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Revision of the larvae of West-Palaearctic **Cordulegaster** Leach, 1815 (Odonata, Cordulegastridae), with a key to the considered taxa and a discussion on their affinity

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Abstract

Larval morphology of the 12 West-Palaearctic *Cordulegaster* taxa is studied, and several new discriminating characters are assessed. Full diagnoses are given for each taxon, three of which had not been described before: *C. boltoni immaculifrons, C. boltoni algiricus* and *C. bidentatus sicilicus*. Possible phylogenetic relationships between the considered taxa, as revealed by larval morphology, are discussed. The following conclusions are reached:

1. The division of West-Palaearctic *Cordulegaster* in two species-groups is justified. The *C. boltoni*-group comprises *C. boltoni* s. l., *C. princeps, C. pictus* and *C. heros*. The *C. bidentatus*-group comprises *C. bidentatus, C. mzymtae* and *C. insignis*.
2. Interspecific differences within the *C. boltoni*-group urge the definition of two subgroups. *C. boltoni* s. l. and *C. princeps* constitute the first subgroup, referred to as the subgroup of western taxa. *C. pictus* and *C. heros* constitute the subgroup of eastern taxa.
3. The taxon *trinacriae* is either a separate species or a subspecies of *C. boltoni*, but not a subspecies of *C. pictus* as previously has been suggested.

A concise key to final instar larvae of West-Palaearctic *Cordulegaster* species and subspecies is provided.

Introduction

The affinities between the West-Palaearctic taxa of *Cordulegaster* have been a matter of discussion in several previous studies dealing with adult morphology, e.g. MORTON (1916), FRASER (1929), BARTENEF (1930), ST QUENTIN (1952), JURZITZA (1965), AKRAMOWSKI & SHENGELIA (1967), WATERSTON (1976) and DUMONT & SCHNEIDER (1984). The results suffer from a general lack of material and defective knowledge of the distribution of most taxa. More fundamentally, however, current adult discriminating features seem to be unreliable, highly variable, and, as in the case of the components of the key-lock system for copulation, subject to different interpretations.

Recent discoveries of the larvae of *C. boltoni algiricus, C. bidentatus sicilicus* and *C.*

mzymtae, unknown thus far, together with the availability of extensive material of *C.pictus* and *C.insignis* (leg. H. MALICKY (Lunz)), stimulated a comprehensive study of *Cordulegaster*'s larval morphology.

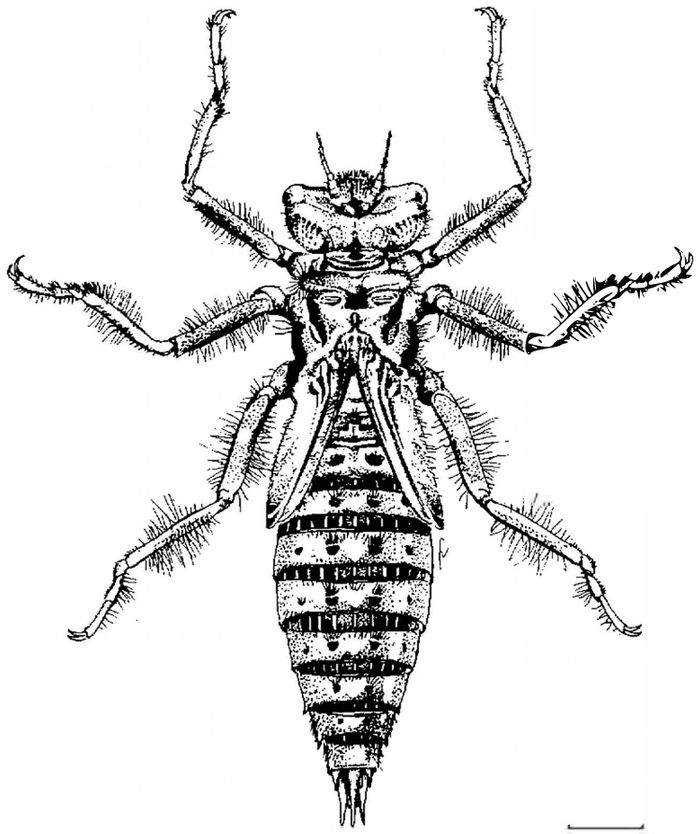

Fig. 1. Habitus of a fullgrown larva of *Cordulegaster boltoni boltoni* (DONOVAN, 1807). Elsenborn, Belgium. Scale = 5 mm.

Material and methods

A total of 371 specimens were examined, obtained from private collections, the Rijksmuseum voor Natuurlijke Historie (RMNH) in Leiden, the Oberösterreichisches Landesmuseum in Linz and the Museo Civico di Storia Naturale (MCSN) in Milano. The material comprises 43 fullgrown larvae, 109 immature larvae and 219 exuviae, found at 89 localities throughout Europe, Morocco and Turkey. 11 species and subspecies could be examined by us; the diagnosis of *C. h. heros* is based upon THEISCHINGER (1979).

Cordulegaster larvae are striking for their generalized bodyplan and the apparent lack of qualitative discriminating features. Close examination of selected characters, however, revealed gradual differences (short to long, narrow to broad, stout to slender) from one taxon to another. Quantitative expressions of the presumed specific differences were sought by means of a biometrical analysis. For each specimen, 35 variables were counted or measured under a dissecting microscope Wild M5 at magnifications of 12X and 25X, with an accuracy of 0.04 mm and 0.02 mm, respectively. Whenever specific «tendencies» exceeded intraspecific variation, critical values between the groups of conspecific specimens were fixed (figs. 2,3,4). Basic statistics (mean, standard deviation) were systematically computed, but proved to be of restricted value because of the small numbers of available data in the majority of taxa studied.

Aberrant specimens, not following the general tendency for a certain character, were encountered in most taxa. In the following diagnoses, their occurrence is expressed as the number of exceptions found on the total of examined specimens. The substantial character variation in *Cordulegaster* might be related to their scattered occurrence and small population sizes. The virtual isolation of many populations enhances the effect of genetic drift, finding expression in characters that are not subject to selection.

As body-colour cannot be appreciated properly on dried exuvial skins, it is only described when full-grown larvae were available for study. Chaetotaxy of the labium provided three relevant characters, viz. the number of palpal setae and the numbers of long and short premental setae. Aberrant setal formulas usually can be imputed to feeding accidents during larval life. The setae on the posterior margin of sternite 9 showed great variability when studied with SEM (fig. 5). Size and shape of the setae varies considerably from one population to another, and different types may occur on one and the same specimen. The almost exclusive occurrence of bi- and trifurcate setae in members of the *C. bidentatus*-speciesgroup forms a useful discriminating feature. Unfortunately, this character can only be fully appreciated under high magnifications (100-200x) with a compound microscope.

The pattern of incisions on the distal margin of the labial palps shows great variation too. Although this variability is not merely random, it is nonspecific and thus unsuitable for identification. Teeth on the left palp interlock with complementary teeth on the right palp. There is always a single deep incision on one palp, and two on the other (arrows in fig. 6). The teeth located between two deep incisions constitute a single «supertooth». The size of the supertooth above the upper deep incision of each palp depends upon the position of the incision along the distal margin. In this way, the different types of tooth-pattern constitute a series, in which successive superteeth seemingly move along the palpal margin, from the movable hook towards the bifid tooth of the prementum. This phenomenon, which is not at all a dynamical process but merely a case of continuous variation, may incorrectly raise the supposition that «left-handed» and «right-handed» specimens occur within a single population or species.

The majority of larvae and exuviae were assigned to an individual taxon on the basis of adult dragonflies, which were reared to emergence or collected in association. The remainder were assigned on the basis of mere locality. In the case of *Cordulegaster*, assignement by locality is justified by the fact that within the two major speciesgroups, larvae of which are easy to distinguish, taxa usually have an allopatric distribution. We nevertheless checked our a priori classification by means of discriminant analysis.

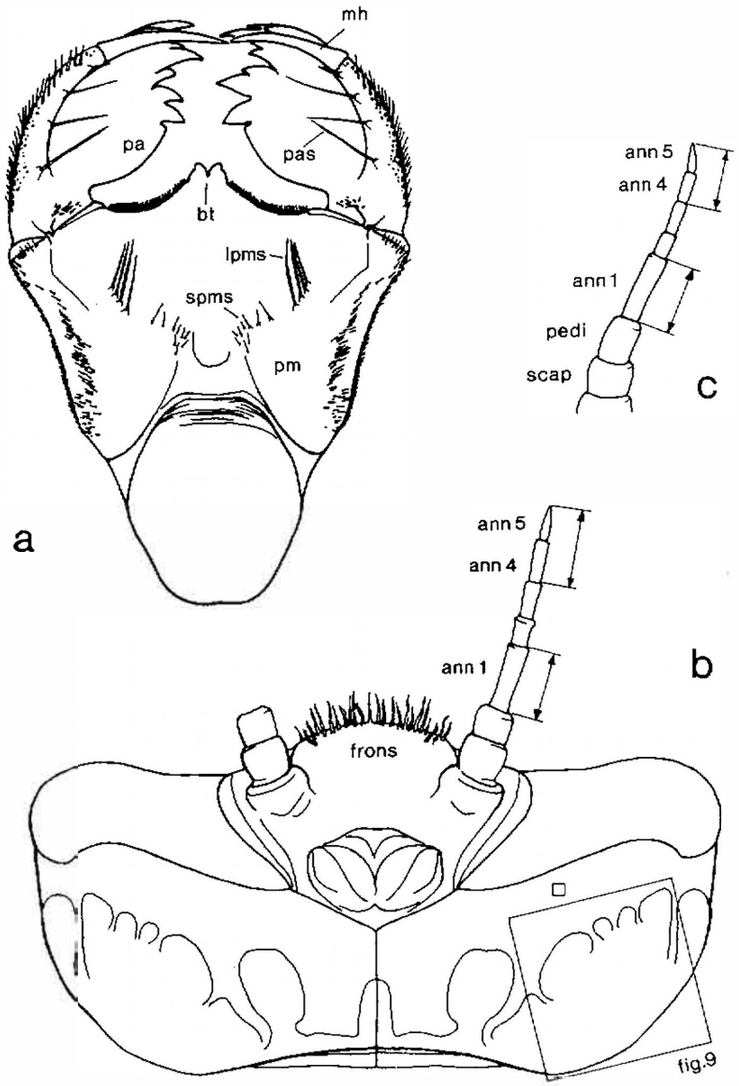

Fig. 2. Biometric variables. a. Inner side of labium (*C. insignis*). b. Dorsal view of head with antenna of the *C. boltoni*-type: ann 1 < ann 4+5. Insets: cf. Fig. 9 a-b. c. Antenna of the *C. bidentatus*-type: ann 1 > ann 4+5. bt: bifid tooth. mh: movable hook. pa: labial palp. pas: palpal setae. pm: prementum. lpms: long premental setae. spms: short premental setae. ann: annulus. frons: frontal shelf. scap: scapus. pedi: pedicellum.

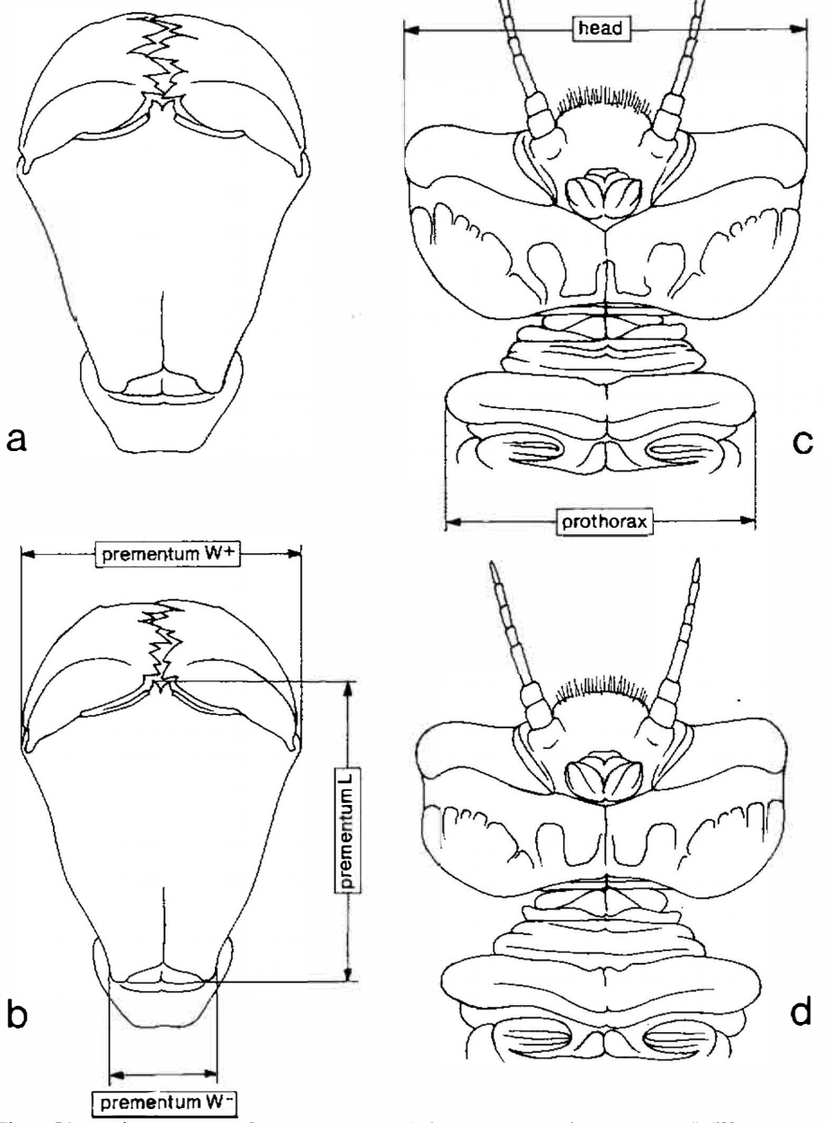

Fig. 3. Biometric variables. a. Stout prementum (*C. bidentatus*-group): prementum L/W+ ⩽ 1.05. b. Slender prementum (*C. boltoni*-group): prementum L/W+ > 1.05. c. Narrow prothorax (*C. insignis*): head/prothorax > 1.30. d. Broad prothorax (*C. pictus*): head/prothorax < 1.25. Prementum L: prementum length. W+: maximal width of prementum, at the articulation of the labial palps. W-: minimal width of the prementum, at the postmental hinge.

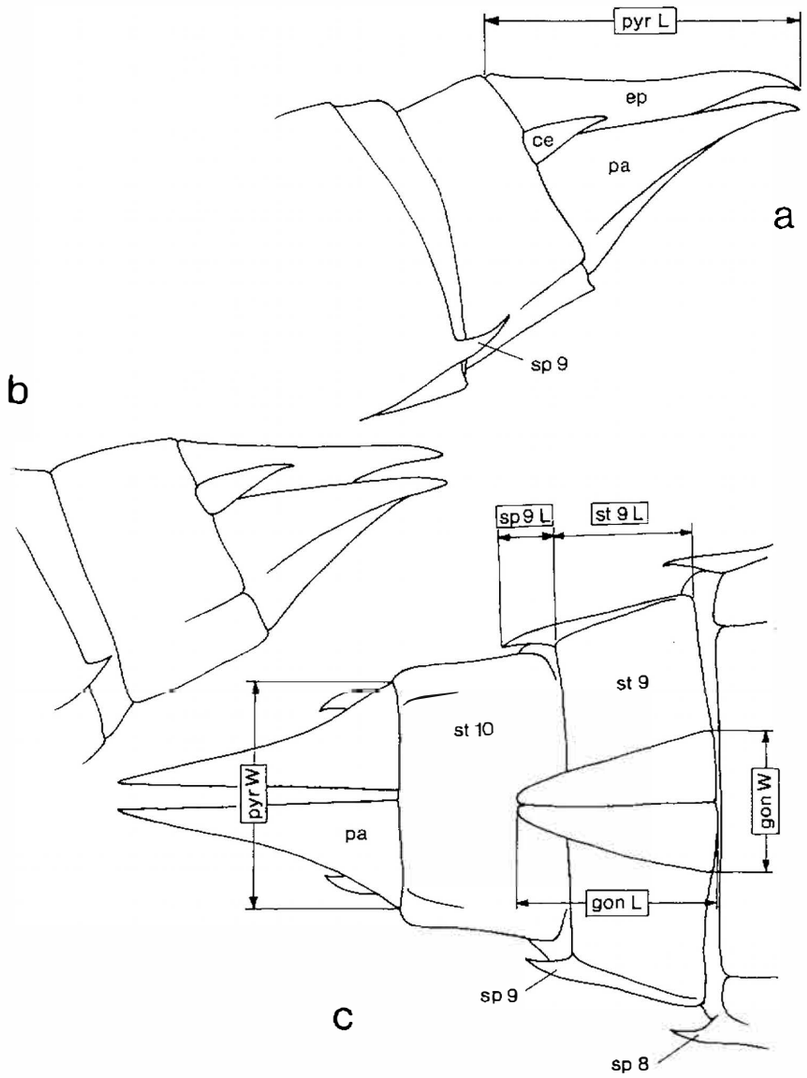

Fig. 4. Biometric variables. a. Slender anal pyramid (*C. bidentatus*-group and western *C. boltoni*-subgroup: anal pyramid L/W > 1.20. b. Short anal pyramid (eastern *C. boltoni*-subgroup): anal pyramid L/W < 1.20. c. Tip of ♀ abdomen, ventral view (*C. b. boltoni*). ce: cercus. ep: epiproct. gon L/gon W: length/width of ♀ gonapophyses. pa: paraproct. pyr L/pyr W: length/width of anal pyramid. sp 8: lateral spine on 8th segment. sp 9: lateral spine on 9th segment. sp 9 L: length of spine on segment 9. st 9: sternite 9. st 9 L: length of sternite 9. st 10: sternite 10.

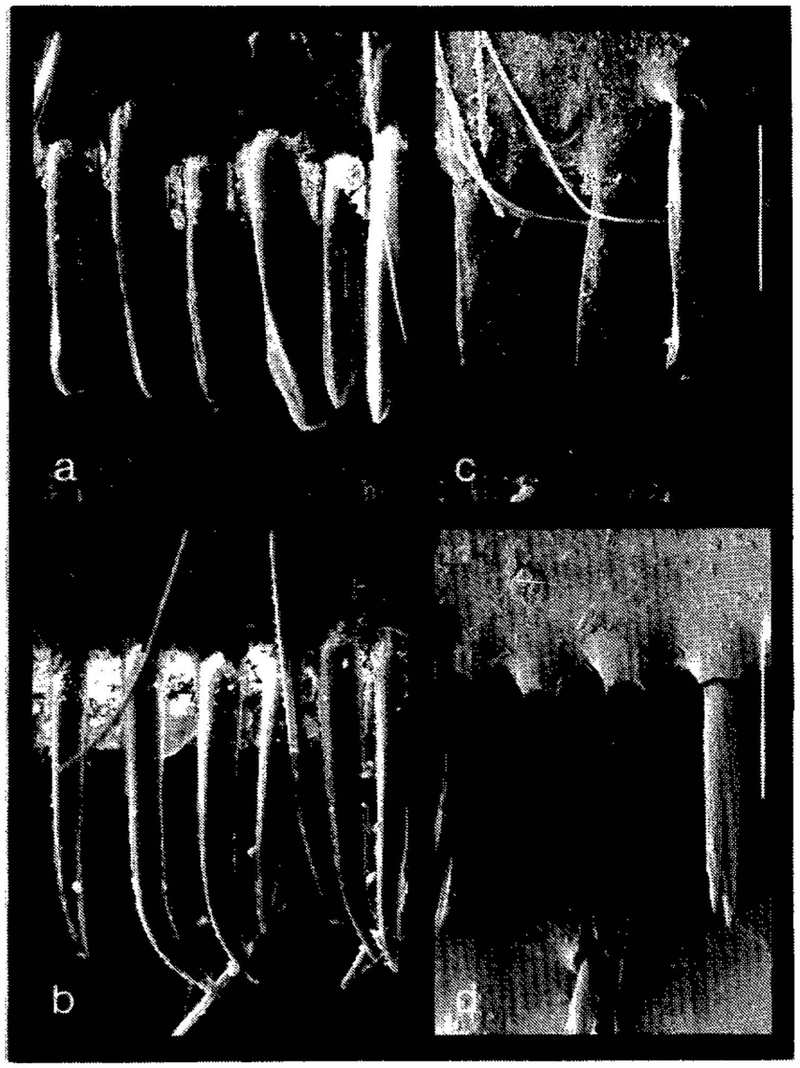

Fig. 5. Variability of the setae on the rear margin of sternite 9 in *Cordulegaster* larvae. Two or more types of setae may occur on one and the same specimen. Scale = 100 µm. a. Flattened, pointed or truncate (*C. b. boltoni*). b. Slender, curved and pointed (*C. b. immaculifrons*). c. Robust, bi- or trifurcate (*C. b. bidentatus*). d. Slender, bifurcate and pointed (*C. insignis*).

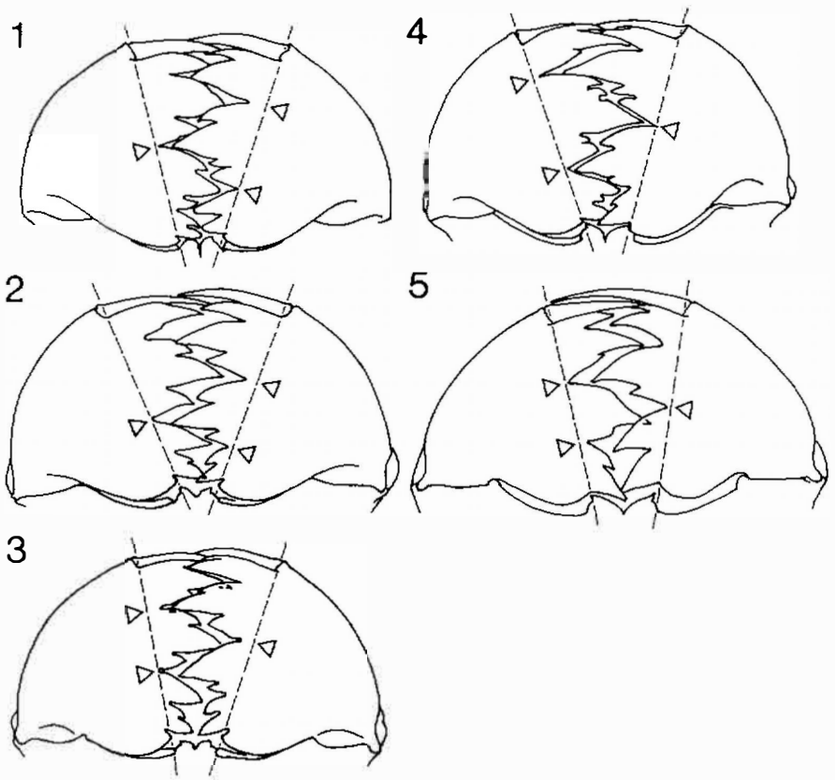

Fig. 6. Variability in the pattern of incisions on the distal margin of the labial palp in *Cordulegaster* larvae. Arrows indicate deep incisions between neighbouring superteeth (see text). 1, 2 and 3: *C. insignis* F_{-0}. 4: *C. pictus* F_{-0}. 5: *C. pictus* F_{-5}.

Biometric analysis yielded about 20 discriminating variables, which measure or count characteristics on which the respective groups of individuals were expected to differ. Discriminant analysis then attempts to distinguish between the N groups by forming N-1 linear combinations of the discriminating variables. The discriminant functions are formed in such a way as to maximize the separation of the groups, and the results are plotted as a histogram or scatterdiagram along one or two axes with the respective discriminant function scores (figs. 7 and 8). In order to make the grouping independent of sexe and absolute size, data on the ♀ gonapophyses (diagnostic to some extent) were omitted and all variables were divided by the head-width. The use of head-width as a measure of absolute size is common in Odonate growth studies (e.g. DUNKLE, 1985; LEGGOTT & PRITCHARD, 1985), and avoids erroneous measurements of body length due to the extension of the abdomen. Data on the antennae were omitted too, as they were missing from

too many exuviae. *C. b. algiricus* and *C. heros* were not included in the analysis, due to lack of intact specimens. Discriminant analysis reached complete separation between *C. b. bidentatus* and *C. insignis* by means of the single discriminant function (fig. 7). The discriminant function score of the *C. b. sicilicus*-specimen was fitted in afterwards. Complete separation between the 5 considered taxa of the *C. boltoni*-group was reached with the combined effort of all 4 discriminant functions, whereas the first two functions reach a separation of 87% (fig. 8). The confirmation of our a priori classification by discriminant analysis forms a guarantee for the correct assignment of all studied specimens.

Application of diagnoses to exuviae and immature larvae

The following diagnoses and key strictly apply to fullgrown larvae only, which can be readily recognized by their wingsheaths extending to the fourth abdominal segment (fig. 1). Exuvial skins of *Cordulegaster*, however, are more readily collected. For identification purposes, they are as useful as fullgrown larvae, because the shape of the sclerotized bodyparts and exocuticular features is unaffected by metamorphosis and emergence. After emergence, however, the exuvial abdomen dries in extended position. Therefore, the total lengths of an exuvia and a fullgrown larva are not comparable. Apart from the apparent sexual dimorphism (♀ ♀ usually exceed ♂ ♂ in length), this also should be considered when interpreting the relative body size of different taxa. Further, the specific orientation of the wingsheaths is distorted during emergence and cannot be reliably checked on exuviae. Finally, the width of the ecdysial split should be taken into account when measuring the width of head and prothorax in exuviae.

In order to establish discriminatig features that remain constant throughout larval life, thereby suitable for identification of immature larvae, attention was given to the variation of characters during development. Extensive material of *C. b. boltoni, C. pictus* and *C. insignis* yielded following conclusions:

1. The antennae are 7-jointed approximately from the F_{-5} - instar onwards. Due to the stretching of annulus 1 during subsequent moultings, the proportionate length of the flagellar segments changes considerably, causing the terminal segments (annulus 4 and 5) to become relatively shorter. In larvae belonging to the *C. bidentatus*-group, annulus 1 ultimately becomes longer than both terminal segments combined, resulting in an annulus 1/4 + 5 ratio above 1. In members of the *C. boltoni*-group, the stretching of annulus 1 is usually insufficient to overcome the size difference with the two terminal segments, resulting in an annulus 1/4 + 5 ratio below 1 (VERSCHUREN *et al.*, 1987).

2. In larvae of the *C. boltoni*-group, the length-width ratio of the prementum progressively increases during development. The higher length-width ratio in members of the *C. boltoni*-group, as compared to members of the *C. bidentatus*-group, can only be used as a discriminating character in later instar larvae (F_{-2} - F_{-0}). In younger larvae, values for this ratio show a considerable overlap between the two speciesgroups.

3. The anal pyramid is relatively shorter in the younger stages of all species.

4. The long premental setae reach their final number in the F_{-4}-instar, the palpal setae already from the F_{-6}-instar.

5. The head/prothorax ratio remains fairly constant throughout development.

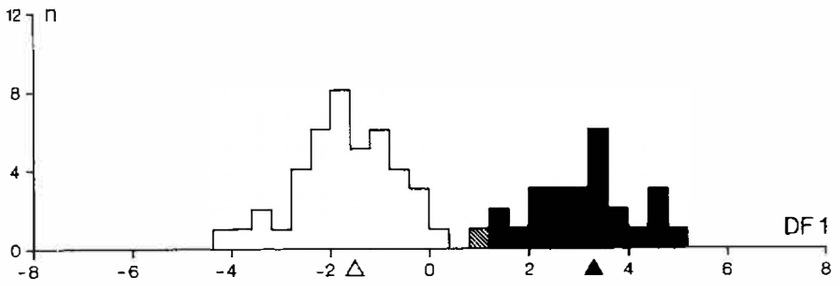

Fig. 7. Frequency distribution for larvae belonging to 3 taxa of the *C. bidentatus*-group along the discriminant function continuum. White: *C. insignis*. Hatched: *C. b. sicilicus*. Black: *C. b. bidentatus*. Arrows indicate the group means.

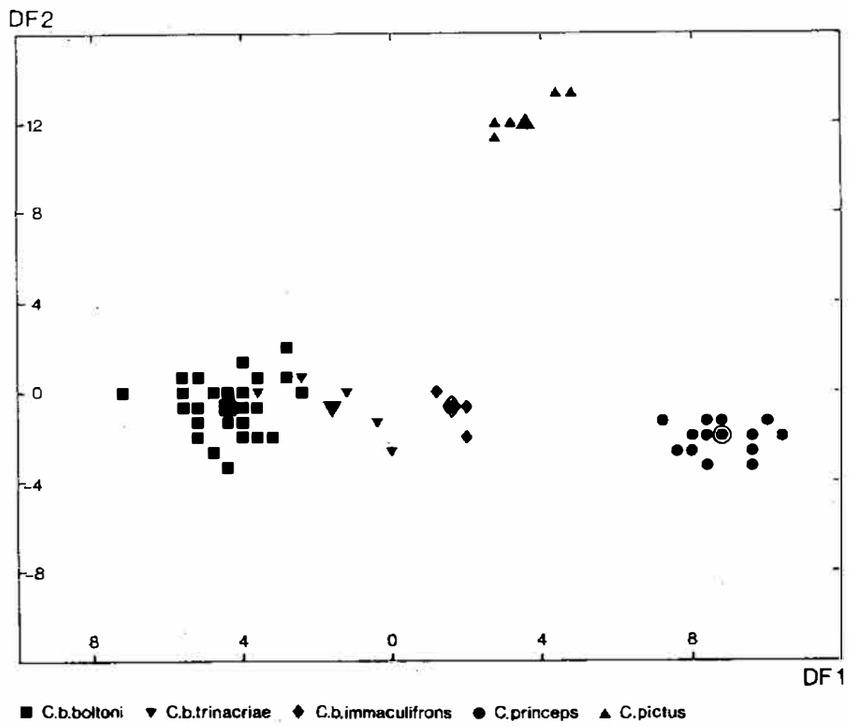

Fig. 8. Distribution of larvae belonging to 5 taxa of the *C. boltoni*-group along the continua of their first two discriminant functions. Enlarged symbols indicate the group centroids.

6. The presence or absence of lateral spines can be checked in any instar, but in younger larvae their relative length to the 9th sternite is unreliable for identification of the various *C. boltoni*-related taxa.

On the basis of the three latter characters, immature larvae from the F_{-5}-instar onwards (body length approx. 1 cm) can be attributed to one of the four following groups:
1. *C. boltoni*-subgroup of western taxa
2. *C. boltoni*-subgroup of eastern taxa
3. *C. bidentatus* + *C. mzymtae*
4. *C. insignis*

Generic Diagnosis of larval *Cordulegaster*

Body stout and hairy (fig. 1). Labium spoon-shaped, covering the face up to the eyes. Distal margin of labial palps with conspicuous, deep and irregularly interlocking teeth. Median lobe of prementum protruding in a bifid tooth (fig. 2a).

In the European Odonate fauna, larval as well as adult *Cordulegaster* are easy to recognize and unlikely to be confused with anything else. At the specific level, however, most descriptions found in literature appear to be defective or incorrect. Therefore, and because of the introduction of several new discriminating characters, we felt the necessity to include an exhaustive generic description of *Cordulegaster* and full diagnoses of the respective taxa.

Description of a *Cordulegaster* larva

Body stout, covered with long hairs and short bristles (fig. 1). Abdomen without mid-dorsal keel, subcylindrical and gradually tapering towards its tip from beyond the 5th segment. Lateral keels weakly pronounced; lateral spines, if present, only on the 8th and 9th segment. Middle and hind legs entirely covered with long hairs. Inner edges of tibiae and tarsal segments bearing stout spines. Front legs hirsute close to the body, but devoid of hairs from the middle of the femora onwards and set here with small, fan-shaped setae (see further). Front tibiae somewhat bent distally, front tarsi heavily spined on their inner edges. Prothorax broad, usually about 3/4 to 5/6 of the head-width (fig. 3c-d). Pronotum laterally produced into two flattened, transverse shoulders, denoted as prothoracic processes or «epaulets» (NEEDHAM & WESTFALL, 1954), which are marginally set with long, stiff hairs. Mesothoracic spiracles conspicuous. Two pairs of wingsheaths lying parallel (e.g. *C. bidentatus, C. insignis, C. pictus)* or divergent (e.g. *C. boltoni*) upon the back.

Head square and transversely broadened. Eyes narrow and protruding, capping the anterolateral corners of the head (fig. 2b). Antennae seven-jointed and rather long, at least 2/5 of the head-width. Scapus and pedicellum subspherical, flagellum slender and consisting of 5 elongated annuli. Frontal shelf projecting anteriorly between the eyes, not particularly prominent, about 1/4 of the width of the head and flanked on both sides by the antennal pedestals, its regularly curved anterior margin fringed with stiff, twisted hairs (fig. 2b). Occiput with long stiff bristles along the rear and side margins, its dorsum covered with fan-shaped setae, which are arranged in a typical pattern of merging rows on the expanded postocular lobes (fig. 9). The same type of modified setae also covering part of the frons and the antennal segments, the upper side of the front tibiae, and the distal end of the front femora.

Fig. 9. a: Pattern of fan-shaped setae on the postocular lobe (cf.fig.2) of *C. insignis*. Scale = 100 μm. b. Fan-shaped seta on the occiput (cf.fig.2). Scale = 10 μm.

Spoon-shaped labium large, covering the face up to the eyes and frontal shelf. Pentagonal prementum (fig. 2a) protruding anteriorly in a conspicuous bifid median tooth; outer margins swollen, covered with short, spiniform setae; a row of 3 to 6 (exceptionally 7) long premental setae present on each side of the midline, and medially to the latter a variable group of short premental setae (general premental formula: 3-6(7) + n / n + 3-6(7)). Labial palps triangular and concave, their outer margin bearing short spiniform setae on the outer edge and a row of longer palpal setae along the inner edge. Number of long palpal setae ranging from 2 to 5, usually 3 or 4, apart from the short additional one at the base of the movable hook (general palpal formula: (2)3-4(5) + 1 / 1 + (2)3-4(5)). Movable hook stout, slightly curved, about half as long as outer palpal margin. Distal margin of labial palp with conspicuous, deep and asymmetrical interlocking teeth.

Anal pyramid of variable length (fig. 4a-b). Epiproct and keeled paraprocts short and rather blunt, or strongly curved and attenuated. Location of male primary genitalia weakly indicated on the 9th sternite. Anterior gonapophyses of female ovipositor appear on the posterior margin of sternite 8 in the F_{-3}-instar; in fullgrown larvae conspicuous, triangular, and extending beyond the rear margin of the 9th sternite (fig. 4c).

The description is valid for West-Palaearctic taxa of *Cordulegaster*. East-Palaearctic and Nearctic representatives, as well as members of the related genera *Neallogaster* and *Anotogaster*, are similar. The generalized bodyplan of all these Cordulegastrinae contrasts with the quite dissimilar larval habitus of the Chlorogomphinae, the other subfamily within the Cordulegastridae.

Revision of the larvae of West-Palaearctic *Cordulegaster*

a. the *C. boltoni*-group, partim: the subgroup of western taxa

1. *Cordulegaster boltoni boltoni* (DONOVAN, 1807)

1763 *Libellula grandis*. SCOPOLI, *Fauna Carniolica*: 259.

Material examined:

15 fullgrown larvae (8 ♂♂, 7 ♀♀), 21 immature larvae and 58 exuviae (26 ♂♂, 32 ♀♀), from 26 localities in Belgium (1), France (16), Germany (1), Switzerland (1) and Italy (7): 1 fullgrown ♀ larva, Wolfsbach, Elsenborn, Belgium, 05.VII.86, leg. D. VERSCHUREN; 1 ♂ exuvia, Célé River, Brengues (Lot), France, 17.VI.67, leg. M. LIEFTINCK (coll. RMNH Leiden); 1 ♀ exuvia, Chasselouve (Ardèche), France, 11.VII.67, leg. L. D. BRONGERSMA (coll. RMNH Leiden); 1 ♀ exuvia, Ruisseau de Brunissart, Les Chambons (Ardèche), France, 11.VII.67, leg. L. D. BRONGERSMA (coll. RMNH Leiden); 2 exuviae (1♂,1♀), La Beune (Dordogne), France, 23.VI.82, leg. J. VAN TOL (coll. RMNH Leiden); 25 exuviae (10 ♂♂, 15 ♀♀), Le Pont Noir (Indre), France, 09.VII.84, leg. J. L. DOMMANGET; 1 ♂ exuvia, Gargilesse, Le Pont Noir (Indre), France, 01.VII.82, leg. J. L. DOMMANGET; 3 fullgrown larvae (2 ♂♂, 1 ♀), Gargilesse (Indre), France, IX.80, leg. J. L. DOMMANGET; 1 ♀ exuvia, Brenne (Indre), France,82, leg. J. L. DOMMANGET; 1 fullgrown ♀ larva, Lancosme, Brenne (Indre), France, VII.82, leg. J. L. DOMMANGET, 1 fullgrown ♀ larva, Assay (Indre & Loire), France, 12.IV.81, leg. J. L. DOMMANGET; 1 ♀ exuvia, reared to emergence, and 3 fullgrown ♂ larvae, Castelculier (Lot & Garonne), France, 31.XII.79, leg. J. L. DOMMANGET; 1 ♂ exuvia, ruisseau de la Baccaule, Requista (Aveyron), France, 6.VII.83, leg. J. L. DOMMANGET; 3 exuviae (2 ♂♂, 1 ♀), Saint-Rome de Tarn (Tarn), France, 8.VII.83, leg. J. L. DOMMANGET; 1 ♂ exuvia, Holzlar bei Bonn (Bonn), Germany,78, leg. J. LEMPERT; 1 ♀ exuvia, Wiessbad, Appenzell, Switzerland, 12.VII.34 (coll. RMNH Leiden); 5 fullgrown larvae (3 ♂♂, 2 ♀♀), Fossa della Mola, Formello (Roma), Italy, 11.II.72 & 9.III.72, leg. C. UTZERI; 1 ♂ exuvia, Pian di Nesso (Como), Italy, 23.VII.72, leg. I. BUCCIARELLI (coll. MCSN Milano), 15 exuviae (5 ♂♂, 10 ♀♀), reared to emergence, San Martino sul Ticino (Novara), Italy, 22.IV.72 & 17.IV.73; leg. I. BUCCIARELLI (coll. MCSN Milano); 1 fullgrown ♀ larva, Naviglio Langosco, Tromello (Pavia), Italy, 10.VII.73, leg. I. BUCCIARELLI (coll. MCSN Milano); 3 ♂♂ exuviae, reared to emergence, Gravellona Toce (Novara), Italy, 21.IV.84, leg. I. BUCCIARELLI (coll. MCSN Milano). 21 immature larvae were examined additionally.

Biometric data:

total length	♂ larvae	: 29.5 - 38 mm ($\bar{x}$ = 32 mm; n = 8)
	♀ larvae	: 33.5 - 44 mm ($\bar{x}$ = 37 mm; n = 6)
	♂ exuviae	: 35.5 - 42 mm ($\bar{x}$ = 39 mm; n = 19)
	♀ exuviae	: 39.5 - 45 mm ($\bar{x}$ = 43 mm; n = 27)
head/prothorax		: 1.21 - 1.35 ($\bar{x}$ = 1.28; n = 59)
annulus 1/4+5		: 0.79 - 1.16 ($\bar{x}$ = 0.93; n = 42)
prementum L/W+		: 1.03 - 1.14 ($\bar{x}$ = 1.08; n = 59)
prementum W+/W-		: 2.40 - 2.67 ($\bar{x}$ = 2.48; n = 59)
anal pyramid L/W		: 1.24 - 1.53 ($\bar{x}$ = 1.39; n = 58)

Diagnosis:

Medium-sized, yellow ochreous to chestnut-brown. lateral spines on the 9th abdominal segment curved and large, usually about 1/3 (1/4 to 2/5) of the length of sternite 9. Lateral spines on the 8th segment scarcely shorter, but straighter and divergent. Length of antennal annulus 1 less than the combined length of antennal annuli 4 and 5, with frequent exceptions (9 out of 42 specimens). Moderately broad-shouldered, prothorax with epaulets between 3/4 and 4/5 of the head-width. Prementum slender, slightly longer than wide (length/width ratio usually above 1.05), with a correspondingly narrow postmental

hinge. Usually 5, sometimes 6 (5 out of 58 specimens) long and 2 to 4 short premental setae. 4 long palpal setae, exceptionally 5 (2 out of 58 specimens). Setae on the rear margin of sternite 9 simple, flattened, and pointed or truncate (fig. 5a). ♀ gonapophyses variable, extending with 1/7 to 1/3 of their length beyond the rear margin of the 9th sternite. Anal pyramid slender (length/width ratio above 1.20), epiproct and paraprocts evenly curved and attenuated.

Affinity:

The *C. boltoni*-speciesgroup is characterized by the presence of lateral spines on the 9th and (usually) the 8th abdominal segments, a slender prementum, the lack of bifurcate setae on the rear margin of the 9th sternite, less than 5 short premental setae, and relatively short basal annulus of the antenna. Members of the western subgroup (*C. boltoni* s.l. and *C. princeps*) share a relatively narrow prothorax and slender anal pyramid, as compared to eastern taxa such as *C. pictus*. In *C. boltoni* s.l., the lateral spines on the 8th segment are constantly present and almost as long as those on the 9th segment.

In order to distinguish the 4 subspecies of *C. boltoni*, the seemingly diagnostic shape of the setae on sternite 9 should be used with caution. Other differences between the 4 subspecific taxa are merely gradual. Being subject to substantial variation, characters such as the wideness of prothorax and length of the lateral spines show a considerable overlap between subspecies (fig. 10). Adult populations with features intermediate between *C. b. boltoni* and *C. b. immaculifrons* have been reported from several localities along the range borders in northern Spain and southeastern France, and signs of their common ancestry are to be expected in larval morphology too. The nominate subspecies usually has shorter lateral spines than *C. b. trinacriae*, but longer ones than *C. b. immaculifrons* and *C. b. algiricus*.

A short first flagellar annulus is typical for all members of the *C. boltoni*-group, contrary to the *C. bidentatus*-group. However, *C. b. boltoni* itself is the only taxon within the group in which exceptions to this rule were frequently found (9 specimens out of 42). The great variability of this character in *C. b. boltoni* resembles the comparable but opposite situation in *C. insignis*.

Literature:

SCOPOLI (1763) first described a larva of *Cordulegaster boltoni*, attributing it to *Libellula grandis* (= *Aeshna grandis* (LINNAEUS, 1758)). CABOT (1872) distinguished *C. boltoni* (and the Nearctic *C. sayi*) from *C. bidentatus* by the presence of lateral spines and the shape of the epiproct. The second character was based on an aberrant or damaged specimen of *C. bidentatus*, and is invalid. ROUSSEAU (1909) copied the erroneous feature. Furthermore, he apparently looked at an immature larva when stating that the ♀ gonapophyses do not reach the rear margin of the 9th sternite. CONCI & NIELSEN (1956) likewise adopted CABOT's defective characters. ROBERT (1958) found a second reliable character to distinguish both taxa: wingsheaths parallel in *C. bidentatus*, divergent in *C. boltoni*. As noted before, this feature cannot be appreciated on exuviae. Besides, this character does not separate the *C. boltoni*- and *C. bidentatus*-groups as a whole, because *C. pictus* possesses parallel wingsheaths as well.

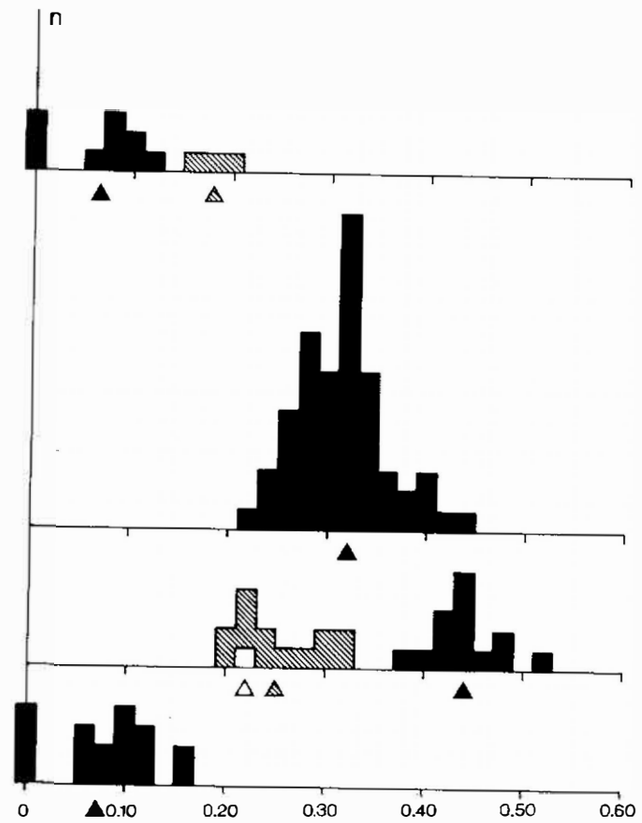

Fig. 10. Relative length of the lateral spines on segment 8 (sp 8/st 8L) in 7 taxa of the *C. boltoni*-group. Upper row: *C. pictus* (black) and *C. h. pelionensis* (hatched). 2nd row: *C. boltoni*. 3rd row: *C. b. algiricus* (white), *C. b. immaculifrons* (hatched) and *C. b. trinacriae* (black). Lower row: *C. princeps*. Arrows indicate the respective mean values.

2. *Cordulegaster boltoni immaculifrons* SÉLYS, 1850

Material examined:

1 fullgrown ♀ larva, Arroyo Pedroches, Sierra Morena (Cordoba), Spain, 13.III.78, leg. M. FERRERAS-ROMERO; 1 fullgrown ♂ larva, Arroyo de El Molino, Sta Maria de Trassiera, Sierra Morena (Cordoba), Spain, 13.IV.78, leg. M. FERRERAS-ROMERO; 1 fullgrown ♀ larva, Arroyo Aljabaros, Hornachuelos, Sierra Morena (Cordoba), Spain, 25.II.83, leg. M. FERRERAS-ROMERO; 1 fullgrown ♀ larva, Rio Cereceda, Fuencaliente, Sierra Madrona (Ciudad Real), Spain, 28.I.84, leg. M. FERRERAS-ROMERO; 13 exuviae (3♂♂, 10♀♀), Rio Blanco, Calomarde (Teruel), Spain, 27.VII.85, leg. A. ANSELIN. 6 immature larvae were examined additionally.

Biometric data:

total length	♂ larva	: 33.5 mm (n = 1)
	♀ larvae	: 35 - 41 mm ($\bar{x}$ = 38.5; n = 3)
	♂ exuviae	: 38.5 - 42 mm ($\bar{x}$ = 39.5; n = 3)
	♀ exuviae	: 41 - 44 mm ($\bar{x}$ = 43; n = 7)
head/prothorax		: 1.27 - 1.37 ($\bar{x}$ = 1.33; n = 14)
annulus 1/4+5		: 0.79 - 1.02 ($\bar{x}$ = 0.90; n = 5)
prementum L/W+		: 1.04 - 1.12 ($\bar{x}$ = 1.07; n = 15)
prementum W+/W-		: 2.49 - 2.60 ($\bar{x}$ = 2.54; n = 15)
anal pyramid L/W		: 1.29 - 1.47 ($\bar{x}$ = 1.34; n = 16)

Diagnosis:

Medium-sized chestnut-brown larva, with lateral spines on segment 9 medium to large, usually about 1/4 (1/5 to 1/3) of the length of sternite 9. Spines on the 8th segment divergent and scarcely shorter. Length of antennal annulus 1 less than the combined length of annuli 4 and 5. Narrow-shouldered, prothorax with epaulets about 3/4 of the head-width. Prementum slender, longer than wide (length/width ratio usually above 1.05), with a narrow postmental hinge. Usually 5, sometimes 6 (4 out of 14 specimens) long premental setae and 2 to 4, exceptionally 5 short premental setae. 4 long palpal setae, exceptionally 5 (1 out of 14 specimens). Setae on the rear margin of segment 9 simple (exceptionally bifurcate), long and slender, distally curved and pointed (fig. 3b). ♀ gonapophyses short, extending with about 1/8 of their length beyond sternite 9. Anal pyramid slender (length/width ratio above 1.20), epiproct and paraprocts evenly curved and attenuated.

Affinity:

This Atlantomediterranean subspecies of *C. boltoni* differs from the nominate subspecies mainly by its shorter lateral spines. This character is not exclusive, however (fig. 10), as are other gradual differences like the narrower prothorax and shorter gonapophyses. *C. b. immaculifrons* is the only taxon of the *C. boltoni*-group in which bifurcate setae on the rear margin of sternite 9 were occasionally found, although in very low numbers: at most 2 or 3 along the entire margin.

3. *Cordulegaster boltoni algiricus* MORTON, 1915

Material examined:

1 ♀ exuvia (damaged, antennae missing), Aarabene between El Jabaa and Bui Hamed, El Rif, Morocco, 23.VI.83, leg. G. JACQUEMIN.

Biometric data:

total length	♀ exuvia	: 40 mm (n = 1)
head/prothorax		: 1.39 (n = 1)

prementum L/W+	: 1.06 (n = 1)
prementum W+/W-	: 2.60 (n = 1)
Anal pyramid L/W	: 1.36 (n = 1)

Diagnosis:

A relatively small larva, with lateral spines on the 9th segment medium-sized, less than 1/4 of the length of sternite 9. Spines on the 8th segment divergent and slightly shorter, about 1/5 of the length of the corresponding sternite. Prothorax with epaulets narrow, distinctly less than 3/4 of the head-width. Prementum slender (length/width ratio above 1.05), with a narrow postmental hinge. 6 long and 4 short premental setae. 4 long palpal setae. Setae on rear margin of sternite 9 simple, slender and slightly curved. ♀ gonapophyses short, hardly extending beyond sternite 9. Anal pyramid slender (length/width ratio above 1.20), epiproct and paraprocts curved and attenuated.

Affinity:

The narrow prothorax and slender anal pyramid include this exuvia in the western subgroup. It shares short gonapophyses and strikingly narrow shoulders with the much larger *C. princeps*. The divergent lateral spines on the 8th segment, on the other hand, scarcely shorter than the ones on the 9th, are typical for *C. boltoni* s.l. The size of the lateral spines, smaller than in *C. b. boltoni*, and the width of the prothorax, narrower than in the nominate subspecies, are reminiscent of the other Atlantomediterranean subspecies *C. b. immaculifrons*, to whom *C. b. algiricus* likely is most closely related. The single specimen at hand also possesses 6 long premental setae, a number which appears to be less exceptional in *C. b. immaculifrons* (4 out of 14 specimens) than in *C. b. boltoni* (5 out of 58 specimens).

4. *Cordulegaster boltoni trinacriae* WATERSTON, 1976

1982 *C. pictus (?) trinacriae* WATERSTON. BALESTRAZZI, BUCCIARELLI & GALLETTI, *Giornale Italiano di Entomologia* 1: 70 fig. 3-5.

Material examined:

17 exuviae (10 ♂♂, 7 ♀♀), Torrente Castelbuono at Piano Zucchi, La Madonie (Palermo), Sicilia, Italy, 27.VI.73 & 3-6.VII.75, leg. I. BUCCIARELLI & M. PAVESI (coll. MCSN Milano); 1 ♂ exuvia, Fiume Anopo near Cassaro, Sicilia, Italy, 17.VIII.85, leg. M. PAVESI; 4 ♀♀ exuviae, San Christina d'Aspromonte, Aspromonte (Reggio di Calabria), Italy, 8.VII.86, leg. M. PAVESI.

Biometric data:

total length	♂ exuviae	: 39 - 41.5 mm ($\bar{x}$ = 40.5; n = 8)
	♀ exuviae	: 44.5 - 48 mm ($\bar{x}$ = 45.5; n = 4)
head/prothorax		: 1.27 - 1.37 ($\bar{x}$ = 1.33; n = 13)
annulus 1/4+5		: 0.72 - 0.92 ($\bar{x}$ = 0.81; n = 11)
prementum L/W+		: 1.06 - 1.14 ($\bar{x}$ = 1.10; n = 12)

prementum W + /W- : 2.57 - 2.70 ($\bar{x}$ = 2.63; n = 12)
anal pyramid L/W : 1.31 - 1.44 ($\bar{x}$ = 1.37; n = 14)

Diagnosis:

Large larva, with lateral spines on the 9th segment between 2/5 and 3/5 of the length of sternite 9. Lateral spines on the 8th segment strongly divergent and likewise long, about 2/5 to 1/2 the length of the corresponding sternite. Moderately broadshouldered, prothorax with epaulets between 3/4 and 4/5 of the head-width. Length of antennal annulus 1 less than the combined length of annuli 4 and 5. Prementum distinctly longer than wide (length/width ratio above 1.05); proximal hinge area narrower than in the nominate subspecies (mean ratio of maximal to minimal prementum width = 2.63, against 2.48 in *C. b. boltoni*), giving the prementum a still more slender appearance. 4 or 5 long, and 2 to 4 short premental setae. 4 long palpal setae. Setae on rear margin of sternite 9 slender, not flattened, and slightly curved. ♀ gonapophyses slender, with a length/width ratio always above 1.65, and extending with about 2/5 of their length beyond the margin of sternite 9. Epiproct and paraprocts slender (length/width ratio of anal pyramid above 1.20), strongly curved and attenuated.

Affinity:

GALLETTI & PAVESI (1985) stated that the taxon *trinacriae* cannot be conspecific with *C. boltoni*, because of their co-occurrence at GERANO (Roma), Italy. This record is based upon two adult ♂♂, one of each taxon, collected by Dr. C. NIELSEN. The authors therefore follow BUCCIARELLI (1977) in ascribing *trinacriae* to *C. pictus*. The present study reveals that larval morphology of *trinacriae* agrees with the *C. boltoni*-habitus (moderately broad shoulders, slender anal pyramid), quite unlike larvae of *C. pictus* (very broad shoulders, short anal pyramid). Within *C. boltoni* s.l., *trinacriae* moreover possesses the most slender prementum, the most slender ♀ gonapophyses, and the longest, most strongly divergent lateral spines on sternite 8. It thereby exhibits most conspicuously the characteristic traits of *C. boltoni* s.l. Therefore, if *trinacriae* and *C. boltoni* do co-occur at the border of their ranges, *trinacriae* deserves a specific status within the subgroup of western taxa.

Literature:

BALESTRAZZI *et al.* (1982) described a female exuvia from Piano Zucchi in Sicily. Upon examination of 21 specimens of *C. b. trinacriae* and 58 of *C. b. boltoni*, the presumed differences between the two taxa in slenderness and acuteness of the anal pyramid, mentioned by the above authors, were found to be insignificant.

5. *Cordulegaster princeps* MORTON, 1915

1966 *C. princeps* MORTON, 1915. LIEFTINCK, *Bull. K. Belg. Inst. Nat. Wet.* 42, 35: 58, fig. 31-32.

Material examined:

13 exuviae (5 ♂♂, 8 ♀♀), Ifrane, Moyen-Atlas, Morocco, 26.V.66 & 07-12.VI.73, leg. M. LIEFTINCK (coll. RMNH Leiden); 5 exuviae (3 ♂♂, 2 ♀♀), Imouzzèr, Moyen-Atlas, Morocco, 06-12.VI.73, leg. M. LIEFTINCK (coll. RMNH Leiden).

Biometric data:

total length ♂ exuviae : 44 - 48 mm ($\bar{x}$ = 46; n = 8)
♀ exuviae : 46 - 52 mm ($\bar{x}$ = 49; n = 10)
head/prothorax : 1.34 - 1.43 ($\bar{x}$ = 1.38; n = 18)
annulus 1/4 + 5 : 0.75 - 0.96 ($\bar{x}$ = 0.86; n = 15)
prementum L/W + : 1.06 - 1.13 ($\bar{x}$ = 1.09; n = 18)
prementum W + /W- : 2.34 - 2.62 ($\bar{x}$ = 2.47; n = 18)
anal pyramid L/W : 1.24 - 1.43 ($\bar{x}$ = 1.31; n = 18)

Diagnosis:

Largest West-Palaearctic *Cordulegaster* larva. Lateral spines on 9th segment small to medium-sized, about 1/6 to 1/4 of the length of sternite 9. Spines on the 8th segment highly variable: usually acute but small, only about 1/10 of the length of sternite 8; sometimes lacking (3 out of 18 specimens) or nearly as long as the spines on segment 9 (2 out of 18 specimens). Prothorax with epaulets narrow, always less than the combined length of annuli 4 and 5. Prementum slender (length/width ratio above 1.05), with a correspondingly narrow postmental hinge. 4 or 5 long and 2 to 4 short premental setae. 4 or 5 (the latter number in 1 out of 8 ♂♂ and 5 out of 10 ♀♀) long palpal setae. Setae on rear margin of sternite 9 simple, slender and slightly curved. ♀ gonapophyses relatively short, extending with only about 1/8 of their length beyond the margin of sternite 9. Length/width ratio of anal pyramid above 1.20; epiproct and paraprocts slender, strongly curved and attenuated.

Affinity:

C. princeps is the only taxon of the western subgroup in which the lateral spines on segment 8 are usually small or missing, and in which the combination of 5 + 1 palpal setae is not exceptional.

Literature:

LIEFTINCK (1966) described a ♀ larva of *C. princeps* from Ifrane. Unfortunately, he took the sole specimen in his collection that lacks the lateral spines on segment 8. LIEFTINCK thus incorrectly considered this to be a useful character to distinguish the taxon from *C. boltoni* and *C. bidentatus*. The error was taken over by AGUESSE (1968). LIEFTINCK further noted that *C. princeps* approaches *C. insignis*, as figured by BUCHHOLZ (1954), in the proportionate length of the antennal segments. LIEFTINCK's comparison is invalid, however, because the figured specimen in the latter publication is aberrant from normal *C. insignis*.

b. the *C. boltoni*-group, partim: the subgroup of eastern taxa

6. *Cordulegaster pictus* SÉLYS, 1854

1979 *C. pictus* SÉLYS, 1854. THEISCHINGER, *Odonatologica* 8: 26.

Material examined:

2 exuviae (1 ♂, 1 ♀), Katundere, Malko Turnovo (Burgas), Bulgaria, 15-16.VI.80, leg. H. MALICKY; 1 ♂ exuvia, Mladeschko (Burgas), Bulgaria, 16.VI.80, leg. H. MALICKY; 4 exuviae (2 ♂♂, 2 ♀♀), Kruschewez (Burgas), Bulgaria, 19.VI.80, leg. H. MALICKY; 1 ♀ exuvia, Marié, Thassos, Greece, 18.VI.79, leg. H. MALICKY; 1 fullgrown ♀ larva, Prinos, Thassos, Greece, 16.X.80, leg. H. MALICKY; 1 ♂ exuvia, Kastel Deresi, Surmene (Trabzon), Turkey, 28.VII.85, leg. D. VERSCHUREN; 1 fullgrown ♀ larva, Eserkiyi Koyu, Hopa (Artvin), Turkey, 17.VII.86, leg. L. BRENDONCK. 46 immature larvae were examined additionally.

Biometric data:

total length	♂ larva	: 36 mm (n = 1)
	♀ larva	: 37.5 mm (n = 1)
	♂ exuviae	: 42 - 43 mm ($\bar{x}$ = 42.5; n = 3)
	♀ exuviae	: 43.5 - 44 mm ($\bar{x}$ = 44; n = 3)
head/prothorax		: 1.16 - 1.26 ($\bar{x}$ = 1.19; n = 9)
annulus 1/4+5		: 0.81 - 0.98 ($\bar{x}$ = 0.91; n = 8)
prementum L/W+		: 1.08 - 1.12 ($\bar{x}$ = 1.09; n = 9)
prementum W+/W-		: 2.54 - 2.66 ($\bar{x}$ = 2.59; n = 9)
anal pyramid L/W		: 1.05 - 1.17 ($\bar{x}$ = 1.11; n = 10)

Diagnosis:

Medium-sized dark ochreous larva, sometimes with a purplish shade. Possessing the smallest lateral spines in the *C. boltoni*-group: on the 9th segment, ranging between 1/8 and 1/5 of the length of sternite 9; lacking on the 8th segment (3 out of 10 specimens) or small, blunt tubercles, less than 1/10 of the length of the corresponding sternite. Length of antennal annulus 1 less than the combined lengths of annuli 4 and 5. Prothorax with epaulets broad, 5/6 or more of the head-width. Wingsheaths lying parallel upon the back. Prementum slender (length/width ratio above 1.05), with a correspondingly narrow postmental hinge. 6 long premental setae (exceptionally 5: 1 out of 9 specimens) and 2 to 4 short premental setae. 4 long palpal setae. Setae on rear margin of sternite 9 simple; usually slender and pointed, sometimes distally flattened and truncate. ♀ gonapophyses of normal proportions, extending about 1/5 to 1/4 of their length beyond sternite 9. Anal pyramid typically short, with a length/width ratio always below 1.20. Epiproct and paraprocts relatively blunt and hardly curved.

Affinity:

The presence of lateral spines, the slender prementum, the simple setae on the margin of sternite 9 and the short first flagellar annulus characterize each member of the *C. boltoni*-group. In belonging to the eastern subgroup, *C. pictus* is distinct from *C. boltoni* and the other western taxa by its broad prothorax and short anal pyramid. It differs from the related *C. heros* by having shorter lateral spines, which are sometimes even lacking on segment 8, and the number of 6 long premental setae, against 5 in *C. heros*.

Literature:

THEISCHINGER (1979) ascribes a ♀ exuvia from Brussa, Turkey, to *C. pictus*, whose larva was unknown until then. The specimen could not be traced in the collections of the Naturhistorisches Museum in Wien, where it was deposited. According to THEISCHINGER's description, its anal pyramid is short and blunt, and its lateral spines are said to be shorter than in *C. heros*. However, it deviates from nearly all *C. pictus* examined by us in bearing only 5 long premental setae, which is the typical number for *C. heros*.

7. *Cordulegaster heros heros* THEISCHINGER, 1979

1979 *C. heros heros* THEISCHINGER, 1979. THEISCHINGER, *Odonatologica* 8: 32.

No material examined by us. Diagnosis based on the description of a ♀ exuvia, Niederösterreich, Austria (coll. Naturhistorisches Museum, Wien), in THEISCHINGER (1979).

Biometric data:

total length ♀ exuvia: 48 mm.

Diagnosis:

Large *Cordulegaster* with lateral spines on the 8th abdominal segment shorter than those on the 9th. Epiproct and paraprocts short and rather blunt.

Affinity:

C. heros apparently is closely related to *C. pictus*, sharing with this species the typical short anal pyramid of the eastern subgroup. It differs from *C. pictus* by its larger lateral spines and the number of long premental setae (5, against 6 in *C. pictus*). The only recently established specific status of adult *C. heros* (THEISCHINGER, 1979) is thus supported by its larval morphology.

Literature:

THEISCHINGER (1979) attributed this *Cordulegaster* larva of the *C. boltoni*-group to *C. h. heros* mainly because of three reasons: it differs distinctly from nominate *C. b. boltoni*, it had been found within the presumed range of THEISCHINGER's newly described taxon *C. h. heros*, and it closely resembles Greek material of *C. h. pelionensis*. Apart from the features mentioned in the diagnosis, *C. heros* (both subspecies) is also said to differ

from *C. b. boltoni* in having straight cerci instead of curved ones (THEISCHINGER, loc. cit.). Upon examination of 61 specimens, however, the cerci of nominate *C. b. boltoni* were often found to be nearly straight as well, or at least much less strongly curved as in the specimen figured by THEISCHINGER. Finally, this author also described slightly longer caudal appendages in *C. heros* than in *C. pictus*. However, the length/width ratio of the anal pyramid in the three examined specimens of *C. h. pelionensis* (see below) properly falls within the range of *C. pictus*.

8. *Cordulegaster heros pelionensis* THEISCHINGER, 1979

1979 *C. heros pelionensis* THEISCHINGER, 1979. THEISCHINGER, *Odonatologica* 8: 33, fig. 20-22, 25-32.

Material examined:

3 exuviae (1 ♂, 2 ♀♀), brook between Makryrrachi and Anelion, Pilion Mountains (Thessalia), Greece, 21-26.VII.78, leg. C., D. & G. THEISCHINGER (coll. Oberösterreichisches Landesmuseum, Linz); 2 immature larvae, Xeriasbrook, Boulgara River, Elasson (Thessalia), Greece, 25.VI.84, leg. G.-J. VAN PELT (coll. RMNH Leiden); 2 immature larvae, Livaderon, Drama (Makedhonia), Greece, 23.VI.84, leg. G.-J. VAN PELT (coll. RMNH, Leiden).

Biometric data:

total length	♂ exuvia	: 42 mm (n = 1)
	♀ exuvia	: 44 mm (n = 1)
head/prothorax		: 1.15 - 1.22 ($\bar{x}$ = 1.19; n = 2)
annulus 1/4+5		: 0.95 (n = 1)
prementum L/W+		: 1.07 (n = 1)
prementum W+/W-		: 2.62 (n = 1)
anal pyramid L/W		: 1.01 - 1.11 ($\bar{x}$ = 1.08; n = 3)

Diagnosis:

Large *Cordulegaster*. Lateral spines on the 9th segment medium-sized, about 1/4 of the length of sternite 9; spines on the 8th segment straight and distinctly shorter, length about 1/6 to 1/5 of the corresponding sternite. Length of antennal annulus 1 less than the combined length of annuli 4 and 5. Broad-shouldered, prothorax with epaulets about 5/6 of the head-width. Prementum slender, distincly longer than wide (length/width ratio above 1.05), with a narrow postmental hinge. Usually 5 long premental setae (6 setae in 1 out of 5 specimens) and 2 to 4 short premental setae. 4 long palpal setae. ♀ gonapophyses of normal proportions, extending with about 1/4 of their length beyond sternite 9. Anal pyramid short (length/width ratio below 1.20); epiproct and paraprocts blunt and hardly curved.

Affinity:

See under *C. h. heros*.

Literature:

THEISCHINGER (1979) stated: «Die Larve von *C. h. pelionensis* gleicht der der Nominatrasse vollig.» although he found the lateral spines to be generally shorter than in the single specimen of *C. h. heros*. Considering the paucity of material available, the reliability of this character in separating both taxa is highly uncertain.

c. the *C. bidentatus*-group.

9. *Cordulegaster bidentatus bidentatus* SÉLYS, 1843

1853 *C. bidentatus* SÉLYS. Hagen, *Stett. Ent. Zeitg.*, Bd. 14: 265.

Material examined:

8 fullgrown larvae (3 ♂♂, 5 ♀♀) and 38 exuviae (21 ♂♂, 17 ♀♀), from 11 localities in Yugoslavia (1), Greece (3), Italy (1), Germany (5) and Switzerland (1): 3 exuviae (1 ♂, 2 ♀♀), Plitvice, Yugoslavia, 24-26.VI.85, leg. J. LEMPERT; 12 exuviae (7 ♂♂, 5 ♀♀), Chania, Volos (Thessalia), Greece, 18.VI.84, leg. G.-J. VAN PELT (coll. RMNH, Leiden); 2 fullgrown larvae (1 ♂, 1 ♀), Mount Aristi, Timfi Oros, Pindos, Ioannina (Makedhonia), Greece, 31.VII.80, leg. M. PAVESI; 8 exuviae (2 ♂♂, 6 ♀♀), Ar'achova (Fokis), Greece, 26.VI.85 & 21.VI.86, leg. C. PESARINI; 4 fullgrown larvae (1 ♂, 3 ♀♀), Lago di S. Anna, Auronzo (Bolzano), Italy, 28.VII.71 & 22-28.III.72, leg. I. BUCCIARELLI (coll. MCSN Milano); 1 ♂ exuvia, Königssee, Oberbayern, Germany, 9.VII.26, leg. K. MARTIN (coll. RMNH Leiden). 1 ♂ exuvia, Bonndorf, Schwarzwald, Germany, 27.VI.30, leg. D. GEIJSKES (coll. RMNH Leiden); 1 ♂ exuvia, reared to emergence (01.IV.85), Kasbach, Bad Honnef, Westerwald, Germany, III.85, leg. U. FRANZEL; 3 exuviae (2 ♂♂, 1 ♀), reared to emergence, Marienfoster Bach, Niederrheinische Bucht, Bonn, Germany, V.85 & 1.VI.85, leg. U. FRÄNZEL; 2 fullgrown larvae (1 ♂, 1 ♀) and 4 exuviae (3 ♂♂, 1 ♀), Ohbach, Siebengebirge NR, Bad Honnef, Westerwald, Germany, 19.VI.85 & 18-19.VII.85, leg. U. FRÄNZEL; 2 exuviae (1 ♂, 1 ♀), reared to emergence, Ohbach, Siebengebirge NR, Bad Honnef, Westerwald, Germany, 20.IV.85, leg. U. FRANZEL; 3 exuviae (2 ♂♂, 1 ♀), Roserenbach, Switzerland, 17.V.33, 31.V.33 & 27.IV.34, leg. D. GEIJSKES (coll. RMNH Leiden).

Biometric data:

total length	♂ larva	: 37 - 37.5 mm ($\bar{x}$ = 37; n = 2)
	♀ larvae	: 36 - 37.5 mm ($\bar{x}$ = 36.5; n = 3)
	♂ exuviae	: 36 - 42 mm ($\bar{x}$ = 39; n = 7)
	♀ exuviae	: 40 - 43.5 mm ($\bar{x}$ = 41.5; n = 4)
head/prothorax		: 1.20 - 1.29 ($\bar{x}$ = 1.24; n = 34)
annulus 1/4+5		: 1.02 - 1.54 ($\bar{x}$ = 1.16; n = 29)
prementum L/W+		: 0.97 - 1.05 ($\bar{x}$ = 1.01; n = 36)
prementum W+/W-		: 2.21 - 2.47 ($\bar{x}$ = 2.33; n = 36)
anal pyramid L/W		: 1.13 - 1.36 ($\bar{x}$ = 1.26; n = 35)

Diagnosis:

Medium-sized, dark ochreous to chocolate-brown larva, without lateral spines on abdominal segments 8 and 9. Antennal annulus 1 longer than combined length of annuli 4 and 5. Broad-shouldered, prothorax with epaulets usually about 4/5 of the head-width. Wing-

sheaths lying parallel upon the back. Prementum robust, about as broad as long (length/width ratio below 1.05), with a correspondingly wide postmental hinge. Usually 4, but often 3 or 5 (respectively 5 and 8 out of 32 specimens) long premental setae and a group of at least 5 short premental setae. 4 long palpal setae, exceptionally 3 or 5 (respectively 2 and 1 out of 35 specimens). Setae on rear margin of sternite 9 robust and flattened; about half of them is clearly bi- or trifurcate. ♀ gonapophyses of variable dimensions, extending with 1/5 to 2/5 of their length beyond sternite 9. Anal pyramid moderately slender (length/width ratio above 1.10), epiproct and paraprocts curved and attenuated.

Affinity:

The stout prementum, long basal annulus of the antenna, large number of short premental setae, bifurcate setae on the rear margin of sternite 9, and the lack of lateral spines characterize all members of the *C. bidentatus*-speciesgroup. Within this group, *C. bidentatus* mainly differs from its counterpart *C. insignis* by a broader prothorax and the presence of 4 palpal setae.

Literature:

CABOT (1872) was the first to distinguish larvae of *C. boltoni* and *C. bidentatus*, the two only known European *Cordulegaster* species at that time, on the presence or absence of lateral spines and the relative length of the epiproct. In *C. boltoni*, the length of the epiproct equals the paraproct, while in *C. bidentatus* it was said to be only half as long. CABOT undoubtedly based his description on an aberrant specimen, or one with a broken epiproct. ROUSSEAU (1909) and CONCI & NIELSEN (1956) copied this erroneous diagnosis in their keys. ROBERT (1958) ended the confusion in reporting a second reliable character to tell apart both species: wingsheaths divergent in *C. boltoni*, parallel in *C. bidentatus*. BUCHHOLZ (1954) erroneously used the proportionate length of the antennal segments to separate *C. bidentatus* from *C. insignis*.

10. *Cordulegaster bidentatus sicilicus* FRASER, 1929

Material examined:

1 ♀ exuvia, Fiume S. Paolo, Francavilla di Sicilia (Messina), Sicily, Italy, 21.V.81, leg. H. MALICKY.

Biometric data:

total length ♀ exuvia	: 42.5 mm (n = 1)
head/prothorax	: 1.28 (n = 1)
annulus 1/4 + 5	: 0.98 (n = 1)
prementum L/W +	: 1.01 (n = 1)
prementum W + /W-	: 2.40 (n = 1)
anal pyramid L/W	: 1.23 (n = 1)

Diagnosis:

Medium-sized larva, without lateral spines on abdominal segments 8 and 9. Antennal annulus 1 about as long as the combined length of annuli 4 and 5. Prothorax moderately broad-shouldered, slightly less than 4/5 of the headwidth. Prementum robust and as broad as long (length/width ratio nearly equals 1), with a correspondingly wide postmental hinge. 4 long and 5 short premental setae. Only 2 long palpal setae. Setae on rear margin of sternite 9 straight and slightly flattened, about half of them bifurcate. ♀ gonapophyses large, extending with about 1/4 of their length beyond the rear margin of sternite 9. Anal pyramid slender (length/width ratio above 1.20); epiproct and paraprocts curved and attenuated.

Affinity:

This single exuvia can be readily recognized as belonging to the *C. bidentatus*-group by the absence of lateral spines on segments 8 and 9, by the stout prementum and by the bifurcate setae on the rear margin of sternite 9. Its affinities within this speciesgroup, however, are somewhat confused. Antennal annulus 1 is unusually short, an aberrant condition sometimes found in *C. insignis*, but not in *C. bidentatus*. The width of the prothorax is intermediate between normal *C. insignis* and *C. b. bidentatus*, but the latter species again shows greater variability in this character. Finally, the low number of 2 palpal setae distinguishes this larva from all other West-Palaearctic specimens examined, which possess at least 3 (*C. insignis*) or 4 (*C. b. bidentatus, C. mzymtae* and the entire *C. boltoni*-group) palpal setae. According to discriminant analysis, *C. b. sicilicus*' general morphology takes an intermediate position between *C. b. bidentatus* and *C. insignis* (fig. 7). However, because the single exuvia at hand is possibly aberrant in one or more important characters, the taxonomic position of this taxon cannot be correctly evaluated as yet.

11. *Cordulegaster mzymtae* BARTENEF, 1929

1987 *C. mzymtae* BARTENEF, 1929. VERSCHUREN, DEMIRSOY & DUMONT, *Odonatologica* 16: 401-406.

Material examined:

1 ♀ $F_{.2}$-larva, 12 km W of Savsat (Artvin), Turkey, 16.VII.86, leg. L. BRENDONCK.

Biometric data:

head/prothorax	: 1.23 (n = 1)
prementum L/W	: 1.00 (n = 1)

Diagnosis:

A small (*), bristly, light chestnut-brown coloured larva, without lateral spines on abdo-

(*) in comparison with equally aged larvae of *C. b. boltoni, C. pictus* and *C. insignis*.

minal segments 8 and 9. Broad-shouldered: prothorax with epaulets about 4/5 of the headwidth. Prementum robust, maximal width equal to total length. 3 long and 5 short premental setae. 4 long palpal setae.

Affinity:

Upon larval morphology, *C. mzymtae* belongs to the *C. bidentatus*-group because of the lack of lateral spines, the stout prementum and the number of short premental setae. Within this species-group, *C. mzymtae* shares its broad prothorax and its number of palpal setae with *C. bidentatus*. With the single known specimen of *C. mzymtae* at hand, we could not find reliable characters to distinguish it from equally aged larvae of *C. bidentatus*, which is evidently its closest relative in the West-Palaearctic area (VERSCHUREN *et al.*, 1987).

Literature:

On the basis of adult morphology, *C. mzymtae* has alternately been assigned to the *C. bidentatus*- and *C. boltoni*-group. Even BARTENEF himself changed his mind in a double description (1929, 1930). Arguments for both opinions are found in AKRAMOWSKI & SHENGELIA (1967) and DUMONT & SCHNEIDER (1984), respectively.

12. *Cordulegaster insignis* SCHNEIDER, 1845

1954 *C. insignis* SCHNEIDER. BUCHHOLZ, *Bonn. zool. Beitr. Sonderband* I. Teil: 63-65, fig. 7a-d.

Material examined:

14 fullgrown larvae (9 ♂♂, 5 ♀♀), 31 immature larvae and 56 exuviae (26 ♂♂, 30 ♀♀), from 24 localities in Greece (22) and Turkey (2): 1 fullgrown ♂ larva and 17 exuviae (7 ♂♂, 10 ♀♀), Ano Kastritsi, Patrai (Akhaia), Greece, 23.V.79, leg. H. MALICKY; 4 exuviae (2 ♂♂,2 ♀♀), N of Apikia, Andros, Greece, 13.VI.79 & 24.X.80, leg. H. MALICKY; 1 ♀ exuvia, NE of Vourkoti, Andros, Greece, 12.VI.79, leg. H. MALICKY; 2 fullgrown ♀ larvae, Revmata, Andros, Greece, 21.X.80, leg. H. MALICKY; 2 ♂♂ exuviae, Andros, Greece, 27.V.73, leg. H. M.ALICKY; 2 fullgrown ♂ larvae, Andros, Greece, leg. H. MALICKY; 1 ♂ exuvia, E of Alexi, Paradision, Euboa, Greece, 05.VI.79, leg. H. MALICKY; 6 exuviae (1 ♂, 5 ♀♀), S of Komiton, Euboa, Greece, 06.VI.79 & 10.X.80, leg. H. MALICKY; 1 ♀ exuvia, near Stropones, Euboa, Greece, 09.IX.81, leg. H. MALICKY; 2 exuviae (1 ♂, 1 ♀), Pigi Megadendro, Euboa, Greece, 09.IX.81, leg. H. MALICKY; 1 ♂ exuvia, W of Christomos, Ikaria, Greece, 30.V.79, leg. H. MALICKY; 2 ♀ exuviae, E of Raches, Ikaria, Greece, 31.V.79, leg. H. MALICKY; 3 fullgrown larvae (2 ♂♂, 1 ♀) and 5 exuviae (4 ♂♂, 1 ♀), near Koronis, Naxos, Greece, 26-28.X.80, leg. H. MALICKY; 3 exuviae (2 ♂♂, 1 ♀), Naxos, Greece, leg. H. MALICKY; 5 exuviae (2 ♂♂, 3 ♀♀), NE of Kalithea, Samos, Greece, 26.V.79, leg. H. MALICKY; 1 ♂ exuvia, Menolates, Samos, Greece, 27-29.V.79, leg. H. MALICKY; 4 exuviae (1 ♂, 3 ♀♀), E of Kardiani, Tinos, Greece, 08.VI.79, leg. H. MALICKY; 5 fullgrown larvae (4 ♂♂, 1 ♀), Mount Karia, Olimpos (Larissa), Greece, 03.VIII.80, leg. M. PAVESI; 1 fullgrown ♀ larva and 1 ♀ exuvia, Kemalye (Erzincan), Turkey, 10.VII.86, leg. L. BRENDONCK. 31 immature larvae were additionally examined.

Biometric data:

total length	♂ larva	: 34.5 - 36.5 mm ($\bar{x}$ = 35.5; n = 5)
	♀ larvae	: 39 - 39.5 mm ($\bar{x}$ = 39; n = 3)
	♂ exuviae	: 34 - 44.5 mm ($\bar{x}$ = 40; n = 18)
	♀ exuviae	: 40 - 48 mm ($\bar{x}$ = 43.5; n = 25)
head/prothorax		: 1.24 - 1.41 ($\bar{x}$ = 1.33; n = 57)
annulus 1/4 + 5		: 0.85 - 1.41 ($\bar{x}$ = 1.08; n = 55)
prementum L/W +		: 0.98 - 1.07 ($\bar{x}$ = 1.03; n = 60)
prementum W + /W-		: 2.21 - 2.54 ($\bar{x}$ = 2.38; n = 60)
anal pyramid L/W		: 1.09 - 1.33 ($\bar{x}$ = 1.19; n = 63)

Diagnosis:

Moderately large and somewhat thick-set, dark ochreous to chestnut-brown larva, without lateral spines on abdominal segments 8 and 9. Antennal annulus 1 longer than combined length of annuli 4 and 5, with frequent exceptions (8 out of 55 specimens). Relatively narrow-shouldered: prothorax with epaulets usually about 3/4, and always less than 4/5 of the headwidth. Wingsheaths lying parallel upon the back. Prementum robust, about as broad as long (length/width ratio below 1.05), with a correspondingly wide postmental hinge. Mostly 3 or 4, exceptionally 5 (1 out of 61 specimens) long and at least 5 short premental setae. 3 long palpal setae, exceptionally 4 or 5 (respectively 2 and 1 out of 62 specimens). Setae on rear margin of the 9th sternite strait and spiny; at least 1/3 of them is bifurcate or distally flattened and truncate. ♀ gonapophyses variable, extending with 1/5 to 2/5 of their length beyond the 9th sternite. Anal pyramid moderately slender (length/width ratio above 1.10), epiproct and paraprocts curved and attenuated.

Affinity:

Although unmistakably belonging to the *C. bidentatus*-group, *C. insignis* shows great variation in a number of important features. The length of annulus 1 is often surpassed by the combined length of the two terminal annuli, which then gives the antennae a *C. boltoni*-like appearance. Its prothorax is usually rather narrow, but great variability in the head/prothorax ratio causes a considerable overlap with the broad-shouldered *C. bidentatus*. Still, *C. insignis* can readily be distinguished from *C. bidentatus* and *C. mzymtae* by its 3 palpal setae.

Literature:

BUCHHOLZ (1954) described larvae of *C. insignis* from Naxos, Greece. Unfortunately, all three characters proposed by this author to separate *C. insignis* from *C. bidentatus* are erroneous. Firstly, the description of the antenna is based on an aberrant specimen with a *C. boltoni*-like appearance. Secondly, the shape of the ecdysial split across the eyes and vertex in exuviae shows only insignificant interspecific variation and is useless for identification. The presumed differences in size and shape of the frons and the tubercles on the vertex, finally, probably resulted largely from a different orientation of the animals.

Key to fullgrown larvae and exuviae of West-Palaearctic *Cordulegaster* taxa

In this key, discriminating characters are arranged in order of decreasing discriminating power. In case of doubt for any single character, reference should be made to the descriptions for notes on variability. *C. b. algiricus, C. h. heros* and *C. mzymtae* are not separately included in the key, as definite identification of these taxa cannot be achieved at this point. The taxon *C. b. sicilicus* has not been included either, because the only available specimen might be aberrant in some important features.

1. a. Lateral spines on 9th abdominal segment, usually also on 8th segment; length/width ratio of prementum > 1.05; all setae on rear margin of sternite 9 simple; annulus 1 of antenna shorter than annuli 4+5; less than 5 short premental setae .....*C. boltoni*-group 2
   b. 8th and 9th abdominal segments without lateral spines; length/width ratio of prementum ⩽ 1.05; at least 1/4 of the setae on rear margin of sternite 9 bi- or trifurcate; annulus 1 of antenna longer than annuli 4 + 5; 5 or more short premental setae .....*C. bidentatus*-group 7
2. a. Ratio head/prothorax > 1.25; length/width ratio of paraprocts > 1.20 ....subgroup of western taxa 3
   b. Ratio head/prothorax < 1.25; length/width ratio of paraprocts < 1.20 .... subgroup of eastern taxa 6
3. a. Lateral spines on 8th segment small or missing; spines on 9th segment 1/6 to 1/4 of the length of sternite 9; 4+1 or 5+1 palpal setae.....*C. princeps*
   b. Lateral spines on 8th segment divergent, and about as large as the spines on the 9th segment; spines on 9th segment at least 1/4 of the length of sternite 9; 4+1 palpal setae.....*C. boltoni* s.l. 4
4. a. Lateral spines on 9th segment nearly half as long as sternite 9; length/width ratio of ♀ gonapophyses > 1.65.....*C. boltoni trinacriae*
   b. Lateral spines on 9th segment distinctly less than half the length of sternite 9; length/width ratio of ♀ gonapophyses < 1.65.....5
5. a. Lateral spines on 9th segment about 1/3 of the length of sternite 9; setae on rear margin of sternite 9 flattened and robust.....*C. boltoni boltoni*
   b. Lateral spines on 9th segment about 1/4 of the length of sternite 9; setae on rear margin of sternite 9 slender.....*C. boltoni immaculifrons & C. b. algiricus*
6. a. Lateral spines on 9th segment about 1/4 of the length of sternite 9; spines on 8th segment about 1/6 of the length of sternite 8; 5 long premental setae .....*C. heros heros & C. h. pelionensis*
   b. Lateral spines on 9 th segment only 1/6 of the length of sternite 9; spines on 8th segment small or missing; 6 long premental setae.....*C. pictus*
7. a. Ratio head/prothorax > 1.30; 3+1 palpal setae.....*C. insignis*
   b. Ratio head/prothorax < 1.30; 4+1 palpal setae..... .....*C. bidentatus bidentatus & C. mzymtae*

Affinities between West-Palaearctic *Cordulegaster* taxa upon larval morphology

It lies not within the scope of the present paper to establish a phylogeny for West-Palaearctic *Cordulegaster*, as larval as well as adult morphology ought to be considered for that purpose. The major part of larval discriminating features which key out species and speciesgroups are nevertheless likely to reflect natural relationships between the considered taxa. In this respect, our study of larval morphology yields some significant conclusions:

1. The division of West-Palaearctic *Cordulegaster* into a *C. boltoni*-speciesgroup and a *C. bidentatus*-speciesgroup is justified, and profound interspecific differences within the *C. boltoni*-group define two subgroups, comprising the western and eastern taxa, respectively. These three main entities are so clearly defined that they may be considered as natural.

2. Within the *C. bidentatus*-group, *C. b. bidentatus* and *C. mzymtae* appear more closely related to one another than to *C. insignis* (VERSCHUREN *et al.*, 1987). Due to lack of material, the taxonomic position of *C. b. sicilicus* remains unclear.

3. The attribution of the taxon *trinacriae* to *C. pictus* is incorrect, as it possesses all typical features of the western *C. boltoni*-subgroup.

4. Although being subspecies of *C. boltoni*, larvae of *C. b. immaculifrons* and *C. b. algiricus* share a few diagnostic characters with *C. princeps*, unlike *C. b. trinacriae* and nominate *C. b. boltoni*: short ♀ gonapophyses and a remarkably narrow prothorax. Convergent adaptation to their common, more or less xerophilic mediterranean environment seems to provide the most obvious explanation for these similarities. It is not unlikely, however, that the features mentioned above are, in fact, plesiomorphic characters of the western *C. boltoni*-subgroup, and that the three former taxa possess a common ancestor that deviated from the ancient *C. boltoni*-stock at the subspecific level; the *C. boltoni*-stock itself then gave rise to the more apomorphic subspecies *C. b. boltoni* and *C. b. trinacriae* with the development of a broader prothorax, longer ♀ gonapophyses and longer spines on the 8th and 9th segment. If this is true, the present taxonomy merely reflects the extent of isolation of the respective taxa during later history. Indeed, the scattered and ecotopically influenced distribution of *C. b. algiricus, C. b. immaculifrons* and *C. b. boltoni* on the Iberian peninsula (COMPTE SART, 1985; VAN PELT, pers. comm.) suggests that the two southern subspecies *C. b. immaculifrons* and *C. b. algiricus* were never sufficiently isolated to permit allopatric evolution, independent from one another and from the northern nominate subspecies. The Moroccan *C. princeps*, on the other hand, possibly has been subject to evolutionary jumps that followed the repeated decimation of mountainous relict populations, resulting in its present specific status. The somewhat erratic variability in the length of the spines on the 8th segment probably reflects considerable inbreeding in this taxon.

Such intra- and interspecific relations in the western *C. boltoni*-subgroup are still difficult to evaluate, and investigations are hindered by the problems already explained. On a broader scale, our results nevertheless demonstrate that the evaluation of affinities in larval morphology can make a valuable contribution in the discussion of dragonfly phylogeny.

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