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Taxonomic Revision of Eastern Part of Western Palaearctic *Cordulegaster* Using Molecular Phylogeny and Morphology, with the Description of Two New Species (Odonata: Anisoptera: Cordulegastridae) [†]

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Abstract: Taxonomy of the genus *Cordulegaster* Leach in Brewster, 1815 in the Eastern part of the Western Palaearctic is poorly resolved. A two-step approach was applied: sequences of mitochondrial and nuclear DNA fragments were used to sort specimens; poorly known or new taxa with their phenotypic variation were described. The existence of two traditional groups (*boltonii*- and *bidentata*-group) was confirmed. *Cordulegaster coronata* Morton, 1916, however, belongs to a different group. Molecular-analysis supported three known and one new species (*C. heros* Theischinger, 1979, *C. picta* Selys, 1854, *C. vanbrinkae* Lohmann, 1993, and *C. kalkmani* sp. nov.) in the *boltonii*-group. In the *bidentata*-group, all specimens from West-Turkey belonged to *C. insignis* Schneider, 1845, all specimens further east to a complex of four closely related species, which we name *charpentieri*-complex (*C. amasina* Morton, 1916, stat. rev., *C. mzyntae* Bartenev, 1929 *C. charpentieri* (Kolenati, 1846), stat. rev. and *C. cilicia* sp. nov.). The following taxa: *C. insignis nobilis* Morton, 1916, syn. nov., *C. nachitschevanica* Skvortsov and Snegovaya, 2015, syn. nov. *C. plagionyx* Skvortsov and Snegovaya, 2015, syn. nov. and the Caucasian subspecies *C. insignis lagodechica* Bartenev, 1930, syn. nov., were synonymized with *C. charpentieri*. Finally, we provide a key for all Western Palaearctic *Cordulegaster*.

Keywords: Caucasus-Anatolian-Iranian-region; hybridization; identification key; new species; new status; new synonym; variation



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1. Introduction

1.1. General Remarks on the Genus *Cordulegaster*

Cordulegastridae is a family, containing three genera: *Cordulegaster* Leach in Brewster, 1815, *Anotogaster* Selys, 1854 and *Neallogaster* Cowley, 1934. Cordulegastridae is a rather small family with 51 species [1]. They are a morphologically conserved family of robust, black-and-yellow dragonflies. The genus *Cordulegaster* occurs in North Africa, Europe, and South-West Asia as far east as the Himalayan region of India and Nepal with species reported also from China and Vietnam [2,3]. In addition, there is a group of *Cordulegaster* species in North America, with one species extending to Central America [4].

1.2. Threats to Western Palaearctic *Cordulegaster*

Cordulegaster are reophiles, and mainly restricted to clean running springs and brooks. These habitats are under particular threat in the south-eastern part of the Western Palaearctic due to water crisis [5,6]. Therefore, some of the European *Cordulegaster* species are currently classified as endangered, like *C. helladica*, or even critically endangered, like *C. helladica kastalia* [5,7,8]. Other Western Palaearctic members of the genus are listed as data deficient, for example *C. vanbrinkae* [9]. A better taxonomic understanding of these taxa is therefore also of interest from the view of conservation aspects.

1.3. History of the Taxonomy of Western Palaearctic *Cordulegaster*

After the actual understanding, Western Palaearctic *Cordulegaster* are separated in two groups the *boltonii*- and the *bidentata*-group [10,11]. The main difference is that the males of the *boltonii*-group have one tooth on the upper appendages, while the males of the *bidentata*-group have two. This latter point was name giving for the *bidentata*-group. More differences between the two groups are listed and depicted in the Field Guide to the Dragonflies of Britain and Europe [11]. This view is further supported by a study on larvae, and recently by a molecular genetic analysis [12,13].

Species of *Cordulegaster* are remarkably similar in the structure of male appendices and female valvular scale, while the pattern of yellow markings on abdomen, thorax, and occipital triangle may vary, even within a single taxon [14,15]. This has resulted in confusion regarding the identification, distribution and infraspecific division of the species of the Western Palaearctic region. A comprehensive revision is urgently needed, to complement a recent study, which left the Eastern part of the Western Palaearctic region with about 10 taxa unresolved [13]. Recently, two additional taxa from the Caucasus were described, adding even more complexity to the taxonomy of the genus [16].

The research history of this genus in the Western Palaearctic includes some of the earliest works on dragonflies. *Cordulegaster insignis* was described based on a female from Kellemisch (Anatolia, Turkey) [17]. The location of Kellemisch is absent from recent maps and was searched for by Erich Schmidt, who localized it in the Western Mediterranean region of Turkey [18]. *C. insignis* was re-investigated and two males and two females from Syria were assigned to this species [19,20]. Kolenati described a further taxon from the Caucasus, *Aeshna charpentieri* Kolenati, 1846 [21]. The later taxon has caused much confusion since then. Unfortunately, in the region of the Caucasus, where Kolenati collected the type male, two members of this genus occur, one of the *bidentata*-group (*C. charpentieri* (Kolenati 1846)) and one of the *boltonii*-group (*C. picta* Selys, 1854). Selys confused *Aeshna charpentieri* with his *C. picta* and this confusion was ongoing until it culminated in the designation of a neotype of *C. charpentieri* by Waterston which belongs in fact to *C. picta* [22–24]. The complex history of confusion is described in detail by Dumont. In this paper *Aeshna charpentieri* is synonymized with a member of the *bidentata*-group *C. insignis* [25].

Morton proposed the taxa *C. boltonii algerica* Morton, 1916, *C. princeps* Morton, 1916, *C. insignis amasina* Morton, 1916, *C. insignis nobilis* Morton, 1916, and *C. coronata* Morton, 1916 on the basis of colour markings and with no clear structural characters [26]. Fraser made a further revision of the genus, did not change much to Morton's conclusions, but provided new figures for many taxa, including those from the east of the Western Palaearctic [2]. Fraser treated *C. coronata* as a subspecies of *C. insignis*. Bartenev described *C. mzymtae* and *C. insignis lagodechica* from the Caucasus, and *C. magnifica* from an unknown locality [27,28]. Dumont synonymized *C. i. lagodechica* with *C. insignis*, Waterston described *C. trinacriae* and Theischinger recognized *C. heros* as a further species in the *boltonii*-group [24,25,29]. Lohmann's revision of the genus involved new genera, species and subspecies, including *C. helladica* and *C. vanbrinkae* [30]. He assigned some members of the *bidentata*-group like *C. helladica*, *C. insignis charpentieri*, *C. insignis amasina* and *C. insignis* in a new genus *Sonjagaster*, which, however, has not been followed so far by others, and we synonymize here *Sonjagaster* with *Cordulegaster*. Moreover, he raised several subspecies of *C. insignis* (e.g., *C. i. amasina*, *C. i. charpentieri*, and *C. i. montandoni* [31]) to species level without giving

details or plausible reasons for this change. In the Eastern part of the Western Palaearctic, another species, *C. coronata*, is found, occurring from North-East Iran to Kyrgyzstan. This taxon was described by Morton as a separate species, later treated as a subspecies of *C. insignis* [2,26].

Neallogaster schmidti was reported once from North-East Afghanistan near the border to Pakistan [32,33], which is just outside of the Western Palaearctic according to most authors and therefore not treated here.

Thus, the exact taxonomic status of most *Cordulegaster* of the Eastern part of the Western Palaearctic region is unsettled, and the relations between the members of this genus in this region, as well as their exact distribution limits, are not known.

1.4. Geological and Climatic Events Influencing Diversification of Western Palaearctic *Cordulegaster*

The diversification of the biota in the Western Palaearctic has been shaped by geological and climatic events of the last millions of years. We assume that these events were also important for the evolutionary history of the genus *Cordulegaster*. One dramatic episode was the Messinian Salinity Crisis, about 6 million years ago, leading to the evaporation of the Mediterranean Sea. It connected many Mediterranean Islands and North Africa with Europe and allowed for their colonization from the continent [34]. As the Mediterranean Basin refilled, the *Cordulegaster* species of North Africa and Mediterranean Islands may have started to evolve in an allopatric way. A second major driver of *Cordulegaster* diversification may have been the Pleistocene Ice Ages. According to the calculation by Solano *C. trinacriae* and *C. boltonii* separated in the early Pleistocene about 1.32 million years ago [35]. Thus, the European but also the whole Western Palaearctic biota may be a result of the postglacial expansion, which has structured the current distribution concepts of species [36,37]. The last Glacial Maximum shaped the phylogeny and phytogeography of most of the existing taxa. Hewitt emphasized the importance of postglacial colonization events in animals and plants following a similar pattern of expansion from refugia [36,38,39]. These events seem to be particularly important for the understanding of species development of Western Palaearctic *Cordulegaster*, as already recently discussed for the Apennine Peninsula [35]. Following those concepts, the Western Palaearctic *Cordulegaster* may have become restricted to regions like the Mediterranean, Black Sea and Caspian Sea shores. These refugia may have kept populations isolated for a few millions of years and allowed them to evolve into species [35–37]. During interglacials, one of which we live in today, species may have expanded and hybridised in secondary contact zones [35–37]. Hot spots of such events in the case of *Cordulegaster* may be the Aegean region, Anatolia and the Caucasus region, where three glacial refuge population (Mediterranean, Black Sea and Caspian Sea) meet [40,41]. A final factor for species diversification may be aridity and the uplift of the Anatolian Diagonal [42].

The availability of molecular tools has recently revolutionised our species concept. It revealed that the definition of a species as an entity that is reproductively isolated is relative. Many species indeed hybridise under natural conditions, and reproductive isolation is only partial.

The complexity of the systematics of the genus *Cordulegaster* indicates that any revision solely based on morphology and colour patterns is bound to fail. A combination of molecular methods for reconstructing phylogenies with traditional morphological techniques is needed. We provide a revision of the Eastern part of the Western Palaearctic *Cordulegaster* by molecular genetic approach followed by phenotype description.

2. Material and Methods

2.1. Material

A total of 156 *Cordulegaster* specimens of the Eastern part of the Western Palaearctic were investigated (Table 1, Figures 1 and 2, Supplementary Material Figure S1). In the molecular genetic analysis sequences from 72 specimens from Eastern Europe, Turkey, the Caucasus countries, Iran and Kyrgyzstan were included. From these 72 specimens,

59 specimens and 107 genetic data are new; genetic data from 13 specimens (*C. heros*, *C. picta*, and *C. insignis*) were already published [13]. New and published sequences of *Cordulegaster* from the Western part of the Western Palearctic and American *Cordulegaster* were used for the COI overview tree (Figure S2). Many species investigated in this study were collected by Gert Jan van Pelt (G.J.v.P.) and are deposited in the Naturalis Biodiversity Center, Leiden (RMNH). The types and most specimens for re-description are deposited in RMNH (Table 1, Figure S1). Additional material was more recently collected by some of the authors (Thomas Schneider, T.S.; Nataly Snegovaya, N.S.; Henri J. Dumont, H.D.), and others listed in Table 1 and the acknowledgement. For the descriptive part material from RMNH and the private collection of one of the authors (T.S.) was used (detailed information Table 1, Figure S1).

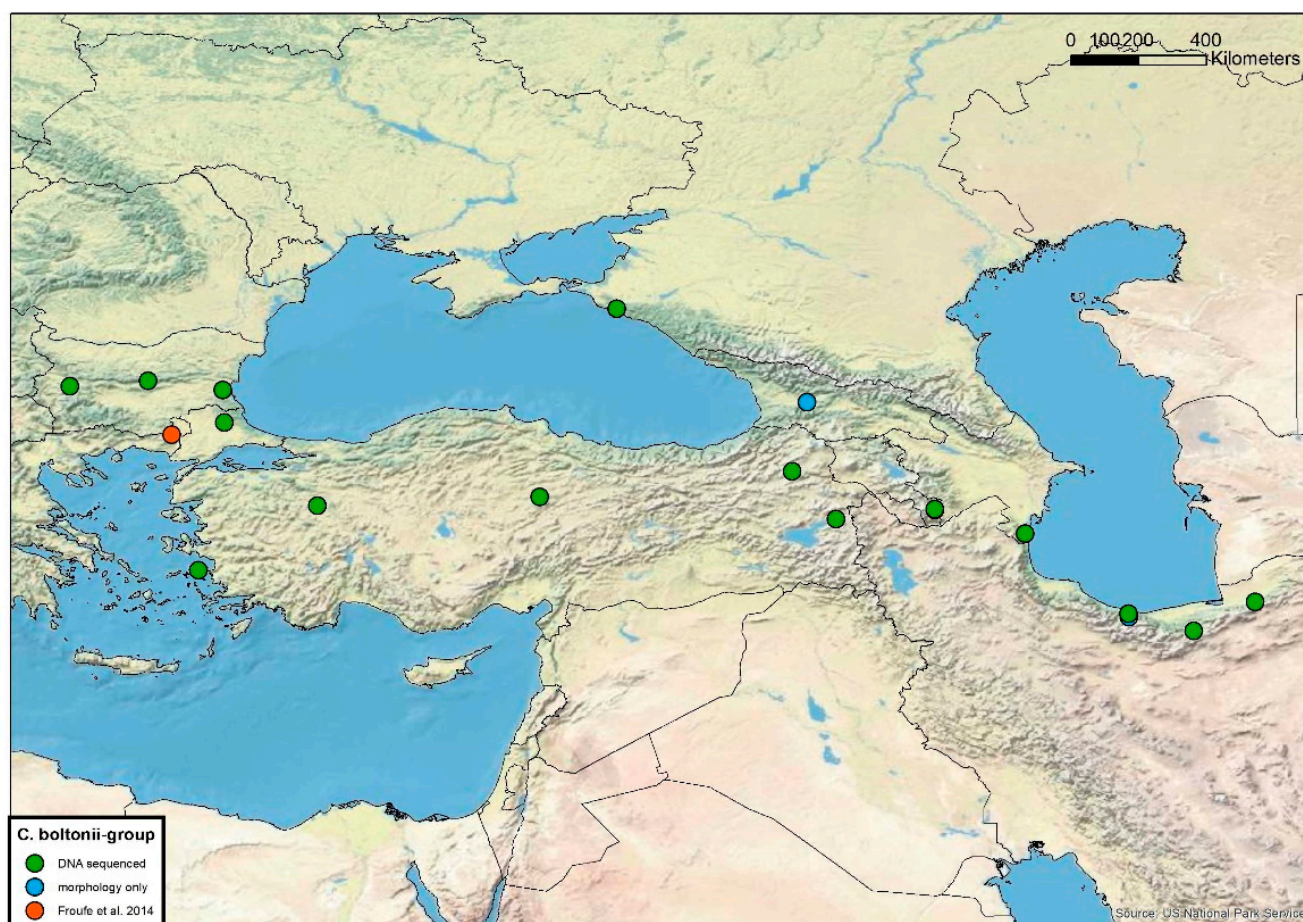


Figure 1. Map showing the origin of investigated specimens of the *C. boltonii*-group.

2.2. General Methods

Our molecular analysis included Genbank sequences of New World and Asian species (Figure S2). Already published sequences of Western Palearctic *Cordulegaster* are included [13,35,43]. From Central Turkey and east of this region, no sequences of *Cordulegaster* from the Western Palearctic have been published so far. Thus, only the sequences published with this manuscript are available. Andy Vierstrate (A.V.) did the molecular phylogenetic work. He received only legs, with exact geographic data, however, without knowing the assumed taxa.

Table 1. *Cordulegaster* specimens investigated are listed here with group name, species names, notes, geo-coordinates, collectors, reference, and gene bank numbers. For further details see Figure S1.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>amasina</i>		39.5629	34.1894	Turkey	leg. G.J. van Pelt	MK779843	MK861474
<i>bidentata</i> -group	<i>amasina</i>		40.9765	34.1894	Turkey	leg. G.J. van Pelt	MK779844	MK861470
<i>bidentata</i> -group	<i>amasina</i>	male redescription	40.5915	32.6597	Turkey	leg. G.J. van Pelt	MK779845	MK861469
<i>bidentata</i> -group	<i>amasina</i>		39.5629	34.1894	Turkey	leg. G.J. van Pelt	no data	MK861473
<i>bidentata</i> -group	<i>bidentata</i>		50.8101	14.7763	Czech Republic	leg. M. Waldhauser	MK779814	no data
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			France	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only			Germany	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	morphology only	39.4386	23.0464	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	was <i>C. b. sicilica</i> , morphology only			Italy	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	was <i>C. b. sicilica</i> , morphology only			Italy	leg. T. Schneider		
<i>bidentata</i> -group	<i>bidentata</i>	was <i>C. b. sicilica</i> , morphology only			Italy	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>		38.9487	46.1958	Armenia	leg. V. Ananian	MK779820	MK861491
<i>bidentata</i> -group	<i>charpentieri</i>		38.9131	46.4604	Armenia	leg. V. Ananian	MK779821	MK861463
<i>bidentata</i> -group	<i>charpentieri</i>		38.8956	46.1875	Armenia	leg. V. Ananian	no data	MK86149
<i>bidentata</i> -group	<i>charpentieri</i>		38.8956	46.1875	Armenia	leg. V. Ananian	no data	MK861467
<i>bidentata</i> -group	<i>charpentieri</i>		38.9487	46.1958	Armenia	leg. V. Ananian	no data	MK861460

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>charpentieri</i>		39.7038	45.3468	Armenia	leg. V. Ananian	no data	MK861462
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nachitschevanica</i>	39.1103	45.9144	Azerbaijan	leg. N. Snegovaya	MK779823	MK861463
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>plagionyx</i>	41.6761	46.4931	Azerbaijan	leg. N. Snegovaya	MK779828	MK861466
<i>bidentata</i> -group	<i>charpentieri</i>	male, was <i>nachitschevanica</i> , morphology only	39.1103	45.9144	Azerbaijan	leg. N. Snegovaya		
<i>bidentata</i> -group	<i>charpentieri</i>	female, was <i>plagionyx</i> , morphology only	41.6761	46.4931	Azerbaijan	leg. N. Snegovaya		
<i>bidentata</i> -group	<i>charpentieri</i>	male, was <i>plagionyx</i> , morphology only	41.6761	46.4931	Azerbaijan	leg. N. Snegovaya		
<i>bidentata</i> -group	<i>charpentieri</i>	<i>charpentieri</i> <i>lagodechica, larva</i>	41.8404	46.2846	Georgia	leg. M. Lemke	MK779824	MK861465
<i>bidentata</i> -group	<i>charpentieri</i>		41.7458	44.7426	Georgia	leg. N. Snegovaya	MK779825	no data
<i>bidentata</i> -group	<i>charpentieri</i>	<i>charpentieri</i> <i>lagodechica, larva</i>	41.8404	46.2846	Georgia	leg. M. Lemke	MK779826	MK861477
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i>	29.4311	53.0842	Iran	leg. T. Schneider	MN623223	MN612638
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , male	33.4597	49.9472	Iran	leg. T. Schneider	MK779819	MK861457
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i>	35.8926	52.0125	Iran	leg. M. Waldhauser	MK779829	MK861459
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , female paratype	30.3339	52.1564	Iran	leg. T. Schneider	MK779830	MK861496
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i>	29.0022	57.5869	Iran	leg. T. Schneider	MK779831	MK861471
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> ; morphology only	29.0022	57.5869	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> ; morphology only	29.0022	57.5869	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> ; morphology only	29.0022	57.5869	Iran	leg. T. Schneider		

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , male paratype , morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , female, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , female, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , female, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , male, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , male, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , male, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , paratype male, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>	was <i>nobilis</i> , paratype male, morphology only	30.3339	52.1564	Iran	leg. T. Schneider		
<i>bidentata</i> -group	<i>charpentieri</i>		40.5616	42.3471	Turkey	leg. G.J. van Pelt	MK779822	MK861458
<i>bidentata</i> -group	<i>charpentieri</i>	male redescription , neotype	38.3834	42.7723	Turkey	leg. G.J. van Pelt	MK779827	MK861476
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , paratype , morphology only	34.2511	36.0111	Lebanon	leg. G.A. Mavromoustakis		
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , paratype , morphology only	34.2511	36.0111	Lebanon	leg. G.A. Mavromoustakis		

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , morphology only	34.2511	36.0111	Lebanon	leg. G.A. Mavromoustakis		
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , female paratype , morphology only	34.4578	35.8414	Lebanon	leg. G.A. Mavromoustakis		
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , morphology only	34.4578	35.8414	Lebanon	leg. G.A. Mavromoustakis		
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , morphology only	34.4578	35.8414	Lebanon	leg. G.A. Mavromoustakis		
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>charpentieri</i> , paratype	40.6114	41.6286	Turkey	leg. G.J. van Pelt	MK779832	MK861494
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , paratype , morphology only	38.7205	36.3950	Turkey	leg. G.J. van Pelt	MK779833	MK861475
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , paratype , morphology only	38.0164	35.0311	Turkey	leg. G.J. van Pelt	MK779834	no data
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , male holotype	38.0614	36.4722	Turkey	leg. G.J. van Pelt	MK779835	MK861498
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i> , male paratype	37.9698	34.6767	Turkey	leg. G.J. van Pelt	MK779836	MK861468
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i>	37.6512	34.5328	Turkey	leg. G.J. van Pelt	MK779837	MK861461
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i>	37.9698	34.6766	Turkey	leg. G.J. van Pelt	MK779839	MK861472
<i>bidentata</i> -group	<i>cilicia</i> sp. nov.	was <i>insignis</i>	40.3334	42.5905	Turkey	leg. G.J. van Pelt	MK779840	MK861495
<i>bidentata</i> -group	<i>cilicia</i> sp. nov./ <i>insignis</i>	hybrid: <i>cilicia</i> × <i>insignis</i>	37.9293	32.5000	Turkey	leg. G.J. van Pelt	MK779838	MK861497
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider	MK779857	MK861452
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	34.9569	60.1672	Iran	leg. T. Schneider		
<i>coronata</i> -group	<i>coronata</i>	was sometimes treated as ssp. of <i>insignis</i>	41.2044	74.7661	Kyrgyzstan	leg. H. Dumont	MK779858	MK861453
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.4887	22.5048	Greece	leg. T. Schneider		

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>helladica</i>	morphology only	38.4887	22.5048	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	48.2132	16.3847	Austria	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	48.2132	16.3847	Austria	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>		42.4929	27.4733	Bulgaria	leg. G.J. van Pelt	MK779810	no data
<i>boltonii</i> -group	<i>heros</i>		42.7339	25.4858	Bulgaria	leg. G.J. van Pelt	MK779810	no data
<i>boltonii</i> -group	<i>heros</i>		42.5937	23.4102	Bulgaria	leg. G.J. van Pelt	MK779812	MK861451
<i>boltonii</i> -group	<i>heros</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>	morphology only	38.0353	22.1098	Greece	leg. T. Schneider		
<i>boltonii</i> -group	<i>heros</i>		42.1837	19.2915	Montenegro	leg. G. De Knijf	MK779813	no data
<i>bidentata</i> -group	<i>insignis</i>		37.7284	26.8196	Greece	leg. T. Schneider	MW353685	MW363787
<i>bidentata</i> -group	<i>insignis</i>		37.5833	26.1667	Greece	leg. T. Schneider	MW353686	MW363788
<i>bidentata</i> -group	<i>insignis</i>		37.5833	26.1667	Greece	leg. T. Schneider	MW353687	MW363789
<i>bidentata</i> -group	<i>insignis</i>		39.0690	26.3468	Greece	leg. W. Lopau	MW353702	no data
<i>bidentata</i> -group	<i>insignis</i>		36.9287	28.7511	Turkey	Froufe et al., 2014	KF584941	KF584979
<i>bidentata</i> -group	<i>insignis</i>		37.0287	28.7554	Turkey	Froufe et al., 2014	KF584941	no data
<i>bidentata</i> -group	<i>insignis</i>		37.0287	28.7554	Turkey	Froufe et al., 2014	KF584941	no data
<i>bidentata</i> -group	<i>insignis</i>		37.0287	28.7554	Turkey	Froufe et al., 2014	KF584941	KF584979
<i>bidentata</i> -group	<i>insignis</i>		37.2196	28.3658	Turkey	Froufe et al., 2014	KF584942	no data
<i>bidentata</i> -group	<i>insignis</i>		37.0287	28.7554	Turkey	Froufe et al., 2014	KF584943	KF584979
<i>bidentata</i> -group	<i>insignis</i>		41.6771	26.5557	Turkey	leg. G.J. van Pelt	MK779846	MK861486

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>insignis</i>		39.3444	29.2579	Turkey	leg. G.J. van Pelt	MK779848	MK861487
<i>bidentata</i> -group	<i>insignis</i>		36.5595	30.3501	Turkey	leg. T. Schneider	MW353707	MW363797
<i>boltonii</i> -group	<i>kalkmani</i> sp. nov.	was <i>picta</i> , male holotype	40.4203	42.7446	Turkey	leg. G.J. van Pelt	MK779808	MK861450
<i>boltonii</i> -group	<i>kalkmani</i> sp. nov.	was <i>picta</i> , female paratype	39.0594	43.7540	Turkey	leg. V. Kalkman	MK779809	MK861449
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	41.6319	42.5680	Georgia	leg. T. Schneider		
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	43.4462	41.7357	Russia	leg. O. Kosterin	MN623222	no data
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	40.6797	37.9573	Turkey	leg. G.J. van Pelt	MK779841	MK861493

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>bidentata</i> -group	<i>mzymtae</i>	was sometimes treated as ssp. of <i>insignis</i>	40.6797	37.9573	Turkey	leg. G.J. van Pelt	MK779842	MK861492
<i>boltonii</i> -group	<i>picta</i>		41.5631	24.9664	Bulgaria	leg. G.J. van Pelt	no data	no data
<i>boltonii</i> -group	<i>picta</i>	morphology only	42.1667	42.9833	Georgia	leg. T. Schneider		
<i>boltonii</i> -group	<i>picta</i>		41.3093	26.1148	Greece	Froufe et al., 2014	KF584944	KF584992
<i>boltonii</i> -group	<i>picta</i>		41.3093	26.1148	Greece	Froufe et al., 2014	KF584944	KF584993
<i>boltonii</i> -group	<i>picta</i>		40.6910	24.6209	Greece	leg. T. Schneider	MK779802	no data
<i>boltonii</i> -group	<i>picta</i>		37.7094	26.8178	Greece	leg. T. Schneider	MW353684	no data
<i>boltonii</i> -group	<i>picta</i>		44.6541	37.9347	Russia	leg. O. Kosterin	MK779799	MK861448
<i>boltonii</i> -group	<i>picta</i>		44.6541	37.9347	Russia	leg. O. Kosterin	MK779800	MK861447
<i>boltonii</i> -group	<i>picta</i>		44.6541	37.9347	Russia	leg. O. Kosterin	MK779801	no data
<i>boltonii</i> -group	<i>picta</i>		39.4200	29.9857	Turkey	leg. G.J. van Pelt	MK779803	no data
<i>boltonii</i> -group	<i>picta</i>		39.6602	35.8823	Turkey	leg. G.J. van Pelt	MK779804	MK861445
<i>boltonii</i> -group	<i>picta</i>		41.6281	27.5122	Turkey	leg. G.J. van Pelt	no data	MK861446
<i>boltonii</i> -group	<i>vanbrinkae</i>		38.6825	48.7831	Azerbaijan	leg. N. Snegovaya	MK779806	no data
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	38.6825	48.7831	Azerbaijan	leg. N. Snegovaya		
<i>boltonii</i> -group	<i>vanbrinkae</i>		36.0965	53.2606	Iran	leg. T. Schneider	MW353704	MW363796
<i>boltonii</i> -group	<i>vanbrinkae</i>		36.8741	54.8872	Iran	leg. T. Schneider	MK779805	MK861442
<i>boltonii</i> -group	<i>vanbrinkae</i>	larva	36.5567	51.5231	Iran	leg. M. Waldhauser	MK779807	MK861443
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.4700	51.5383	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.4700	51.5383	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		

Table 1. Cont.

Group	Species Identified	Former Taxon/Notes	Latitude	Longitude	Country	Collector/Reference	Genbank COI	Genbank ITS
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae</i>	morphology only	36.8741	54.8872	Iran	leg. T. Schneider		
<i>boltonii</i> -group	<i>vanbrinkae/picta</i>	hybrid: <i>vanbrinkae</i> × <i>picta</i>	39.3334	46.3786	Armenia	leg. V. Ananian	MK779798	MK861444
<i>boltonii</i> -group	<i>vanbrinkae/picta?</i>	morphology only	39.3106	46.3775	Armenia	leg. V. Ananian		
<i>boltonii</i> -group	<i>vanbrinkae/picta?</i>	morphology only	39.3106	46.3775	Armenia	leg. V. Ananian		

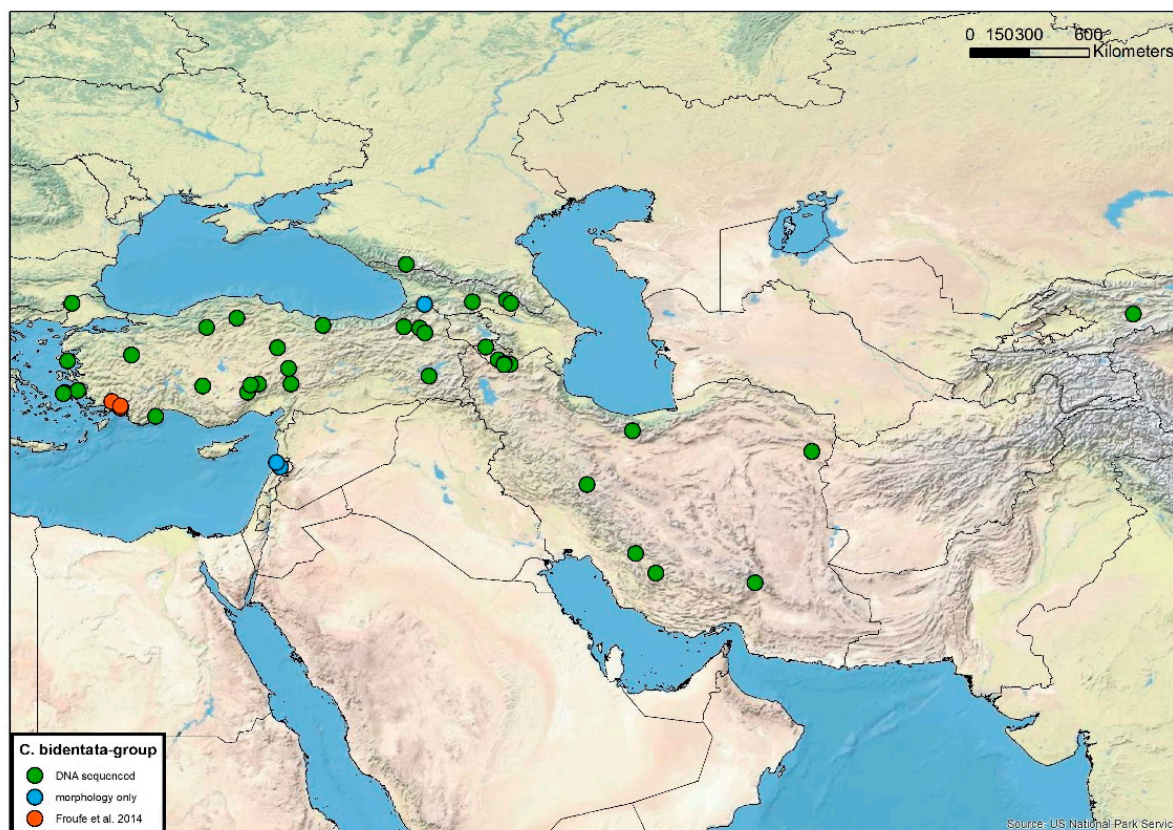


Figure 2. Map showing the origin of the investigated specimens of the *C. bidentata*-group.

At that point of the study, taxonomy of this region was no more than a guess. For example, all members of the *bidentata*-group of the region are currently treated under *C. insignis* or a subspecies of this species [11]. Furthermore, some authors treated *C. charpentieri* or *C. coronata* as separate species without specifying scientific reasons [44–47].

We used at first a molecular genetic approach analysing the COI and ITS genes for constructing bootstrap maximum likelihood trees, Bayesian inference trees and haplotype networks. In addition, evolutionary distance between a pair of sequences was measured by the *p*-distance and the Kimura 2-P distance (K2-P). The latter methods can be translated into taxonomic ranks. In zoology, about 3% difference is considered as a good limit for species difference [48]. For odonata, a difference between 2 to 3% are discussed for species discrimination and may be lower in closely related species [49,50].

A recent analysis for Western Palaearctic odonata revealed for Anisoptera, a K2-P distance above 1.96% as a good threshold [43]. This barcoding analysis on a large set of Italian odonata showed that genetic K2-*p* distance variation within morphospecies ranged from 0% to 9.17% (mean \pm SD = 0.48 \pm 0.62%) in Zygoptera and from 0% to 2.64% (mean \pm SD = 0.33 \pm 0.29%) in Anisoptera. Interspecific K2-*p* distance values ranged from 0% to 27.29% (mean \pm SD = 19.41 \pm 3.71%) and from 0% to 25.28% (mean \pm SD = 18.25 \pm 3.18%) in Zygoptera and Anisoptera, respectively [43]. Therefore, we used beside the Bayesian inference trees and haplotype networks a K2P-distance above 2% as an orientation for species allocation. We observed no relevant difference between P- and K2-P distances.

Possible hybrids were defined when specimens with their maternally inherited COI corresponding to a different species than their ITS.

2.3. Molecular Genetic Analysis

We analyzed the cytochrome c oxidase subunit I (COI) gene from the mDNA and the ITS region (ITS1, 5.8S and ITS2) from the rDNA. For details of the origin of specimens, see maps Figures 5 and 6, Figure S1 and Table 1. For the COI gene, the sequences are 568 bp long, for the ITS region the sequences are between 713 and 815 bp long, depending on the species. We used *Aeshna umbrosa* Walker, 1908 and *Anotogaster chaoi* Zhou, 1998 as outgroups.

2.4. DNA Extraction, PCR Methods, and Sequencing

Per specimen, a 1.0 mm section of a leg was transferred to a tube with 20 μ L 0.05 N NaOH and 2 μ L 5% Tween 20. This was heated for 15 min at 95 °C and cooled on ice. 100 μ L sterile water was added to the tube and mixed. 1 to 5 μ L of this solution was used in a PCR reaction. We amplified and sequenced a fragment of mDNA (the barcoding segment of the cytochrome c oxidase subunit I (COI) gene) and the entire ITS region separating the SSU and LSU region of the 18S nuclear rDNA operon comprising the ITS 1 intergenic ITS, the conserved 5.8S gene and the ITS 2 intergenic ITS, using the PCR on a 2720 Thermal Cycler of Applied Biosystems, Waltham, Massachusetts, USA. Primers used for PCR were CO1490F (5'-GGT CAA ATC ATA AAG ATA TTG G-3') and CO2198R (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') for the COI fragment [51]. Cycle conditions were 95 °C for 3 min followed by 45 cycles of 95 °C for 30 s, 48 °C for 30 s and 72 °C for 1 min. Primers used for amplifying the rDNA fragment are Vrain2F (5'-CTT TGT ACA CAC CGC CCG TCG CT-3') and 28R1 (5'-TGA TAT GCT TAA NTT CAG CGG GT-3') primers. Cycle conditions were 95 °C for 3 min followed by 45 cycles of 95 °C for 30 s, 54 °C for 30 s and 72 °C for 1 min. PCR products were sequenced on an ABI 3130XL automatic sequencer from Applied Biosystems with the BigDye 3.1 kit according to manufacturer instructions.

2.5. Phylogenetic Methods

MAFFT (Multiple Alignment with Fast Fourier Transform)

Multiple sequence alignments were made with the online version of MAFFT [52].

2.6. jModelTest

The model of DNA evolution that best fit the data was determined with JMODELTEST version 2.1.10 [53]. Based on the Bayesian information criteria (BIC), the best model was chosen for Bayesian inference in MRBAYES 3.2.7a [54] and maximum likelihood analysis in PAUP 4.0a168 [55].

2.7. Tree Construction with MrBayes and PAUP

The model parameters from JMODELTEST were used in MRBAYES (nst = 6 and rates = gamma for COI; nst = 1 and rates = equal for the ITS region). The settings were: 10 million generations, a sample frequency of 1000 and a burnin value of 5000 trees.

PAUP 4.0a168 was used for constructing the bootstrap maximum likelihood trees. The model parameters from JMODELTEST were used as model in PAUP (TPM2uf + G base = (0.3247 0.1447 0.1192) nst = 6 rmat = (1.8954 21.0629 1.8954 1.0000 21.0629) rates = gamma shape = 0.1580 ncat = 4 pinvar = 0 for COI, HKY + G base = (0.2011 0.2807 0.3290) nst = 2 ratio = 0.9345 rates = gamma shape = 0.3020 ncat = 4 pinvar = 0 for the ITS region). 100 bootstrap replicates (starting with a Neighbor Joining tree) were performed with a branch swapping limit set to 100,000 or 3 h (whichever comes first) per bootstrap replicate. For creating trees, *Cordulegaster* DNA-sequences from the West Palaearctic, from America and from E-Asia were used. Genbank was searched for credible sequences. Available sequences for COI and the ITS region approximately the same length as our own were added to the alignment. Their accession numbers are listed next to the names in the trees.

2.8. StarBeast

In addition, StarBeast, a multi-individual multi-locus species tree estimation program, using Bayesian coalescent analysis, as implemented in the BEAST package was applied for both genes [56,57]. Xml input files were created in BEAUTI v2.6.3 [57], using the HKY + Γ + I model for both markers. The following settings were used for all analysis: base frequencies 'empirical' clock model 'Strickt clock Clock.rate = 1'; tree prior 'default values (Yule Model)'; The analyses were run in BEAST v.2.6.3 [56,57]. Analyses were run for 50 million generations, sampling every 5000th generation. Tracer v. 1.7.1 [56] was used for examining the effective sample size (ESS) for parameters and determining the burn-in. Trees and posterior probabilities were summarized using TreeAnnotator v. 2.6.3 [56] and showed on the Maximum clade credibility tree, with a Posterior probability limit = 0.5 and Burnin percentage = 0. The trees were drawn in FigTree v.1.4.4 [58].

2.9. BPP

As a third program, we used BPP v. 4.3.8 for coalescent species delimitation [59]. For COI, the input species tree contained 21 species and 151 sequences. For the ITS, the input species tree contained 12 species and 53 sequences. For the combined COI and ITS, the input species tree contained 12 species and 47 sequences.

1. Running species delimitation: Settings were Speciesdelimitation = 1 0 2, Speciestree = 1, speciesmodelprior = 1, burnin = 16,000, samplefreq = 2, nsample = 500,000.
2. Running Species tree Estimation: Settings were Speciesdelimitation = 0, Speciestree = 1, speciesmodelprior = 1, burnin = 16,000, samplefreq = 2, nsample = 500,000.

2.10. Timetree

MEGA X was used to do the Timetree analysis using the RelTime method to estimate divergence times by distinct molecular dating [60]. The estimated log likelihood value is -4139.29 . A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.1688)). The analysis involved 151 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd + Noncoding. There were a total of 568 positions in the final dataset.

2.11. Haplotype Analysis

Haplotype networks were built in POPART with the TCS network interference method from the COI alignment [61]. A haplotype network is the evolutionary sum of mutations that defines the current haplotypes through the DNA lineages that connect the current DNA molecules to the common ancestral DNA molecule.

2.12. Evolutionary Distance Analysis

The evolutionary distance between a pair of sequences is usually measured by the number of nucleotide or amino acid substitutions between them: p -distance. This distance is merely the proportion (P) of nucleotide sites at which the two sequences compared are different. This is obtained by dividing the number of nucleotide differences (nd) by the total number of nucleotides compared (n). This is one of the more simple methods to evaluate differences and to calculate relationships between taxa. Another established technique for evaluating DNA sequences is the Kimura 2-parameter (K2-P) index, which is conveniently expressed in percent differences between sequences. The p - and K2-P distance matrix between groups was constructed in MEGA X [60]. Transitions and transversions were included, uniform rates among sites and gaps were pairwise deleted.

2.13. Morphological Analysis and Systematics

As the molecular work revealed novel taxonomic information, we had to re-describe some poorly defined and described taxa: *C. amasina* (Turkey), *C. mzymtae* (Georgia), *C. charpentieri* (East Anatolia, North-West Iran, Azerbaijan) with its variations in its large geographical range and select a neotype for *C. charpentieri* as the neotype described by

Waterston belongs to *C. picta* and should be exchanged by a new neotype [24,62]. Furthermore, we describe the new taxa *C. kalkmani* sp. nov. (East Anatolia) and *C. cilicia* sp. nov. (South–East Turkey, Lebanon). Furthermore, the phenotypic variations in characters such size and colouration of the poorly known *C. vanbrinkae* (provinces Mazandaran and Golestan in Iran and Lenkoran in Azerbaijan) were compared with the closely related species *C. picta* (Bulgaria, Greece, Turkey, Georgia). The hybrid between *C. vanbrinkae* and *C. picta* from Armenia detected by our molecular analysis is phenotypically characterized, described, depicted and compared with *C. picta* and *C. vanbrinkae*. All specimens used for molecular analysis, description, measurements and verification of characters used for the key are listed in Table 1. More detailed remarks including notes on previous taxonomy, more detailed geographical data and methods on conservation, name-bearing types, neotype, re-description, paratype, DNA isolation, access numbers for gene bank and source are provided in Figure S1. The types, and the neotype are deposited in RMNH.

Specimens were measured (total length, abdomen length, forewing length, hindwing length) with a Vernier caliper in mm (error limit: 0.03 mm). The measurements of total length, abdomen length and wing length were rounded to the nearest millimetre. For differences in the measurements a D’Agostino-Pearson Test was performed to confirm normality of the data sets followed by a two-tailed unpaired *t*-test. Values are given as individual values with means and extremes. All drawings are artwork of Ole Müller (O.M.), made on graphic tablets (Wacom Intuos, Surface Book).

For the description and for the key we used the traditional morphological features of *Cordulegaster* shown in Figure 3.

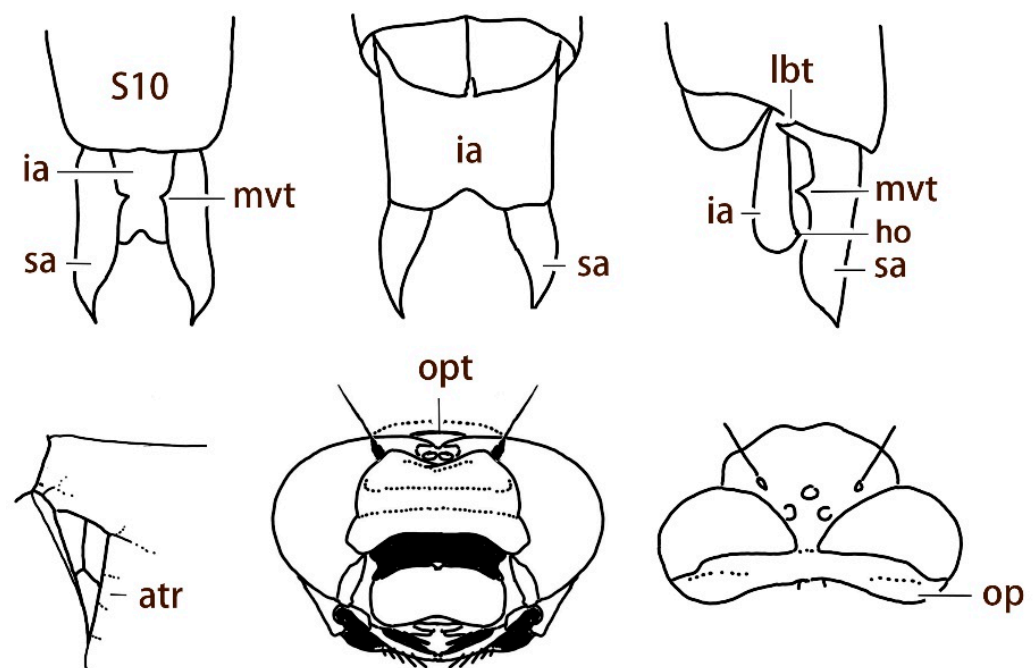


Figure 3. Main morphological characters of *Cordulegaster* used for description and in the key. Abbreviations: ia—inferior appendage, sa—superior appendage, mvt—medioventral tooth, lbt—laterobasal tooth, ho—hook, op—occiput, opt—occipital triangle, atr—anal triangle, S10—abdominal segment 10.

2.14. Distribution Maps

The distribution maps were created as follows: Collecting localities of the specimens were first georeferenced using Google’s Geocoding API (Application Programming Interface). Subsequently, the resulting coordinates were plotted in ARCGIS version 10.2.2 using the geographic coordinate system WGS 1984. The source of the background map for reference was the U.S. National Park Service, publicly available through Esri services. In

Figures 21 and 22 we have drawn the biogeographic boundary known as the Anatolian Diagonal by hand. Its position is based on literature and mountain chains visible on the background map [42].

3. Results

3.1. Molecular Genetic Analysis of the COI and ITS Genes

The COI alignment contained 151 taxa and 568 characters of which 213 were distinct data patterns. The ITS alignment contained 53 taxa and 885 characters, of which 263 were distinct data patterns. The partition alignment with two markers (COI, ITS) contained 47 taxa and 568 characters for COI, 891 for the ITS of which 150 (COI) and 296 (ITS) were distinct data patterns.

All three programs used showed for both genes in the majority-rule consensus trees four distinct major clades: *boltonii*, *bidentata*, *coronata* and a New World clade, shown are the MrBayes trees (Figures 4 and S2). Western Palaearctic *Cordulegaster* species fall in traditional *boltonii*- and *bidentata*-groups. We observed no evidence for hybridization between members of the *bidentata*- and the *boltonii*-group. *C. coronata*, until recently often treated as a subspecies of *C. insignis*, is grouped neither with *bidentata*- nor with the *boltonii*-group. All three programs with both genes and combination of both genes revealed an extra clade, which we named the *coronata*-group (Figures 4, 5 and S3–S6). For better resolution, we separated the MrBayes COI-tree in two parts and added the haplotype analysis (Figures 6 and 7). For better understanding of previously used names of the members of the genus in the region in relation to our molecular genetic results we introduced Table 2.

3.2. *Cordulegaster boltonii*-Group

In the *boltonii*-group of the Eastern region of the Western Palaearctic we recovered with molecular genetic analysis three known taxa (*C. heros*, *C. picta*, *C. vanbrinkae*) and one new taxon, which is described phenotypically below in the descriptive section (*C. kalkmani* sp. nov.). For the little known member of the *boltonii*-group *C. vanbrinkae* specimens from localities of all provinces from which this taxon has been reported so far (Armenia: Syunik; Azerbaijan: Lankaran; Iran: Mazandaran, Golestan) were included in this study (Figures 1 and S1, Table 1). In the case of specimens so far treated as *C. picta*, the whole large geographical range from East–Europe to Russian Black Sea region was covered by our molecular approach. Specimens from the East Anatolian provinces Van and Kars grouped separately from *C. picta* and *C. vanbrinkae* with both genes in MrBayes analysis (Figures 4–6). The additional two programs used for COI and a combination of COI and ITS, placed the two specimens of the new taxon apart from the other members of the *boltonii*-group (Figures S3–S6). Looking at the trees for COI, the *boltonii*-group forms two bigger clades in all three programs applied: the “western” clade with *C. boltonii*, *C. trinacriae*, and *C. princeps*; and the “eastern” clade with *C. heros*, *C. picta*, *C. vanbrinkae*, and *C. kalkmani* (Figures 4, 6, S3 and S5). The alignments suggest that *C. vanbrinkae* and *C. picta* are sister taxa (Figures 4–6 and S3–S6).

The K2-P analysis of the COI gene revealed that the proposed new taxon (*C. kalkmani*) is genetically more distant from *C. picta* than *C. vanbrinkae* is from *C. picta* (Table 3). Thus, these specimens belong, neither to *C. picta* nor to *C. vanbrinkae*. The K2-P distance between *C. picta* and *C. kalkmani* is 5.88%, and between *C. kalkmani* and *C. vanbrinkae* 4.93% (Table 3). The presence of four eastern species in the *boltonii*-group was also supported by the haplotype analysis of the COI gene (Figure 6).

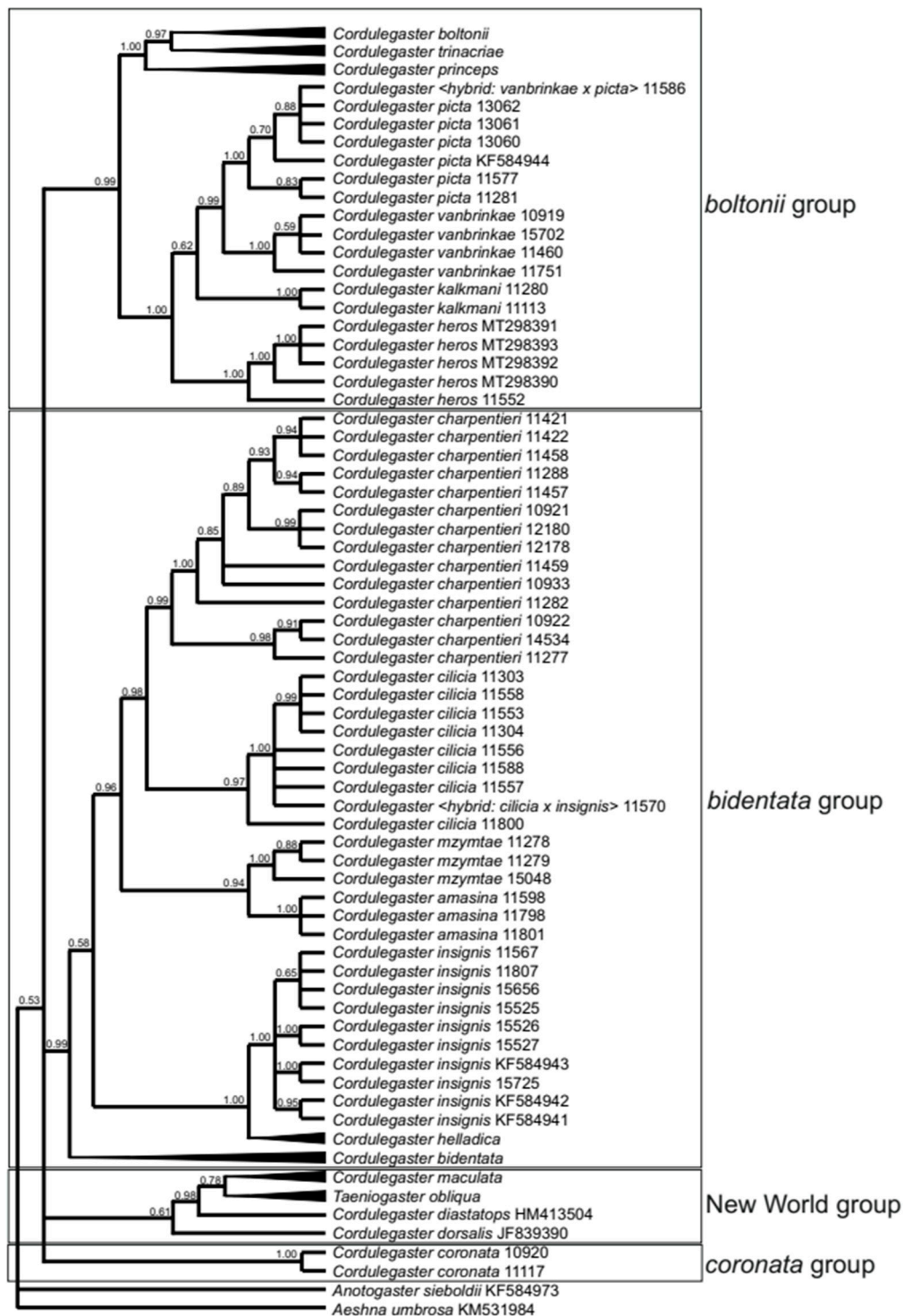


Figure 4. Overview tree for the COI gene, indicating the four major groups: *boltonii*-, *bidentata*-, *coronata*-, New World-group. Maximum likelihood tree inferred with Bayesian analysis using MRBAYESs 3.2.7a using the best-fit model (GTR+I+G) identified with JMODELTEST 2.1.10. Bayesian posterior probabilities values are depicted at the nodes. Included are our own sequences (PCR number next to the name) and those retrieved from GenBank (accession numbers next to the name), if specimens identify different taxa in the COI and ITS analysis they are indicating possible hybrids).



Figure 5. Overview tree from the ITS gene. Maximum likelihood tree inferred with Bayesian analysis using MRBAYES 3.2.7a using the best-fit model (HKY + G) identified with JMODELTEST 2.1.10. Bayesian posterior probabilities values are depicted at the nodes. Included are our isolated sequences (PCR number next to the name) and those retrieved from GenBank (accession numbers next to the name), if specimens identify different taxa in the COI and ITS analysis they are indicating possible hybrids.

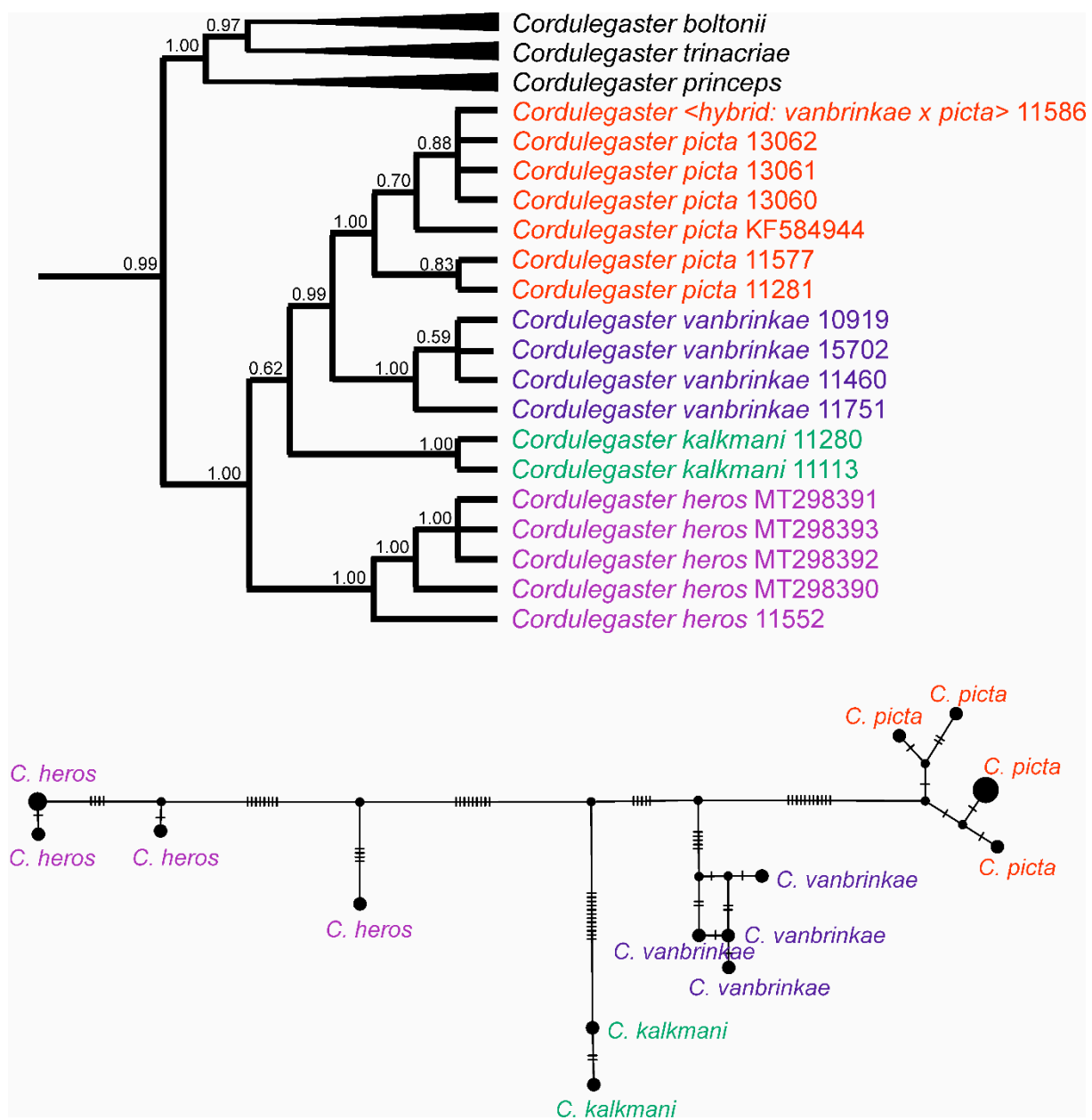


Figure 6. Tree of the COI-analysis for the *C. boltonii*-group and haplotype-analysis (TCS-network made in POPART 1.7). Bayesian posterior probability values are depicted at the nodes.

3.3. Possible Hybridisation in the *Cordulegaster boltonii*-Group

The two available specimens from the new taxon *C. kalkmani* showed no evidence for hybridization with other taxa. However, a specimen labeled under the name *C. vanbrinkae* from Armenia (Genbank MK779798) grouped in the COI analysis (PCR COI: 11586) with *C. picta*, while in the ITS analysis (PCR ITS: 11936) with *C. vanbrinkae* (Figures 4–6).

3.4. *Cordulegaster coronata*-Group

Specimens of supposed *C. coronata* from North-East Iran and Kyrgyzstan formed an extra clade in all analyses performed for both genes and the combination of the two genes (Figures 4, 5 and S3–S6). Thus, *C. coronata* does not group with members of the *bidentata*-group neither in the COI nor in the ITS analysis, which is in contrast to phenotype analysis, in which *C. coronata* is similar to *C. charpentieri* (see below in the descriptive part).

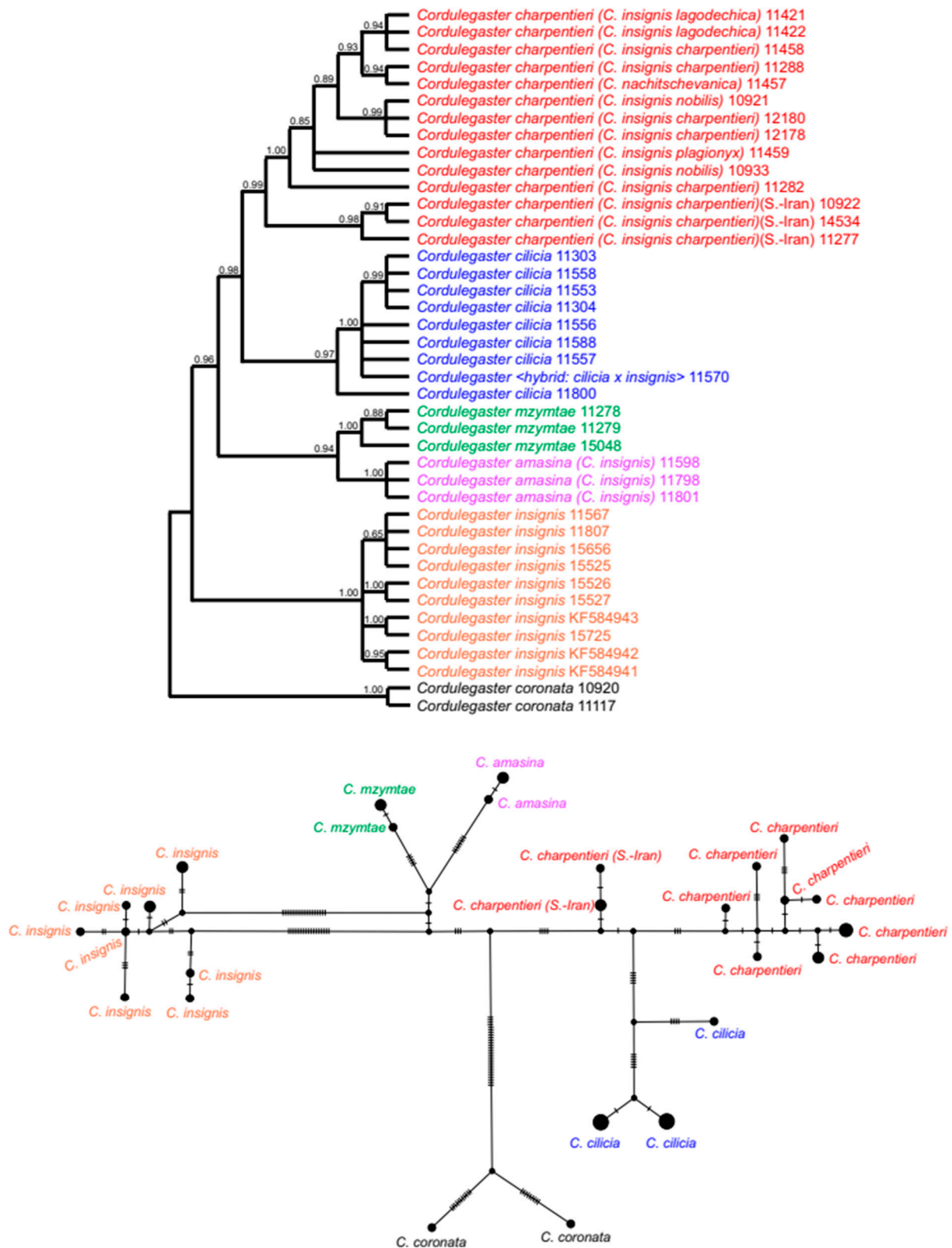


Figure 7. Tree of the COI-analysis for the *C. bidentata*-complex and *C. coronata* including haplotype-analysis (TCS-network made in POPART 1.7). Bayesian posterior probabilities are depicted at the nodes.

Table 2. (Overview Table): Actual used names and taxonomic rank as well as revised names and taxonomic rank, and the country of origin of the *Cordulegaster* specimens investigated.

Actual Used Names and Taxonomic Rank	Revised Name and Taxonomic Rank	Origin of Specimens Studied
<i>C. heros</i>	<i>boltonii</i> -group <i>C. heros</i>	Bulgaria, Montenegro, Greece, Austria
<i>C. picta</i>	<i>C. picta</i>	Bulgaria, Turkey, Greece, Georgia, Russia
<i>C. picta</i>	<i>C. kalkmani</i> sp.nov.	Eastern Anatolia Turkey
<i>C. vanbrinkae</i>	<i>C. vanbrinkae</i>	Armenia, Azerbaijan, Iran
<i>C. insignis</i>	<i>bidentata</i> -group <i>C. insignis</i>	West Turkey, East Greece
<i>C. insignis amasina</i>	<i>charpentieri</i> -complex <i>C. amasina</i> stat. rev.	Turkey
<i>C. insignis mzymtae</i> sometimes also used on species level <i>C. mzymtae</i>	<i>C. mzymtae</i>	Turkey, Georgia, Russia
<i>C. insignis charpentieri</i>	<i>C. charpentieri</i> stat. rev.	Armenia, Turkey, Georgia
<i>C. insignis lagodechica</i>	<i>C. charpentieri</i> stat. rev.	Georgia
<i>C. insignis nobilis</i>	<i>C. insignis lagodechica</i> syn. nov.	
<i>C. nachitschevanica</i>	<i>C. charpentieri</i> stat. rev.	Turkey, Iran
<i>C. plagionyx</i>	<i>C. insignis nobilis</i> syn. nov.	
<i>C. insignis</i>	<i>C. charpentieri</i> stat. rev.	Azerbaijan
	<i>C. nachitschevanica</i> syn. nov.	
	<i>C. charpentieri</i> stat. rev.	Azerbaijan
	<i>C. plagionyx</i> syn. nov.	
	<i>C. cilicia</i> sp. nov.	Eastern Mediterranean Turkey, Lebanon
<i>C. insignis coronata</i> sometimes used on species level <i>C. coronata</i>	<i>coronata</i> -group <i>C. coronata</i>	Iran, Kyrgyzstan

Table 3. Genetic distance, estimated by the Kimura 2-parameter method, between the different species in the *Cordulegaster boltonii*-group and *C. coronata*.

	<i>C. boltonii</i>	<i>C. trinacriae</i>	<i>C. princeps</i>	<i>C. heros</i>	<i>C. picta</i>	<i>C. kalkmani</i>	<i>C. vanbrinkae</i>	Average Distance within the Group
<i>C. boltonii</i>								0.0077
<i>C. trinacriae</i>	0.0583							0.0048
<i>C. princeps</i>	0.0563	0.0632						0.0044
<i>C. heros</i>	0.0811	0.0865	0.0852					0.0151
<i>C. picta</i>	0.0790	0.0794	0.0865	0.0617				0.0060
<i>C. kalkmani</i>	0.0698	0.0884	0.0718	0.0625	0.0588			0.0036
<i>C. vanbrinkae</i>	0.0791	0.0838	0.0941	0.0537	0.0395	0.0493		0.0044
<i>C. coronata</i>	0.1108	0.1083	0.1083	0.0883	0.0950	0.1010	0.0991	0.0402

3.5. *Cordulegaster bidentata*-Group

Within the *bidentata*-group, three major clades were recognized by the majority-rule consensus trees for both genes in all three programs and with the combination analysis of COI and ITS genes with the StarBeast and BPP program (Figures 4–6 and S3–S6), which we name here *C. bidentata*, *helladica-insignis*-complex, and *charpentieri*-complex. Specimens from West Turkey grouped together with specimens from Eastern Greece islands like Samos and Ikaria. They are separated in all trees for both genes in all three programs and with the combination analysis of COI and ITS genes with the StarBeast and BPP program from all specimens collected further east, which belong to the *charpentieri*-complex (Figures 4–6 and S3–S6). Thus, our molecular analysis revealed that *C. insignis* occurs only in the Western part of Turkey further east all specimens of the *bidentata*-group belong to the *charpentieri*-complex.

3.6. *Cordulegaster charpentieri*-Complex

The COI analysis with the two programs MrBayes and StarBeast support four closely related taxa in the *charpentieri*-complex (Figures 4, 5, 7 and S3). The majority-rule consensus tree for the COI created by the BPP program revealed a reduced topology with *C. amasina* and *C. mzymtae* together, as well as *C. charpentieri* and *C. cilicia*, as well as *insignis* and *helladica*, as well as *C. picta* and *C. vanbrinkae*, as well as *C. princeps*, *C. trinacriae*, and *C. boltonii*, all in one group, respectively (Figure S5). This may indicate that the BPP program does not sufficiently distinguish more recently split taxa. Our timetree analysis supports a more recent separation of the taxa within the *charpentieri*-complex (Figure S7). For a more detailed taxonomy in this complex we followed the COI analysis suggested by the majority-rule consensus trees created by the MrBayes and StarBeast program, because these analyses also differentiated the well-established taxa *C. boltonii*, *C. trinacriae* and *C. princeps*. Finally, we suggest the differentiation of the *charpentieri*-complex in four taxa: *C. amasina* stat. rev., *C. mzymtae*, *C. cilicia* sp. nov. and *C. charpentieri* stat. rev. The phenotypical description of the suggested new taxon and the re-description of the poorly described other three taxa in this *charpentieri*-complex are presented below in the descriptive part. The trees for COI by the BPP program, and by the combination of the two genes using the StarBeast program suggest *C. amasina* and *C. mzymtae* as well as *C. charpentieri* and *C. cilicia* as sister taxa, respectively (Figures S4 and S5) supplementary y = COI-ITS combined Starbeast, z = COI BPP).

The K2-P distances in the COI analysis between the four taxa suggested here as species are 2.96–4.24% (Table 4). For Western Palaearctic Anisoptera, a recent large analysis revealed a K2-P distance above 1.96% for a good threshold [43]. The existence of four species (*C. amasina*, *C. mzymtae*, *C. cilicia* and *C. charpentieri*) in the *charpentieri*-complex is also supported by the haplotype analysis (Figure 7). To avoid further taxonomic trouble, we decided not to recognize or create subspecies within the *charpentieri*-complex.

Table 4. Genetic distance, estimated by the Kimura 2-parameter method, between the different species in the *Cordulegaster bidentata*-group and *C. coronata*.

	<i>C. bidentata</i>	<i>C. insignis</i>	<i>C. amasina</i>	<i>C. mzymtae</i>	<i>C. charpentieri</i>	<i>C. cilicia</i>	Average Distance within the Group
<i>C. bidentata</i>							0.0098
<i>C. insignis</i>	0.0686						0.0093
<i>C. amasina</i>	0.0656	0.0623					0.0012
<i>C. mzymtae</i>	0.0590	0.0551	0.0296				0.0012
<i>C. charpentieri</i>	0.0633	0.0633	0.0452	0.0424			0.0110
<i>C. cilicia</i>	0.0566	0.0628	0.0401	0.0421	0.0322		0.0067
<i>C. coronata</i>	0.1028	0.0972	0.1022	0.0966	0.0942	0.0888	0.0402

C. amasina and *C. mzymtae* occur mainly along the Black Sea. *C. amasina* occurs in the western part of this region approximately from the province Kastamonu to the province Samsun and from the Black Sea Coast to central Turkey reaching the province Ankara (Figures 2 and S1, Table 1). *C. mzymtae* the darkest member of the *bidentata*-group occurs eastwards from *C. amasina* reaching Georgia, the Russian Black Sea Coast and even until Karachay Cherkessia region in the North Caucasus (Russia) (Figures 2 and S1, Table 1).

An undescribed species, here named *C. cilicia* sp. nov., occurs in central Anatolia, and along the East Mediterranean Sea.

Surprisingly, there was evidence for a hybrid at the contact between *C. insignis* and *C. cilicia*. In the ITS analysis, *C. cilicia* from Turkey, Konya, Doganbey (Genbank MK779798) grouped in the ITS analysis (PCR ITS: 11622) with *C. insignis*, while in the COI analysis (PCR COI: 11570) it grouped with eight other *C. cilicia* (Figures 4, 5 and 7, Table 4).

C. charpentieri occurs in a large area including East-Central Anatolia, Georgia, Armenia, Azerbaijan and Iran, and most probably in North-East Iraq. This taxon is slightly more heterogeneous in the COI and haplotype analysis (Figures 4 and 7) compared to the other

three species of the *charpentieri*-complex. However, *C. nachitschevanica* was in the COI analysis identical with Armenian *C. charpentieri*, and *C. plagionyx* was identical with North Iranian *C. charpentieri* (Figures 4 and 7). The K2-P distances are far below 2% and the haplotype analysis did not support species level (Figure 7). Therefore, we synonymized *C. nachitschevanica* syn. nov. and *C. plagionyx* syn. nov. with *C. charpentieri*. The COI and haplotype analysis of the Georgian specimens from Lagodechi (*C. i. lagodechica*) did not support a separate species or subspecies as suggested by Bartenev [30]. Therefore, we synonymized *C. insignis lagodechica* syn. nov. with *C. charpentieri*. The *C. charpentieri* specimens from South and South-East Iran (provinces Fars and Kerman) grouped extra in the COI analysis and haplotype analysis (Figures 4 and 7). However, the distance in the COI analysis between these specimens and *C. charpentieri* was less than 2%. To avoid further confusion in this group we refrain from describing further species or subspecies. For better visualization, the morphological variants were illustrated in the descriptive part below.

4. Descriptive Part

4.1. *Cordulegaster boltonii*-Group

Variation of *Cordulegaster vanbrinkae* and characterisation of a hybrid between *C. picta* and *C. vanbrinkae*

Material examined: *C. vanbrinkae*: 1 ♂ (coll. Thomas and Elias Schneider): IRAN: Mazandaran, Veysar, 36.4700° N, 51.5383° E, 1438 m a.s.l., July 2013, leg. Thomas Schneider, July 2013; 2 ♂♂ (collection coden here): IRAN: Golestan, Kaboodval waterfall/river 3 km SW Kordabad ca. 4 km SSE Aliabad, 36.8741° N, 54.8872° E, 343 m a.s.l., vii.2017, leg. Thomas Schneider.

C. picta: 1 ♂ (coll. Thomas and Elias Schneider): GEORGIA: Imereti, 42.0236° N, 43.4588° E, 900 m a.s.l., vii.2015, leg. Thomas Schneider. *C. vanbrinkae* × *C. picta* (**sequenced hybrid**): 1 ♂ (RMNH): ARMENIA: Verin Khotanan village, 39.3334° N, 46.3786° E, 1550 m a.s.l., specimen RMNH.INS.974942, vii.2010, leg. Vasil Ananian.

C. vanbrinkae × *C. picta* (possible hybrid, no DNA could be extracted): same locality as previous specimen, RMNH.INS.975675.

Comments. In the molecular section, we detected a possible hybrid between *C. vanbrinkae* and *C. picta*. The specimen is from Armenia, geographically between known populations of *C. picta* and *C. vanbrinkae*. Therefore, we compared the morphology of this hybrid with *C. picta* and *C. vanbrinkae*.

As shown in Figure 8, by abdominal colour pattern the hybrid cannot be distinguished from *C. vanbrinkae*. *C. vanbrinkae* is usually darker than *C. picta* (Figure 8A–C,F), although more yellow specimens of *C. vanbrinkae* can be found (Figure 8C). The male appendages of the hybrid look intermediate, as the basal tooth of the superior appendages is a bit larger than in typical *C. vanbrinkae* (Figure 8J–L).

Cordulegaster kalkmani sp. nov.

Type material: Holotype: 1 ♂ (RMNH.INS.974903): TURKEY: Kars, 16 km NE Sarikamis, 40.4203° N, 42.7446° E, 1800 m a.s.l., 23.vii.2007, leg. Gert Jan van Pelt.

Paratype: 1 ♀ (RMNH.INS.747180): TURKEY: Van, 8 km N Muradiye, near Bendimahi Selalesi 8 km, 39.0594° N, 43.7540° E, 1850 m a.s.l., 30.vi.2003, leg. Vincent Kalkman.

Etymology. The species is named after Dr. Vincent Kalkman, Naturalis Biodiversity Center, Leiden, Netherlands, who collected the female paratype.

Description of the male holotype. *Head* (Figure 9E,F): anteclypeus black; postclypeus yellow; labrum yellow with thicker black margin and a short black line in the middle; frons yellow, in dorsal view with black bar at the rear edge; labium yellow, mandible black; occipital triangle black with two yellow dots (Figure 9G); antenna and vertex black; eyes green (collector's observation).

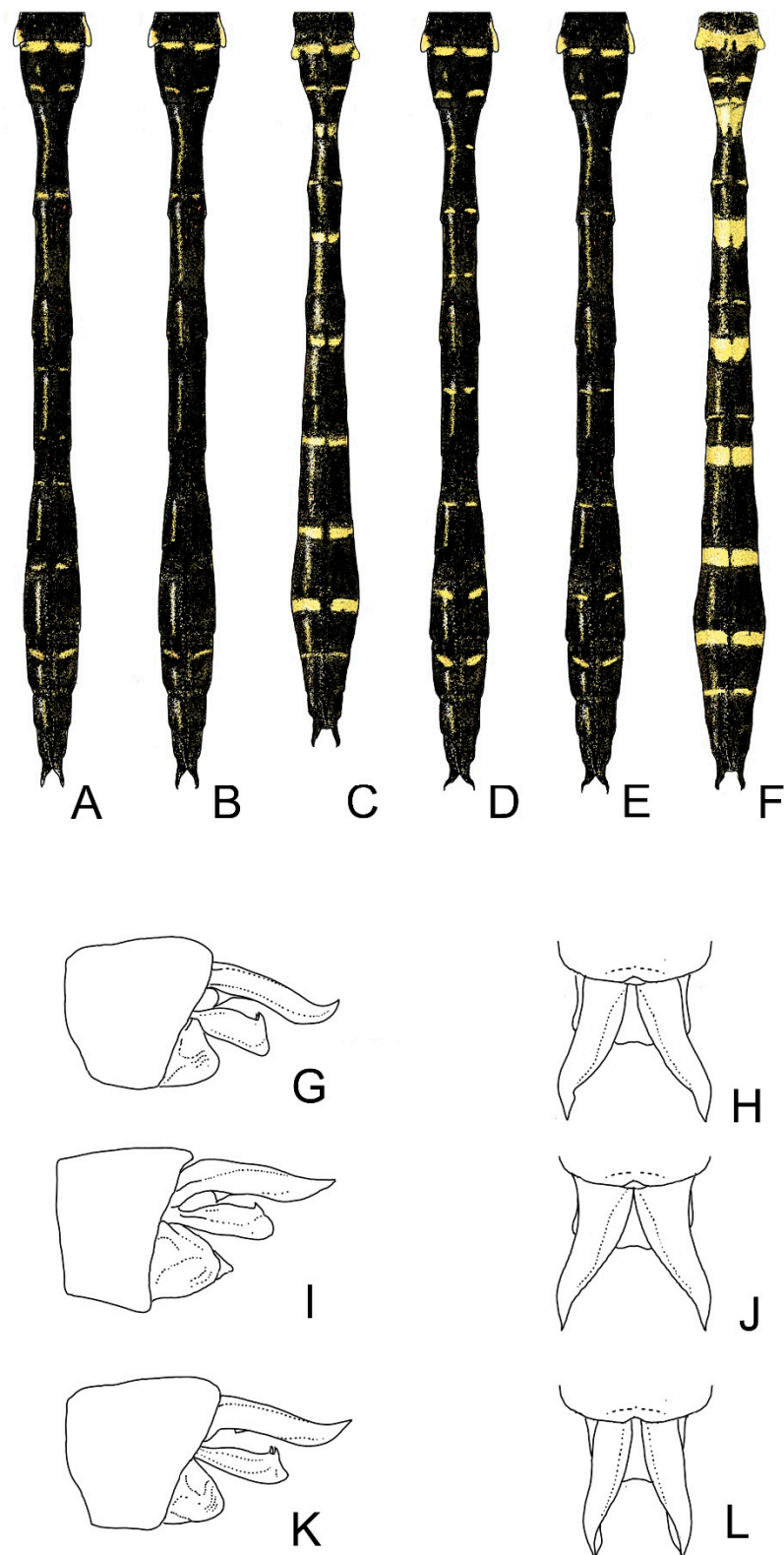


Figure 8. Abdominal variation of *C. vanbrinkae*: (A): Golestan, Iran. (B): Mazandaran, Iran. (C): Golestan. (D): Armenia, possible hybrid: *C. picta* × *C. vanbrinkae* not genetically analyzed. (E): Armenia, hybrid: *C. picta* × *C. vanbrinkae* genetically analyzed. (F): *C. picta* Georgia. (G,H): lateral and dorsal view of the male appendices from *C. picta* Georgia. (I,J): Hybrid *C. picta* × *C. vanbrinkae*, Armenia. (K,L): *C. vanbrinkae*, Mazandaran.

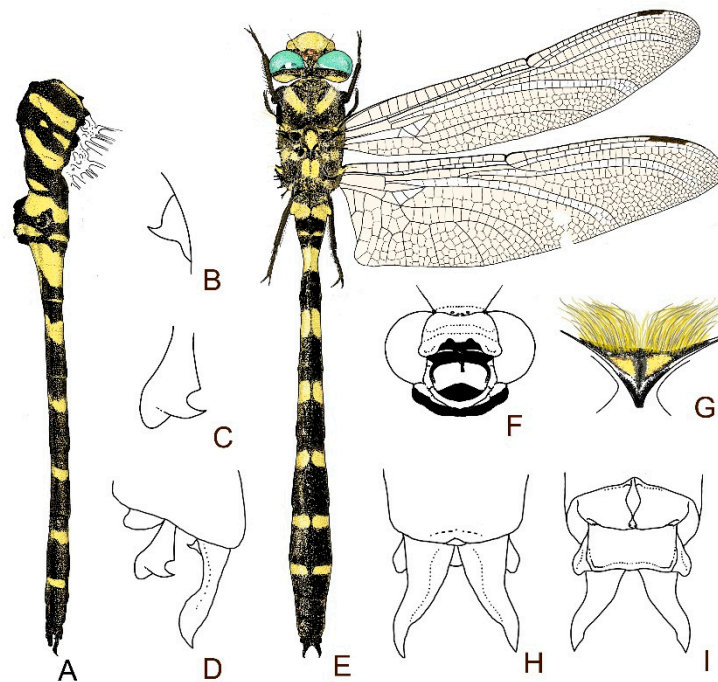


Figure 9. *Cordulegaster kalkmani* sp. nov., holotype ♂ (RMNH, leg. Gert Jan van Pelt, RMNH.INS.974903, 23.07.2007, Turkey, Kars, 16 km NE Sarikamis: 40.4203° N 42.7446° E, 1800 m a.s.l.): (A): habitus, lateral. (B): medioventral tooth, lateral. (C): hook, lateral. (D): appendages, lateral. (E): habitus, dorsal. (F): head, schematically. (G): occipital triangle, frontal. (H): appendages, dorsal. (I): appendages, ventral.

Thorax (Figure 9A,E): anterior lobe with yellow frontal edge, median lobe of pronotum black, posterior lobe with yellow margin at the rear edge that narrows dorsolaterally; front of synthorax with broad yellow antehumeral stripes, narrowing towards pronotum leaving less than 30% black of the antehumeral region; small yellow dot on the mesanepisternum near the antealar ridge; mesepimeron and metepimeron with broad yellow bands; metepisternum black with yellow interrupted stripe-like marking reaching to one third of basal margin; metakatepisternum black; poststernum black; coxae black with yellow parts, trochanter, femora, tibiae and tarsi black.

Wing (Figure 9E hyaline; Pt black; FW 3.8×0.5 ; HW 4.5×0.7 ; anal triangle with 3 cells; all veins black, except costa.

Abdomen (Figure 9A,E): color pattern as in Figure 9A; S1 black with two yellow markings in lateral view, S1 dorsally covered with yellow hairs, yellow marking (abdominal rings) on side of S1 semilunar; S2 to S8: yellow abdominal rings of S2 and S3 dorsally connected, rings of S4 to S8 interrupted by fine black line, yellow abdominal rings leaving a bigger part black but running onto underside; S9–S10 black.

Appendages (Figure 9B–D,H,I): superior appendages in dorsal view slender and diverging, with pointed and slightly curved tips, nearly as long as S10; laterobasal tooth not visible in lateral view because it is covered by the rear edge of S10, prominent medioventral tooth, with a claw-shape tip only visible in lateral view, located at the base of the inferior near S10 (Figure 8B,D); inferior appendage in lateral view at the end with a single pointed hook-shaped tooth on each side (Figure 9C,D). Inferior appendage broad, nearly parallel-sided, the dorsally pointing lobes widen the inferior distally, hind margin not notched (Figure 9I).

Measurements (in mm): TL (inclusive appendages) 74.0, AL 58.0, HWL 46.0, FWL 46.0.

Description of female paratype. Head (Figure 10A): much as in ♂, additional small black line at crest of frons.

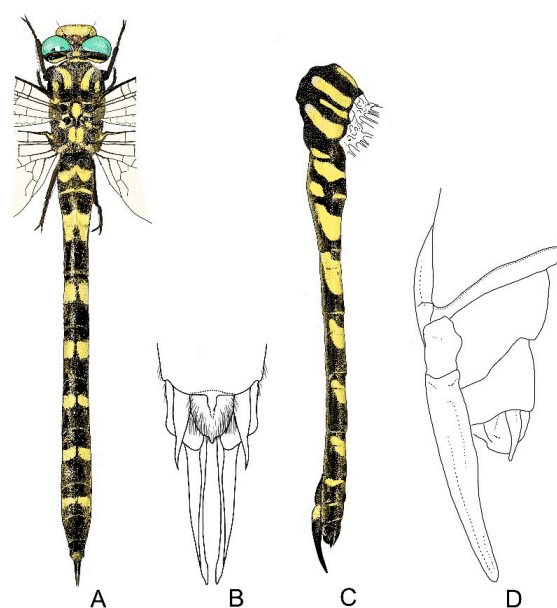


Figure 10. *Cordulegaster kalkmani* sp. nov., paratyp ♀(RMNH, leg. Vincent Kalkman, 30.06.2003, RMNH.INS. 747180, Turkey, Van, 8 km N Muradiye, near Bendimahi Selalesi, 39.0594° N 43.7540° E, 1850 m a.s.l.): (A): habitus, dorsal. (B): appendages, dorsal. (C): habitus, lateral. (D): appendages, lateral.

Thorax (Figure 10A,C): colour pattern of prothorax and synthorax similar to male; in contrast to male yellow band at metepisternum not interrupted; metakatepisternum black with a pale yellow shadow near metastigma.

Wings hyaline; pterostigmata black; costal veins with yellow leading edge.

Abdomen (Figure 10A–D): cylindrical and thicker than in male; ovipositor black, long and bent like a sword, more than three times as long as S10 as seen in lateral view.

Measurements (mm): TL (inclusive ovipositor) 82.0, AL 65.0, HWL 51.0, FWL 53.0.

Differential diagnosis

The male inferior appendage of *C. kalkmani* distally much wider than in all other members of the genus. A single hook-shaped tooth in lateral view at the apex of the inferior appendage separates it from *C. vanbrinkae* and *C. picta*. These latter two species of the Eastern *boltonii*-group have two teeth in lateral view that are often covered by bristles and are therefore difficult to see. In *C. heros* the laterobasal and medioventral teeth on superior appendages are clearly more distal than in the other three Eastern species of the *boltonii*-group. Compared to *C. vanbrinkae*, *C. kalkmani* has a stout inferior appendage in lateral view. In addition, the medioventral teeth are more clearly visible, although are closer to S10 than in *C. vanbrinkae*. In *C. picta* the medioventral teeth are more distal than in *C. kalkmani*. The medioventral teeth are more clearly hooked in *C. kalkmani* than in *C. picta*. The position of the laterobasal teeth are comparable in *C. picta* and *C. kalkmani*. In contrast to *C. vanbrinkae*, *C. kalkmani* has a yellow frons as well as *C. picta* and *C. heros*. Females within the *boltonii*-group are impossible to separate without knowing their geographical origin.

Distribution

East Anatolia and probably North–West Iran. Separated from *C. picta* through the Anatolian Diagonal, and further east by the Armenian Highland and the Caucasus Mountains. *Cordulegaster kalkmani* is separated from *C. vanbrinkae* by the Elburz Mountains, hybridization between *C. picta* and *C. vanbrinkae* occurs in South–East Armenia.

4.2. *Cordulegaster bidentata*-Group

***Cordulegaster charpentieri* (Kolenati, 1846) stat. rev.**

Cordulegaster insignis nobilis Morton, 1916, *syn. nov.*

Cordulegaster insignis lagodechica Bartenev, 1930, *syn. nov.*

Cordulegaster nachitschevanica Skoortsov and Snegovaya, 2015, *syn. nov.*

Cordulegaster plagionyx Skvortsov and Snegovaya, 2015, *syn. nov.*

Redescription. As the type is lost and the original description is poor, we selected a neotype for re-description; in addition we describe the variation of this species in its geographical range.

Material examined: Neotype: 1 ♂ (RMNH.INS.974905): TURKEY: Bitlis Province, 32 km WNW Gevas, 38.3834° N, 42.7723° E, 1950 m a.s.l., 13.vii.2005, leg. Gert Jan van Pelt.

Additional material studied. 1 ♂ (RMHN.INS.974907): TURKEY: Erzurum, Şenkaya, 40.5615° N, 42.3471° E, 1887 m a.s.l., 31.viii.1993, leg. Gert Jan van Pelt; 1 ♂ (collection Thomas and Elias Schneider): AZERBAIJAN: Nakhichevan, Agdere, 39.11028° N, 45.9144° E, 1990 m a.s.l., 26.vii.2017, leg. Nataly Snegovaya; 1 ♂ (collection Thomas and Elias Schneider): AZERBAIJAN: Balakan, 41.6761° N, 46.4931° E, 320 m a.s.l., 03.vii.2014, leg. Nataly Snegovaya; 2 ♂ (collection Thomas and Elias Schneider): IRAN: Lorestan, Bagh Goije 24 km NE Aligudarz, 33.4597° N, 49.9472° E, 1817 m a.s.l., 11.vi.2015, leg. Thomas Schneider; 1 ♂ (RMNH.INS.975673): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 07.vi.2018, leg. Thomas Schneider; 2 ♂ (collection Thomas and Elias Schneider): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 06.vi.2014, leg. Thomas Schneider; 6 ♂ (collection Thomas and Elias Schneider): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 06.vi.2019, leg. Thomas Schneider; 4 ♂ (collection Thomas and Elias Schneider): IRAN: Dalfard waterfalls, Kerman, 29.0022° N, 57.5869° E, 2110 m a.s.l., 28.v.2014, leg. Thomas Schneider; 1 ♀ (RMNH.INS.975674): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 06.v.2017, leg. Elias and Thomas Schneider; 1 ♀ (collection Thomas and Elias Schneider): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 06.v.2017, leg. Elias and Thomas Schneider; 2 ♀ (collection Thomas and Elias Schneider): IRAN: Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l., 06.vi.2019, leg. Elias and Thomas Schneider.

Description of neotype. Head (Figure 11B,D,E): anteclypeus black; postclypeus yellow; labrum yellow with black margin; frons yellow with faint black bar; labium yellow; occiput domed and yellow, occipital triangle domed, yellow with black margins; antenna and vertex black; eyes blue (collector's observation); postocular area yellow with black upper margin.

Thorax (Figure 11A,D): anterior lobe of pronotum with yellow front edge; median lobe black with yellow dorsolateral patterns, middorsal with two small yellow dots; posterior lobe yellow with narrow middorsal line ending in front of rear edge of lobus; front of synthorax with broad big yellow antehumeral stripes, narrowing moderately towards pronotum leaving less than 20% black of antehumeral region; mesepimeron and metepimeron with broad yellow bands, metepisternum black with yellow triangle marking with base to wings and short yellow comma-shaped stripe ending near metastigma; metakatepisternum black; poststernum black; coxae black with yellow ventral parts, trochanter, femora, tibiae and tarsi black.

Wings (Figure 11D): hyaline; costal veins yellow, other veins black; pterostigma black, pterostigma FW 4.2 × 0.5, HW 4.5 × 0.7; anal triangle 3 cells; membranula narrow.

Abdomen (Figure 11A,D): colour pattern as shown in Figure 11A,B; S1 dorsal black, yellow marking on side of S2 to S9 with medium sized yellow markings leaving ca. 40% black, on dorsal view of S2 to S8 there are a pair of small yellow line-art markings on lateral distal part of segment not touching in the middle of segment, on S2 to S10 the black markings reaching lateral sides, yellow markings also present on S9 and S10.

Appendages (Figure 11C,F,G): superior appendages in dorsal view straight, slender, with pointed tips, medioventral teeth clearly visible and directed to each other, in lateral view laterobasal teeth are visible and are located near S10, in lateral view upper medioventral teeth located more ventral far away of crossing with tooth on the end of inferior appendage; inferior appendage is stout trapezoid, not notched on distal margin when viewed from above, in lateral view distally small teeth on end of the inferior appendage

are visible, the three teeth form a crown-shaped complex in which the two outer teeth are fused, the inner tooth is isolated from them.

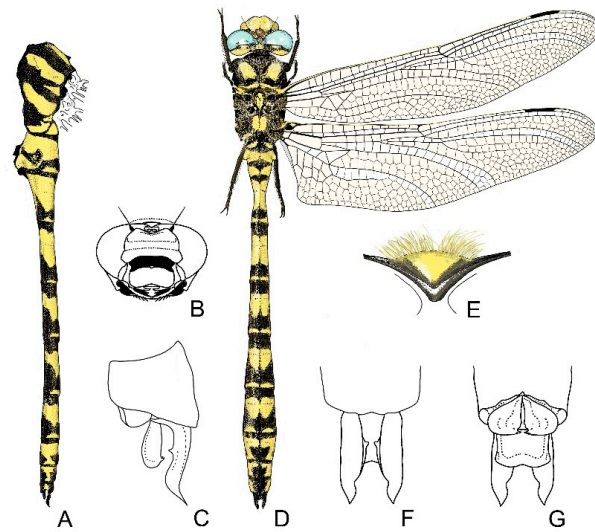


Figure 11. *Cordulegaster charpentieri* neotype ♂ (RMNH, leg. Gert Jan van Pelt, RMNH.INS.974905, 13.07.2005, Turkey, Bitlis Province, 32 km WNW Gevas, 38.3834° N, 42.7723° E, 1950 m a.s.l.): (A): habitus, lateral. (B): head, schematically. (C): appendages, lateral. (D): habitus, dorsal. (E): occipital triangle, frontal. (F): appendages, dorsal. (G): appendages, ventral.

Measurements (mm): TL (including appendages) 65.0, AL 50.0, HWL 41.0, FWL 42.0.

Variation. *C. charpentieri* shows strong variation in colour pattern and size. We visualize this variability in figures that include yellow specimens of females (Figure 12). Individuals from South–East Iran are bigger, and those from Fars Province are more yellow (Figure 13), than typical specimens from Eastern Anatolia, the Caucasus Countries and North Iran (Figure 14). Males from Fars ($n = 9$): TL (including appendages) 79.0–83.0, AL: 60–63.0, HWL 47.0–50.0.

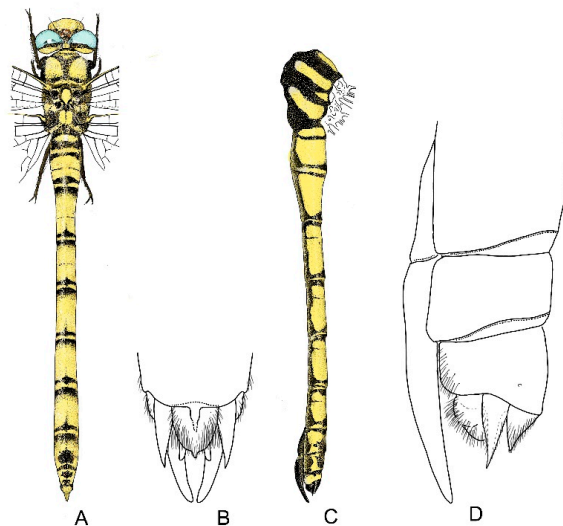


Figure 12. *Cordulegaster charpentieri*, yellow form ♀, (RMNH, leg. Elias and Thomas Schneider, RMNH.INS.975674, 06.05.2018, Iran, Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1564° E, 1800 m a.s.l.): (A): habitus, dorsal. (B): appendages, dorsal. (C): habitus, lateral. (D): ovipositor, lateral.

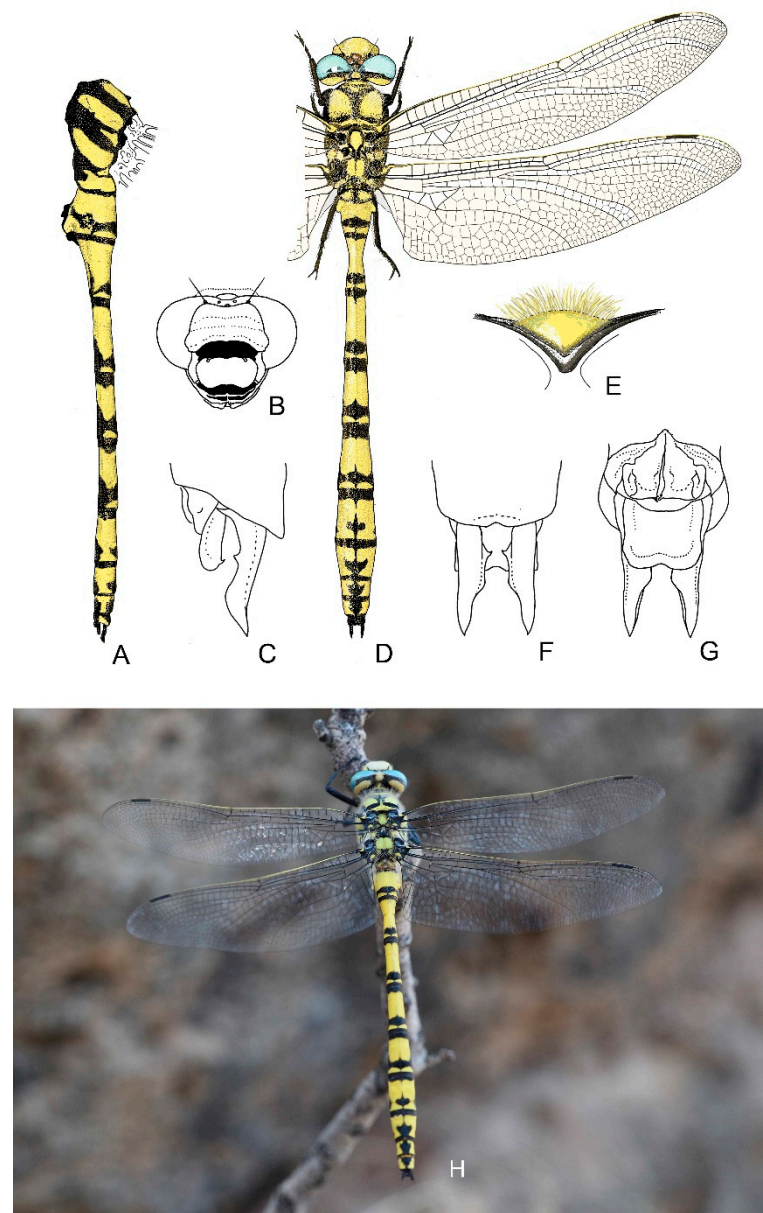


Figure 13. *Cordulegaster charpentieri* paratype ♂ (yellow form) (RMNH, leg. Thomas Schneider, RMNH.INS. 975673, 7 June 2019, Iran, Lost Paradise, Behesht Gomshodeh, Fars, 30.3339° N, 52.1563° E, 1800 m a.s.l.): (A): habitus, lateral. (B): head, schematically. (C): appendages, lateral. (D): habitus, dorsal. (E): occipital triangle, frontal. (F): appendages, dorsal. (G): appendages, ventral. (H): photo of this paratype (Dietmar Ikemeyer).

Individuals from Kerman Province are darker, more similar to typical forms, but much larger and with pterostigma extremely narrow (Figure 13). These individuals are the biggest in the *bidentata*-group, even bigger than *C. heros*, and are therefore among the largest dragonflies in the Western Palaearctic. Males from Kerman ($n = 4$): TL (including appendages) 81.0–85.0; AL 62.0–65.0; HWL 49.0–55.0. Individuals were found between 1700 and 2200 m a.s.l.

Females from Fars are very yellow and are impressive, heavy insects. Females from Fars ($n = 4$): TL (including ovipositor) 84.0–88.0; AL: 63.0–7.0; HWL 51.0–57.0.

Differential Diagnosis

The males have large abdominal markings, those on S9–10 often connect to form «7» shaped markings, apical dorsal pair of yellow spots usually present on S2–10, whereas they are less present in *C. cilicia* sp. nov. and absent in *C. mzymtae*. Individuals of *C. charpentieri*

from South–East Iran are larger than all other members of the *bidentata*-group. The occiput and the postocular area are domed and yellow. The other species (*C. amasina*, *C. mzymtae*, *C. cilicia*) of the *charpentieri*-complex have the occiput and postocular area more flattened and less yellow.

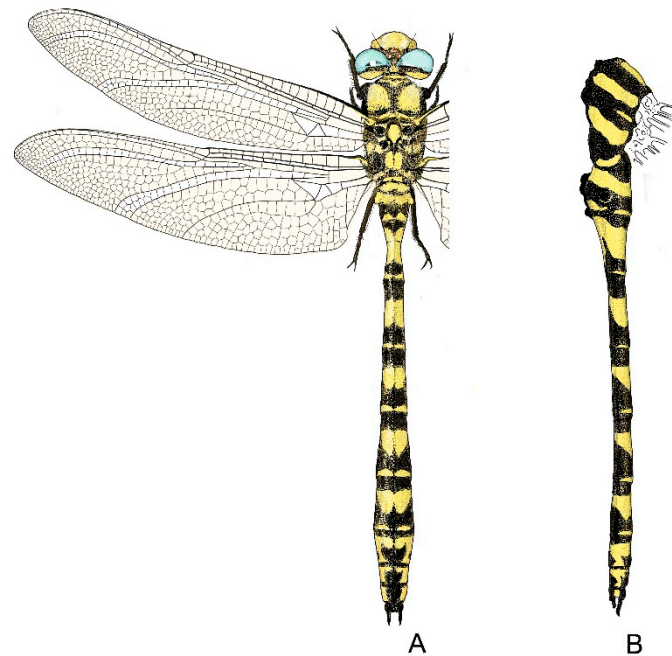


Figure 14. *Cordulegaster charpentieri*, (dark form) ♂, (in coll. Elias and Thomas Schneider, leg. Thomas Schneider, 28 May 2014, Iran Dalfard, 29.0022° N, 57.5869° E, 2110 m a.s.l.): (A): habitus, dorsal. (B): habitus, lateral.

Superior appendages in dorsal view are more straight and slender than in the other two species of the complex, inferior appendage is stout trapezoid, not rectangular as in *C. cilicia* (see below). Only the very big, yellow females of *C. charpentieri* from South–East Iran and the small and dark females of *C. mzymtae* can easily be recognized. Other females are nearly impossible to separate within the *charpentieri*-complex without knowing their geographical origin.

Distribution

Cordulegaster charpentieri has a wide distribution, from East Anatolia (Turkey), Georgia, Armenia, Azerbaijan and Iran to North–East Iraq.

Cordulegaster cilicia sp. nov.

Type material. Holotype: 1 ♂ (RMNH.INS.974914): TURKEY: Kahramanmaraş, Göksun, Gücüksu, Göksun River, 38.0608° N, 36.6494° E, 1350 m a.s.l., 09.vii.2008, leg. Gert Jan van Pelt.

Paratypes: 1 ♂ (RMNH.INS.974912): TURKEY: Nigde, 37.9698° N, 34.6767° E, 1230 m a.s.l., 30.vi.2008, leg. van Pelt; 1 ♂ (RMNH.INS.974906): TURKEY: Erzurum, Uzundere, 40.6114° N, 41.6286° E, 1010 m a.s.l., 03.viii.1996, leg. Gert Jan van Pelt; 1 ♂ (RMNH.INS.974908): TURKEY: Kayseri, Pinarbasi, 38.7205° N, 36.3950° E, 1520 m a.s.l., 19.vii.1996, leg. Gert Jan van Pelt; 1 ♂ (RMNH.INS.974909): TURKEY: Nigde, Kizilören, 38.0164° N, 36.0311° E, 1900 m a.s.l., 11.vii.1996, leg. Gert Jan van Pelt; 2 ♂ (RMNH.INS.1090920 and RMNH.INS.1090922): N LEBANON: Bcharre, 34.2511° N, 36.0111° E, 1400 m a.s.l., 27.vi.1960, leg. G. A. Mavromoustakis; 1 ♀ (RMNH.INS. 1090923): N LEBANON: Bcharre, 34.2511° N, 36.0111° E, 1400 m a.s.l., 27.vi.1960, leg. G. A. Mavromoustakis.

Paratype: 1 ♀ (RMNH.INS.1090164): N LEBANON: Bcharre, 34.2511° N, 36.0111° E, 1400 m a.s.l., 22.vi. 1960, leg. G. A. Mavromoustakis.

Etymology. The name refers to the historical Roman province of Cilicia located on the south coast of Asia Minor. The range of this species exceeds the limits of this historical province to northeast and southeast.

Description of holotype. Head (Figure 15D–F): anteclypeus black; postclypeus yellow; labrum yellow with thicker black margin; frons yellow with faint black seam; labium yellow; occiput less domed than in *C. charpentieri*, black and yellow occipital triangle domed, yellow with pale brown margins; antenna and vertex black; eyes turquoise (collector's observation); postocular area yellow with black upper margin.

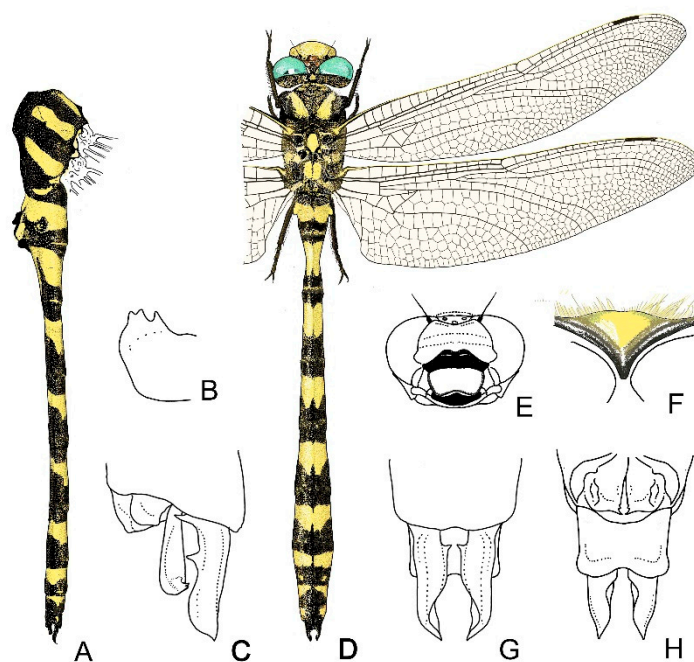


Figure 15. *Cordulegaster cilicia* sp. nov., holotype ♂, (RMNH, leg. Gert Jan van Pelt, RMNH.INS.974914, 9 July 2008, Turkey, Kahramanmaraş, Göksun, 38.0614° N, 36.4722° E, 1350 m a.s.l.): (A): habitus, lateral. (B): detailed latero-dorsal view on the hook of the inferior appendix. (C): appendages, lateral. (D): habitus, dorsal. (E): head, schematically. (F): occipital triangle, frontal. (G): appendages, dorsal. (H): appendages, ventral.

Thorax (Figure 15A,D): anterior lobe of the pronotum with yellow front edge; median lobe black with yellow dorsolateral wing-shaped patterns; posterior lobe yellow interrupted by middorsal black band; front of synthorax with broad big yellow antehumeral stripes, narrowing moderately towards pronotum leaving less than 30% black of the antehumeral region; mesepimeron and metepimeron with broad yellow bands; metepisternum black with tiny yellow markings near base of wings; metakatepisternum black; poststernum black; coxae black with yellow ventral parts, trochanter, femora, tibiae and tarsi black.

Wing (Figure 15D) hyaline; costal veins yellow, other veins black; Pt dark brown, Pt FW 4.2×0.5 , HW 4.5×0.7 ; anal triangle 3-celled; membranula narrow.

Abdomen (Figure 15A,D): colour pattern as in Figure 15A,D; S1 dorsal black, yellow marking on side of S1 small, S2–9 with medium sized yellow markings leaving ca. 50% black, on dorsal view of S2–5 there are a pair of small, linear yellow spots present on the dorsal distal part of abdominal segments not touching in middle of the segment, on S2–10 black markings reaching lateral sides, yellow markings present on S9–10.

Appendages (Figure 15B,C,G,H): superior appendages in dorsal view broad and stout with curved and inward pointing tips, the medioventral teeth clearly visible and directed with the tips slightly in direction of S10, in the lateral view the laterobasal teeth visible and located near S10, in lateral view the medioventral teeth located more ventral and far from crossing with the tooth on end of the inferior appendage; inferior appendage in ventral view stout, nearly rectangular, slightly notched on distal margin, in lateral view distally

small teeth on end of the inferior appendage are visible (Figure 15C), the three teeth form a crown-shaped complex in which the two outer teeth are fused, the inner tooth is isolated from them (Figure 15B).

Measurements (mm): TL (inclusive appendages): 71, AL 54, HWL 43, FWL 43.

Variations in males. *C. cilicia* shows some variability in size and some minor variations in colouration patterns. The eyes of some individuals are greenish, in others more blue (collector's observation). **Measurements (mm)** (paratypes, $n = 6$): TL (inclusive appendages) 70.0–73.0, AL: 53.0–55.0, HWL 40.0–46.0.

Description of female paratype. Head (Figure 16A): like in ♂.

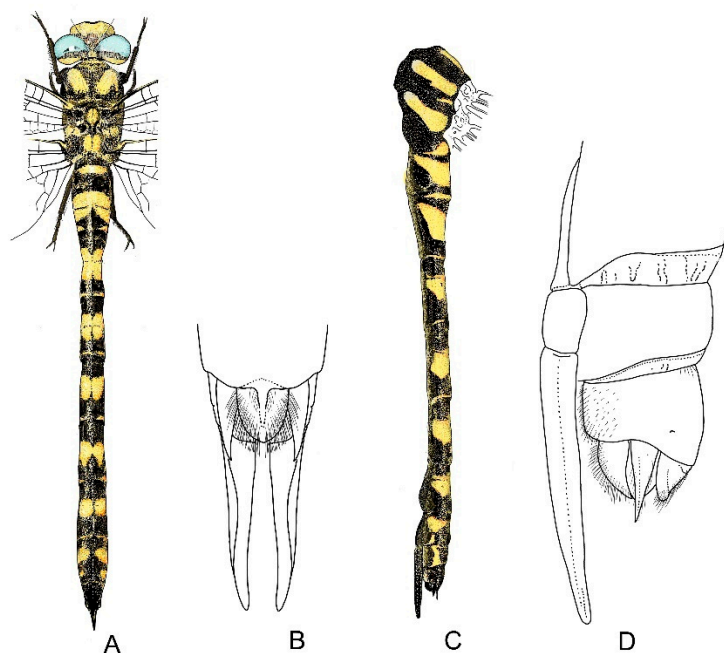


Figure 16. *Cordulegaster cilicia* sp. nov., paratype ♀, (RMNH, leg. G. A. Mavromoustakis, RMNH.INS. 1090164, 21 June 1960, North Lebanon, Bcharre, 34.2511° N, 36.0111° E, 1400 m a.s.l.): (A): habitus, dorsal. (B): appendages, dorsal. (C): habitus, lateral. (D): ovipositor, lateral.

Thorax (Figure 16A,C): much as in male, except the yellow markings of metepisternum; metepisternum black with prominent comma-shaped yellow markings.

Wings: like in male, hyaline; Pt dark brown, Pt FW 4.4×0.7 , HW 4.8×0.6 ; membranula narrow.

Abdomen (Figure 16A,C): cylindrical and thicker than in males, ovipositor 9.0, black, only slightly curved, almost straight and long.

Measurements (mm): TL (including ovipositor) 83.0, AL 67.0, HWL 48.0, FWL 49.0.

Variations in females. Further paratype female much as the other with minor differences in measurements: TL (inclusive ovipositor) 81.0, AL 63.0, HWL 46.0, FWL 47.0.

Differential diagnosis

The males are similar in colour pattern to other species of *charpentieri*-complex, but are usually more yellow than *C. amasina* and less yellow than *C. charpentieri*, pairs of abdominal spots on apical margins of S6–10 usually absent. The occiput less domed and less yellow than in *C. charpentieri*, postocular area is less domed and mostly darker than in *C. charpentieri*; but less dark than in *C. amasina*. The superior appendages in dorsal view curved, widened at base, in contrast to *C. charpentieri*, which has nearly parallel sided superior appendages. The medioventral teeth in dorsal view located more closely to S10 than in *C. charpentieri*. The medioventral teeth in lateral view located more ventral and further from crossing with the teeth on the end of the inferior appendage, as in *C. charpentieri*. In *C. amasina* the inferior appendage slightly wider at the base, in contrast to *C. cilicia* which has a nearly rectangular shape.

Female individuals are nearly impossible to separate within the *charpentieri*-complex not knowing the geographical origin, only the dark and small *C. mzymtae*, and the large and yellow forms of *C. charpentieri* are easily identified.

Distribution

C. cilicia occurs east of Anamur along the Mediterranean coast, reaching Lebanon. It is also distributed to East-Central Turkey reaching Erzurum near Uzundere, where it meets *C. charpentieri*.

Cordulegaster amasina Morton, 1916 stat. rev.

Material examined: 1 ♂ (RMNH.INS.974910): TURKEY: Ankara, near GÜvem, 40.5915° N, 32.6597° E, 1100 m a.s.l., 31.vii.2008, leg. Gert Jan van Pelt.

Additional males: 2 ♂ (RMNH.INS.974929): TURKEY: Yozgat, 13 km SW of Akdagmadeni, 39.5629° N 35.7954° E, 1680 a.s.l., 27.vii.2006, leg. Gert Jan van Pelt; 1 ♂ (RMNH.INS.974932): TURKEY: Kastamonu, Tosya, 20 km SE of Tosya, spring and brook, 40.9765° N, 34.1894° E 1200 m a.s.l., 05.viii.2006, leg. Gert Jan van Pelt.

Redescription of male

Head (Figure 17D,E): anteclypeus black; postclypeus yellow; labrum yellow with black margin; frons yellow and labium yellow; occipital triangle black fringed with yellowish hairs above; occiput not domed and yellow; antenna and vertex black; eyes green; postocular area yellow with black upper margin.

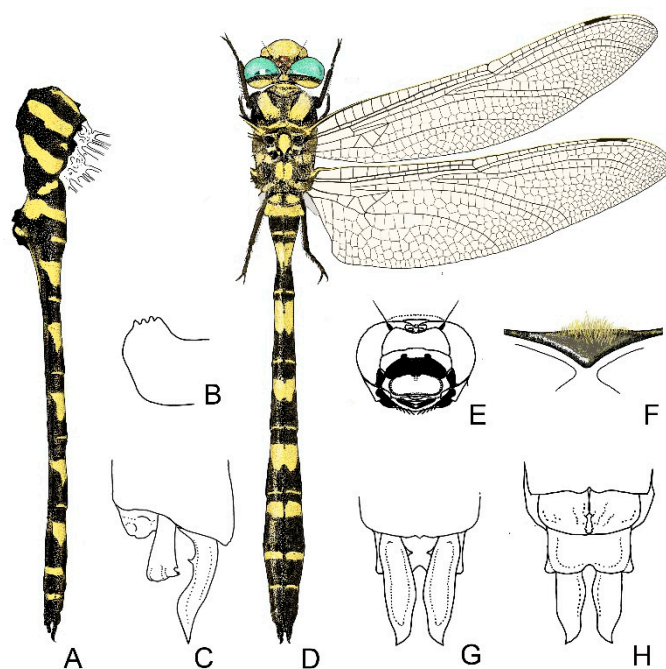


Figure 17. *Cordulegaster amasina*, re-description ♂, (RMNH, Gert Jan van Pelt, RMNH.INS.974910, 31 July 2008, Turkey, Ankara, near GÜvem, 40.5915° N, 32.6596° E, 1100 m a.s.l.): (A): habitus, lateral. (B): detailed latero-dorsalview on the hook of the inferior appendix. (C): appendages, lateral. (D): habitus, dorsal. (E): head, schematically. (F): occipital triangle, frontal. (G): appendages, dorsal. (H): appendages, ventral.

Thorax (Figure 17A,D): anterior lobe of pronotum with yellow front edge; median lobe black with yellow dorsolateral ellipsoid patterns, two yellow middorsal dots; posterior lobe yellow interrupted by a middorsal black band; front of synthorax with broad big yellow antehumeral stripes, narrowing moderately towards pronotum leaving less than 20% black of antehumeral region; mesepimeron and metepimeron with broad yellow bands; metepisternum black with small yellow triangle near base of wings; metakatepisternum black; poststernum black; coxae, trochanter, femora, tibiae and tarsi black.

Wings (Figure 17D) hyaline; costal veins yellow, other veins black; Pt black, Pt FW 3.6×0.4 , HW 4.0×0.5 ; anal triangle 3-celled; membranula narrow.

Abdomen (Figure 17A,D): colour pattern as shown in Figure 17A,D; S1 dorsally black, yellow marking on side of S2–9 with medium sized yellow markings leaving ca. 40% black, in dorsal view of S2–8 there are a pair of small, linear yellow spots present on the dorsal distal part of abdominal segments not touching in the middle of segment, on S2–10 black markings reaching sides, yellow markings also on S9–10.

Appendages (Figure 17B,C,G,H): superior appendages in dorsal view paddle-like, with tips pointing outwards, medioventral teeth visible and directed towards each other; in lateral view, laterobasal tooth visible, located near S10. In lateral view, medioventral tooth visible with a relatively broad base and a prominent hook-shaped curved tip; inferior appendage stout, inverse trapezoid, deeply notched on distal margin seen from above, in lateral view distally small teeth on end of the inferior appendage are visible (Figure 17C), the four single teeth form a small wreath that is visible from latero-dorsal view (Figure 17B), the single teeth inclined distally, in lateral view the caudal end of the inferior is slightly elongated to the rear in the ventral area (Figure 17C).

Measurements (mm): TL (inclusive appendages) 68.0, AL 53.0, FWL 39.0, HWL 39.0.

Variability: other males similar to the described one with minor variability in measurements: (mm) (males, $n = 3$): TL (including appendages) 71.0–68.0, AL 53.0–55.1, FWL 39.0–42.5, HWL 39.0–42.7.

Differential diagnosis

The males are usually smaller than in other species of the *charpentieri*-complex, *C. amasina* is only comparable in size to *C. mzyntae*. However, *C. mzyntae* is much darker than *C. amasina*. Pairs of abdominal spots on dorsal apical margin of S2–8 present in *C. amasina* are absent in *C. mzyntae*. The occipital triangle usually dark, not regular yellow as in other species of *charpentieri*-complex, in some individuals the occipital triangle of *C. amasina* and *C. mzyntae* has small yellowish markings, occiput not domed as in *C. charpentieri*, postocular area not domed and darker than in *C. charpentieri* and *C. cilia*.

The tips of superior appendages of *C. amasina* are bent outwards (possibly an artefact of desiccation), not inwards like in *C. charpentieri*, the medioventral teeth smaller than in two other species of the group. The medioventral teeth in *C. amasina* are closer to S10 than in *C. charpentieri*. The females are smaller and darker than those of other species of *charpentieri*-complex. In contrast to the other species of the group, the small teeth at the caudal end of the inferior appendage form a regularly shaped crown consisting of four teeth. *C. amasina* shares this character with *C. mzyntae*. The size of the teeth varies among male individuals.

Distribution

C. amasina occurs approximately from the province Kastamonu to the province Samsun and from the Black Sea Coast to central Turkey reaching the province Ankara (Figure S1, Table 1).

Cordulegaster mzyntae Bartenev, 1929

Redescription

Material examined: 1 ♂ (coll. Thomas and Elias Schneider): GEORGIA: Adjara, 5 km E Goderdzi Pass, 41.3755° N, 42.3405° E, 1800 m a.s.l., 29.vii.2015, leg. Thomas Schneider; 1 ♂ (coll. Thomas and Elias Schneider): GEORGIA: Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l., 30.vii.2015, leg. Thomas Schneider; 1 ♂ (coll. Thomas and Elias Schneider): GEORGIA: Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l., 30.vii.2015, leg. Thomas Schneider; 1 ♂ (coll. Thomas and Elias Schneider): GEORGIA: Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l., 30.vii.2015, leg. Thomas Schneider; 1 ♂ (RMNH.INS.974901): TURKEY: Ordu, SE of Turnasuyu, 40.6797° N, 37.9573° E, 1300 m a.s.l., 05.viii.1998, leg. Gert Jan van Pelt; 1 ♂ (RMNH.INS.974902): TURKEY: Ordu, SE of Turnasuyu, 40.6797° N, 37.9574° E, 1500 m a.s.l., 02.viii.1998, leg. Gert Jan van Pelt; 2 ♀ (coll. Thomas and Elias Schneider): GEORGIA: Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l., 30.vii.2015, leg. Thomas Schneider.

Description of the male. Head (Figure 18B,D): anteclypeus black; postclypeus yellow; labrum yellow with thicker black margin and a pigmented comma-shaped line in the middle; frons yellow with faint black seam; labium yellow; occiput yellow, not domed, occipital triangle black with yellowish hairs above; antenna and vertex black; eyes green (collector's observation); postocular area black.

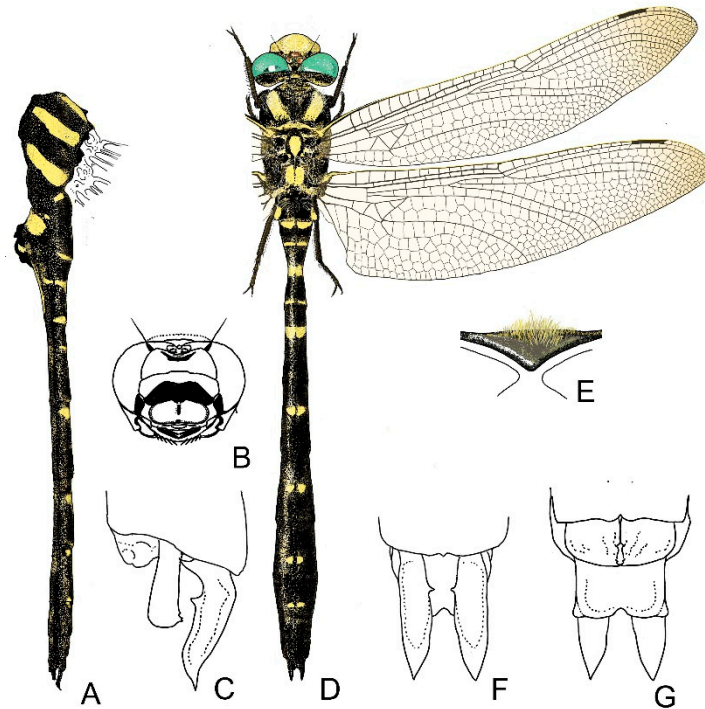


Figure 18. *Cordulegaster mzyntae*, ♂ (collection Elias and Thomas Schneider, leg. Thomas Schneider, 30 July 2015, Georgia, Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l.): (A): habitus, lateral. (B): head schematically. (C): appendages, lateral. (D): habitus, dorsal. (E): occipital triangle. (F): appendages, lateral. (G): appendages, ventral.

Thorax (Figure 18A,D): anterior lobe of pronotum black; median lobe black with yellow dorsolateral spindle-shaped patterns; posterior lobe black; front of synthorax with broad big yellow antehumeral stripes, narrowing moderately towards pronotum leaving less than 20% of antehumeral region black; mesepimeron and metepimeron with broad yellow bands; metepisternum black with small yellow dot near base of wings; metakatepisternum black; poststernum black; coxae, trochanter, femora, tibiae and tarsi black.

Wings (Figure 18D) hyaline, older individuals with semihyaline brownish wings in the distal region, costal veins yellow, other veins black; Pt black, Pt FW 3.7×0.4 , HW 4.0×0.5 ; anal triangle 3-celled; membranula grey and narrow.

Abdomen (Figure 18A,D): dorsal yellow spots on abdomen are reduced to small pairs of semi-lunar markings leaving over 90% black; S9 and S10 completely dark in dorsal and lateral view.

Appendages (Figure 18C,F,G): superior appendages in dorsal view paddle-like, with pointed tips, medioventral teeth visible and directed towards each other, in lateral view, laterobasal teeth visible, located near S10. In lateral view, medioventral teeth visible located at the first half of the superiores, with a relatively broad base, gradually narrowing, slightly pointed; inferior appendage stout, slightly trapezoid, notched on distal margin seen from above, in lateral view distally small teeth on end of the inferior appendage are visible, the four hook-shaped single teeth form a small comb that is visible from caudal view, the single teeth inclined slightly distally, the caudal end of the inferior appendages is almost rounded in lateral view.

Measurements (mm): TL (inclusive appendages) 65.7, AL 49.6, FWL 41.4, HWL 40.8.

Variability: other males much as the described one with minor variation in measurements: (mm) (males, $n = 7$): TL (including appendages) 63.8–65.7, AL 49.5–49.9, FWL 41.2–42.1, HWL 40.4–42.0.

Description of female. Head (Figure 19A): much as in ♂.

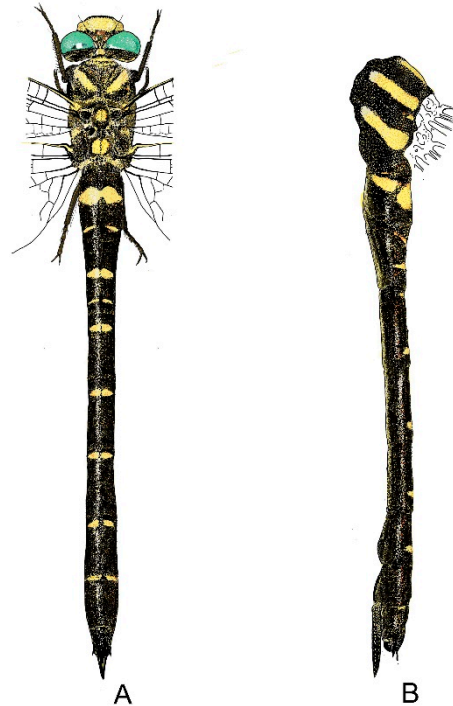


Figure 19. *Cordulegaster mzymtae*, ♀ (collection Elias and Thomas Schneider, leg. Thomas Schneider, 30 July 2015, Georgia, Adjara, 5 km E Goderdzi Pass, 41.6319° N, 42.5680° E, 1820 m a.s.l.): (A): habitus, dorsal. (B): habitus, lateral.

Thorax (Figure 19A,B): much as in male, exception the yellow markings of metepisternum; metepisternum black with small comma-shaped yellow markings,

Wings: much as in male, hyaline; Pt black, Pt FW 4.0×0.5 , HW 4.1×0.6 .

Abdomen (Figure 19A,B): cylindrical and thicker than in males, ovipositor 5.3 mm, black, only slightly curved, almost straight and long.

Measurements (mm): TL (inclusive ovipositor) 68.5, AL 51.7, FWL 43.4, HWL 44.6.

Variability in females: second female looks much as described above, but slightly larger. **Measurements (mm)** (females, $n = 2$): TL (inclusive ovipositor) 68.5–68.6, AL 51.7–51.8, FWL 43.4–43.5, HWL 44.6–44.7.

Differential diagnosis

Male and female are smaller than all other species of the *C. charpentieri*-complex. They are easily recognized by their dark colour pattern. Pairs of abdominal spots on dorsal apical margin of S2–8 are absent. The occipital triangle is black, not yellow as in most other species of *charpentieri*-complex, in some individuals the occipital triangle has yellowish markings, occiput not domed as in *C. charpentieri*, postocular area not domed and darker as in all other species of this complex. Superior and inferior appendages are very similar to the appendices of *C. amasina*. As in *C. amasina*, there is also a four-tooth crown in *C. mzymtae* at the end of the inferior. In all other species of the group there are usually three teeth of different sizes visible at the end of the inferior.

Distribution

C. mzymtae and other *Cordulegaster* in its natural environment are shown in Figure 20.

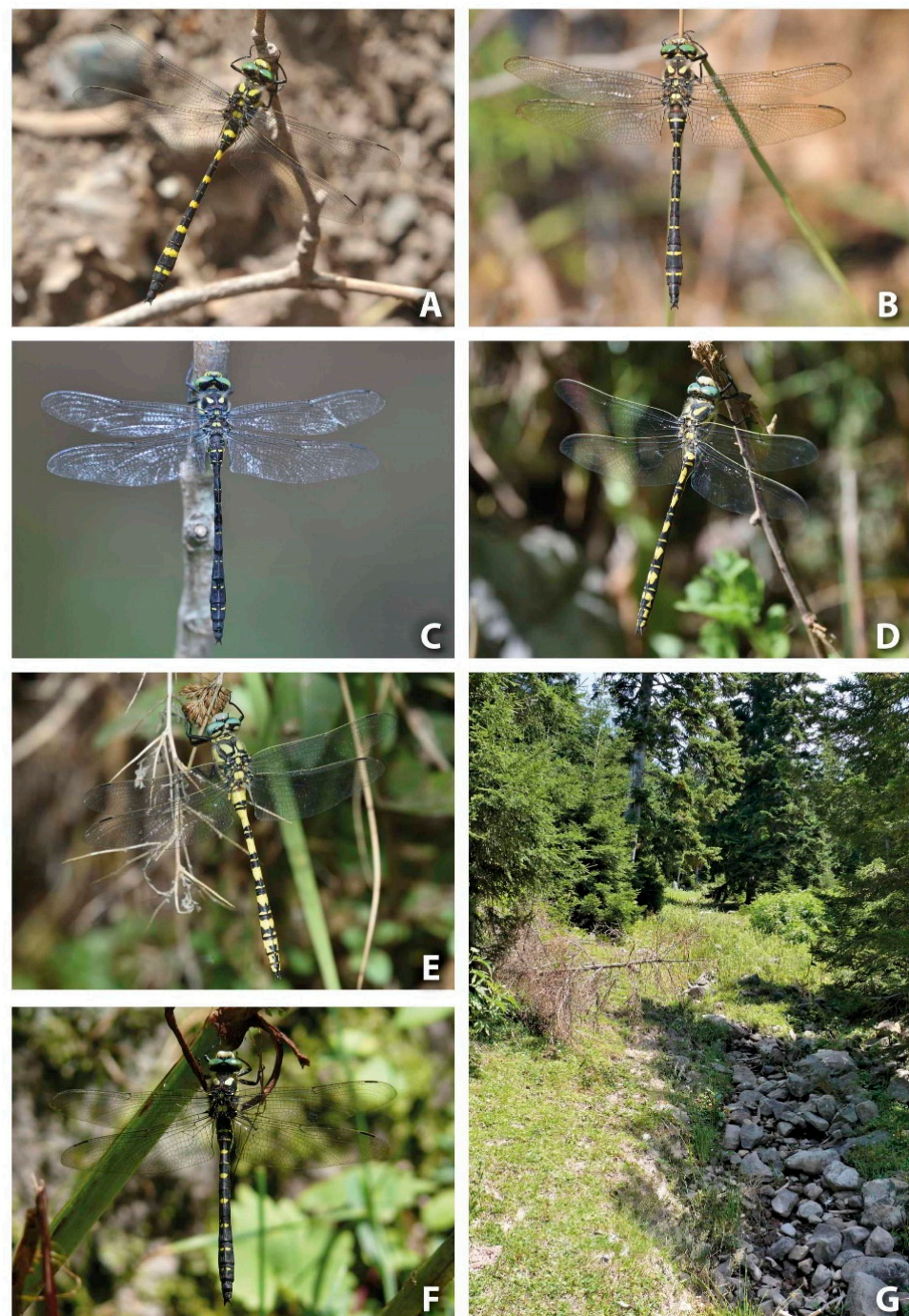


Figure 20. Some *Cordulegaster* in their natural environment and some of their habitats: (A): yellow form of *C. picta* (near Köycegiz, Turkey). (B): dark form of *C. picta* (near Mengen, Turkey). (C): *C. vanbrinkae* (Hyrcanian forest near Veysar, Iran). (D): *C. coronata* (near Arzaneh, Iran): (E): *C. charpentieri* (near Dorud, Iran): (F): *C. mzymtae* (Georgia, Adjara, 5 km E Goderdzi Pass). (G): *C. mzymtae* Habitat (Georgia, Adjara, 5 km E Goderdzi Pass). (A–E): photos Dietmar Ikemeyer, (F,G): photos Elias Schneider.

C. mzymtae the darkest member of the *bidentata*-group occurs eastwards from *C. amasina* reaching Georgia, the Russian Black Sea Coast and even until Karachay Cherkessia Region in the North Caucasus (Russia) (Figure S1, Table 1).

5. Discussion

5.1. General Discussion on the Genus *Cordulegaster* in the Western Palaearctic

The taxonomic debate on the genus *Cordulegaster* in the Western Palaearctic has been ongoing for over one and half centuries [2,13,14,19,26,30,35,63,64]. For the Western part of the Western Palaearctic, a molecular approach exists [13]. However, for the more complex and unsettled Eastern part of the Western Palaearctic, no molecular studies have been conducted until now, and no published sequences are available so far. From the east of the Western Palaearctic, including Turkey, the Caucasus countries and Iran, several species and subspecies have been described (Table 2). All these were based on external morphology and the colour patterns of imagines, especially of the male appendices. However, colour patterns and structure of the appendices may vary and hybrids may complicate phenotypic taxonomy. *C. boltonii* and *C. trinacriae* interbreed in a broad zone in Italy [35]. In a similar way, our data support hybridization in the *boltonii*-group between *C. vanbrinkae* and *C. picta* in Armenia and in the *bidentata*-group between *C. insignis* and *C. cilicia* sp. nov. Such hybridization supports the view that pre- and post-mating barriers are inefficient, and structural differences in the genital apparatus do not prevent gene flow. It explains the limitations of morphological characters for species recognition in this genus. Only part of the variation observed is taxonomically relevant and it is sometimes impossible to identify specimens to species. As an alternative, we undertook a molecular genetic approach, which reveals the genotype, not the phenotype. It helped us to clarify the status of several doubtful subspecies and species in this region. Furthermore, an inherent limitation of the morphological method is that not all hybrids are intermediate and can only be detected by molecular genetic approach.

5.2. *Cordulegaster boltonii*-Group

In the *boltonii*-group of the Eastern region of the Western Palaearctic, we recovered with molecular genetic analysis three known (*C. heros*, *C. picta*, *C. vanbrinkae*) and one new species (*C. kalkmani*). These four eastern species of the *boltonii*-group (*C. heros*, *C. picta*, *C. kalkmani*, and *C. vanbrinkae*) seem to be geographically separated but may meet in contact zones (Figure 21). The existence of the new taxon *C. kalkmani* was supported by the alignments of both genes separately or combined as well by the haplotype-analysis and the K2-P distances. *C. heros* is known from rather Central and Southeast Europe, reaching Ukraine in the North–East [65]. *C. picta* inhabits an area extending from North–Eastern Greece and Bulgaria, through West and North Turkey, including Samos and Lesbos in the Aegean, along the Black Sea coast as far as Russia, Georgia and Azerbaijan [16,66,67]. However, the presence of *C. picta* in Azerbaijan may be questioned, as the only voucher specimen is old and in bad condition; it is not clear whether it belongs to *C. picta*, to *C. vanbrinkae* or is a hybrid between them [16]. *Cordulegaster picta* from South–West Turkey and Samos are rather yellow, where those from the Black Sea region are much darker (Figure 20). *C. vanbrinkae* is restricted to the South Caspian Sea region [68,69]. In East Anatolia, possibly reaching Armenia and North–West Iran, a new species, *C. kalkmani* was found. The record of *C. picta* by Rastegar in North–West Iran may belong to the latter species [70]. *C. kalkmani* seems to be geographically separated from *C. picta* and *C. vanbrinkae* by the Anatolian Diagonal and further east by the Armenian Highlands and the Caucasus (Figure 21). *C. vanbrinkae* and *C. kalkmani* seem to be separated by the Armenian Highland (Figure 21). As mentioned before, we found hybridization between *C. picta* and *C. vanbrinkae* in Armenia. These hybrids may be phenotypically indistinguishable from one of their parents. This is the case of the hybrid from Armenia, which looks like *C. vanbrinkae*, causing specimens from this population to be initially described as *C. vanbrinkae* [71]. We found no evidence for hybridisation between *C. picta* and *C. kalkmani* and between *C. vanbrinkae* and *C. kalkmani*. The K2-P distances of the COI sequences revealed that *C. kalkmani* is more distant from *C. picta* (5.88%) than *C. vanbrinkae* from *C. picta* (3.95%). Correspondingly, the male appendices of *C. kalkmani* are more different from *C. picta* than those of *C. vanbrinkae* from *C. picta*.

This suggests that the latter two were separated more recently (see also timetree-analysis, Figure S7) and may be regarded as sister taxa.



Figure 21. Map with species identified in this study for *C. boltonii*-group relative to the Anatolian Diagonal.

Hybridization may occur also between *C. boltonii* and *C. heros* as both are locally syntropic [72], and may also occur in still undocumented contact zones in Greece or Bulgaria between *C. heros* and *C. picta*, and even in Ukraine and Russia north of the Black Sea.

Thus, we highlight broad variation in colour pattern in some taxa. Male appendages, often used as diagnostic, have limits for discriminating species, and the distinction between intraspecies variation and significant differences is often hard to make. This was a source of confusion in the past. The work by Froufe showed that all European subspecies of *C. boltonii*; *C. b. immaculifrons* Selys, 1850; *C. b. iberica* Boudot & Jacquemin, 1995; *C. b. algerica* Morton, 1916, although statistically representative, may just be colour variations [13]. We conclude, including the data of Froufe, that the following species in the *boltonii*-group live in the West Palaearctic: *C. princeps*, *C. boltonii*, *C. trinacriae*, *C. heros*, *C. picta*, *C. kalkmani*, and *C. vanbrinkae*. The division of the *boltonii*-group in a “western” group, with *C. princeps*, *C. b. algerica* (North Africa only), *C. boltonii*, *C. trinacriae* and an “eastern” group with *C. heros*, *C. picta*, *C. kalkmani* and *C. vanbrinkae* is supported by our molecular data. This view was already suggested by Verschuren based on the morphology of the larvae without knowing the latter two species at that time [12].

5.3. *Cordulegaster bidentata*-Group

In the *bidentata*-group of the Eastern region of the Western Palaearctic, two complexes were revealed by molecular analysis: the *helladica-insignis*-complex in South-East Europe

and Western Turkey, and the *charpentieri*-complex in Eastern Anatolia, Levant, Caucasus countries and Iran (Figure 22). These species are geographically separated by mountains of Anatolia and the Caucasus, although overlapping zones exist in East Anatolia (Figure 22). As widely accepted, the nominotypic *C. insignis* inhabits Western Turkey and eastern Greece islands like Samos. However, the molecular analysis of all specimens collected east of the Marmara and Aegean region grouped away from *C. insignis* using both programs for both genes separately or combining the COI and ITS genes. All the eastern specimens of the *bidentata*-group were therefore summarized here in the *charpentieri*-complex.

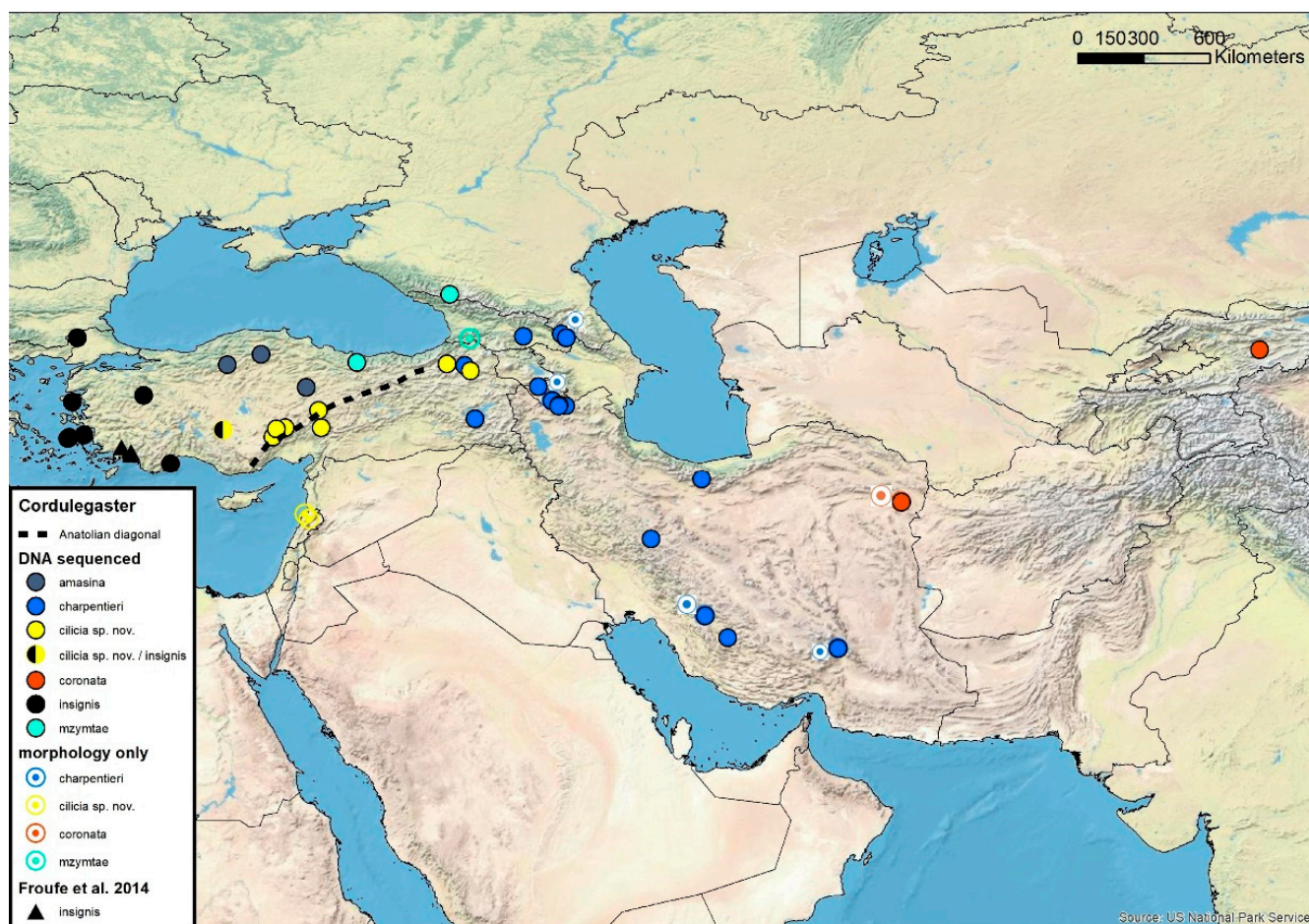


Figure 22. Map of both *C. bidentata*-complex and *C. coronata* with species identified in this study relative to the Anatolian Diagonal.

The COI analysis of the *charpentieri*-complex with two programs is in favour of four species (*C. amasina*, *C. mzymtae*, *C. cilicia*, and *C. charpentieri*). The K2-P distance between these four taxa is 2.96–4.24% (Table 4), in agreement with a full species level [43,45,46]. The ITS analysis by the MAFT program, however, put them all together indicating a more recent diversification in this taxa complex (supported by our timetree, Figure S7). This may be due to special glacial events in Anatolia as discussed below. For several aspects, including the conservation of highly endangered and unique biotopes, we would suggest to hold up these three traditional and the new taxa.

Morton introduced *C. amasina* as a race, based on five males from Amasya, Turkey [26]. As our results support the occurrence of a separate species along the western part of Black Sea Coast, we adopted the existing name for this lineage. Further east, reaching Georgia and Russia, *C. mzymtae* occurs. This taxon was sometimes treated as a subspecies of *C. insignis* [10,11]. More extensive fieldwork along the Black Sea Coast may clarify the exact distribution borders between *C. insignis*, *C. amasina*, and *C. mzymtae*. The separation

between these taxa may be due to the glacial events discussed in a recent paper on banded newts in this region [73].

We did not find any published name for another clade defined by molecular data in the *charpentieri*-complex, and therefore we name it *C. cilicia*. The name refers to the historical province of Cilicia located on the south coast of Asia Minor. However, the range of this species exceeds the limits of this historical province to northeast and southeast and it inhabits East Anatolia and extends along the East–Mediterranean Sea reaching Lebanon. *C. cilicia* and *C. charpentieri* meet in Central–East Anatolia in the province of Kars (Figure 22). *C. cilicia* is well separated in the COI and haplotype analysis, and the K2-P distance to its next relative *C. charpentieri* is 3.22% and in agreement with species level for Anisoptera [43].

C. charpentieri is a widespread species occurring in Central-East Anatolia, Armenia, Georgia, and Iran. It is most likely also present in northern Iraq taking the description by Asahina into account [74]. *C. charpentieri* exhibits some variation in the colour-pattern across its range; therefore, we have depicted representative examples in this study. The size of this species is also variable, and the largest animals of this taxon exist in the South and South-Eastern Zagros Mountains. These individuals belong with *C. heros* and *Anax immaculifrons* to the largest dragonflies of the Western Palaearctic.

Anatolia emerges as a hotspot for the *charpentieri*-complex. Here, three refugia meet and interact: the Caucasus, Irano–Anatolian and the Mediterranean [40,41]. Two refugia, one in western and one in Eastern Anatolia, separated by the Anatolian diagonal, have been suggested, based on non-genetic data [75,76]. More have been found by genetic analysis of different animal groups [77,78]. The lake system was present in central Anatolia during the Pliocene and the inhabitability of the Central Anatolian Plateau in the glacial maxima of the Pleistocene probably broke up previously continuous faunal ranges leading to subspeciation [79]. Vicariant events related to the formation of the Anatolian diagonal and the orogenesis of the mountain chains in southern and Eastern Anatolia are what led to current distribution patterns of animals like *Cordulegaster*. The Anatolian diagonal was originally described for plants, but also applies to animals [41,42,77,78]. In the case of the *charpentieri*-complex it separates *C. amasina* from *C. cilicia* and the western Taurus, nominal *C. insignis* from all others. The Eastern Anatolian Mountains and the Armenian Highland separate *C. charpentieri* from *C. amasina*, and *C. cilicia* (Figure 22). However, hybridization may have occurred and may still occur in postglacial contact zones (Figure 22).

For *C. magnifica*, described by Bartenev based on a single female of unknown origin, we did not find any support in the investigated region [28]. The type is lost. The description fits to most females of ‘mid-yellow’ *Cordulegaster* of the *bidentata*-group in the East Mediterranean, the Middle East and the South Caucasus. In view of its unknown origin and as no other specimen or living population is known, it is not possible to ascribe it to any taxon and the name should be deleted.

Thus, in the *bidentata*-group the following species occur from West to East: *C. bidentata*, *C. helladica*, *C. insignis*, *C. amasina*, *C. mzymtae*, *C. cilicia* and *C. charpentieri*. The species *C. coronata* is genetically distant from this group, although morphologically close to the *charpentieri*-complex (Figure 23).

5.4. *Cordulegaster coronata*-Group

The *coronata*-group formed an extra clade with all three programs for both genes and also in combination of these two genes. This is the reason why this taxon was sometimes treated as a subspecies of *C. insignis* in the past [2,14]. *C. coronata* is a Middle Asian taxon, which has its Western distribution limits in North-East Iran (Razavi Khorasan) as recently documented [46,47]. In North-Khorasan, *C. coronata* and *C. charpentieri* may meet, therefore, it would be of interest to investigate specimens from this region to see if hybridisation between them is possible.

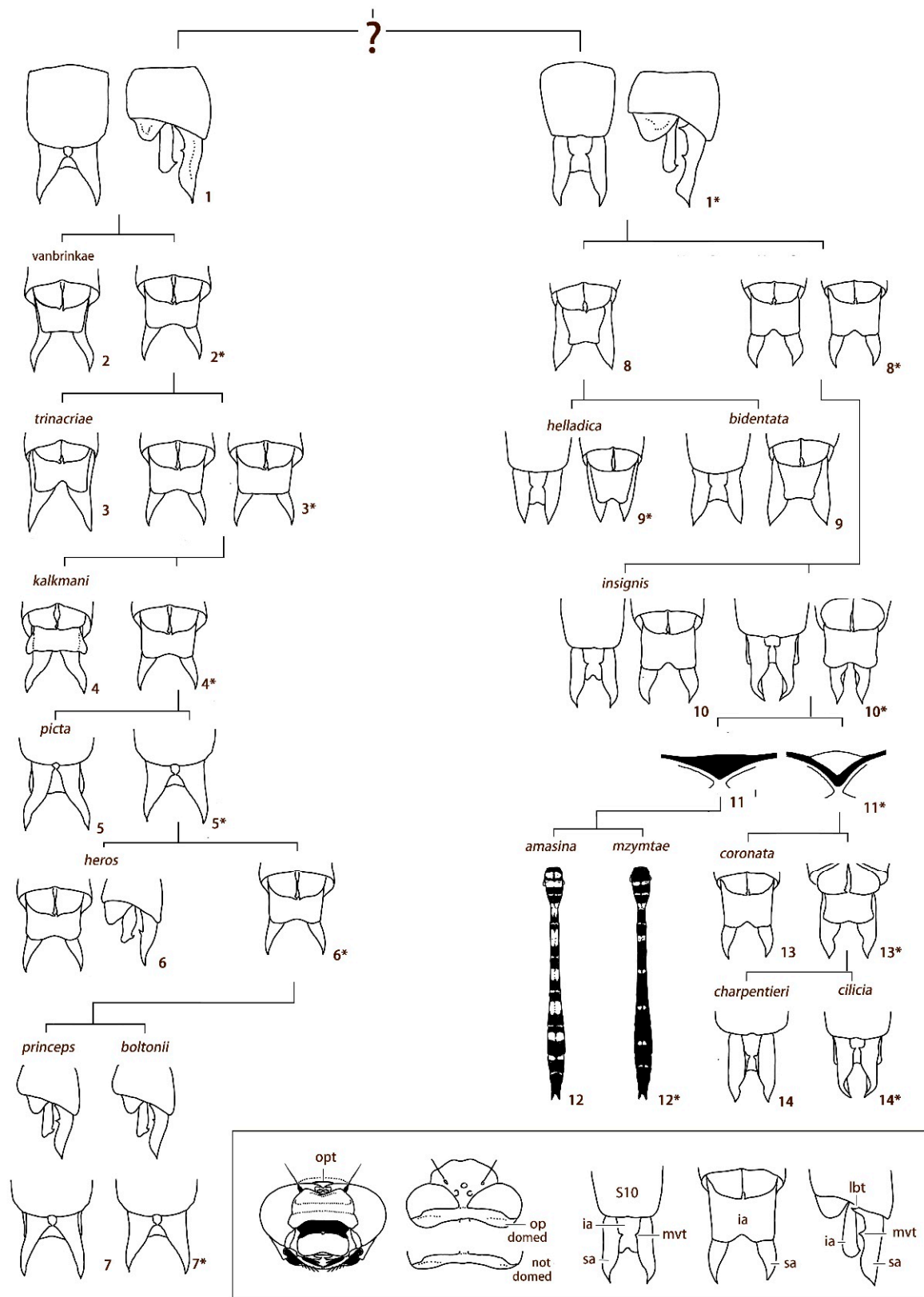


Figure 23. Dichotomous identification tree for all Western-Palaeartic *Cordulegaster* (males, graphically represented features in the text, additional features in square brackets).

5.5. Key for the Western–Palearctic *Cordulegaster*

Finally, we provide a preliminary key for the Western–Palearctic *Cordulegaster* (Figure 23). This key should be regarded as a working version for future studies. As *Cordulegaster* species seem to have separated rather recently and hybridization in contact zones is common, the phenotypical approach based upon male appendices as a discriminating character is limited. Moreover, male appendices are mobile and may become fixed at death in different positions, which may influence later interpretation. This may have led to confusion in the past. Despite all these difficulties, our key uses the known characters used for differentiation of *Cordulegaster* species (Figure 3). In contact zones this key may not work, especially where hybrids are present.

Key (only for males):

1 superior appendages in dorsal view diverging with curved outer borders and nearly close at the base, one visible tooth (medioventral tooth), laterobasal tooth not visible in lateral view ... *boltonii*-group ... 2.

1* superior appendages nearly parallel with straight outer borders and separated at the base, two teeth visible (medioventral tooth, laterobasal tooth) in lateral view ... *bidentata*-group and *coronata*-group ... 8.

2 inferior appendage trapezoid with a narrower hind margin, [frons with a thick black bar, occipital triangle black, hind margin of the inferior appendage weakly concave, narrowing distally, hooks of the inferior bifid, medioventral teeth on superior appendages very close to S10 and small] ... *vanbrinkae*.

2* inferior appendage nearly parallel-sided ... 3.

3 hind margin of the inferior appendage not or weakly notched ... 4.

3* hind margin of the inferior appendage clearly notched, [inferior appendage clearly notched, hooks of the inferior with one single tip, 3–5 cells in anal triangle, occipital triangle mostly yellow, frons mostly unmarked] ... *trinacriae*.

4 hind margin of the inferior appendage not notched or curved inwards, the dorsally pointing lobes of the inferior appendage widen the inferior distally, [inferior appendage at the end with a single pointed hook-shaped tooth on each side, medioventral teeth on superior appendages larger and more distal than in *C. vanbrinkae* but more proximal than in *C. picta*, 3 cells in anal triangle] ... *kalkmani*.

4* hind margin of the inferior appendage slightly curved inwards, the dorsally pointing lobes of the inferior appendage not significantly widen the inferior distally, [4–5 cells in anal triangle] ... 5.

5 superior appendages narrow, reaching outwards, longer than S10, [hooks of the inferior bifid, frons with a narrow black bar, occipital triangle with two yellow spots, never completely black, superior appendages long and slender, clearly divergent, longer than S10, inferior appendage slightly notched, widened distally in ventral view, 4–5 cells in anal triangle] ... *picta*.

5* superior appendages stout, weakly pointing outwards, shorter than S10 ... 6.

6 margins of inferior appendage not parallel-sided, widened distally, [#teeth with one single tip, 3–6 cells in anal triangle, medioventral teeth on superior appendages small, more distal than in *C. vanbrinkae*, *C. kalkmani*, and *C. picta*] ... *heros*.

6* margins of inferior appendage nearly parallel-sided ... 7.

7 superior appendages slender,–medioventral tooth prominent, [hooks of the inferior small, dull and only with one single tip, species endemic to the High and Middle Atlas (Africa)] ... *princeps*.

7* superior appendages stout,–medioventral tooth very small hooks of the inferiores with one single tip] ... *boltonii*.

8 inferior appendage significantly narrower at the distal end than at the base, sometimes slightly waisted ... 9.

8* inferior appendage not significantly narrower at the distal end than at the base ... 10.

9 superior appendages reaching outwards, inferior appendage slightly waisted and with notch at the hind margin, [occipital triangle usually black although sometimes yellowish in South Italy and Sicilia] . . . *bidentata*.

9* superior appendages not reaching outwards, inferior appendage tapering towards hind margin, significantly notched at the hind margin . . . *helladica*.

10 lateral margins of the inferior appendage nearly parallel-sided over its entire length, shape rectangular, hind margin significantly notched, in dorsal view—medioventral tooth far from S10, [occiput little arched, mostly black coloured with a yellow hem, flat] . . . *insignis*.

10* lateral margins of the inferior appendage parallel-sided only at their base, inferior appendage distally getting wider . . . 11.

11 occipital triangle only slightly domed, mainly black, [sometimes with yellow markings, occiput little arched, abdomen mostly black coloured] . . . 12.

11* occipital triangle domed, mainly yellow . . . 13.

12 abdomen [and thorax] with large extended yellow spots, [wings not coloured, hooks of the inferiores forming a 4-toothed crown] . . . *amasina*.

12* abdomen [and thorax] with only some yellow spots, hooks of the inferior appendage forming a 4-toothed crown] . . . *mzyntae*.

13 inferior appendage distally slightly smaller than at base, [occipital triangle yellow, not domed, occiput flattened, mostly black coloured] . . . *coronata*.

13* inferior appendage distally slightly wider than at base (teeth pointing outwards, this widens the inferior appendage outwards), [occipital triangle yellow and domed, occiput yellow and domed] . . . 14.

14 inferior appendage longer than one half the length of superior appendages, in dorsal view medioventral teeth inserted far away from S10, [occiput mostly yellow and domed] . . . *charpentieri*.

14* inferior appendage as long as the middle of superior appendages, in dorsal view—medioventral tooth inserted nearby S10, superior appendages are shorter in relation to the inferior appendage, [short distance between laterobasal tooth and—medioventral tooth in lateral view, occiput mostly black, slightly domed] *cilicia*.

6. Conclusions

This is the first revision of the Western Palaearctic *Cordulegaster* including the complex eastern part of the Western Palaearctic since Morton over 100 years ago [26]. We applied a two-step approach, first using molecular genetic sorting and, in a second step, morphology and description. The existence of the two traditional groups, the *boltonii*- and *bidentata*-group, is confirmed. Two new species are suggested and described, one in each group (*C. kalkmani*, *C. cilicia*). *C. coronata* Morton, 1916, however, is assigned to a different group based on its separate position in molecular trees and despite its morphological similarity to the *charpentieri*-complex. We synonymize four taxa with *C. charpentieri*: *C. insignis nobilis* Morton, 1916, *C. nachitschevanica* Skvortsov and Snegovaya, 2015, *C. plagionyx* Skvortsov and Snegovaya, 2015, and *C. insignis lagodechica* Bartenev, 1930. In contact zones of members of the *boltonii*- and the *bidentata*-group, hybridization is possible, therefore taxonomy in these areas should rule out hybrids by using not only the COI barcoding gene.

Thus, we suggest 16 taxa in *Cordulegaster* in the Western Palaearctic, eight in the *boltonii*-group (*C. princeps*, *C. b. algerica* (genetically distinct only in North Africa), *C. boltonii*, *C. trinacriae*, *C. heros*, *C. picta*, *C. kalkmani* and *C. vanbrinkae*); and seven in the *bidentata*-group (*C. bidentata*, *C. helladica*, *C. insignis*, *C. amasina*, *C. mzyntae*, *C. cilicia* and *C. charpentieri*). *C. coronata* a Middle East species with its western distribution limits in the Western Palaearctic is genetically distant from these groups ([13] and the present publication).

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13120667/s1>, Figure S1: Detailed information about the *Cordulegaster* specimens investigated in this study. Figure S2: CordWPalaeartcis COI overview. Figure S3: COI StarBEAST. Figure S4: StarBEAST COI and SPACER. Figure S5: COI_BPP. Figure S6: COI_SPACER_BPP. Figure S7: COI timetree.

Author Contributions: T.S. designed the study and led the writing of the manuscript. A.V. conducted the molecular analysis and created the phylogenetic trees, O.M. created all drawings of the manuscript and made general contributions, G.J.v.P. and N.S. collected and analyzed data, M.C. helped finding specimens in RMNH, created the maps, H.J.D. and D.I. helped interpretation and writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

Collections. RMNH—Naturalis Biodiversity Center; **Genetic; BIC**—Bayesian information criteria; **COI**—mitochondrial cytochrome oxidase subunit I; **ITS**—internal transcribed ITS; **K2-P**—Kimura 2-parameter; **PCR**—polymerase chain reaction; **Morphology.** **AL**—abdomen length; **FW**—forewing; **FWL**—forewing length; **HW**—hindwing; **HWL**—hindwing length; **Pt**—pterostigma; **S**—abdominal segment; **TL**—total length.

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