



The classification and phylogenetic status of *Jekelius (Reitterius) punctulatus* (Jekel, 1866) and *Jekelius (Jekelius) brullei* (Jekel, 1866) (Coleoptera: Geotrupidae) using molecular data

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Abstract

The phylogenetic placement of *Jekelius brullei* (Jekel, 1866) and *J. punctulatus* (Jekel, 1866) (Coleoptera: Geotrupidae) was assessed using mitochondrial and nuclear molecular data to discern contrasting nomenclatural views provided by López-Colón (1996) and the *Catalogue of Palaearctic Coleoptera* (Löbl *et al.* 2006). Our results support both the monophyletic and classification status of the genus *Jekelius* López-Colón, 1989; and the splitting of the genus into the subgenera *Jekelius* López-Colón, 1989 and *Reitterius* López-Colón, 1996. The basal phylogenetic placement of these two species also suggests an oriental origin for *Jekelius* within the western Palaearctic region. Finally, we include a potential distributional map of *Jekelius (Reitterius) punctulatus* (Jekel, 1866) based on an exhaustive search of occurrence data.

Key words: Geotrupinae, dung beetles, Balkan Peninsula, potential distribution

Introduction

Thorectes Mulsant, 1842 (Coleoptera: Geotrupidae: Geotrupinae) sensu lato (including *Jekelius* López-Colón, 1989, which we consider a genus) is an apterous genus comprising 43 species according to the recent catalogue of Palaearctic Coleoptera (Löbl *et al.* 2006) and the world Scarabaeidae database (Schoolmeesters 2014). Following the taxonomic criteria of López-Colón (2003), most of these species are distributed in the western Palaearctic region (Fig. 1): 20 species in the Ibero-Balearic region, 15 in the western part of northern Africa (including *J. brullei africanus* (Baraud, 1965)), with one species that is doubtfully shared among both regions (*T. intermedius* (Costa, 1839)), and two species in other western Mediterranean areas (*T. sardous* (Erichson, 1847) and *T. sericeus* (Jekel, 1866)). From the nine species occurring east of the Italian Peninsula, three live in the Balkan Peninsula and the Middle East (*T. intermedius*, *J. punctulatus* (Jekel, 1866), and four subspecies of *J. brullei*) and the other six occur beyond the European region: one in Turkey (*T. asperifrons* (Fairmaire, 1866)), one from Tajikistan (*T. banghaasi* (Reitter, 1892)), one from northern India (*T. stellosum annapurnicus* (Krikken, 1981) and *T. stellosum stellosum* (Krikken, 1981)), and three have been cited from Nepal (*T. martensi* (Krikken, 1981), *T. nepalensis* (Baraud, 1974), and *T. shankara* Carpaneto & Mignani, 1999).

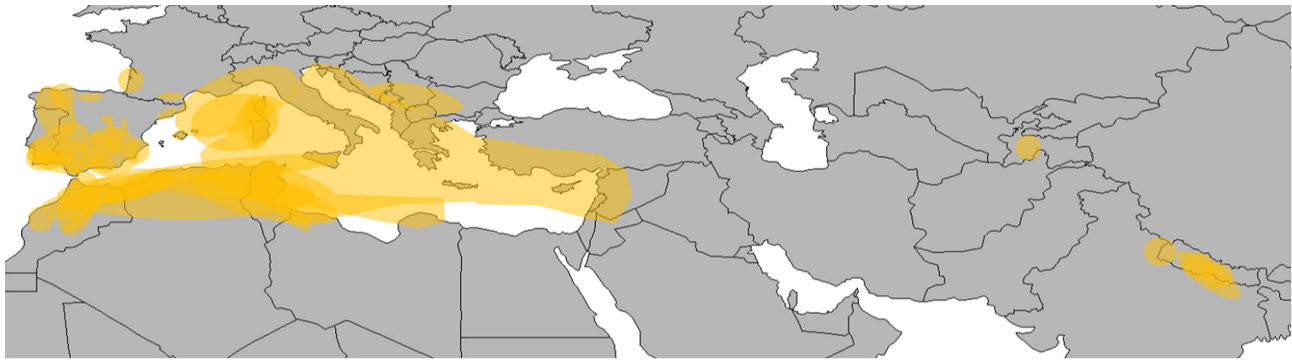


FIGURE 1. Schematic map showing the approximate distribution of all known *Thorectes* sensu lato species according to the general distributional data provided by Krikken (1981), López-Colón (1996), Löbl *et al.* (2006), and Palmer and Cambefort (1997).

Although they are relatively similar externally, the study of the male genital morphology of *Thorectes* by López-Colón (1989) enabled recognition of four different subgenera (*Thorectes* sensu stricto, *Silphotrupes* Jekel, 1866, *Jekelius*, and *Zuninoe* López-Colón, 1989). Subsequently, the same author (López-Colón 1996) suggested elevating these subgenera to full generic status, and also delimited a new genus (*Baraudia* López-Colón, 1996) for *Thorectes geminatus* (Gené, 1839). Simultaneously, López-Colón (1996) proposed new subgeneric denominations for both *Thorectes* (*Thorectes* sensu stricto and *Renaudia* López-Colón, 1996) and *Jekelius* (*Jekelius* sensu stricto, *Reitterius* López-Colón, 1996, and *Petrovitzia* López-Colón, 1996). Subsequently, Rey & López-Colón (2003) proposed the replacement of *Petrovitzia* with *Rudolfpetrovitzia* and López-Colón (2006) proposed the replacement of *Renaudia* with *Renaudtrupes*. Branco and Ziani (2006), in the *Catalogue of Palaearctic Coleoptera*, considered that “most of these generic names are unnecessary” synonyms and eliminating them. Independent of the nomenclatural controversy (see López-Colón & Alonso-Zarazaga 2006), the splitting of *Thorectes* into several genera is not considered adequate because the described differences “are not important enough to justify its split” (Branco & Ziani 2007) despite the results provided by the only morphological phylogenetic hypothesis available at the time (Palmer & Cambefort 1997). More recently, a phylogenetic study based on molecular characters (Cunha *et al.* 2011) suggested that Iberian flightless *Thorectes* lineages are most likely paleoendemics surviving from the Tertiary in this refugial area and suggested that the proposed genera of López-Colón represent independent lineages appeared at a time similar to other well-established Geotrupidae genera.

In this study, we use newly acquired and previously published molecular data (Cunha *et al.* 2011) from 17 species of *Thorectes* sensu lato (2 species of *Silphotrupes* Jekel, 1866, 5 species of *Thorectes* Mulsant, 1842, and 10 species of *Jekelius* López-Colón, 1989) to examine the phylogenetic placement of two of the three species occurring in eastern Europe (*T. brullei anatolicus* (Jekel, 1866) and *T. punctulatus* (Jekel, 1866)). These two species were recognised as belonging to the genus *Jekelius* by López-Colón (1996). Because this author included these two species in different subgenera: *Jekelius* (*Reitterius*) *punctulatus* (Jekel, 1866) and *Jekelius* (*Jekelius*) *brullei* (Jekel, 1866), the results provided in this work should be considered a further test of the validity of these proposed but unrecognised taxonomic categories. Additionally, we also compile the available distributional data of *J. punctulatus* for the first time, showing the main environmental characteristics of the localities in which this species occurs.

Methods and material

Molecular analyses

Two specimens of *J. brullei anatolicus* and two of *J. punctulatus* were collected from Kütahya (Turkey; 39.30°N, 30.12°E) and Ledenika (Bulgaria; 43.20°N, 23.49°E), respectively. The other species of the genera *Silphotrupes*, *Thorectes*, and *Jekelius* used in this work are indicated in Table 1. Based on a previous study (Cunha *et al.* 2011), two species of Geotrupini were selected as outgroups (*Geotrupes ibericus* Baraud, 1958 and *Trypocopris pyrenaicus* (Charpentier, 1825); see Zunino 1984) (see Table 1).

TABLE 1. List of species used in this study, collection locality , GenBank accession number for mitochondrial and nuclear gene fragments, code of the voucher specimen deposited in the DNA and Tissues Collection of the National Museum of Natural Sciences of Madrid, Spain (see <http://www.mncn.csic.es/>) (*: current study; **: Cunha *et al.*, 2011).

Species	Locality	COI-COII	GenBank accession number		
				<i>nuc</i>	Voucher number
<i>Silphotrupes orocantabricus</i> (Verdú & Galante, 2000)	Spain. Lugo: Hospital	GU984623**	KP6576 60*	GU9845 91**	MNCN/ADN 58018
<i>Silphotrupes punctatissimus</i> (Chevrolat, 1840)	Spain. Zamora: Laguna de los Peces	GU984622**	KP6576 61*	GU9845 88**	MNCN/ADN 58020
<i>Thorectes armifrons</i> (Reitter, 1892)	Morroco: Ifrane		KP6576 73*	KP65767 9*	MNCN/ADN 57485
<i>Thorectes baraudi</i> López-Colón, 1981	Spain. Albacete: Sierra de Alcaraz	GU984636**	KP6576 62*	GU9845 98**	MNCN/ADN 58024
<i>Thorectes ferreri</i> López-Colón, 1983	Spain. Badajoz: Santo Domingo	GU984635**	KP6576 63*	GU9845 85**	MNCN/ADN 58028
<i>Thorectes lusitanicus</i> (Jekel, 1866)	Spain. Cádiz: Los Alcornocales		KP6576 74*	KP65768 0*	MNCN/ADN 57480
<i>Thorectes valencianus</i> (Baraud, 1966)	Spain. Alicante: Sierra Carrasqueta	GU984632**	KP6576 64*	GU9845 84**	MNCN/ADN 58036
<i>Jekelius albarracinus</i> (Wagner, 1928)	Spain. Albacete: El Balletero	GU984604**	KP6576 65*	GU9845 92**	MNCN/ADN 57991
<i>Jekelius balearicus</i> López-Colón, 1985	Spain. Baleares: Mallorca	HM625867**	KP6576 66*	GU9845 80**	MNCN/ADN 58080
<i>Jekelius castillanus</i> López-Colón, 1985	Spain. Madrid: Loeches	GU984603**	KP6576 67*	GU9845 97**	MNCN/ADN 58001
<i>Jekelius catalonicus</i> López-Colón, 1991	Spain. Tarragona: Sierra de los Cortijos	GU984629**	KP6576 68*	GU9845 78**	MNCN/ADN 58006
<i>Jekelius hernandezi</i> López-Colón, 1988	Spain. Albacete: Bonete	GU984627**	KP6576 69*	GU9845 93**	MNCN/ADN 58008
<i>Jekelius hispanus</i> (Reitter, 1892)	Spain. Huelva: Doñana	GU984628**	KP6576 70*	GU9845 99**	MNCN/ADN 58007
<i>Jekelius nitidus</i> (Jekel, 1866)	Spain. Ávila: El Tiemblo	GU984626**	KP6576 71*	GU9845 83**	MNCN/ADN 58010
<i>Jekelius punctatolineatus</i> (François, 1904)	Spain. Alicante: Bussot	GU984625**	KP6576 72*	GU9845 82**	MNCN/ADN 58014
<i>Thorectes punctulatus</i> (Jekel, 1866)	Bulgaria: Ledenika cave		KP6576 75*	KP65768 1*	MNCN/ADN 57481
<i>Thorectes punctulatus</i> (Jekel, 1866)	Bulgaria: Ledenika cave		KP6576 76*	KP65768 2*	MNCN/ADN 57482
<i>Thorectes brullei</i> (Jekel, 1866)	Turkey: Kutahya		KP6576 77*	KP65768 3*	MNCN/ADN 57483
<i>Thorectes brullei</i> (Jekel, 1866)	Turkey: Kutahya		KP6576 78*	KP65768 4*	MNCN/ADN 57484
<i>Geotrupes ibericus</i> Baraud, 1958	Spain. Castellón: Villabona	GU984608**	KP6576 58*	GU9845 90**	MNCN/ADN 57984
<i>Trypocopris pyrenaicus</i> (Charpentier, 1825)	Spain. León: Puerto Ancares	GU984621**	KP6576 59*	GU9845 96**	MNCN/ADN 58038

Total DNA was extracted from frozen tissue with a DNA Easy extraction kit (Qiagen). COI-Sca-Frevc (5'-GCTAATCATCTAAAAATTTTAATTCC -3') (this study), HCO2198 (Folmer *et al.* 1994), C1-J-2183 (Simon *et al.* 1994), COI-Sca-R, COIIam-Sca, and COIIB-605-Sca (Villalba *et al.* 2002) were the primers used to amplify with PCR three overlapping fragments comprising the 3' end of mitochondrial cytochrome oxidase I (COI), the adjacent complete tRNA-Leu (UUR), and the 5' end of cytochrome oxidase II (COII) genes. Additionally, the primers Sca-nuc-F and Sca-nuc-R (Cunha *et al.* 2011) were used to amplify a 420 base pair fragment of the nuclear gene neurofibromin by polymerase chain reaction (PCR). A total of 40 PCR cycles (denaturing at 94 °C for 30 seconds, annealing at 40–42 °C for 30 seconds, and extension at 72 °C for 60 seconds) with an initial denaturing step at 94 °C for five minutes and a final extension step at 72 °C for five minutes were performed to amplify both mitochondrial and nuclear fragments. All PCR amplifications were conducted in 25 µL reactions containing 3 mM MgCl₂, a 0.4 mM of each dNTP, 0.2 µM of each primer, template DNA (10–100 ng), and DNA polymerase (one unit, Biotools). After, PCR purification samples were directly sequenced using the corresponding PCR primers. Samples were sequenced in an automated DNA sequencer (ABI PRISM 3700) using the Big-Dye Deoxy Terminator cycle-sequencing kit (Applied Biosystems) following the manufacturer's instructions. Sequences were deposited in GenBank under the accession numbers provided in Table 1.

DNA sequences were aligned with BioEdit v7.2.5 (Hall 1999) using the default options and further optimised manually. The partial nucleotide sequences of the mitochondrial COI, COII genes, and the complete sequence of the mt ARNtleu (UUR) gene were concatenated with the partial sequences of the neurofibromin nuclear gene into a single dataset of 2435 base pairs. The combined data set included 1700 constant and 540 parsimony-informative positions. The Akaike information criterion (AIC) and the Bayesian information criterion (BIC) as implemented in jModelTest v2.1.4 (Darriba *et al.* 2012) selected GTR + I + G (I = 0.584; G = 0.891) as the evolutionary model that best fit the data. The selected model and model parameters were used in the maximum likelihood (ML) analysis performed with PhyML v3.1 (Guindon *et al.* 2010). The robustness of the inferred trees was tested by nonparametric bootstrapping (BP) using 1000 pseudoreplicates. Bayesian inference was also performed with MrBayes v3.2.2 (Ronquist *et al.* 2012), running for 1×10^7 generations (four simultaneous Markov chains; sample frequency, 100). Four independent runs were performed. Eight data partitions were analysed: mitochondrial COI gene (first, second, and third codon positions), mitochondrial COII gene (first, second, and third codon positions), mitochondrial ARNtleu (uur) gene, and the nuclear neurofibromin gene. Model parameters were estimated independently for each one of the respective data partitions using the unlink command in MrBayes. Burn-in was set to the first 1 000 000 generations. The robustness of the inferred Bayesian trees was determined using Bayesian posterior probabilities (BPP; as obtained from majority-rule consensus trees of the post burn-in trees).

Distributional data

The distributional data of *T. punctulatus* was compiled following bibliographic sources as well as unpublished material collected by the authors (Table 2). All localities have been georeferenced using Google Maps (www.maps.google.com) and the Geonames geographical database (www.geonames.org). In total, 148 valid georeferenced localities were available (Table 2), which corresponded to 103 cells at an approximate resolution of 0.04° ($\approx 5 \times 5$ km) after eliminating redundant data belonging to the same cell.

One topographic variable (altitude) and eight climatic variables were considered: mean annual temperature (in °C), annual precipitation (in mm), minimum temperature of the coldest month, maximum temperature of the warmest month, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality (coefficient of variation of monthly values), and temperature seasonality (standard deviation of monthly values). The values of these variables have been calculated for each terrestrial cell (0.04° resolution) within the extent comprised between 15° and 29° longitude, and 38° and 46° latitude ($n = 45356$ terrestrial cells). Climatic data were obtained from WorldClim (version 1.3, www.worldclim.org; see Hijmans *et al.* 2005), and mean altitude was extracted from a digital elevation model (Clark-Labs 2000). The values of these variables in all the cells with observed occurrences were extracted to examine the range of environmental conditions at which the species has been observed. Subsequently, all the cells of the considered territory with environmental values similar to those existing within the range of observed occurrences (*i.e.*, within maximum and minimum values) were mapped to represent those areas with *a priori* favourable conditions for the species (potential distribution).

TABLE 2. List of the citations of *Jekelius* (*Reitterius*) *punctulatus* (Jekel, 1866) considering both bibliographic references (showed at the end) and public or private collections. The records in bold (column A) should be considered erroneous or doubtful. * *Nomen nudum*.

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Geotrupes</i> (<i>Thorectes</i>) <i>punctulatus</i>	Pazaric	Bosnia & Herzegovina	<= 1890	43.78	18.17	Apfelbeck (1890)
<i>Geotrupes</i> (<i>Thorectes</i>) <i>punctulatus</i>	Konjica [= Konjic]	Bosnia & Herzegovina	<= 1890	43.65	17.95	Apfelbeck (1890)
<i>Thorectes laevigatus</i>	Stara Planina Mt., Yurushka gramada above Kaloferski	Bulgaria	24/07/1898	42.73	24.97	Ioakimov (1904)
<i>Thorectes laevigatus</i>	Sofia	Bulgaria	5/06/1898	42.65	23.29	Ioakimov (1904)
<i>Thorectes punctulatus</i>	Stara Planina Mt., Kalofer	Bulgaria	6/07/1899	42.62	24.97	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>“Thorectes laevigator”</i> *	Rila Mt., Kirilova polyana place	Bulgaria	<= 1899	42.15	23.40	Ioakimov (1899)
<i>“Thorectes laevigator”</i> *	Rila Mt., Rila Monastery	Bulgaria	<= 1899	42.13	23.33	Ioakimov (1899)
<i>“Thorectes laevigator”</i> *	Rila Mt., "on the path between Dupnista town and Rila village"	Bulgaria	<= 1899	42.14	23.07	Ioakimov (1899)
<i>“Thorectes laevigator”</i> *	Rila Mt., Rila vill.	Bulgaria	<= 1899	42.13	23.13	Ioakimov (1899)
<i>Geotrupes punctulatus</i>	Rila Mountain	Bulgaria	<= 1900	42.23	23.77	Mikšic (1953)
<i>Thorectes punctulatus</i>	Makljen (= Maklen Pass)	Bosnia & Herzegovina	1902	43.85	17.59	private collection Oliver Hillert (Berlin, Germany)
<i>Thorectes laevigatus</i>	Sredna Gora	Bulgaria	<= 1909	42.59	24.52	Nedelkov (1909)
<i>Geotrupes punctulatus</i>	Vitosha Mt., Knyazhevo	Bulgaria	16/03/1909	42.65	23.24	Mikšic (1956)
<i>Thorectes punctulatus</i>	Rila Mt., Kostenets Bath	Bulgaria	30/05/1909	42.25	23.81	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Osogovo Mt. "Kyustendil"	Bulgaria	25/05/1910	42.26	22.68	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Rila Mt., Kostenets	Bulgaria	11/05/1912	42.25	23.81	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Sredna gora Mt., Pancharevo	Bulgaria	01/05/1913	42.22	23.42	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Kruma	Albania	05/06/1918	42.18	20.42	museum collections; Magyar Természettudományi Múzeum, Budapest, Hungary
<i>Thorectes punctulatus</i>	Rila Mt. Borovets resort	Bulgaria	15–25/08/1921	41.57	23.62	Guéorguiev & Bunalski (2004)

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Rila Mt., Ovnarsko Place	Bulgaria	17/05/1923	42.22	23.42	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Livno	Bosnia & Herzegovina	<= 1925	43.82	17.00	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Krug planina	Bosnia & Herzegovina	<= 1925	43.83	17.02	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Hrbljina	Bosnia & Herzegovina	<= 1925	43.93	16.85	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Kupreško polje	Bosnia & Herzegovina	<= 1925	44.07	17.23	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Olovo	Bosnia & Herzegovina	<= 1925	44.12	18.57	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Sarajevo	Bosnia & Herzegovina	<= 1925	43.83	18.33	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Vučja Luka nr. Sarajevo	Bosnia & Herzegovina	<= 1925	43.90	18.50	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Trebević planina	Bosnia & Herzegovina	<= 1925	43.82	18.47	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Reljevo	Bosnia & Herzegovina	<= 1925	43.88	18.30	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Ivan planina	Bosnia & Herzegovina	<= 1925	43.77	18.02	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Pazaric (Kijevo)	Bosnia & Herzegovina	<= 1925	43.78	18.17	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Zelengora planina	Bosnia & Herzegovina	<= 1925	43.23	17.47	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Konjić	Bosnia & Herzegovina	<= 1925	43.65	17.95	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Nevesinje	Bosnia & Herzegovina	<= 1925	43.25	18.10	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Gacko	Bosnia & Herzegovina	<= 1925	43.17	18.53	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Baba planina	Bosnia & Herzegovina	<= 1925	43.65	18.93	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Osogovo Mt. Kamenets (=Tash-Tepe) Peak, the state border	Bulgaria	21/04/1926	42.17	22.51	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Rila Mt., Kostenets	Bulgaria	02/05/1926	42.25	23.81	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Stara Planina Mt., Jumrukcal [= Botev Peak]	Bulgaria	--/07/1928–1929	42.70	24.92	museum collections; Magyar Természettudományi Múzeum, Budapest, Hungary

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes laevigatus</i>	Rila Mt., alpin zone	Bulgaria	1929	41.94	23.36	Tesař (1935)
<i>Geotrupes punctulatus</i>	Dumitor Massif	Montenegro	<= 1932	43.10	19.02	Roubal (1932)
<i>Thorectes punctulatus</i>	Rila, Chamkoriya [= resort Borovets]	Bulgaria	--/06/1933	42.26	23.60	museum collections, National Museum Prague, Czech Republic
<i>Geotrupes punctulatus</i>	Rila Mt., Kostenets town	Bulgaria	<= 1935	42.07	23.86	Tesař (1935)
<i>Thorectes punctulatus</i>	Prokletje Mts., Gusinje	Montenegro	20/06/1937	42.55	19.83	museum collections, National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vodno	Macedonia	06/06/1937	41.82	21.38	museum collections, Magyar Természettudományi Múzeum, Budapest, Hungary
<i>Thorectes punctulatus</i>	Golo Bardo Mt.	Bulgaria	28/04/1937	42.14	23.07	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Golo Bardo Mt.	Bulgaria	11/05/1938	42.56	23.03	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Lyulin Mt.	Bulgaria	07/05/1939	42.68	23.11	Guéorguiev & Bunalski (2004)
<i>Geotrupes punctulatus</i>	Koprivnik Mt	Kosovo	<= 1940	42.65	20.23	Csiki (1940)
<i>Thorectes punctulatus</i>	Sredna Gora Mt., Buzovgrad vill.	Bulgaria	27/04/1948	42.57	25.37	museum collections, National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Igman planina - Gornja Grkarica	Bosnia & Herzegovina	14/06/1949	43.72	18.30	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Central Stara Planina Mt., Zhaltets Peak (=Sara-Kaya)	Bulgaria	05/08/1949	42.71	24.86	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., Dragalerski Monastery	Bulgaria	08/05/1949	23.30	23.30	museum collections, National Museum of Natural History Sofia, Bulgaria
<i>Geotrupes punctulatus</i>	Treskavitsa Mt.	Bosnia & Herzegovina	24/05–08/1951	43.60	18.32	Mikšić (1956)
<i>Thorectes punctulatus</i>	Vlašić planina	Bosnia & Herzegovina	01/05/1951	44.30	17.67	Mikšić (1953), Lelo (2006)
<i>Thorectes punctulatus</i>	Stara Planina Mt., Botev Peak env.	Bulgaria	28/05/1951	42.70	24.93	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha, road above Knyazhevo	Bulgaria	06/05/1951	42.64	23.24	museum collections, National Museum of Natural History Sofia, Bulgaria
<i>Geotrupes punctulatus</i>	"Kopaonik Mt." [?] = Rogozna Mt. J. Šanac	Serbia	20/05/1953	43.07	20.61	Mikšić (1956)
<i>Geotrupes punctulatus</i>	Stara Planina Mt. "Etropol Balkan" Mt.	Bulgaria	<= 1953	42.81	24.05	Mikšić (1953)

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Vitosha Mt., BAS holiday station	Bulgaria	13/05/1953	42.61	23.24	Guéorguiev & Bunalski (2004)
<i>Geotrupes punctulatus</i>	Perućica	Bosnia & Herzegovina	--/06/1956	43.83	17.02	Mikšić (1956)
<i>Thorectes punctulatus</i>	Stara Planina Mt., Karlovo – Kalofer	Bulgaria	11/06/1956	42.62	24.93	museum collections; Magyar Természettudományi Múzeum, Budapest, Hungary
<i>Thorectes punctulatus</i>	Vitosha Mt., Vladaia vill., "at the river"	Bulgaria	08/07/1956	42.63	23.21	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Geotrupes punctulatus</i>	Kopaonik Mt., Glog	Serbia	--/05–06/1957	43.27	20.75	Miksic (1956)
<i>Thorectes punctulatus</i>	Stara Planina Mt., near Sofia	Bulgaria	24/04/1957	42.55	23.42	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Vitosha Mt., Kiselishte Pl. above Vladaia vill	Bulgaria	13/07/1957	42.63	23.23	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Vitosha Mt., Cherni Vrah	Bulgaria	22/05/1959	42.55	23.25	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., Cherni Vrah	Bulgaria	04/09/1959	42.13	23.33	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Rila Mt., Rila Monastery	Bulgaria	10/07/1959	42.13	23.33	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., Zlatnite mostove Pl	Bulgaria	27/06/1960	42.61	23.24	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Sredna Gora Mt., Oborishte Place near Panagyurishte	Bulgaria	24/05/1961	42.53	24.12	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., Cherni Vrah	Bulgaria	29/04/1962	42.54	23.24	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt.	Bulgaria	12/06/1963	42.62	23.27	Král & Malý (1993)
<i>Thorectes punctulatus</i>	Vitosha Mt., Zlatnite mostove Pl - Kumata Hut	Bulgaria	21/07/1965	42.60	23.24	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Geotrupes punctulatus</i>	Stara Planina Mt., Levski Hut	Bulgaria	<= 1965	42.70	24.85	Angelov (1965)
<i>Geotrupes punctulatus</i>	Vitosha Mt., "below Aleko Hut"	Bulgaria	<= 1965	42.59	23.31	Angelov (1965)
<i>Geotrupes punctulatus</i>	Rodopi Mt., Yundola	Bulgaria	<= 1965	42.07	23.86	Angelov (1965)
<i>Geotrupes (Thorectes) levigatus</i>	Stara Planina Mt., Chuprene Vill. near Vratsa	Bulgaria	08/07/1966	42.26	22.68	Zacharieva-Stoilova (1969)
<i>Geotrupes (Thorectes) intermedius</i>	Stara Planina Mt., Parshevitza Hut near Vratsa	Bulgaria	24/06/1966	43.15	23.47	Zacharieva-Stoilova (1969)

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Vitosha Mt. Simeonovo, Bunkera Pl.	Bulgaria	10/06/1966	42.04	23.38	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Pirin Mt., Vihren Hut	Bulgaria	20/07/1972	41.79	23.43	Král & Malý (1993)
<i>Thorectes punctulatus</i>	Rila Mt., Rila Monastery	Bulgaria	01/07/1976	42.13	23.33	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Bjelasica Mt., Kolašin env	Montenegro	--/06/1978	42.85	19.47	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Bjelašnica Mt., Mojkovac	Montenegro	16/06/1980	42.95	19.52	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Pirin Mt. above Dobrinishte	Bulgaria	23/07/1980	41.76	23.54	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., Kopitoto	Bulgaria	19–24/06/1986	42.63	23.24	Král & Malý (1993)
<i>Thorectes punctulatus</i>	Stara Planina Mt., reserve Dzendema, south of Botev Peak	Bulgaria	22/06/1989	42.69	24.91	museum collections; National Museum Prague, Czech Republic & Deutsches Entomologisches Institut,
<i>Thorectes punctulatus</i>	Golo Bardo Mt.	Bulgaria	21/05/1993	42.56	23.05	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Stara Planina Mt. Vrachanska pl., Ledenika	Bulgaria	26–28/05/1996	43.20	23.48	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Pirin Mt., Orelek peak	Bulgaria	--/06–08/1996– 1998	41.28	23.68	Bunalski (2000)
<i>Thorectes punctulatus</i>	Stara Planina, Vrachanska Mt., Chernite kamani Locality	Bulgaria	10/06/1997	43.21	23.48	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Stara Planina Mt., Troyanska Planina, south Troyan Town	Bulgaria	23/06/1997	42.84	24.71	private collection Ekehard Roßner (Schwerin, Germany)
<i>Thorectes punctulatus</i>	Skopska Crna Gora, Mon. Sv. Jovan.	Macedonia	27/06/1998	42.11	21.45	Rozner & Rozner (2009)
<i>Thorectes punctulatus</i>	Skopska Crna Gora.	Macedonia	28/05/1998	42.13	21.50	Rozner & Rozner (2009)
<i>Thorectes punctulatus</i>	Rila Mt., Krilova poyana	Bulgaria	11/06/1998	42.16	23.40	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vitosha Mt., Kopitoto env.	Bulgaria	03/06/1999	42.64	23.24	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Plana Mt., above the "St. Archangel Michail" Monastery	Bulgaria	19/05/2000	41.79	23.43	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Zemenska Mt.	Bulgaria	14/05/2000	42.48	22.72	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" prophylactic hotel	Bulgaria	27/05/2000	42.18	22.62	private collection Yana Petrova (Sofia, Bulgaria)

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Bjelasica Mts., Biogradska gora NP, ca. 9 km SE of Mojkovac,	Montenegro	--/09/2001	42.90	19.63	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vitosha Mt., Momina skala-Ofeliste	Bulgaria	08/07/2002	42.62	23.25	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Durmitor Mt., Zupej	Montenegro	10/06/2003	43.10	19.13	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vitosha Mt., "Ivanov's path"	Bulgaria	01/07/2003	41.77	23.36	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Maleshevska Mt., W of Gorna Breznitsa vill	Bulgaria	--/05-07/2003	41.75	23.04	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Maleshevska Mt., on the state border between Bulgaria and	Bulgaria	03/07/2003	41.75	23.02	Guéorguiev & Bunalski (2004)
<i>Thorectes punctulatus</i>	Vitosha Mt., above Knyazhevo	Bulgaria	22/04/2004	42.65	23.24	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Vitosha, above Zheleznitisa Vill.	Bulgaria	03-05/06/2005	42.54	23.34	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Vitosha, above Zheleznitisa Vill.	Bulgaria	1-3/08/2005	42.13	23.33	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Rila Mt., near Parangalitsa Reserve	Bulgaria	10/07/2005	42.04	23.38	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Rila Mt., near Parangalitsa Reserve	Bulgaria	11/07/2005	41.94	23.36	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Vitosha, above Zheleznitisa Vill.	Bulgaria	27-29/06/2006	42.54	23.34	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Stara Planina Mt., Ledenika Hut	Bulgaria	19/06/2007	42.59	23.50	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Vitosha, above Zheleznitisa Vill.	Bulgaria	14-16/05/2007	42.54	23.34	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Ledenika cava	Bulgaria	21/06/2007	43.20	23.49	museum collections; National Museum of Natural History Madrid, Spain
<i>Thorectes punctulatus</i>	Rila Mt., near Parangalitsa Reserve	Bulgaria	24/06/2007	42.04	23.36	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Osoгово Mt., Choveka Peak - Tri buki Hut	Bulgaria	17/05/2008	42.18	22.59	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Valbonë	Albania	06/06/2009	42.45	19.88	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Çerem	Albania	07/06/2009	42.48	19.95	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Lozenska Planina Mt., the road to monastery "St. Spas"	Bulgaria	16/07/2010	41.76	23.54	private collection Yana Petrova (Sofia, Bulgaria)

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Stara Planina Mt., near Belediehan Village	Bulgaria	15/10/2011	42.89	23.16	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Sokobanja, hills around city	Serbia	8-10/06/2014	43.63	21.88	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Lozenska Planina Mt. Germanski monastery	Bulgaria	15/06/2014	42.60	23.44	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Lozenska Planina Mt., above Dohi Lozen vill.	Bulgaria	27/06/2014	42.59	23.50	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Erma Riv. Gorge, at the first tunnel	Bulgaria	20/05/2014	42.86	22.65	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Erma Riv. Gorge at the second tunnel	Bulgaria	20/05/2014	42.87	22.66	private collection Yana Petrova (Sofia, Bulgaria)
<i>Thorectes punctulatus</i>	Vitosha, above Zhelezitsa Vill.	Bulgaria	08/07/2014	42.54	23.34	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	27/07/2014	42.17	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	28/07/2014	42.17	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	27/07/2014	42.17	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	26/07/2014	42.17	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	30/07/2014	42.17	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	29/07/2014	42.18	22.63	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., around "Tri buki" phililactic hotel	Bulgaria	28/07/2014	42.18	22.62	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Osogovska planina Mt., 0.4 km N "Tri buki" Chalet	Bulgaria	8-9/07/2014	42.18	22.62	museum collections; Biological Faculty of Sofia University, Bulgaria
<i>Thorectes punctulatus</i>	Rila Mt., above Bistrisa vill.	Bulgaria	15/07/2014	42.03	23.27	museum collections; Institute of Biodiversity and Ecosystem Research, Bulgaria
<i>Thorectes punctulatus</i>	Bosnek Village, pitfall traps in Zhivata Voda Cave	Bulgaria	22/06/2014	42.53	23.20	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	Jahorina Mt., Pale near Saraevo	Bosnia & Herzegovina	?	43.72	18.58	http://www.entomologistitaliani.net/public/forum/phpBB3/viewtopic.php?f=166&t=28051
<i>Thorectes punctulatus</i>	Tisovica	Bosnia & Herzegovina	?	44.18	18.62	museum collections; Magyar Természettudományi Múzeum, Budapest, Hungary
<i>Thorectes punctulatus</i>	Nevesinje	Bosnia & Herzegovina	?	43.25	18.10	museum collections; National Museum Prague, Czech Republic

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TABLE 2. (Continued)

Species name (as they were published)	Location	Country	Date	Latitude	Longitude	Source data
<i>Thorectes punctulatus</i>	Sarajevo	Bosnia & Herzegovina	?	43.83	18.33	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Tmova	Bosnia & Herzegovina	?	44.61	16.54	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vareš	Bosnia & Herzegovina	?	44.15	18.32	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Reljevo near Sarajevo	Bosnia & Herzegovina	?	43.89	18.31	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Stara Planina Mt., "Kalofer Balkan", above Kalofer Town	Bulgaria	?	42.68	24.95	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vitosha Mt., Dragalevtsi Vill.	Bulgaria	?	42.62	23.31	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Bišina	Bosnia & Herzegovina	?	44.19	19.12	private collection Wolfgang Ziegler, Rundeshausen, Germany
<i>Thorectes punctulatus</i>	Pirin Mt, Cherna voda	Bulgaria	?	41.77	23.36	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Vrontous Mt.	Greece	?	41.28	23.68	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Herceg Novi	Montenegro	?	42.47	18.55	museum collections; National Museum Prague, Czech Republic
<i>Thorectes punctulatus</i>	Kapaonik	Serbia	?	43.28	20.78	museum collections; Magyar Természettudományi Múzeum, Budapest, Hungary
<i>Geotrupes (Thorectes) punctulatus</i>	Sernéc	Bosnia & Herzegovina	<= 1890	?	?	Apfelbeck (1890)
<i>Geotrupes laevigatus</i>	Razgrad	Bulgaria	<= 1909	43.53	26.52	Markovich (1909)
<i>Thorectes punctulatus</i>	Kresna Gorge	Bulgaria	--/06/1935	41.76	23.15	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Thorectes punctulatus</i>	South Black Sea Coast, Tsarevo	Bulgaria	29/07/1935	42.16	27.82	museum collections; National Museum of Natural History Sofia, Bulgaria
<i>Geotrupes punctulatus</i>	Varna	Bulgaria	1892	43.24	27.91	Mikšić (1953)
<i>Thorectes punctulatus</i>	Bilina	Bosnia & Herzegovina	?	?	?	private collection Oliver Hillert (Berlin, Germany)

Results

The reconstructed ML ($-\ln L = 11884.25$) and Bayesian ($-\ln L = 11071.78$) phylogenies (Fig. 2) support that *Thorectes*, *Silphotrupes*, and *Jekelius* can be considered independent and monophyletic lineages with very strong bootstrap and posterior probability support. Furthermore, and notably, the two species considered in this study are included within the *Jekelius* branch, also with high support. *T. brullei anatolicus* is basal to the Ibero-Balearic *Jekelius* species, and *T. punctulatus* is in the root of all considered *Jekelius* species, thus supporting the subgeneric status of both species (Fig. 2). The percentage of genetic divergence between *Thorectes* and *Jekelius* species is between 16.4% and 23.4%. Within *Thorectes*, the intraclade genetic divergence among species varies from 8.4% to 20.6%. Concerning *Jekelius* species, this genetic divergence is between 0.8% (*J. hispanus* (Reitter, 1892)—*J. nitidus* (Jekel, 1866)) and 17.0%. Both the basal position of *Jekelius* (*Reitterius*) *punctulatus* and its relatively high genetic divergence from all the other considered *Jekelius* species (from 12.4% to 17.0%) support its adscription to the subgenus *Reitterius* López-Colón, 1996.

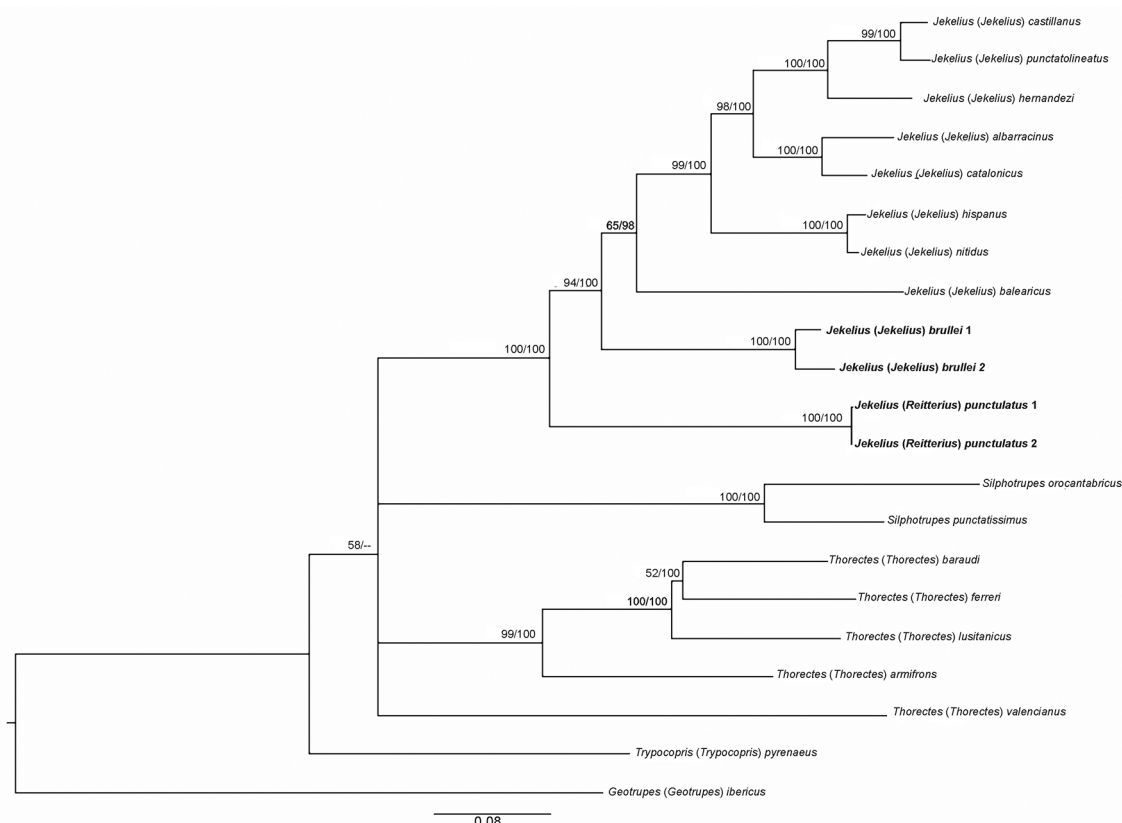


FIGURE 2. Phylogenetic relationships of the considered species based on maximum likelihood (ML) and Bayesian inference analysis (both procedures generate similar trees) using mitochondrial (COI, COII, tRNA-Leu) and nuclear (neurofibromin) genes and the GTR + I + G evolutionary model. Numbers at nodes correspond to ML bootstrap proportions (first number) and Bayesian posterior probabilities (second number). The specimens of the two east European species are in bold. Nomenclature as proposed by López-Colón (1996).

The potential distribution area of *Jekelius* (*Reitterius*) *punctulatus* (Fig. 3) according to the selected topoclimatic variables shows that it is possible to find suitable conditions across Balkan montane areas, from the Dinaric Alps to the Rhodope Mountains. The mean altitude of the observed occurrences is approximately 1150 m, being collected in areas with precipitation throughout the year and monthly minimum temperatures below zero (Table 3). This potential distribution includes all countries in which the species has been previously observed (Bosnia and Herzegovina, Montenegro, Albania, Kosovo, Republic of Macedonia, Serbia, and Bulgaria; see Löbl *et al.* 2006) and also some small areas of southern Romania, Croatia, and northern Greece.

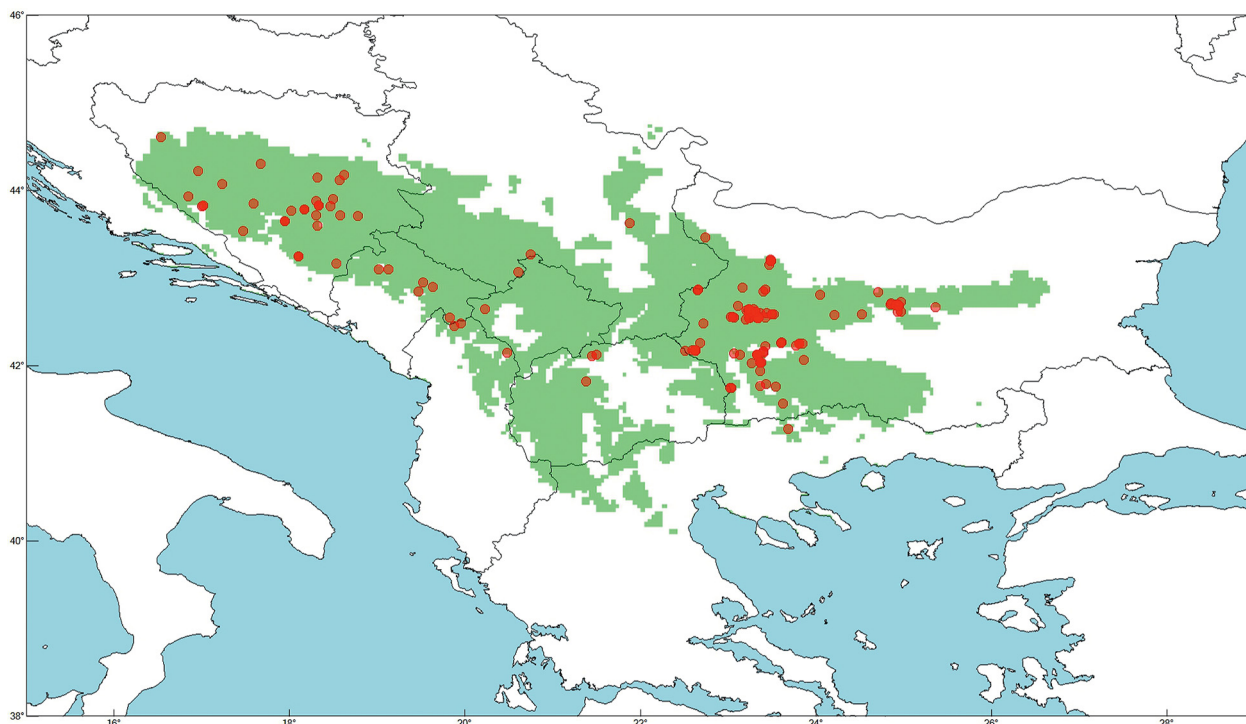


FIGURE 3. Distribution of *Jekelius (Reitterius) punctulatus* (Jekel, 1866) (see Table 2). The green area represents localities with suitable climatic conditions within the extreme values observed for the eight considered climatic variables in the analysis of occurrence localities (Table 3).

TABLE 3. Means and ranges of the considered environmental variables in the 0.04° cells in which *Jekelius (Reitterius) punctulatus* (Jekel, 1866) has been observed.

	Altitude	Precipitation seasonality	Temperature seasonality	Mean annual temperature	Maximum temperature of the warmest month	Minimum temperature of the coldest month	Mean annual precipitation	Precipitation of the wettest month	Precipitation of the driest month
mean	1142	20	67.8	6.8	21.9	-6.4	814	94	49
maximum	1913	29	76.8	11.3	27.8	-2.1	1228	151	85
minimum	529	11	60.8	1.5	15.3	-10.4	511	60	29
lower quartile	851	18	64.6	5.5	19.9	.7.5	635	75	36
upper quartile	1398	23	70.1	8.6	24.1	-5.3	1043	112	68

Discussion

Our results are consistent with previous findings (see Cunha *et al.* 2011) clearly supporting the splitting of the former genus *Thorectes* sensu lato as recommended by López-Colón (1996), at least for the genera *Thorectes*, *Silphotrupes*, and *Jekelius* as well as the subgenera *Jekelius* and *Reitterius*. Considering the deep divergence and the strongly supported monophyly of these genera shown by the molecular analyses (Cunha *et al.* 2011), we consider that this taxonomic hypothesis should be considered those more accurately reflect the common ancestry of these species. Of course, we are aware of the opposing systematic and nomenclatural treatments proposed by López-Colón (1989, 1996) and Branco & Ziani (2007), originating in the acceptance of different type species for *Thorectes* and the different ranking of the divisions of the former *Thorectes* sensu lato. In a recently submitted application for the International Commission on Zoological Nomenclature (Case 3699) we address this issue (Alonso-Zarazaga *et al.* submitted). Thus, according to the spirit of Art. 82.1 (maintenance of prevailing usage) of the International Code of Zoological Nomenclature, we advocate in this application that the taxonomic proposal found in López Colón (1989, 1996) should be maintained by their usage in recently published paper as those Verdú & Galante (2004), Lobo *et al.* (2006), Pérez-Ramos *et al.* (2007), Verdú *et al.* (2010), or Cunha *et al.* (2011).

Apart from the taxonomic and conservation implications derived from the existence of more narrowly distributed species with a higher taxonomic rank, the results also shed some light on the probable origin of *Jekelius*. The basal phylogenetic placement of *Jekelius* (*Jekelius*) *balearicus* (López-Colón 1984) concerning the other Iberian *Jekelius* species, in addition to *Jekelius* (*Jekelius*) *brullei anatolicus* and *Jekelius* (*Reitterius*) *punctulatus* appearing in even more basal positions, suggests an oriental origin for this genus within the western Palaearctic region. The dates of major lineage-splitting (Cunha *et al.* 2011) advocate that the three main genera (*Thorectes*, *Jekelius*, and *Silphotrupes*) would have arisen under the isolated conditions experienced by current European areas during the Cretaceous-Tertiary boundary. According to our results, *Jekelius* would be a monophyletic lineage that could have an eastern origin because both *J. punctulatus* and *J. brullei anatolicus* show a basal branching/rooting within the *Jekelius* tree (Fig. 2), and the two have current distributional ranges in southeast Europe and the eastern Mediterranean region.

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