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Diversity of benthic marine mollusks of the Strait of Magellan, Chile (Polyplacophora, Gastropoda, Bivalvia): a historical review of natural history

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Abstract

An increase in richness of benthic marine mollusks towards high latitudes has been described on the Pacific coast of Chile in recent decades. This considerable increase in diversity occurs specifically at the beginning of the Magellanic Biogeographic Province. Within this province lies the Strait of Magellan, considered the most important channel because it connects the South Pacific and Atlantic Oceans. These characteristics make it an interesting area for marine research; thus, the Strait of Magellan has historically been the area with the greatest research effort within the province. However, despite efforts there is no comprehensive and updated list of the diversity of mollusks within the Strait of Magellan up to now. This study consisted of a complete bibliographic review of all available literature that included samples of mollusks in the Strait of Magellan. More than 300 articles were reviewed, covering 200 years of scientific knowledge. There were 2579 records belonging to 412 taxa, of which 347 are valid species. Of the total valid species, 44 (~13%) are considered of doubtful presence in the Strait. This work increases the known richness of mollusks of the Strait of Magellan by 228%; it is also the first report that integrates all available diversity studies of the three most speciose classes of benthic mollusks (Gastropoda, Bivalvia and Polyplacophora) from the Strait of Magellan.

Keywords
benthos, Magellanic Biogeographic Province, Mollusca, South Atlantic, South Pacific, species richness

Introduction

It has been described that mollusks show an increase in diversity towards high latitudes in the Chilean southeastern Pacific coast (Valdovinos et al. 2003). This increase in mollusk richness occurs around 42°S, coinciding with the beginning of the Magellanic Biogeographic Province (Spalding et al. 2007). The Magellanic Province has been the focus of study of several scientific expeditions that contributed to the knowledge of marine mollusks. The first reports were made by King and Broderip (1832), d'Orbigny (1835–1846) and Philippi (1845). Other reports that contributed considerably to the knowledge of mollusks of the Magellanic Province were Smith (1881), Rochebrune and Mabille (1889), Strebel (1904, 1905a, b, 1906, 1907, 1908), Odhner (1926), Marcus (1959) and Soot-Ryen (1959). Carcelles and Williamson (1951) published the first checklist of species of marine mollusks of the Magellanic Province in the 1950s, defining the province from around 37°S in the Pacific coast and 43°S in the Atlantic coast, to 56°S. In their checklist 614 species were reported. Many taxonomic revisions of specific groups have been published (e.g., McLean 1984a; Castellanos 1988; Castellanos and Landoni 1988, 1989, 1990, Castellanos 1990, 1992a, b; Castellanos and Landoni 1993a, b; Castellanos et al. 1993; Ponder and Worsfold 1994; Schrödl 1996), therefore the checklist of Carcelles and Williamson (1951) had to be updated, for species synonyms and newly found species. Linse (1999) presented a new checklist of mollusks of the Magellanic Province, defining the province from around 41°S in the Pacific and Atlantic coasts to 56°S. However, the classes Polyplacophora and Cephalopoda were excluded from this checklist, which included 397 species of mollusks.

One of the most important channels in the Magellanic Province is the Strait of Magellan, where most historical reports of mollusks are focused. This extensive channel connects the Pacific and Atlantic Oceans and is considered the most important one of the province. It is influenced by water masses of the Pacific, Atlantic and Southern Oceans, and it possess several geological characteristics derived from the last glaciation (Antezana 1999). For these reasons the Strait of Magellan offers unique characteristics for the study of biodiversity and related aspects of the biogeography of mollusks (Linse et al. 2006). Linse et al. (2006) presented the only report of mollusk richness in the Strait of Magellan, which contains 116 species. However, a list of species is not provided and only the classes Gastropoda and Bivalvia are included. Between the year 2000 and the present there have been several studies that have provided more information about the diversity of mollusks in the Strait of Magellan (e.g., Ríos et al. 2003; Ríos et al. 2005; Ríos et al. 2007; Thatje and Brown 2009; Aldea et al. 2011; Rosenfeld et al. 2013; Rosenfeld et al. 2015), presenting new records of species. Several taxonomic revisions of specific groups have been published in recent years, where erroneous records, changes in nomenclature, synonymized species and descriptions of new species have been made (e.g., Sirenko 2006a; Zelaya and Geiger 2007; Aranzamendi et al. 2009; Zelaya 2009; González-Wevar et al. 2011; Güller et al. 2016; Pastorino 2016; Güller and Zelaya 2017; Korshunova et al. 2017). In order to have a comprehensive list of species in the most important channel of the Magellanic Province it is necessary to provide an updated list of records of the malacofauna of the Strait of Magellan. The objective of this study is to provide the first list of species of benthic marine mollusks of the three most speciose and best documented classes (Polyplacophora, Gastropoda, Bivalvia) of the Strait of Magellan, integrating all studies throughout history.

Materials and methods

To make the list of mollusks as complete as possible, information was gathered from all the available scientific publications that have sampled or reviewed benthic marine mollusks in the Magellanic Province, from the expedition of the HMS Beagle in the 19th century (King and Broderip 1832) to the present. A total of 323 articles were reviewed, of which 146 contained species within the Magellanic Province. The records and their respective geographical positions were entered into a spreadsheet structured with the Darwin Core Standard (Wieczorek et al. 2012), adjusted taxonomically according to the MolluscaBase (2019) and the revisions of classification and systematics of gastropods (Bouchet et al. 2017), bivalves (Nevesskaja 2009) and polyplacophorans (Sirenko 2006b). The Strait of Magellan was divided into 420 quadrants of 6×6 minutes of latitude and longitude. The records located within this area were analyzed (Fig. 1), taking into account their georeference or approximate location. This analysis was developed using tools for Google Earth (http://www.earthpoint.us), which transforms XLS extension files (Excel format) to KML (files that contains geographic data). In total, 108 articles provided records for the Strait of Magellan.

Dubious records were counted as were species that were recorded only once in history. Criteria were followed to determine doubtful species records, as follows: species that were cited once and later questioned in taxonomic revisions or never reported again; species that greatly exceed their distribution limit and do not appear in taxonomic revisions or alpha diversity studies; and species that have a huge geographical discontinuity and are not explained or figured in the article.

A new matrix was elaborated with the Darwin Core standard from the database, with presence-absence data of each taxon per quadrant entered as 1 or 0, respectively. The quadrants with no species were removed from the matrix and species/taxa considered doubtful and/or with imprecise locations were not included in the matrix. However, the above cases were considered in the quantification of total richness. On the other hand, the records up to or above genus level (registered as “indet.” or “sp.”) were not considered as valid species for both species richness values and estimation models, except for those in which the author commented that it could be a new species.

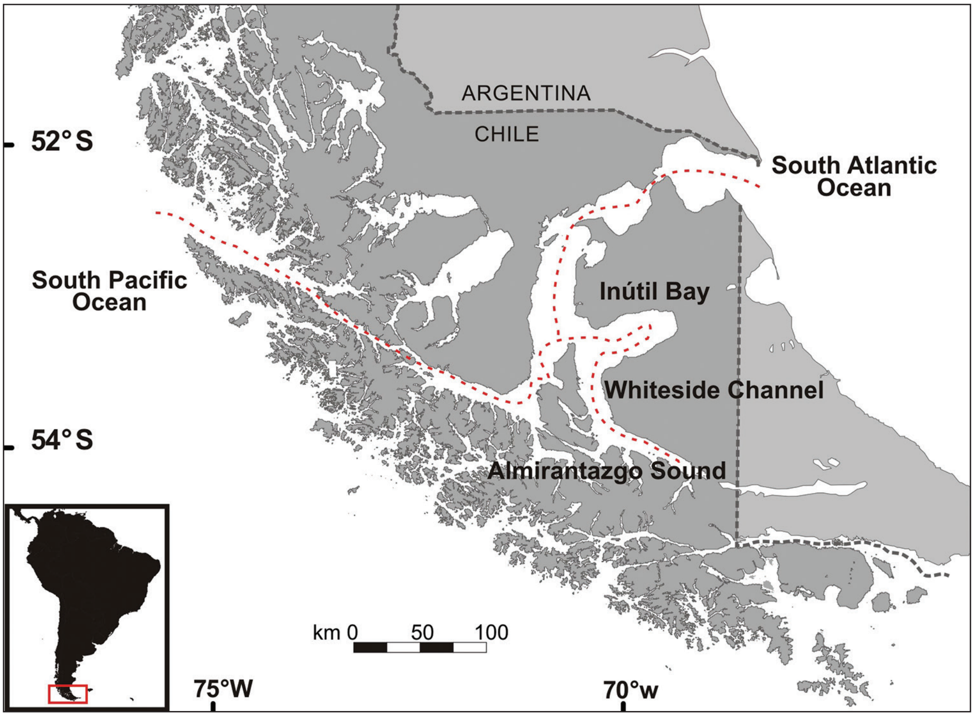

Figure 1. Study area. Location of the Strait of Magellan (marked by the red line), including Inútil Bay, Whiteside Channel and Almirantazgo Sound.

Finally, to detect whether the historial sampling effort was able to estimate all the species of mollusks in the Strait of Magellan, the non-parametric species accumulation models Chao 2 and Jacknife 1 (Burnham and Overton 1978; Burnham and Overton 1979; Chao 1987; Colwell and Coddington 1994) were used to evaluate the sampling effort spatially and estimate the number of species expected theoretically in the Strait of Magellan. These methods require only presence-absence data; Chao 2 is calculated with the species that occur in only one sample (single or singleton species) and those that occur exactly in two samples (doubletons). Jacknife 1 is a more accurate and less biased estimator, since it only uses the number of singletons and the number of samples (Moreno 2001). Complementarily, parametric accumulation models were used to detect whether the historical sampling effort was able to estimate the total species of mollusks (Soberón and Llorente 1993); the linear dependence and Clench models were used. All samples were randomized so as not to affect the shape of the curve (Colwell and Coddington 1994; Moreno and Halffter 2000). The estimation of the coefficients of each nonlinear regression model was done using the Simplex and Quasi-Newton estimation methods of the statistical package STATISTICA 7. For all models, species with imprecise locations were not included.

Results

A total of 134 articles summarizing two centuries of study were entered in the spreadsheet, representing 2579 records corresponding to 412 taxa distributed in the three classes studied (Table 1, Appendix I). Of the total taxa, 65 were reported up to or above genus level (i.e., "indet." or "sp."), finding no evidence that they may correspond to new species. On the other hand, 44 species were considered doubtful. Of the total 303 validated species with effective distribution in the Strait of Magellan (Fig. 2), 57.1% belong to the class Gastropoda (173 species); 24.1% of these correspond to the most diverse families: Buccinidae, Muricidae, Calliostomatidae, Fissurellidae, Eatoniellidae, Nassariidae, Rissoidae and Naticidae. The family Buccinidae was the most diverse in the class, with 15 species. The class Bivalvia was represented by 35.3% of the species (107 in total); 17.5% of these correspond to the most diverse families: Mytilidae, Philobryidae, Lasaeidae, Mactridae, Veneridae, Cyamiidae, Neoleptonidae, Nuculidae and Thyasiridae. The remaining 7.6% correspond to the class Polyplacophora (23 species). The family Chitonidae was the most diverse, with 2.0% of the species. In total, 106 families were recorded.

There has been a constant increase since the decade of the 1980s in the number of studies (Fig. 3a) and records (Fig. 3b). The largest number of records in history were incorporated for the Strait of Magellan in the last decade (2007–2018) (Fig. 3b).

Of the 420 quadrants proposed, 163 presented species (Fig. 4, Appendix II). Ordering the matrix of absence and presence of species according to these quadrants, 1229 mollusk records were counted. The eastern microbasin had 35 quadrants with records, while the central microbasin had 104. The western microbasin proved to be the least historically sampled, with only 24 quadrants with records. The total richness of the Strait of Magellan was 303 species. However, 47 species had imprecise locations, as they were described as inhabitants of the Strait of Magellan, but the site of their habitat was not defined with geographical accuracy. These species include three polyplacophorans (*Leptochiton* sp., *Notoplax magellanica* and *Hemiarthrum setulosum*), 25 gastropods (*Fissurella nigra*, *Anatoma euglypta*, *Scissurella petermannensis*, *Diloma nigerrimum*, *Prisogaster niger*, *Capulus compressus*, *Hydrobia antarctica*, *Crucibulum quiriquinae*, *Buccinanops cochlidium*, *Savatieria frigida*, *Concholepas concholepas*, *Tromina dispectata*, *Xymenopsis subnodosus*, *Mangelia martensi*, *Mathilda malvinarum*, *Atomiscala xenophyes*, *Doris fontainii*, *Gargamella immaculata*, *Diaulula punctuolata*, *Geitodoris patagonica*, *Thecacera darwini*, *Tyrinna delicata*, *Ancula fuegiensis*, *Tritonia vorax* and *Eubranchus fuegiensis*) and 19 Bivalvia (*Solemya notialis*, *Solemya occidentalis*, *Malletia chilensis*, *Modiolus patagonicus*, *Mytilus galloprovincialis*, *Barbatia platei*, *Limopsis perieri*, *Philobrya antarctica*, *Aequipecten tehuelchus*, *Cardium parvulum*, *Macoploma inornata*, *Lasaea petitiana*, *Mulinia levicardo*, *Diplodonta patagonica*, *Proteopitar patagonicus*, *Netastoma darwinii*, *Entodesma cuneata*, *Entodesma solemyalis* and *Luzonia chilensis*).

The quadrants that had species records cover ~37% of the total area of the Strait of Magellan; most of the studies are concentrated in the central microbasin. The quad-

Table 1. Species checklist of benthic marine mollusks of the Strait of Magellan (Polyplacophora, Gastropoda and Bivalvia). Those species with a single record are marked with an asterisk (*) and those which are dubious with a square (▪). Their presence is indicated (+) in the eastern (E), central (C) and western (W) microbasins. References provided at the end of the list.

Taxa	Reference	E	C	W
Class Polyplacophora				
Polyplacophora indet.	ab, as, bo, cp		+	
Order Lepidopleurida				
Leptochitonidae				
Leptochitonidae indet.	f		+	
Leptochiton sp.	cc			
Leptochiton kerguelensis Haddon, 1886	t, cd, bm, b, cq, as	+	+	+
Leptochiton laurae Schwabe & Sellanes, 2010	cd		+	+
Leptochiton linseae Sirenko, 2015	cd		+	
Leptochiton medinae (Plate, 1899)	as, cd, cq, bm, h	+	+	+
Leptochiton smirnovi▪ Sirenko, 2016	as		+	
Lepidopleurus cullierti▪ Rochebrune, 1899	as, bm	+	+	
Order Chitonida				
Ischnochitonidae				
Ischnochiton sp.*	e		+	
Ischnochiton punctulatissimus (Sowerby I, 1832)	b		+	+
Ischnochiton pusio (Sowerby I, 1832)	b, cq, br		+	+
Ischnochiton stramineus (G. B. Sowerby I, 1832)	p, cq, cc, b, t, bv, am, ej	+	+	+
Ischnochiton striolatus▪ (Gray, 1828)	br			
Stenosemus exaratus (Sars G. O., 1878)	cq		+	
Chaetopleuridae				
Chaetopleura angulata▪ (Spengler, 1797)	br			
Chaetopleura isabellei▪ (d'Orbigny, 1841)	br			
Chaetopleura peruviana▪ (Lamarck, 1819)	h, e		+	
Callochitonidae				
Callochiton bouveti Thiele, 1906	bm, as	+	+	
Callochiton gaussi Thiele, 1908	t, as		+	
Callochiton puniceus (Gould, 1846)	am, as, bm, ct, i, b, cq, bn, bo, e, t, br, am, bv, ej	+	+	+
Callochiton steinenii (Pfeffer, 1886)	bm, as	+	+	
Chitonidae				
Acanthopleura granulata▪ (Gmelin, 1791)	p			
Chiton sp.	bl		+	
Chiton bowenii King, 1833	b, j, bv, cc, ct, ej	+	+	
Chiton magellanicus▪ Gmelin, 1791	dd			
Chiton magnificus▪ Deshayes, 1827	h, j		+	
Chiton olivaceus▪ Spengler, 1797	p			
Tonicia sp.	b, i, j		+	
Tonicia atrata (G. B. Sowerby II, 1840)	cq, ct, j, as, bm, bo, e, s, bu, bv, ar, ej	+	+	+
Tonicia calbucensis Plate, 1897	cq, j		+	+
Tonicia chilensis (Frembly, 1827)	j, as, bm, bu, bv	+	+	
Tonicia disjuncta▪ (Frembly, 1827)	as		+	
Tonicia lebruni Rochebrune, 1884	bm, cq, ej	+	+	+
Tonicia smithi Leloup, 1980	b, cc, bu, bv, b, a, am, cc			+
Mopaliidae				
Nuttallochiton hyadesi▪ (Rochebrune, 1884)	p		+	
Nuttallochiton martiali (Rochebrune, 1884)	b, cq, br, t, bv		+	+
Plaxiphora aurata (Spalowsky, 1795)	bu, bv, cq, bm, bo, e, j, am, a, br, ar, bk, ba, bl, t, i, b	+	+	+
Acanthochitonidae				
*Notoplax magellanica** Thiele, 1909	am			
Hemiarthridae				
Hemiarthrum setulosum Carpenter in Dall, 1876	br, cc			
Class Gastropoda				
Gastropoda indet.	as, j, bo		+	

Taxa	Reference	E	C	W
Order Patellida				
Lottiidae				
Lottia sp.	bl, bk, cb		+	
Lottia orbignyi■ (Dall, 1909)	h			
Scurria ceciliana (d'Orbigny, 1841)	br, b, a, cs	+	+	+
Scurria ceciliana magellanica (Strebel, 1907)	co, de		+	+
Scurria plana■ (Philippi, 1846)	bg			
Scurria variabilis■ (G. B. Sowerby I, 1839)	e		+	
Lepetidae				
Lepetidae indet.*	as		+	
Iothia emarginuloides (Philippi, 1868)	co, bm, b, ce, bv, v, ad	+	+	+
Nacellidae				
Nacellidae indet.*	as		+	
Nacella sp.*	as, bv, bl		+	
Nacella sp. juvenile	b		+	+
Nacella deaurata (Gmelin, 1791)	cv, co, as, ab, aa, b, a, bm, aq, cb, bw, e, y, d, bu, bv, ba, bg, bk, bl, br, cd, j	+	+	+
Nacella flammea (Gmelin, 1791)	b, bu, bv, bw, j, e, i, y, ar, bk, bl, aa		+	+
Nacella magellanica (Gmelin, 1791)	as, bw, an, ah, ai, y, cs, aq, co, b, a, cv, bl, bk, bg, br, e, bu, aa, h, j, ar, cb, ab, d	+	+	+
Nacella mytilina (Helbling, 1779)	co, cv, z, bw, cs, bg, i, as, b, bv, br, x, aa, bk, ar, ba, bo, cg, cp	+	+	+
Order Seguenziida				
~Seguenzioidea				
*Lissotesta impervia** (Strebel, 1908)	b			+
Order Lepetellida				
Fissurellidae				
Fissurellidae indet.	as		+	+
*Diodora patagonica** (d'Orbigny, 1839)	bg		+	
Fissurella sp.	as, b, e, bo, bl, ab, j		+	+
*Fissurella nigra** Lesson, 1831	k			
Fissurella oriens G. B. Sowerby I, 1834	co, b, bu, bv, i, br, bo, ce, ao		+	+
Fissurella picta (Gmelin, 1791)	co, bu, e, ar, bo, bk, bl, bg	+	+	
Fissurella picta picta (Gmelin, 1791)	a, b, ao, bv	+	+	
Fissurella radiosa Lesson, 1831	b, ao, ar, e, br, bu, cr, ba		+	+
Fissurellidea patagonica (Strebel, 1907)	bw, ap		+	
Lucapinella henseli (Martens, 1900)	k, av		+	
Parmaphorella sp.*	as		+	
Puncturella sp.	bm, as	+	+	
Puncturella conica (d'Orbigny, 1841)	b, f, k, cy		+	+
Puncturella noachina■ (Linnaeus, 1771)	as, co		+	+
Scissurellidae				
Scissurella clathrata Strebel, 1908	cz, b, dj, eb		+	
*Scissurella petermannensis** Lamy, 1910	cz			
Anatomidae				
Anatoma conica (d'Orbigny, 1841)	cz		+	
Anatoma euglypta (Pelseneer, 1903)	df			
Order Trochida				
Trochidae				
Trochidae indet.*	as		+	
*Diloma nigerrimum** (Gmelin, 1791)	h			
Calliostomatidae				
Calliostoma sp.*	b			+
Calliostoma irisans Strebel, 1905	cl		+	+
Calliostoma modestulum Strebel, 1908	bv, as		+	+
Calliostoma moebiusi Strebel, 1905	bm, as, l	+	+	
Calliostoma nudum (Philippi, 1845)	as, bm, b, j, bv, cl, l	+	+	+
Margarella sp.*	as		+	
Margarella expansa (G. B. Sowerby I, 1838)	a, b, bv, ci, bt	+	+	

Taxa	Reference	E	C	W
Margarella jason▪ Powell, 1951	av, as		+	
*Margarella pruinosa** (Rochebrune & Mabille, 1885)	bq, l		+	
Margarella violacea (King, 1832)	as, cl, b, bt, av, i, bd, cg, bm, ar, bv, s, bo, bw, e, j, ak, ba	+	+	+
Photinastoma taeniatum (G. B. Sowerby I, 1825)	as, bm, bv, bq, f, av, l	+	+	
Photinula coerulescens (King, 1832)	br, av, bm, ar, i, as, bn, bk, ce, bg, s, ak, bp, cl, al	+	+	
*Photinula crawshayi** E. A. Smith, 1905	cg		+	
Photinula roseolineata (E. A. Smith, 1885)	bm, bw	+		
Colloniidae				
Homalopoma cunninghami (E. A. Smith, 1881)	bm, as, b, h, cl	+	+	+
Margaritidae				
Margarites sp.*	bm	+		
Margarites sigaretinus▪ (Sowerby I, 1838)	ci	+		
Tegulidae				
Tegula atra (Lesson, 1830)	b, as, bw, j, o		+	+
Tegula patagonica (d'Orbigny, 1835)	bg, l	+		
Turbinidae				
*Prisogaster niger** (W. Wood, 1828)	h			
Caenogastropoda unassigned				
Turritellidae				
Turritellidae indet.*	as	+		
Epitoniidae				
Epitoniidae indet.	as		+	+
Cirsotrema magellanicum (Philippi, 1845)	br, bh		+	
Cirsotrema strebeli Zelaya & Güller, 2018	cm, ed		+	+
Newtoniellidae				
Eumetula michaelseni (Strebel, 1906)	as, cm, ef		+	
Eumetula pulla (Philippi, 1845)	b, bm, bv, as, sm, ce, bh	+	+	+
Order Littorinimorpha				
Eatoniellidae				
Eatoniella sp.	as, b, bm	+	+	+
Eatoniella afronigra Ponder & Worsfold, 1994	bv, bc		+	
*Eatoniella argentinensis** Castellanos & Fernández, 1972	bm	+		
Eatoniella denticula Ponder & Worsfold, 1994	bc, b		+	+
Eatoniella ebenina Ponder & Worsfold, 1994	bc, b		+	+
*Eatoniella glomerosa** Ponder & Worsfold, 1994	bc		+	
*Eatoniella picea** Ponder & Worsfold, 1994	bc		+	
Eatoniella turricula Ponder & Worsfold, 1994	bc			+
Capulidae				
*Capulus compressus** Pelseneer, 1903	m			
Capulus subcompressus▪ Pelseneer, 1903	as		+	
*Capulus ungaricoides** (d'Orbigny, 1841)	av		+	
Littorinidae				
Laevilitorina caliginosa (Gould, 1849)	b, ar, co, bk		+	+
Naticidae				
Naticidae indet.*	as			+
*Euspira constricta** Dall, 1908	bh			+
Falsilunatia carcellesi Dell, 1990	as, bm, al, dj	+	+	
Falsilunatia falklandica▪ (Preston, 1913)	bm	+		
Falsilunatia patagonica (Philippi, 1845)	br, av, bw, bh, cn, b, v, i, f, dj, dz		+	+
Natica sp.*	s	+		
*Natica limbata** d'Orbigny, 1837	cg, dz		+	
Notocochlis isabelleana▪ (d'Orbigny, 1840)	bm	+		
Polinices sp.	dz			
Tectonatica impervia (Philippi, 1845)	bh, cn, bm, v, b, o, dz	+	+	+
Rissoidae				
Onoba georgiana (Pfeffer, 1886)	bc		+	
Onoba lacuniformis Ponder & Worsfold, 1994	bc		+	

Taxa	**Reference**	**E**	**C**	**W**
Onoba schythei (Philippi, 1868)	b, bc, as, af		+	+
Onoba subincisa Ponder & Worsfold, 1994	bc		+	
*Onoba sulcula** H. Adams & A. Adams, 1852	b			+
Powellisetia microlirata Ponder & Worsfold, 1994	bc, b		+	+
Caecidae				
*Caecum chilense** Stuardo, 1962	b			+
Caecum magellanicum (di Geronimo, Privitera & Valdovinos, 1995)	dg			+
Cochliopidae				
*Littoridina angustiarum** Preston, 1915	bh		+	
*Littoridina faminensis** Preston, 1915	bh		+	
*Littoridina limosa** Preston, 1915	bh		+	
*Littoridina lioneli** Preston, 1915	bh		+	
Hydrobiidae				
Hydrobia antarctica Philippi, 1868	bh			
Eulimidae				
Eulimidae indet.	as			+
Calyptraeidae				
Calyptraeidae indet.*	as		+	
Crepipatella sp.	dh		+	
Crepipatella dilatata (Lamarck, 1822)	b, br, ar, e, bw, as, bn, bo, cn	+	+	+
Crucibulum quiriquinae (Lesson, 1830)	di			
Trochita pileolus (d'Orbigny, 1841)	as, av, bm, bn, b, f, dj, ec	+	+	+
Trochita pileus (Lamarck, 1822)	bm, bw, cn, av, as, a, bu, bv, ar, o, i, bn, bh, ce, dj, ec	+	+	+
Velutinidae				
Lamellaria sp.*	j		+	
Lamellaria ampla Strebel, 1906	dj		+	
Lamellaria elata Strebel, 1906	dj, m		+	
*Lamellaria hyadesi** Mabille & Rochebrune, 1889	br		+	
Lamellaria mopsicolor▪ Ev. Marcus, 1958	dk			
Lamellaria patagonica Mabille & Rochebrune, 1889	as, cn		+	+
Lamellaria perspicua (Linnaeus, 1758)	dl		+	
Marseniopsis pacifica▪ Bergh, 1886	m			
Cymatiidae				
Argobuccinum pustulosum (Lightfoot, 1786)	b, s, j		+	+
Fusitriton magellanicus (Röding, 1798)	j, b, s		+	+
Order Neogastropoda				
Volutidae				
Volutidae indet.*	as		+	+
Adelomelon ancilla (Donovan, 1824)	cn, bi, as, bm, s, av, e, b, br, f, i, ba	+	+	+
Adelomelon beckii (Powell, 1951)	bi, cn	+		
Adelomelon ferussacii (Donovan, 1824)	s, cn	+	+	
Odontocymbiola magellanica (Gmelin, 1791)	as, e, bi		+	
Cancellariidae				
Admete sp.*	f		+	
Admete magellanica (Strebel, 1905)	as, bm, cm	+	+	+
*Admete philippi** Ihering, 1907	s	+		
Admete schythei (Philippi, 1855)	b, bi		+	+
Buccinidae				
Buccinidae indet.	as, dj		+	+
Anomacme smithi Strebel, 1905	as, bm	+	+	
Antistreptus magellanicus Dall, 1902	bi, as, dj		+	+
Argeneuthria cerealis (Rochebrune & Mabille, 1885)	b, bv		+	+
*Argeneuthria euthrioides** (Strebel, 1905)	cm		+	
Argeneuthria paessleri (Strebel, 1905)	cm, b, bv		+	+
Argeneuthria philippii (Strebel, 1905)	az, cm		+	
Falsimacme kobelti (Strebel, 1905)	cm, az	+	+	+
Glypteuthria meridionalis (E. A. Smith, 1881)	as, az, cm, ce		+	+

Taxa	Reference	E	C	W
Meteuthria martensi (Strebel, 1905)	cm, az, b	+	+	+
Microdeuthria michaelseni (Strebel, 1905)	as, az, b, bm, cm, bv	+	+	+
Pareuthria atrata (E. A. Smith, 1881)	as, b, cm, ak, bm, av, az, o, ce, dj	+	+	+
Pareuthria fuscata (Bruguière, 1789)	az, j, bw, ar, cm, bu, bv, as, a, f, i, ab, cb, b, bd, bk, e, bn, ak, o	+	+	+
*Savatieria areolata** Strebel, 1905	bm	+		
Savatieria coppingeri (E. A. Smith, 1881)	as, cm		+	
Savatieria frigida Rochebrune & Mabille, 1885	as, cm, dm		+	+
Savatieria meridionalis (E. A. Smith, 1881)	b, cm, bv, ce		+	+
Nassariidae				
*Buccinanops cochlidium** (Dillwyn, 1817)	c			
*Buccinanops deformis** (King, 1832)	c		+	
Buccinanops monilifer (Kiener, 1834)	c	+		
Buccinanops paytensis (Kiener, 1834)	c, bw,r	+	+	
*Nassarius coppingeri**(E. A. Smith, 1881)	b			+
Nassarius gayii (Kiener, 1834)	h, r		+	
Nassarius taeniolatus▪ (Philippi, 1845)	r			
Muricidae				
Acanthina monodon (Pallas, 1774)	bw, e, ar, bu, bk, bl, cg		+	
Acanthina unicornis▪ (Bruguière, 1789)	w		+	
Concholepas concholepas (Bruguière, 1789)	dn			
Coronium acanthodes (Watson, 1882)	ay			+
*Enixotrophon veronicae** Pastorino, 1999	ax			+
Fuegotrophon pallidus (Broderip, 1833)	as, ce, bm, ar, bv, ak, a, ck, dj, eg	+	+	+
Tromina sp.*	bm	+		
Tromina dispectata Dell, 1990	cu, q			
Trophon sp.	as, ab		+	
Trophon geversianus (Pallas, 1774)	b, e, i, j, s, ar, av, ay, ck, ce, cf, bu, bv, bw, br, bk, bl, bi	+	+	+
*Trophon minutus** Melvill & Standen, 1907	as		+	
Trophon ohlini Strebel, 1904	as, ck, dj, eg		+	
Trophon plicatus (Lightfoot, 1786)	ar, ck, av, ce, b, ay, cu, f		+	+
Xymenopsis buccineus (Lamarck, 1816)	cn, ak, av, aw	+	+	
Xymenopsis muriciformis (King, 1832)	b, ak, ar, as, av, aw, bi, bk, bl, bo, br, bv, bw, cu, ce, cn, eg, p	+	+	+
Xymenopsis subnodosus (Gray, 1839)	aw			
Borsoniidae				
Typhlodaphne filostriata (Strebel, 1905)	cm, eh		+	+
Typhlodaphne payeni (Rochebrune & Mabille, 1885)	b		+	+
Typhlodaphne strebeli Powell, 1951	b		+	+
Cochlespiridae				
Aforia sp.	bm	+		
Drilliidae				
Agladrillia fuegiensis (Smith, 1888)	bm, as, bi	+	+	
Leptadrillia elissa▪ (Dall, 1919)	bm, as	+	+	
Mangeliidae				
*Belalora cunninghami** (E. A. Smith, 1881)	b, eh		+	
Lorabela sp.	bm	+		
Mangelia martensi (Strebel, 1905)	do			
Mangelia michaelseni (Strebel, 1905)	bm, cm	+	+	
Oenopota magellanica (Martens, 1881)	br, cm, dj		+	+
Pseudomelatomidae				
Leucosyrinx sp.*	as		+	
Raphitomidae				
Pleurotomella ohlini (Strebel, 1905)	cm, eh	+	+	
Thesbia michaelseni (Strebel, 1905)	cm, eh	+	+	
Turridae				
Turridae indet.	as		+	

Taxa	**Reference**	**E**	**C**	**W**
Infraclass “Lower Heterobranchia”				
Mathildidae				
Mathilda magellanica Fischer, 1873	b		+	
Mathilda malvinarum (Melvill & Standen, 1907)	df			
Cimidae				
Atomiscala xenophyes (Melvill & Standen, 1912)	df			
Infraclass Euthyneura				
Acteonidae				
Acteon biplicatus (Strebel, 1908)	bm, bv, bj	+	+	
Acteon delicatus▪ Dall, 1889	bj			
Ringiculidae				
*Microglyphis curtula** (Dall, 1890)	as			+
Order Pleurobranchida				
Pleurobranchidae				
Berthella platei (Bergh, 1898)	bn	+	+	
Order Nudibranchia				
Dorididae				
*Doris fontainii** d’Orbigny, 1837	by			
Doris kerguelenensis (Bergh, 1884)	bx, by, at	+	+	
Doris magellanica▪ Cunningham, 1871	s			+
Discodorididae				
Diaulula hispida (d’Orbigny, 1834)	by, bx		+	
*Diaulula punctuolata** (d’Orbigny, 1837)	by			
*Gargamella immaculata** Bergh, 1894	by			
*Geitodoris patagonica** Odhner, 1926	by			
Polyceridae				
Holoplocamus papposus Odhner, 1926	bx, by, bj		+	+
*Thecacera darwini** Pruvot-Fol, 1950	by			
Chromodorididae				
Tyrinna delicata (Abraham, 1877)	dp			
Cadlinidae				
Cadlina magellanica Odhner, 1926	by, bz		+	
Onchidorididae				
Acanthodoris falklandica Eliot, 1907	by, j		+	
Goniodorididae				
*Ancula fuegiensis** Odhner, 1926	by			
Janolidae				
Janolus sp.*	j		+	
Tritoniidae				
*Tritonia australis** (Bergh, 1898)	h		+	
Tritonia challengeriana Bergh, 1884	by, bx, j		+	
*Tritonia vorax** (Odhner, 1926)	by			
Coryphellidae				
Itaxia falklandica (Eliot, 1907)	by, bx		+	
Cuthonidae				
Cuthona valentini (Eliot, 1907)	by, bx		+	
Eubranchidae				
*Eubranchus fuegiensis** Odhner, 1926	by			
Aeolidiidae				
Aeolidia sp.	as, bk	+	+	
Aeolidia campbellii (Cunningham, 1871)	by, ar, h, dq		+	
Facelinidae				
*Phidiana patagonica** (d’Orbigny, 1836)	bx		+	
Order Cephalaspidea				
Cylichnidae				
*Cylichna gelida** (E. A. Smith, 1907)	as			+
Toledonia sp.*	as			+

Taxa	**Reference**	**E**	**C**	**W**
*Toledonia parelata** Dell, 1990	bs		+	
Toledonia perplexa Dall, 1902	cm, b, n, bj, dj		+	+
Diaphanidae				
Diaphana paessleri (Strebel, 1905)	b, dj		+	+
Superorder Sacoglossa				
Plakobranchidae				
Elysia hedgpethi Marcus, 1962	bx		+	
Limapontiidae				
*Ercolania evelinae** (Marcus, 1959)	bx		+	
Limapontia sp.*	bx		+	
Hermaeidae				
Aplysiopsis brattstroemi▪ (Marcus, 1959)	bx		+	
Order Siphonariida				
Siphonariidae				
*Siphonaria fuegiensis** Güller, Zelaya & Ituarte, 2016	a, ea	+	+	
Siphonaria laeviuscula▪ G. B. Sowerby I, 1835	dr			
Siphonaria lateralis Gould, 1846	b, co, ar, bk, ab, ea	+	+	+
Siphonaria lessonii Blainville, 1824	b, bw, ab, ar, e, co, a, bu, bk, bl, ba, cb, ea	+	+	+
Williamia magellanica Dall, 1927	n			+
Superorder Pylopulmonata				
Pyramidellidae				
Odostomia sp.	b		+	
Turbonilla sp.*	as			+
*Turbonilla sanmatiensis** Castellanos, 1982	bm	+		+
Turbonilla smithi (Strebel, 1905)	as, bm	+		+
Turbonilla strebeli Corgan, 1969	b		+	+
Order Systellommatophora				
Onchidiidae				
Onchidella marginata (Couthouy in Gould, 1852)	b		+	
Class Bivalvia				
Bivalvia indet.	as, bm		+	
Order Nuculida				
Nuculidae				
Ennucula eltanini Dell, 1990	as, v		+	+
Ennucula grayi (d'Orbigny, 1846)	as, cw, cp, bn		+	
Ennucula puelcha (d'Orbigny, 1842)	t, cw		+	
Linucula sp.*	as		+	
Linucula pisum (G. B. Sowerby I, 1833)	cw		+	
Nucula sp.	as, cp	+		+
Nucula falklandica Preston, 1912	b, cw, dj		+	+
Order Solemyida				
Solemyidae				
Acharax patagonica (E. A. Smith, 1885)	as		+	+
Solemya notialis Simone, 2009	du			
Solemya occidentalis Deshayes, 1857	dt			
Order Nuculanida				
Sareptidae				
Aequiyoldia sp.*	i		+	
Nuculanidae				
Nuculana sp.*	s			+
*Propeleda longicaudata** (Thiele, 1912)	cp		+	
Malletiidae				
*Malletia chilensis** Desmoulins, 1832	h			
Malletia inequalis Dall, 1908	ds		+	
Malletia subaequalis (G. B. Sowerby II, 1870)	as, cw, be, f		+	
Neilonellidae				
Neilonella sulculata (Gould, 1852)	b, f, as, br, cw		+	+

Taxa	Reference	E	C	W
Siliculidae				
Silicula patagonica (Dall, 1908)	as, v		+	+
Tindariidae				
Tindaria virens (Dall, 1890)	as			+
Yoldiidae				
Yoldia sp.*	as		+	
Yoldiella chilenica (Dall, 1908)	as, cw		+	
Yoldiella granula (Dall, 1908)	ds		+	
Yoldiella indolens (Dall, 1908)	as, cw		+	+
Yoldiella valettei▪ (Lamy, 1906)	cp		+	
Order Mytilida				
Mytilidae				
Mytilidae indet.	as		+	
Aulacomya atra (Molina, 1782)	bn, j, ab, bw, cb, bo, as, e, bk, bl, bu, bv, bm, ar, ch, ba, u, t	+	+	+
Choromytilus chorus (Molina, 1782)	i, bw		+	
Crenella sp.*	as			+
Crenella decussata▪ (Montagu, 1808)	as			+
Crenella magellanica Linse, 2002	b		+	+
Modiolus patagonicus (d'Orbigny, 1842)	dt			
Mytilus chilensis Hupé, 1854	a, b, e, f, g, j, t, u, ar, ab, as, bk, bl, bm, bo, bp, br, bu, bv, bw, cb, ch, ei	+	+	+
Mytilus galloprovincialis Lamarck, 1819	dv, ei		+	
Mytilus platensis d'Orbigny, 1842	as, ba		+	
Perumytilus purpuratus (Lamarck, 1819)	g, j, ab, e, bk, bl, b, bu, cb, ch		+	+
Order Arcida				
Arcidae				
Barbatia platei (Stempell, 1899)	dt			
Limopsidae				
Limopsis sp.	as		+	+
Limopsis hirtella Rochebrune & Mabille, 1889	as, v		+	
Limopsis marionensis E. A. Smith, 1885	as, v, bn		+	+
Limopsis perieri P. Fischer in de Folin & Périer, 1870	dt			
Philobryidae				
Lissarca miliaris (Philippi, 1845)	b, as, v		+	+
Philobrya sp.	bm, b, bv	+	+	+
Philobrya aequivalvis▪ (Odhner, 1922)	bm, as	+	+	
Philobrya antarctica (Philippi, 1868)	dt			
*Philobrya atlantica** Dall, 1896	as			+
Philobrya blakeana▪ (Melvill & Standen, 1914)	b, bm	+	+	
*Philobrya capillata** Dell, 1964	as		+	
Philobrya crispa Linse, 2002	as, bm	+	+	
Philobrya magellanica (Stempell, 1899)	as		+	
Philobrya sublaevis Pelseneer, 1903	as, bm, be	+	+	
Order Pectinida				
Pectinidae				
Pectinidae indet.	as		+	
Aequipecten tehuelchus (d'Orbigny, 1842)	dt			
Austrochlamys natans (Philippi, 1845)	b, h, as, bv		+	+
Chlamys sp.*	as		+	
Delectopecten vitreus (Gmelin, 1791)	as, v			+
Zygochlamys patagonica (King & Broderip)	bn, bo, as, h, bm, b, f, bv, be, cx, t, i	+	+	+
Propeamussiidae				
Cyclopecten sp.*	as			+
Cyclopecten subhyalinus (Smith, 1885)	as			+
Cyclochlamydidae				
Cyclochlamys multistriata (Linse, 2002)	b		+	+

Taxa	**Reference**	**E**	**C**	**W**
Order Limida				
Limidae				
Limidae indet.	as		+	
*Acesta patagonica** (Dall, 1902)	bn		+	
Limea pygmaea (Philippi, 1845)	as, v, t, b, bv, bm, ch	+	+	+
Limatula deceptionensis▪ Preston, 1916	as		+	
Limatula hodgsoni (E. A. Smith, 1907)	as, v		+	
Order Lucinida				
Lucinidae				
Epicodakia falklandica Dell, 1964	as, b		+	+
Lucinoma lamellata (E. A. Smith, 1881)	as, aj, cf		+	+
Loripes pertenuis▪ E. A. Smith, 1881	ce, br			
Thyasiridae				
Adontorhina pisum (Dall, 1908)	ac, be		+	+
Parathyasira magellanica (Dall, 1901)	db		+	
Thyasira debilis (Thiele, 1912)	db, cp, as		+	
*Thyasira fuegiensis** Dall, 1890	db		+	
Thyasira patagonica Zelaya, 2010	dc		+	+
Order Carditida				
Carditidae				
Cyclocardia compressa (Reeve, 1843)	as, ce, b		+	+
*Cyclocardia thouarsii** (d'Orbigny, 1845)	s			+
Cyclocardia velutina (E. A. Smith, 1881)	as, bn, f, bf		+	
Condylocardiidae				
Carditella exulata▪ E. A. Smith, 1885	bf		+	
Carditella naviformis (Reeve, 1843)	ag, as, bv		+	
Carditella tegulata (Reeve, 1843)	b		+	+
Carditopsis flabellum (Reeve, 1843)	u, b, ag		+	+
Carditopsis malvinae▪ (d'Orbigny, 1845)	as		+	+
Astartidae				
Astarte longirostra d'Orbigny, 1842	as, bm, ce, bv, b, u, v	+	+	+
Order Cardiida				
Cardiidae				
Cardium parvulum Dunker, 1861	ag			
Tellinidae				
*Macoploma inornata** (Hanley, 1844)	br			
Superorder Imparidentia				
Cyamiidae				
Cyamiocardium sp.*	as			+
Cyamiocardium dahli Soot-Ryen, 1957	b		+	+
Cyamiocardium denticulatum (E. A. Smith, 1885)	v, bm, as	+	+	
Cyamiocardium yeskumaala Urcola & Zelaya, 2018	dy			+
Cyamium sp.*	b		+	
*Cyamium antarcticum** Philippi, 1845	br	+		
Kidderia pusilla (Gould, 1850)	br			
Gaimardiidae				
Gaimardia trapesina (Lamarck, 1819)	b, bw, bv, i, br, cg, ak		+	+
Order Galeommatida				
Lasaeidae				
Altenaeum mabillei (Dall, 1908)	be, v			+
Kellia bullata Philippi, 1845	bm, br, as	+	+	
Lasaea adansoni▪ (Gmelin, 1791)	b		+	+
*Lasaea miliaris** (Philippi, 1845)	u		+	
*Lasaea petitiana** (Récluz, 1843)	h			
Mysella sp.	cp, bm, b	+	+	
Mysella rochebrunei (Dall, 1908)	ds		+	
Pseudokellya cardiformis (E. A. Smith, 1885)	bm, v, as	+	+	

Taxa	Reference	E	C	W
-Galeommatoidea				
Montacutidae indet.*	f		+	
Order Venerida				
Mactridae				
Darina solenoides (King, 1832)	ca, s, br, al, cg	+	+	
Mactra fuegiensis E. A. Smith, 1905	ca		+	
Mulinia byronensis Gray, 1837	ca		+	
Mulinia edulis (King, 1832)	w, s, bw, bf, bm, al, br	+	+	
Mulinia exalbida (King, 1832)	s, ca			+
*Mulinia levicardo** (E. A. Smith, 1881)	br, ca			
Ungulinidae				
*Diplodonta patagonica** (d'Orbigny, 1842)	o			
Diplodonta punctata▪ (Say, 1822)	dx			
Veneridae				
Veneridae indet.*	as		+	
Eurhomalea exalbida (Dillwyn, 1817)	as, b, bf, i, bm, f, bp, cj,	+	+	+
Leukoma antiqua (King, 1832)	b, bw, cj, o		+	+
Petricola dactylus G. B. Sowerby I, 1823	dw		+	
Pitar rostratus (Philippi, 1844)	b, bf		+	
Proteopitar patagonicus (d'Orbigny, 1842)	br			
Tawera elliptica (Lamarck, 1818)	bw, cp, bl, b, as, ce, cg		+	
Venus inflata▪ King & Broderip, 1832	al		+	
Neoleptonidae				
Neolepton sp.	b		+	+
*Neolepton amatoi** Zelaya & Ituarte, 2004	b		+	
*Neolepton cobbi** (Cooper & Preston, 1910)	as		+	+
Neolepton concentricum (Preston, 1912)	b, da, bm, as	+		+
Neolepton hupei Soot-Ryen, 1957	as			+
Neolepton yagan Zelaya & Ituarte, 2004	b, da		+	+
Order Myida				
Myidae				
*Sphenia hatcheri** Pilsbry, 1899	bf	+		
Pholadidae				
Netastoma darwinii (G. B. Sowerby II, 1849)	dt			
Teredinidae				
Bankia martensi (Stempell, 1899)	h, bf		+	
Order Adapedonta				
Hiatellidae				
Hiatellidae indet.*	as		+	
Hiatella sp.	bv, as, ce		+	
Hiatella antarctica (Philippi, 1845)	b		+	+
Hiatella arctica (Linnaeus, 1767)	as, bu, e, i, u, ar, f, bm, bo, ch	+	+	+
Pharidae				
Ensis macha (Molina, 1782)	s, as		+	
Superorder Anomalodesmata				
Pandoridae				
Pandora braziliensis G. B. Sowerby II, 1874	br, bm, as, f, ae	+	+	
Pandora cistula▪ Gould, 1850	as, br		+	
Lyonsiidae				
Entodesma cuneata (Gray, 1828)	dt			
Entodesma elongatulum Soot-Ryen, 1957	bm, as	+	+	
*Entodesma solemyalis**(Lamarck, 1818)	bf			
Laternulidae				
Laternula elliptica▪ (King, 1832)	as		+	
Cuspidariidae				
Cuspidaria sp.	as		+	
Cuspidaria patagonica (E. A. Smith, 1885)	as, bm, cp, bf	+	+	+
*Cuspidaria tenella** E. A. Smith, 1907	as		+	

Taxa	Reference	E	C	W
Luzonia chilensis (Dall, 1890)	dt			
Poromyidae				
Dermatomya mactroides▪ (Dall, 1889)	as			+
Lyonsiellidae				
Policordia radiata (Dall, 1889)	as		+	+

References: **a** (Aldea and Rosenfeld 2011); **b** (Aldea et al. 2011); **c** (Allmon 1990); **d** (Andrade and Brey 2014); **e** (Andrade et al. 2016); **f** (Arntz and Gorny 1996); **g** (Astorga et al. 2007); **h** (Brattström and Johanssen 1983); **i** (Cañete et al. 2014); **j** (Cárdenas 2008); **k** (Castellanos and Landoni 1988); **l** (Castellanos and Landoni 1989); **m** (Castellanos and Landoni 1990); **n** (Castellanos et al. 1993); **o** (Castellanos 1970); **p** (Castellanos 1988); **q** (Castellanos 1992a); **r** (Castellanos 1992b); **s** (Cunningham 1871); **t** (Dell 1964); **u** (Dell 1971); **v** (Dell 1990); **w** (d'Orbigny 1835–1846); **x** (González-Wevar et al. 2010); **y** (González-Wevar et al. 2016a); **z** (González-Wevar et al. 2016b); **aa** (González-Wevar et al. 2017a); **ab** (Guarda 2015); **ac** (Güller and Zelaya 2011); **ad** (Güller and Zelaya 2016a); **ae** (Güller and Zelaya 2016b); **af** (Güller and Zelaya 2017); **ag** (Güller and Zelaya 2013); **ah** (Guzmán and Ríos 1987); **ai** (Guzmán 1978); **aj** (Holmes et al. 2005); **ak** (Hombron and Jacquinot 1854); **al** (King and Broderip 1832); **am** (Leloup 1956); **an** (Mancilla 2010); **ao** (McLean 1984a); **ap** (McLean 1984b); **aq** (Menéndez 2013); **ar** (Mutschke et al. 1998); **as** (OBIS 2018); **at** (Odhner 1926); **av** (Osorio 1999); **aw** (Pastorino and Harasewych 2000); **ax** (Pastorino 1999); **ay** (Pastorino 2005a); **az** (Pastorino 2016); **ba** (Pelseneer 1903); **bc** (Ponder and Worsfold 1994); **bd** (Powell 1951); **be** (Ramírez 1993a); **bf** (Ramírez 1993b); **bg** (Ramírez 1996a); **bh** (Ramírez 1996b); **bi** (Ramírez 1997); **bj** (Ramírez 2000); **bk** (Ríos and Gerdes 1997); **bl** (Ríos and Mutschke 1999); **bm** (Ríos et al. 2003); **bn** (Ríos et al. 2005); **bo** (Ríos et al. 2007); **bp** (Ríos et al. 2010); **bq** (Rochebrune and Mabille 1885); **br** (Rochebrune and Mabille 1889); **bs** (Rosenfeld and Aldea 2011); **bt** (Rosenfeld et al. 2011); **bu** (Rosenfeld et al. 2013); **bv** (Rosenfeld et al. 2015); **bw** (Rosenfeld et al. 2016); **bx** (Schrödl 1996); **by** (Schrödl 1999); **bz** (Schrödl 2000); **ca** (Signorelli and Pastorino 2011); **cb** (Silva 2015); **cc** (Sirenko 2006a); **cd** (Sirenko 2015); **ce** (Smith 1881); **cf** (Smith 1885); **cg** (Smith 1905); **ch** (Soot-Ryen 1959); **ci** (Sowerby 1838); **cj** (Sowerby 1847); **ck** (Strebel 1904); **cl** (Strebel 1905a); **cm** (Strebel 1905b); **cn** (Strebel 1906); **co** (Strebel 1907); **cp** (Thatje and Brown 2009); **cq** (Thiele 1908); **cr** (Tryon and Pilsbry 1890); **cs** (Tryon and Pilsbry 1891); **ct** (Tryon and Pilsbry 1892); **cu** (Tryon 1880); **cv** (Valdovinos and Ruth 2005); **cw** (Villarroel and Stuardo 1998); **cx** (Waloszek 1984); **cy** (Watson 1886); **cz** (Zelaya and Geiger 2007); **da** (Zelaya and Ituarte 2004); **db** (Zelaya 2009); **dc** (Zelaya 2010); **dd** (Kaas et al. 2006); **de** (Nakano and Ozawa 2007); **df** (Di Luca and Zelaya 2019); **dg** (di Geronimo et al. 1995); **dh** (Nuñez et al. 2012); **di** (Dall 1909); **dj** (Linse 2002); **dk** (Marcus 1959); **dl** (Bergh 1898); **dm** (Di Luca and Pastorino 2018); **dn** (Osorio 2002); **do** (Tucker 2004); **dp** (Schrödl 2003); **dq** (Kienberger et al. 2016); **dr** (Álamo and Valdivieso 1987); **ds** (Dall 1908); **dt** (Huber 2010); **du** (Huber 2015); **dv** (Araya 2015); **dw** (Coan 1997); **dx** (Dall 1901); **dy** (Urcola and Zelaya 2018); **dz** (Pastorino 2005b); **ea (**Güller et al. 2016); **eb** (Geiger 2012); **ec** (Pastorino and Urteaga 2012); **ed** (Zelaya and Güller 2017); **ef** (Castellanos 1990); **eg** (Castellanos and Landoni 1993a); **eh** (Castellanos and Landoni 1993b); **ei** (Oyarzún et al. 2016); **ej** (Sellanes 2018).

rant with the highest richness was Punta Santa Ana and Fuerte Bulnes (C59), 60 km south of Punta Arenas with 112 nominal taxa, greatly exceeding the diversity of other quadrants (Fig. 4). The most common species was the gastropod *Nacella magellanica*, present in 33 quadrants, followed by *Pareuthria fuscata* (25 quadrants), *Callochiton puniceus* (23), *Nacella deaurata* (23), *Margarella violacea* (23), *Nacella mytilina* (22), *Trophon geversianus* (22), *Aulacomya atra* (22), *Trochita pileus* (21), *Plaxiphora aurata* (20), *Zygochlamys patagonica* (20), *Mytilus chilensis* (19), *Pareuthria atrata* (18), *Leptochiton kerguelensis* (17), and *Xymenopsis muriciformis* (17).

The estimated prediction for the richness of species associated with the sampling effort for the Strait of Magellan determined by the Clench model showed that the values of the constants were a = 5.664075 and b = 0.014764. The relation of these values (a / b) obtained a maximum expected richness of 383.6 species (value of the asymptote of the species accumulation curve with $R^2 = 0.97$), higher than the 270 species observed. The constants of the linear dependence model were a = 4.953160 and b = 0.017756, thus the maximum expected richness (a / b) was 279 species with $R^2 = 0.97$, obtaining a higher value in 9 species than observed in this study (Fig. 5a).

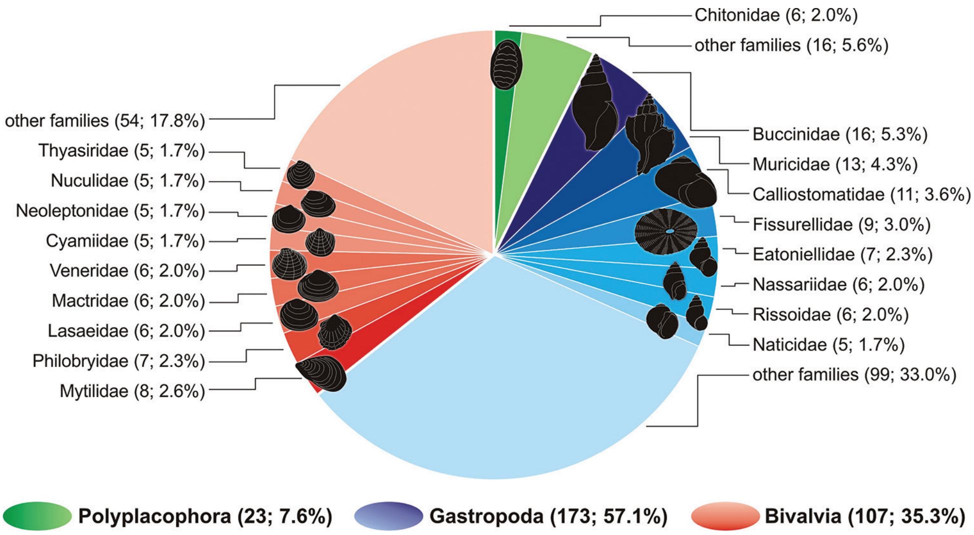

Figure 2. Species richness of mollusks from the Strait of Magellan, highlighting the families with higher diversity. The numbers of species and their percentages are indicated in parentheses.

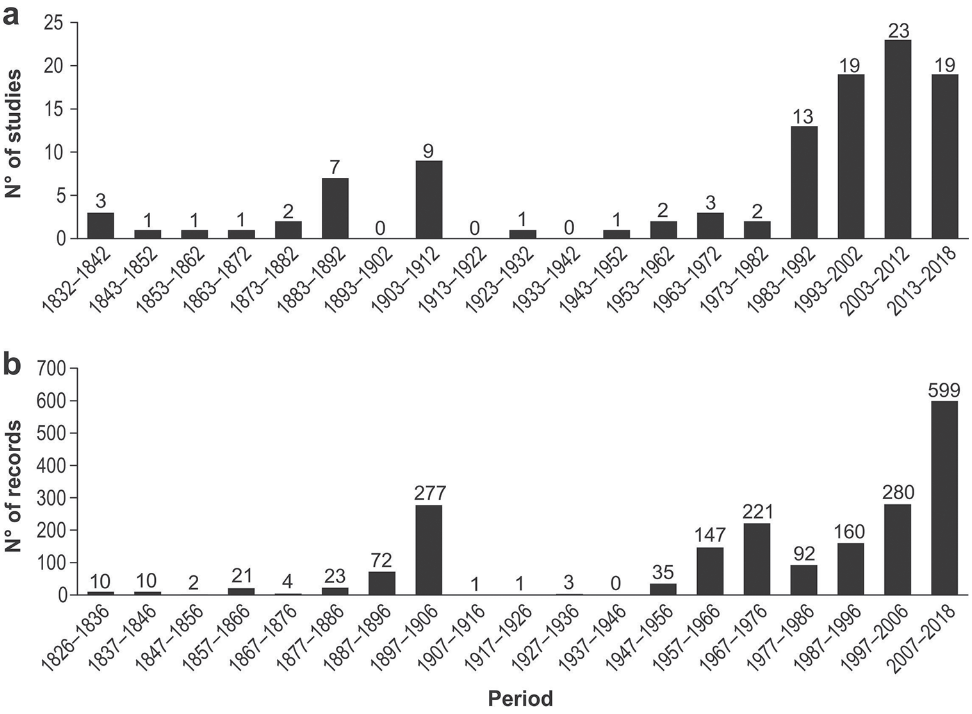

Figure 3. A number of studies per decade of the Strait of Magellan mentioned in this study **B** number of mollusk records per decade reported in the Strait of Magellan.

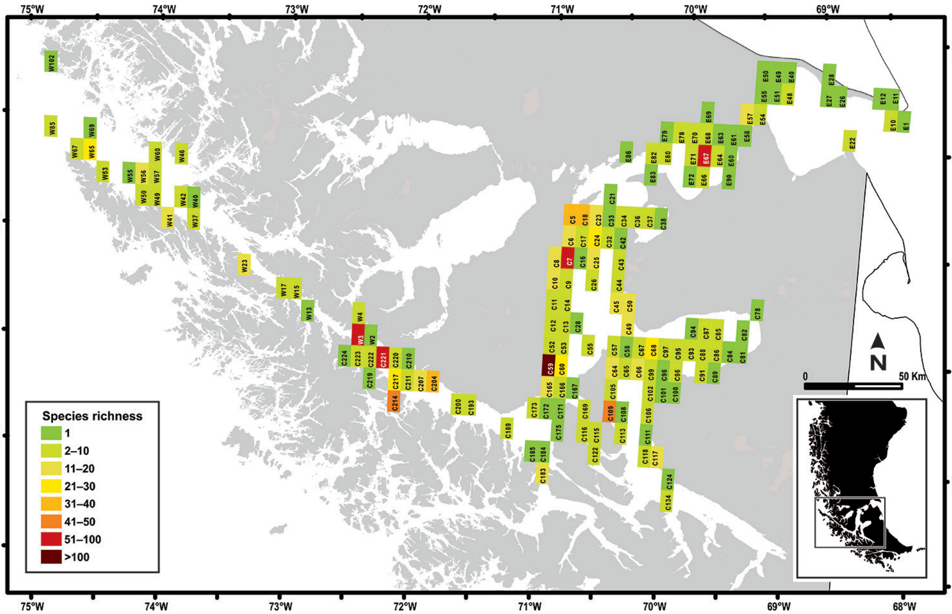

Figure 4. Species richness by quadrant in the Strait of Magellan.

Therefore, neither of the two theoretical models predicted exactly the observed number of mollusk species for the Strait of Magellan. Both non-parametric models estimated an expected richness much higher than that observed empirically (Chao 2 = 353.49; Jacknife 1 = 360.39), and both curves were above that of observed richness (Fig. 5b).

Discussion

According to Valdovinos (1999), the Chilean coast has about 959 species of the three most diverse classes of benthic marine mollusks (671 gastropods, 226 bivalves and 62 polyplacophorans), including Antarctic and oceanic island species. The Magellan Biogeographic Province (41°S to 56°S) is one of the geographical areas with the highest diversity of mollusks on the Chilean coast (Valdovinos et al. 2003). Taking into account this database, the 303 mollusk species recorded in this study correspond to ~31.6% of the species cited for the Chilean coast (Fig. 6). About 400 species of marine mollusks, 250 gastropods, 131 bivalves (Linse 1999) and 19 polyplacophorans (Sirenko 2006a) have been reported for the Magellan Province. Therefore, the 303 species recorded for the Strait of Magellan represent 75% of the mollusks reported for the MBP. However, comparing the value of richness found in this study (303 species) to the 116 species of gastropods and bivalves reported for the Strait of Magellan by Linse et al. (2006), plus 17 species of polyplacophorans by Sirenko (2006a), the richness of mollusks for the Strait of Magellan was increased by 228% (Fig. 6). Most of the records were reported in the last 70 years. However, records of the late 19th century and early 20th century

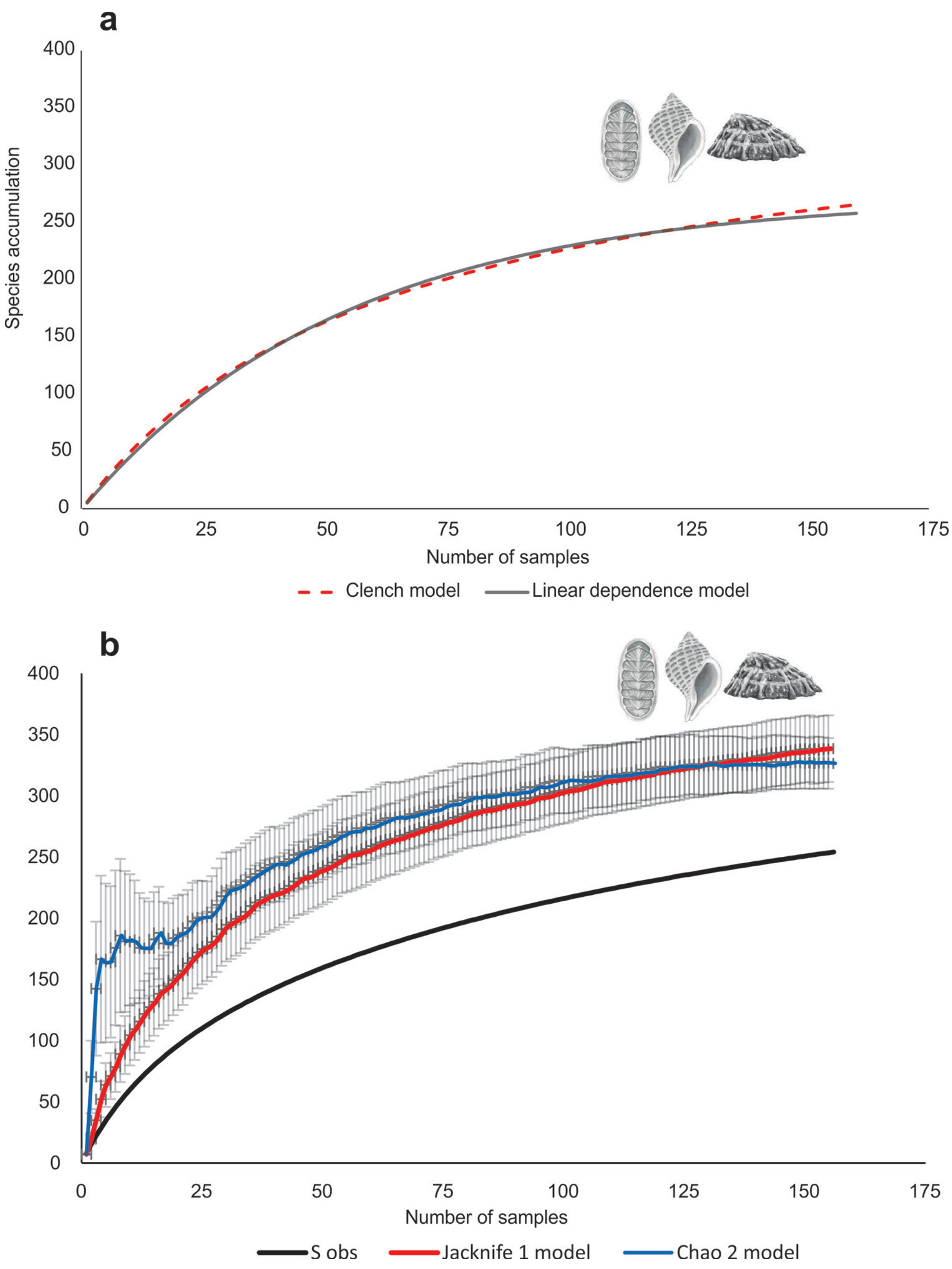

Figure 5. a accumulation curves of mollusk species according to the parametric estimators Clench and linear dependence, and **b** according to the non-parametric estimators Chao 2 and Jack 1 for the Strait of Magellan.

greatly increased the knowledge of the zone, surpassing previous reports (see Fig. 3). This is mainly due to the publications of Rochebrune and Mabille (1889) and Strebel (1904, 1905a, b, 1906, 1907) which reported 267 records in the Strait. The number of

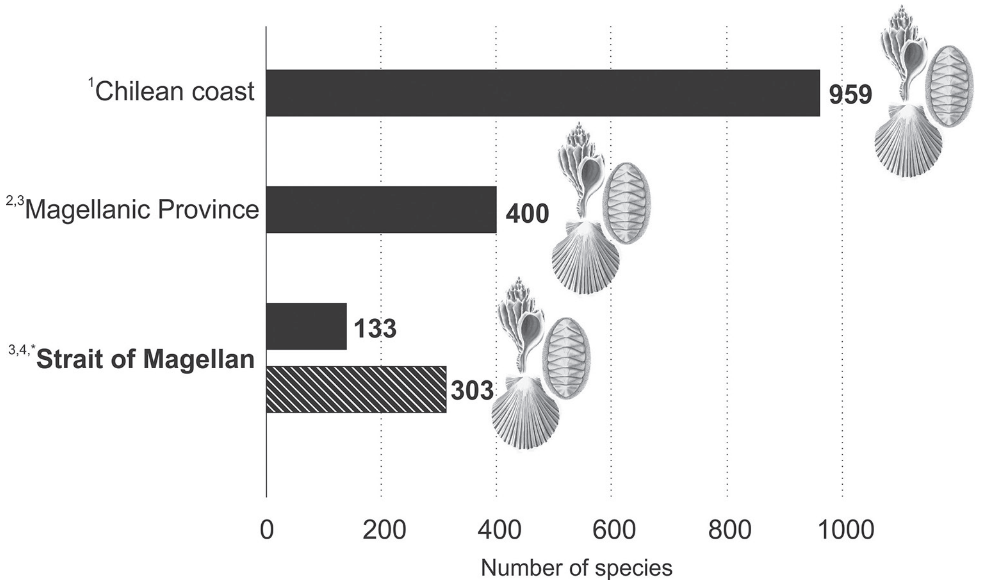

Figure 6. Number of mollusk species cited for the Chilean coast (1: Valdovinos 1999), Magellan Province (2: Linse 1999; 3: Sirenko 2006a) and Strait of Magellan (4: Linse et al. 2006; * this study).

studies has increased in the last 40 years, and therefore the records (see Fig. 3). However, some of these records belong to reviews of biological collections and older studies.

One criterion was followed to determine doubtful species; those records that were cited in the past and have been questioned in taxonomic reviews. Species such as *Carditella exulata* or *Pandora cistula* were identified as dubious according to these criteria (Güller and Zelaya 2013; Güller and Zelaya 2016b). Other criteria included records in which the same taxonomist discussed the species described such as the case of *Doris magellanica* (Cunningham, 1871), records that considerably exceed their distribution limit and do not appear in taxonomic revisions or alpha diversity studies or are simply dismissed, such as *Lottia orbignyi*, *Leptochiton smirnovi*, *Falsilunatia falklandica*, etc. (Espoz et al. 2004; Pastorino 2005b; Sirenko 2016), and records that have a huge biogeographical discontinuity and are not explained or figured in the article, is the case of *Ischnochiton striolatus*, *Puncturella noachina* and *Acteon delicatus* (Rochebrune and Mabille 1889; Strebel 1907; Ramírez 2000). On the other hand, of the taxa reported up to or above genus level (“indet.” or “sp.”), only two could correspond to new species, according to the authors’ remarks: *Leptochiton* sp. (Sirenko 2006a) and *Crepipatella* sp. (Nuñez et al. 2012).

Recent studies using molecular tools have observed that several species co-distributed in the Antarctic Peninsula and South America actually belong to different lineages, with evolutionary units separated by millions of years (Poulin et al. 2014). This has been mainly observed in species of the genus *Aequiyoldia* Soot-Ryen, 1951 (González-Wevar et al. 2019).

Finally, there are species in the list that do not qualify as doubtful, but which have been classified as unknown species due to their low number of records or due to its small body size, which makes it difficult to identify the species, with poor ecological or descriptive information (Castellanos 1979; Geiger 2012; Rosenfeld et al. 2017), e.g., *Notoplax magellanica*, *Lissotesta impervia*, *Onoba sulcula*, *Onoba georgiana*, *Microglyphis curtula*, *Cylichna gelida*, *Turbonilla sanmatiensis*, *Philobrya atlantica*. In this sense, it should be noted that much of the mollusk information that was collected in this work comes from manual collections and various types of sampling gears, trawl and grabs (e.g., Watson 1886; Rochebrune and Mabille 1889; Strebel 1907; Linse 2002; Ríos et al. 2003). However, taxonomic works on specific groups have allowed a good representation of unknown micromollusks (Ponder and Worsfold 1994; Geiger 2012; Pastorino 2016; Di Luca and Pastorino 2018). Despite the aforementioned contributions, micromollusks could continue to be underestimated, since the comparative morphology of various species is only beginning to be illustrated and described in detail (Di Luca and Pastorino 2018).

This historical compilation of the richness of benthic mollusks of the Strait of Magellan promotes the need and urgency for the management of coastal environments. Despite the historical sampling effort and about 192 years of records, the Strait of Magellan has a high diversity of mollusk species which is not yet fully known. The richness estimated by the parametric models was greater than that observed. Two reasons may explain this: i) the sampling effort along the Strait of Magellan has been low (only about 36% of the total area is recorded), and ii) there is still a lack of knowledge about the taxonomy of many mollusk groups, since many species remain undetermined and are not included in the listings or are not recognized in the field. According to Soberón and Llorente (1993), the probability of finding a new species in the Clench model will increase according to experience in the field. Therefore, the Clench model suggests increasing the sampling effort but at a broader spatial and temporal scale to reach the asymptote in the estimation of mollusk species from the Strait of Magellan.

The richness estimated by non-parametric models was higher than the observed. These non-parametric models work based on the number of unique (number of species that occur only in one sample) and duplicate (number of species that occur in exactly two samples). This is based on the assumption that individuals of a species do not live alone in ecosystems, but in populations (Magurran 1988), therefore many unique species in a sample may be indicating that a sufficient number of sampling units has not been used. This historical compilation showed that there are many places in the Strait of Magellan that only have one or two records, which was reflected in both estimators.

However, it is important to consider that in order to evaluate the behavior of the different estimators, it is necessary to know the number of species in the community (Walther and Moore 2005; González-Oreja et al. 2010). Unless the community has been thoroughly sampled, these curves may not work properly (Magurran 2004). Therefore, some authors recommend not working with only one estimator, but testing several models to see how they behave with the data (González-Oreja et al. 2010), since these may vary depending on the situation or for a specific group of organisms

(Walther and Moore 2005). The results of the four models used in this study allows us to infer that greater sampling effort is needed in the Strait of Magellan, mainly because the largest number of records and species richness are concentrated at the same points within the Strait of Magellan, in the central microbasin.

Conclusion

This study provides a clearer idea of the diversity of mollusks in the Strait of Magellan, identifying erroneous records and those that need verification, encouraging other researchers to sample less-studied areas of the strait. This will update knowledge of the diversity of mollusks of the Strait of Magellan, contributing to Chile's biodiversity heritage and future studies of biogeographical models that are currently based on the 116 species of gastropods and bivalves cited by Linse et al. (2006) and the 17 species of polyplacophorans cited by Sirenko (2006a) for the Strait of Magellan. Finally, with this information of all the records, it will be possible to identify the hotspots of diversity for study and gaps in knowledge, among other things.

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Appendix I

Registration in GBIF database.

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Endpoints: http://gbif-chile.mma.gob.cl/ipt/archive.do?r=moluscos-estrecho-magallanes (Darwin Core Archive), http://gbif-chile.mma.gob.cl/ipt/eml.do?r=moluscos-estrecho-magallanes (EML)

Preferred identifier, DOI: https://doi.org/10.15468/znrbm9

Alternative identifiers: http://gbif-chile.mma.gob.cl/ipt/resource?r=moluscos-estrecho-magallanes

Appendix II

Quadrants of the Strait of Magellan in which mollusks are recorded.

Quadrant	Location	Latitude (S) / Longitude (W)
E1	Dungeness Point 1	52°24’12"S, 68°25’40"W
E10	Dungeness Point 2	52°24’1"S, 68°26’35"W
E11	Dungeness Point 3	52°21’58"S, 68°26’50"W
E12	Dungeness Point 4	52°20’59"S, 68°28’23"W
E22	Point Catalina	52°27’55"S, 68°46’17"W
E26	Cape Posession 1	52°19’40"S, 68°51’5"W
E27	Cape Posession 2	52°19’3"S, 68°56’50"W
E28	Cape Posession 3	52°16’20"S, 69°0’33"W
E40	Posession Bay 1	52°14’25"S, 69°12’30"W
E48	Posession Bay 2	52°17’8"S, 69°12’30"W
E49	Posession Bay 3	52°13’30"S, 69°17’12"W
E50	Tandy Point	52°15’20"S, 69°21’58"W
E51	Posession Bay 4	52°17’8"S, 69°17’17"W
E54	Punta Anegada	52°25’59"S, 69°25’26"W
E55	Nunición Bay	52°20’09"S, 69°26’38"W
E57	Punta Delgada	53°27’12"S, 69°32’7"W
E58	First Narrow 1	52°32’25"S, 69°34’10"W
E60	Punta Remo	52°38’20"S, 69°39’27"W
E61	First Narrow 2	52°32’55"S, 69°40’31"W
E63	Punta Barranca 1	52°32’28"S, 69°43’12"W
E64	Punta Barranca 2	52°37’7"S, 69°43’53"W
E66	Punta Piedras 1	52°44’48"S, 69°50’40"W
E67	Punta Piedras 2	52°38’58"S, 69°50’43"W
E68	Santiago Bay 1	52°34’6"S, 69°50’40"W
E69	Santiago Bay 2	52°29’33"S, 69°51’3"W
E70	Santiago Bay 3	52°31’44"S, 69°55’33"W
E71	Triton Bank 1	52°36’52"S, 69°55’39"W
E72	Triton Bank 2	52°41’44"S, 69°56’6"W
E78	Gregorio Bay 1	52°34’34"S, 70°4’47"W
E79	Gregorio Bay 2	52°35’00"S, 70°08’23"W
E80	Gregorio Bay 3	52°38’13"S, 70°7’58"W
E82	Cape Gregorio	52°39’27"S, 70°14’25"W
E83	Second Narrow 1	52°43’5"S, 70°14’48"W

Quadrant	Location	Latitude (S) / Longitude (W)
E86	Second Narrow 2	52°41’44"S, 70°26’17"W
E90	Punta Remo	52°42’43"S, 69°40’28"W
C5	Cabo Negro 1	52°56’30"S, 70°47’46"W
C6	Río Seco	53°2’27"S, 70°49’50"W
C7	Punta Arenas 1	53°8’8"S, 70°51’30"W
C8	Punta Arenas 2	53°11’47"S, 70°55’52"W
C9	Leñadura 1	53°15’24"S, 70°51’35"W
C10	Leñadura 2	53°15’46"S, 70°56’32"W
C11	Santa María Point 1	53°21’57"S, 70°57’37"W
C12	Colorado River 1	53°29’10"S, 70°56’49"W
C13	Colorado River 2	53°28’47"S, 70°51’4"W
C14	Santa María Point 2	53°21’53"S, 70°51’51"W
C16	Paso Ancho 1	53°8’53"S, 70°43’11"W
C17	Paso Ancho 2	53°4’5"S, 70°42’43"W
C18	Cabo Negro 2	52°56’29"S, 70°44’50"W
C21	Marta Island	52°52’57"S, 70°34’48"W
C23	Paso Ancho 3	52°58’19"S, 70°39’54"W
C24	Paso Ancho 4	53°2’11"S, 70°40’1"W
C25	Paso Ancho 5	53°7’34"S, 70°41’34"W
C26	Paso Ancho 6	53°13’4"S, 70°42’24"W
C28	Paso Ancho 7	53°23’35"S, 70°48’47"W
C32	Paso Ancho 8	53°2’15"S, 70°32’49"W
C33	Paso Ancho 9	52°56’34"S, 70°32’5"W
C34	Paso Ancho 10	52°56’19"S, 70°27’31"W
C36	Zegers Point	52°56’20"S, 70°18’52"W
C37	Gente Grande Bay 1	52°55’44"S, 70°12’33"W
C38	Gente Grande Bay 2	52°55’40"S, 70°7’41"W
C42	Gente Point	53°3’13"S, 70°25’45"W
C43	Paso Ancho 10	53°9’47"S, 70°26’17"W
C44	Paso Ancho 11	53°16’46"S, 70°28’16"W
C45	Porvenir Bay 1	53°20’57"S, 70°27’33"W
C49	Paso Boquerón	53°25’59"S, 70°19’40"W
C50	Porvenir Bay 2	53°18’29"S, 70°22’45"W
C52	Carrera Bay	53°33’53"S, 70°54’57"W
C53	Paso del Hambre 1	53°32’47"S, 70°49’20"W
C55	Paso del Hambre 2	53°32’30"S, 70°39’57"W
C57	Cape Valentín 1	53°32’12"S, 70°24’51"W
C58	Inútil Bay 1	53°32’8"S, 70°17’0"W
C59	Santa Ana Point	53°37’55"S, 70°54’41"W
C60	Paso del Hambre 3	53°37’51"S, 70°49’53"W
C64	Cape Valentín 2	53°39’16"S, 70°27’59"W
C65	Inútil Bay 2	53°39’4"S, 70°19’33"W
C66	Inútil Bay 3	53°38’40"S, 70°14’8"W
C67	Cape Boquerón	53°32’26"S, 70°13’43"W
C68	Inútil Bay 4	53°31’49"S, 70°9’20"W
C78	Puerto Nuevo	53°22’23"S, 69°22’14"W
C81	Inútil Bay 5	53°31’36"S, 69°23’42"W
C82	Inútil Bay 6	53°26’59"S, 69°23’58"W
C84	Inútil Bay 7	53°31’5"S, 69°30’41"W
C85	Inútil Bay 8	53°25’58"S, 69°35’25"W
C86	Inútil Bay 9	53°29’40"S, 69°35’4"W
C87	Inútil Bay 10	53°26’28"S, 69°44’32"W
C88	Inútil Bay 11	53°32’24"S, 69°44’48"W
C89	Inútil Bay 12	53°37’18"S, 69°39’42"W
C91	Inútil Bay 13	53°39’9"S, 69°45’59"W
C93	Inútil Bay 14	53°33’13"S, 69°52’27"W
C94	Inútil Bay 15	53°27’20"S, 69°52’32"W

Quadrant	Location	Latitude (S) / Longitude (W)
C95	Inútil Bay 16	53°33’38"S, 69°59’57"W
C96	Cameron Point 1	53°39’3"S, 69°59’10"W
C97	Inútil Bay 17	53°35’41"S, 70°7’51"W
C98	Inútil Bay 18	53°40’22"S, 70°8’39"W
C99	Inútil Bay 19	53°40’23"S, 70°15’42"W
C100	Cameron Point 2	53°43’38"S, 69°59’20"W
C101	Cape Nose 1	53°44’21"S, 70°5’37"W
C102	Cape Nose 2	53°45’22"S, 70°10’58"W
C104	Whiteside Channel 1	53°45’35"S, 70°22’4"W
C105	Kelp Point	53°47’10"S, 70°25’49"W
C106	Chown Point	53°52’8"S, 70°10’17"W
C107	Whiteside Channel 2	53°52’7"S, 70°14’29"W
C108	Whiteside Channel 3	53°52’12"S, 70°18’59"W
C109	Harris Bay	53°51’18"S, 70°25’33"W
C111	Cóndor River	53°56’44"S, 70°7’46"W
C113	No Entres Bay	53°58’37"S, 70°21’2"W
C115	Owen Sound 1	53°59’8"S, 70°35’16"W
C116	Owen Sound 2	53°59’14"S, 70°38’46"W
C117	Karukinka Point	54°3’57"S, 70°5’17"W
C118	Whiteside Channel 4	54°4’10"S, 70°8’44"W
C122	Owen Sound 3	54°4’8"S, 70°32’47"W
C124	Port Castillo	54°9’47"S, 69°54’58"W
C134	Alta Island	54°16’21"S, 69°55’49"W
C165	Árbol Point	53°45’50"S, 70°57’51"W
C166	Paso del Hambre 4	53°45’57"S, 70°51’16"W
C167	Lomas Bay 1	53°45’50"S, 70°44’45"W
C169	Lomas Bay 2	53°50’6"S, 70°39’51"W
C171	Amigo Bay	53°51’3"S, 70°52’12"W
C172	Paso del Hambre 5	53°52’12"S, 70°57’27"W
C173	Glascott Point	53°51’45"S, 71°5’25"W
C175	Valdés Point	53°55’9"S, 70°52’54"W
C183	Magdalena Channel	53°55’36"S, 70°56’51"W
C184	Magdalena Sound 1	54°5’5"S, 70°57’30"W
C185	Magdalena Sound 2	54°3’8"S, 71°4’51"W
C189	Paso Froward 1	53°58’35"S, 71°13’35"W
C193	Paso Froward 2	53°51’23"S, 71°31’58"W
C200	Cape Holland	53°50’34"S, 71°37’16"W
C204	Andrés Bay	53°45’50"S, 71°49’0"W
C207	West Point	53°44’38"S, 71°55’28"W
C210	Fortescue Bay	53°42’25"S, 72°1’36"W
C211	Charles Island 1	53°44’22"S, 72°4’14"W
C214	Bárbara Bay	53°48’42"S, 72°9’6"W
C217	Charles Island 2	53°45’25"S, 72°8’42"W
C219	Choiseul Bay	53°45’14"S, 72°19’21"W
C220	Charles Island 3	53°40’56"S, 72°8’34"W
C221	Rupert Island	53°39’55"S, 72°14’14"W
C222	Ballena Sound 1	53°40’38"S, 72°19’31"W
C223	Ballena Sound 2	53°40’9"S, 72°25’25"W
C226	Cape Froward	53°53’52"S, 71°15’9"W
W2	Carlos III Island	53°34’32"S, 72°20’6"W
W3	Paso Tortuoso	53°33’25"S, 72°26’20"W
W4	Jerónimo Channel	53°30’13"S, 72°25’4"W
W13	Spider Island	53°31’14"S, 72°40’26"W
W15	Glacier Bay	53°22’9"S, 72°55’35"W
W17	Paso Largo	53°20’52"S, 73°2’12"W
W23	Lewis Bay	53°15’0"S, 73°19’51"W
W37	Chapman Isles	53°3’18"S, 73°45’13"W

Quadrant	Location	Latitude (S) / Longitude (W)
W40	Cape Tamar	52°56’38"S, 73°44’54"W
W41	Brazo Damián	53°1’31"S, 73°55’23"W
W42	Tamar Island	52°55’31"S, 73°50’14"W
W46	Sholl Bay	52°43’42"S, 73°50’16"W
W49	Patranca Island	52°56’46"S, 74°1’59"W
W50	Félix Point	52°56’6"S, 74°8’12"W
W53	Tuesday Bay	52°50’43"S, 74°24’40"W
W55	Paso Tamar 1	52°50’27"S, 74°14’40"W
W56	Paso Tamar 2	52°50’43"S, 74°7’21"W
W57	Paso Tamar 3	52°50’24"S, 74°1’10"W
W60	Paso Tamar 4	52°44’34"S, 74°0’41"W
W65	Cape Pilar 1	52°43’29"S, 74°33’11"W
W67	Cape Pilar 2	52°41’56"S, 74°38’45"W
W69	Western entrance	52°37’40"S, 74°33’38"W
W85	Western entrance	52°33’27"S, 74°45’44"W
W102	Victoria Island	52°18’31"S, 74°50’10"W

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Rugitermes tinto: A new termite (Isoptera, Kalotermitidae) from the Andean region of Colombia

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Abstract

The imago and soldier castes of a new *Rugitermes* Holmgren, 1911 species, *R. tinto* **sp. nov.** are described. It is the ninth species of *Rugitermes* from South America and the first record of this genus from Colombia. Unlike its congeners, the soldier of *R. tinto* has very dark head capsule pigmentation and acute protuberances projecting from frontolateral ridges.

Keywords

frontolateral ridges, imago, new species, soldier, South America, taxonomy

Introduction

Rugitermes Holmgren, 1911 is a widespread termite genus in Central and South America (Scheffrahn 2019a) where twelve species are described (Krishna et al. 2013). A curious thirteenth species, *R. athertoni* (Light, 1932), occurs in Oceania. Eight species of *Rugitermes* are currently known from South America: *R. bicolor* (Emerson, 1925) from Amazonia (Scheffrahn 2019b), *R. laticollis* Snyder, 1957 from the Andean highlands (Scheffrahn 2015), *R. flavicinctus* (Emerson, 1925) and *R. magninotus* (Emerson, 1925) from Guyana, *R. niger* Oliveira, 1979, *R. nodulosus* (Hagen, 1858), and *R. rugosus* (Hagen, 1858)

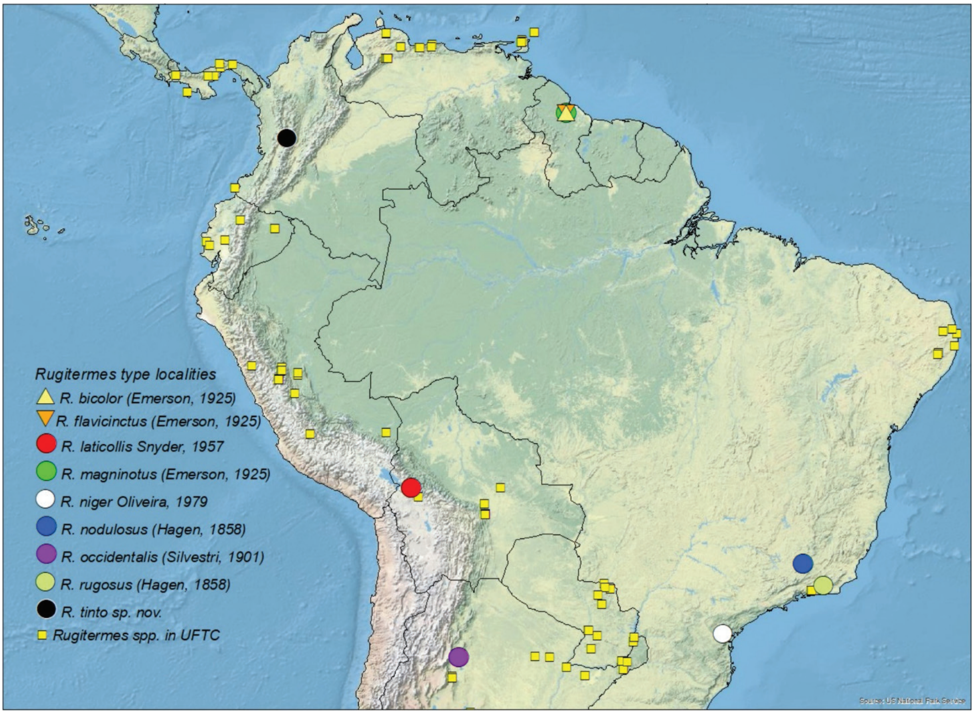

Figure 1. Type localities for all *Rugitermes* species described from South America and collection localities for *Rugitermes* spp. in the University of Florida Termite Collection (UFTC).

from southern Brazil, and *R. occidentalis* (Silvestri, 1901) from Argentina. The type localities for the South American species, including *Rugitemes tinto* sp. nov., are given in Fig. 1.

In South America, only four kalotermitid genera have soldiers with virtually no head capsule phragmosis: *Comatermes*, *Incisitermes*, *Neotermes*, and *Rugitermes* (Scheffrahn, 2019a). In his generic description, Krishna (1961) wrote that the *Rugitermes* soldier can be differentiated from the other three genera by the former's "prominent ridge…present in front of and medial to the antennal socket". The *Rugitermes* imago is distinguished by its "short, sclerotized median vein in the forewing which joins the radial sector very close to the wing suture" (Krishna 1961). The coloration of the head and pronotum contrast sharply in the majority of species.

Herein, we describe the imago and soldier of *Rugitermes tinto* sp. nov. This is the first record of *Rugitermes* from Colombia.

Material and methods

Microphotographs were taken as multi-layer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Preserved specimens were taken from 85 % ethanol and suspended in a pool of Purell Hand Sanitizer to position the specimens on a transparent Petri dish background.

Taxonomy

Rugitermes tinto Scheffrahn & Pinzón Florian, sp. nov.

http://zoobank.org/601947D7-EF34-4209-A9A2-7B43A11BF317
Figures 2, 3

Diagnosis. The soldier of *R. tinto* is the only non-phragmotic kalotermitid worldwide with dark coloration of the anterior head capsule. Aside from head color, it differs from congeneric soldiers in that the anterolateral corners of the frontal ridges project to form acute angles. In other South American (Fig. 4), Central American, and Oceanian *Rugitermes*, the anterolateral corners of the frontal ridges are either at right or obtuse angles.

Among South American species, the imago of *R. tinto*, with contrasting coloration of the head and pronotum, is similar to *R. bicolor*, *R. flavicinctus*, *R. magninotus*, and *R. nodulosus*. Of these, the imago of *R. bicolor* is larger, while that of *R. flavicinctus* is smaller than *R. tinto* and the head/pronotum coloration of the former two are similar to *R. magninotus*. The imago of *R. magninotus* has a brown head and a yellow pronotum while the imago of *R. tinto* has a black head and a brownish pronotum. The distribution of *R. nodulosus* is known only from southern Brazil (Minas Gerais).

Description. ***Imago*** (Fig. 2A, B). Single female damaged: distal half of left wings torn, right wings absent. Head capsule black; pronotum brownish orange. Compound eye small, nearly circular. Ocellus very small, circular, black; difficult to see as there is no contrast with

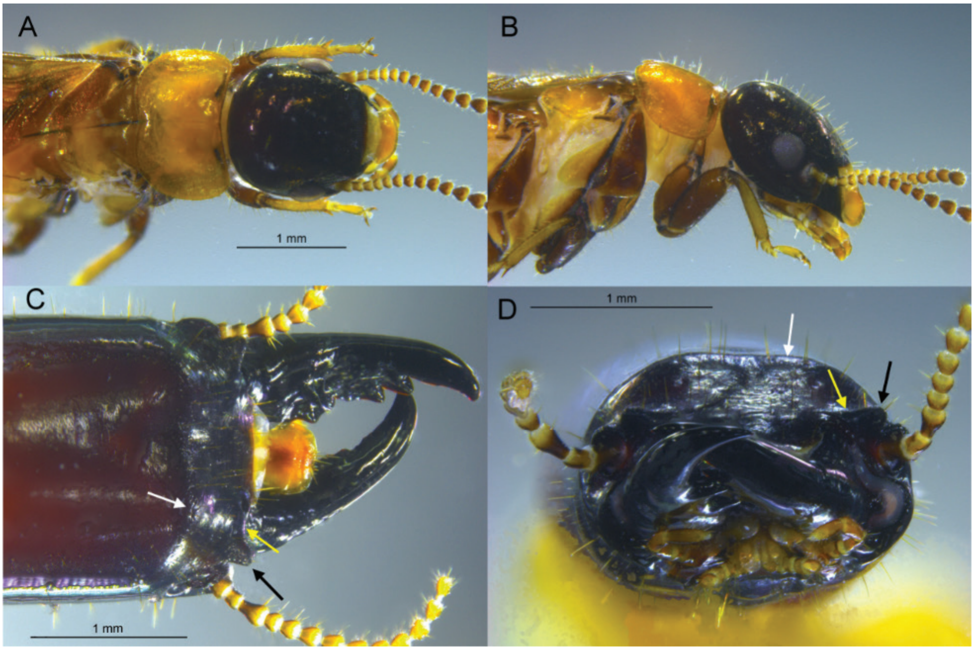

Figure 2. *Rugitermes tinto* sp. nov. **A** Dorsal **B** lateral views of head and thorax of imago **C** dorsal **D** frontal views of anterior soldier head capsule (white arrows mark frontal flange, yellow arrows mark frontolateral ridge, and black arrows mark protuberance of frontolateral ridge).

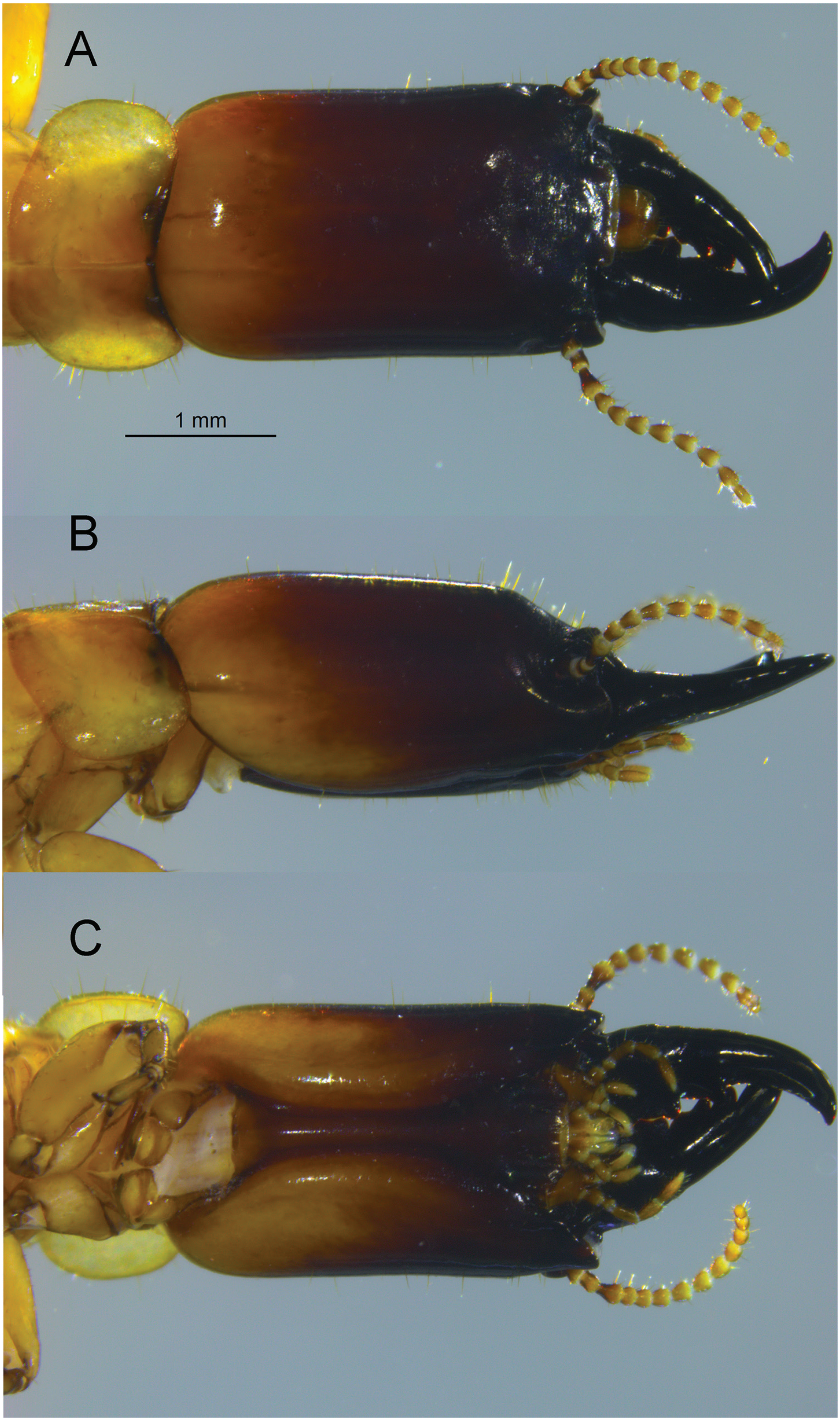

Figure 3. *Rugitermes tinto* sp. nov. soldier head and pronotum. **A** Dorsal **B** lateral **C** ventral view.

head capsule cuticle; ocellus well removed from eye margin. Head vertex and frons not depressed; frons with faint rugosity; covered with dozens of erect setae ca 0.15-mm-long. Pronotum slightly wider than head capsule; anterior margin slightly incised; posterolateral corners evenly rounded, posterior margin narrowly concave. Pronotum pilosity congruent with vertex. Antennae with at least 16 articles, basal article relative lengths 1>2=3>4. Forewing anterior half as per genus; median vein very short, joins radial 0.9 mm from wing scale. Wing scale covered with about 20 setae of similar length and density as those on head and pronotum. Wing membrane smokey brown, covered with darker nodules. Legs dark brown. Arolium present. Measurements (maximum, mm): head width 1.31, pronotum width 1.43, eye diameter 0.32, ocellus diameter 0.01, and body length 7.9.

Soldier (Figs 2C, D, 3). Head capsule, in dorsal view, dark castaneous brown from posterior margin of postclypeus to posterior one fourth; posterior one fourth grading from dark reddish brown to brownish orange at occiput. In ventral view, head capsule coloration grades gradually from dark castaneous brown to brownish orange with exception of postmentum which remains dark reddish brown at posterior. Pronotum yellowish with reddish interior, in obvious contrast with head capsule coloration. Head capsule long, rectangular; lateral margins very slightly concave in middle, covered with a few setae except at frons where setae are denser. Pronotum much wider than long; with scattered setae, denser along lateral margins; anterior margin weakly incised. In dorsal view, the frontal flange forms a weak hemispherical border surrounding the frons. The frontal flange forms a 30° angle with plane of vertex. Frons finely rugose. In dorsal view (Fig. 2C), frontolateral ridges form shelves on each side of the frons almost in-line with posterior margin of postclypeus. The outer margins of each ridge are adorned with protuberance forming acute angles of ca 65°. In frontal view, the ridges rise slightly at their protuberances; dorsal margins of antennal carinae ("sockets") positioned well below ridges. Eye spots small, concolorous with head capsule. Third antennal article club-shaped, about twice as long as second and fourth articles. Mandibles about half length of head capsule; outside margin of each blade curving gradually, with very slight hump at base. Measurements in mm [mean (range, $N = 6$)]: Head length lateral base of mandibles: 2.83 (2.47–2.99), max. head width 1.72 (1.52–1.90), max. head height with postmentum 1.42 (1.29–1.47), max. pronotum width 1.86 (1.58–2.04), max. pronotum length 0.90 (0.86–0.95), third antennal article length 0.19 (0.18–0.20).

Type material examined. ***Holotype*** (soldier). Colombia: Risaralda, Pereira (4.810, -75.695); 1410 meters a.s.l., 11APR1998, J. Navarro, A. Arevalo; two soldiers (one labelled holotype), one damaged female imago University of Florida Termite Collection (UFTC) no. CO919, subsample from Colección Entomológica Forestal Universidad Distrital "Francisco José de Caldas" (CEFUDFJC) no. 009942 of which remains one soldier and three pseudergates.

Other material examined. Colombia: Cundinamarca, Villeta (5.017, -74.467); 842 meters a.s.l., no date, A. Moreno; one soldier and two pseudergates; CEFUDFJC no. 009940. Colombia: Risaralda, Pereira (4.810, -75.695); 1410 meters a.s.l., 11APR1998, J. Navarro, A. Arevalo. Same location; two soldiers, three pseudergates; CEFUDFJC no. 009942.

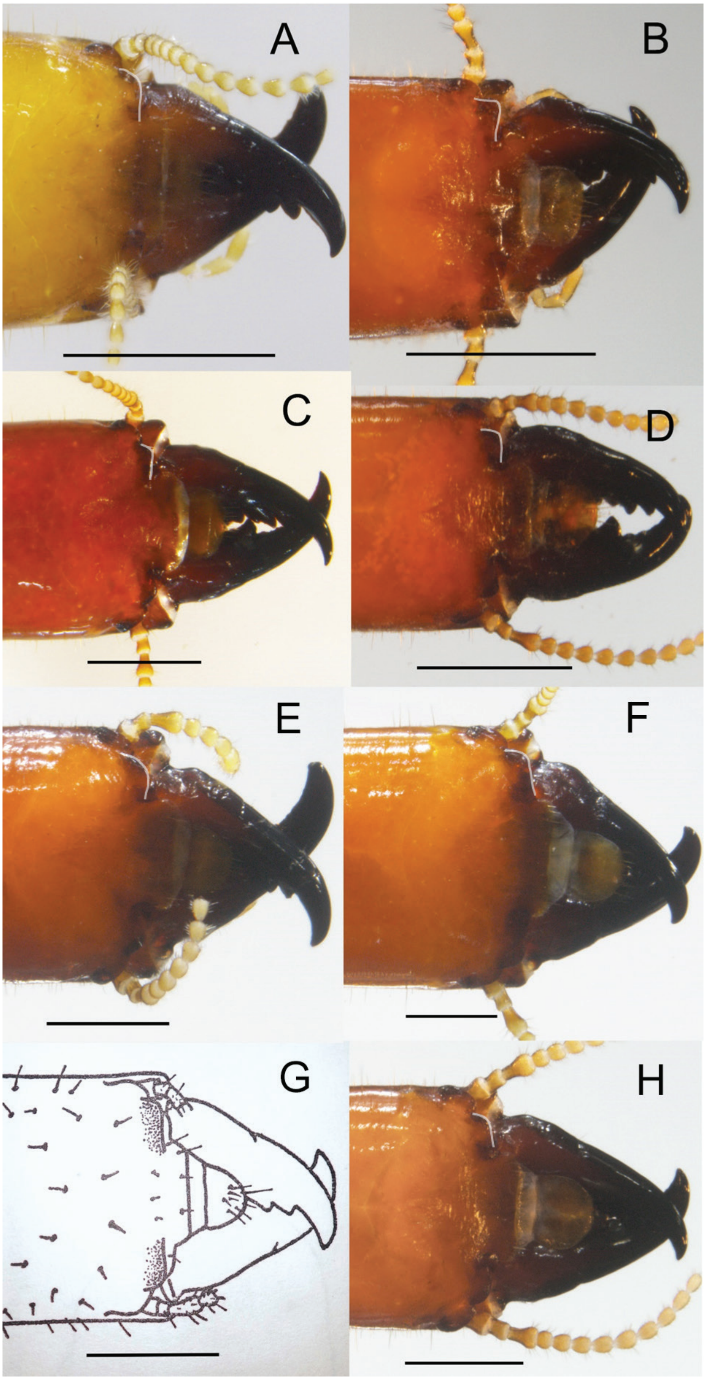

Figure 4. Anteriodorsal views of *Rugitermes* soldier heads from South America. Margins of left frontolateral ridges enhanced. **A** *R. bicolor*, PU946 **B** *R. flavicinctus*, TT88 **C** *R. laticollis*, EC1465 **D** *R. magninotus*, PU1087 **E** *R. occidentalis*, AG380 **F** *R. niger*, AG500 **G** *R. nodulosus* (modified from fig. 14, Krishna 1961) **H** *R. rugosus* PA1186. Accession numbers from UFTC (Scheffrahn 2019b). Scale bars: 1 mm.

Distribution. *Rugitermes tinto* is known from the Cauca River Valley montane ecoregion (Pereira) which has a mesic climate (Olson et al. 2001) and from the higher slopes of the Magdalena River Valley ecoregion (Villeta) which is characterized by more xeric forests (Sánchez-Cuervo et al. 2012).

Etymology. "Tinto" is the Colombian name for plain black coffee which is reminiscent of the dark coloration of the *R. tinto* soldier head capsule. The type locality of *R. tinto*, Pereira, is also in the major coffee growing area of Colombia.

Discussion

Authoritative records of the kalotermitid diversity for Colombia are reported almost entirely from the Caribbean Region (Casalla et al. 2016a, b; Snyder 1925; Krishna and Emerson 1962; Scheffrahn 2019a, b). An Andean termite survey by Parra and Soto (1992) is a remarkable exception as they report ten kalotermitids from this region. Except for *Cryptotermes brevis* (Walker), their generic and specific assignments are mostly incorrect. Furthermore, the drawings by Parra and Soto (1992) do not allow for positive identification below family. Aside from *R. tinto* and *C. brevis*, the only other confirmed kalotermitid from Andean Colombia is *Glyptotermes truncatus* (Krishna & Emerson, 1962).

It is hoped that future termite collecting in Andean Colombia will uncover many new termite species and expand known species distribution records. The Magdalena River Valley recently also yielded a new non-kalomitid termite, *Rhynchotermes armatus* Scheffrahn (2019c).

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RESEARCH ARTICLE

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Taxonomic revision of the Afrotropical *Agabus raffrayi* species group with the description of four new species (Coleoptera, Dytiscidae)

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Abstract

We revise the Afrotropical *Agabus raffrayi* species group, motivated by the discovery of new diversity in Kenya and South Africa. Whilst *Agabus* is mainly a holarctic genus, the *Agabus raffrayi* group is restricted to high altitude regions of eastern Africa and temperate parts of South Africa, from where we describe the southernmost *Agabus* in the world. The following new species are introduced: *Agabus anguluverpus* **sp. nov.** from Mount Kenya in central Kenya, *Agabus austellus* **sp. nov.** a widespread species in South Africa, *Agabus riberae* **sp. nov.** from the Kamiesberg and northeastern Cederberg ranges in the Northern and Western Cape Provinces of South Africa and *Agabus agulhas* **sp. nov.** from the Agulhas Plain, Western Cape Province, South Africa. We provide a distribution map, a determination key for males, quantitative measurements of diagnostic characters, habitus photos and detailed photos of male genitalia for all described species in the group, as well as images of diagnostic characters and habitats. The presence or absence of an elongated section between the subapical broadening and the base of the apical and subapical teeth of the male aedeagus is a useful novel character, first revealed by our study. In contrast with the most recent revision of Afrotropical *Agabus*, we show that *Agabus ruwenzoricus* Guignot, 1936 is restricted to eastern Africa; South African records of this species having been based on misidentifications, no species of the group being common to southern and eastern Africa. We speculate that the *raffrayi* group may display phylogenetic niche conservatism, being restricted, as an originally temperate taxon, to higher elevations in tropical eastern Africa, but occurring at lower altitudes in temperate South Africa.

Keywords
Afromontane, diving beetles, freshwater, new species, taxonomy

Introduction

With over 170 species, *Agabus* Leach, 1817 is a large and complex genus of diving beetles which is particularly diverse in temperate regions of the Holarctic. Species-level identification characters in *Agabus* are often subtle, with the taxa known from the Afrotropical region being no exception. Nilsson (1992a) made a significant contribution to our understanding of Afrotropical *Agabus*, defining species groups and providing keys for the identification of all species known at the time. Afrotropical *Agabus* are mainly high altitude specialists, distributed from Ethiopia to South Africa. There are currently 17 described species, placed in four distinct species groups, the *ambulator*, *ragazzi*, *cordatus* and *raffrayi* groups (Nilsson 1992a). With the exception of some species in the *raffrayi* group, all Afrotropical taxa are endemic to Ethiopia (Nilsson 1992a). Recently, a combination of newly collected material together with problems encountered with certain morphological characters have prompted us to conduct a revision of the *Agabus raffrayi* group. At present this group consists of five species: *A. dytiscoides* Régimbart, 1908, *A. pallidus* Omer-Cooper, 1931, *A. raffrayi* Sharp, 1882, *A. ruwenzoricus* Guignot, 1936 and *A. sjostedti* Régimbart, 1908. This revision aims to clarify morphological species delimitations for these taxa, describe four new species which have come to light more recently, and present a new identification key for the group.

With the exception of the three taxa described here from South Africa, species of the *Agabus raffrayi* group are apparently restricted to relatively high elevations, between 1900 and 4300 m (see Fig. 1). The high number of montane specialists in the group could be related to the environmental history of the region. African tropico-alpine ecosystems are believed to be relatively young (Linder 2014) and Nilsson (1992a) suggested that the cold, dry climate of the Quaternary may have forced Afrotropical *Agabus* to adapt to higher altitudes in order to survive, and that this adaptation cannot easily be reversed. Additionally, species of this largely temperate genus may display a degree of phylogenetic niche conservatism (sensu Morinière et al. 2016), physiologically restricting them to relatively cool climates. Such suggestions correlate with the apparent lack of high-altitude specialist *Agabus* in South Africa, an area that has retained a relatively temperate climate throughout the Quaternary period, particularly in the Cape (Meadows and Baxter 1999; Dupont et al. 2011).

Material and methods

Abbreviations

Material studied is deposited in the following collections:

AMG	Albany Museum, Grahamstown, South Africa
BMNH	The Natural History Museum, London, UK
CBP	Collection D T Bilton, Plymouth, UK
IBE	Institut de Biologia Evolutiva, Barcelona, Spain
ISAM	Iziko South African Museum, Cape Town, South Africa
MfN	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
MZLU	Biological Museum, Entomological collections, Lund, Sweden
NHRS	Swedish Museum of Natural History, Stockholm, Sweden
NMK	National Museums of Kenya, Nairobi, Kenya
SANC	South African National Collection of Insects, Pretoria, South Africa
ZSM	Zoologische Staatssammlung, München, Germany

Additional acronyms used:

WC	Width of metacoxal plate
WS	Width of metasternal wing (correct term is lateral extension of the metaventrite but we use here the term "metasternal wing" to adhere to previous literature on the group, e.g., Nilsson and Persson 1990).

Measurements

Characters were measured using a WILD 445111 10x/21B ocular on a LEICA M125 microscope.

Individual measurements were taken as follows:

Metatarsomeres 2 and 5 were measured from a lateral perspective, using the maximum length and width.

The ratio of the width of metacoxal plate to the width of metasternal wing (WC/WS) was measured as in Nilsson and Persson (1990): WS was measured at the shortest distance between the mesocoxa and the metacoxal plate, with WC continuing along the line of WS (see Fig. 2).

Protarsal claw/protarsomere 4. The length of the protarsal claw was measured from a lateral perspective, using the maximum distance between the base and apex of the claw (see Fig. 3); maximum length of protarsomere 4 was also measured from a lateral perspective.

Pronotum/Interocular distance was measured in dorsal view, using the maximum distance for pronotum width and minimum interocular distance (see Fig. 4).

Body length was measured in dorsal view, from the anterior margin of the head to the tip of the elytra.

Preparation of genitalia

Male genitalia were extracted from the tip of the abdomen using fine forceps. The aedeagus and parameres were then carefully separated from the last divided sternite (VIII) and glued onto a mounting card on the same pin as the specimen. The removed sternites of the abdomen as well as parts removed during extraction of genitalia were also mounted on the same card. Dry specimens were submerged in hot water for 15 minutes prior to preparation in order to soften the body to facilitate extraction.

Photographs, figures and tables

Photographs were taken using a Canon EOS 5D Mark II DSLR camera with a Canon MP-E 65 mm 1–5× macro lens mounted on a motorized rail (Cognisys Stackshot). Elytral microreticulation was imaged using a Canon EOS 600D camera attached to a Leica Z6 APO macroscope with a 2× objective lens. Aedeagal apices of South African species were imaged with the same system, as temporary mounts in hand sanitizer gel. Images were stacked using the PMax algorithm in Zerene Stacker and manually edited in Photoshop. Boxplots were made using R version 3.4.3.

Taxonomic results

Agabus raffrayi group

Nilsson (1992a) gives a full diagnosis of the *Agabus raffrayi* group. It is noteworthy that Nilsson was unable to find a single synapomorphic character for the group, but states that the very similar appearance of the aedeagus amongst the species of the group might suggest a common evolutionary history. The aedeagus shape of the four new species described here does differ somewhat from the five species known to Nilsson, but follows the same basic design. Nilsson (1992b) described larval morphology of some species belonging to the *raffrayi*, *ambulator* and *ragazzi* groups. He concluded that *A. raffrayi* (and probably also *A. ruwenzoricus*) larvae can be distinguished from the two other groups by its short urogomphus as well as terga with long spiniform setae (among other characters).

The nine species of the group recognised in this revision are all endemic to the Afrotropical region (see Fig. 1). Three species are endemic to the Republic of South Africa, one of which is widespread there. Two species are endemic to Ethiopia, two species endemic to Tanzania, and one endemic to Kenya. Based on current understanding, only one of the nine species has a geographical range spanning over several countries, namely *A. ruwenzoricus*, collected in Kenya, Rwanda, Uganda and the Democratic Republic of the Congo.

Key to males of the *Agabus raffrayi* group

1 Aedeagus not prolonged between subapical broadening and base of apical and subapical teeth (as in Figs 5D, 6) **2**

– Aedeagus prolonged between subapical broadening and base of apical and subapical teeth (as in Fig. 5A–C) **5**

2 Pronotal bead broad, especially anteriorly. Aedeagus in ventral view with apex straight (Fig. 7A), in lateral view evenly thickened and not distinctly broadened subapically; subapical tooth slightly angled both at base and apex (see Fig. 8F). Females with coarse microreticulation on pronotum and elytra, much coarser than in males. Known only from Mt. Kenya .... ***A. anguluverpus* sp. nov.**

– Pronotal bead narrower and not becoming broader anteriorly. Aedeagus in ventral view with apex asymmetrically curved (see Fig. 7B), in lateral view usually subapically broadened (see Fig. 8G–I); subapical tooth not distinctly angled twice. Female microreticulation much more similar to males. South Africa **3**

3 Base of subapical tooth of aedeagus distinctly angled (Figs 6G, 8I). Scutellum lighter than elytra .... ***A. agulhas* sp. nov.**

– Base of subapical tooth of aedeagus not distinctly angled (Figs 6A–F, 8G–H). Scutellum same colour as elytra **4**

4 Metasternal wing narrow, WC/WS > 3.1 in all specimens. Microreticulation of elytral disc dominated by relatively small, approximately isodiametric meshes in most specimens (Fig. 9B, C) .... ***A. austellus* sp. nov.**

– Metasternal wing wide, WC/WS < 3.0 in most specimens. Microreticulation of elytral disc dominated by relatively large, uneven meshes (Fig. 9E) .... ***A. riberae* sp. nov.**

5 Hypomeron broadly visible in strict lateral view (see Fig. 10A, B). Protarsal claw < 1.6× as long as protarsomere 4. Known only from high mountains of Tanzania **6**

– Hypomeron not visible in strict lateral view (see Fig. 10C, D). Protarsal claw usually > 1.6× as long as protarsomere 4. Known from Kenya, Rwanda, the Democratic Republic of the Congo, Uganda and Ethiopia 7

6 Large species, body length > 8 mm. Pronotum broad, width of pronotum > 2× interocular distance. Metasternal wing broad, WC/WS > 3.6 in most specimens. Subapical tooth of aedeagus robust, with tip angled downwards .... ***A. sjostedti***

– Smaller species, body length < 8 mm long. Pronotum narrow, width of pronotum < 2× interocular distance. Metasternal wing narrow, WC/WS < 3.6 in most specimens. Subapical tooth of aedeagus less robust, with tip not distinctly angled downwards .... ***A. dytiscoides***

7 Interocular spots clearly visible (as in Fig. 4B). Known from Kenya, Rwanda, the Democratic Republic of the Congo and Uganda .... ***A. ruwenzoricus***

– Specimens normally without interocular spots (as in Fig. 4D). Ethiopia **8**

8 Metasternal wing narrow, WC/WS > 3.0 in most specimens .... ***A. pallidus***

– Metasternal wing broad, WC/WS < 2.9 in most specimens .... ***A. raffrayi***

Agabus raffrayi Sharp, 1882

Figures 1, 2B, 3B, 5A–C, 8D, 10D, 11D, 11I, 12, 13, 14

Agabus raffrayi Sharp, 1882: 501–502
Agabus limbicollis Régimbart, 1905: 224–225 (Syn. Nilsson 1992a)

Type locality. *raffrayi* "Abyssinia" [Ethiopia]; *limbicollis* "Abyssinie: Auato, au bord du Nil Bleu, dans le Gindeberat" [Ethiopia: Auato, on the banks of the Blue Nile, in the Gindeberat].

Type material. ***Lectotype*** ♂ of *raffrayi* (BMNH) labelled: "♂ Abyssinia, Raffray 782", "Type", "Sharp Coll 1905-313.", "Type 782 Agabus Raffrayi n.sp. Abyssinia", "LECTOTYPUS ♂ Agabus raffrayi Sharp, 1882 Des. A.Nilsson, 1989". ***Lectotype*** ♂ of *limbicollis* (MNB) labelled: "N.O. – Africa, Schoa, Falle O. Neumann S.", "610 Falle", "Agabus limbicollis Rég. Type.", "LECTOTYPUS ♂ Agabus limbicollis Régimbart, 1905. Des. Nilsson -90".

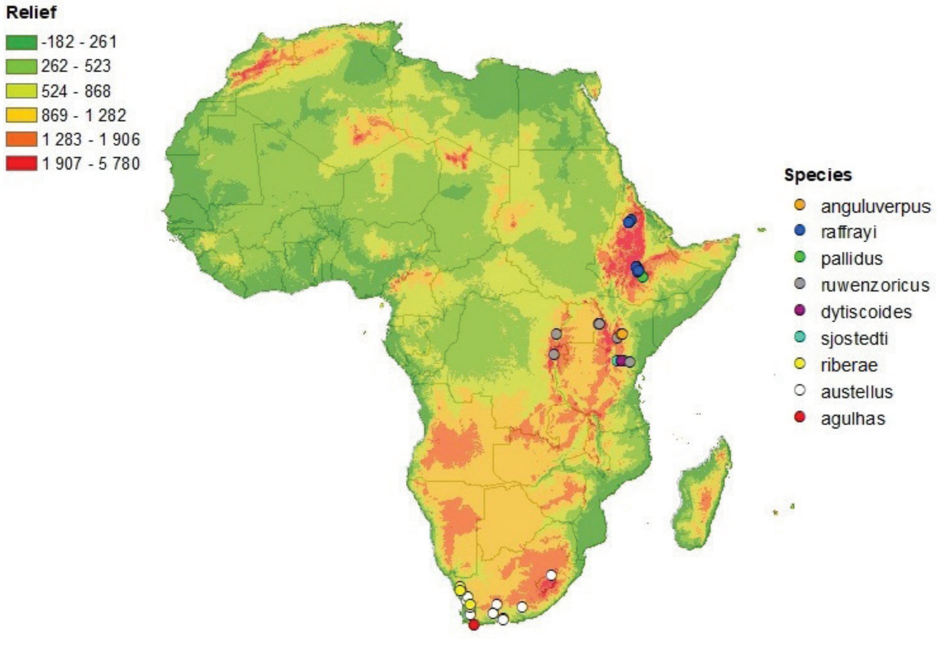

Figure 1. Distribution map of the *Agabus raffrayi* group. Relief is expressed in meters above sea level.

Figure 2. *Agabus* spp., metasternal wing and metacoxal plate in ventral view **A** *A. pallidus* **B** *A. raffrayi*. Dashed lines indicate measurements used; red: metasternal wing (WS), blue: metacoxal plate (WC).

Diagnosis. With a prolonged preapical section of male aedeagus and a pronotal hypomeron which is not visible in lateral view, this species is most similar to *A. pallidus* and *A. ruwenzoricus*. From the former it is separated by its broader metasternal wing (Figs 2, 12) and from the latter by the lack of interocular spots (compare Fig. 4D, B).

Description. Habitus as in Fig. 11D, I.

***Colour*:** Head black, most specimens with a small rufous anterior area, interocular spots not present. Pronotum black with rufous margins. Elytra rufotestaceous to brown. Ventral surface black, hypomeron and epipleuron testaceous. Legs rufous to rufopiceous. Antennae and palpi testaceous to rufotestaceous.

***Microreticulation*:** Medium impressed on head, pronotum and elytra, similar in both sexes. Composed of a mixture of small and somewhat larger, uneven meshes.

***Structural features*:** Body length: 6.96–8.24 mm (see Table 1). Hypomeron not visible in strict lateral view (Fig. 10D), lateral bead of pronotum well defined (see Fig. 10D). Metasternal wing broad, WC/WS less than 2.9 (see Table 1, Figs 2B, 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1, as in Fig. 4B).

***Legs*:** Protarsal claws long, > 1.6× as long as protarsomere 4 in all males and most females (see Table 2, Fig. 14). Metatarsomeres short and broad; metatarsomere 2 < 1.6× as long as broad (see Table 2), metatarsomere 5 < 3.0 times as long as broad (see Table 2).

Table 1. Morphological characters in the *Agabus raffrayi* group. WC/WS = width of metacoxal plate / width of metasternal wing, PW/ID = width of pronotum/interocular distance, TL = total body length, N = number of specimens, Min = minimum value, Max = maximum value, SD = standard deviation, NA = not applicable.

Species	Sex	WC/WS					PW/ID					TL				
		N	Min	Max	Mean	SD	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
A. sjostedti	♀	2	3.60	3.69	3.64	0.06	2	2.05	2.10	2.07	0.04	2	8.08	8.24	8.16	0.11
	♂	4	3.29	3.65	3.55	0.17	4	2.07	2.24	2.13	0.08	4	8.40	9.12	8.70	0.31
A. dytiscoides	♀	2	3.00	3.27	3.13	0.19	2	1.93	1.93	1.93	0.00	2	7.36	7.60	7.48	0.17
	♂	5	2.88	3.40	3.14	0.22	5	1.93	1.98	1.96	0.02	5	7.36	7.76	7.55	0.18
A. anguluverpus sp. nov.	♀	1	3.47	3.47	3.47	NA	1	2.10	2.10	2.10	NA	1	7.52	7.52	7.52	NA
	♂	2	3.19	3.53	3.36	0.25	2	2.05	2.15	2.10	0.07	2	7.36	7.44	7.40	0.06
A. austellus sp. nov.	♀	17	3.11	4.15	3.55	0.23	17	2.12	2.30	2.22	0.05	17	6.80	8.16	7.53	0.40
	♂	27	3.17	4.0	3.52	0.25	27	2.12	2.49	2.28	0.08	27	7.04	8.40	7.67	0.36
A. ruwenzoricus	♀	9	2.90	3.41	3.16	0.19	9	2.05	2.33	2.19	0.10	9	7.36	8.08	7.67	0.21
	♂	17	2.73	3.63	3.05	0.28	17	2.09	2.33	2.24	0.07	17	7.52	8.08	7.86	0.20
A. raffrayi	♀	5	2.11	2.84	2.58	0.28	5	2.16	2.33	2.25	0.06	5	6.96	8.16	7.70	0.45
	♂	7	2.46	2.71	2.61	0.10	7	2.25	2.29	2.27	0.01	7	7.52	8.24	7.82	0.31
A. pallidus	♀	6	3.06	3.53	3.29	0.16	6	2.15	2.29	2.22	0.05	6	7.52	8.08	7.79	0.25
	♂	5	3.05	3.81	3.39	0.27	5	2.30	2.45	2.34	0.06	5	7.92	8.40	8.14	0.18
A. riberae sp. nov.	♀	6	3.00	3.17	3.05	0.07	6	2.24	2.33	2.27	0.03	6	7.21	8.08	7.70	0.35
	♂	16	2.65	3.53	2.91	0.19	16	2.21	2.37	2.28	0.05	16	7.21	8.24	7.83	0.29
A. agulhas sp. nov.	♀	2	3.67	3.75	3.71	0.06	2	2.15	2.18	2.16	0.02	2	7.94	7.94	7.94	0
	♂	4	3.67	4.54	4.01	0.38	4	2.10	2.24	2.17	0.06	4	7.60	8.00	7.86	0.19

Table 2. Morphological characters in the *Agabus raffrayi* group. MT2L/MT2W = length/width of metatarsomere 2, MT5L/MT5W = length/width of metatarsomere 5, CL/PT4L = length of protarsal claw/length of protarsomere 4, N = number of specimens, Min = minimum value, Max = maximum value, SD = standard deviation, NA = not applicable.

Species	Sex	MT2L/MT2W					MT5L/MT5W					CL/PT4L				
		N	Min	Max	Mean	SD	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
A. sjostedti	♀	2	1.71	1.90	1.81	0.14	2	3.31	3.57	3.44	0.19	2	1.33	1.38	1.36	0.03
	♂	4	1.68	1.92	1.80	0.10	4	3.12	3.67	3.39	0.22	4	1.3	1.39	1.35	0.04
A. dytiscoides	♀	2	2.00	2.05	2.03	0.04	2	3.77	4.17	3.97	0.28	2	1.53	1.59	1.56	0.04
	♂	5	1.81	2.00	1.91	0.07	5	3.69	4.17	4.02	0.19	5	1.26	1.47	1.35	0.10
A. anguluverpus sp. nov.	♀	1	1.85	1.85	1.85	NA	1	3.07	3.07	3.07	NA	1	1.80	1.80	1.80	NA
	♂	2	1.86	1.95	1.90	0.07	2	3.33	3.46	3.40	0.09	2	1.69	1.87	1.78	0.13
A. austellus sp. nov.	♀	17	1.38	1.84	1.57	0.14	17	2.46	3.55	2.88	0.25	17	1.44	2.00	1.77	0.14
	♂	27	1.29	1.80	1.61	0.14	27	2.54	3.50	3.06	0.25	26	1.50	1.88	1.70	0.09
A. ruwenzoricus	♀	9	1.40	1.67	1.49	0.08	8	2.46	3.09	2.76	0.23	9	1.43	1.73	1.64	0.09
	♂	17	1.32	1.75	1.46	0.12	17	2.46	3.23	2.71	0.20	17	1.53	1.88	1.70	0.09
A. raffrayi	♀	5	1.31	1.43	1.37	0.05	5	2.50	2.67	2.59	0.09	5	1.46	1.93	1.69	0.18
	♂	7	1.22	1.52	1.35	0.10	6	2.31	2.92	2.54	0.21	6	1.63	1.87	1.74	0.11
A. pallidus	♀	6	1.30	1.50	1.37	0.09	6	2.46	2.92	2.65	0.17	6	1.67	1.86	1.77	0.07
	♂	5	1.25	1.36	1.30	0.05	5	2.36	2.67	2.48	0.12	5	1.63	1.86	1.75	0.12
A. riberae sp. nov.	♀	6	1.67	1.76	1.71	0.04	6	2.93	3.31	3.12	0.15	6	1.53	1.68	1.62	0.07
	♂	16	1.64	1.88	1.72	0.06	16	2.94	3.54	3.24	0.21	16	1.60	1.75	1.66	0.05
A. agulhas sp. nov.	♀	2	1.48	1.52	1.50	0.03	2	2.64	2.71	2.68	0.05	2	1.78	1.88	1.83	0.07
	♂	4	1.43	1.52	1.48	0.04	4	2.62	2.83	2.70	0.09	4	1.80	2.21	2.00	0.18

***Male genitalia*:** Subapically broadened, and prolonged between the subapical broadening and the apical and subapical teeth. Subapical tooth with quite variable shape (see Figs 8D, 5A–C).

Female: Externally similar to males but colour of the elytra tends to be slightly lighter.

Distribution. Ethiopia (see Fig. 1). Rocchi (1975) listed the distribution of *A. raffrayi* to also include the Democratic Republic of the Congo, Uganda, Rwanda, Tanzania, Zimbabwe, and South Africa but these specimens are likely to belong to other species.

Habitat. Found in small, often temporary, streams and pools in streambeds at elevations between 2100 to 3200 m (Nilsson and Persson 1990, 1993; Nilsson 1992a).

Etymology. The name refers to the collector of the type specimens, Achille Raffray. The name of the synonym *A. limbicollis* refers to the well-defined lateral bead of the pronotum (Latin: *limbus* = border, *collum* = neck).

Comments. The fact that *A. raffrayi* and *A. pallidus* are distinguishable only on the width of the metasternal wing led some previous authors to suggest the occurrence of a single species which was dimorphic with regard to this character (Jackson 1956). Nilsson and Persson (1990) provided a detailed account of this argument, analysed a large series of specimens and concluded that the variation should rather be interpreted as two separate species. We agree with this assessment and concur that male genitalia are not diagnostic for these two species, only the width of the metasternal wing being reliable. In our measurements, the pronotum is marginally broader in *A. pallidus* but the small sample size forbids any strong conclusions at present (Fig. 13).

Nilsson (1992b) described the larval morphology of *Agabus raffrayi* along with some representatives of two other Afrotropical *Agabus* groups.

Agabus pallidus Omer-Cooper, 1931

Figures 1, 2A, 3B, 4D, 8E, 11E, 11J, 12, 13, 14

Agabus pallidus Omer-Cooper, 1931: 786–787, fig. 3a, pl. 9: 7

Type locality. “Between Addis Abeba and Addis Alem” [Ethiopia].

Type material. ***Lectotype*** ♀ (BMNH) labelled: “Type”, “Abyssinia: Between Addis Abeba and Addis Alem 7,500 ft. 18.ix.1926. J.Omer-Cooper.”, “Agabus pallidus, Joyce Omer-Cooper. 1931. TYPE.”, “A. pallidus.O.C.”, “LECTOTYPUS ♀ Agabus pallidus Omer-Cooper, 1931 Des. A. Nilsson, 1989”.

Diagnosis. Similar in all diagnostic features to *A. raffrayi* except for the narrower metasternal wing (Table 1, Figs 2, 12).

Description. Habitus as in Fig. 11E, J.

***Colour*:** Head black, most specimens with a small rufous anterior area, interocular spots not present. Pronotum black with rufous margins. Elytra rufotestaceous to brown. Ventral surface black, hypomeron rufous, epipleuron testaceous to rufotestaceous. Legs rufous to rufopiceous. Antennae and palpi testaceous to rufotestaceous.

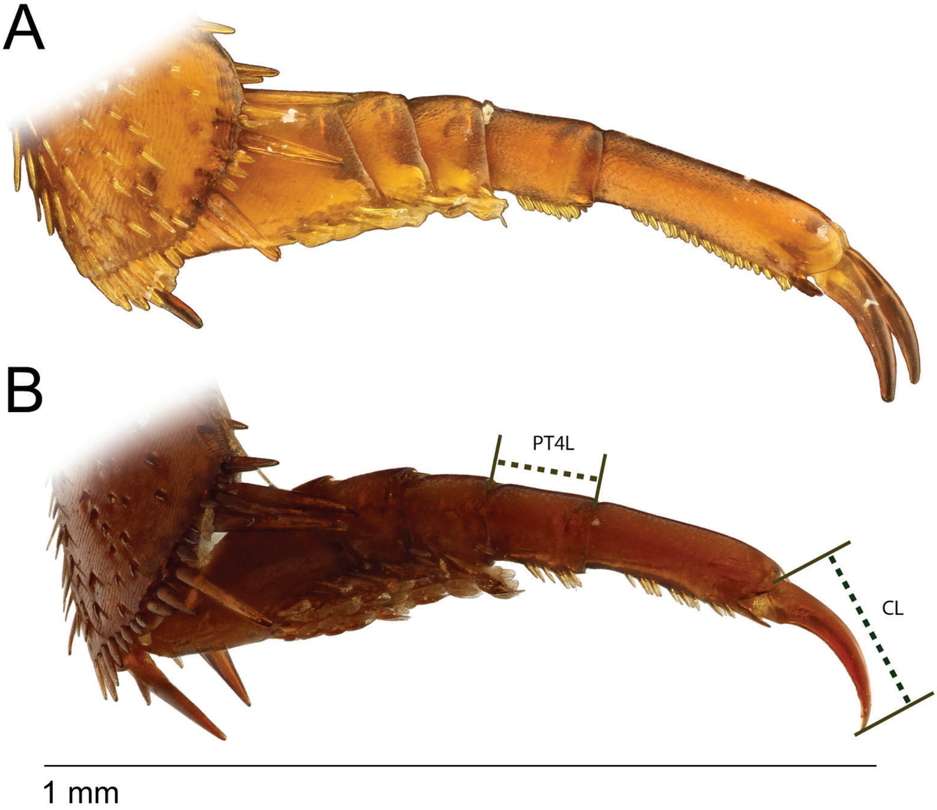

Figure 3. *Agabus* spp., protarsomeres in anterior view **A** *A. dytiscoides* **B** *A. raffrayi*. PT4L = measured distance for length of protarsomere 4; CL = measured distance for length of protarsal claw.

***Microreticulation*:** Medium impressed on head and pronotum, similar in both sexes. Composed of a mixture of small and somewhat larger, uneven meshes. Elytral microreticulation similar, but less strongly impressed and more uneven, with some relatively elongate meshes, especially close to suture. One female examined (Ethiopia, Arsi, 13 km E Bekoji) has more strongly impressed elytral reticulation, with distinctly wider grooves between meshes.

***Structural features*:** Body length: 7.52–8.40 mm (see Table 1). Hypomeron not visible in lateral view (as in Fig. 10C, D), lateral bead of pronotum well defined (Fig. 10D). Metasternal wing narrow, WC/WS > 3.0 (see Table 1, Figs 2A, 12). Pronotum very broad, more than or equal to 3.3× as broad as interocular distance in males (see Table 1, Figs 4D, 13).

***Legs*:** Protarsal claws long, > 1.6× as long as protarsomere 4 (see Table 2 and Fig. 14). Metatarsomeres short and broad; metatarsomere 2 < 1.6× as long as broad (see Table 2), metatarsomere 5 < 3.0 times as long as broad (see Table 2).

***Male genitalia*:** Subapically broadened, and prolonged between the subapical broadening and the apical and subapical teeth (Fig 8E). Subapical tooth with varying appearance (similar to magnitude in variation seen in Fig. 5A–C).

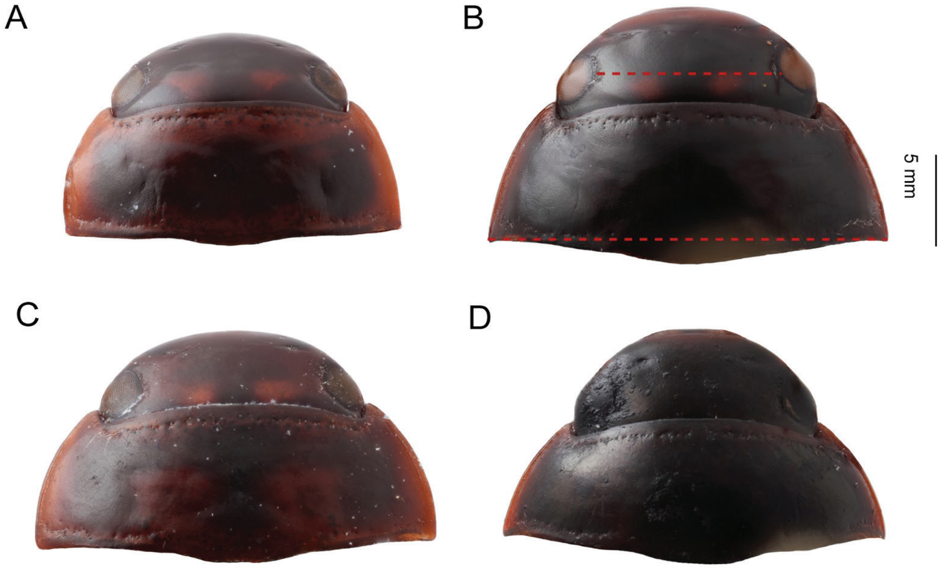

Figure 4. *Agabus* spp., head and pronotum in dorsal view **A** *A. dytiscoides* **B** *A. ruwenzoricus* **C** *A. sjostedti* **D** *A. pallidus*. Red dashed lines indicate measurements used for interocular distance and pronotal width.

Female: Externally similar to males.

Distribution. Ethiopia (see Fig. 1).

Habitat. Found in small streams and often temporary waterbodies at elevations of 2250 to 4000 m (Nilsson and Persson 1990; Nilsson 1992a; Nilsson and Persson 1993).

Etymology. The name refers to the pale nature of the type specimens (Latin: *pallidus* = pale).

Comments. See comments for *A. raffrayi*.

***Agabus ruwenzoricus* Guignot, 1936**

Figures 1, 4B, 8C, 11C, 11H, 12, 13, 14, 15

Agabus (*Agabinectes*) *pallidus* var. *ruwenzoricus* Guignot, 1936: 49

Type locality. "Uganda. Mons Ruwenzori, versant est, 3.000 à 4.000 m." [Uganda, Mount Ruwenzori, eastern slope, 3000 to 4000 m].

Type material. [Not examined]: Information about type specimens from Nilsson (1992a): "Lectotype here designated in NMNH (coll. Guignot) labelled: 'Monts Ruwenzori versant est zone alpine 3000 4000 m Ch. Alluaud I 1909', '3000 m', '♂', and my lectotype label; paralectotype ♂ with same original labels and my paralectotype label.".

Diagnosis. Most similar to *A. pallidus* and *A. raffrayi* but separated from these taxa by the presence of distinct interocular spots on head (compare Fig. 4B and D). The

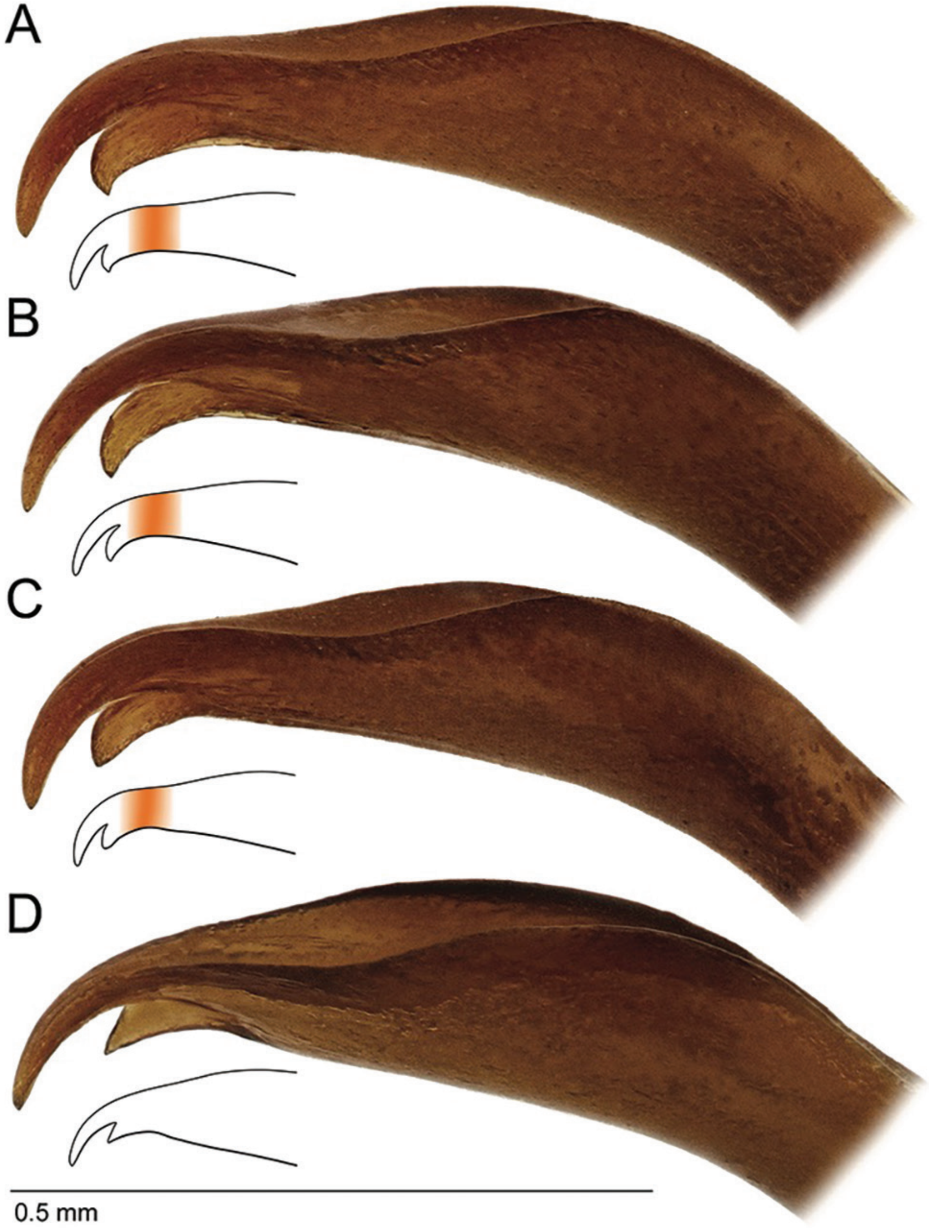

Figure 5. *Agabus* spp., lateral view of tip of aedeagus **A–C** *A. raffrayi*, different specimens showing the variation in shape of the subapical tooth **D** *A. austellus* sp. nov. Note the prolonged section between subapical broadening and base of apical and subapical teeth in *A. raffrayi* (indicated with orange in the smaller outline illustrations).

metasternal wing is rather narrow; the WC/WS frequency distribution being intermediate between *A. pallidus* and *A. raffrayi*, but most similar to *A. pallidus* (see Table 1, Fig. 12). The aedeagus has an extended portion between the subapical broadening and the apical teeth, and the pronotal hypomeron is not visible in lateral view.

Description. Habitus as in Fig. 11C, H.

***Colour*:** Head black with rufous anterior area; rufous interocular spots present. Pronotum black with minute to well-defined rufous margin. Elytra ferrugineous to rufopiceous. Ventral surface black, hypomeron rufotestaceous to rufous and epipleuron testaceous to rufotestaceous. Legs rufous to black. Antennae and palpi testaceous.

***Microreticulation*:** Medium impressed on head, pronotum and elytra, and rather similar in both sexes. Composed of a mixture of small and somewhat larger, uneven meshes.

***Structural features*:** Body length: 7.36–8.08 mm (see Table 1). Hypomeron not visible in strict lateral view (as in Fig. 10C, D, compare with 10A, B), lateral bead of pronotum narrow and well defined. Metasternal wing narrow, WC/WS 3.0 or more in most specimens (see Table 1, Fig. 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1, Fig. 13).

***Legs*:** Protarsal claws long, > 1.6× as long as protarsomere 4 in most specimens (see Table 2, Fig. 14). Metatarsomeres short and broad; metatarsomere 2 < 1.8× as long as broad (see Table 2), metatarsomere 5 < 3.3× as long as broad (see Table 2).

***Male genitalia*:** Subapically broadened and prolonged between the subapical broadening and the apical and subapical teeth (Fig. 8C). Subapical tooth with varying appearance (similar to magnitude in variation seen in Fig. 5A–C).

Female: Externally similar to males.

Distribution. Kenya, Rwanda, Uganda and the Democratic Republic of the Congo. Nilsson (1992a) and Omer-Cooper (1965) also give South Africa and Zimbabwe but these records are likely to belong to other species (see below).

Habitat. Most records are from small mountain streams and rivers at elevations of 1900 to 3100 m, but it has also been found in stagnant waterbodies (Nilsson 1992a). We found the species in a very small cold-water forest stream at an elevation of 1900 m in the Taita Hills, Kenya (Fig. 15).

Etymology. The name refers to the locality where the species was first collected, Mount Ruwenzori.

Agabus sjostedti Régimbart, 1908

Figures 1, 4C, 8A, 10A, 11A, 11F, 12, 13, 14

Agabus sjostedti Régimbart, 1908: 5–6

Type locality. "mont Meru, entre 3,500 et 4,300 mèt" [Tanzania, Mount Meru, between 3500 and 4300 m].

Type material. ***Lectotype*** ♂ (NHRS) labelled: "Meru Regenwald", "Meru Sjöstedt", "Type", "Typus", "Agabus sjöstedti Rég. n.sp. ♂ et ♀ "LECTOTYPUS ♂ Agabus sjostedti Régimbart 1908, Des. A.Nilsson -90". Paralectotypes 2 ♂ 1 ♀ (NHRS) labelled: "Meru Regenwald", "Meru Sjöstedt", "22 dec", "PARALECTOTYPUS ♂/♀ Agabus sjostedti Régimbart 1908 Des. A.Nilsson 1990".

Diagnosis. Most similar to *A. dytiscoides* but separated by its larger size (see Table 1), narrower metasternal wing (see Table 1), broader prontoum (see Table 1 and compare Fig. 4C with Fig. 4A) and by the curvature of the aedeagal subapical tooth (compare Fig. 8A with Fig. 8B). The aedeagus is prolonged preapically as in the preceeding three species, but the pronotal hypomeron is clearly visible in strict lateral view (see Fig. 10A).

Description. Habitus as in Fig. 11A, F.

***Colour*:** Head black to rufous with testaceous to rufous interocular spots. Pronotum rufopiceous to black and rufous to testaceous at margins; some specimens with two diffuse rufous to testaceous spots in the middle of the pronotum. Elytra ferruginous to rufopiceous. Ventral surface rufopiceous to black, hypomeron and epipleuron testaceous. Legs rufous to rufopiceous. Antennae and palpi testaceous to rufous.

***Microreticulation*:** Males with medium impressed reticulation on head and pronotum and slightly finer reticulation on elytra giving a shiny appearance, all meshes being a mix of smaller and somewhat larger meshes.

The two females studied varied greatly in microreticulation, but shared having mostly isodiametric meshes on elytra and the same variable meshes on head and pronotum as males. One female (Mt. Meru) had very coarse meshes; giving head, pronotum and elytra a matte appearance while the other female (Kilimanjaro Bismarck hut) had the same shiny appearance as males.

***Structural features*:** Body length: 8.08–9.12 mm (see Table 1). Hypomeron broadly visible in strict lateral view (see Fig. 10A), lateral bead of pronotum broad and well defined (see Fig. 10A). Metasternal wing very narrow, WC/WS > 3.6 in most specimens (see Table 1, Fig. 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1, Figs 5C, 13).

***Legs*:** Protarsal claws short, < 1.4× as long as protarsomere 4 (see Table 2, as in Figs 3A, 14). Metatarsomeres long and slender; metatarsomere 2 > 1.6× as long as broad (see Table 2), metatarsomere 5 > 3.3× as long as broad in most specimens (see Table 2).

Male genitalia: Subapically broadened, and prolonged between the subapical broadening and the apical and subapical teeth. Subapical tooth robust, with distinct curvature (see Fig. 8A).

Female: Elytral and pronotal microreticulation much coarser than in males.

Distribution. Known from Meru and Kilimanjaro mountains in northern Tanzania (see Fig. 1).

Habitat. Régimbart (1908) reports that the type specimens (from Mt. Meru) were found in very cold water, at an altitude of 3500 to 4300 m. On Mt. Kilimanjaro it has been found at lower altitudes between 2200 and 3100 m (Nilsson 1992a).

Etymology. The name refers to the collector of the type specimens, Yngve Sjöstedt.

Comments. Nilsson (1992a) studied the material collected by G.F. De Witte and concluded that the animals that Gschwendtner (1938) and Guignot (1959) referred to as *Gaurodytes sjostedti* from Park National Albert [=Virunga NP in DRC], bordering the Ruwenzori mountains, were in fact *A. ruwenzoricus*. Older records of *A. sjostedti* must be interpreted with caution.

Agabus dytiscoides Régimbart, 1908

Figures 1, 3A, 4A, 8B, 10B, 11B, 11G, 12, 13, 14

Agabus dytiscoides Régimbart, 1908: 6–7

Type locality. "Kiboscho, au Kilimandjaro … entre 3,000 et 3,500 mèt." [Tanzania, Kiboscho, Mount Kilimanjaro, between 3000 and 3500 meters].

Type material. ***Lectotype*** ♂ (NHRS) labelled: "Kilimandj. Sjöstedt", "Kiboscho 3' -4000 m.", "20 febr", "LECTOTYPUS ♂ Agabus dytiscoides Régimbart 1908 Des. Nilsson 1990". Paralectotypes 5 ♂ 3 ♀ (NHRS) labelled: "Kilimandj. Sjöstedt", "Kiboscho 3' -4000 m.", "20 febr", "PARALECTOTYPUS ♂/♀ Agabus dytiscoides Régimbart 1908 Des. Nilsson 1990".

Diagnosis. The very narrow pronotum, distinctly narrower than the base of elytra, is characteristic and separates *A. dytiscoides* from all other species in the group (see Table 1, Fig. 4A). With the pronotal hypomeron clearly visible in strict lateral view (see Fig. 10B), *A. dytiscoides* is most similar to *A. sjostedti* but can be separated, apart from the pronotal shape, by its smaller size (see Table 1), broader metasternal wing (see Table 1), and by the shape of the less robust aedeagal subapical tooth (compare Fig. 8A, B).

Description. Habitus as in Fig. 11B, G.

***Colour*:** Head rufopiceous to black with testaceous to rufous interocular spots. Pronotum rufopiceous to black with testaceous margins; some specimens with two diffuse rufous to testaceous spots in the middle of the pronotum. Elytra ferruginous to brown. Ventral surface rufopiceous to black, hypomeron and epipleuron testaceous. Legs rufous. Antennae and palpi testaceous.

***Microreticulation*:** Males with medium impressed reticulation on head and pronotum. Females with much coarser meshes than males, giving pronotum and elytra a matte appearance. Females also with mostly elongate meshes on pronotum. Males with a mixture of small and somewhat larger meshes on both pronotum and elytra, while female elytra tends to have more uniform small meshes. Both sexes with overall larger meshes on pronotum than elytra.

***Structural features*:** Body length: 7.36–7.76 mm (see Table 1). Pronotal hypomeron broadly visible in strict lateral view (see Fig. 10B), lateral bead of pronotum well defined. Metasternal wing relatively broad, WC/WS < 3.6 (see Table 1, Fig. 12). Pronotum very narrow, < 2.0× as broad as interocular distance (see Table 1, Figs 4A, 13), clearly narrower than base of elytra and therefore with a non-continuous outline between pronotum and elytra.

***Legs*:** Protarsal claws short, < 1.6× as long as protarsomere 4 (see Table 2, Figs 3A, 14). Metatarsomeres very long and slender; metatarsomere 2 > 1.8× as long as broad (see Table 2), metatarsomere 5 > 3.6× as long as broad (see Table 2).

***Male genitalia*:** Subapically broadened, and prolonged between the subapical broadening and the apical and subapical teeth. Subapical tooth with curvature as in Fig. 8B, less robust than in *A. sjostedti*.

Female: Elytral and pronotal microreticulation much coarser than in males.

Distribution. Known from Kilimanjaro and the Loolmalasin mountains in northern Tanzania (see Fig. 1).

Habitat. Régimbart (1908) reports that the type specimens were found in cold runoff water from a glacier at 3000 to 3500 m.

Etymology. The name literally translates to "*Dytiscus*-like". In his original description Régimbart (1908) explains that "J'ai donné à l'*A. dytiscoides* ce nom à cause de la grande similitude de forme et de couleur des males dans les deux especes. [I gave it the name *A. dytiscoides* because of the great similarity in form and colour between the males in the two species.]". Despite great differences in size and many other characters, the pale pronotal margins and the distinct shoulder between the pronotum and elytra are somewhat reminiscent of a *Dytiscus*. That said, Régimbart also mentioned similarities with *A. raffrayi*, making it difficult to be sure exactly what he was referring to in choosing this name.

Agabus anguluverpus Englund, Njoroge & Bergsten, sp. nov.

http://zoobank.org/78EDD21C-BB25-4472-872C-6159BBAD12E8

Figures 1, 7A, 8F, 10C, 11K, 11O, 12, 13, 14, 20, 21

Type locality. Kenya, Mount Kenya, Chogoria, Lake Ellis, -0.123N, 37.401E.

Type material. ***Holotype*** ♂ (NMK) labelled: "Kenya, Mt. Kenya, Lake Ellis, Chogoria. -0.123S 37.401E. 17.IX.2015 Leg. W. Wamiti". ***Paratypes*** 1 ♂ 1 ♀ (NHRS, NMK) labelled: "Kenya, Mt. Kenya, Lake Ellis, Chogoria. -0.123S, 37.401E. 17.IX.2015 Leg. W. Wamiti".

Diagnosis. This species is in some respects similar to *A. sjostedti* and *A. dytiscoides* in that females are matte due to a coarse dorsal microsculpture, and although the pronotal hypomeron is not or barely visible in strict lateral view, the pronotal bead is broader anteriorly (see Fig. 10C). The subapical portion of aedeagus is not prolonged, which is similar to South African species of the group, but the apex is straight in ventral view which is unique in the group. The aedeagus is evenly thickened, and essentially lacks the subapical broadening seen in most *raffrayi* group taxa (see Fig. 8).

Description. Habitus as in Fig. 11K, O.

***Colour*:** Head rufopiceous with testaceous interocular spots and an anterior testaceous area. Pronotum brown to rufopiceous with testaceous margins; some specimens with a diffuse rufotestaceous area in the middle of the pronotum. Elytron brown to testaceous brown. Ventral surface rufous, hypomeron testaceous, epipleuron testaceous brown. Legs rufous to testaceous. Antennae and palpi testaceous. The three specimens collected were all teneral individuals, especially the two paratypes, and as a result there is a probability that non-teneral individuals of this species will be somewhat darker than described here. In particular the pronotum may be darker medially in non-teneral individuals.

***Microreticulation*:** Males with medium impressed reticulation on head and pronotum. Females with much coarser and larger meshes than males, giving pronotum and elytra a matte appearance. Both sexes with a mixture of small and somewhat larger meshes.

***Structural features*:** Body length: 7.36–7.52 mm (see Table 1). Hypomeron not or barely visible in strict lateral view (see Fig. 10C), lateral bead of pronotum broad and well defined, broader anteriorly (see Fig. 10C). Metasternal wing narrow, WC/WS 3.0 or more in both males and females (see Table 1 and Fig. 12). Pronotum more than twice as broad as interocular distance (see Table 1 and Fig. 13), lateral margins straighter anteriorly and more curved posteriorly.

***Legs*:** Protarsal claws long, > 1.6× as long as protarsomere 4 (see Table 2, Fig. 14). Metatarsomeres very long and slender; metatarsomere 2 > 1.8× as long as broad in both females and males (see Table 2), and metatarsomere 5 > 3.3× as long as broad in males (see Table 2).

***Male genitalia*:** Aedeagus without distinct subapical broadening and without subapical prolongation; subapical tooth angled both basally and subapically (see Fig. 8F). Aedeagus with straight apex in ventral view.

Female: Elytral and pronotal microreticulation much coarser than in males.

Distribution. Only known from Mount Kenya in central Kenya (see Fig. 1).

Habitat. Lake Ellis is situated at an altitude of about 3500 m on Mount Kenya's eastern slope (Figs 20, 21).

Etymology. The species name refers to the angled subapical tooth of the male genitalia (Latin: *angulus* = angle, *verpus* = penis).

Agabus austellus Englund, Bilton & Bergsten, sp. nov.

http://zoobank.org/290F05EF-3F4E-4971-B957-1071B64FBD13
Figures 1, 5D, 6A–D, 7B, 8G, 9A–D, 11L, 11P, 12, 13, 14, 16, 17

Type locality. South Africa, Western Cape Province, Tributary stream to Keurboom river crossing R339 road, 33.8612S, 23.1729E, 250 m (Fig. 16).

Type material. ***Holotype*** ♂ (AMG) labelled: "South Africa W Cape Province Tributary stream to Keurboom river x-ing R339. 33.8612S, 23.1729E, 250m. Foreststream with gravel and veg. At edges RSA15-21 13.XII.2015 Leg. J. Bergsten & A. Désamoré". ***Paratypes:*** 1 ♂ (NHRS) labelled: "South Africa E Cape Province. Small fish river x-ing road r337, NW of Somerset East. 32.5913S, 25.4510E, 1017m. Waterpools in streambed RSA15-27 15.XII.2015 Leg. J. Bergsten & A. Désamoré"; paratypes 1 ♂ (NHRS) labelled: "Rep. South Africa, W. Cape Gydo Pass at junc R303 & Witzenberg Valley Rd. Aug. 25, 2004 G. Challet"; paratypes 6 ♂ 2 ♀ (MZLU) labelled: "S. Afr. Cape Prov., Swartbergpas, Platberg, Alt.: ab. 5000 ft., 5–6.I.51 No. 120", "Swedish South Africa Expedition 1950–1951, Brinck-Rudebeck", "Agabus ruwenzoricus Guignot, det AN Nilsson 1990", one male and one female had an extra label containing "Agabus raffrayi sharp, Det. J. Omer-Cooper"; paratypes 2 ♂ 3 ♀ (MfN) labelled: "R.S.Africa 17.xi.1997 32°15.3'S, 22°29.9'E Cape Province:Karoo NP. Swamp at Puttersvlei, swamp vegetation treating, watercatcher, lg. M.Uhlig+J.

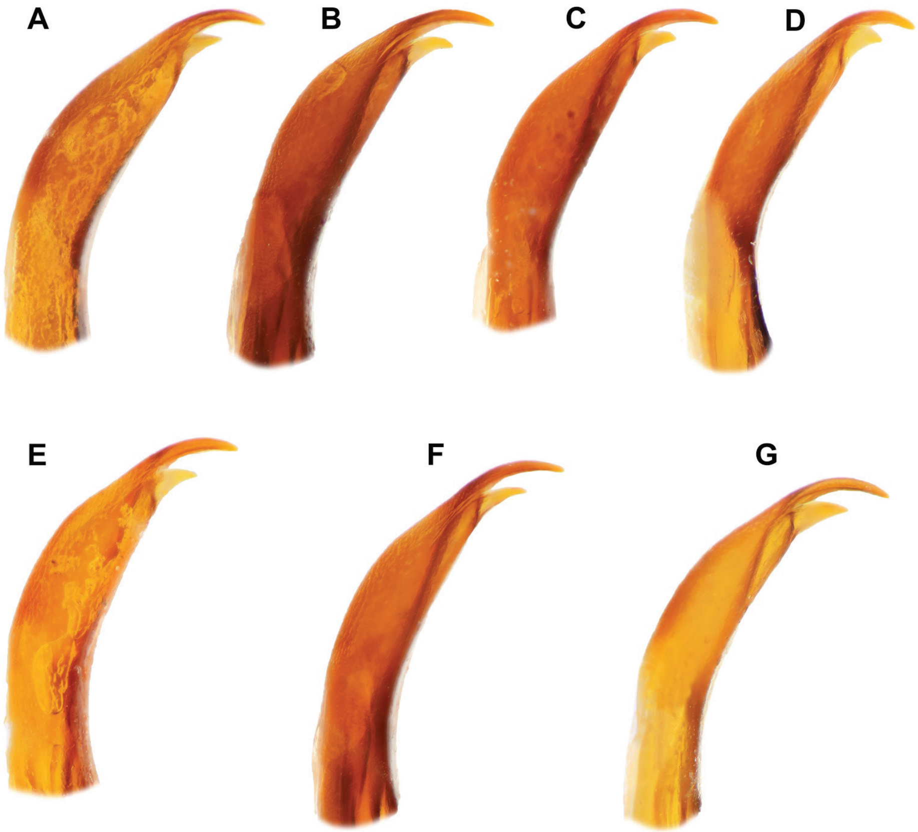

Figure 6. South African *Agabus* spp., aedeagal apices, lateral view **A** *A. austellus* sp. nov. holotype, Keurboom, Western Cape **B** *A. austellus* sp. nov., Gydo Pass, Western Cape **C** *A. austellus* sp. nov. Groote Swartberg, Western Cape **D** *A. austellus* sp. nov. Sentinel Peak, KZN Drakensberg **E** *A. riberae* sp. nov. holotype, Kamiesberg, Northern Cape; **F** *A. riberae* sp. nov. paratype, Kamiesberg, Northern Cape **G** *A. agulhas* sp. nov. holotype, Rattelrivier, Western Cape.

Ndamane", one male had an extra label containing "Agabus ruwenzoricus Guignot det. K.B. Miller 1999"; paratypes 2 ♂ 3 ♀ (AMG, CBP) labelled: "Sept. 2002 South Africa WC Pools beside Brée River below Mitchell's Pass, Ceres. D T Bilton leg."; paratypes 4 ♂ 1 ♀ (CBP, ZSM) labelled: "24/ix/2009 South Africa WC Groote Swartberg stream on R328 1 km N of De Top, on N side of pass. D.T. Bilton leg."; paratypes 1 ♂ 1 ♀ (CBP) labelled: "20/ix/2014 South Africa WC Gifberg – stream in Gifberg Pass above Vanrhynsdorp rocky stream. D T Bilton leg."; paratype 1 ♂ (CBP) labelled: "11/ii/2017 South Africa WC Harkerville Forest pool 1 survey site 16. M Bird & D T Bilton leg."; paratypes 6 ♂ 6 ♀ dry mounted, 18 ♂ 16 ♀ in ethanol (AMG, CBP, NHRS) labelled: "28/v/2018 South Africa KZN Drakensberg – river nr. Sentinel Peak

Figure 7. *Agabus* spp., ventral view (following Miller and Nilsson 2003) of apex of aedeagus **A** *A. anguluverpus* sp. nov. **B** *A. austellus* sp. nov.

28°45'30.80"S, 28°54'14.82"E 2960m M. Mlambo leg."; paratype 1 ♀ (IBE) labelled: "25/viii/2008 South Africa WC Gydo Pass – pool at Jnct. R303 & Witzenberg Valley Rd. G Challet leg."; paratypes 1 ♂ (IBE) labelled: "2/x/2010 South Africa WC Cederberg Dwarsrivier 32°30'59.51"S, 19°21'E 735 m Hidalgo-Galiana & Kleynhans leg."; paratypes 1 ♂ (CBP) labelled: "6/x/2015 South Africa NC Bokkeveld, Avontuur – stream below Fynbos Cottage D T Bilton leg."; paratypes 4 ♂ 3 ♀ (CBP, ISAM, SANC) labelled: "22/ix/2010 South Africa WC Gydo Pass stream along Witzenberg Valley road ca 1 km SW of Jnct. with R303 985 m D T Bilton leg.".

Diagnosis. Most similar to *A. riberae* sp. nov. and *A. agulhas* sp. nov., but distinguishable by a combination of having a scutellum darker than or as dark as elytra, base

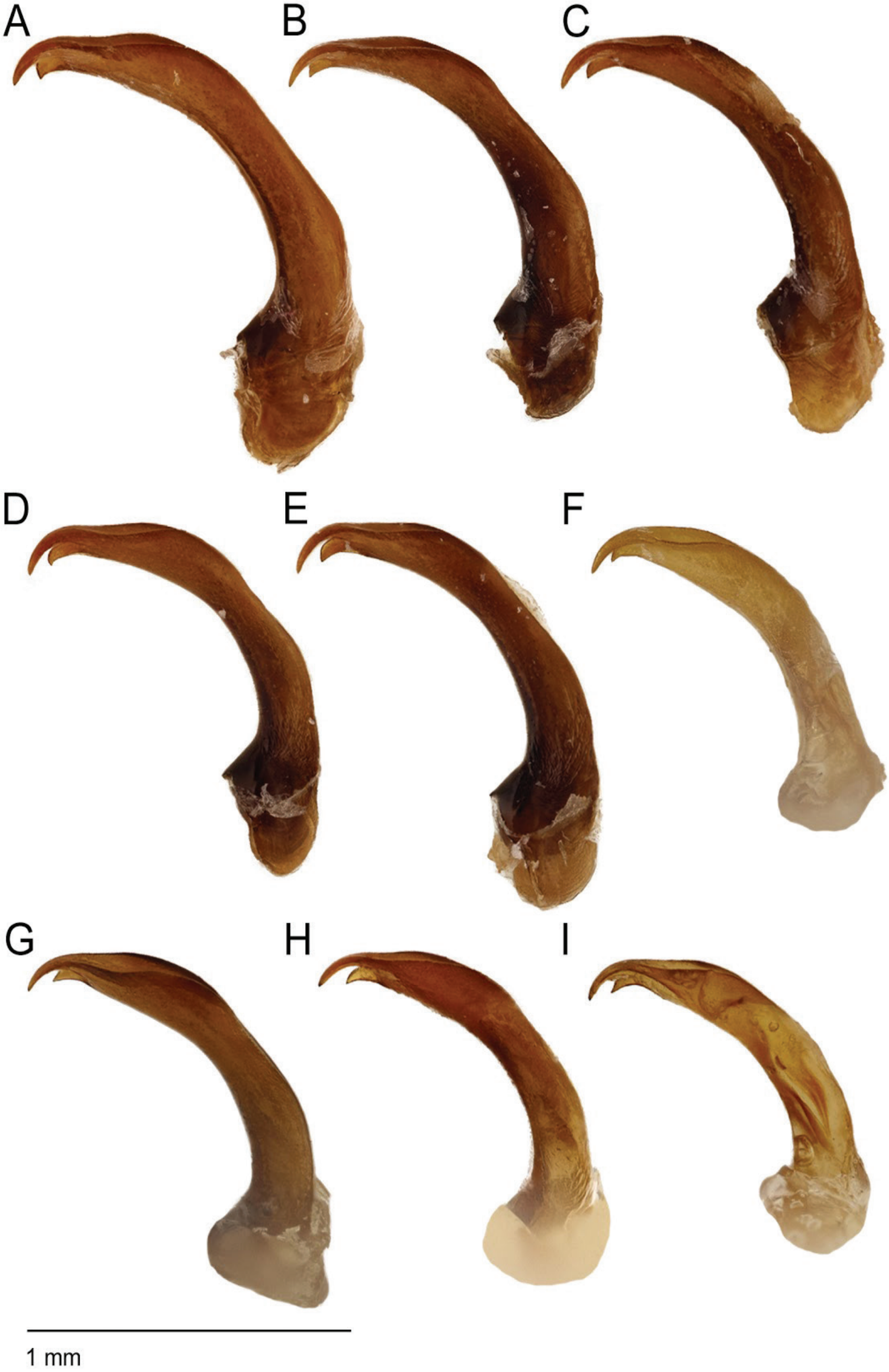

Figure 8. *Agabus* spp., aedeagus in lateral view **A** *A. sjostedti* **B** *A. dytiscoides* **C** *A. ruwenzoricus* **D** *A. raffrayi* **E** *A. pallidus* **F** *A. anguluverpus* sp. nov. **G** *A. austellus* sp. nov. **H** *A. riberae* sp. nov. **I** *A. agulhas* sp. nov.

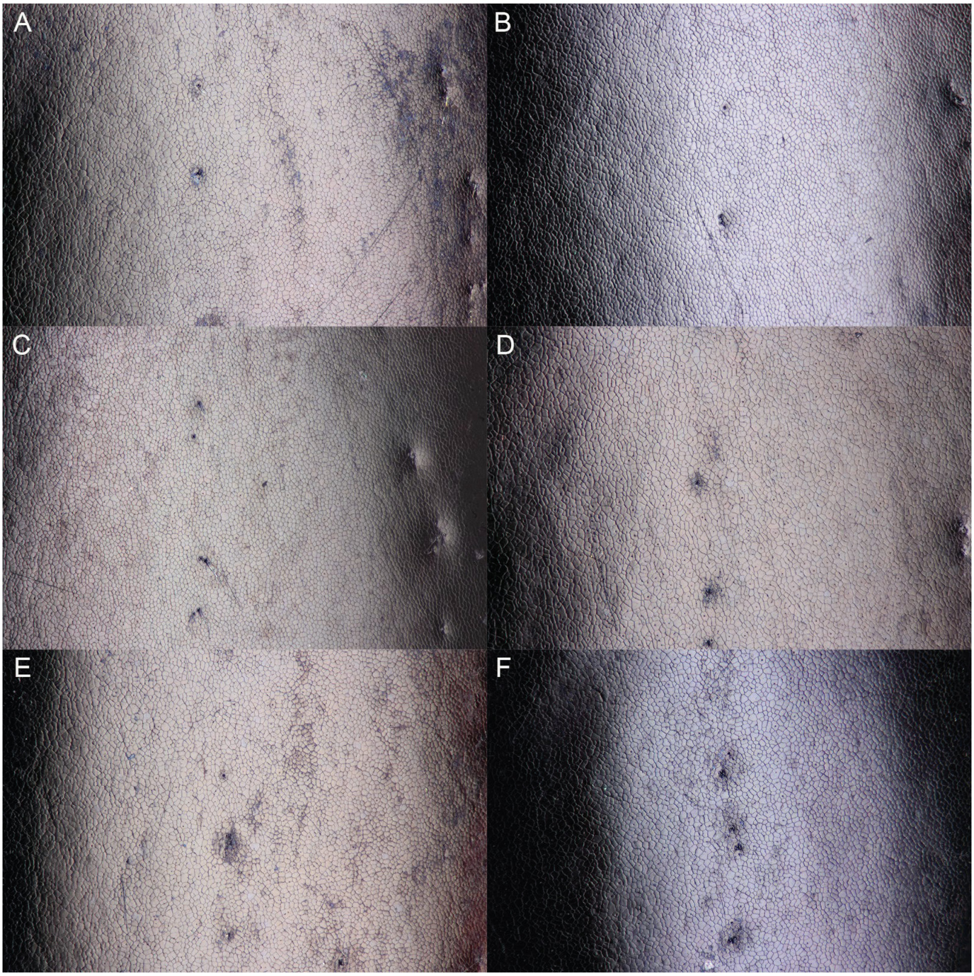

Figure 9. South African *Agabus* spp., microreticulation of male elytral disc **A** *A. austellus* sp. nov. holotype, Keurboom, Western Cape **B** *A. austellus* sp. nov. Groote Swartberg, Western Cape **C** *A. austellus* sp. nov. Sentinel Peak, KZN Drakensberg **D** *A. austellus* sp. nov. Harkerville Forest, Western Cape **E** *A. riberae* sp. nov. Kamiesberg, Northern Cape **F** *A. agulhas* sp. nov. holotype, Rattelrivier, Western Cape.

of aedeagal subapical tooth lacking a distinct incurvation (compare Fig. 8G, I) and a relatively narrow metasternal wing (see Table 1). The pronotal hypomeron is not visible in strict lateral view, the aedeagus does not have a prolonged subapical portion and in ventral view its apex is asymmetrically curved. The discal elytral microreticulation of most specimens is dominated by relatively small, isodiametric meshes.

Description. Habitus as in Fig. 11L, P.

***Colour*:** Head black, with rufous interocular spots; some specimens with an additional anterior rufous area. Pronotum rufopiceous to black. Elytra rufopiceous to black. Ventral surface rufous to black; testaceous lines on abdominal segments rarely

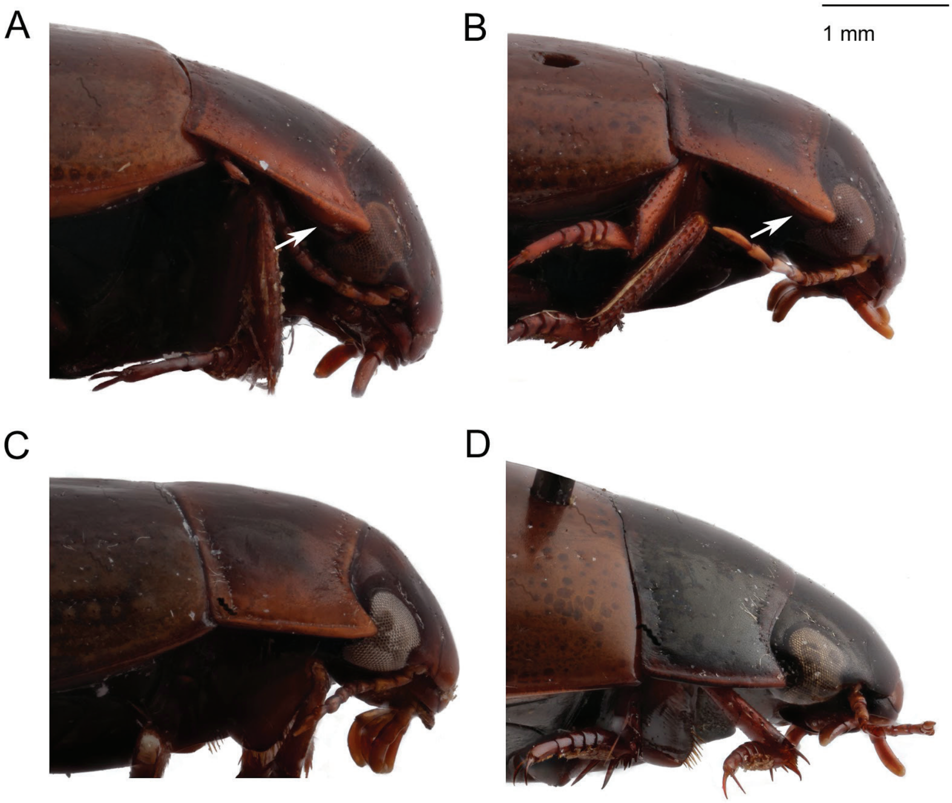

Figure 10. *Agabus* spp., hypomeron in lateral view **A** *A. sjostedti* **B** *A. dytiscoides* **C** *A. anguluverpus* sp. nov. **D** *A. raffrayi*. White arrows indicate hypomeron.

present; hypomeron and epipleuron rufopiceous to rufous. Legs rufous to rufopiceous. Antennae and palpi testaceous.

***Microreticulation*:** Relatively fine on both pronotum and elytra, and rather similarly impressed in both sexes. The microreticulation of the elytral disc is dominated by relatively small, somewhat isodiametric meshes in most specimens examined (e.g. Fig. 9B, C), although this character does vary somewhat between populations in this relatively widespread species (see Fig. 9). In particular, the male from Harkerville Forest (see Fig. 9D) has a reticulation composed of much larger meshes than seen in other material of this species. This specimen conforms to *A. austellus* sp. nov. on other morphological characters, and COI sequence data (I. Ribera, pers. comm.).

***Structural features*:** Body length: 6.80–8.40 mm (see Table 1). Hypomeron marginally visible in strict lateral view, lateral bead of pronotum narrow and well defined. Metasternal wing narrow, WC/WS 3.1 or more in both males and females (see Table 1 and Fig. 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1 and Fig. 13).

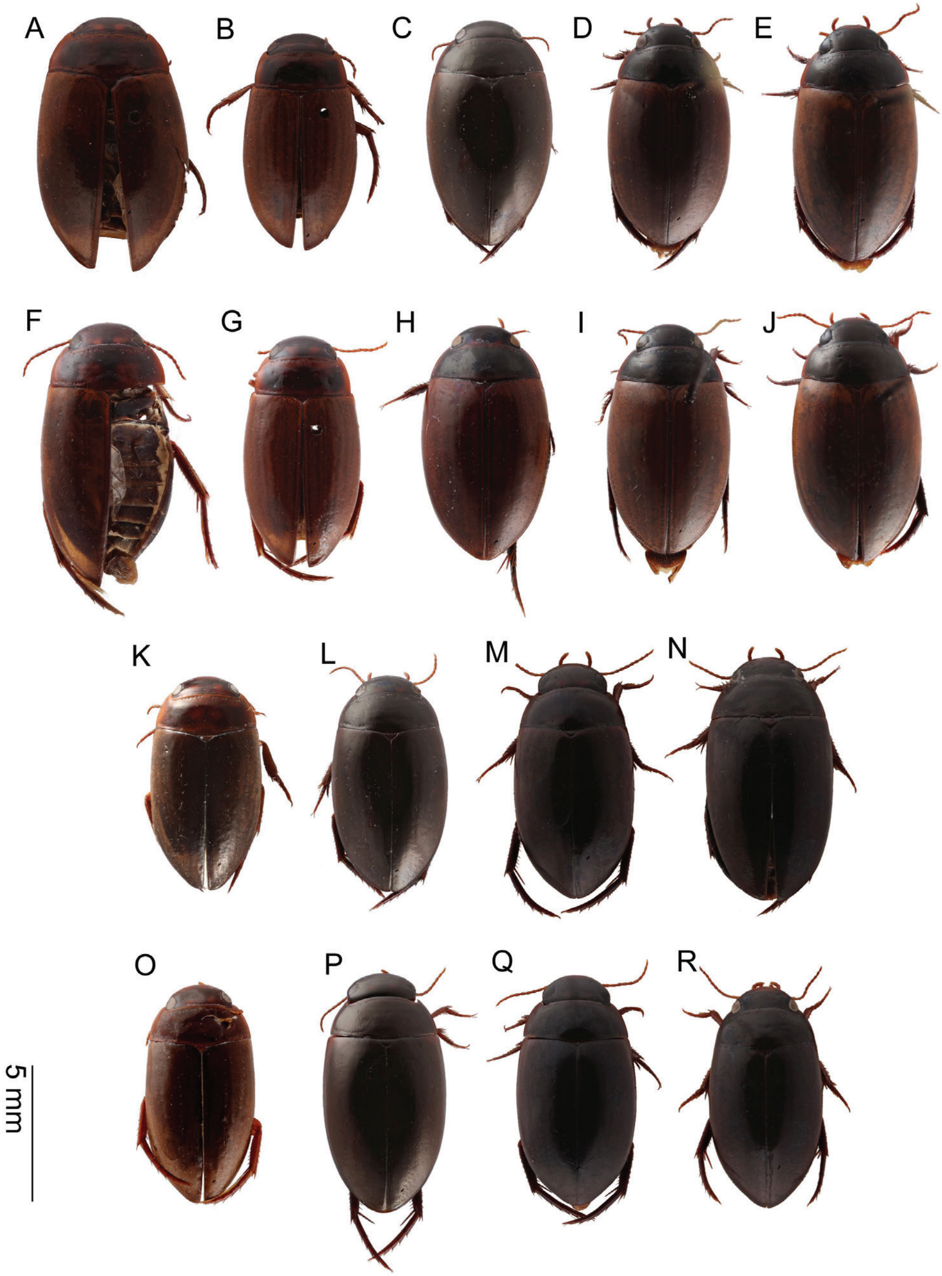

Figure 11. *Agabus* spp., habitus of males in dorsal view **A, F** *A. sjostedti* **B, G** *A. dytiscoides*; **C, H** *A. ruwenzoricus* **D, I** *A. raffrayi* **E, J** *A. pallidus* **K, O** *A. anguluverpus* sp. nov. **L, P** *A. austellus* sp. nov. **M, Q** *A. riberae* sp. nov. **N, R** *A. agulhas* sp. nov.

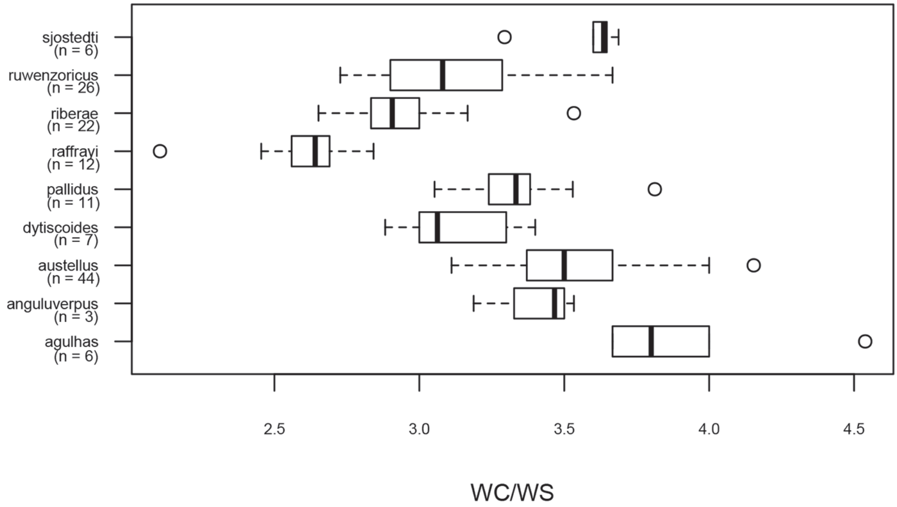

Figure 12. The ratio between width of the metacoxal plate and metasternal wing (WC/WS) in the *A. raffrayi* group (incl. specimens of both sexes). Thick black line inside boxes represents medians, left and right box borders 25th (Q1) and 75th (Q3) percentiles respectively. Whiskers were calculated with the boxplot. stats function in R using the default coefficient value of 1.5 (drawn to the highest and lowest value within 1.5*IQD (Inter Quartile Distance = Q3-Q1) away from the 75th and 25th percentiles respectively). Note that this character fully separates *A. raffrayi* from *A. pallidus*.

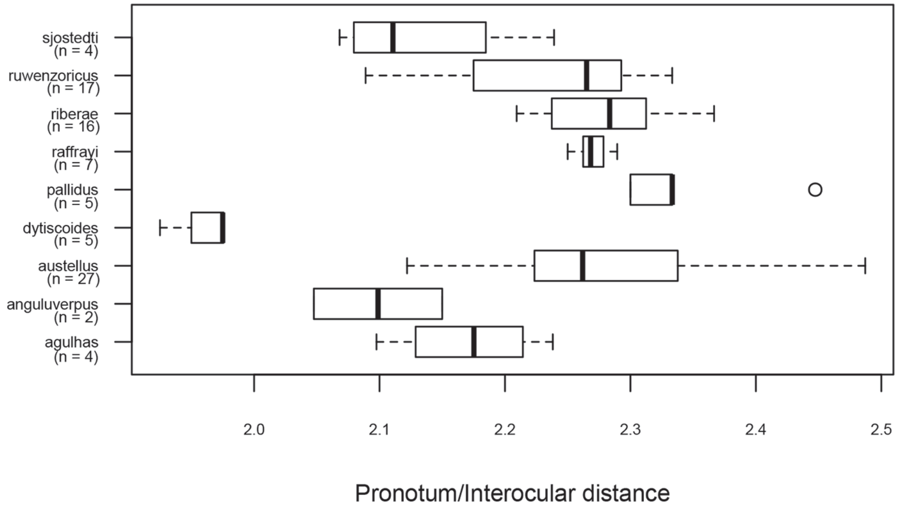

Figure 13. The ratio between pronotal width and interocular distance in males of the *Agabus raffrayi* group. Symbols as in Fig. 12. Note the very narrow pronotum of *A. dytiscoides*, a distinguishing feature of this species.

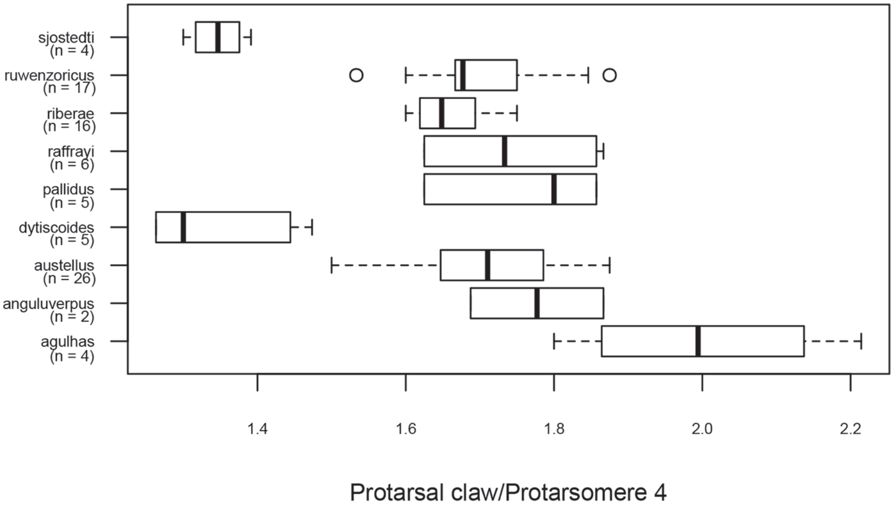

Figure 14. The ratio between length of protarsal claw and length of protarsomere 4 in males of the *Agabus raffrayi* group. Symbols as in Fig. 12. Note the short claws of *A. sjostedti* and *A. dytiscoides*.

***Legs*:** Protarsal claws long, > 1.6× as long as protarsomere 4 in most specimens (see Table 2 & Fig. 14). Metatarsomeres usually short and broad; metatarsomere 2 < 1.8× as long as broad in most specimens (see Table 2), metatarsomere 5 < 3.3× as long as broad in most specimens (see Table 2).

***Male genitalia*:** Aedeagus lack the prolonged section between the subapical broadening and the apical and subapical teeth present in some species in the group (see Fig. 8G). In ventral view the apex is asymmetrically curved (Fig. 7B). There is some variation in the shape and size of the subapical tooth of the aedeagus (Fig. 6A–D), this being relatively small in most populations (Fig. 6A–C).

Female: Externally similar to males. Some specimens with dorsal microreticulation slightly more strongly impressed.

Distribution. Republic of South Africa, where the species is relatively widespread, from the Bokkeveld Plateau in the south of the Northern Cape Province, most mountain systems of the Western Cape Province and east along the Great Escarpment to the Drakensberg (see Fig. 1). This wide geographical range encompasses winter, summer and bimodal rainfall regimes.

Ecology. Found in streams, pools beside streams and remnant pools in seasonal running watercourses. Most localities are situated in Fynbos or alpine grassland (e.g., Fig. 17), but also recorded from densely forested streams. Sites span a wide range of altitudes, from the type locality at 250 m (Fig. 16) to almost 3000 m in the Kwazulu-Natal, Drakensberg (Fig. 17), most being at intermediate elevations.

Figure 15. Small forest stream at 1900 m in remaining fragment of afromontane cloud forest on Vuria, the highest mountain in the Taita Hills, Taita-Taveta district, northeastern part of Eastern Arc Mountains, Kenya. Albeit minute, the small pools seen in the photo were inhabited by tens of individuals of *Agabus ruwenzoricus*. January 19, 2016.

Etymology. The name refers to the fact that the species is widespread in South Africa and therefore truly an *Agabus* of the south (Latin: *austellus* = southern parts).

Comments. Nilsson (1992a) and Omer-Cooper (1965) assigned specimens from South Africa and S. Rhodesia [=Zimbabwe] to *A. ruwenzoricus*. We have studied one series of specimens cited by both authors from the Swartberg Pass (Swartbergpas) W. Cape Province, housed in Lund (MZLU), which correspond to *A. austellus* sp. nov. Males of this species do not have a prolonged preapical section of the aedeagus, a distinguishing character not previously noted in the *raffrayi* group. It seems likely that all previous records of *A. raffrayi*, *A. pallidus* or *A. ruwenzoricus* from South Africa, and also possibly those from Zimbabwe, are misidentified and mostly refer to *A. austellus* sp. nov. This species is somewhat variable in body shape, elytral microreticulation (see Fig 9A–D) and the shape and size of the subapical tooth of the aedeagus (see Fig. 6A–D). We interpret this variation as comprising a single species, however, particularly given the very similar mtDNA COI sequences observed amongst populations spanning the entire known range in South Africa (i.e., Bokkeveld Plateau to Drakensberg, I. Ribera, pers. comm.).

Figure 16. Diep River at 250 m, tributary to Keurbooms River, R339 towards Prince Alfred's Pass, Langkloof Mountains, Western Cape province, South Africa. Type locality of *Agabus austellus* sp. nov. December 13, 2015.

Figure 17. River nr Sentinel Peak, 2960 m, Drakensberg, KwaZulu-Natal, South Africa. Locality for *Agabus austellus* sp. nov. May 28, 2018. Photo Samuel Motitsoe.

Agabus riberae Bilton, Englund & Bergsten, sp. nov.

http://zoobank.org/A391EC84-95B1-480F-B4DD-E7DEA2AE3076
Figures 1, 6E, F, 8H, 9E, 11M, 11Q, 12, 13, 14, 18, 19

Type locality. South Africa, Northern Cape Province, Kamiesberg, stream on Witwater-Langkloof Road ca 1 km S. of junction, 30°23'41.30"S 18°08'07.95"E, 1100 m.

Type material. ***Holotype*** ♂ (AMG) labelled: "19/ix/2010 South Africa NC Kamiesberg Stream on Witwater-Langkloof road ca 1 km S. of junction. D.T. Bilton leg.". ***Paratypes:*** 5 ♂ 5 ♀ (CBP, SANC, ZSM) labelled: "19/ix/2010 South Africa NC Kamiesberg Stream on Witwater-Langkloof road ca 1 km S. of junction. D.T. Bilton leg."; paratype 4 ♂ 4 ♀ (AMG, CBP, ISAM, NHRS) labelled: "19/1x/2010 South Africa NC Kamiesberg – stream above Studer Pass ca 5 km W of Witwater 30°23'13.49"S, 18°07'05.78"E 1,105 m D T Bilton leg."; paratype 1 ♀ (IBE) labelled: "22/viii/2004 South Africa NC Kamiesberg – stream at top of Studer Pass G. Challet leg."; paratype ♂ (CBP) labelled: "19/ix/2014 South Africa NC Kamiesberg temporary stream in Kamiesberg Pass D T Bilton leg."; paratypes 2 ♂ (CBP) labelled: "18/ix/2014 South Africa NC Kamiesberg spring pool on Rondefontein Farm 30°30'05.59"S, 18°08'56.35"E 1023 m D T Bilton leg."; paratypes 4 ♂ 1 ♀ (CBP, NHRS) labelled: "17/ix/2014 South Africa NC Kamiesberg stream nr. Damsland on N. side of Rooiberg 30°23'36.33"S, 18°06'32.12"E 1111 m D T Bilton leg."; paratype 1 ♂ (CBP) labelled: 19/ix/2014 South Africa NC Kamiesberg stream nr. De Kuilen 30°10'44.94"S, 18°04'37.71"E 940 m D T Bilton leg."; paratypes 2 ♂ (CBP) labelled: "18/ix/2014 South Africa NC Kamiesberg – stream at bottom of Langkloof 30°33'16.98"S, 18°08'19.13"E 594 m D T Bilton leg."; paratypes 2 ♂ 4 ♀ (AMG, CBP) labelled: "28/ix/2018 South Africa WC Cederberg Tra-Tra river @ Wupperthal 32°16'45.35"S, 19°13'04.32"E 485 m D T Bilton leg.".

Diagnosis. Very similar to *A. austellus* sp. nov., differing from this species in having a relatively broad metasternal wing (see Table 1), and an elytral microreticulation dominated by larger, more irregular meshes than seen in most *A. austellus* sp. nov. specimens (see above). Metatarsomere 5 is also somewhat longer in this species than in most *A. austellus* sp. nov.

Description. Habitus as in Fig. 11M, Q.

***Colour*:** Head black with rufous interocular spots and an anterior rufous area. Pronotum black with rufous borders. Elytra rufopiceous to black. Ventral surface black, testaceous lines on abdominal segments rarely present, hypomeron and epipleuron rufotestaceous to rufous. Legs rufous to rufopiceous. Antennae and palpi testaceous.

***Microreticulation*:** Relatively fine on both pronotum and elytra, and rather similarly impressed in both sexes. The microreticulation of the elytral disc is typically dominated by relatively large, somewhat irregular meshes (Fig. 9E).

***Structural features*:** Body length: 7.21–8.24 mm (see Table 1). Hypomeron marginally visible in strict lateral view, lateral bead of pronotum narrow and well defined. Metasternal wing broad, WC/WS 3.0 or less in most specimens (see Table 1 and Fig. 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1 and Fig. 13).

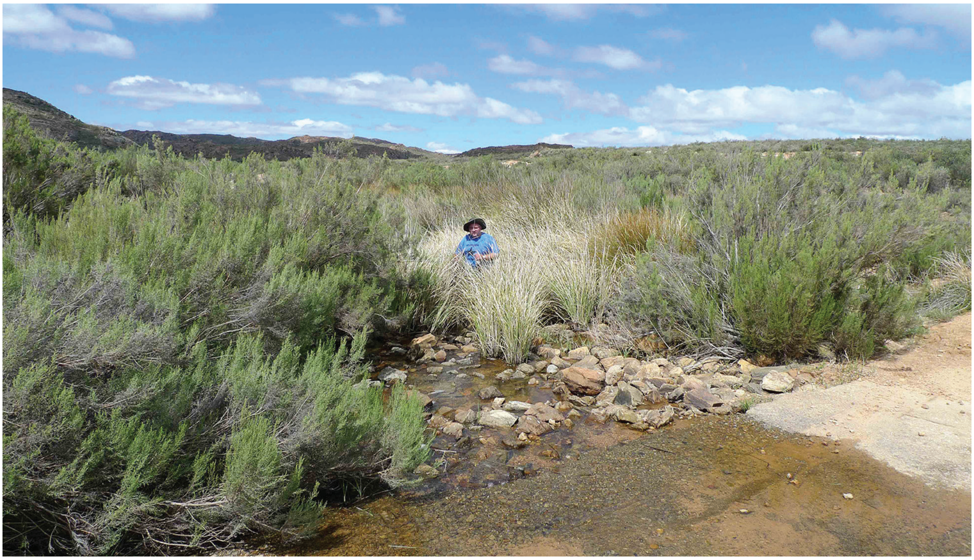

Figure 18. Stream at 1100 m on Witwater-Langkloof road ca 1 km S. of junction, Kamiesberg, Northern Cape Province, South Africa. Type locality of *Agabus riberae* sp. nov., with DTB. September 19, 2010. Photo Rebecca Bilton.

Figure 19. Tra-Tra River at 485 m at Wupperthal, Cederberg range, Western Cape Province, South Africa. Locality for *Agabus riberae* sp. nov. September 28, 2018. Photo Stacey DeAmicis.

***Legs*:** Male protarsal claws long, > 1.6× as long as protarsomere 4 (see Table 2 and Fig. 14). Metatarsomere 2 short and broad, < 1.8× as long as broad (see Table 2) in most specimens. Metatarsomere 5 long and slender, > 3.3× as long as broad in most males (see Table 2).

***Male genitalia*:** Tip of aedeagus short, lacking the prolongation of the area located between the subapical broadening and the apical and subapical tooth present in some species in the group (see Fig. 8H). There is some variation in the shape and size of the subapical tooth (Fig. 6E, F), this being relatively long and narrow in most specimens examined (Fig. 6F), but with both narrow and broader teeth being observed within the same population.

Female: Externally similar to males. Some specimens with dorsal microreticulation slightly more strongly impressed.

Distribution. To date known only from Kamiesberg Range in the Northern Cape Province, and the eastern fringes of the Cederberg, Western Cape Province, Republic of South Africa (see Fig. 1), material from both areas being confirmed from COI sequences. The Kamiesberg represents a northerly outlier of Fynbos and Renosterveld vegetation in predominantly arid Namaqualand, and consequently have a diverse flora with a number of localised endemics (Helme and Desmet 2006). The mountains support the bulk of the global population of the endemic dytiscid *Andex insignis* Sharp, 1882 and a number of new, apparently endemic, water beetles have been described

Figure 20. Lake Ellis on Mount Kenya, Kenya. Type locality for *Agabus anguluverpus* sp. nov. September 17, 2015. Photo Wanyoike Wamiti.

Figure 21. Part of Lake Ellis on Mount Kenya, Kenya. Type locality for *Agabus anguluverpus* sp. nov. September 17, 2015. Photo Wanyoike Wamiti.

from the area in recent years (Bilton 2013, 2015, 2016). *Agabus riberae* sp. nov. appears to be the only *Agabus* present in Kamiesberg, where it is abundant. In the Cederberg the species has been found close to Wupperthal, in the relatively dry northeastern fringes of the range. *A. austellus* sp. nov. is the only species so far recorded from the wetter central areas of the Cederberg. All sites known to date experience predominantly winter rainfall.

Ecology. Found in streams and associated pools in the Kamiesberg and northeastern Cederberg ranges (Figs 18, 19), in either Fynbos or Renosterveld vegetation between 480 and 1000 m elevation. Typically netted from marginal vegetation, including at the base of tussocks. Also found amongst grasses in a spring pool with cold water. Ecological differences between this species and *A. austellus* sp. nov. are unclear, but may relate, at least in part, to rainfall.

Etymology. Named after our late friend and colleague Ignacio Ribera, who will be sorely missed.

Comments. Despite the relatively minor morphological differences between this species and *A. austellus* sp. nov. we consider these two taxa distinct. COI sequences for four specimens of *A. riberae* sp. nov. investigated differed by 4.5–4.7% from *A. austellus* sp. nov., more than that observed between many well-established species in the subgenus *Acatodes* Thomson, 1859 (I. Ribera pers. comm.). This is supportive of the recognition as a distinct taxon, particularly given the relative uniformity in COI sequence observed across the wide geographical range of *A. austellus* sp. nov.

Agabus agulhas Bilton, Englund & Bergsten, sp. nov.

http://zoobank.org/FD6B9312-065E-4B96-9FDF-9B1C45EA8D69
Figures 1, 6G, 8I, 9F, 11N, 11R, 12, 13, 14

Type locality. South Africa, Western Cape Province, Rooistrandveld, Bredasdorp, natural viei beside road to Die Dam at Ratelrivier 34°43'00.47"S, 19°41'53.81"E, 31 m.

Type material. ***Holotype*** ♂ (AMG) labelled: "26/ix/2010 South Africa WC Rooistrandveld, Bredasdorp natural viei beside road to Die Dam @ Ratelrivier FW marsh with tussocks etc. D. T. Bilton leg.". ***Paratypes*** 3 ♂ 2 ♀ (AMG, CBP, NHRS, ZSM) labelled: "26/ix/2010 South Africa WC Rooistrandveld, Bredasdorp natural viei beside road to Die Dam @ Ratelrivier FW marsh with tussocks etc. D. T. Bilton leg.".

Diagnosis. Very similar to *A. austellus* sp. nov. and *A. riberae* sp. nov., but distinguishable by the distinctly curved base of the aedeagal subapical tooth (compare Fig. 8I with Fig. 8G, H and see Fig. 6G), the scutellum being lighter than the elytra and its relatively narrow metasternal wing (see Table 1 and Fig. 12).

Description. Habitus as in Fig. 11N, R.

***Colour*:** Head black with weak rufous interocular spots and an anterior rufous area. Pronotum black with slightly rufous margins. Elytra blackish brown to black, with a lighter scutellum. Ventral surface black, testaceous lines on abdominal segments reduced or absent, hypomeron and epipleuron rufotestaceous to rufous. Legs rufopiceous to rufous. Antennae and palpi testacous.

***Microreticulation*:** Relatively fine on both pronotum and elytra, and slightly more impressed in females. The microreticulation of the elytral disc is composed of a mix of small and larger, somewhat irregular meshes (Fig. 9F).

***Structural features*:** Body length: 7.60–8.00 mm (see Table 1). Hypomeron marginally visible in strict lateral view, lateral bead of pronotum narrow and well defined. Metasternal wing very narrow, WC/WS > 3.6 in all specimens (see Table 1 and Fig. 12). Pronotum broad, more than twice as broad as interocular distance (see Table 1 and Fig. 13).

***Legs*:** Protarsal claws very long, > 1.8× as long as protarsomere 4 in all males (see Table 2 & Fig. 14). Metatarsomeres short and broad; metatarsomere 2 < 1.8× as long as broad (see Table 2), metatarsomere 5 < 3× as long as broad in all specimens (see Table 2).

***Male genitalia*:** Aedeagus without the prolonged section between subapical broadening and the apical and subapical teeth which is present in some species in the group. In ventral view the apex is asymmetrically curved. Base of subapical tooth distinctly curved basally (see Figs 8I, 6G).

Female: Externally similar to males. Dorsal microreticulation slightly more impressed than in males.

Distribution. Only known from the type locality, a lowland valley wetland at 31 m on the Agulhas Plain, Western Cape Province, Republic of South Africa (see Fig. 1). The most southerly distributed *Agabus* species in the world.

Ecology. Collected from the base of large tussocks in a valley wetland. Despite having largely lentic conditions, this is likely to experience some seepage flow, particularly following periods of high rainfall in winter and spring.

Etymology. Named after the Agulhas Plain, on which the type locality is situated. The Agulhas Plain is itself named in reference to nearby Cape Agulhas (Portuguese – Cabo das Agulhas = Cape of Needles), the most southerly point on the African continent. As with other members of the species group, *A. agulhas* sp. nov. has sharp, needle-like, teeth at the aedeagal apex.

Comments. COI sequence divergence between *A. agulhas* sp. nov. and *A. austellus* sp. nov. ranges from 3.9 to 4.7%; that between *A. agulhas* sp. nov. and *A. riberae* sp. nov. being 6.4% (I. Ribera, pers. comm.).

Discussion

Agabus is one of a number of largely temperate northern hemisphere water beetle lineages which have colonised the Afrotropical region. Other examples include *Nebrioporus* Régimbart, 1906 and *Ilybiosoma* Crotch, 1873 within the Dytiscidae and *Helophorus* Fabricius, 1775 (Hydrophiloidea, Helophoridae). In all cases, these genera are restricted to relatively high elevations in East Africa, from Ethiopia southwards, but occur across a much greater range of altitudes in temperate regions of South Africa, particularly the Cape. South African *Agabus* have to date been considered to belong to *Agabus ruwenzoricus* (Nilsson 1992a), or prior to the recognition of *A. ruwenzoricus*, *Agabus pallidus* (Omer-Cooper 1965). Instead of forming part of a widespread species, distributed from East Africa to the Cape, we demonstrate that South African *Agabus* are all endemic to the region, and comprise a group of three semi-cryptic species, one of which is relatively widespread. These species constitute the southernmost records in the world for this otherwise largely Holarctic genus which is most diverse in the northern hemisphere and absent from South America and Australia (Miller and Bergsten 2016). The discovery of *Agabus anguluverpus* sp. nov. on Mount Kenya, shows that our knowledge of the *Agabus* fauna of high altitude areas in East Africa is also incomplete. Many of the mountain systems associated with the Rift remain poorly investigated for aquatic insects, and we suspect that additional, new, species of the genus remain undiscovered.

In his revision of the *raffrayi* species group, Nilsson (1992a) considered that the shape of male genitalia, although universally used for species-level identification in the genus elsewhere, was largely uninformative and consequently this character was not used in the determination key to the group. Here we show instead that the three distinct species found in South Africa differ from other *raffrayi* group species by having a preapically shorter male aedeagus. Coincidentally, this genitalic feature is also characteristic of the new species we describe from high elevations on Mount Kenya. We hypothesize, however, that a preapically prolonged aedeagus may be a synapomorphy of *A. ruwenzoricus* and its relatives, and that the shorter plesiomorphic state may not necessarily indicate a close relationship, at least between South African and Kenyan beetles.

Acknowledgements

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RESEARCH ARTICLE

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Catalogue, distribution, taxonomic notes, and conservation of the Western Palearctic endemic hunchback beetles (Tenebrionidae, *Misolampus*)

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Abstract

Hunchback darkling beetles of the Ibero-Maghrebian genus *Misolampus* Latreille, 1807 (Tenebrionidae, Stenochiinae) encompass six species: *M. gibbulus* (Herbst 1799), *M. goudotii* Guérin-Méneville, 1834, *M. lusitanicus* Brême, 1842, *M. ramburii* Brême, 1842, *M. scabricollis* Graells, 1849, and *M. subglaber* Rosenhauer, 1856. Previously known distribution ranges of the species were delineated using many old records, the persistence of such populations being questionable under the current situation of global biodiversity loss. Additionally, the status of geographically isolated populations of the genus have been the subject of taxonomic controversy. An exhaustive bibliographical revision and field search was undertaken, and the *Misolampus* collection of the Museo Nacional de Ciencias Naturales (MNCN-CSIC) was revised. The aims are to (i) provide an updated geographic distribution range for the species of *Misolampus*; (ii) to determine the taxonomic status of controversial populations; (iii) to provide a catalogue for *Misolampus*; and (iv) to discuss the conservation status of these saproxylic beetles. As a result, a catalogue including synonymies and type localities, geographical records, diagnoses, and information on natural history for all species of *Misolampus* is presented. The results reveal that the distribution ranges of the species of *Misolampus* have not undergone a reduction in the last century, and indicate the presence of the genus in areas where it had never been recorded before. The morphological variability of *M. goudotii* drove the proposal of different taxa that are here formally synonymised as follows: *M. goudotii* Guérin-Méneville, 1834 = *M. erichsoni* Vauloger de Beaupré, 1900, **syn. nov.** = *M. peyerimhoffi* Antoine, 1926, **syn. nov.**

Keywords

Coleoptera, geographic range, morphological variability, new synonymies, population persistence, saproxylic, scientific collections, Stenochiinae

Introduction

Species identification is an essential process for almost all biodiversity studies and can constitute a major constraint for conservation evaluation and legislation due to the inherent difficulty of identifying many of the groups, the long time needed for processing the samples, and the extensive taxonomic experience that this process requires (Gauld et al. 2000; Guerra-García et al. 2008; Wheeler 2013; de Oliveira et al. 2020; Saoud 2020). Meeting this goal for megadiverse groups such as insects is often arduous considering the vast number of species that must be identified and the limited number of taxonomists, which make correct identification a very time-consuming process (De Carvalho et al. 2005; Evenhuis 2007; Wheeler 2008; Moore 2011; Yang et al. 2015). It is therefore necessary to create easy-to-use identification tools, such as visually enhanced guides, to overcome the difficulties involved in the identification process (Kirchoff et al. 2011). Easy-to-use tools are also a key instrument for biodiversity study and conservation, since they can be used by both specialists and non-specialists and their implementation improves outcome, thereby facilitating decision-making for conservation actions (Norton et al. 2000; Yang et al. 2015; Rosas-Ramos et al. 2019).

Tenebrionidae is one of the most species-rich families of beetles, with approximately 20,000 species worldwide and many more taxa yet to be described (Bousquet et al. 2018). The large number of species, combined with the high morphological diversity that this family exhibits (Matthews et al. 2010), can hinder species identification of tenebrionids. Thus, providing easy-to-use, photographically illustrated identification tools can greatly facilitate data acquisition on this group of beetles (e.g., Matthews and Bouchard 2008; Pérez-Vera and Ávila 2012). The problem represented by the local absence of taxonomists and lack of adequate identification tools for non-specialists, is often reflected in a general lack of appropriate identifications, use of not-actualised names, or worst, inclusion of misidentified specimens in scientific collections or databases (Vilgalys 2003; Guerra-García et al. 2008; Kholia and Fraser-Jenkins 2011; Shea et al. 2011). This situation renders Tenebrionidae collections of little use for any scientific purpose, as it can be easily recognised by their poor representation in biodiversity databases (e.g., GBIF – Gaiji et al. 2013). One example of this problem is represented by the saproxylic hunchback darkling beetles of the genus *Misolampus* Latreille, 1807, paradoxically one of the better studied genera of Tenebrionidae at taxonomic and phylogenetic levels in the Western Palearctic Region (Palmer 1998; Palmer and Cambefort 2000).

The genus *Misolampus* [type species: *Misolampus hoffmannseggii* Latreille, 1807 (= *Pimelia gibbula* Herbst, 1799), by monotypy], currently included within Cnodalonini Oken, 1843, in the subfamily Stenochiinae Kirby, 1837 (= Coelometopinae Schaum, 1859; = Cnodaloninae; see Bouchard et al. 2005, 2011), encompasses six species: *M. gibbulus* (Herbst 1799), *M. goudotii* Guérin-Méneville, 1834, *M. lusitanicus* Brême, 1842, *M. ramburii* Brême, 1842, *M. scabricollis* Graells, 1849, and *M. subglaber* Rosenhauer, 1856 (Löbl et al. 2008; Martínez Fernández 2018), all of them linked to woodlands (Español 1949, 1954b; Molino Olmedo 1996; Palmer 1998). Five of them are endemic to the Iberian Peninsula, while *M. goudotii* is distributed throughout Morocco, Algeria and the Balearic Islands (Löbl et al. 2008). Reitter (1917), Antoine (1949, 1954), and Español (1949) provided identification keys for the species of *Misolampus*, and Palmer (1998) illustrated the female genitalia and specific diagnostic characters. Palmer (1998) and Palmer and Cambefort (2000) presented analyses of their geographic distribution and phylogenetic relationships, based on morphological traits. However, a search in the GBIF database (https://www.gbif.org; searched 22-mar-2020), only retrieved a total of 49 records for *Misolampus* (once records for other genera were discarded), three of them identified at genus level, and at least one misidentified species; 14 of 49 had geographic coordinates data, eleven of which corresponded to a single locality. Excluding all additional specimens with imprecise locality data, fewer than 30 specimens remained available for scientific use.

Despite database records shortfall, the distribution ranges of the species of *Misolampus* are relatively well known (Palmer 1998). Nevertheless, a few new eccentric geographical records have recently been published, suggesting that the distribution areas might be larger than what is currently recognised (Ibáñez Orrico 2002; Pérez and López-Colón 2010; Novoa et al. 2014). Regretfully, many of the specimens used to delineate the distribution areas of the species were collected between 50 and 100 years ago (Palmer 1998). The continuity of those populations through time, under the current scenario of drastic increase in land-use and climate change is, however, questionable (Vanwalleghem et al. 2017), all the more so given the saproxylic nature of these species, which often can lead to conservation issues (García-López et al. 2016).

In the light of these considerations, first, we aimed to provide an updated geographic distribution range for all the species of *Misolampus*, to evaluate their persistence in the areas where they were reported. For this purpose, we undertook a thorough bibliographical revision, an exhaustive field search, and we revised the *Misolampus* collection of the Museo Nacional de Ciencias Naturales (MNCN-CSIC) in Madrid (Spain). Secondly, and as a result of the field data collection, we aimed to determine the taxonomic status of geographically isolated populations of the genus, including those that have been the subject of taxonomic controversy (Reitter 1917; Español 1949; París García et al. 2011). Thirdly, with all that information, we aimed to provide an easy to use, photographically illustrated catalogue for *Misolampus*, and to discuss the potential threats and conservation status of the species of the genus.

Materials and methods

Field work to locate *Misolampus* was carried out by members of the research team for two periods, a non-intensive period from 1982 to 2000 in which specimens were collected, georeferenced, and dry-mounted for their morphological study, and a more intensive period from 2001 to 2013, with additional collections in 2019–2020, aimed to detect changes in populations previously known from records dating from the 19th and 20th centuries. Field data collection was carried out along most of the areas where the presence of the genus was documented (Spain, Portugal, and Morocco). Information on the location of previously known populations was obtained by undertaking an exhaustive bibliographic revision and by reviewing the *Misolampus* collection held at the MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain).

We studied 1304 specimens representing all known taxa of *Misolampus* (812 collected before 1945, and 492 collected after 1982). Of those, 355 specimens are preserved in ethanol, and 949 specimens dry-mounted (Table 1), all forming part of the entomological collections of the Museo Nacional de Ciencias Naturales (MNCN-CSIC, Madrid). The list of examined specimens is included in the corresponding paragraph of the species catalogue. Collectors are specified when different from authors or members of the research team; collector name is indicated for old collections only when printed in the labels; "ex." or "exx." is used to abbreviate "specimen" or "specimens".

Unresolved taxonomic issues, such as the validity of subspecies within the North African taxon, the specific assignation of the populations from Algarve (Reitter 1917; Español 1949), and taxonomic status of the isolated population from Ifni (Morocco) (París García et al. 2011), were addressed by comparing these problematic populations with specimens from near type localities, or from areas of undisputed taxonomy.

Distribution maps based on current data represent the extent of occurrence of each species following a relaxed modification of IUCN criteria (IUCN 2012). We performed species distribution models (SDMs) to obtain the potential distribution of each species (Kamiński et al. 2017). We used Maximum entropy algorithm (MaxEnt) (Elith et al. 2006, 2011) and the set of WorldClim v 2.0 environmental variables, with a resolution of 30 s (~ 1 km) (Fick and Hijmans 2017). The SDMs were modelled considering the studied specimens as presences and generating pseudo-absences fol-

Table 1. Specimens of *Misolampus* studied. Number of specimens by preservation mode (ethanol or dry-mounted) and date of collection (before 1945 or after 1982). The total number of specimens of each species is also provided.

Species	Before 1945	After 1982	Dry-mounted	Alcohol	Total
Misolampus gibbulus	339	163	392	110	502
Misolampus goudotii	108	66	145	29	174
Misolampus lusitanicus	1	27	1	27	28
Misolampus ramburii	11	26	32	5	37
Misolampus scabricollis	310	178	328	160	488
Misolampus subglaber	43	32	51	24	75

lowing Gil-Tapetado et al. (2018). This methodology creates a preliminary presence-only coverage model based on the maximum and minimum values of each variable. Areas with environmental values that fall out of the maximum and minimum range were considered liable to be pseudo-absences. This is considered as a more reliable approach than generating pseudo-absences entirely at random. SDMs were run 50 times, with random test percentage set to 25 and "subsample" as the sampling technique. The model was validated by estimating the area under the curve (AUC) value (Fielding and Bell 1997). All SDMs have AUC > 0.95 (*M. gibbulus*: 0.958; *M. goudotii*: 0.965; *M. lusitanicus*: 0.998; *M. ramburii*: 0.963; *M. scabricollis*: 0.964; *M. subglaber*: 0.958).

To obtain morphological data, dry-mounted specimens were examined under a stereomicroscopy. Specimen length was measured in dorsal view as the distance between the anterior margin of the pronotum and the elytral apex (ignoring elytral convexity). The head was excluded from measurement since it is usually directed ventrally. Maximum width was measured as the distance between the outer edges of the elytra at approximately three-fourths of the elytral length, also in dorsal view. Photographs of live specimens were taken with a Nikon digital camera. Extended depth-of-focus images of dry-mounted specimens, were taken on a Leica M165C stereo-microscope, with a digital camera Leica DFC450, using the LAS X software from Leica Microsystems.

Results

Species catalogue, distribution, notes on natural history, and taxonomy

***Misolampus gibbulus* (Herbst, 1799)**

Pimelia gibbula Herbst, 1799: 51. Terra typica: unknown: "Das vaterland ist mir unbekannt".

Misolampus hoffmannsegii Latreille, 1807: 161. Terra typica: "e Lusitania allatus". Latreille's (1807) species name has been often misspelled. Guérin-Méneville (1829–1838: 115, pl. 29; 1834: 27) spelled it as: "*M. hoffmansegii*" and "*M. hoffmanseggii*", respectively, Solier (1848: 185): "*M. hoffmanseggii*", and Laporte de Castelnau (1850: 204): "*M. hoffmansseggii*". Synonymy with *M. gibbulus* proposed by Solier (1848).

Misolampus gibbulus (Herbst, 1799): Solier 1848: 185.

Studied material. Portugal – Beja: Beja: 1 ex.; Beja, V-1909 (exp. del Museo): 1 ex.; São Martinho das Amoreiras, 200 m, 37°36'57.4"N, 08°27'57.3"W, 4-I-2013: 10 exx. – Evora: Evoramonte, 17-X-1992: 1 ex.; Monte São Bento, 353 m, 38°34'54.33"N, 7°56'12.10"W, 11-III-2010: 1 ex.; Valverde, 232 m, 38°31'39.8"N, 8°00'25.4"W, 4-X-2002: 1 ex.; – Faro: Alferce: 1 ex.; Alferce, V-1909 (Exp. del Museo): 2 exx.; carretera Monchique-Laranjeira [Gil Bordalo], 21-X-1992: 6 exx.; Foia, 742 m, 37°18'29.4"N, 08°35'56.2"W, 4-I-2013: 1 ex.; Monchique, 439 m, 37°21'40.3"N, 08°32'23.6"W, 4-I-2013: 8 exx.; San Marcos da Serra [São Marcos da Serra]: 2 exx.; San Marcos da Serra [São Marcos da Serra], V-1909 (exp. del Museo): 23 exx.; São Marcos da Serra, 140 m, 37°21'02.5"N, 08°22'48.4"W, 3-I-2013: 24 exx.; Sierra de Monchique, V-1909 (exp. del Museo): 1 ex.; Portalegre: Santo Antonio de Alcorrego, 150 m, 38°58'59.5"N, 7°56'54.1"W, 18-IV-2013: 6 exx. Spain – Andalucía: Córdoba: Córdoba (Col. del Sr. Pérez Arcas): 2 exx.; Córdoba: 2 exx.; Córdoba, IV-1901 (Escalera leg.): 4 exx.; Córdoba, VI-1909 (Exp. del Museo): 3 exx.; Manueles, 30SUH82, 7-V-1982 (M.A. Alonso Z. leg.): 1 ex.; Huelva: Barranco Riofrío [La Nava], 28-XII-1985: 1 ex.; Cala (C. Bolívar leg.): 15 exx.; Cortegana, Puerto del Corzo (hacia Gil Márquez), 664 m, 37°52'56.1"N, 06°50'42.3"W, 3-I-2013: 7 exx.; Patrás, 397 m, 37°48'04.4"N, 6°43'30.8"W, 1-V-2004: 3 exx.; Jaén: [3 km al SO de] Aldeaquemada, 25-IV-1992: 3 exx.; Lugar Nuevo, 24-X-1991: 2 exx.; Santa Elena, carretera hacia La Aliseda, 795 m, 38°20'53.1"N, 03°33'20.6"W, 28-XII-2010: 14 exx.; Santa Elena, 12-III-1901: 2 exx.; Santa Elena: 2 exx.; Sierra Morena: 1 ex.; Sevilla: Constantina: 1 ex.; – Castilla –La Mancha: Ciudad Real: Almadén (Belbeze leg.): 1 ex.; Navas de Estena: 1 ex.; Pueblo Nuevo del Bullaque, 7-XII-1992: 2 exx.; Puerto Madrona, 20-XI-1992: 8 exx.; Saceruela (Paz leg.): 1 ex.; Solana del Pino: Puerto Madrona, 38°25'07.3"N, 4°03'33.1"W, 06-III-2012: 1 ex.; Toledo: Santa Cruz del R. [Retamar] (Paz leg.) (Col. del Sr. Pérez Arcas): 1 ex.; – Castilla y León: Ávila: Candeleda, XI-1933: 1 ex.; 8 km NE Hoyo de Pinares, 40°31'40.6"N, 4°20'04.5"W, 1-IV-2013: 2 exx.; Mombeltrán – Navalperal [de Pinares]: 1 ex.; Extremadura: Badajoz: Aljucén (Pacheco leg.): 2 exx.; Cáceres: Alcuéscar: I-1894: 3 exx.; Belvís de Monroy, 373 m, 39°48'04.8"N, 5°37'01.1"W, 24-XII-2011: 6 exx.; Castillo de Trevejo, 714 m, 40°10'20.9"N, 6°46'48.9"W, 17-IV-2011: 1 ex.; Valdemorales, 420 m, 39°12'08.1"N, 06°03'57.8"W, 2-I-2012: 2 exx. Madrid: Brunete (Bolívar leg.): 2 exx.; Cadalso [de los Vidrios] (J. Ardois leg.): 120 exx.; Cadalso de los Vidrios, hacia Almorox, 12-IV-1992: 1 ex.; Cerro de San Pedro, 29-X-2004: 4 exx.; Collado Mediano (C. Bolívar leg.): 1 ex.; Collado Mediano: 13 exx.; Collado Mediano (G. Schramm leg.): 4 exx.; Collado Mediano (Moróder leg.): 5 exx.; Fresnedillas de la Oliva, 941 m, 40°29'38.57"N, 4°10'12.90"W, 14-III-2001: 14 exx.; Galapagar (Col. del Sr. Pérez Arcas) (*Misolampus gibbulus* Hbst.): 1 ex.; Manzanares [El Real], 30-III-1928: 1 ex.; Moralzarzal: Cerro del Telégrafo, 23-IV-2017: 1 ex.; Navas del Rey, 2-XII-1990: 2 exx.; Pelayos de la Presa, 799 m, 40°20'19.40"N, 4°21'34.84"W, 3-III-2001: 1 ex.; [3 km al S de] Quijorna, 5-II-1992: 1 ex.; Robledo de Chavela: 7 exx.; Santa María de la Alameda (estación), 1-IV-1991: 10 exx.; Sierra de Guadarrama (J. Lauffer leg.): 1 ex.; Torrelodones, 7-XI-1992: 4 exx.; Valdemaqueda, 40°30'30.0"N, 4°17'00.1"W, 1-IV-2013: 2 exx.; Valdemorillo, 12-IV-1992: 7 exx.; Villa del Prado (J. Ardois leg.): 105 exx.; Villa del Prado: 4 exx.; Villa del Prado, Encinar del Alberche, 742 m, 40°17'29.7"N, 04°21'11.9"W, 4-I-2009: 5 exx.; Villalba: 1 ex.

Diagnosis. Total length 6.6–12 mm (Reitter 1917; Español 1949; López-Pérez 2014a). Easily recognisable by its general shiny appearance and small size. *Misolampus gibbulus* presents acutely protruding prothoracic anterior angles, strong pronotal punctation, deep, and densely covering most of its surface; elytra with well-marked deeply excavated striae, with large and deep punctation, and shiny interstriae intervals often with additional series of punctures (Fig. 1A–D). Female genitalia figured by Palmer

(1998). The species presents marked variability on the development and depth of the elytral and pronotal sculpture. Pronotal punctation is usually less developed, and elytral striae shallower, not so excavated, in populations of southwestern Portugal (Faro district) (see taxonomic discussion).

Geographic distribution. Endemic to Spain and Portugal (Löbl et al. 2008) (Fig. 2). Its general distribution includes most of the southwestern area of the Iberian Peninsula. Published records are however scanty, from central and southern Portugal, and from the Spanish provinces of Cáceres, Ciudad Real, Córdoba, Huelva, Jaén, Ma-

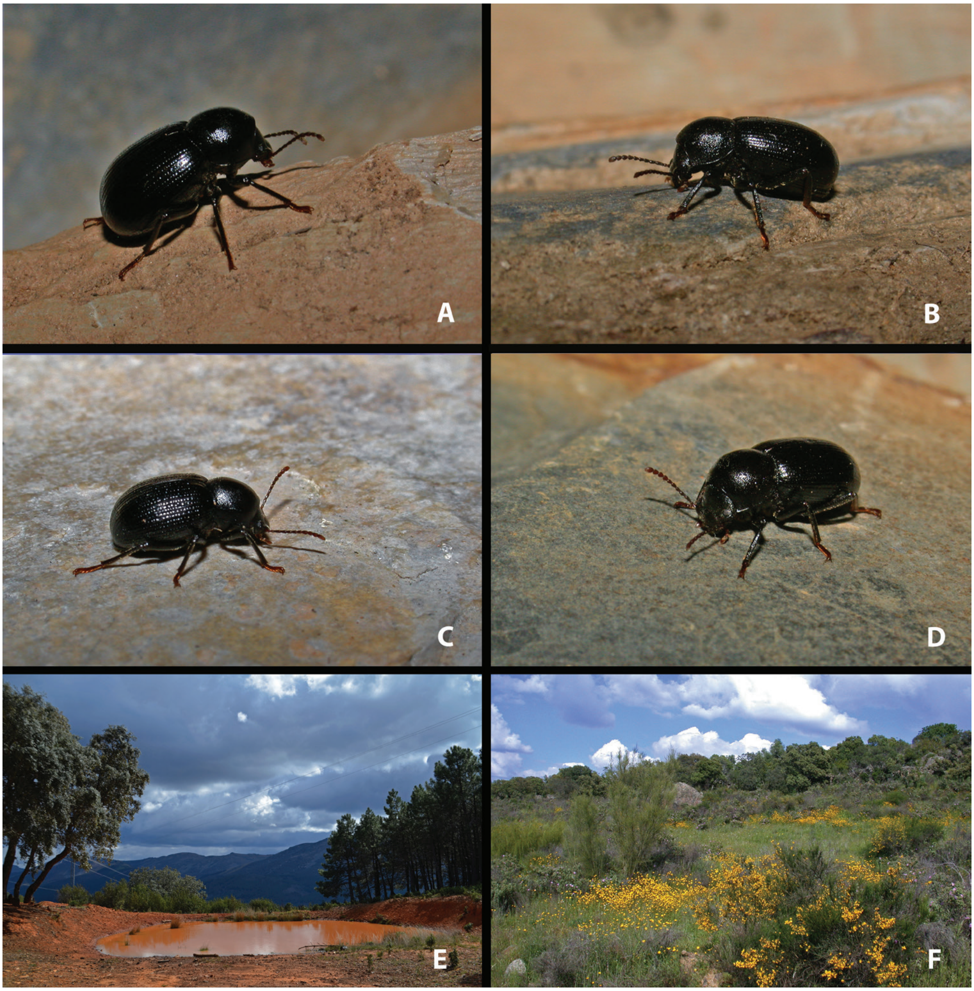

Figure 1. Live specimens and habitat of *Misolampus gibbulus* **A–D** live adult specimens of *Misolampus gibbulus* from Portugal (**A** Foia; **B** Monchique; **D** São Martinho das Amoreiras) and Spain (**C** Santa Helena, Jaén); specimens **A**, **B**, and **D** represent the diversity of sculptural patterns in elytra and pronotum within the Faro population, see the contrast with typical specimen **C**; **E, F** typical habitats of *M. gibbulus* in Spain (**E** native *Quercus ilex* and *Pinus* plantations at Robledo del Mazo, Toledo **F** *Q. ilex* open forest with *Cytisus* and *Retama* at Puerto de Santa Cruz, Cáceres). Photographs by MGP.

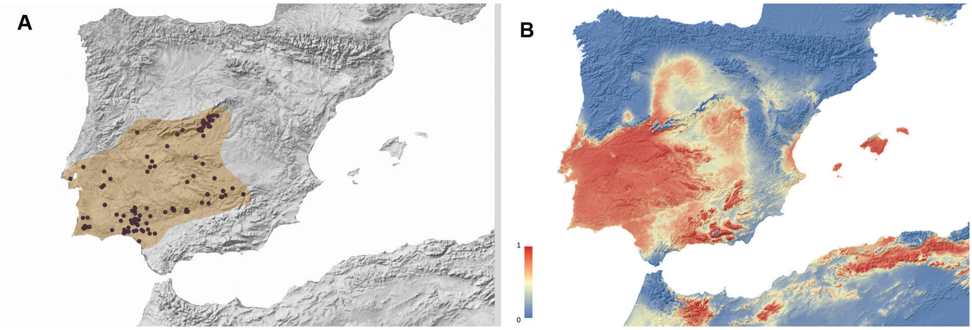

Figure 2. A Geographic distribution of *Misolampus gibbulus.* Map of the Iberian Peninsula depicting the geographic distribution range of the Iberian endemic *Misolampus gibbulus* (orange area). Purple dots correspond to the species' records, including both recent and old, as well as previously published data **B** potential geographic distribution of *Misolampus gibbulus*: Red indicates areas of high suitability, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al. 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

drid and Sevilla (Latreille 1807; von Heyden 1870; Paulino de Oliveira 1894; Reitter 1917; Lindberg 1933; De la Fuente 1934–1935; Español 1949; Cabral 1983; Cárdenas Talaverón and Bujalance de Miguel 1985; Cárdenas 2003; Grimm and Aistleitner 2009; López-Pérez 2014a, 2014c; Bujalance de Miguel 2015; Barreda 2018).

Our new records considerably expand the known distribution of *M. gibbulus*. In addition to previously published data, we add new records for the district of Évora and Portalegre in Portugal, and from the provinces of Ávila, Badajoz, and Toledo in Spain; together with numerous localities for some provinces represented by a few records, such as Cáceres, Ciudad Real, and Madrid. With the addition of these records, the distribution of *M. gibbulus* seems to be more or less continuous along the southern slopes of the Sistema Central: from Cáceres and Ávila to Madrid, along both slopes of Montes de Toledo and Sierra Morena, and in a more or less extended area in southern Portugal, from Évora to Serra de Monchique in the Algarve region. The Guadalquivir river basin seems to conform the southeastern distribution limit for the species (Fig. 2A). The potential distribution map identifies southwestern Iberia as a high suitable area for the species occurrence, together with some areas where the species does not occur: the Betic Mountain ranges, the Balearic Islands, and northern Africa (Fig. 2B).

Notes on natural history. *Misolampus gibbulus* is a low altitude species, ranging from 4 to 1278 m a.s.l., although 81% of the populations recorded are located below 800 m of altitude. Geological substrates are very diverse across its distribution area, but mostly siliceous, including sandstones, gneisses, granites, and schists, which generate acid soils (see Vera 2004; Oliveira and Quesada 2019a, 2019b). It occupies mainly the meso-Mediterranean thermoclimatic belt and, to a lesser extent, the thermo – (at the southermost portion of its range) and supra-Mediterranean (on a narrow northern strip), with ombrotypes from dry to humid (Rivas-Martínez 1987; Rivas-Martínez et al. 2002; Rivas-Martínez 2007). It is found over an extensive variety of forest and subforestry habitats, including both coniferous (*Pinus* L.) and broadleaved trees (*Quercus*

L., *Fraxinus* L.), and also dense shrublands of *Cistus* L. ("jarales"), *Retama* Raf. and *Cytisus* Desf. ("retamares") (Fig. 1E, F). The species also occupies areas densely reforested with native and non-native *Pinus* and *Eucalyptus* L'Hér. (Cabral 1983), as well as open man-modified agroforestry systems ("dehesas" of *Quercus*) and montane agrosystems with olive and chestnuts trees (*Olea europaea* L. and *Castanea sativa* Mill.) (see Ladero 1987; Rivas-Martínez et al. 1987; Valle 2003; Costa Tenorio et al. 2005).

Misolampus gibbulus is commonly found under bark or within decomposing dead logs and stumps of pines (mainly of *Pinus pinea* L. and *Pinus sylvestris* L.), including reforested areas (especially *Pinus pinaster* Aiton), where they appear to be particularly common. It is also found in dead or old trunks of perennial or deciduous oaks (*Quercus ilex* L., *Quercus suber* L., *Quercus pyrenaica* Willd. and *Quercus faginea* Lam.), under the dry layers that cover roots and thick stems of *Cistus ladanifer* L. and *Cistus laurifolius* L., and at the base of brooms, mainly *Cytisus scoparius* (L.) Link and *Retama sphaerocarpa* (L.) Boiss. Occasionally found under loose bark or at the base, among decaying wood of standing *Eucalyptus* trees, and also in rotten *Eucalyptus* stumps (Cabral 1983; López-Pérez 2014a; pers. obs.). Sometimes found also under stones in open areas, near forest or shrub patches. Almost all these habitat locations are coincident to those described by López-Pérez (2014a) for the province of Huelva. Its food source is unknown (as in the other species of the genus), although Barreda (2018) pointed out mistakenly that it is a moss eater (quoting Español 1949 and Bujalance de Miguel 2015); nevertheless, Español (1954b) commented that the species of *Misolampus* are saprophagous, without further specification.

Misolampus gibbulus has been found in microsympatry with *M. scabricollis* along western Sierra Morena (Huelva), northern Extremadura (Cáceres), Montes de Toledo (Toledo) (Fig. 1E), and southern slopes of the Sistema Central (Madrid, Ávila, Toledo), and with *M. subglaber* at the eastern end of Sierra Morena (Jaén) (pers. obs.). Adults can be found across most of the year (Cárdenas Talaverón and Bujalance de Miguel 1985; López-Pérez 2014a; Barreda 2018) but according to our observations they are more easily encountered during the wetter months (October to May).

Misolampus goudotii Guérin-Méneville, 1834

Misolampus goudotii Guérin-Méneville, 1834: 28. Terra typica: "trouvée à Tanger... ...à trois lieues de Tanger, sur les bords d'une rivière, dans le tronc d'un olivier." Vauloger de Beaupré (1900), Reitter (1917), Antoine (1949), and Español (1949) among others, wrote the species name with a single final -i. Solier (1848) and Vauloger de Beaupré (1900) mentioned the unavailable name: "*Misolampus nigrita* Dejean", and Español (1954a): "*M. moraguesi*".

Misolampus goudotii Erichson in Wagner, 1841: 184 (non Guérin-Méneville 1834). Terra typica: not indicated, but "von Algier" according to Erichson's (1841) work title.

Misolampus erichsoni Vauloger de Beaupré, 1900: 674 syn. nov. Terra typica: "Algérie: O., Oran...; Daya...; Tlemcen...; Mascara..., Ammi Moussa; A.: Blidah...; La Chiffa...; Margueritte...; forêt de Boghar...; mont Ouarsenis...; forêts de la Grande-Kabylie...".

Misolampus peyerimhoffi Antoine, 1926: 257 syn. nov. Terra typica: "Grand Atlas, région du Glaoui: plateau des Aït Rba...".

Studied material. Algeria: "Argelia" (Dufour leg.): 1 ex. Morocco – Marrakech-Tensift-Al Hauz: Toufliht, 1483 m, 31°28'34.6"N, 7°26'06.5"W, 11-III-2013: 4 exx. – Meknès – Tafilalet: Ain Leuh, 17-V-1925: 1 ex.; Azrou, 1900 m (Alluaud 79) (*Misolampus goudoti var. laevior* Alluaud): 1 ex.; Azrou, 19-V-1925: 1 ex.; Dj. [Yebel] Hebri, 20-V-1925: 1 ex.; Timadit [Timahdite], 21-V-1923: 1 ex. – Tanger – Tétouan: Rif: Beni Siyyel: Bab Ruadi: VI-1932 (C. Bolívar leg.): 6 exx.; Tanger, 1897: 3 exx.; Tanger (M. Escalera leg.) (small square-label pinned): 36 exx., plus 3 exx. only square-labelled; 2 km al O de Bab Berret, 1318 m, 35°00'02.57"N, 4°55'31.91"W, 12-VI-2011: 3 exx.; Crtra. Zinat-Mulay Abdeselam, P-4702, Beni Aros, Yebala, 513 m, 35°22'04"N, 5°32'17"W, 29-IV-2016: 5 exx.; Yebel Bou-Hachem, Beni Aros, Yebala, 1160 m, 35°15'31"N, 5°30'49"W, 12-V-2012: 6 exx.; Crtra. Mulay Abdeselam-Al Hamra, P-4704, Beni Aros, 985 m, 35°15'50"N, 5°25'36"W, 28-XI-2019: 2 exx.; Larache: Yebala: Beni Arós: Yebel Bou-Hachem, 35°15'31"N, 5°30'49"W, 9-VI-2012: 2 exx.; Pinsapar del Talassemtane, 1900 m, 35°08'36.7"N, 5°08'13.0"W, 11-VI-2011: 2 exx.; Bab Taza: Talassemtane, 1401 m, 35°06'10.9"N, 5°08'21.3"W, 27-VII-2013: 1 ex.; Bab Taza: Talassemtane: Plaza de España, 1667 m, 35°09'03.7"N, 5°08'28.6"W, 27-VII-2013: 1 ex.; Casa Forestal, Yebel Lekraa, P.N. Talasemtane, Chefchaouen, 35°07'56"N, 5°08'11"W, 1695 m, 7-VI-2008: 3 exx.; Yebel Talassemtane-vertiente sur, P.N. Talasemtane, Chefchaouen, 35°07'53"N, 5°08'01"W, 1650 m, 11-IV-2011: 4 exx.; P.N. Yebel Tazaot, Pinsapar, P.N. Talasemtane, Chefchaouen, 35°15'N, 5°07'W, 1670 m, 7-V-2011: 2 exx.; Pista hacia Casa Forestal, Yebel Lekraa, P.N. Talasemtane, Chefchaouen, 35°07'45"N, 5°08'09"W, 1700 m, 28-VII-2011: 1 ex.; E. de Yebel Talaousisse, P.N. Talasemtane, Chefchaouen, 35°07'33"N, 5°04'03"W, 1350 m, 1-XII-2018: 2 exx.; Pista hacia Haout Taznout, P.N. Talasemtane, Chefchaouen, 35°08'20"N, 5°07'24"W, 1712 m, 27-IV-2019: 2 exx.; Yebel Tizirhen, Bab Berred, Rif Central, 1585 m, 35°00'54"N, 4°54'57"W, 27-IV-2017: 3 exx.; Yebel Tizirhen, Bab Berred, Rif Central, 1570 m, 35°00'47"N, 4°54'03"W, 28-IV-2018: 1 ex.; Pista de Bab El Kar, Montañas de Fifi, Rif, 1512 m, 34°59'13"N, 5°11'20"W, 2-VI-2019: 2 exx. – Taza – Al Hoceima – Taounate: Iguermalen [Targuist]: Beni Mesdui, VI-1932 (M. Escalera leg.): 6 exx.; Rif: Beni Seddat: Imosiner: VI-1930 (exp. C. Bolívar leg.): 3 exx.; Rif: Beni Seddat: Tizi Taka, VI-1932 (C. Bolívar leg.): 4 exx.; Rif: Beni Seddat: Tizi Taka, VI-1932 (Exp. C. Bolívar leg.): 1 ex.; Rif: Iguermalen (Targuist), VI-1930 (exp. C. Bolívar leg.): 4 exx.; Rif: Ketama, Bab Chiquer, VI-1932 (C. Bolívar leg.): 8 exx.; Rif: Ketama, Bab Chiquer, VI-1932 (M. Escalera leg.): 2 exx.; Rif: Ketama: Tainza, VI-1930 (exp. C. Bolívar leg): 3 exx.; Rif: Ketama: Tidiguin [Tidghine], VI-1930 (exp. C. Bolívar leg.): 1 ex.; Rif: Ketama: Zoco Telata, VI-1932 (M. Escalera leg.): 7 exx.; Lurdeka [?]: 1 ex.; Yebel Tidighin, Azila, Rif central, 1705 m, 34°51'14"N, 4°32'19"W, 29-XI-2019: 1 ex; Carretera P-5420, P.N. Tazzeka, Medio Atlas nororiental, 1000 m, 34°03'N, 4°15'W, 25-XI-2004 (F.J. Martínez leg.): 2 exx. – Souss-Massa-Drâa: Yebel Tual, 28-VII-1934: 1 ex.; Ifni: Yebel Tamarrut [25 km SE Ifni], I-1935 (F. Escalera leg.): 1 ex.; Sidi Ifni: Akarkor, Jbel Toual, 627 m, 29°13'48.9"N, 10°00'44.1"W, 21-I-2020: 4 exx. Spain – Islas Baleares: Mallorca (Mas de Xaxars leg.) (*Misolampus erichsoni*): 2 exx.; Escorca, 26-III-1985, 1 ex.; Escorca, Coll de Femenia, 545 m, 39°51'33.68"N, 2°54'19.27"W, 25-III-2012: 10 exx.; Menorca (Cardona leg.): 2 exx. plus 6 exx. without data; 2 exx.; Menorca: 2 exx.; Algaiarens, 14 m, 40°02'28.3"N, 03°55'28.4"W, 27-IV-2006: 2 exx.

Diagnosis. With a total length from 10 to 14 mm, this is the largest species of the genus (Vauloger de Beaupré 1900; Reitter 1917; Antoine 1926; Español 1949). This species is well characterised and isolated within the genus *Misolampus* by the following traits: fore angles of the prothorax not protruding, almost rounded, forming an obtuse angle at apex; lateral surface of pronotum shallowly rugose, with the rugosity progressively erased towards the dorsal areas that appear smoother, propleural punctation fine and often erased; elytra with longitudinal series of small elongated tubercles, more apparent on the sides of the posterior half of the elytra (Español 1949, 1954a; Palmer 1998) (Fig. 3A–C). Female genitalia figured by Palmer (1998). Specimens from the Balearic Islands have been studied karyologically (Juan and Petipierre 1986, 1989; Juan et al. 1993; Pons et al. 1993; Pons 2004), presenting a chromosome number of 20 (2n) (Juan and Petitpierre 1986, 1989). There is marked geographical variability on the sculpture and shape of pronotum and propleurae, and on the development of elytral tubercles (Vauloger de Beaupré 1900; Antoine 1949; Español 1954a) (Fig. 3A–C). Specimens from northern Morocco (excluding the Tingitane Peninsula), Algeria and the Balearic Islands, present a well-developed and evident elytral tuberculation that may form rugose ridges (Fig. 3A). On the other extreme, elytral tubercles are reduced in the Rif and Atlas populations (Fig. 3B), to become almost completely absent in the specimens from Sidi Ifni (Fig. 3C). Pronotum sculpture is formed by fine spaced punctures intermixed with granules, much denser on the sides in the Balearic Islands population (Fig. 3A); pronotal rugose areas are more marked and extended in the specimens from the High Atlas (Fig. 3B), and formed by sparse punctation, without granulose areas, in the specimens from Ifni (Fig. 3C). The anterior edge of the pronotum, in the Rif and Balearic populations, is straight at the middle, while it appears convex in the populations from the High Atlas (Antoine 1949). The geographic distribution of this variability has been the subject of taxonomic discussion resulting in the proposal of different taxa, here formally synonymised (see synonymic list, and taxonomic discussion).

Geographic distribution. Distributed throughout Morocco, northern Algeria and the Balearic Islands in Spain (Antoine 1926, 1949; Español 1949; Löbl et al. 2008). Precise records are well distributed in northern Morocco and Mallorca, scanty in all other areas (Solier 1848; Lucas 1849; Cardona Orfila 1872; Pérez Arcas 1873; Moragues 1889; Champion 1891; Vauloger de Beaupré 1900; Martínez de la Escalera 1914; Reitter 1917; Peyerimhoff 1919; Antoine 1926; Lindberg 1933; De la Fuente 1934–1935; Palau 1945; Antoine 1949; Español 1949, 1953, 1954a; Cobos 1955; Pardo Alcaide 1955; Kocher 1958; Cobos 1961; Español 1967; Mouna and Arahou 1986; Juan and Petitpierre 1989; Whitehead 1993; París García et al. 2011; Benyahia et al. 2015, 2016; Núñez et al. 2016; Chavanon 2020) (Fig. 4). The record from Ceu-

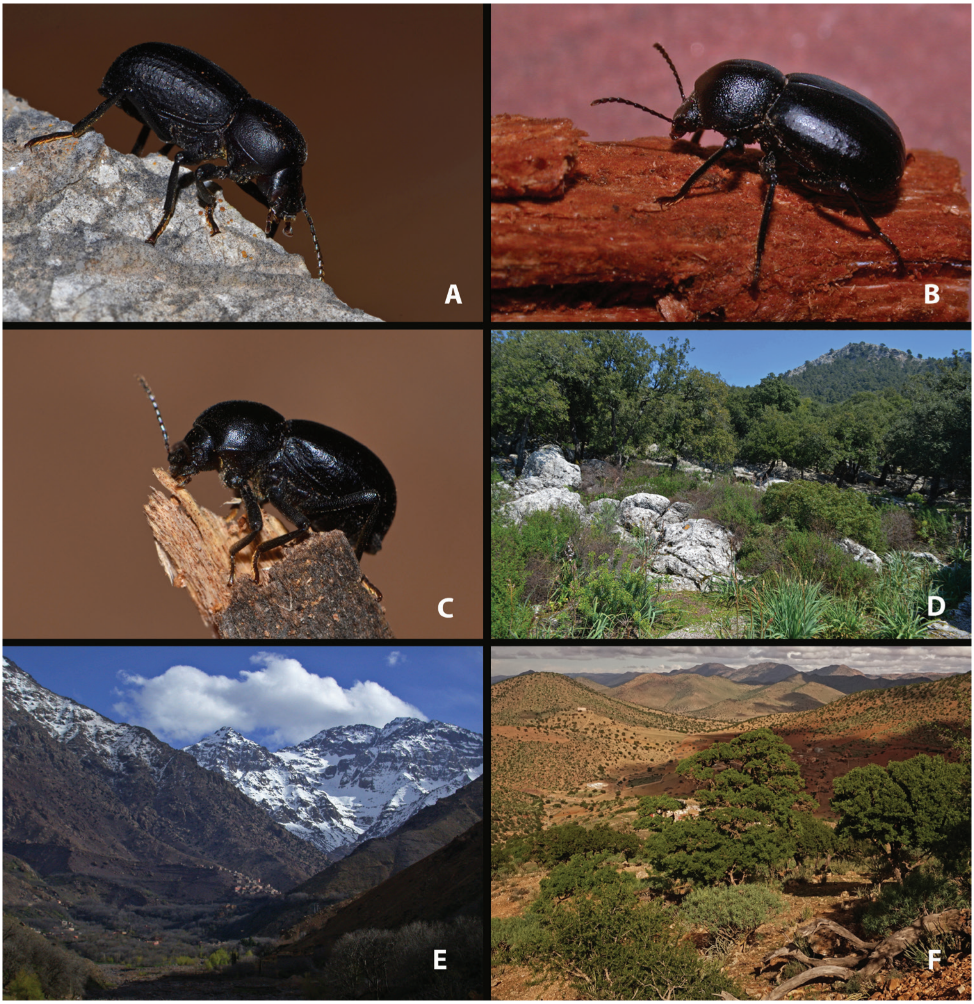

Figure 3. Live specimens and habitat of *Misolampus goudotii* **A–C** Live adult specimens of *Misolampus goudotii* from the Balearic Islands (**A** Cap Formentor, Mallorca) and Morocco (**B** Toufliht, High Atlas **C** Akarkor, Sidi Ifni); the specimens selected represent the diversity of sculptural patterns in elytra and pronotum reported for the species **D–F** A summary of the impressive habitat diversity used by *M. goudotii* from the Balearic Islands (**D** *Quercus ilex* forest at Creu de Menut, Mallorca), to southwestern Morocco (**E** deep valleys in the Toubkal National Park, High Atlas **F** *Argania spinosa* open forests at Jbel Toual in Sidi Ifni). Photographs by MGP and NRR.

ta, Spain (Vauloger de Beaupré 1900) corresponds to the mountain Yebel Musa (just 1.5 km west of Ceuta), currently in Moroccan territory (region of Tanger-Tétouan).

The studied materials include recent and old records of populations from the Balearic Islands (Mallorca and Menorca) and from the Moroccan regions of Meknès-Tafilalet, Souss-Massa-Drâa, Tanger-Tétouan, and Taza-Al Hoceima-Taounate. Recent data are available from all four regions, with a large number of localities from the Rif, and less numerous in the Middle and High Atlas. Among these records, we emphasise the re-discovery of the population from the province of Sidi Ifni, in January-2020, 85 years after its original finding, by F. Martínez de la Escalera in 1934 and 1935 (París García et al. 2011). The latter is a singular population, apparently isolated in the arid mountains near Ifni; its closest known population is located in the Western High Atlas, ca. 250 km to the northeast (Fig. 4A). The potential distribution map locates high suitable areas for this species along the mountain ranges of northwestern Africa, the coastal and mountain areas in the Tingitane peninsula, and along the coast of Rabat-Salé-Kénitra region. It also identifies areas where the species does not occur as high suitable, including sothwestern Iberia, the Balearic Islands and Sardinia. The Ifni population is located in a very fragmented area of high suitability, suggesting a possible Pleistocene relict status for this population (Fig. 4B).

Notes on natural history. *Misolampus goudotii* is widely distributed over northwestern Africa, though restricted to mountain ranges and adjacent areas: Rif, Middle Atlas, western High Atlas, Beni Snassen mountains, southwestern foothills of the Anti-Atlas (Morocco) and Tellian Atlas (Algerie) (Fig. 4). Altitudinal range in the Maghreb from 2 to 2064 m a.s.l., with 70.5% of records above 800 m of altitude (62% above 1000 m). In the Balearic Islands its altitudinal range is lower, between 15 and 718 m a.s.l., but the species is found mainly in areas of mountainous topography (e.g., Serra de Tramuntana in Mallorca). It inhabits a wide range of geological substrates, both acid and basic, from plutonic and metamorphic types to calcareous and dolomitic rocks (see Michard 1976; Vera 2004; Oliveira and Quesada 2019a, 2019b). *Misolampus goudotii* is a euryecious species that occurs at infra-, thermo-, meso- and supra-Mediterranean thermoclimatic belts, in regions with ombrotypes from arid to hyperhumid (Benabid 1985; Rivas-Martínez 1987; Le Houerou 1989; Rivas-Martínez et al. 2002; Rivas-Martínez 2007; Sebbar et al. 2013), and occupies a wide variety of forest formations, both coniferous [*Tetraclinis articulata* (Vahl) Mast., *Abies maroccana* Trab., *Cedrus atlantica* (Endl.) Manetti ex Carrière, *Juniperus phoenicea* L., *Juniperus thurifera* L., *Pinus nigra* J.F. Arnold, *Pinus halepensis* Mill., *P. pinaster*] and broadleaved [deciduous: *Quercus canariensis* Willd., *Quercus afares* Pomel, *Q. faginea*, *Q. pyrenaica*; perennial: *Quercus ilex*, *Q. suber*, *Olea europaea* var. *sylvestris* (Mill.) Lehr] (see Benabid 1982, 1984, 1985; Benabid and Fennane 1994; Bolòs 1997; Charco 1999; Benabid 2000; Taleb and Fennane 2019). It also occurs in areas reforested with pines (pers. obs.) (Fig. 3D, E). The population of Ifni inhabits mountains (620–1225 m of altitude) at the infra-Mediterranean thermoclimatic belt, probably affected by the proximity to the Atlantic Ocean and consequently by the presence of some degree of cryptic precipitation (Géhu and Biondi 1998). The vegetation of the area is dominated by open forest of *Argania spinosa* (L.) Skeels, with sparse cactiform and arbustive *Euphorbia* L. (Médail and Quézel 1999; Ruiz and García-París 2015), and large areas covered by formerly cultivated *Opuntia* Mill (Fig. 3F).

In the Moroccan Rif, *M. goudotii* is often encountered under bark, inside fallen logs or stumps, and at the base of dead old oaks (perennial: *Q. ilex*, *Q. suber*; deciduous: *Q. canariensis*, *Q. faginea* and *Q. pyrenaica*), arbutus trees (*Arbutus unedo* L.), wild olive trees (*O. europaea* var. *sylvestris*), pines (*P. nigra*, *P. pinaster*, *P. halepensis*), firs (*Abies maroccana*), and cedars (*Cedrus atlantica*), as already reported partially by Vauloger de Beaupré (1900), Cobos (1955, 1961), and Benyahia et al. (2015, 2016).

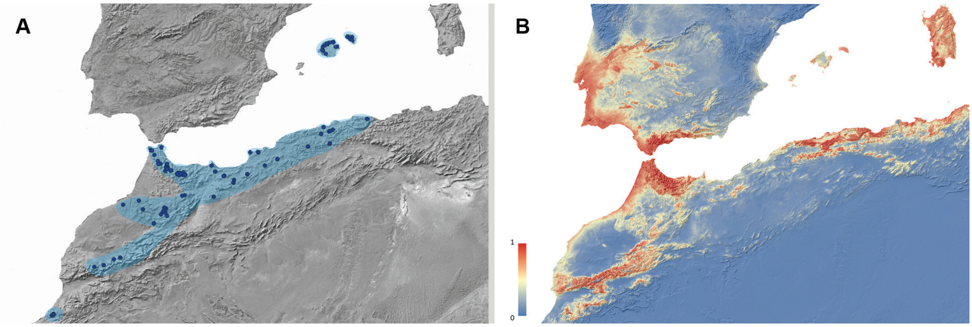

Figure 4. A Geographic distribution of *Misolampus goudotii*. Map for the distribution range of *Misolampus goudotii* (pale blue spot). Blue dots correspond to the species records, including both recent and old, as well as previously published data. The population from Ifni remains isolated from the main distribution range, by a distance of ca. 250 km **B** potential geographic distribution of *Misolampus goudotii*: Red indicates high suitable areas, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al. 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

They can also be found under bark of standing dead trees (*A. maroccana*, *C. atlantica*, *Q. suber*, *Q. pyrenaica*). In the Middle and High Atlas, it is usually found under bark and inside large decaying logs of *Q. ilex* (Antoine 1926), but also in old decomposing logs of *P. nigra* and *C. atlantica*. Mouna and Arahou (1986) collected the species on thuya (*Tetraclinis articulata*) in the Korifla Valley (northwestern Morocco). Sidi Ifni specimens were found within crevices in old dead logs of *Argania spinosa*, almost buried on the ground of a steep slope (Fig. 3F). Nearby standing dead trunks were occupied by *Nesotes tuberculipennis villarubiai* (Español, 1943) as described by Nabozhenko (2015). In Algeria, they have been found under bark of fallen pines (Vauloger de Beaupré 1900). In Menorca, it has been found in oak forests of *Q. ilex*, under bark or under stones and leaf litter (Cardona Orfila 1875), and in Mallorca it is frequent in decaying wood of fallen pines (*P. pinea*) and old oaks (*Q. ilex*) (Fig. 3D).

Adult specimens are often found in aggregations. We found aggregations of approximately 15 specimens close together in a single large rotting pine log in Mallorca. We also found aggregations of *M. goudotii* together with *Helops insignis maroccanus* (Fairmaire, 1873) (Tenebrionidae, Helopinae) under bark of dead trees of *Q. suber*, *A. maroccana* and *C. atlantica* in the Rif Mountains. Whitehead (1993) relates the finding on two occasions of groups of individuals between the annual rings of dead pines (*P. halepensis*) in active colonies of ants of the genus *Messor* Forel, 1890 and of the species *Monomorium bicolor* Emery, 1877 (probably another species of *Monomorium* Mayr, 1855, since the invasive *M. bicolor* is not present in Balearic Islands; Salata et al. 2019).

Adults are present all year round, but they are more commonly seen in winter and spring in middle and low elevations (Vauloger de Beaupré 1900; Español 1967; pers. obs.), and in summer at higher altitude (Antoine 1926), however, Moragues (1889) mentioned collections during the summer in Mallorca.

Misolampus lusitanicus Brême, 1842

Misolampus lusitanicus Brême, 1842: 82. Terra typica: "Portugal".

Studied material. Portugal – Porto: Fervença – Eido, 585 m, 41°14'28.98"N, 7°57'00.34"W, 24-IV-2012: 23 exx. Spain – Castilla y León: León: Lago de la Baña, 1418 m, 42°15'23.2"N, 6°44'58.6"W, 22-VIII-2016: 1 ex. – Galicia: Ourense: Fumaces, 804 m, 41°56'50.2"N, 7°21'05.7"W, 20-XI-2012: 3 exx.; Sierra de Oneija [Queixa] (A. Kricheldorff leg.): 1 ex.

Diagnosis. Total length 7.5–8.0 mm, one of the smaller species within the genus (Reitter 1917; Español 1949; pers. obs.). Antennae relatively short, not reaching the base of prothorax (Español 1949). Pronotum with relatively deep, dense, well-defined punctation covering all its surface. Elytra covered by dense punctation somewhat confused with shallow granulation, or partially erased at the disc (Fig. 5A–D). Female genitalia figured by Palmer (1998). We have not observed any relevant morphological variability among the populations studied.

Geographic distribution. Endemism of northern Portugal and northwestern Spain (Löbl et al. 2008) (Fig. 6). Published records are very scarce but distributed in the district of Braga (Portugal) and provinces of León, Ourense, Pontevedra, and Zamora (Spain) (Brême 1842; von Heyden 1870; Paulino de Oliveira 1894; Reitter 1917; De la Fuente 1934–1935; Español 1949, 1955, 1956; Español and Comas 1981; Novoa et al. 2014).

The material we studied includes recent representation from the provinces of León and Ourense in Spain, and from the Porto district in Portugal. To date, the species is only known from ten localities (Fig. 6A). The potential distribution map locates high suitable areas for this species mainly in the northwestern region of the Iberian Peninsula (Fig. 6B).

Notes on natural history. *Misolampus lusitanicus* is a medium altitude species (altitudinal range 572–1680 m a.s.l.; 59% of records above 1000 m), typical of mountainous reliefs of northwestern Iberian Peninsula (Macizo Galaico-Leonés mountain range: Serra San Mamede-Queixa, Serra do Eixe, Serra do Gêres, Serra Segundeira y do Porto, Serra dos Ancares, Serras Occidentais and Montes de León). Geological substrates in its geographic range are mainly granite, gneiss and, to a lesser extent, quartzite, which form acid soils (Vera 2004; Oliveira and Quesada 2019a, b). It occupies meso- and supra-Temperate thermoclimatic belts, and more locally meso- and supra-Mediterranean, mostly in the Atlantic European biogeographic province, in high rainfall regions, with ombrotypes humid and hyperhumid (Rivas-Martínez 1987; Rivas-Martínez et al. 2002; Rivas-Martínez 2007). The species inhabits humid forest habitats, mainly of deciduous oak trees (*Quercus robur* L., *Q. pyrenaica*), hazel (*Corylus avellana* L.), birch (*Betula pubescens* ssp. *celtiberica* Rothm. & Vasc.), chestnut trees (*Castanea sativa*), and yews (*Taxus baccata* L.), but also heathlands and rocky open areas covered by broom shrubs (*Cytisus oromediterraneus* Rivas Mart. & al. and *C. scoparius*) (see Izco 1987; Rivas-Martínez 1987; Costa Tenorio et al. 2005) (Fig. 5E, F).

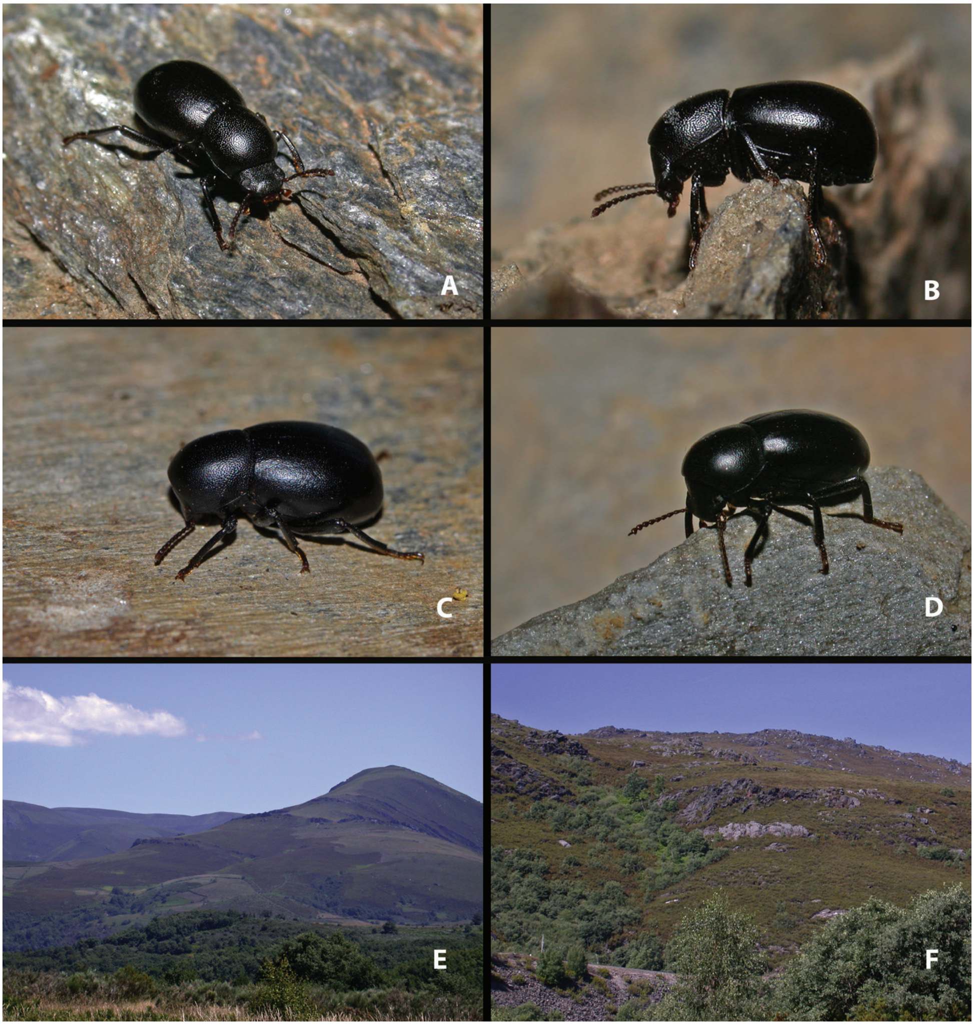

Figure 5. Live specimens and habitat of *Misolampus lusitanicus* **A–D** live specimens of *Misolampus lusitanicus* from Spain (**A, B** Fumaces, Ourense **C** Laguna de La Baña, León) and Portugal (**D** Fervença-Eido, Porto) **E, F** two examples of typical habitat of *M. lusitanicus* from **E** Sierra de Queixa (Ourense) and **F** Mountains of Sanabria (Zamora). Photographs by MGP.

Adults are usually found at the base of trees, under bark, under stones or in leaf litter of forests (Español 1956; Español and Comas 1981), but also under stones in mountain shrub-lands (pers. obs.). It has also been found in densely reforested areas with *P. pinaster*, and also in chestnut groves (*C. sativa*). It has not been recorded in sympatry with any other species of *Misolampus*, but it has been found in company of *Coelometopus clypeatus* (Germar, 1813) (Tenebrionidae, Cnodalonini) (Español and Comas 1981). According to the limited available data, adults seem to be present all year round.

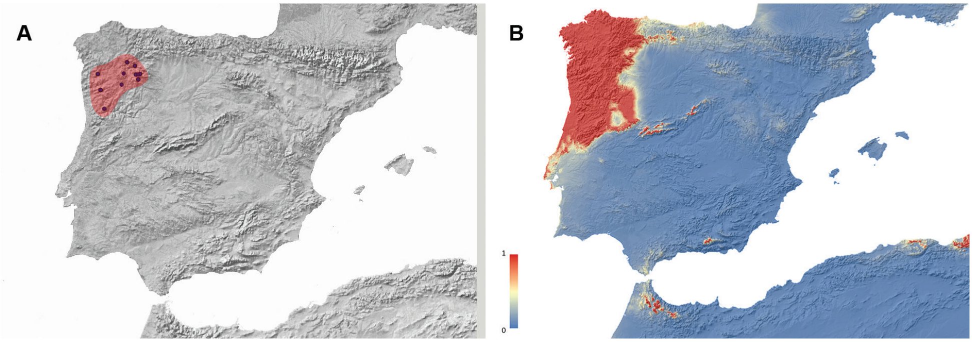

Figure 6. A Geographic distribution of *Misolampus lusitanicus*. Map depicting the distribution range of the Iberian endemic *Misolampus lusitanicus* (red spot). Purple dots correspond to the species records, including both recent and old, as well as previously published data **B** potential geographic distribution of *Misolampus lusitanicus*: Red indicates areas of high suitability, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al., 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

Misolampus ramburii Brême, 1842

Misolampus ramburii Brême, 1842: 82. Terra typica: "De l'Espagne meridionale". Some authors wrote the species name with a single final -i (Rosenhauer 1856; Paulino de Oliveira 1894; Reitter 1917; De la Fuente 1934–1935; Palau 1945; Español 1949).

Studied material. Spain – Andalucía: Almería: Fondón: 2 exx.; Sierra Bacares: 1900 (Escalera leg.): 3 exx.; Sierra Alhamilla, Almería, 1240 m, 36°59'25"N, 02°20'13"W, 30-XII-2003 (P. Barranco leg.): 1 ex.; Sierra de Gádor, 892 m, 36°55'32.18"N, 2°35'57.07"W, 27-III-2012: 3 exx.; Granada: Jayena, 30-VII-1920: 4 exx.; Puerto de la Mora, 1294 m, 37°15'19.71"N, 3°29'01.80"W, 26-III-2012: 2 exx.; Pista La Alcaicería-El Robledal (encinar), Sierra Tejeda, 1020 m, 36°57'07"N, 4°00'56"W, 5-I-2005: 1 ex.; Málaga: Málaga (Aragoncillo leg.) (Col. del Sr. Pérez Arcas): 1 exx.; Arroyo Güi, Torrox, 155 m, 36°46'36"N, 3°59'29"W, 23-XII-2000: 4 exx.; Lagos, Velez-Málaga, 102 m, 36°45'00"N, 4°00'28"W, 15-IV-2006: 2 exx.; Área El Pinarillo, Nerja, Sierra de Almijara, 485 m, 36°47'53"N, 3°50'55"W, 3-I-2003: 6 exx.; Área El Pinarillo, Nerja, Sierra de Almijara, 471 m, 36°47'52"N, 3°50'58"W, 4-I-2012: 3 exx.; Cerro El Cañuelo, Acantilados de Maro-Cerro Gordo, Nerja, 130 m, 36°44'57"N, 3°47'12"W, 29-XII-2007: 1 ex.; Carril Cuevas de Nerja-El Pinarillo, Sierra de Almijara, 340 m, 36°46'58"N, 3°50'24"W, 30-III-2018: 2 exx.; Alrededores Cuevas de Nerja, Maro, Nerja, 171 m, 36°45'46"N, 3°50'43"W, 2-XI-2018: 1 ex. – Murcia: Sierra Espuña: VIII-1943 (G. Menor leg.): 1 exx.

Diagnosis. Total length 9–11 mm (Reitter 1917; Español 1949). *Misolampus ramburii* is characterised by its shiny appearance and by presenting the anterior angles of prothorax slightly protruding forward. Pronotal punctation deep and dense, not as strong as in *M. gibbulus*, without granular areas. Elytra with shallow striae formed by series of punctures in longitudinal series, sometimes almost absent (Fig. 7A, B). Elytral inter-striae smooth. Female genitalia figured by Palmer (1998) and aedeagus by Español (1949). Adults present a marked variability in elytral sculpturing, smoother with elytral striae almost erased in the western populations of Sierra de Almijara and Sierra de Huétor (Fig. 7B); more marked in the eastern areas (Fig. 7A) (see taxonomic discussion).

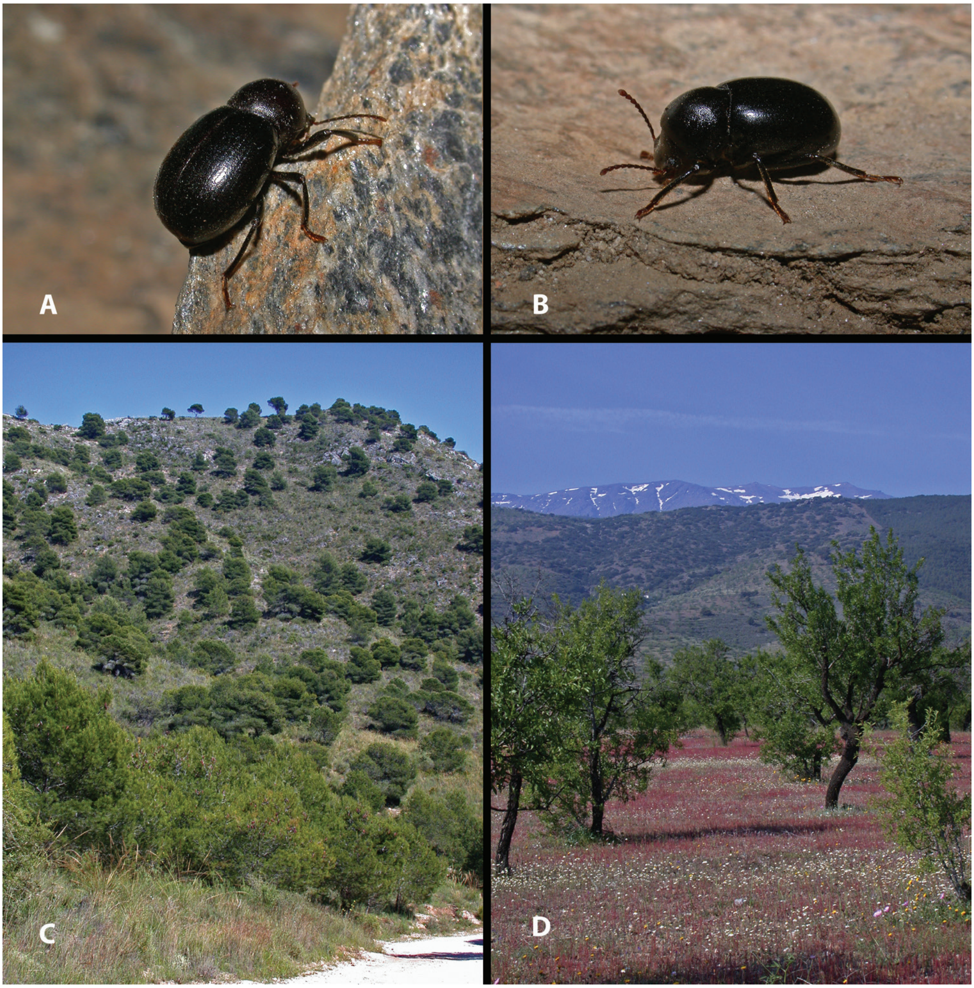

Figure 7. Live specimens and habitat of *Misolampus ramburii* **A, B** adult *Misolampus ramburii* from Spain (**A** Sierra de Gádor, Almería **B** Sierra de Huétor, Granada); the specimens selected represent the diversity of sculptural patterns in elytra and pronotum, smoother in western populations, without elytral striae (**B**), marked in eastern areas (**A**) **C, D** two examples of typical habitat of *M. ramburii* from **C** coastal ravines with scattered *Pinus halepensis* (Maro, Málaga) and **D** slope of Sierra Nevada with open forests of *Q. ilex* and almond trees (Almería). Photographs by MGP.

Geographic distribution. Endemism of southeastern Spain and Mallorca in the Balearic Islands (Fig. 8). Records from Portugal, as Serra de Monchique (Paulino de Oliveira 1894; Reitter 1917; Löbl et al. 2008), are based on misidentifications (see taxonomic discussion). Published records are scarce, but covering most of the known species range, from the provinces of Almería, Granada, Málaga, Murcia, and the island of Mallorca (Rosenhauer 1856; von Heyden 1884 sub *M. scabricollis*; Reitter 1917; De la Fuente 1934–1935; Palau 1945; Cobos 1949; Español 1949, 1954a, 1954b, 1963; Sánchez-Piñero et al. 2013; Valladares et al. 2013). All published records are relatively old, except those from Almería and Granada. According to the current records, *M. ramburii* is restricted to the Betic Mountain ranges (Montes de Málaga, Sierra Nevada, Sierra de Huétor, Sierras de Tejeda and Almijara, Sierra de Filabres, Sierra de Gádor, Sierra Alhamilla, Sierra Espuña), and in Malllorca to the southwestern foothills of the Sierra de Tramuntana, including Palma Bay (Fig. 8A). The record of an unidentified *Misolampus* from Sierra de Contraviesa (Granada) (Español 1963), found in the company of *Coelometopus cobosi* Español, 1963, probably corresponds to *M. ramburii* (see taxonomic discussion).

Materials studied by us include specimens from all previously reported areas except Mallorca (not searched for). Records are recent for all localities except for those from the Murcia region (Sierra Espuña). The potential distribution map (Fig. 8B) shows that highly suitable areas are primarily located in the coasts and mountain ranges of the south of Almería, Granada, and Málaga and the northwest of Mallorca island, coinciding with the recorded presence of the species. The northwestern coast of the Iberian Peninsula and the mountain ranges of Northwestern Africa are also pointed as areas of high suitability.

Notes on natural history. *Misolampus ramburii* is a low-medium mountain species, even sub-coastal, with an altitudinal range between 14 and 1673 m a.s.l. (60% of records below 1000 m of altitude); in Mallorca it is also found at low altitude, 14–398 m a.s.l. Lithological substrates of its area of occupancy are very diverse, due to the high

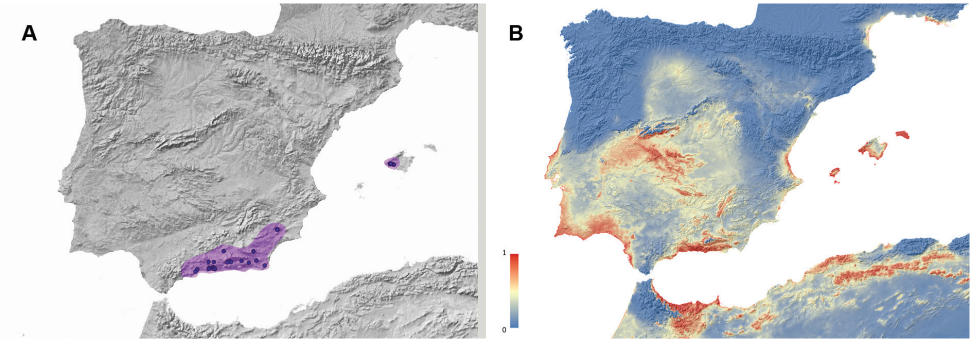

Figure 8. A Geographic distribution of *Misolampus ramburii*. Map of the Iberian Peninsula depicting the geographic distribution of *Misolampus ramburii* (purple spot), an endemic species to Spain. Blue dots correspond to the species records, including both recent and old, as well as previously published data **B** potential geographic distribution of *Misolampus ramburii*: Red indicates areas of high suitability, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al. 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

geostructural complexity of the Betic Mountain ranges, but are mainly dolomites, limestones, slates, phyllites, mycaschists, and, very locally, plutonic rocks (Sanz de Galdeano 1997; Vera 2004; Oliveira and Quesada 2019a, 2019b). It inhabits usually the thermo- and meso-Mediterranean bioclimatic levels, and very locally at the supra-Mediterranean, with ombrotypes from semiarid to subhumid (Rivas-Martínez 1987; Rivas-Martínez et al. 2002; Valle 2003; Valle et al. 2004). According to the known localities and our observations, the species occurs in an extensive variety of habitats, with preference for more or less open forested areas with pines (*Pinus halepensis*, *P. pinaster*, *P. nigra*, both natural and reforested), oaks (*Quercus ilex*, *Q. faginea* and *Q. suber* in Sierra de Contraviesa), wild olive trees (*Olea europaea* var. *sylvestris*), and carob trees (*Ceratonia siliqua* L.), but also in shrub-lands of *Quercus coccifera* L., *Genista umbellata* (L'Hér.) Dum. Cours., *Rosmarinus officinalis* L., *Pistacia lentiscus* L., *Pistacia therebinthus* L., *Buxus balearica* Lam., *Maytenus europaeus* (Boiss.) Rivas Mart., *R. sphaerocarpa*, and *Cistus* and *Lavandula* L. species, among other typical shrubs (Rivas-Martínez and Costa 1987; Bolòs 1997; Valle 2003; Costa Tenorio et al. 2005). Sometimes, it has been found in almond tree crops (*Prunus dulcis* (Mill.) D.A. Webb) with scattered oaks (*Q. ilex*) (pers. obs.) (Fig. 7C, D).

Commonly found under bark or inside dead logs and stumps of pines (*P. halepensis*, *P. pinaster* and *P. nigra*), and oaks (*Q. ilex*), or under stones in forests and shrublands. Occasionally found under the lose bark of standing live isolated *Eucalyptus* trees. In the island of Mallorca, it has been found in oak forests (*Q. ilex*), under bark or under stones and leaf litter (Español 1949, 1954a). Adults can be found in autumn, winter, and spring, with no records in the summer months of August and September.

Misolampus scabricollis **Graells, 1849**

Misolampus scabricollis Graells, 1849: 621. Terra typica: "Guadarrama". Graells (1851a) mentioned the unavailable name "*Misolampus graellsi* Dufour".

Studied material. Portugal – Guarda: 2 km al O de Vale de Estrela, 977 m, 40°29'35.7"N, 7°19'12.1"W, 18-IV-2011: 1 ex.; [6 km al SO de] Guarda, 11-X-1992: 7 exx.; S. de Estrella [Serra da Estrela] (Sanz leg.): 1 ex. – Portalegre: Monte Palheiros, 632 m, 39°20'03.91"N, 7°25'38.63"W, 10-III-2012: 12 exx.; Ribeira de Nisa, [4 km al NE de Nisa], 23-X-1990: 1 ex. Spain – Andalucía: Huelva: Andalucía: Huelva: Cortegana, 706 m, 37°53'55.6"N, 06°50'16.3"W, 3-I-2013: 2 exx.; Cortegana: Puerto del Corzo (hacia Gil Márquez), 664 m, 37°52'56.1"N, 06°50'42.3"W, 3-I-2013: 9 exx. – Castilla – La Mancha: Ciudad Real: Fuencaliente (Sierra Morena) (J. Cabré leg.): 1 ex.; Navas de Estena: 2 exx.; Puebla de Don Rodrigo: El Vivero, 39°02'29.2"N, 4°33'40.9"W, 5-III-2012: 1 ex.; Saceruela: 1 ex., plus 1 without label; Guadalajara: 3 km al O de La Mierla, 1023 m, 40°56'27.6"N, 3°16'13.4"W, 26-X-2013: 12 exx.; Alpedrete de la Sierra, hacia el Atazar, 17-IV-1992: 3 exx.; Retiendas: Embalse del Vado, 931 m, 41°00'09.8"N, 3°17'41.6"W, 26-X-2013: 2 exx.; Umbralejo, 1256 m, 41°07'33.2"N, 3°10'39.4"W, 26-X-2013: 18 exx.; Toledo: Belvís de la Jara (N502 km 153), 584 m, 39°43'59.3"N, 4°58'14.6"W, 1-XI-2008: 1 ex.; Las Honfrías, Robledo del Mazo, 39°35'48"N, 04°53'15"W, 9-II-2011: 1 ex.; Navamorcuende: Sierra de San Vicente: El Piélago, 1154 m, 40°08'34.4"N, 4°44'09.2"W, 27-XII-2011: 3 exx.; Sierra de San Vicente: El Piélago, 1224 m, 40°08'03.91"N, 4°43'48.79"W, 13-V-2012: 1 ex. – Castilla y León: Ávila: Chamartín de la Sierra: Castro de la Mesa de Miranda, 40°43'24.7"N, 4°56'57.6"W, 10-II-2013: 1 ex.; [Navarredonda de] Gredos: 1 ex.; [Navarredonda de] Gredos (J. Ardois leg.): 10 exx.; Arenas [de San Pedro] (J. Ardois leg.): 1 ex.; Ávila (197) (Pérez leg.): 1 ex.; Casillas, 1158 m, 40°19'25.6"N, 4°35'14.0"W, 16-XI-2012: 1 ex.; Casillas: 4 exx.; Las Navas [del Marqués]: [Sierra de] Guadarrama (G. Schramm leg.): 75 exx.; 5 km S Navas del Marqués, 40°33'24.4"N, 4°19'32.5"W, 1-IV-2013: 1 ex.; Mombeltrán – Navalperal: 2 exx.; Navalperal [de Tormes], VII-1904 (Escalera leg.): 1 ex.; Navamorcuende (Ardois leg.): 1 ex.; Navas del Marqués: Carretera de Valdemaqueda, 1021 m, 0°32'14.3"N, 4°20'26.5"W, 20-III-2010: 1 ex.; Peguerinos: Valle de Enmedio, 1-VII-1992: 2 exx.; Puerto de Casillas, 1590 m, 40°20'37.1"N, 4°35'06.7"W, 15-V-2011: 1 ex.; Sierra de Gredos: 2 exx.; Valle de Iruelas, 10-V-1919 (J. Abajo leg.): 8 exx.; Valle de Iruelas, V-1920: 7 exx.; Villarejo [del Valle]): 1 ex. plus 1 without label; Burgos: Quemada, 848 m, 41°43'20.4"N, 3°33'00.3"W, 9-V-2013: 4 exx.; Salamanca: 1 km al N del Puerto de Perales, 884 m, 40°15'18.3"N, 6°41'22.2"W, 16-IV-2011: 2 exx.; Navasfrías, 959 m, 40°17'03.1"N, 6°49'49.1"W, 23-XII-2011: 9 exx.; Peña de Francia: 1 ex.; Puerto de Perales, 917 m, 40°14'46.2"N, 6°41'20.5"W, 22-XII-2011: 3 exx.; Serradilla del Llano, 13-X-1992: 2 exx.; Segovia: Balsaín (C. Bolívar leg.): 1 ex.; Balsaín (J. Abajo leg.): 1 ex.; Balsaín (J. Ardois leg.): 15 exx.; Collado Ventoso, 1964 m, 40°47'13.2"N, 4°02'32.8"W, 11-VIII-2013: 3 exx.; El Espinar: 1 exx.; Puerto de Los Cotos – Dos Hermanas, 40°49'27.1"N, 3°57'51.4"W, 19-XI-2012: 1 ex.; Puerto de Los Cotos – Dos Hermanas, 1900 m, 2-IX-1991: 2 exx.; Puerto de Navacerrada, 40°47'11"N, 4°01'05"W, 13-V-2012: 1 ex.; Puerto de Navacerrada, 40°47'17.83"N, 4°00'36.27"W, 30-V-2012: 1 ex.; Zamora: Santa Ana, 872 m, 41°42'17.66"N, 6°24'22.65"W, 25-IV-2012: 11 exx. – Extremadura: Cáceres: Alcuéscar, I-1894: 2 exx.; Carretera Villamiel – San Martín de Trevejo, 868 m, 40°11'43.8"N, 6°47'30.3"W, 23-XII-2011: 6 exx.; Casares de Las Hurdes: Puerto de Robledo, 1074 m, 40°27'07.06"N, 6°17'48.82"W, 17-IV-2012: 4 exx.; Hurdes: 1 exx.; Madrigal [de la Vera]: 1 exx.; Madrigal [de la Vera] (J. Ardois leg.): 21 exx.; Pico Villuercas, 1394 m, 39°28'19.72"N, 5°23'54.70"W, 12-V-2012: 7 exx. – Madrid: Dehesa de Braojos, 1400 m, 41°03'27.4"N, 3°38'51.1"W, 12-X-2013: 1 ex.; Cadalso [de los Vidrios] (J. Ardois leg.): 3 exx.; Cercedilla, 1460 m, VII-1945 (L. Esteban leg.): 1 ex.; Cercedilla, 1500 m, VIII-1935 (J. Hernández leg.): 4 exx.; Cercedilla, [Sierra de] Guadarrama (G. Schramm leg.): 11 exx.; Cercedilla, [Sierra de] Guadarrama (E. Zarco leg.): 2 exx.; Cercedilla (Lauffer leg.): 1 exx.; Cercedilla (Moróder leg.): 10 exx.; Cercedilla (Exp. del Museo): 20 exx.; Cercedilla (C. Bolívar leg.): 23 exx.; Cercedilla, 25-VII-1926: 1 ex.; Cercedilla (J. Ardois): 5 exx.; Cercedilla (Museo): 5 exx.; Cercedilla: 6 exx.; Cercedilla: El Ventorrillo, 1480 m: VIII-1960 (J. Abajo leg.): 2 exx.; Cercedilla: El Ventorrillo, 1478 m, 40°45'17.3"N, 4°01'21.6"W, 11-VI-2013: 11 exx.; Cercedilla: Estación Alpina, 1460 m (J. Abajo leg.): 1 ex.; Cercedilla: Estación Alpina, 1500 m: 2 exx.; Cercedilla: Estación Alpina, XII-1941 (E. Zarco leg.): 1 ex.; El Escorial (J. Dusmet leg.): 1 ex.; El Escorial (*Misolampus scabricollis* Graells): 1 ex. plus 1 without label; El Escorial, 10-V-1926: 3 exx.; El Escorial, 10-VI-1927:

2 exx.; El Escorial, 20-V-1925: 2 exx.; El Escorial, 22-V-1953 (W. Steiner leg.) (T-29) (*Misolampus scabricollis* Graells, F. Español det.): 4 exx.; El Escorial (C. Bolívar leg.): 4 exx.; El Escorial: 4 exx.; El Escorial (Lauffer leg.): 5 exx.; El Escorial: Cuelgamuros, 1337 m, 40°38'53.8"N, 4°09'19.8"W, 10-VI-2013: 9 exx.; El Escorial: Puerto [de Malagón]: 1 ex.; El Paular (Exp. del Museo): 11 exx.; Garganta de Los Montes, 1346 m, 40°54'46.9"N, 3°40'05.5"W, 26-V-2013: 2 exx.; Lozoyuela, 1288 m, 40°55'31.4"N, 3°39'44.9"W, 26-V-2013: 5 exx.; Manzanares [El Real], 30-III-1928: 1 exx.; Manzanares El Real, 1156 m, 40°45'28.1"N, 3°54'56.0"W, 28-II-2012: 3 exx.; Pelayos de la Presa, 799 m, 40°20'19.40"N, 4°21'34.84"W, 3-III-2001: 1 ex.; Puerto de Cotos, 12-VIII-1925: 1 ex.; Puerto de La Hiruela, 1354 m, 41°03'42.5"N, 3°28'36.8"W, 6-IV-2011: 1 ex.; Puerto de La Puebla, 1633 m, 41°02'27.7"N, 3°28'48.9"W, 27-IV-2011: 3 exx.; Puerto de Navacerrada, 18-VIII-1923): 1 ex.; Puerto de Navacerrada (E. Zarco leg.): 2 exx.; San Lorenzo del Escorial, 40°35'58"N, 4°09'42"W, 14-III-2015 (A. Sánchez Vialas): 2 exx.; Santa María de la Alameda (estación), 1-IV-1991: 1 ex.; Santa María de la Alameda, 1437 m, 40°36'11.11"N, 4°15'18.93"W, 30-V-2012: 1 ex.; Sierra de Guadarrama (Lauffer leg.): 2 exx.; Tablada, 12-V-1957 (J. Álvarez leg.): 1 ex.; Valdemanco, 1090 m, 40°51'10.5"N, 3°38'48.5"W, 8-V-2013: 1 ex.

Diagnosis. Total length 11–13 mm (Graells 1849, 1851a, 1851b; Reitter 1917; Español 1949; López-Pérez 2014a). Pronotum with strong punctation intermixed with raised granules and small tubercles, particularly developed on the lateral sides, which gave them a strongly rugose appearance. Propleural sides with dense strong punctation. Elytra smooth, without traces of striae, series of punctures, or tubercles (Fig. 9A, B). Female genitalia figured by Palmer (1998) and aedeagus by Español (1949). Morphological variability seems to be restricted to individual variation in size and in the extent of the pronotal rugose areas.

Geographic distribution. Endemism of Portugal and Spain (Löbl et al. 2008) (Fig. 10). Bibliographic records are scarce, covering a large portion of the centre and western areas of the Iberian Peninsula, including Aveiro, Bragança, Alto Douro, and Guarda in Portugal, and the provinces of Ávila, Cáceres, Huelva, Madrid, Ourense, and Segovia in Spain (Graells 1849, 1851a, 1851b; Seidlitz 1867; Paulino de Oliveira 1894; Reitter 1917; De la Fuente 1934–1935; Español 1949; López-Pérez 2014a; Novoa et al. 2014). Published records of *M. scabricollis* from Sierra Espuña (von Heyden 1884), Murcia (De la Fuente 1934–1935) and Sierra de Alcaraz (Reitter 1917) are erroneous and probably correspond to *M. subglaber*. *Misolampus scabricollis* is widely distributed throughout the main mountain ranges of the central and western areas of the Iberian Peninsula (Sistema Central, Sierra de Gata, Sierra de Guadalupe, Montes de León, Montes de Toledo, eastern Sierra Morena, Serra da Estrêla), with an apparently isolated population in the western extreme of Sierra Morena (Sierra de Aracena, province of Huelva) separated ca. 240 km from the eastern population of this same mountain system (Fig. 10A).

All previously existing records except those of Huelva and Ourense, correspond to data published more than 70 years ago. The material studied or collected by us, includes records from all provinces of Spain previously reported in the literature, except from Ourense, with the addition of new records from Castelo Branco and Portalegre in Portugal, and from the provinces of Burgos, Ciudad Real, Guadalajara, Salamanca,

Figure 9. Live specimens and habitat of *Misolampus scabricollis* **A, B** live adult specimens of *Misolampus scabricollis* from Spain (**A** Sierra de Guadalupe, Cáceres **B** Las Honfrías, Montes de Toledo) **C–F** typical habitats of *M. scabricollis* (**C** granitic outcrops with *Cytisus*, *Juniperus communis*, and *Quercus ilex* along the Sistema Central Mountain Chain, Avila **D** densely reforested area with *Pinus sylvestris* at Santa Ana, Zamora) **E** *Pinus sylvestris* forests at the southern slopes of Pico del Lobo, Guadalajara **F** dense forests of *Quercus pyrenaica* at Montes de Toledo). Photographs by MGP.

Toledo, and Zamora in Spain. All these new records correspond to recent observations, together with old ones for Ciudad Real and Salamanca. The potential distribution map for this species (Fig. 10B) locates the main high suitable areas in central and western regions and along mountain ranges of the Iberian Peninsula. The SDM does not consider the isolated population of Sierra de Aracena as present in a high suitability area.

Notes on natural history. *Misolampus scabricollis* is a medium-low mountain species, with an elevation range of 224 to 1964 m a.s.l. (78% of the records are above

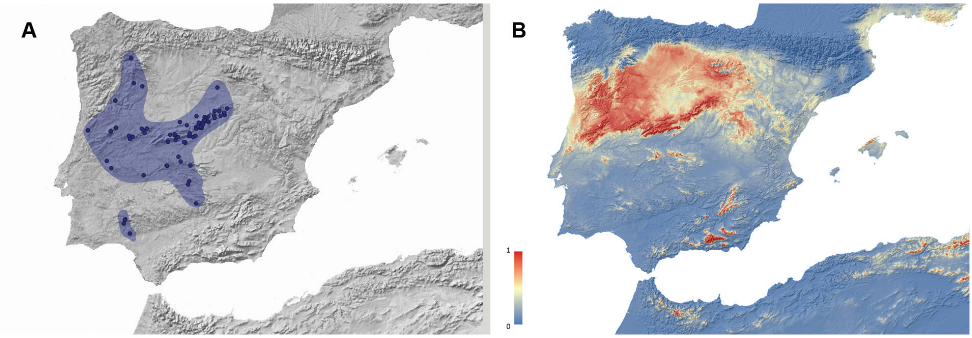

Figure 10. A Geographic distribution of *Misolampus scabricollis*. Distribution range of the Iberian endemic *Misolampus scabricollis* (dark blue spot). Blue dots correspond to the species records, including both recent and old, as well as previously published data. The populations from Huelva (southwestern Spain) remain isolated, since no intermediate populations are known in a distance of at least 150 km, however intervening habitat seems favourable in many areas **B** potential geographic distribution of *Misolampus scabricollis*: Red indicates areas of high suitability, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al. 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

800 m, 56 % above 1000 m of altitude). Lithological materials of its area of occupancy are siliceous and very diverse, mainly granites, schists, gneisses, quartzites, and plutonic rocks (Vera 2004; Oliveira and Quesada 2019a, 2019b). Most of its distribution area is located in the meso- and supra-Mediterranean thermoclimatic belts, and more locally at higher altitude in the oro-Submediterranean (exceptionally, one location is in the upper thermo-Mediterranean: Niebla, province of Huelva), with ombrotypes dry, subhumid and humid (Rivas-Martínez 1987; Rivas-Martínez et al. 1987, 2002; Valle et al. 2004; Rivas-Martínez 2007). It occurs in a large variety of forested habitats with different degrees of coverage, usually composed by pines (*Pinus sylvestris*, *P. pinea*, *P. pinaster*, natural or reforested), oaks (perennial: *Quercus suber*, *Q. ilex*; deciduous: *Q. pyrenaica*, *Q. faginea*) and chestnut trees (*Castanea sativa*), as well as substitution shrubs, mainly of *Cistus*, *Cytisus*, *Ulex* L. and *Genista* L. (Ladero 1987; Rivas-Martínez 1987; Rivas-Martínez et al. 1987; Valle 2003; Costa Tenorio 2005) (Fig. 9C–F).

According to our observations, *M. scabricollis* is usually found inside dead and decaying tree trunks, or under bark, usually in standing or lying pine logs, oaks, and chestnut trees. These observations are coincident with the few disperse available data on the habitat of this species (Graells 1851a, 1851b; López-Pérez 2014a). Areas covered by dense bushes of *Q. pyrenaica* and *Q. ilex* (recovering after fires or logging) are also frequently used by this species. *Misolampus scabricollis* can also be found in areas reforested with pines, and under stones, small pieces of wood, or inside tight clusters of branches, in shrub areas dominated by *Cytisus scoparius*, *C. oromediterraneus*, and less frequently by *Cistus ladanifer* (Fig. 9C–F). They are usually more easily found on logs and under stones at the edge of dense forests, but they can also be found deep inside the forest or in nearby grasslands.

This species is usually found forming small groups of 2–21 specimens in a single log. Graells (1851a, 1851b) reported groups of five or six specimens per log in the Guadarrama Mountains. According to Graells (1851a, 1851b), when disturbed they pretend to be dead (thanatosis) and expel an unpleasant light odour.

Misolampus scabricollis has been found in microsympatry with *M. gibbulus* along western Sierra Morena (Huelva), northern Extremadura (Cáceres), Montes de Toledo (Toledo) and southern slopes of the Sistema Central (Madrid, Ávila, Toledo) (Fig. 1E), however, *M. scabricollis* is usually found at higher altitudes than *M. gibbulus*. Adults can be found across most of the year, but are more easily encountered during the wetter, colder, months (October to May). It is often found in company of *Coelometopus clypeatus* in old chestnut trunks.

Misolampus subglaber Rosenhauer, 1856

Misolampus subglaber Rosenhauer, 1856: 204. Terra typica: "in der Sierra de Ronda".

Studied material. Spain – Andalucía: Córdoba: Córdoba: 1 ex.; Granada: Güejar Sierra: 1 ex.; La Sagra (Escalera 1900): 4 exx.; Puebla de Don Fadrique (Escalera 1900): 5 exx.; Puebla de Don Fadrique: Nablanca, 1517 m, 38°00'23.6"N, 2°28'28.2"W, 10-IV-2011: 2 exx.; Valdeiglesias, 975 m, 36°56'49.3"N, 4°04'29.6"W, 24-X-2019: 3 exx.; Jaén: 3 km SO Aldeaquemada, 38°23'53.7"N, 3°24'00.5"W, 7-III-2012: 5 exx.; [3 km al SO de] Aldeaquemada, 26-IV-1992: 2 exx.; Cazorla: 7 exx.; Vadillo de Castril, Sierra de Cazorla, 995 m, 37°55'14"N, 2°55'50"W, 8-V-2008 (D. Ruiz leg.): 1 ex.; Santa Elena, carretera hacia La Aliseda, 768 m, 38°20'18.0"N, 3°32'56.8"W, 11-IV-2011: 3 exx.; Santa Elena, carretera hacia La Aliseda, 795 m, 38°20'53.1"N, 03°33'20.6"W, 28-XII-2010: 1 ex.; Santiago de la Espada (J. Martínez): 1 ex.; Segura [de la Sierra]: 1 ex.; Sierra Morena (Laguna leg.): 1 ex.; Málaga: 3 km al E de Jubrique, 786 m, 36°33'37.5"N, 5°10'40.9"W, 14-IV-2013: 6 exx.; Nerja: 1 ex.; El Colmenar, Gaucín, P.N. Los Alcornocales, 255 m, 36°32'29"N, 5°23'22"W, 17-II-2018 (S. Yubero leg.): 3 exx.; Carril Llanada de Sedella-Bco. de Valdeinfierno, Sierras de Tejeda y Almijara, 1495 m, 36°53'15"N, 3°56'40"W, 4-I-2017: 2 exx. – Castilla – La Mancha: Albacete: Agramón: 2 exx., plus 1 without label; Alcaraz: 3 exx.; Calar del Mundo, V-1904 (G. Schramm leg.): 1 ex.; Cañadillas, 15-VI-1938: 1 ex.; Cañadillas, 16-VI-1938: 1 ex.; Cañadillas, 17-VII-1938: 1 ex.; Los Collados, 20-II-1938: 1 ex.; Molinicos: 1 ex., plus 4 exx. without labels; Riópar, 25-VII-1926: 1 ex.; San Juan de Alcaraz [Fábricas de Riópar] (Paz leg.): 1 ex.; Ciudad Real: Solana del Pino: Puerto Madrona, 38°25'07.3"N, 4°03'33.1"W, 06-III-2012: 3 exx.; Cuenca: Puerto de Cabrejas, 1167 m, 40°04'17.9"N, 2°18'39.5"W, 10-XI-2012: 1 ex. – Murcia: Jumilla: 3 exx.

Diagnosis. Total length 10–12 mm (Reitter 1917; Español 1949). Species clearly characterised by the combination of the following traits: smooth silky appearance; antennae graceful, reaching the base of pronotum; pronotal punctation very fine and sparse on the disc, somewhat stronger and denser to the sides; elytral punctation very fine and irregular, not forming longitudinal series of points or striae (Reitter 1917; Español 1949; Palmer 1998) (Fig. 11A, B). Female genitalia figured by Palmer (1998). The species has been studied karyologically and presents 2n = 20 chromosomes (Palmer and Petitpierre 1997). Morphological variability within this species seems limited to the depth and density of pronotal punctation, and it does not appear geographically structured.

Geographic distribution. Endemism of southeastern Spain (Löbl et al. 2008) (Fig. 12). Published records are scarce, but well distributed throughout Andalucía: Granada, Jaén, Málaga; Castilla – La Mancha: Albacete; Comunidad Valenciana: Valencia; and Murcia (Rosenhauer 1856; Piochard 1866; Reitter 1917; De la Fuente 1934–1935; Cobos 1949; Español 1949, 1960; Molino Olmedo 1996; Palmer and Petitpierre 1997; Ibáñez Orrico 2002; Pérez and López-Colón 2010; López-Pérez 2014a sub *M. erichsoni*, 2014b; Grimm and Aistleitner 2009; Bujalance de Miguel 2015). Records are distributed through time in all areas, except for the recent one from Valencia region (Fig. 12A).

The material studied or collected by us includes specimens from all provinces reported in the literature, except from Valencia. In addition, we studied material from the provinces of Córdoba, Ciudad Real and Cuenca; specimens of Ciudad Real and Cuenca are represented by recent collections (2012). According to these data, *M. subglaber* is located in the Betic Mountain range (Sierras del Campo de Gibraltar, Serranía de Ronda, Sierra Nevada, Sierras de Tejeda and Almijara, Sierra de Cazorla, Sierra de

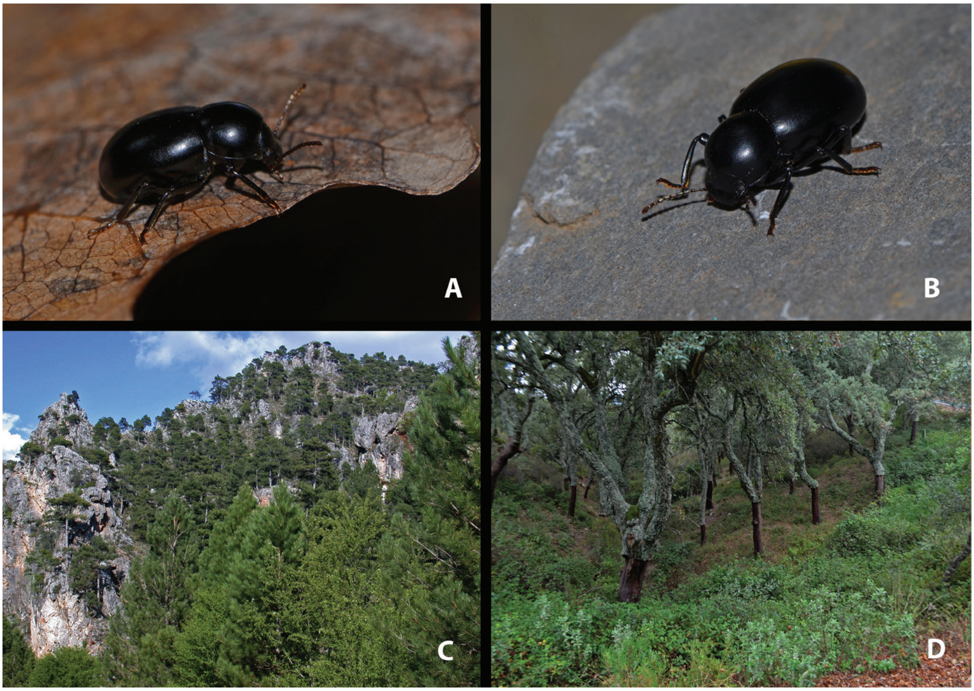

Figure 11. Live specimens and habitat of *Misolampus subglaber* **A, B** live specimens of *Misolampus subglaber* from Spain (**A** Valdeiglesias, Sierra Tejeda, Granada **B** Miranda del Rey, Sierra Morena, Jaén) **C, D** general habitat occupied by *M. subglaber* (**C** limestone outcrops with *Pinus nigra* along the Sierra de Alcaraz, Albacete **D** *Quercus suber* forests at Cortes de la Frontera, Sierra de Grazalema, Málaga). Photographs by MGP.

Alcaraz, Sierra de Cartagena), eastern and central Sierra Morena mountain range, and two apparently isolated populations in the Southern Iberian mountain range (Serranía de Cuenca and Sierra de Malacara, separated between them by ca. 150 km). There is a gap of records in the arid regions of the southeastern end of Spain, throughout the provinces of Almería and southern Murcia, including the eastern half of Sierra Nevada and Sierra de Filabres. The record from Cartagena, Murcia (Reitter 1917), requires further confirmation (Fig. 12A). The potential distribution map identifies the Betic Mountain ranges as the most suitable area for the species. The coastal areas of Almería, Granada, and Málaga provinces are however not included as very suitable. The southern Iberian Plateau and the northwestern African mountain ranges are also suggested as areas of high suitability for the species occurrence (Fig. 12B).

Notes on natural history. *Misolampus subglaber* behaves as a low-medium altitude montane element, distributed within an altitudinal range of 56 to 1662 m a.s.l. (with 61% of its records above 800 m). Geological substrates along its distribution area are diverse, both acid and basic, including mainly sandstones, limestones, dolomites, slates, gneisses, schists and mycaschists (Sanz de Galdeano 1997; Vera 2004; Oliveira and Quesada 2019a, 2019b). *Misolampus subglaber* occupies mostly the thermo- and meso-Mediterranean thermoclimatic belts and locally supra-Mediterranean, in areas with ombrotype semiarid, dry, subhumid and, exceptionally, humid (Rivas-Martínez 1987; Rivas-Martínez et al. 2002; Valle 2003; Rivas-Martínez 2007). It occurs on an extensive variety of pre-forest and forest systems, more or less dense and open, including oaks (deciduous: *Quercus pyrenaica*, *Q. canariensis* and *Q. faginea*; perennial: *Q. suber* and *Q. ilex*) and pines (natural or reforested: *Pinus nigra*, *P. pinaster*, *P. halepensis*, and *P. sylvestris*), all of them usually with diverse undergrowth (Alcaraz Ariza and Peinado Lorca 1987; Peinado Lorca and Martínez Parras 1987; Laguna 1997; Valle 2003; Costa Tenorio et al. 2005) (Fig. 11C, D).

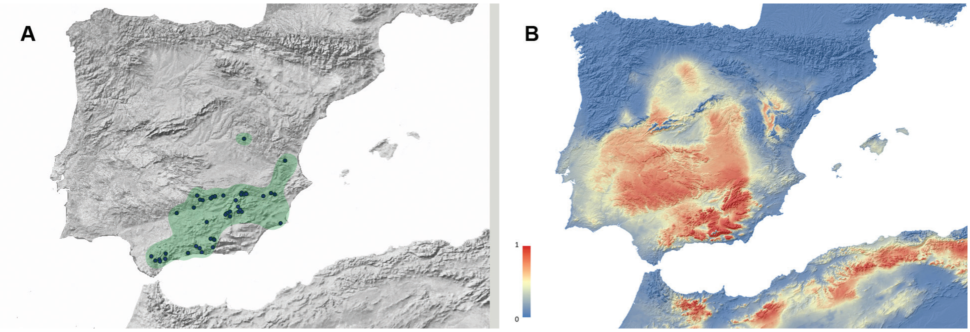

Figure 12. A Geographic distribution of *Misolampus subglaber*. Distribution range of *Misolampus subglaber* (green spot). Blue dots correspond to the species records, including both recent and old, as well as previously published data. Cuenca population is isolated from all other known populations by a distance of 150 km. The old bibliographic record from Cartagena (province of Murcia, south western Spain) requires confirmation **B** potential geographic distribution of *Misolampus subglaber*: Red indicates high suitable areas, and blue, areas of low suitability. Species distribution model was generated using MaxEnt v 3.4.1 (Elith et al. 2006) and the set of WorldClim v 2.0 (Fick and Hijmans 2017) environmental variables.

Adult specimens of *M. subglaber* have been found at the base and under mosses of old oak trunks and inside hollow branches on the ground (*Q. suber*, *Q. pyrenaica*, *Q. canariensis*, *Q. faginea*) (Fig. 11D), inside rotten logs, and under stones and leaf litter in pine forests (*P. nigra*, *P. pinaster*, *P. halepensis*) (Piochard 1866; Español 1960; Molino Olmedo 1996; Ibáñez Orrico 2002; pers. obs.). Pérez and López-Colón (2010) found a specimen inside a natural cavity in the province of Jaén, where it possibly came by stochastic passive dispersal. Often found in groups (Español 1960; pers. obs.).

Molino Olmedo (1996) found larvae inside decaying wood of branches and logs of *Q. pyrenaica*, *Q. canariensis*, *Q. faginea*, *Q. suber*, *Q. ilex* and *P. pinaster* and Ibañez Orrico (2002) on rotten logs of *P. halepensis* (however, the larva of *M. subglaber* has not been described yet). According to Molino Olmedo (1996), *M. subglaber* is a typical saproxylic species.

The general distribution area occupied by *M. subglaber* (Fig. 12) is largely coincident with that of *M. ramburii* (Fig. 8), however they have not been found in microsympatry, a possible indication of ecological segregation between them. Adults are mainly active in fall, winter and spring, but can be found all year round (pers. obs.). Large larvae and pupae have been observed at the end of August in Valencia (Ibañez Orrico 2002).

Identification key for adult specimens of the genus *Misolampus* (modified from Español 1949)

1 Elytra with series of deep to shallow punctures forming strongly to almost erased, excavated striae; additional series of punctures often present on the elytral intervals (Fig. 14A, B). Small size (6.9–12 mm) **2**

– Elytra without any trace of longitudinal series of punctures forming striae (Fig. 14C, D); if very weak striae are present, then interstriae show slightly raised longitudinal series of more or less developed and separated tubercles (Fig. 14D). Medium to small size (7.5–14 mm)... **3**

2 Anterior angles of pronotum slightly prominent (Figs 15A, 1C). Elytra with poorly marked striae, formed by longitudinal series of shallow to almost erased punctures; interstriae smoothly curved (Figs 7, 14A) .... ***M. ramburii***

– Anterior angles of pronotum markedly prominent (Figs 15B, 16D). Elytra with strong to shallow striae, formed by longitudinal series of deep to shallow punctures; interstriae clearly convex (Figs 1, 14B)......................***M. gibbulus***

3 Anterior angles of pronotum rounded, forming an open angle (Figs 16E, F). Elytra with shallow to almost erased striae, often showing longitudinal series of more or less developed elongated tubercles, or sometimes shallow fossae on the interstriae, better marked on the second half of the elytra and on the sides (Fig. 14D). Medium size (10–14 mm), long antennae (Fig. 3) ....***M. goudotii***

– Anterior angles of pronotum forming a widely acute to right angle (Figs 16A, B, 17). Elytra without any trace of striae or tubercles. Medium to small size (7.5–13 mm), relatively short antennae.. **4**

4 Pronotum sculpture formed by deep large confluent punctures (Fig. 16A); the surface between punctures progressively transforms in irregular raised areas that become small irregular granules and wrinkles, giving a strongly rugose appearance to the pronotum sides (Figs 9, 16A). Medium size (11–13 mm) ....***M. scabricollis***

– Pronotum sculpture formed by deep to shallow, dense or sparse, never confluent, well-defined punctures which cover all the pronotal surface, including the lateral sides, which can present somewhat more confused punctation, but not forming rugose areas (Fig. 16B). Large to small size............................**5**

5 Elytra covered by dense punctures somewhat confused or partially erased at the disc. Pronotum sculpture formed by deep, dense, well-defined punctation. Antennae relatively short, not reaching the base of pronotum (Fig. 5). Small size (7.5–8 mm) ....***M. lusitanicus***

– Elytra covered with very fine, shallow and sparse punctation that gave a silky shine to the elytral surface (Fig. 14C). Pronotum sculpture formed by shallow, spaced, and very fine well-defined punctation (Fig. 16B). Antennae usually reaching the base of pronotum (Fig. 11). Medium size (10–12 mm) ....***M. subglaber***

Discussion

Comments on the taxonomy of Misolampus

North African *Misolampus* were described originally as three independent entities: *M. goudotii* from Tanger in northwestern Morocco (Guérin-Méneville 1834), *M. erichsoni* from Algeria (Erichson in Wagner 1841; Vauloger de Beaupré 1900; Reitter 1917) (Fig. 3A), and *M. peyerimhoffi* from the High Atlas in Morocco (Antoine 1926) (Fig. 3B). Additional variability was recorded, but not published, in the labels assigned by M. Martínez de la Escalera to specimens from the Rif region ("*M. g.* var. *riffensis*" Escalera *in litt.*; "*M. g.* var. *laevior*" Alluaud *in litt.*) and from Ifni ("*M. g.* var. *ifnicus*" Escalera *in litt.*) (Fig. 3C) at the MNCN collection (París García et al. 2011). Antoine (1949) described morphologically intermediate populations (Middle Atlas) and showed that male genital structures were similar between the three taxa. Accordingly, Antoine (1949), followed by Español (1949, 1954a), considered that the morphological traits used to separate the three described North African taxa were insufficient, and treated them as subspecies (*M. g. goudotii*, *M. g. erichsoni*, and *M. g. peyerimhoffi*). Español (1953, 1967) went further, and suggested that *M. g. erichsoni* should be included in the synonymy of *M. goudotii*, while Kocher (1958) indicated that all three taxa were just local varieties of a unique taxon. However, the criterion of Español (1953, 1967) and Kocher (1958) was not followed by subsequent authors (Löbl et al. 2008). Meanwhile, the morphological variability implied by Martínez de la Escalera and Vauloger identifications (in litt.), raises further problems for the characterisation of North African populations as subspecies.

Characters initially used for separation of the North African taxa were: pronotal punctation, shape of the anterior margin of the pronotum, shape and sculpture of the propleurae, and width of the second interstria on the elytra (Vauloger de Beaupré 1900; Antoine 1949; Español 1954a). A close examination of the specimens studied by Vauloger and Escalera (see materials and methods) reveals that some of the Rif specimens present intermediate traits between the specimens of the Tingitane Peninsula (Tanger, western Rif) and those from the Middle and High Atlas (Fig. 3B). At the same time, specimens from Ifni (Fig. 3C), roughly located at the coastal western end of the Anti-Atlas mountains, are more similar morphologically to the specimens from the Rif than to those geographically closer from the High Atlas.

Morphological similarity between specimens located in geographically isolated areas, separated by hundreds of kilometres, reflects that the morphological diversity documented across populations, lies within the phenotypic variability of a single evolutionary entity, rather than being a consequence of ancient isolation processes (Montori et al. 2008; Gonçalves et al. 2009). Alternatively, the observed morphological diversity could be consequence of a rapid response to recent geographic isolation of local populations subjected to local strong selective pressures (Velo-Antón et al. 2007). These hypotheses could be tested by genetic analyses, since the phylogeographic outcome of these two processes would be markedly different in each case: Geographically unstructured nuclear marker networks, accounting for the lack of geographic structure at the morphological level, with or without deep mtDNA lineage differentiation in the first case (Recuero and García-París 2011); or alternatively, geographically congruent nuclear and mtDNA marker phylogeographic patterns, with recent, shallow, multiple mtDNA lineage differentiation, accounting for the recency of the isolation processes, not enough to allow sorting out morphological differences, in the second case (Vörös et al. 2006; Rodríguez-Flores et al. 2017). However, none of these processes is consistent with the recognition of independent evolutionary units within North African *Misolampus*, and therefore we consider necessary to synonymise all three subspecies (*M. goudotii* Guérin-Méneville, 1834 = *M. erichsoni* Vauloger de Beaupré, 1900, syn. nov. = *M. peyerimhoffi* Antoine, 1926, syn. nov.), retaining thus a single North African species: *M. goudotii* Guérin-Méneville, 1834. The morphological similarity between the Balearic specimens and the Eastern Moroccan and Algerian ones drove Palmer and Cambefort (2000) to consider a very recent origin for the Balearic populations, possibly as a consequence of human-mediated dispersal.

There has been some confusion in the identification of specimens of *Misolampus* from southern Portugal (Serra de Monchique). Specimens from that region often present not strongly marked elytral striae, and relatively smooth thoracic impressions (Fig. 1A, B), resembling *M. ramburii* (Fig. 7A, B). However, a close examination of the Serra de Monchique specimens (Foia, Monchique, São Marcos da Serra) indicates that based on all other characters (mainly, prothorax morphology, and pronotal punctation), they correspond to *M. gibbulus*. The morphological differentiation shown by the population of *M. gibbulus* from Serra de Monchique with respect to other populations of the species, is quite marked, and led Reitter (1917), Paulino de Oliveira (1894) and De la Fuente (1934–1935) to mention erroneously the presence of *M. ramburii* in Serra de Monchique.

A similar situation occurs within *M. ramburii*. Specimens from populations of Granada (Sierras de Contraviesa and Huétor) have smoother pronotal sculpture, and less marked, almost absent elytral striae (Fig. 7B), while specimens from Almería show stronger sculpturing in elytra and pronotum, with elytral striae, marked by a series of aligned punctation, faint, but visible (Fig. 7A). This contrasting variation is probably the reason Español (1963) reported an unidentified species of *Misolampus* from the Sierra de Contraviesa. Lack of elytral striae made these specimens key to *M. subglaber*, *M. lusitanicus*, or *M. scabricollis* using Reitter's (1917) identification table, but other characters, including pronotal structure, allow for an easy separation.

These evident patterns of morphological differentiation within *M. ramburii*, *M. gibbulus*, and *M. goudotii* may reflect a relatively recent history of isolation across populations, probably consequence of the existence of multiple isolated Pleistocene refugia (Abellán and Svenning 2014), as proposed for other flightless Iberian Coleoptera (Sánchez-Vialas et al. 2020). In any case, these hypotheses require phylogeographic analyses to be properly tested.

Historical population continuity and current conservation status

Species of *Misolampus* have often been considered to present allopatric or, at most, parapatric distributions (Palmer 1998; Palmer and Cambefort 2000). However, old records of *Misolampus* are, in most species, scarce and unevenly distributed. Indeed, by filling large gaps where no records were present, the newly gathered specimens allow for a better understanding of the distribution patterns of all species.

Our data show some level of sympatry among several species pairs (i.e., *M. gibbulus* – *M. scabricollis*, *M. ramburii* – *M. subglaber*), even with cases of microsympatric distribution. These levels of sympatry among ecologically similar, phylogenetically closely related taxa are not common because of demographic processes such as competitive exclusion (Hardin 1960; Waters et al. 2013). Assuming the existence of ecological niche overlap among species pairs of *Misolampus*, areas of sympatric distribution can be explained by simultaneous colonisation from their respective glacial refugia, rapidly spreading into areas with favourable habitats while population densities are still very low, allowing for the establishment of two species (Recuero and García-París 2011; Escoriza et al. 2016; Yackulic 2017). In this way, areas traditionally considered glacial refugia in the Iberian Peninsula (e.g., southern Portugal, Atlantic Coasts of Galicia and Northern Portugal, southeastern Spain) (Martínez-Solano et al. 2006; Sánchez-Montes et al. 2018), where population sizes would have remained high, and thus favouring processes as competitive exclusion, are typically inhabited by a single species of *Misolampus*. The species distribution models show that the species of *Misolampus* present almost complementary potential distributions, supporting the hypothesis that current sympatry areas are the result of recent contact among taxa. The map including highest suitability areas (suitability > 0.7) for all the Iberian species combined (Fig. 13), shows that most of the high suitable areas do not overlap. Species suitable areas remain mainly restricted to the following regions: *M. gibbulus* in the southwest, *M. lusitanicus* in the northwest, *M. ramburii* in the southern coasts, *M. scabricollis* over the northern Iberian Plateau, and *M. subglaber* in the southeastern areas of the Iberian Plateau and along the Betic Mountains.

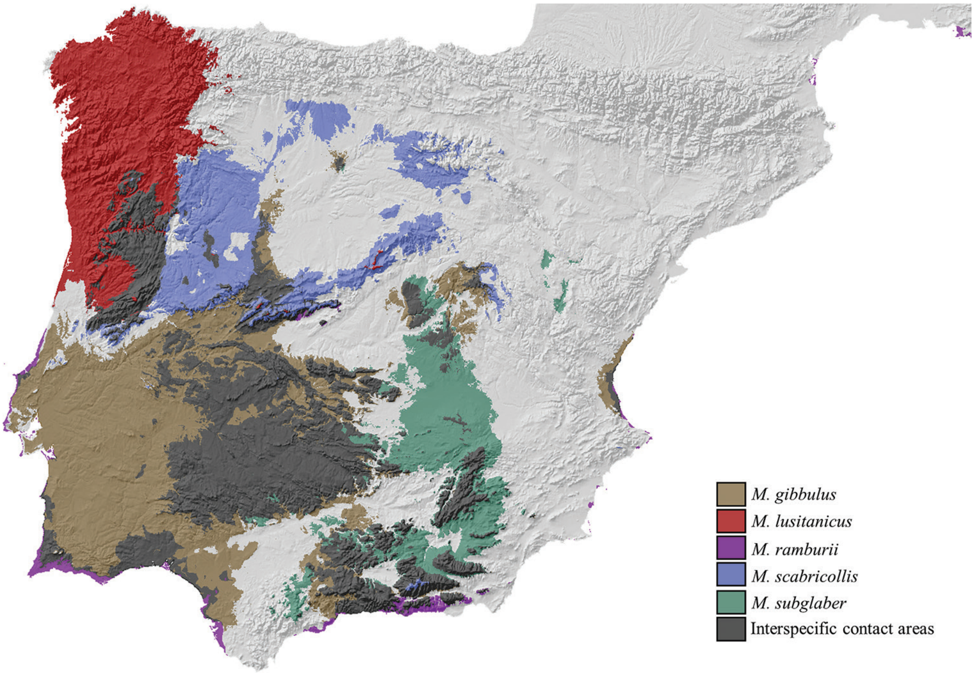

Figure 13. Map of the potential geographic distribution of the Iberian species of *Misolampus*, with the areas of high suitability (suitability > 0.7) depicted for all the species combined: *M. gibbulus* (orange), *M. lusitanicus* (red), *M. ramburii* (purple), *M. scabricollis* (dark blue), *M. subglaber* (green). Dark grey areas correspond to interspecific contact areas. The areas of low suitability for the occurrence of Iberian species of *Misolampus* are represented in pale grey.

Additionally, our results indicate the presence of the genus in geographical areas where it had never been recorded. The absence of *Misolampus* from most part of the Sistema Ibérico mountain chain is particularly striking, considering the huge extension of favourable forest habitats. The recent finding of *M. subglaber* in the province of Cuenca, as well as the published record from the province of Valencia (Ibañez Orrico 2002), suggests that further populations could be discovered with more intensive sampling, at least in the southern parts of the Sistema Ibérico. Similarly, our records of *M. scabricollis* from the provinces of Burgos and Guadalajara are relatively close to the Sistema Ibérico mountains, where the species could be present, but still undetected. Similar cases of long undetected presence of arthropod species in the Sistema Ibérico have been recently published (Valladares et al. 2000; Pérez-Onteniente et al. 2015; Ruiz 2015; Recuero and Rodríguez-Flores 2019).

Field data collection, although essential, has the disadvantage of being limited across space, time and taxa, which can constitute a constraint for biodiversity monitoring and conservation (Kuussaari et al. 2009; Meineke et al. 2019). Lack of information on changes in biodiversity through time and on the direction of these changes can make it difficult to identify and counteract negative impacts derived from disturbances (Magurran et al. 2010). However, scientific collections hold in a single location an

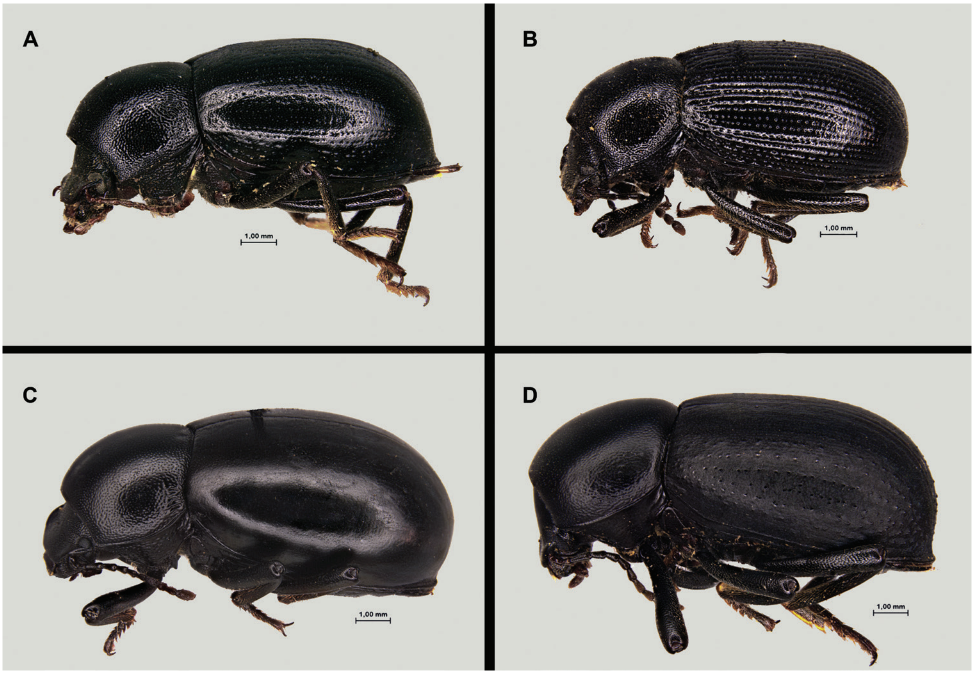

Figure 14. Lateral view of specimens of *Misolampus* **A** *Misolampus ramburii* from Málaga **B** *Misolampus gibbulus* from Santa Elena (Jaén) (MNCN_Ent 270070) **C** *Misolampus subglaber* from Cazorla (Jaén) (MNCN_Ent 270037) **D** *Misolampus goudotii* from Menorca Island (MNCN_Ent 270032). Note the marked differences in sculpture of elytra among all four species.

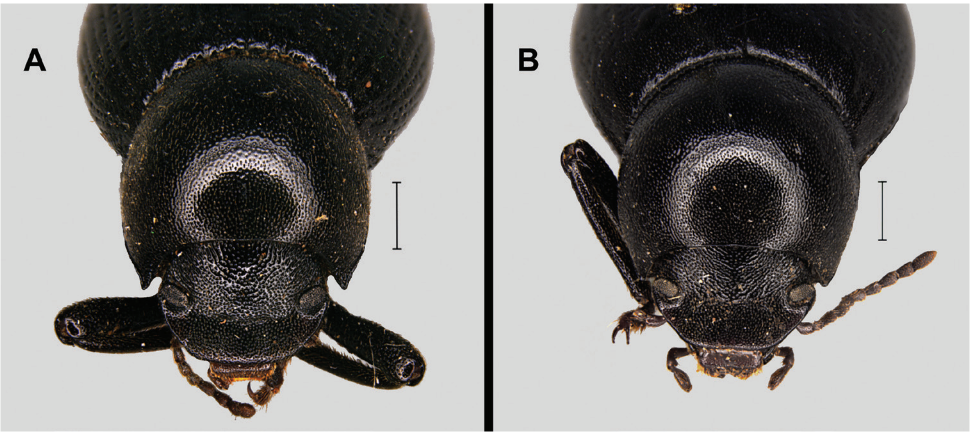

Figure 15. Fronto-dorsal view of specimens of *Misolampus* **A** *Misolampus gibbulus* from Santa Elena (Jaén) (MNCN_Ent 270070) **B** *Misolampus ramburii* from Málaga (MNCN_Ent 270037). Note the differences between the two species in the shape of the anterior angles of the prothorax. Scale bars: 1 mm.

enormous amount of information regarding a wide variety of taxa and, even though their potential has been historically under-appreciated, they are currently considered invaluable resources for biological studies (Meineke et al. 2019; Salvador and Cunha

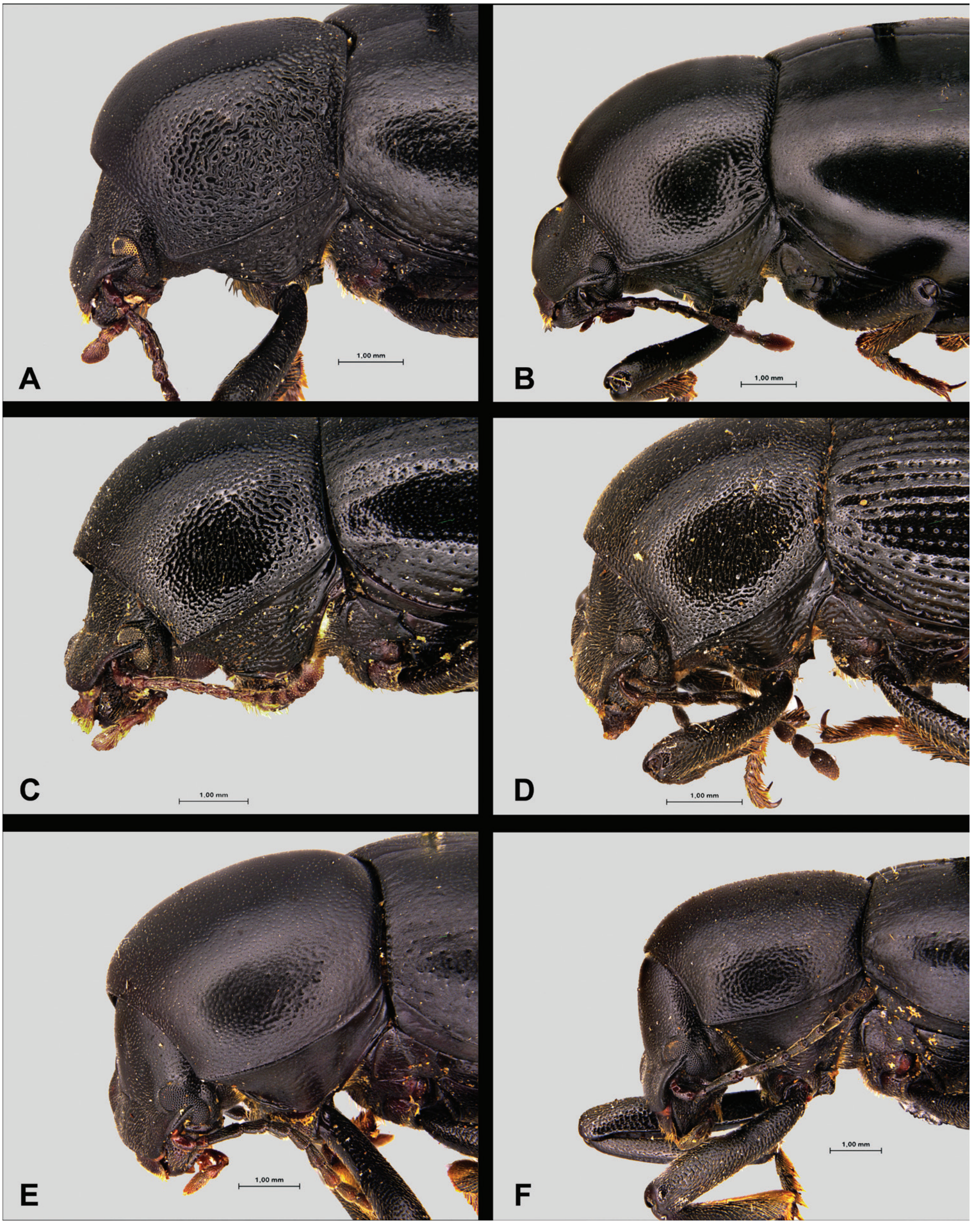

Figure 16. Lateral view of the head and prothorax of specimens of *Misolampus* **A** *Misolampus scabricollis* from Puerto de Navacerrada (Madrid) (MNCN_Ent 270049) **B** *Misolampus subglaber* from Cazorla (Jaén) (MNCN_Ent 270209) **C** *Misolampus ramburii* from Málaga (MNCN_Ent 270037) **D** *Misolampus gibbulus* from Santa Elena (Jaén) (MNCN_Ent 270070) **E** *Misolampus goudotii* from Menorca Island (MNCN_Ent 270032) **F** *Misolampus goudotii* from Iguermalen, Beni Mesdui (Rif Mountains, Morocco) (MNCN_Ent 270188). Note the marked differences in sculpture and anterior angles of pronotum among all five species represented. Photographs **E, F** represent some of the geographic variability observed within *M. goudotii*.

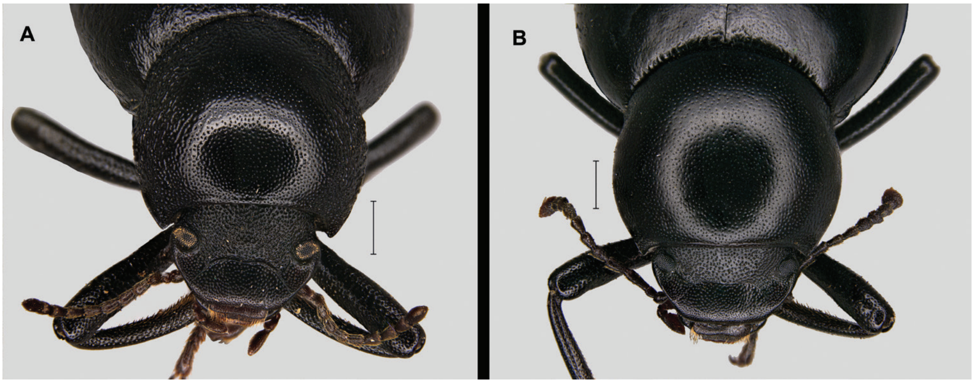

Figure 17. Fronto-dorsal view of specimens of *Misolampus* **A** *Misolampus scabricollis* from Puerto de Navacerrada (Madrid) (MNCN_Ent 270049) **B** *Misolampus subglaber* from Cazorla (Jaén) (MNCN_Ent 270209). Note the differences in the lateral sculpture of pronotum. Scale bars: 1 mm.

2020). These collections provide data on taxon distributions over a vast time, offering a unique perspective on species response to habitat loss and fragmentation, land use intensification or climate change, thus providing critical information to reconstruct species decline and develop conservation strategies (Ponder et al. 2001; Suarez and Tsutsui 2004; Grixti et al. 2009; Doadrio et al. 2019).

The way scientific collections were gathered and the form in which they have been preserved, offer a vast array of possibilities for past-present comparisons in this era of biodiversity loss (Short et al. 2018). Large entomological collections are often formed by the addition of multiple smaller collections (Cambefort 2006; Doadrio et al. 2019). Each taxonomist's collection is a summary of the general biodiversity knowledge at the time, for each of their groups of study. In this sense, scientific collections represent temporal windows opened to a now unreachable past biodiversity, and access to them should be essential and promoted (Mantle et al. 2012; Short et al. 2018).

The saproxylic nature of *Misolampus* calls into question their conservation status, since saproxylic beetles have been identified as a highly threatened animal assemblage due to habitat loss derived from logging and the decline of veteran trees throughout the landscape (Davies et al. 2008; Ricarte et al. 2009; Nieto and Alexandre 2010; Marcos García and Galante 2013; García-López et al. 2016; García et al. 2018). Despite the potential threats to which the species of *Misolampus* can be subjected to, their current level of threat has not been evaluated within the frame of the regional IUCN Red List of Mediterranean saproxylic beetles (García et al. 2018).

However, our comparison of historical data with recent records to assess the current population trends of the species of *Misolampus*, reveals that their distribution ranges show no reduction in the last century, since these species currently persist in most areas of historical occurrence. This fact, combined with the addition of new recent records for some of the species, enables us to state that, from a general perspective, the species of *Misolampus* are not in decline, but rather seem to exhibit an adequate conservation status. This status could be further guaranteed, because the distribution range of all species of *Misolampus* include numerous protected areas (National and Natural Parks, Natura 2000 protected areas; see https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ENP.aspx), which could ensure to some extent the long-term persistence of these saproxylic beetles, if combined with the implementation of adequate agroforestry practices, consistent with the general strategies of saproxylic arthropods conservation from the Mediterranean forests ecosystems (Sánchez Martínez et al. 2012; Marcos García and Galante 2013; García et al. 2018).

Considering the habitat specificity of *Misolampus*, disjunct distribution records such as Ifni for *M. goudotii* (Fig. 4), or Cuenca and Valencia for *M. subglaber* (Fig. 12), can involve threats for the species conservation, derived from local population extinctions, which can be irrevocable in the case of isolated populations. However, disjunct distributions might be not only the result of a reduction of the species range (Teixeira et al. 2018), but also a consequence of recent expansion (Mas-Peinado et al. 2015). Distinguishing between these two situations is highly relevant when evaluating the conservation status of a given species (Hampe and Petit 2005).

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RESEARCH ARTICLE

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Metapogonia snizeki sp. nov. and a previously unknown female of *M. elgonensis* (Burgeon, 1945) (Coleoptera, Scarabaeidae, Melolonthinae, Diplotaxini)

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Abstract

Metapogonia snizeki **sp. nov.** from northeastern Tanzania is described. The new species is compared with the morphologically closely similar species *M. elgonensis* (Burgeon, 1945). A previously unknown female of *M. elgonensis* is described, and the species is recorded from Uganda for the first time. Relevant diagnostic characters (parameres, shape of male protarsomeres, female pygidium) are illustrated.

Keywords

Mount Elgon, new species, Tanzania, Uganda

Introduction

The Afrotropical diplotaxine genus *Metapogonia* Lacroix, 2008 (replacement name for *Metagonia* Kolbe, 1899) currently comprises 10 species from northwestern Africa (Senegal, Gambia) to southernmost Africa (Bezděk 2004). Nearly all of these species are known from primary descriptions only, with no comprehensive revisions and faunistic studies available. The members of *Metapogonia* differ from the species-rich and widely distributed genus *Apogonia* Kirby, 1819 mainly in the shape of the male genitalia. Parameres of *Apogonia* are often complex, asymmetrical, and only in some rare cases rather simple and laterally flattened, while those of *Metapogonia* are symmetrical and dorsoventrally flattened. This shape of the male genitalia is shared with the closely related Afrotropical genus *Dichecephala* Brenske, 1895. The main difference between *Metapogonia* and *Dichecephala* is in the shape of the clypeus. In both sexes of *Metapogonia*, the clypeus is simply rounded and slightly emarginated in the middle. The clypeus of *Dichecephala* is, however, strongly sexually dimorphic. The male possesses a clypeus triangularly produced anteriad, the apex of which is deeply emarginate and often bent upward. The clypeus of the *Dichecephala* female is less prominent and always displays two more or less visibly blunt teeth (but never broadly rounded as in *Metapogonia*).

The history of the generic nomenclature of this group of chafers is rather complicated. Kolbe (1899) proposed the genus-group name *Metagonia* as a subgenus of *Apogonia*. Subsequently, Moser (1918) and Burgeon (1945) elevated it to genus rank. This approach was followed by Bezděk (2004), who catalogued all Old World diplotaxine chafers. Unfortunately, all of these authors overlooked the fact that the genus-group name *Metagonia* Kolbe, 1899 was preoccupied by *Metagonia* Simon, 1893 (Aranae, Pholcidae). Nearly simultaneously, Lacroix (2008) and Özdikmen and Demir (2008) proposed replacement names for *Metagonia* Kolbe, 1899. *Metapogonia* Lacroix, 2008 was published on 4 April 2008, while *Bezdekia* Özdikmen & Demir, 2008 on 24 June 2008. Thus, based on the principle of priority, *Metapogonia* is the valid name for this group of chafers (see also Lacroix and Bezděk 2009 for a detailed discussion).

Studies of recently collected material of Diplotaxini from the northeastern part of the Afrotropical Region has revealed a new distinct species of *Metapogonia* as well as additional specimens of both sexes of *M. elgonensis*, a species previously known from the holotype male only.

Material and methods

A total of 139 specimens were studied. Specimens were examined with an Olympus SZX9 stereomicroscope; measurements were taken with an ocular grid. The habitus photographs were taken using a Canon MP-E 65mm/2.8 1–5× Macro attached to a Canon EOS 550D camera. Partially focussed images of each specimen were combined using Helicon Focus 3.20.2 Pro software. Specimens of the newly described species are provided with one printed red label: "*Metapogonia snizeki* sp. n. | holotypus [or paratypus with type number], sex symbol | Aleš Bezděk det. 2018". Exact label data are cited for the type material examined. Separate labels are indicated by a double vertical bar "||", lines within each label are separated by a single vertical bar "|". Information in quotation marks indicates the original spelling. My remarks and additional comments are placed in brackets, [p] – preceding data (within quotation marks) are printed; [hw] – the same but handwritten. HT – holotype, PT – paratype. The map was composed using SimpleMappr (Shorthouse 2010).

The following codes identify the collections housing the material examined:

BMNH	The Natural History Museum, London, United Kingdom (Maxwell Barclay, Michael Geiser);
IECA	Biology Centre CAS, Institute of Entomology, České Budějovice, Czech Republic (Aleš Bezděk);
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (Alain Drumont);
MFNB	Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (Bernd Jäger, Joachim Willers);
MNHN	Muséum National d'Histoire naturelle, Paris, France (Antoine Mantilleri, Olivier Montreuil);
MRAC	Musée royal de l'Afrique centrale, Tervuren, Belgium (Alice-Marie Buset, Stéphane Hanot);
NMPC	National Museum, Prague, Czech Republic (Jiří Hájek).

Taxonomy

Metapogonia snizeki sp. nov.

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Figures 1, 2, 6, 7, 10, 12

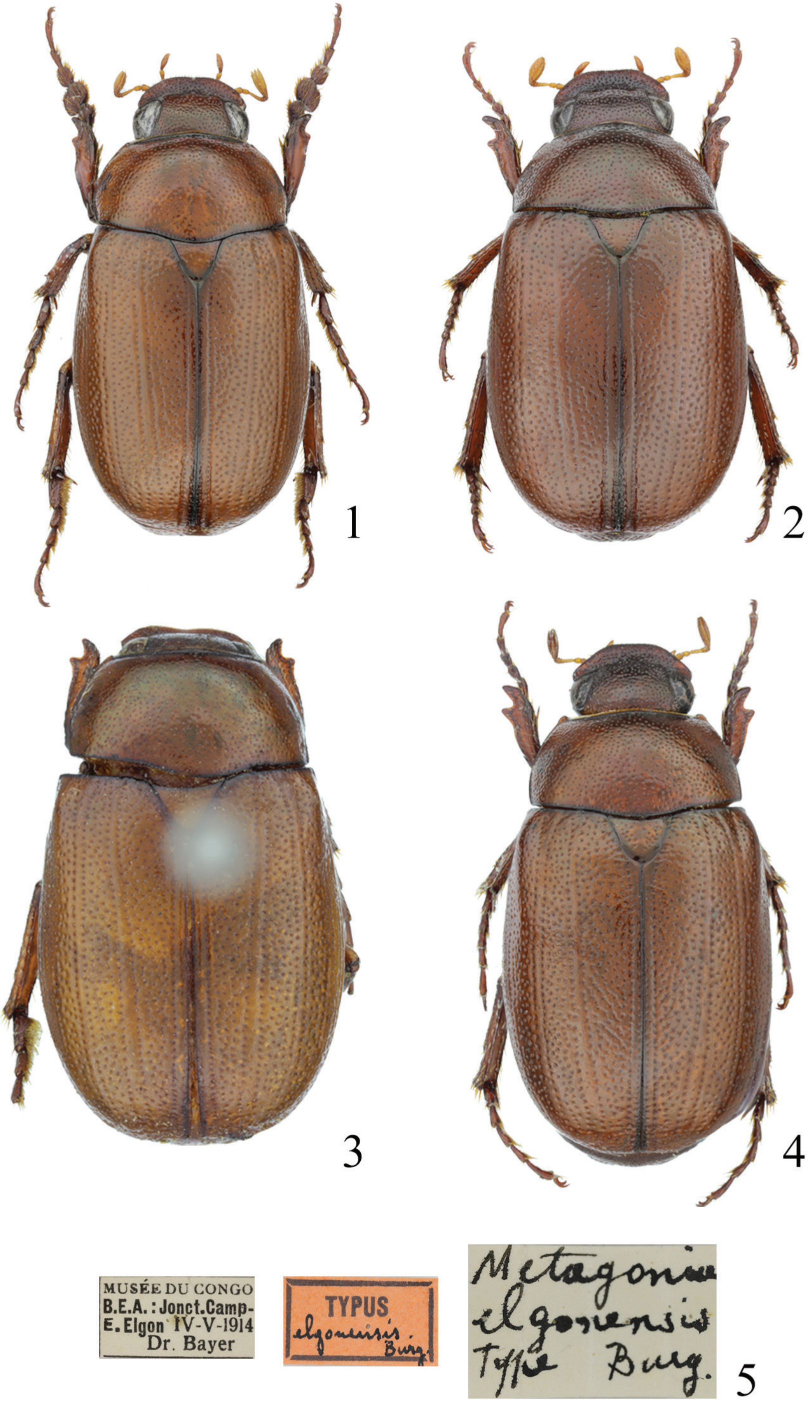
Type locality. NEE Tanzania, SSW of Pangani, environs of Pande.

Type material. HT, male, labelled: "TANZANIA NEE | SSW OF PANGANI | PANDE env. | 10.3.2002 | lgt. M. Snížek [p]"; PT Nos. 1–8 (males) and 9–35 (females), same data as holotype; PT Nos. 36–46 (males) and 47–83 (females), same data as holotype, but "coast | Forest [p]"; PT Nos. 84–91 (males) and 92–119 (females): "TANZANIA NE | HANDENI | MAKINDA env. | 14.3.2002 | lgt. M. Snížek [p]"; PT Nos. 120–121 (females): "TANZANIA NE | E of KIBERASHI | 15.3.2002 | lgt. M. Snížek [p]"; PT Nos. 122–129 (females): "Tanzania c.or., 350 m | 6°25.4'N, 37°30.4'E | 60 km N of Morogoro | leg. L. Hálková, 13.I.2007 [p]".

Type depositories. HT and PT no. 1–19, 24–36, 41–84, 87–91, 94–129 in IECA, PT no. 20, 37 in BMNH, PT no. 21, 38 in ISNB, PT no. 22, 39 in MFNB, PT no. 23, 40 in MNHN, PT no. 85, 92 in MRAC, PT no. 86, 93 in NMPC.

Description of holotype (male). Body length 7.9 mm. Body elongate, convex, surface brown, moderately shiny, anterior and basal margins of pronotum and sutura narrowly darkened (Fig. 1). Antennae and palpi yellowish brown. Head (except for a few setae on eye-canthus), pronotum and elytra bare, epipleura covered with short but well-visible setae. Legs and ventral surface with sparse, pale setation.

Head. Clypeus transverse, broadly rounded, slightly emarginate in the middle, with coarse and dense punctures. Frons and vertex less densely punctate. Eye canthus prominent, largely fused with clypeus; borderline between eye canthus and clypeus



MUSÉE DU CONGO
B.E.A.: Jonct.Camp-
E.Elgon IV-V-1914
Dr. Bayer

TYPUS
elgonensis
Burg.

Metagonia
elgonensis
Type Burg.

Figures 1–5. Habitus of *Metapogonia* spp. and associated labels. **1** *M. snizeki* sp. nov., HT, 7.9 mm **2** *M. snizeki* sp. nov., female PT No. 27, 7.4 mm **3** *M. elgonensis* (Burgeon, 1945), HT, 8.1 mm **4** *M. elgonensis*, female from Uganda: Kelim River, 7.8 mm **5** labels associated with the holotype of *M. elgonensis*.

invisible. Eye large, distinctly extended beyond the canthus. Antenna with 10 antennomeres; club trimerous, slightly shorter than antennal shaft. Antennomeres 1–7 with few isolated, erect setae; club sparsely covered with moderately long, erect setae. Labrum transverse, narrow, completely covered by clypeus, thus not visible from above, with coarse irregular punctures bearing moderately long, erect setae.

Pronotum transverse, convex, widest at about the middle, base broader than anterior margin. Anterior angles prominent, acute-angulate; posterior angles obtuse. Anterior margin with membranous border; anterior marginal line incomplete, interrupted in the middle. Lateral marginal line complete; basal marginal line absent. Punctation coarse, punctures separated by 0.5 or less of their diameter, but never confluent. Scutellum triangulate, approximately as wide as long; apex broadly rounded, sparsely punctate in basal half, nearly impunctate apically, completely bare.

Elytron convex, widest about at middle; sutural angle obtuse-angulate. Surface of elytron covered with coarse, irregular punctures. Basal half of epipleuron with a row of short, recumbent setae. Apical half of lateral margin of elytron with membranous border. Macropterous.

Protibia bidentate, basal teeth in some specimens subobsolete; terminal calcar present. Mesotibia and metatibia slightly expanded apically, covered with semirecumbent setae, at about the middle with short, incomplete, transversal carina armed with 2 or 3 short, thick setae. Terminal calcars of mesotibia and metatibia flattened, nearly blunt apically; upper calcar about 1.2 times as long as lower calcar. Protarsomeres 1–4 considerably dilated (Fig. 12); mesotarsomeres and metatarsomeres 1–4 slightly dilated. Tarsomeres 1–4 on all legs with remarkably shortly and densely macrosetaceous pads ventrally. Tarsomere 5 elongate, ventrally and dorsally with few isolated setae. Claws equal, cleft at the apex.

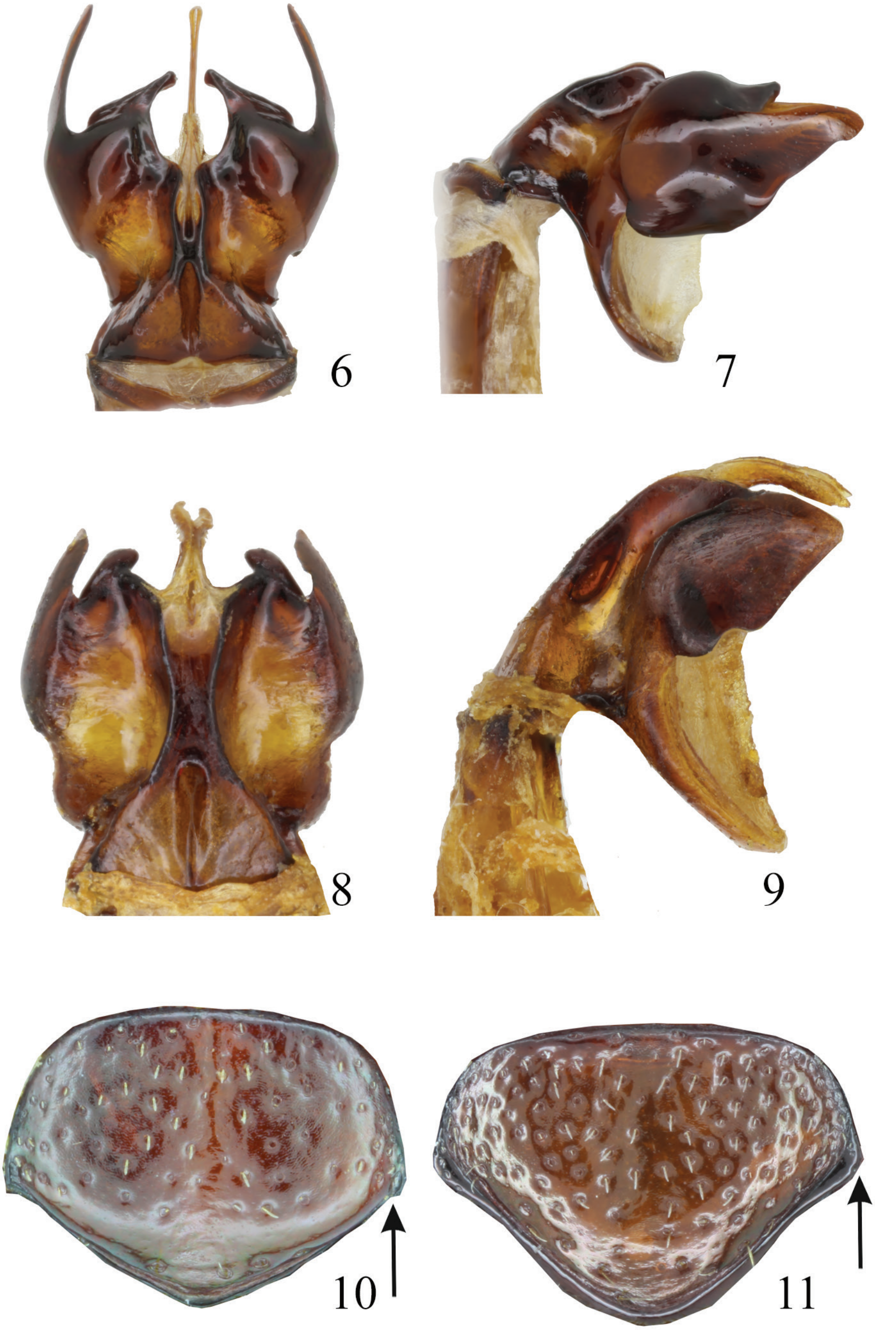
Ventral surface of thorax densely covered with setiferous punctures, setae short, recumbent. Abdominal sternites 3–7 covered with irregular punctures bearing short recumbent or semirecubent setae, setae becoming denser laterally. Abdominal sternites 6 and 7 distinctly narrowed at midline. Abdominal sternite 8 nearly completely retracted beneath abdominal sternite 7, bare, only apical margin with row of erect setae. Propygidium (= abdominal tergite 7) and abdominal sternite 7 completely fused. Pygidium extremely large, convex, irregularly coarsely punctate, apically covered with moderately long, semirecumbent setae, except of smooth depressed midline. Apical and lateral margins of pygidium distinctly bordered.

Male genitalia. Parameres symmetrical (Figs 6, 7), complex, bare, fused basally.

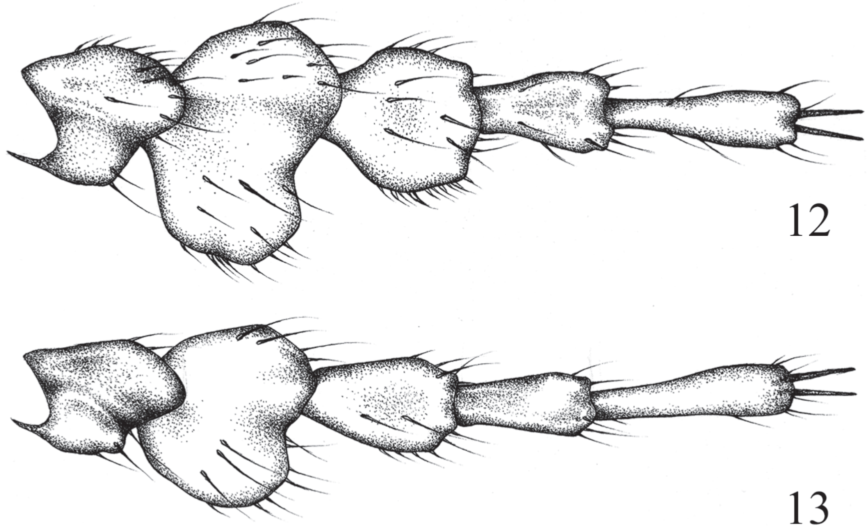
Variability. Male paratypes slightly differs in size (total body length 6.8–8.0 mm, 27 specimens measured), some of them are slightly darker than holotype.

Sexual dimorphism. Female differs from male in the following characters: body length 6.8–7.8 mm (102 specimens measured); antennal club shorter, as long as 6 antecedent antennomeres. Tarsomeres without patches of macrosetae ventrally; pygidium less prominent, nearly flat, with distinct tooth in the centre of lateral margin (Fig. 10).

Differential diagnosis. *Metapogonia snizeki* sp. nov. and *M. elgonensis* are the only *Metapogonia* species with deeply bilobed parameres (Figs 6, 8). All other *Metapogonia* species share parameres that are more simply shaped (see e.g. Figs 14–16). The males of



Figures 6–11. Comparison of diagnostic characters of *Metapogonia* spp. **6** *M. snizeki* sp. nov., parameres of HT, dorsal view **7** the same, ventral view **8** *M. elgonensis* (Burgeon, 1945), parameres of HT, dorsal view **9** the same, lateral view **10** *M. snizeki* sp. nov., female pygidium of PT No. 27 **11** *M. elgonensis*, female pygidium of specimen from Uganda: Kelim River. Not to scale.



Figures 12, 13. Male protarsomeres of *Metapogonia* spp., dorsal view. **12** *M. snizeki* sp. nov., HT **13** *M. elgonensis* (Burgeon, 1945), male from Uganda: Atari. Not to scale.

M. snizeki sp. nov. differ from those of *M. elgonensis* in the shape of the genitalia (compare Figs 6, 7 and 8, 9) and by the shape of protarsomeres, which are more dilated in *M. snizeki* sp. nov. (Figs 12, 13). The females of these two species are very difficult to differentate from the dorsal view, the best identification character seeming to be the shape of the pygidium. The tooth of the pygidium is located nearly in the middle of its lateral margin in *M. snizeki* sp. nov. (Fig. 10), but distinctly more basally in *M. elgonensis* (Fig. 11).

There are three more *Metapogonia* species currently known from Tanzania: *M. kaszabi* (Frey, 1974), *M. parvula* (Moser, 1918), and *M. platypus* (Kolbe, 1899). They are easily distinguishable from *M. snizeki* sp. nov. by the shape of the male genitalia (Figs 14–16) and smaller overall body size (length up to 6.2 mm).

Collecting events. The majority of type material was captured when attracted to light (M. Snížek pers. comm.).

Etymology. The species is named after Miroslav Snížek (Homole near České Budějovice, Czech Republic), one of the collectors of the new species.

Distribution. Northeastern Tanzania (Fig. 17).

Metapogonia elgonensis (Burgeon, 1945)

Figures 3–5, 8, 9, 11, 13

Metagonia elgonensis Burgeon 1945: 17, fig. 19 (primary description); Bezděk 2004: 66 (catalogue).

Metapogonia elgonensis: Lacroix 2008: 69 (new generic combination); Lacroix 2010: 78 (catalogue).

Type locality. "Jonction Camp E. Elgon".

Type material examined. HT, male, fixed by original designation, 8.1 mm: "MUSÉE DU CONGO | B.E.A.: Jonct. Camp - | E. Elgon, IV-V-1914 | Dr. Bayer [p] || Metagonia | elgonensis | Type Burg. [hw] || TYPUS [p] | elgonensis Burg. [h, red label, black frame] || Metagonia elgonensis | Burgeon, 1945 | holotypus, ♂ | det. A. Bezděk, 2017 [p, red label]". Deposited in MRAC.

Additional material examined (8 specimens). UGANDA • 1 male and 6 females (IECA), Kelim River, 17.IV.1976, leg. I. Hájek • 1 male (IECA), Kapchorwa district, 5 km NE of Atari, 1066 m a.s.l., 1.47633N, 34.42011E, 26.I.2016, leg. W. & M. Grosser.

Diagnosis of females. Body length 6.9–8.5 mm (6 specimens measured). Body elongate (Fig. 4), convex, surface brown, moderately shiny, anterior and basal margins of pronotum and sutura very narrowly darkened. Antennae and palpi somewhat paler. Head, pronotum, and elytra bare. Legs and ventral surface with sparse, pale setation. Clypeus transverse, broadly rounded, with coarse and dense punctures. Eye canthus prominent, largely fused with clypeus. Eye large, distinctly extended beyond the canthus. Antenna with 10 antennomeres; club trimerous, shorter than antennal shaft. Labrum transverse, narrow, completely covered by clypeus. Pronotum transverse, convex, widest at about the middle. Anterior angles prominent; posterior angles obtuse. Anterior margin with membranous border; lateral marginal line complete; basal marginal line absent. Punctation coarse. Elytron convex, widest about at middle. Surface of elytron covered with coarse, irregular punctures. Macropterous. Protibia bidentate; terminal calcar present. All tarsomeres normally developed. Claws equal, cleft at the apex. Ventral surface

Figures 14–16. Parameres of *Metapogonia* spp., dorsal view. **14** *M. kaszabi* (Frey, 1974) **15** *M. parvula* (Moser, 1918) **16** *M. platypus* (Kolbe, 1899). Not to scale.

of thorax densely covered with setiferous punctures, setae short, recumbent. Pygidium large, almost flat, with distinct tooth in the basal third of lateral margin (Fig. 11).

Distribution. Kenya (Burgeon 1945), first record for Uganda. The species is known from the Mount Elgon area only (Fig. 17).

Remark. The holotype of *M. elgonensis* was collected by Leon Bayer during his 1914 expedition to eastern Africa in the so called "Junction Camp" (Bayer 1923). According to Moreau et al. (1946), the "Junction Camp" was built on a foothill of Mount Elgon in Kenya, the coordinates of the location are approximately 1°7'N, 34°50'E.

The following additional specimens were used for comparison (Figs 14–16):

Metapogonia kaszabi (Frey, 1974). Tanzania • 1 male (IECA), Arusha distr., Macumira near Arusha, 1200 m, 15.II.2008, leg. A. Bellmann.

Metapogonia parvula (Moser, 1918). Tanzania • 1 male (IECA), Handeni, Makinda env., 14.III.2002, leg. M. Snížek.

Metapogonia platypus (Kolbe, 1899). Tanzania • 1 male (IECA), SSW of Pangani, Pande env., 10.III.2002, leg. M. Snížek.

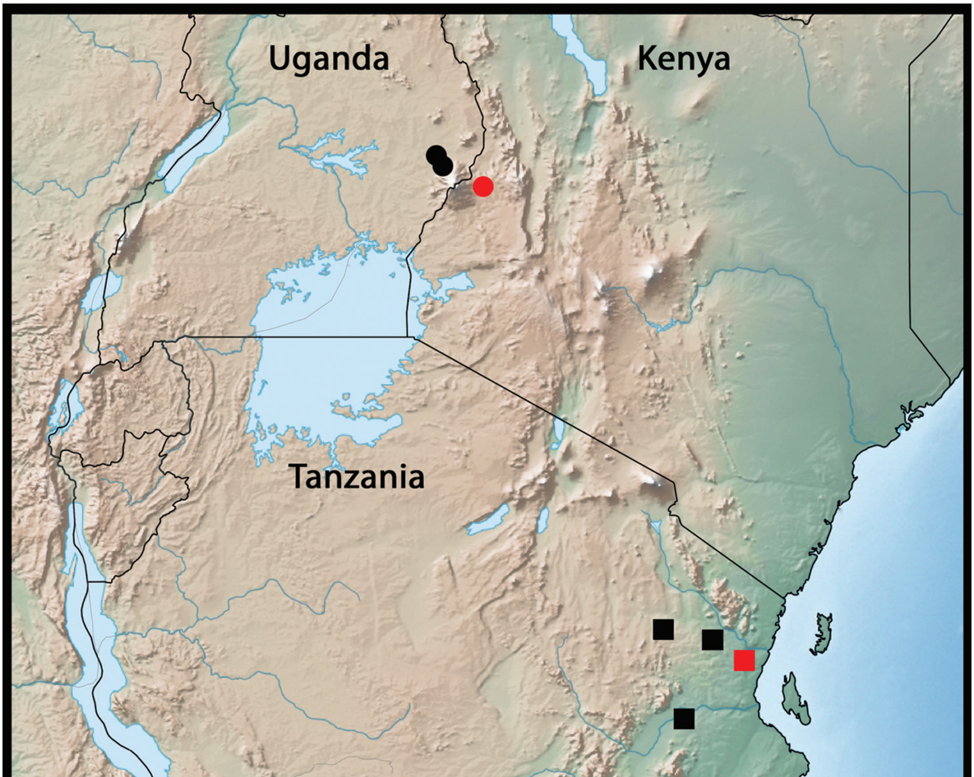


Figure 17. Geographic distribution of *Metapogonia snizeki* sp. nov. (squares) and *M. elgonensis* (Burgeon, 1945) (circles). Red symbols indicate type localities.

Acknowledgements

I extend my sincere appreciation to Marc de Meyer, former curator at MRAC, who enabled me to study the holotype of *Metapogonia elgonensis*, Richard Sehnal (Czech University of Life Sciences, Prague, Czech Republic), who provided me with the habitus photographs, Dana Bláhová (Plzeň, Czech Republic), who prepared the line drawings, and Christopher Steer (University of South Bohemia, České Budějovice, Czech Republic), who kindly improved the English of the manuscript.

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RESEARCH ARTICLE

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Megacraspedus cottiensis sp. nov. (Lepidoptera, Gelechiidae) from northern Italy – a case of taxonomic confusion

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Abstract

Megacraspedus cottiensis **sp. nov.** is described from the western Alps (prov. Torino, Italy). The dorsal habitus and genitalia for both the male and brachypterous female are provided. The new species belongs to the *M. faunierensis* species group based on genitalia morphology and DNA barcodes, and was hitherto confused with *M. neli* Huemer & Karsholt, 2018 from the southwestern Alps. However, it clearly differs in morphology and DNA barcode sequences from that species and from *M. faunierensis* Huemer & Karsholt, 2018. The new species is suspected of being a regional endemic of the Cottian Alps.

Keywords

brachyptery, Cottian Alps, DNA barcoding, morphology, misidentification, new species

Introduction

Megacraspedus comprises 85 described species, therefore one of the most diverse genera of Palearctic Gelechiidae. It was recently revised by Huemer and Karsholt (2018) with 44 species introduced as new to science. Almost half of the genus (46 species) are diagnosed from only male specimens and the biology of the majority is unknown. Species diversity in the genus, not associated or incorrectly associated males and females, and limited biological knowledge has created some recent problems in identification and classification. Fortunately, descriptions of the unknown females for five species were recently provided (Nel and Varenne 2019), and additionally, likely overlooked or unknown species were detected (Corley pers. comm.) as a result of this work.

As part of a survey of the fauna of Lepidoptera from the Cottian Alps (northwest Italy), a large number of specimens identified as *M. neli* were collected, including associated female specimens which were unknown when the species was described. *Megacraspedus neli* Huemer & Karsholt, 2018 was described based on the male holotype collected in the south of France and two male paratypes from the Cottian Alps (northwestern Italy). It therefore seemed reasonable to publish the newly discovered, brachypterous female in a short note. However, examination of the genitalia of both sexes revealed that the specimens identified as *M. neli* collected in the new survey from the Cottian Alps differed morphologically from the holotype. The relevant diagnostic characters were overlooked as a result of the *M. neli* description (Huemer and Karsholt 2018) being based on the genitalia of a paratype in glycerol. These characters are more easily recognised in permanent preparations. The new species hypothesis was corroborated by comparing the DNA barcode of the holotype of *M. neli*, obtained using Next Generation Sequencing methods, to the DNA barcode sequences from specimens collected in the Cottian Alps. The new species is therefore described below.

Materials and methods

The study is based on 248 specimens of the *Megacraspedus faunierensis* species group: *M. faunierensis* (127 specimens), *M. neli* (1 specimen), and *M. cottiensis* sp. nov. (120 specimens). Specimens were pinned, wings spread, and dried. Genitalia preparations followed standard techniques (Robinson 1976) adapted for male genitalia of Gelechiidae by the "unrolling technique" as described by Pitkin (1986). In the absence of properly set specimens, the forewing length measured from the base to the apex of fringes is given instead of the wingspan (Huemer and Karsholt 2018).

Habitus photographs were taken with an Olympus SZX 10 binocular microscope and an Olympus E-3 digital camera. Images were z-stacked using the software Helicon Focus 4.3 and digitally edited in Adobe Photoshop CS4 and Lightroom 2.3. Genitalia photographs were taken with an Olympus E-1 Digital Camera on an Olympus BH2 microscope.

DNA samples were extracted from dried legs in order to sequence the 658 base-pair long barcode segment of the mitochondrial COI gene (cytochrome c oxidase 1) according to the prescribed standards. In addition to specimens previously treated by Huemer and Karsholt (2018), legs from five specimens of the *M. faunierensis* species group were successfully processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain DNA barcodes using the standard high-throughput protocol described in deWaard et al. (2008). The DNA sequence of the holotype of *M. neli* was recovered using Next Generation Sequencing techniques (Prosser et al. 2016). New sequences were submitted to GenBank, and further details including complete voucher data and images can be accessed in the public dataset "DS-MEGAFAUN *Megacraspedus faunierensis* species group" https://dx.doi.org/10.5883/DS-MEGAFAUN in the Barcode of Life Data Systems (BOLD systems v. 4.0. http://www.boldsystems.org; Ratnasingham and Hebert 2007, Ratnasingham 2018). Degrees of intra- and interspecific variation of DNA barcode fragment were calculated under Kimura 2-parameter model of nucleotide substitution using analytical tools of BOLD. Neighbour-Joining analysis from previously published sequences of *Megacraspedus* (Huemer & Karsholt, 2018) and the additional samples was conducted in MEGA7 (Kumar et al. 2016).

Abbreviations of specimen repositories:

LMK	Landesmuseum Kärnten, Klagenfurt, Austria
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
ZMUC	Zoological Museum, University of Copenhagen, Denmark

Taxonomy

Megacraspedus faunierensis species group

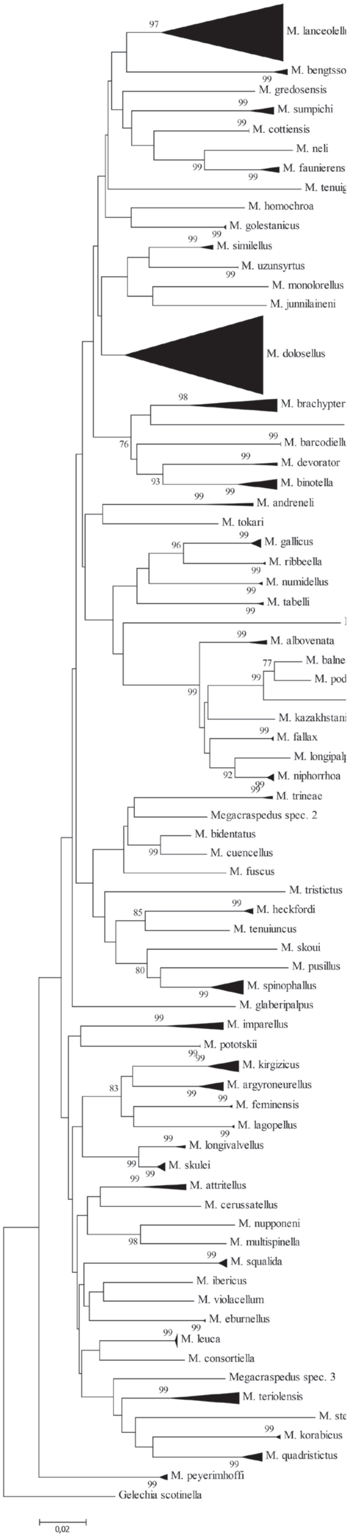
The *M. faunierensis* species group includes three species: *M. neli*, *M. faunierensis*, and *M. cottiensis* sp. nov. Male genitalia are characterised by the proportionally small uncus as compared to the tegumen, the straight and long gnathos hook, the longitudinal medial ridge of the saccular area, the oblong saccus with a longitudinal medial ridge, and the shape of the phallus with wrinkles. Females of *M. faunierensis* and *M. cottiensis* are brachypterous but unknown for *M. neli*. For detailed morphological descriptions and diagnoses, see Huemer and Karsholt (2018).

***Megacraspedus cottiensis* sp. nov.**

http://zoobank.org/16E7C5ED-3271-473B-B5D7-B48D50128A20
Figures 2–4, 7

Type material. *Holotype.* ITALY; • ♂; prov. Torino, Parco Naturale N Orsiera – Rocciavrè, Fenestrelle, ca. 0.7 km NE Pequerel; 45°3'6"N, 7°4'16"E; 1820 m; 29 Jun. 2019; leg. P. Huemer; [Barcode identification number] TLMF Lep 27447; [genitalia slide number] GEL 1299 ♂ P. Huemer; coll. TLMF (Fig. 2).

Paratypes. ITALY; • 39 ♂, 2 ♀; same data as holotype; 1 ♂; [Barcode identification number] TLMF Lep 27448; 1 ♀; [Barcode identification number] TLMF Lep 27446; [genitalia slide number] GEL 1300 ♀ P. Huemer; coll. TLMF; • 31 ♂, 2 ♀; same data as holotype; 23 Jul. 2019; coll. TLMF; • 10 ♂; same data as holotype; leg.


97
M. lanceolell
M. bengtsso
99
M. gredosensis
99
M. sumpichi
99
M. cottiensis
M. neli
99
M. faunierens
99
M. tenuig
M. homochroa
M. golestanicus
99
99
M. similellus
M. uzunsyrtus
99
M. monolorellus
M. junnilaineni
M. dolosellus
98
M. brachypter
76
99
M. barcodiell
99
M. devorator
93
M. binotella
99
99
M. andreneli
M. tokari
99
96
M. gallicus
M. ribbeella
99
M. numidellus
99
M. tabelli
99
99
M. albovenata
77
M. balne
99
M. pod
99
M. kazakhstani
99
M. fallax
M. longipal
92
M. niphorrhoa
99
99
M. trineae
Megacraspedus spec. 2
M. bidentatus
99
M. cuencellus
M. fuscus
M. tristictus
99
85
M. heckfordi
M. tenuiuncus
M. skoui
M. pusillus
80
M. spinophallus
99
M. glaberipalpus
99
M. imparellus
M. pototskii
99
99
M. kirgizicus
83
M. argyroneurellus
99
99
M. feminensis
M. lagopellus
99
99
M. longivalvellus
99
M. skulei
99
99
M. attritellus
M. cerussatellus
M. nupponeni
98
M. multispinella
99
M. squalida
M. ibericus
M. violacellum
M. eburnellus
99
99
M. leuca
M. consortiella
Megacraspedus spec. 3
99
M. teriolensis
M. ste
99
M. korabicus
M. quadristictus
99
M. peyerimhoffi
99
Gelechia scotinella
0,02

C. Wieser; coll. LMK; • 7 ♂; prov. Torino, Parco Naturale N Orsiera – Rocciavrè, Via Colle delle Finestre, Forte Serre Mariae E; 45°2'58.88"N, 7°3'5.29"E; 1840 m; 30 Jun. 2019; leg. C. Wieser; coll. LMK; • 1 ♂; prov. Torino, Valsusa, Mompantero, Monte Rocciamelone; 2200 m; 3 Jul. 1993; leg. G. Bassi; genitalia prep. (in glycerin); coll. ZMUC [misidentified paratype of *M. neli*]; • 1 ♂; same data, but loc. Riposa; 2200 m; 16 Jul. 1993, leg. G. B. Delmastro; coll. TLMF [misidentified paratype of *M. neli*]; • 5 ♂; prov. Torino, Parco Naturale Orsiera – Rocciavrè, Usseaux, Colle delle Finestre N, 45°4'21"N, 7°3'11"E; 2180 m; 24 Jul. 2019; leg. P. Huemer; coll. TLMF; • 14 ♂; prov. Torino, Parco Naturale Gran Bosco di Salbertrand, 2 km SE Colle dell´Assieta; 45°3'38"N, 6°58'44"E; 2240 m; 25 Jul. 2019; leg. P. Huemer; coll. TLMF; • 5 ♂; prov. Torino, Parco Naturale Gran Bosco di Salbertrand, 1.8 km SE Colle dell´Assieta; 45°3'40"N, 6°58'21"E; 2350 m; 21 Jul. 2020; leg. P. Huemer; coll. TLMF.

Diagnosis. *Megacraspedus cottiensis* belongs to a group of species with three distinct black spots in the forewing. It is characterised by the dark basal part of the costa and the dark grey-brown costal area of the forewing in the males, but otherwise it is very similar to other species of the *M. faunierensis* species group. This species is also similar to *M. tristictus* Walsingham, 1910 and *M. pentheres* Walsingham, 1920 in external appearance.

Major diagnostic characters are found in the male genitalia (Figs. 4–6). The male genitalia of *M. cottiensis* differs from that of *M. neli* by the slightly narrower uncus, the long lateral sclerites of the saccus exceeding the maximum width of the saccus, and the slender phallus. The new species is easily separated from *M. faunierensis* by the smaller, less triangular-shaped saccus with proportionally longer lateral sclerites, and several other subtle characters such as the proportionally larger uncus, and more slender valva and phallus.

The female genitalia differ from that of *M. faunierensis* by the convex anterior projection of the subgenital plate and the transverse, suboval signum whereas characters such as the differing lengths and widths of the ductus and corpus bursae may be variable (Figs. 7, 8). The female genitalia are similar to those of several other species of *Megacraspedus* and the documented characters generally seem of limited diagnostic value in the delimitation of species.

Finally, all species are easily separated by DNA barcode sequences (Fig. 1).

Description. Adult. Male (Fig. 2). Forewing length 4.0–5.8 mm. Segment 2 of labial palpus with moderately long scale brush, brown on outer surface, white mottled with brown on inner surface, white on lower and upper surface; segment 3 creamy white. Antennal scape without pecten; flagellum dark brown, at most weakly ringed with white. Head and thorax creamy white to cream. Forewing light yellowish brown,

Figure 1. Neighbor-Joining tree (built with MEGA7) of cytochrome c oxidase subunit I (COI) barcode fragments. Values on branches represent bootstrap values of ≥ 75 % inferred from 500 replicates, scale bar represents substitutions per site. Note: the scale bar only applies to internal branches between species. The width of the triangles represents the sample size, and the depth the relative genetic variation within the cluster (2× scale bar). Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

Figures 2–3. *Megacraspedus cottiensis* sp. nov., adult. **2** male, holotype; **3** female, paratype. Scale bar: 2 mm, all to scale.

more or less intensively mottled with brown, costal half variably covered with grey-brown scales, dorsal half lighter, base of costa dark grey-brown, a black dot in fold at 2/5 and two black dots in middle of wing and at end of cell; some black-tipped scales along termen; fringes light grey. Hindwing light grey with concolourous fringes. Female (Fig. 3). Flagellum distinctly ringed with white. Head and thorax yellowish brown. Forewing length 4.1–4.2 mm. Forewing narrow, apically pointed, almost unicolourous light yellowish brown, without grey brown costal half, darker towards apex, fringes whitish. Hindwing lanceolate, whitish grey. Otherwise similar to male.

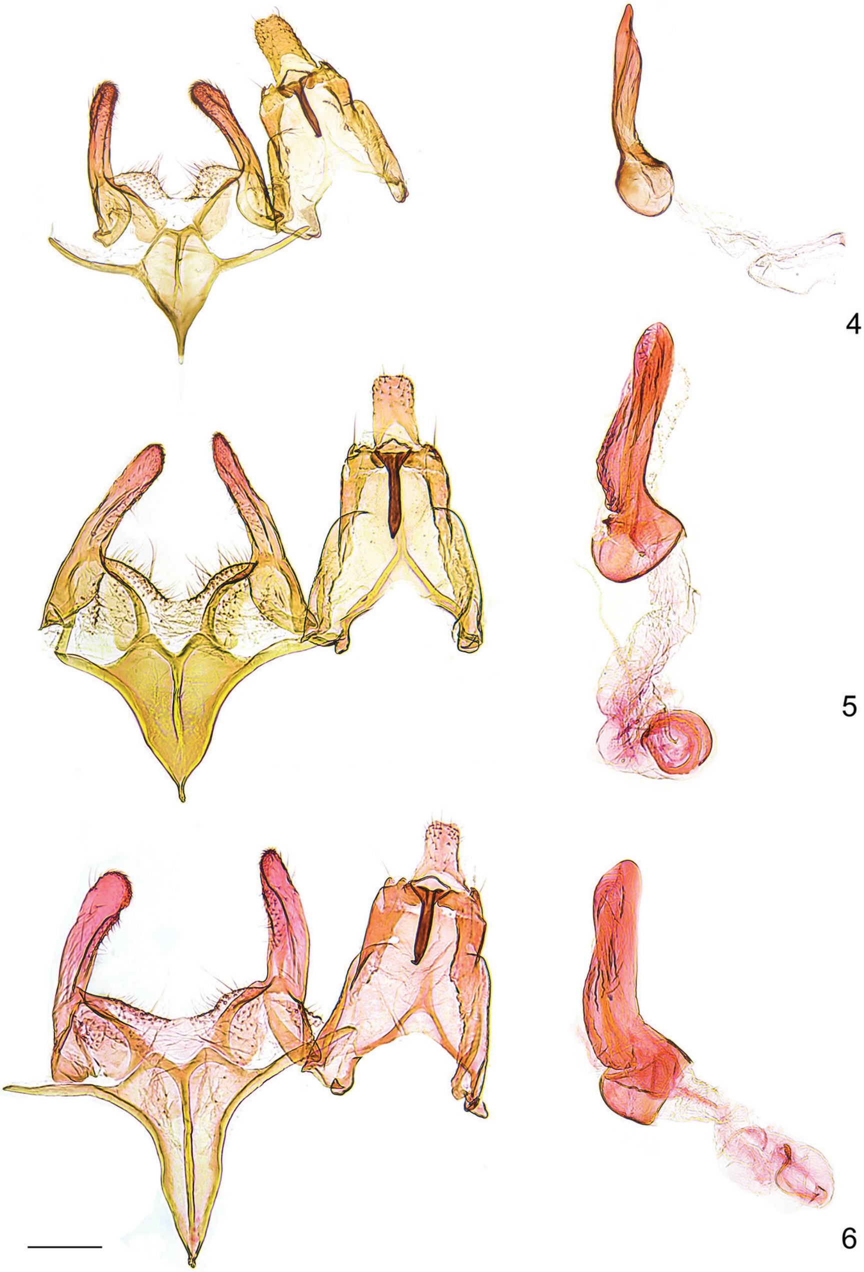
Variation. The extension of the darkened part of the costa as well as the amount of black scales on the forewings is variable.

Male genitalia (Fig. 4). Uncus moderately small, nearly sub-rectangular, apical corners rounded, apical edge with weak medial emargination; gnathos hook moderately slender, straight, apically pointed, approximately length of uncus; anterior margin of dorsal surface of tegumen with suboval emargination, sclerotised ridges from anterior edge converge in medial part of tegumen; pedunculi small, suboval, with small ridge; valva approximately width of uncus, stout, extending slightly beyond base of uncus, digitate distal part, apex broadly rounded; saccular area densely covered with setae, with longitudinal ridge, without separated sacculus; posterior margin of vinculum medially emarginated, with lateral humps, vincular sclerite elongated subovate, with nearly straight sclerotised posterior edge; saccus moderately small, slightly shorter than valva, slender V-shaped, ratio maximum width to length 0.6, posterior margin with weak convex projections, separated by minute incision, medial part with sclerotised ridge from posterior margin to approximately middle, lateral sclerites approximately 1.3 times length of maximum width of saccus; phallus weakly curved at ca. one-third, with inflated coecum, two times wider than distal part, distal part 2.5 times length of coecum, sclerotised dorsal ridge, apex slender; ductus ejaculatorius with small internal sclerotisation.

Female genitalia (Fig. 7). Papilla analis small, apically rounded; apophysis posterior slender rod-like, ca. 2.5 mm long, with short, bifurcate posterior end, bordered by small sclerotised field; segment VIII long and slender, ca. 0.7 × 0.4 mm, largely membranous; subgenital plate with sub-triangular subostial sclerotisation, posteriorly weakly extended sclerites delimiting small ostium bursae, anterior margin with rod-like edge connected with apophysis anterior, medially with moderately short convex projection; apophysis anterior slender, rod-like, free-standing part approximately length of segment VIII, posteriorly becoming rod-like venula of segment VIII, extending to posterior margin of segment VIII; colliculum short; ductus bursae short, slender; corpus bursae, moderately short and slender, distinctly delimited from ductus bursae, entire length of ductus and corpus bursae ca. 1.7 mm; signum small, transverse, suboval spiny plate.

Distribution. Northern part of the Cottian Alps in northwestern Italy.

Biology. Host plant and early stages are unknown. Adults were collected from late June to late July in a xeromontane grassland (Fig. 9) at artificial light sources. Males were attracted in the first 3 hrs of the night, with females, discovered by lighting the



Figures 4–6. Male genitalia of *Megacraspedus faunierensis* species group. **4** *M. cottiensis* sp. nov., holotype; **5.** *M. neli*, holotype; **6** *M. faunierensis*, paratype, genitalia slide GEL 1219. Scale bar: 200 µm, all to scale.

Figures 7–8. Female genitalia of *Megacraspedus faunierensis* species group. **7** *M. cottiensis* sp. nov., paratype, genitalia slide GEL 1300; **8** *M. faunierensis*, paratype, genitalia slide GEL 1235. Scale bar: 200 µm, all to scale.

Figure 9. Habitat of *Megacraspedus cottiensis* sp. nov., Parco Naturale Orsiera – Rocciavrè, Forte Serre Mariae environs (photograph M. Vilgut).

Table 1. Intraspecific mean K2P (Kimura 2-parameter) divergences, maximum pairwise distances and distance to Nearest Neighbour in the *Megacraspedus faunierensis* species group.

Species	Mean Div.	Max Div.	Nearest Species	Nearest Neighbour	Distance to NN
Megacraspedus faunierensis	1.01	1.71	*Megacraspedus neli*	DEPAL068-20	7.12
Megacraspedus neli	N/A	N/A	*Megacraspedus faunierensis*	LEASU040-18	7.12
Megacraspedus cottiensis	N/A	N/A	*Megacraspedus faunierensis*	LEASU040-18	9.04
Megacraspedus sumpichi	N/A	N/A	*Megacraspedus cottiensis*	LEASV695-19	12.14

vegetation with a headlamp. Specimens were collected at altitudes ranging from ca. 1800 to 2350 m.

Etymology. The specific name is an adjective derived from the Cottian Alps, where the new species was discovered.

Molecular analysis. Eight specimens of the *Megacraspedus faunierensis* species group, covering all three described species, were successfully sequenced (sequence length 599 to 658 bp). Intraspecific distances are generally low (not applicable for *M. neli*), ranging from a minimum of 0% to a maximum of 1.71%, whereas interspecific divergence is much higher, ranging between 7.12 and 9.04% among members of the species group and 12.14% to the nearest species *M. sumpichi* Huemer & Karsholt, 2018 (Table 1, Fig. 1) These values, however, are based on a low number of samples. All species in the group belong to different BINs (Ratnasingham and Hebert 2013); the BIN ID for *M. cottiensis* is BOLD:AEA4020 (n = 3). All the individuals of the new species share the same haplotype and the distance to the nearest congeneric neighbour, *M. faunierensis*, is 9.04% (p-dist).

Discussion

We were surprised to discover another undescribed species of *Megacraspedus* in the Alps given the recent revisionary treatment (Huemer and Karsholt 2018), but, at the same time, it supports the hypothesis of even more species diversity and local endemism in a region where the genus is already rich. *Megacraspedus cottiensis* is another apparently small-scale endemic to the western Alps. The difference between this species' DNA barcode and its nearest neighbour, *M. faunierensis*, is quite high for these taxa (ca. 9%); and this despite their geographic proximity to each other (i.e., the type localities are only ca. 70 km apart.). There is a high probability that the divergence from a possible common ancestor pre-dates the last glacial period. It is precisely for taxa such as these that the need for standardised morphological examinations and the greatest possible completeness of DNA barcode reference libraries are evident. By way of example, in this study, the successful morphological differentiation of the new species from closely related taxa was corroborated with the DNA barcode of the holotype of *M. neli* made possible only by NGS methods. Other equally rich and enigmatic taxa may benefit from similar sampling and methodological approaches.

Acknowledgements

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