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# DNA barcoding and male genital morphology reveal five new cryptic species in the West Palearctic bee *Seladonia smaragdula* (Vachal, 1895) (Hymenoptera: Apoidea: Halictidae)

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## Abstract

Several forms or variants have long been recognized in the West Palearctic sweat bee *Seladonia smaragdula* (Vachal, 1895). Using DNA barcoding and morphological characters, primarily of the male genitalia, these variants are here recognized and described as five new species: *S. gemmella* Pauly **sp. nov.**, *S. submediterranea* Pauly **sp. nov.**, *S. orientana* Pauly & Devalez **sp. nov.**, *S. phryganica* Pauly & Devalez **sp. nov.**, and *S. cretella* Pauly & Devalez **sp. nov.** Also, we designate a lectotype for *Halictus smaragdulus* Vachal, consider *Seladonia butea* (Warncke, 1975) and *S. morinella* (Warncke, 1975) as nomina dubia, and discuss the identity of the *Seladonia* specimens from Australia currently determined as *S. smaragdula*.

**Key words:** Australia, integrative taxonomy, invasive species, new species

## Introduction

*Seladonia* Robertson, 1918 (Halictidae: Halictini) consists of approximately 65 species occurring across the Holarctic, Sub-Saharan and Oriental Regions; one species has been recorded as invasive in Australia (Gollan *et al*. 2008). Herein we follow Pesenko (2004) and Pauly (2008; 2015) in treating *Seladonia* at the genus level, not as a subgenus of *Halictus* Latreille, 1804 (Michener 2007). Several variants or forms have long been known in *S. smaragdula* (Vachal, 1895), a rather common species in the Mediterranean Basin (Figs 1, 2), occurring in Europe from Portugal to Greece, and in North Africa from Morocco to the Sinai Peninsula in Egypt; eastwards, this species extends to the Middle East, Central Asia and the Boro Horo Mountains in Xinjang, China. It has a scattered distribution in Central Europe, where it is mostly restricted to warm areas. Adult males and females often forage on flowers of Asteraceae, Apiaceae and Lamiaceae. The nesting biology and social behaviour are unknown; however, phenological data and variations in the size of the female head suggest some degree of eusociality (Pesenko *et al*. 2000).

Blüthgen (1923; 1955) pointed out that "this species forms numerous subspecies and it needs a revision". Ebmer (1976; 1987; 1988) also considered *S. smaragdula* as a highly variable species ("Eine der variabelsten Arten der Westpaläarktis ohne geographische Subspezies auszubilden"). Females of these forms resemble each other and cannot be identified by morphological characters alone. However, the genitalia of males show consistent differences, which allowed Pauly & Rassel (1982) to distinguish five morphs provisionally named forms A to E.

In the present work, we use morphological and genetic data in order to evaluate the status of the forms A–E recognized by Pauly & Rassel (1982). The analysis of DNA sequences can complement morphological investigations for species delimitation and have been used to reveal cryptic bee species, such as those in the *Colletes succinctus* (Linnaeus, 1758) (Kuhlmann *et al.* 2007) and the *Bombus lucorum* (Linnaeus, 1761) groups (Murray *et al.* 2008). Recently, Schmidt *et al.* (2015) used DNA barcoding, a standard approach based on a

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fragment of the mitochondrial cytochrome oxidase subunit 1 (COI) gene, to analyse 4118 specimens representing 561 species of bees from Central Europe, including 12 of *S. smaragdula* [as *Halictus* (*Seladonia*) *smaragdulus*]. These authors found four different clusters of sequences showing divergences that range from 4.6–8.7%, values that have been observed among species of *Halictus*. To test the hypothesis that *S. smaragdula* is composed of a complex of different species, herein we used barcoding data from 87 other West Palaearctic *Seladonia* specimens, most of them of the *S. smaragdula* complex. Herein, we also refine observations of the male genitalia among the currently recognized forms in *S. smaragdula* and describe them as new species.

a b

**FIGURE 1.** *Seladonia smaragdula* "form B" (Spain, Almeria, Almerimar); a, female; b, male.

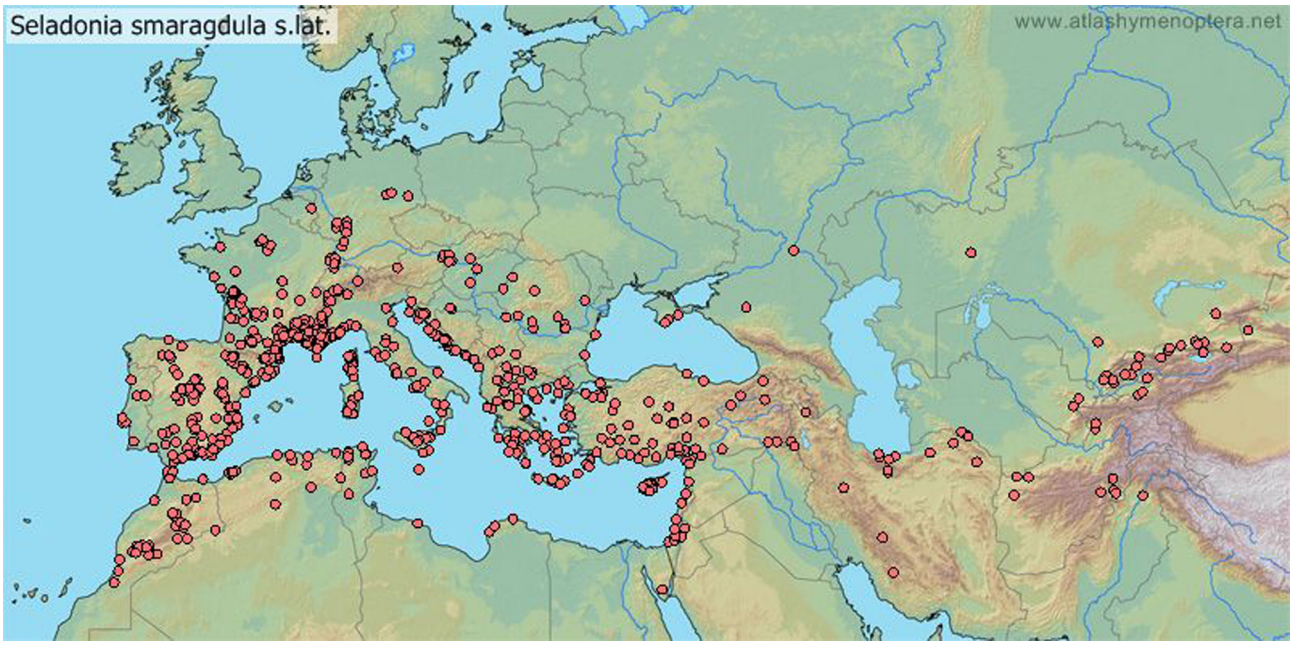


**FIGURE 2.** Geographic distribution of bees in the *Seladonia smaragdula* complex (= *S. smaragdula* sensu lato).

## Materials and methods

We examined the primary types of names associated with *S. smaragdula*, including proposed synonyms. A total of 1668 male and female dry specimens were borrowed and identified from museums and private collections. The following acronyms are used in the text for repository collections with the contact person in parentheses: The Natural History Museum, London, UK (formerly British Museum, Natural History) (BMNH) (D. Notton); Faculté Universitaire des Sciences Agronomiques, Gembloux, Belgium (now Agrobiotech) (FSAG) (E. Haubruge, F. Francis); The Hebrew University of Jerusalem, Rehovot, Israel (HUJ) (G. Pisanti); Institut National de Recherche

Agronomique, Avignon, France (INRA) (B. Vaissière, L. Guilbaud); Museo Nacional de Ciencias Naturales, Madrid (MNCN) (M. Paris); Museum National d'Histoire Naturelle, Paris, France (MNHNP) (C. Villemant); Museum für Naturkunde, Berlin, Germany (MNHUB) (F. Koch, V. Richter); Musée Zoologique de Strasbourg (MZS) (F. Gouin); Naturhistorisches Museum, Wien, Austria (NMW) (M. Madl); Niederösterreichisches Landesmuseum, St Pölten, Austria (NÖLM) (C. Dietrich); Oberösterreichisches Landesmuseum, Linz, Austria (OOLM) (M. Schwarz); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS) (W. Dekoninck); Museum Naturalis, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie) (RMNHL) (W. Hogenes, F. Bakker); Universitat Autònoma di Barcelona, Bellatera, Spain (UAB) (J. Bosch); University of the Aegean, Greece (UAEG) (T. Petanidou); University of Mons-Hainaut, Mons, Belgium (UMH) (P. Rasmont); University of Nottingham, Nottingham, UK (UNOT) (O. Norfolk); Yasouj University, Iran (YASU) (R. Kodarahmi); Zoologische Staatssammlung München, München, Germany (ZSM) (S. Schmidt); A.W. Ebmer (Linz, Austria); S. Gadoum (OPIE, Guyancourt); D. Genoud (Carcassone, France); A. Livory (Manche, France); X. Lair (Sournia, Pyrénées Orientales, France); F. J. Ortiz-Sanchez (Almeria, Spain); M. Schwarz (Ebenfeld, Austria); E. Scheuchl (Germany); C. Schmid-Egger (Berlin, Germany).

Male genitalia were extracted, examined, and photographed with a scanning electron microscope Quanta 200. Specimens were coated with gold and micrographs were taken at 15 or 20 KV. The shape of the underplate of the "large projection" and the thickness of the "small projection" of the gonocoxites were used to identify the forms A to E. The "large projection" corresponds to the gonostylus while the "small projection" is probably homologous to the retrorse ventral membrane observed in the genus *Lasioglossum* Curtis, 1833, as its base is inserted under the gonocoxite. Color pictures of the head, mesosoma, propodeum and metasoma of both sexes were taken with a Nikon camera D7000, a Zuiko Macro 20 mm F3.5 Olympus mounted on a Nikon PB6 bellows, two speedlights Nikon SB-900 and an altoglass dome to obtain highest diffuse light conditions.

One middle leg per specimen (n = 87) was used for DNA barcoding. Fresh material was collected, especially from Greece, France, Spain, and the Sinai. Fourteen other museum specimens of *Seladonia* were included to expand geographical coverage. Females were used to associate the two sexes of each form and to increase the sample size (Table 1). We also used 12 specimens of *S. smaragdula* sequenced by Schmidt *et al.* (2015) that were collected in Germany, Northern France, Cyprus, Greece, and Northern Italy (Table 2).

Location data were digitized with the Data-Fauna-Flora software (Barbier *et al.* 2015) and maps produced with Atlas Hymenoptera (Pauly 2015).

Genomic DNA was extracted with the commercial NucleoSpin Tissue Kit (Macherey-Nagel, Germany). Primers LCO1490 and HCO2198 (Folmer *et al.* 1994) were used to amplify the 5' end of the cytochrome *c* oxidase subunit I (COI) marker (standard DNA barcode region) by PCR. Each reaction of 25 µl contained 2 µl of DNA template, 0.03 U/µl of Platinum® Taq DNA polymerase (Life Technologies, USA), 1X PCR buffer, 0.2 mM dNTPs, 0.4 µM of each primer and 1.5 mM MgCl2. The temperature profile started with 3 min at 94° C, followed by 40 cycles of three steps: 30 s at 94° C, 30 s at 48° C and 60 s at 72° C. The profile ended with 7 min at 72° C. PCR products were purified using the NucleoFast 96 PCR Plate (Macherey-Nagel, Germany). PCR products were sequenced in both directions with an ABI 3130xl sequencer using BigDye® Terminator v3.1 Cycle Sequencing Kit (Life Technologies, USA).

All sequences were edited and trimmed in CodonCode Aligner© v5.0.1 (CodonCode Corp., Centerville, Massachusetts). In total, COI sequences were obtained for 57 out of 87 specimens (BOLD process ID from VARIA002-15 to VARIA088-15 and GenBank accession numbers from KT601640 to KT601696, see Table 1). The sequences were aligned with all COI sequences of *Seladonia* available in GenBank. We also included one outgroup, *Lasioglossum semilucens* (accession number KJ837947). The shortest sequences were removed (9 of the 57 new sequences) in order to obtain an alignment of 658 bp, including a stretch of 560 bp without missing data. Only unique haplotypes were kept for the subsequent analyses. MEGA v.6.06. (Tamura *et al.* 2013) was used to calculate p-distances (i.e. proportion of variable sites) and to construct a neighbour-joining tree with the default parameters implemented in the software. Parsimony trees were calculated in R using the packages ape (Paradis *et al.* 2004) and phangorn (Schliep 2011) with 1000 bootstrap replicates (non-parametric bootstrapping). For maximum likelihood analysis and Bayesian inference of phylogeny, we first used PartitionFinder v1.0 (Lanfear *et al.* 2012) to estimate the best partition scheme (one partition for each codon position) and best-fit substitution models. A maximum likelihood analysis was conducted using RaxML (Stamatakis 2014) on the CIPRES Science Gateway (Miller *et al.* 2010) where rapid bootstrapping was automatically stopped after 750 replicates according to

**TABLE 1**. List of specimens analysed here using morphology and DNA barcoding. Species correspond to initial identification names. Forms A–E refer to Pauly & Rassel (1982).

| Code | Species | Sex | Form | Locality | Date | GenBank |
|---|---|---|---|---|---|---|
| AP001 | *Seladonia seladonia* | ♂ | | Spain, Paraela, Riaza Ermita Kontanares | 2013 | KT601676 |
| AP002 | *Seladonia subaurata* | ♀ | | Spain, Paraela, Riaza Ermita Kontanares | 2013 | KT601687 |
| AP003 | *Seladonia smaragdula* | ♂ | A | Spain, Avila, Debresa de Olalla | 2013 | - |
| AP004 | *Seladonia smaragdula* | ♀ | | Spain, Segovia, Cerezo de Abajo | 2013 | KT601689 |
| AP005 | *Seladonia smaragdula* | ♀ | | Spain, Segovia, Cerezo de Abajo | 2013 | - |
| AP006 | *Seladonia smaragdula* | ♀ | | Spain, Avila, Dehesa de la Cogota | 2013 | KT601683 |
| AP007 | *Seladonia smaragdula* | ♀ | | Spain, Avila, Dehesa de la Cogota | 2013 | KT601690 |
| AP008 | *Seladonia smaragdula* | ♀ | | Spain, Avila, Dehesa de la Cogota | 2013 | KT601682 |
| AP009 | *Seladonia smaragdula* | ♀ | | Spain, Avila, Dehesa de la Cogota | 2013 | - |
| AP010 | *Seladonia smaragdula* | ♀ | | Spain, Avila, Dehesa de la Cogota | 2013 | KT601680 |
| AP011 | *Seladonia smaragdula* | ♀ | | Egypt, Sinai, St Katherines | 2013 | KT601652 |
| AP012 | *Seladonia smaragdula* | ♀ | | Egypt, Sinai, St Katherines | 2013 | - |
| AP013 | *Seladonia smaragdula* | ♂ | B | Egypt, Sinai, St Katherines | 2013 | KT601654 |
| AP014 | *Seladonia smaragdula* | ♂ | B | Egypt, Sinai, St Katherines | 2013 | KT601650 |
| AP015 | *Seladonia smaragdula* | ♂ | E | Israel, Bet Guvrim | 2012 | - |
| AP016 | *Seladonia smaragdula* | ♂ | E | Israel, Bet Guvrim | 2012 | KT601675 |
| AP017 | *Seladonia smaragdula* | ♀ | | France, Deux-Sèvres, Fontenay-R.-R. | 2006 | KT601693 |
| AP018 | *Seladonia smaragdula* | ♀ | | France, Deux-Sèvres, Belleville | 2011 | - |
| AP019 | *Seladonia smaragdula* | ♀ | | Spain, Almeria, El Ejido | 2005 | - |
| AP020 | *Seladonia smaragdula* | ♂ | B | Spain, Almeria, El Ejido | 2005 | KT601649 |
| AP021 | *Seladonia smaragdula* | ♀ | | France, île de Porquerolles | 2007 | - |
| AP022 | *Seladonia smaragdula* | ♂ | A | France, île de Porquerolles | 2007 | KT601678 |
| AP023 | *Seladonia smaragdula* | ♂ | A | France, île de Porquerolles | 2007 | - |
| AP024 | *Seladonia smaragdula* | ♂ | D | Greece, Mt Olympus | 2013 | - |
| AP025 | *Seladonia hotoni* | ♀ | | South Africa, 40 km NE Vanrhynsdorp | 2003 | - |
| AP026 | *Seladonia atroviridis* | ♀ | | South Africa, Nieuwoudtville | 2006 | KT601640 |
| AP027 | *Seladonia lucidipennis* | ♀ | | Iran, Esfahan, Zazeran | 2012 | KT601655 |
| AP028 | *Seladonia lucidipennis* | ♀ | | Iran, Fars, Shiraz | 2013 | - |
| AP029 | *Seladonia subauratoides* | ♀ | | Iran, Esfahan | 2012 | KT601688 |
| AP030 | *Seladonia smaragdula* | ♀ | | Iran, Khorasan, E. Shomali, Esfaraen Ruin | 1973 | - |
| AP031 | *Seladonia orientalis* | ♀ | | France, Ile de la Réunion | 2012 | KT601656 |
| AP032 | *Seladonia smaragdula* | ♀ | | Libya, Cyrenaica, Bersis | 1954 | - |
| AP033 | *Seladonia smaragdula* | ♀ | | Morocco, Taza, Sfsofat | 1996 | - |
| AP034 | *Seladonia smaragdula* | ♂ | E | Greece, Santorini, Panagia Kalou | 2013 | KT601672 |
| AP035 | *Seladonia smaragdula* | ♂ | E | Greece, Santorini, Panagia Kalou | 2013 | KT601667 |
| AP036 | *Seladonia smaragdula* | ♂ | E | Greece, Anafi, Vagia | 2013 | KT601664 |
| AP037 | *Seladonia smaragdula* | ♂ | E | Greece, Anafi, Helicodrome | 2013 | - |
| AP038 | *Seladonia smaragdula* | ♀ | | Greece, Antiparos, Antiparos village | 2004 | - |
| AP039 | *Seladonia smaragdula* | ♀ | | Greece, Sifnos, Ag Anna | 2013 | - |
| AP040 | *Seladonia smaragdula* | ♀ | | Greece, Syros, Kambos | 2013 | KT601673 |
| AP041 | *Seladonia smaragdula* | ♀ | | Greece, Iraklia | 2013 | - |
| AP042 | *Seladonia smaragdula* | ♀ | | Greece, Attica, Athens, Daphni | 2013 | - |
| AP043 | *Seladonia smaragdula* | ♀ | | Turkey, Mugla Koycegiz | 2013 | KT601662 |

*.....continued on the next page*

**TABLE 1.** (Continued)

| Code | Species | Sex | Form | Locality | Date | GenBank |
|---|---|---|---|---|---|---|
| AP044 | *Seladonia smaragdula* | ♀ | | Greece, Kea Poisses, Koundouros | 2013 | - |
| AP045 | *Seladonia smaragdula* | ♀ | | Greece, Samothrace, Panagia | 2012 | KT601660 |
| AP046 | *Seladonia smaragdula* | ♀ | | Greece, Thasos, Potos | 2012 | |
| AP047 | *Seladonia smaragdula* | ♀ | | Greece, Naxos, Fragma | 2012 | KT601666 |
| AP048 | *Seladonia smaragdula* | ♀ | | Greece, Zante, col. Vachal | 1890 | - |
| AP049 | *Seladonia smaragdula* | ♂ | C | France, Deux-Sèvres, Prissé-la-Charrière | 2011 | KT601692 |
| AP050 | *Seladonia smaragdula* | ♂ | C | France, Deux-Sèvres, Fontenay-RR | 2012 | - |
| AP051 | *Seladonia smaragdula* | ♂ | A | France, Var, Porquerolles | 2007 | - |
| AP052 | *Seladonia smaragdula* | ♂ | D | Greece, Evros, Dadia | 2012 | - |
| AP053 | *Seladonia smaragdula* | ♂ | D | Greece, Samothrace, Panaigia | 2012 | KT601657 |
| AP054 | *Seladonia smaragdula* | ♂ | D | Greece, Samothrace, Dafnes | 2012 | KT601659 |
| AP055 | *Seladonia seladonia* | ♂ | | Spain, Paraela, Riaza Ermita Kontanares | 2013 | KT601677 |
| AP056 | *Seladonia smaragdula* | ♀ | | Iran, Golestan, Park E Melli | 2013 | - |
| AP057 | *Seladonia smaragdula* | ♀ | | Iran, Golestan, Minoudasht | 2013 | - |
| AP058 | *Seladonia smaragdula* | ♀ | | Iran, Esfahan, Dehagan Astaneh | 2013 | KT601671 |
| AP059 | *Seladonia smaragdula* | ♂ | B | Spain, Almeria, Almerimar | 2014 | KT601648 |
| AP060 | *Seladonia smaragdula* | ♂ | B | Spain, Almeria, Almerimar | 2014 | KT601647 |
| AP061 | *Seladonia gemmea* | ♂ | | Spain, Almeria, Almerimar | 2014 | KT601643 |
| AP062 | *Seladonia smaragdula* | ♂ | B | Spain, Almeria, Almerimar | 2014 | KT601646 |
| AP063 | *Seladonia smaragdula* | ♂ | B | Spain, Almeria, Almerimar | 2014 | KT601645 |
| AP064 | *Seladonia smaragdula* | ♀ | | Spain, Almeria, Sierra Alhamilla | 2014 | KT601653 |
| AP065 | *Seladonia smaragdula* | ♂ | A | Spain, Almeria, Berchules | 2014 | KT601679 |
| AP066 | *Seladonia smaragdula* | ♀ | | Spain, Almeria, Berchules | 2014 | KT601681 |
| AP067 | *Seladonia gemmea* | ♂ | | Spain, Almeria, Berchules | 2014 | KT601644 |
| AP068 | *Seladonia smaragdula s.l.* | ♀ | | Spain, Almeria, Sorbas | 2014 | KT601651 |
| AP069 | *Seladonia smaragdula* | ♀ | | Spain, Barcelona, Montseny | 2012 | KT601684 |
| AP070 | *Seladonia smaragdula* | ♀ | | Spain, Barcelona, Montseny | 2012 | KT601695 |
| AP071 | *Seladonia smaragdula* | ♀ | | Spain, Barcelona, Montseny | 2012 | KT601685 |
| AP072 | *Seladonia smaragdula* | ♀ | | Spain, Barcelona, Montseny | 2012 | KT601686 |
| AP073 | *Seladonia smaragdula* | ♂ | E | Greece, Chios, Ag Georgios Sikousis | 2013 | KT601663 |
| AP074 | *Seladonia cephalica* | ♂ | | Greece, Lesvos, Mytilène | 2013 | KT601641 |
| AP075 | *Seladonia smaragdula* | ♂ | E | Greece, Ios | 2013 | KT601674 |
| AP076 | *Seladonia cephalica* | ♂ | | Greece, Lesvos, Mytilène | 2013 | KT601642 |
| AP077 | *Seladonia smaragdula* | ♂ | E | Greece, Crete, Heraklion | 2013 | KT601670 |
| AP078 | *Seladonia smaragdula* | ♀ | | Greece, Crete, Heraklion | 2013 | KT601665 |
| AP079 | *Seladonia smaragdula* | ♀ | | Greece, Lesvos, Mytilène | 2013 | KT601668 |
| AP080 | *Seladonia smaragdula* | ♀ | | Greece, Ios, central area | 2013 | KT601669 |
| AP081 | *Seladonia smaragdula* | ♀ | | Greece, Anafi | 2013 | - |
| AP082 | *Seladonia smaragdula* | ♂ | D | Greece, Evros, Dadia | 2012 | KT601661 |
| AP083 | *Seladonia smaragdula* | ♀ | | France, Deux-Sèvres, Doeuil-sl-M. | 2012 | KT601696 |
| AP084 | *Seladonia smaragdula* | ♀ | | France, Deux-Sèvres, Marigny | 2011 | - |
| AP085 | *Seladonia smaragdula* | ♂ | D | Greece, Pieria, Litochoro | 2013 | KT601658 |
| AP086 | *Seladonia smaragdula* | ♂ | C | Iran, Gilan Prov., Tulkabo near Roodbar | 2010 | KT601694 |
| AP087 | *Seladonia smaragdula* | ♂ | C | Iran, Gilan Prov., Tulkabo near Roodbar | 2010 | KT601691 |

the MRE-based bootstopping criterion. Bayesian analyses were performed with MrBayes v3.2.3 (Ronquist *et al.* 2012). Two parallel runs with four chains each were run for five million generations, with unlinked nucleotide substitution parameters for each data partition. Every 1000th generation was sampled, and the first 25% of the trees were discarded ("burn-in").

**TABLE 2.** List of specimens sequenced by Schmidt *et al.* (2015).

| Species | Sex | Locality | GenBank |
|---|---|---|---|
| *Seladonia smaragdula* | ♀ | Italy, Valle d'Aoste | KJ838161 |
| *Seladonia smaragdula* | ♀ | Italy, Valle d'Aoste | KJ838692 |
| *Seladonia smaragdula* | ♀ | Italy, Valle d'Aoste | KJ837319 |
| *Seladonia smaragdula* | ♀ | Germany, Rheinland-Pfalz | HQ948048 |
| *Seladonia smaragdula* | ♀ | Germany | KJ837404 |
| *Seladonia smaragdula* | ♀ | France, Haut-Rhin | HM401095 |
| *Seladonia smaragdula* | ♀ | Germany, Rheinland-Pfalz | KJ838383 |
| *Seladonia smaragdula* | ♀ | Germany | KJ838728 |
| *Seladonia smaragdula* | ♂ | Greece, Crete | KJ839319 |
| *Seladonia smaragdula* | ♀ | Cyprus | KJ838248 |
| *Seladonia smaragdula* | ♀ | Cyprus | KJ838440 |
| *Seladonia smaragdula* | ♀ | Cyprus | KJ837345 |

## Results

All museum male specimens examined (n = 421) were sorted into the five morphological forms previously recognized by Pauly & Rassel (1982). All COI sequences were segregated into five distinct groups, thus in total accordance with these morphological forms. These sequences also revealed a sixth divergent haplotype (Fig. 3).

Divergences at COI (Table 3) observed among each of the five forms recognized by morphology were systematically larger than within them (p-distances: 3.3–9.8% and 0–2.7%, respectively). In addition, the divergences within each of the five forms were in the same range as intraspecific distances observed in the genus (0–1.6%) and those among the five forms fall within the range of the interspecific distances observed in the genus (1.7–10.3%). All phylogenetic trees constructed on the basis of COI (Fig. 3) support the monophyly of each of five forms (bootstrap values ≥ 99% and posterior probabilities = 1). Relationships among these forms were not resolved, except for those of forms A and E, whose sister relationship was strongly supported (bootstrap values ≥ 97% and posterior probabilities = 1), both sister to *S. cephalica* (Morawitz, 1873) (bootstrap values ≥ 93% and posterior probabilities = 1). GenBank sequences of *S. smaragdula* from Germany and France clustered within form C (divergence with closest sequence < 0.3%), those from Italy within form D (divergence < 2.7%), and those from Cyprus within form E (divergence = 0%). In contrast, the sequence of a single specimen from Crete was highly divergent from all COI sequences of *Seladonia* available (≥ 6%) and thus, suggesting a distinct form. The similarity of the sequences obtained here also allowed us to associate sexes, which is not feasible on the basis of the morphology alone.

The results from the genetic analysis and the morphological study of the male genitalia, in addition to their geographic distribution, consistently allowed us to recognize these forms as distinct species, which are described below.

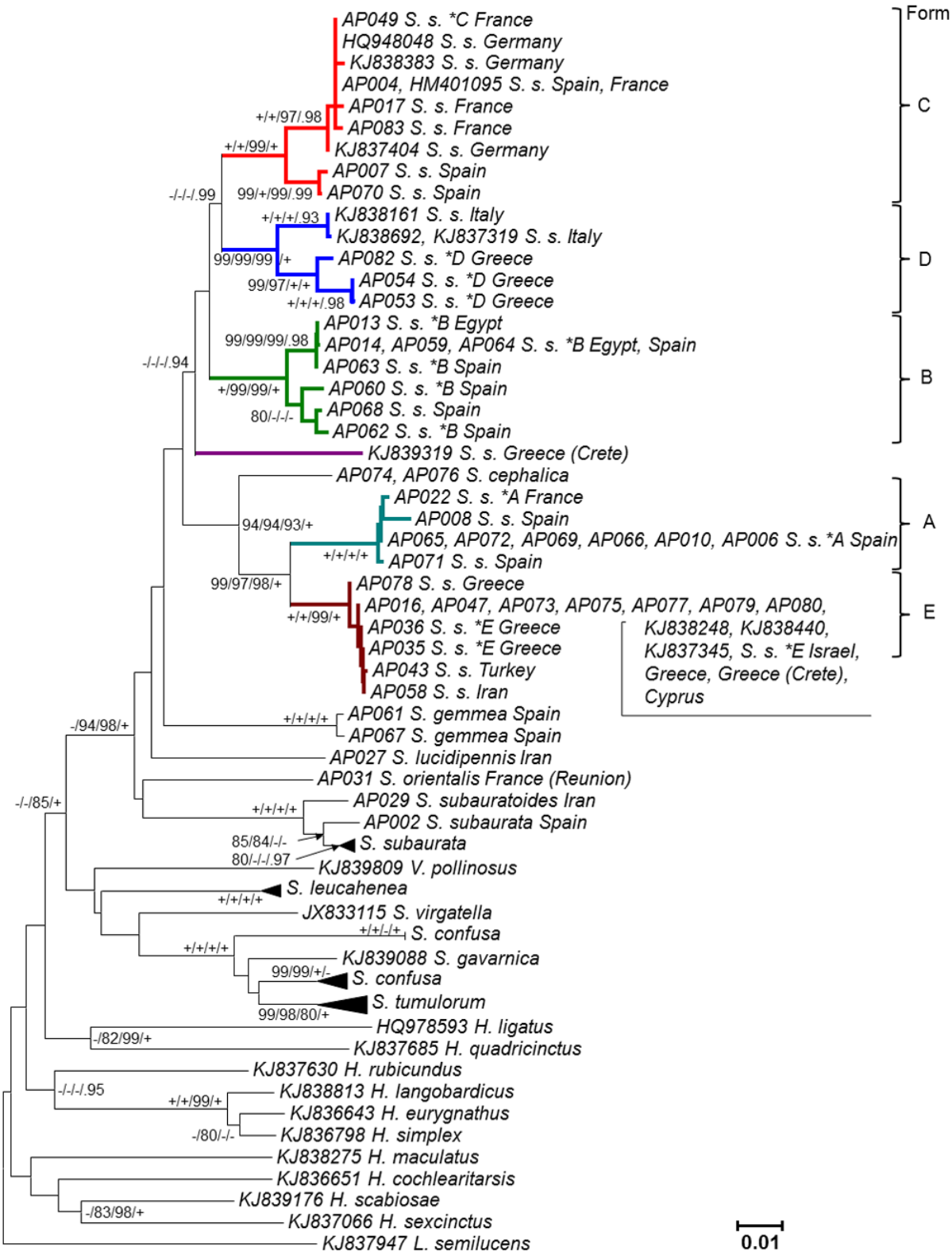


**FIGURE 3.** Neighbour-joining tree showing p-distances at COI (658bp) among *Seladonia* specimens. Outgroup: *Lasioglossum semilucens*. Label at the end of each branch includes field ID or GenBank accession number, species identification [L = *Lasioglossum*, H = *Halictus*, S = *Seladonia*, S s = *Seladonia smaragdula* sensu lato, V = *Vestitohalictus*, *A–E = each of the currently recognized forms within *Seladonia smaragdula* based on the male genitalia according to Pauly & Rassel (1982)] and country of collection. Values at nodes: bootstrap support (%) in the neighbour-joining / parsimony / maximum likelihood analyses / and posterior probabilities in the Bayesian inference ("+": maximum support; "-" support of bootstrapping < 80% or posterior probability < 0.9). Colors of branches are according to each *S. smaragdula* form; black triangles at the end of a branch represent several similar haplotypes with identical species identifications.

**TABLE 3**. Ranges of distances (number of substitutions/length of sequence) within ("intra") each form or each *Seladonia* species (when more than one sequence is available per species) and between ("inter") forms or *Seladonia* species.

| | intra | | inter (but within *S. smaragdula* complex) | | inter (but within *Seladonia*) | |
|---|---|---|---|---|---|---|
| Form | min | max | min | max | min | max |
| A | 0 | 0.007 | 0.033 | 0.098 | 0.033 | 0.099 |
| B | 0 | 0.016 | 0.043 | 0.089 | 0.043 | 0.090 |
| C | 0 | 0.022 | 0.043 | 0.092 | 0.043 | 0.104 |
| D | 0 | 0.027 | 0.046 | 0.084 | 0.046 | 0.093 |
| E | 0 | 0.002 | 0.033 | 0.088 | 0.033 | 0.101 |
| "Crete" | | | 0.060 | 0.098 | 0.060 | 0.099 |
| gemmea | 0.003 | 0.003 | | | 0.076 | 0.103 |
| subaurata | 0 | 0.016 | | | 0.017 | 0.103 |

## Species account

## Systematics

### Family Halictidae Thomson, 1869

### Tribe Halictini Thomson

### Genus *Seladonia* Robertson, 1918

### *Seladonia smaragdula* complex

**Diagnosis.** Members of the *S. smaragdula* complex can be distinguished from all other *Seladonia* by the following combination of characters: small body size (length 5.0–6.5 mm); body with golden green metallic reflexions; femora dark; tibiae and tarsi yellow brown with dark central maculations; head short (female length/width 0.92–1.02; male 0.95–1.22); vertex short, rounded; punctation of scutum minute and dense, spaces between punctures equivalent to a puncture width; propodeal area rounded, surrounded by shiny area; terga with apical hair bands, minutely and densely punctate, spaces between punctures equivalent to a puncture width; male gonocoxite with a large and a small projection, the large projection bearing a tuft of setae on its inner side and with a thin apical appendice (Fig. 7).

Two species may be easily confused with those of the *S. smaragdula* complex: *S. cephalica* (Morawitz, 1873) and *S. gemmea* (Dours, 1872). *Seladonia cephalica* differs by the first tergum with apical margin more depressed, vertex and gena more developed, propodeum with larger shining area, and the male fourth antennal segment longer (length/width 1.54). The female of *S. gemmea* differs from those of the *S. smaragdula* complex by the lack of apical hair bands on the terga, vertex and gena more developed and propodeum with larger shining area. The male differs by the lack of an apical appendice on the large projection of the gonocoxite and the specialized pilosity on the inner side of this projection, which is reduced to a single long setae.

### *Seladonia smaragdula* (Vachal, 1895)

(Figs 4–9, 22a,b, 24a)

*Halictus smaragdulus* Vachal, 1895: 150, ♂. Lectotype ♂: Spain, Sevilla, col. Medina (MCSNM) (**new lectotype designation**).

*Halictus barcelonicus* Pérez, 1903: 211, ♀. Lectotype ♀: Barcelona (MNHNP), designated by Ebmer 1972: 619, examined.

*Halictus smaragdulus* form *vinulus* Blüthgen, 1923: 300, ♀, ♂. Holotype ♀: "Sicilien, Zeller S., n°1892" (MNHUB), examined.

*Halictus smaragdulus* Form A in Pauly & Rassel, 1982: 142.

**Diagnosis.** The male of this species differs from other species of the *S. smaragdula* complex by the racket-shaped underplate of the large projection of the gonocoxite, which is rounded as in *S. phryganica*. This plate is very similar to that of *S. cephalica* but the latter species differs by the longer fourth antennal segment (length/width = 1.54 in *S. cephalica* vs. 1.25 in *S. smaragdula*) and the more depressed apical margin of tergum 1. The small projection of the gonocoxites is rather thin in *S. smaragdula* but not as thin as in *S. phryganica*. *Seladonia smaragdula* and *S. phryganica* are also geographically separated (Figs 9 and 19).

Females of *S. smaragdula* cannot be distinguished from the other species of the *S. smaragdula* complex by morphological characters.


a b

**FIGURE 4.** *Seladonia smaragdula*, male lectotype; a, genitalia, ventral view; b, lectotype labels.

**Description**. Male. Length 5.0–6.5 mm. Colouration. Body with golden green metallic reflexions. Femora black with metallic reflexions. Apex of femora, tibiae and tarsi yellow. Antennae brown below. Labrum and apical margin of clypeus pale yellow. Head (Fig. 6a). Face relatively short (length/width 0.95). Fourth antennal segment relatively short (length/width = 1.25) (Fig. 6b). Vertex short, rounded. Mesosoma. Punctation of scutum minute and dense, spaces between punctures equivalent to a puncture width (Fig. 6c). Propodeal area rounded, its surrounding area shining (Fig. 6d). Metasoma. First tergum with weakly depressed apical margin (Fig. 6e). Terga with apical hair bands, minutely and densely punctate, spaces between punctures equivalent to a puncture width (Fig. 6f). Underplate of the large projection of gonocoxite rounded or racquet-shaped (Figs 7, 22a,b); small projection of gonocoxite relatively thin (Figs 7, 24a).

Female. As in the male except as follows: Colouration. Middle and hind tibiae with central dark maculation. Head (Fig. 8a). Face relatively short (length/width = 0.92), minutely and densely punctate. Mesosoma. Punctation of scutum minute and dense, spaces between punctures equivalent to a puncture width (Fig. 8c). Propodeal area rounded, its surrounding area shining (Fig. 8d). First tergum with apical margin weakly depressed (Fig. 8e). Terga with apical hair bands, the punctation minute and dense, the spaces between punctures equivalent to a puncture width (Fig. 8f). Inner metatibial spur with three or four teeth.

**Comments.** The type locality of this species according to the original description of Vachal (1895: 150) is "Sevilla", Spain. The first revisor (Blüthgen 1924: 333) in the introduction of his paper on Spanish halictids wrote: "Finalmente, fue my interesante para mi el hecho de poder ver los tipos de las especies españolas descritas por Vachal, que se encuentran en las colecciones de la Universidad de Sevilla". The types of bees from the Medina collection are now deposited in the Museum de Ciencias naturales de Madrid (Rasmussen 2012). We examined and dissected the metasoma to extract the genitalia of the lectotype (herein designated) with the authorization of the curator Mercedes Paris. It belongs to the form A, here recognized as the true *S. smaragdula* (Fig. 4a). The lectotype bears a locality label "Sevilla" and a label of identification with the handwriting of Blüthgen (Fig. 4b). A second specimen bearing a label with the locality "Guadalcanal" in the Province of Sevilla is designated here as paralectotype, and its metasoma is missing.


**FIGURE 5.** *Halictus smaragdulus* form *vinulus*, female holotype and male paratype; a, female head; b, female propodeum; c, male head; d, male antenna; e, male genitalia, ventral view; f, labels of the female holotype.

*Halictus barcelonicus* was described from a female specimen collected in Barcelona, a locality where males fall within the form A. Thus, despite being based on a female specimen we considered *H. barcelonicus* as part of *S. smaragdula*.

The type series of *Halictus smaragdulus* form *vinulus* is composed of three females and two males from Sicily (Fig. 5). One female bears a "type" label while the remaining specimens each a "cotype" label. We dissected one of the males and the gonostylus is identical to that of *S. smaragdula* (Fig. 5e), and thus it is here placed under this

species. The head of the type series of the form "*vinulus*" (Figs 5a, c) is longer (female length/width = 1.02) than the head of the Spanish "*smaragdula*", suggesting a differentiate population.

**Distribution.** West Mediterranean, from Spain to Western Greece, and from Morocco to Tunisia (Fig. 9).

**Visited plants**. *Eryngium campestre* L. (Apiaceae), *Tolpis virgata* Bertol (Asteraceae), *Lavandula latifolia* Medlk, *Origanum vulgare* L. (Lamiaceae), *Heliotropium europaeum* L. (Boraginaceae), *Malva sylvestris* L. (Malvaceae).

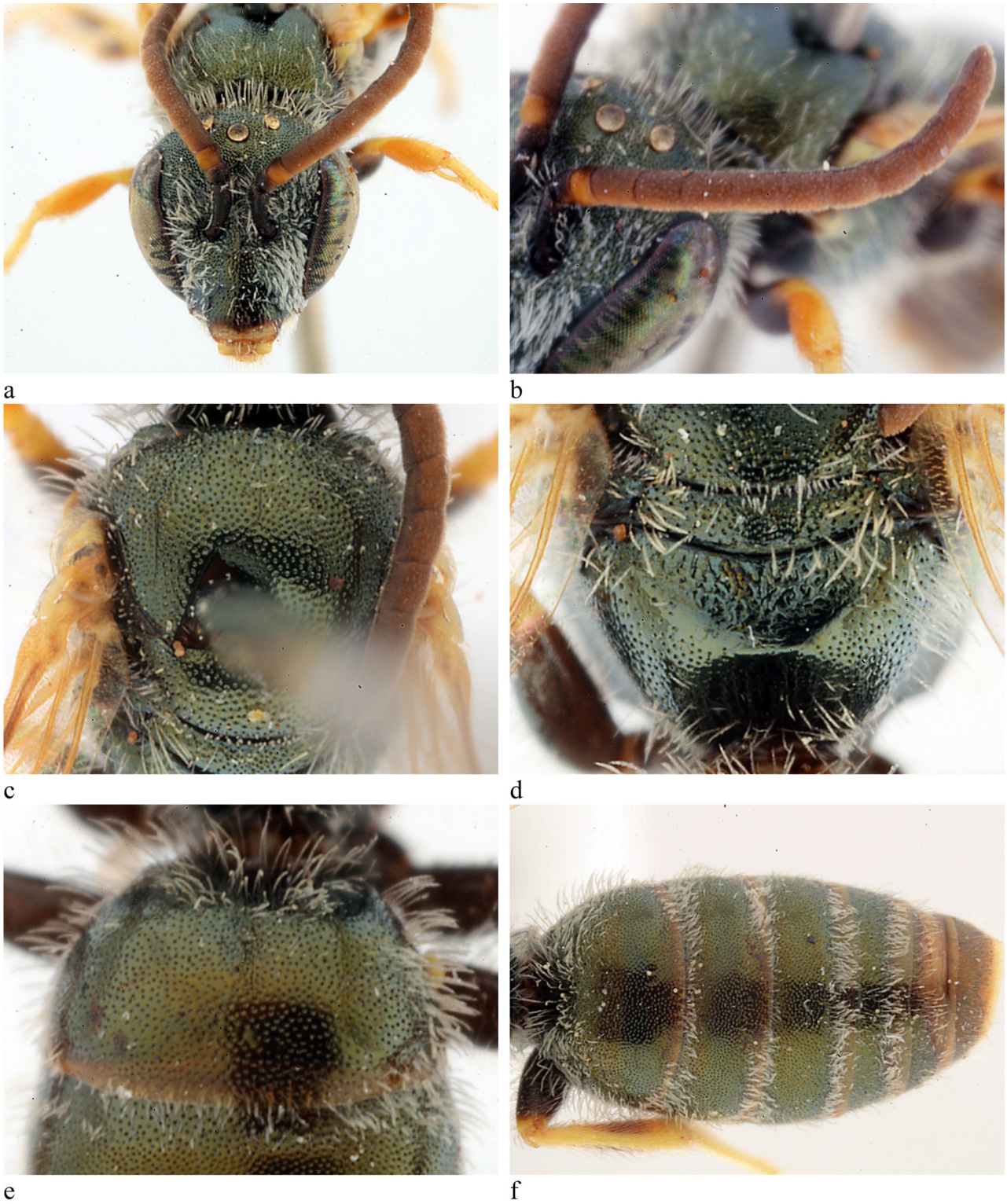


**FIGURE 6.** *Seladonia smaragdula*, male (= Form A) (Spain: Avila); a, head; b, antenna; c, scutum; d, propodeum; e, first tergum; f, metasoma.

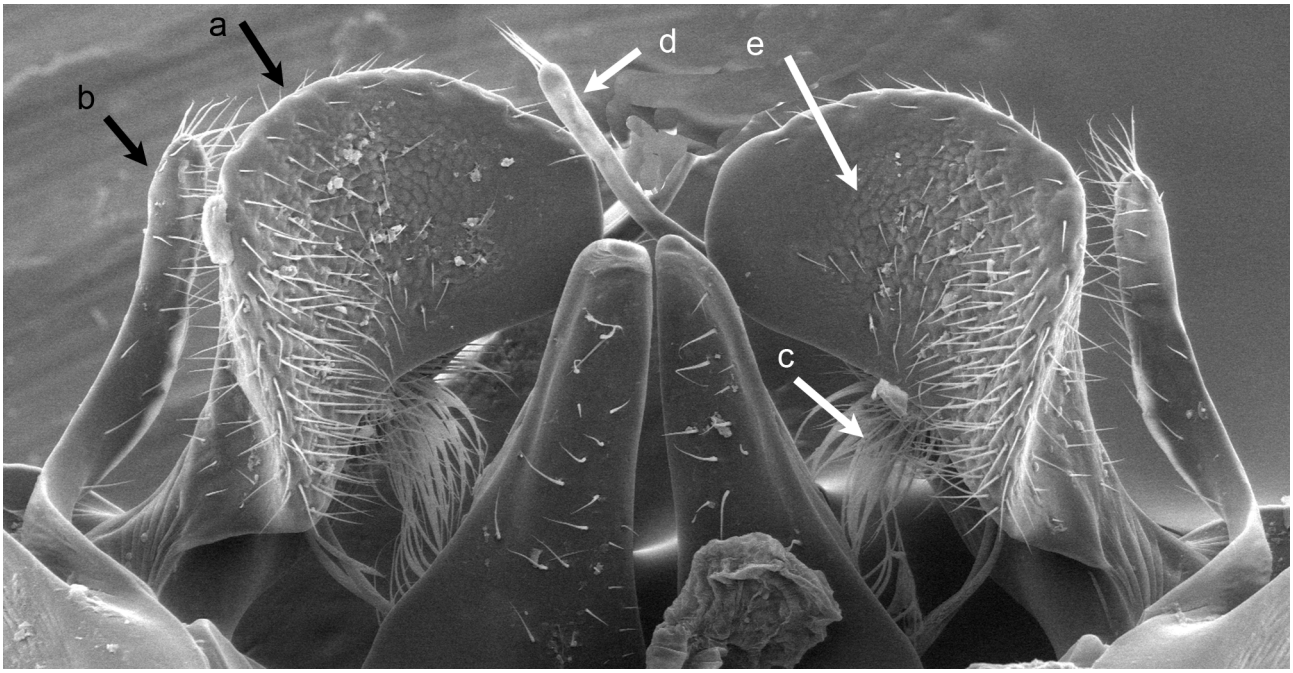


**FIGURE 7.** *Seladonia smaragdula*, male (= form A) (France, Var, Porquerolles Island), ventral view of the projections of the gonocoxites; a, large projection; b, small projection; c, tuft of setae; d, appendice; e, underplate.

**Material examined** (138 males, 3 females). PORTUGAL. Lisboa Province, Cascais, 16.IX.1960, 1♂, leg. H. Wiering (RMNHL).—Beja Province, Odemira Est, 20.IX.1960, 2♂, leg. H. Wiering (RMNHL).—Lisbon, Parque Florestal de Monsanto, 25.VII.1962, 1♂, thin dry forest, leg. J. Abraham & L. Horacsek (BMNH).

SPAIN. Madrid, Montarco, 1911, 1♂, leg. G. Mercet, col. J. Vachal (MNHNP).—Madrid, Camping Osuna near Madrid, 30.VII.1970, 1♂, leg. Ph. Pronk (RMNHL).—Madrid, Collado Mediano, Sierra de Guadarrama, 30TVL1404, 1075m, 27.VIII.2011, 1♂, leg. F.J. Ortiz-Sanchez.—Tarragona, 25 km SW Salou, 17.X.1952, 1♂, leg. B.B. de Jong & Osse (RMNHL).—Ciudad Real, Pozuelo de Calatrava, 1914, 1♂, leg. Ernest André (MNHNP).—Cordoba, Penarroya, 13.VIII.1925, 4♂, 26.VIII.1925, 2♂, leg. R. Benoist (MNHNP).—Huesca, Jaca, Pena de Oroel, 1210m, 2.VIII.1995, *Eryngium campestre*, 1♂, leg. M. Terzo (UMH).—Leon, Ferral de Bernesga, 900m, 28.VIII.1969, 1♂, leg. M.C. & G. Kruseman (RMNHL).—Avila, Brieva, 30TUL620047, 1180m, 20.VIII.2010, 1♂, leg. F.J. Ortiz-Sanchez.—Avila, Gd Parada, Debresa de Olalla, 6.VIII.2013, leg. F.J. Ortiz-Sanchez.—Avila, Dehesa de la Cogota (AV), 6.VIII.2013, 1♀, leg. F.J. Ortiz-Sanchez.—Almeria, Ermita Virgen de la Cabeza, Sierra de Maria, 30SWG7271, 4.VII.1994, 1♂, leg. F.J. Ortiz-Sanchez.—Almeria, Berchules, 1169m, 4.VIII.2014, leg. A. Pauly (RBINS).—Granada, Carco Mecina Bombaron, 20.VIII.1985, 1♂, leg. F.J. Ortiz-Sanchez.—Barcelona, Montseny, 2012, 3♀, leg. J. Bosch.

FRANCE. Pyrénées Orientales, Argelès-sur-Mer, 10.VIII.1966, 1♂, leg. Ch. Jeuniaux (FSAG).—Pyrénées Orientales, Argelès, 1–4.VII.1980, 2♂, dunes, leg. H. Wolf (OOLM).—Pyrénées Orientales, col de Banyuls, 250–500m, 12.VI.1990, 2♂, leg. H. & J.E. Wiering (RMNHL).—Pyrénées Orientales, Bocal du Tech, 18.VI.1990, 1♂, leg. H. & J.E. Wiering (RMNHL).—Gers, Laymont, "prairie sous terrain de foot", 5.IX.2010, 1♂, leg. D. Genoud.—Aude, Narbonne, 11.VIII.1975, 1♂, leg. R.L. Veenendaal (RMNHL).—Aude, Ile Sainte Lucie, 30.VIII.1910, 1♂, leg. R. Benoist (MNHNP).—Aude, Villegaihenc, Villardonnel, 14–20.VII.1980, 1♂, leg. H. Wiering (RMNHL).—Ardèche, St Thomé, Dausseron, 140m, 15–23.VII.1986, 1♂, leg. R. Wahis (FSAG).—Vaucluse, Carpentras, 13.IX.1957, 1♂, leg. J. van der Vecht (RMNHL).—Vaucluse, Cadenet, Rue Neuf, 24–27.VII.1985, 2♂, leg. H. Wiering (RMNHL).—Vaucluse, 1 km SSE Merindol, La Guarrigue, 27.VII.2004, *Eryngium campestre*, 1♂ (INRA). –Vaucluse, 3.8 km W Mallemort, Pas des Lanciers, 140m, 28.VII.2004, *Lavandula latifolia*, 1♂ (INRA).—Bouches-du-Rhône, Saint-Marc-Jaumegarde, Lac du Bimont, 19.VII.1985, 4♂, leg. H. Wiering (RMNHL).—Hautes Alpes, Vallée du Durance, 6 km SW Briançon, Prelles, 1200m, 1♂, leg. Schmidt-Egger.—Hautes Alpes, Mont Dauphin, 1000m, 31.VII–1.VIII.1981, 2♂, leg. H. Wiering (RMNHL).—Var, Gonfaron, Notre-Dame-du-Figuier, 240m, 15.IX.1979, 1♂, 27–28.IX.1984, 1♂, leg. P. Rasmont


**FIGURE 8.** *Seladonia smaragdula*, female (barcoded specimen from Barcelona); a, head; b, vertex; c, scutum; d, propodeum; e, first tergum; f, metasoma.

(FSAG).—Var, Gonfaron, 150m, 30.VII.1991, *Origanum vulgare*, 3♂, leg. M. Terzo (UMH).—Var, Gonfaron, Les Cours des Longs, 100m, 20.VII.1991, *Eryngium campestre*, 1♂, leg. M. Terzo (UMH).—Var, Bormes-les-Mimosas, 10.VIII.1983, 1♂ (FSAG).—Var, Callian, 1920, 1♂, leg. L. Berland (MNHNP).—Var, Saint Zacharie, 3.VII.1938, 1♂, leg. R. Benoist (MNHNP).—Var, Valescure, 4.VII.1968, 1♂, leg. K. Guichard (BMNH).—Var, Pignans, 25.VII.1965, 1♂, leg. J. Barbier (MNHNP).—Var, Ollioules, 15.X.1955, 1♂, leg. J. Barbier (MNHNP).—

Var, Ile de Porquerolles, 9.VIII.2007, *Malva sylvestris*, 1♂, n°P2007.1446, leg. N. Crouzet (INRA).—Var, Ile de Porquerolles, 9.VIII.2007, *Tolpis virgata*, 1♂, n°P2007.1443, leg. N. Crouzet (INRA).—Var, Ile de Porquerolles, 4.VIII.2007, *Heliotropium europaeum*, 1♂, n°P2007.1476, leg. B. Vaissière (INRA).—Alpes de Haute Provence, Annot, 2–5.VIII.1938, 1♂, 12.VIII.1938, 2♂, leg. R. Benoist (MNHNP).—Alpes de Haute Provence, Simiane-la-Rotonde, 700m, 12.IX.1999, 1♂, leg. H. Wiering (RMNHL).—Alpes Maritimes, La Napoule, 27.VI.1971, 1♂ (FSAG).—Corse, Calvi, 25–27.VIII.1971, 1♂, leg. A.C. & W.N. Ellis (RMNHL).—Alpes Maritimes, Opio near Grasse, 340m, 22.IX.1980, 1♂, leg. W. Perraudin (OOLM).—Corse, Calvi, La Figarella, 12–14.VII.1993, 2♂, leg. R. Wahis (FSAG).—Corse, Vivario, 1♂ (MNHNP).—Corse, Tattone near Vizzavona, 700m, 23.VIII.1956, 1♂, leg. Blöte & Hesselbach (RMNHL).—Corse, Ajaccio, 4–10.VI.1969, 1♂, leg. K.M. Guichard (BMNH).

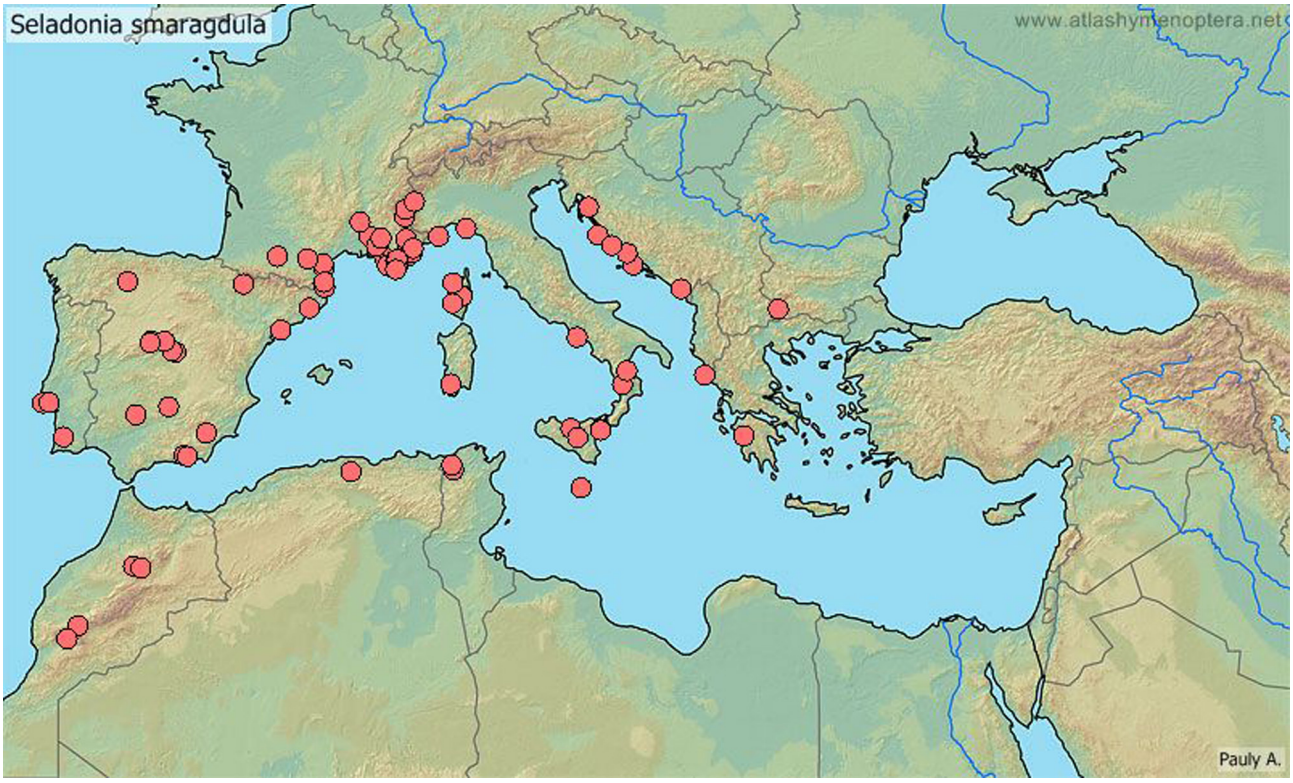


**FIGURE 9.** Geographic distribution of *Seladonia smaragdula* (males with genitalia form A and barcoded females).

ITALIA. Piemonte, 50 km W. Torino, 2 km W. Susa, 750m, 3.VIII.1995, 1♂, leg. Schmidt-Egger.—Liguria, Ortovero, 4.IX.1985, 1♂, leg. Pagliano.—Cosenza, Scalea, 1984, 1♂ (FSAG).—Cosenza Prov., Sibari, 25.VIII.1987, 1♂, leg. F. Gusenleitner (OOLM).—Lavagna, 7.VII.1962, 1♂, leg. Grunwaldt (BMNH).—Naples, 9.VIII.1966, 1♂, leg. J. Osborne (BMNH).—Sardegna, Domusnovas, 28.VIII.1982, 1♂, leg. Pagliano.—Sicily, Enna, San Giorgio di Marco, 508m, 7.VII.1993, *Eryngium campestre*, 1♂, leg. M. Terzo (UMH).—Sicily, Madonia, Serra del Contrasto, 1000m, 26.VI.1961, 1♂ (FSAG).—Sicily, Taormina, 26.VI.1941, 1♂, leg. G. Soika (BMNH).—Sicily, Taormina, Naxos, 14.V.1961, 1♂, leg. M. Schwarz.—Sicily, Naxos, 9.V.1961, 1♂, leg. J. Gusenleitner, col. M. Schwarz.—Sicilia, Taormina, Sirinatal, 6.V.1961, 1♂, 29.IX.1970, 1♂, 3.X.1970, 2♂, leg. M. Schwarz.

MALTA. Mosta, 4.IV.1965, 1♂, leg. K.M. Guichard (BMNH).

CROATIA. Hvar, 12.VI.1962, 1♂, leg. J. Gusenleitner, col. M. Schwarz.—Krk Island, Baska, 1–24.VIII.1975, 1♂, leg. J. Heinrich (OOLM).—Ugljan island, Preko, 3.VIII.1970, 1♂, leg. R. Wahis (FSAG).—Vodice, 43.76°N 15.78°E, 18.VII.1972, 1♂, leg. A. Pauly (RBINS).—Split, 26.VII.1962, 4♂, leg. H. Asbök, col. M. Schwarz.

BULGARIA. (SW) Vlahi, 14.VIII.1993, 2♂, leg. M. Halada, col. M. Schwarz.

GREECE. Corfou, 23.VII–4.VIII.1954, 3♂, leg. P.M. Verhoeff (RMNHL).—Ilia, Olympia, 4–11.VII.1979, 1♂, leg. M.C. Day, G.R. Else & D. Morgan (BMNH).

MOROCCO. High Atlas, Agaiouar, 1500m, 10.VII.1975, 1♂, leg. A.W. Ebmer.—Tizi-n-Test S., 1900m, 30.VI.1987, 14 ♂, leg. & col. M. Schwarz.—Timahdite 30 km SW, 1600m, 16.VIII.1988, 7♂, leg. K. Warncke (OOLM).—Ain Leuh 10 km S, 1750m, 15.VIII.1988, 10♂, leg. K. Warncke (OOLM).

ALGERIA. Gr Kabylia, Djurdjura, 1000m, 11.VI.1971, 1♂, leg. A. Hoffer & J. Horek (OOLM).

TUNISIA. 2 km N. Fernana, Oued Daguidour, 18.VII.1979, 1♂, leg. A.W. Ebmer.—Jendouba 20 km S, 11.VII.1979, 1♂, leg. J. Gusenleitner (OOLM).

***Seladonia gemmella* Pauly sp. nov.**
(Figures 1, 10–13, 23a,b, 24c)

*Halictus gemmellus* Blüthgen, 1924 in Schulthess, 1924: 306. Nomen nudum. Cyrenaica, ♂, ♀, col. Mader (NÖLM). Ebmer 1988: 566 (comment on nomen nudum).
*Halictus smaragdulus* Form B in Pauly & Rassel 1982: 144.

**Diagnosis.** The male of *S. gemmella* differs from that of *S. smaragdula* and *S. phryganica* by the boomerang-shaped underplate of the large projection of the gonocoxite (Figs 11,12, 23a,b). The distal part of the plate is larger than in *S. submediterranea* and *S. orientana*. The shape of the large projection is remarkably stable among specimens from Spain (Fig. 11) as far as to the Sinai in Egypt (Fig. 12). Females of *S. gemmella* cannot be distinguished from the other species of the *S. smaragdula* complex by morphological characters. However, most female specimens collected in North Africa belong to this species.

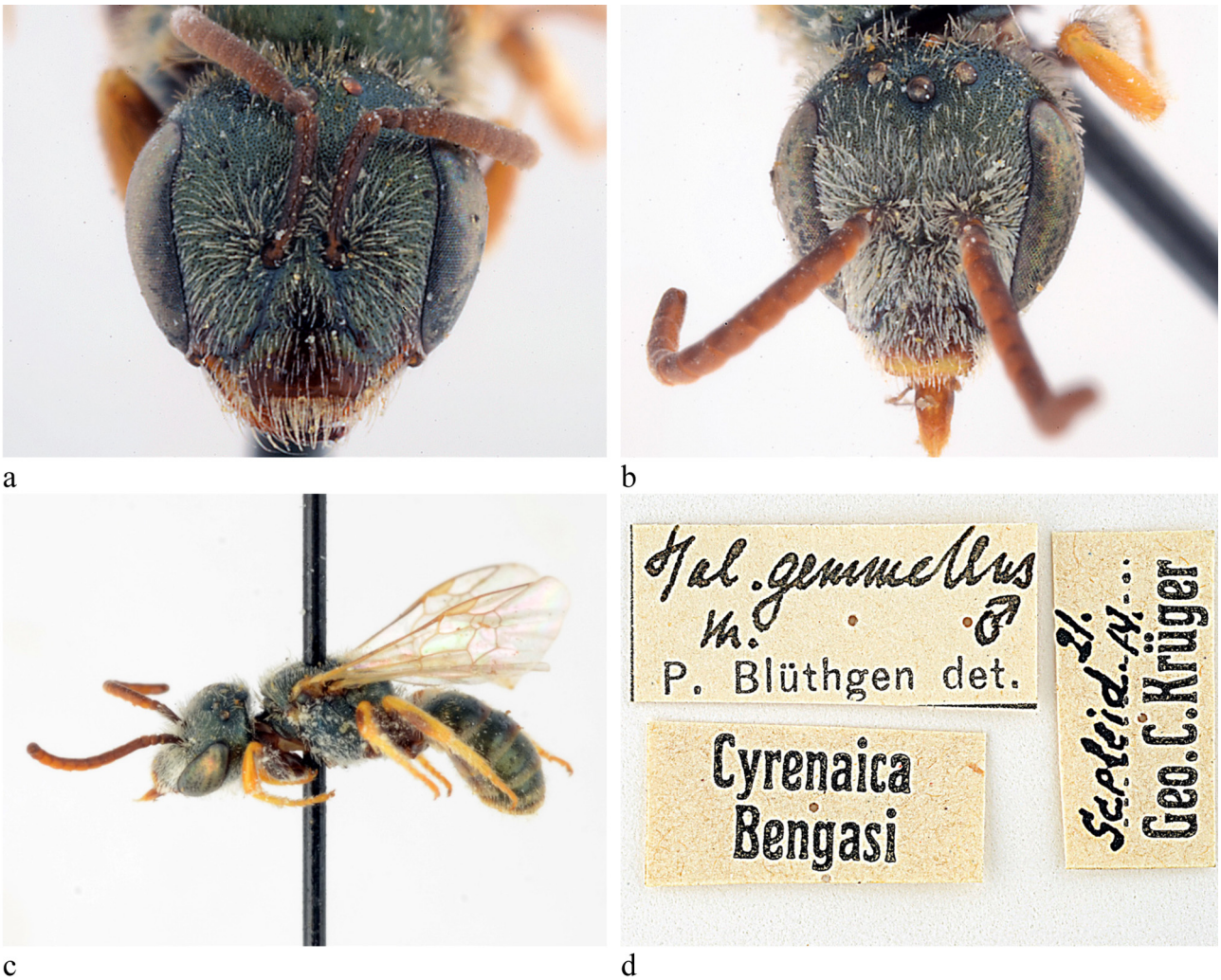


**FIGURE 10.** "*Halictus gemmellus*", nomen nudum, male and female in collection Schulthess in the Niederösterreiches landesmuseum; a, female head; b, male head; c, male habitus; d, labels of the male.

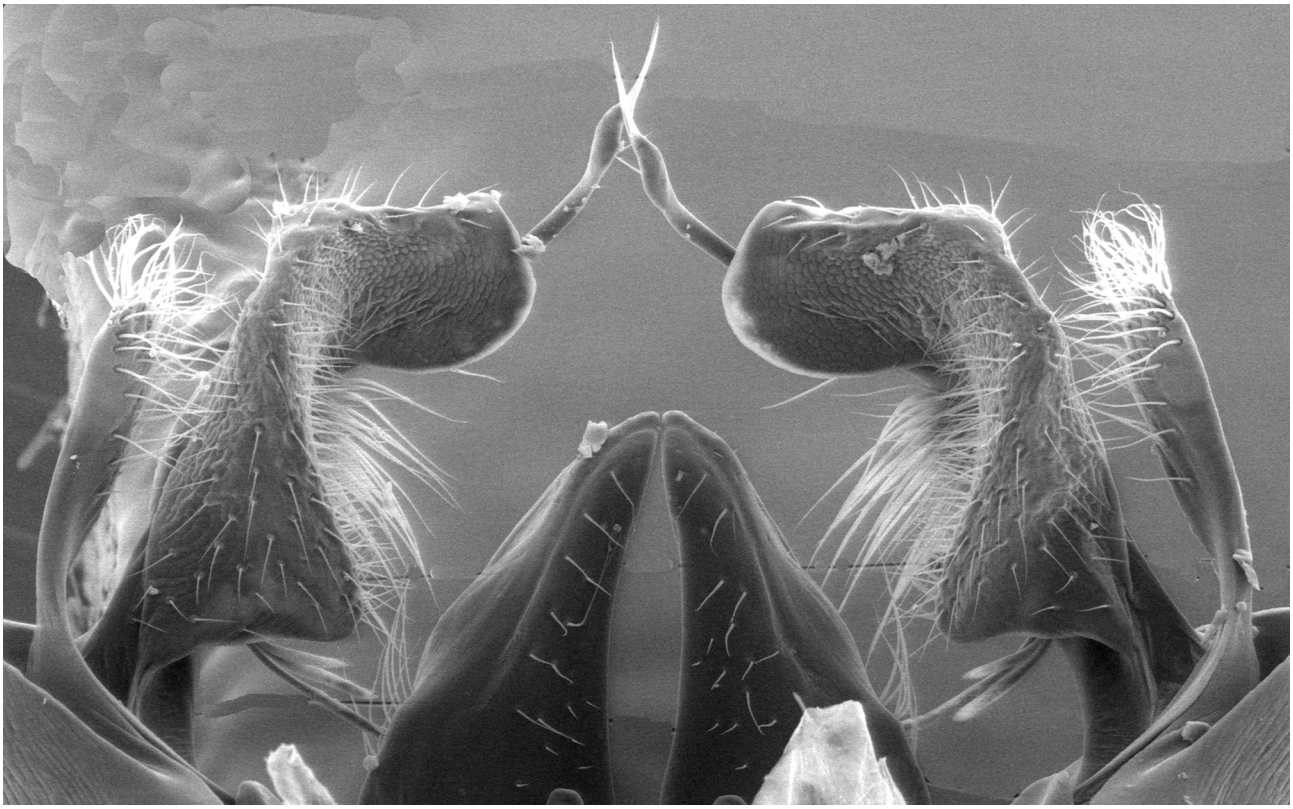

**FIGURE 11.** *Seladonia gemmella* **sp. nov.** (= form B) (Spain, Almeria, Almerimar), ventral view of the projections of the gonocoxites.

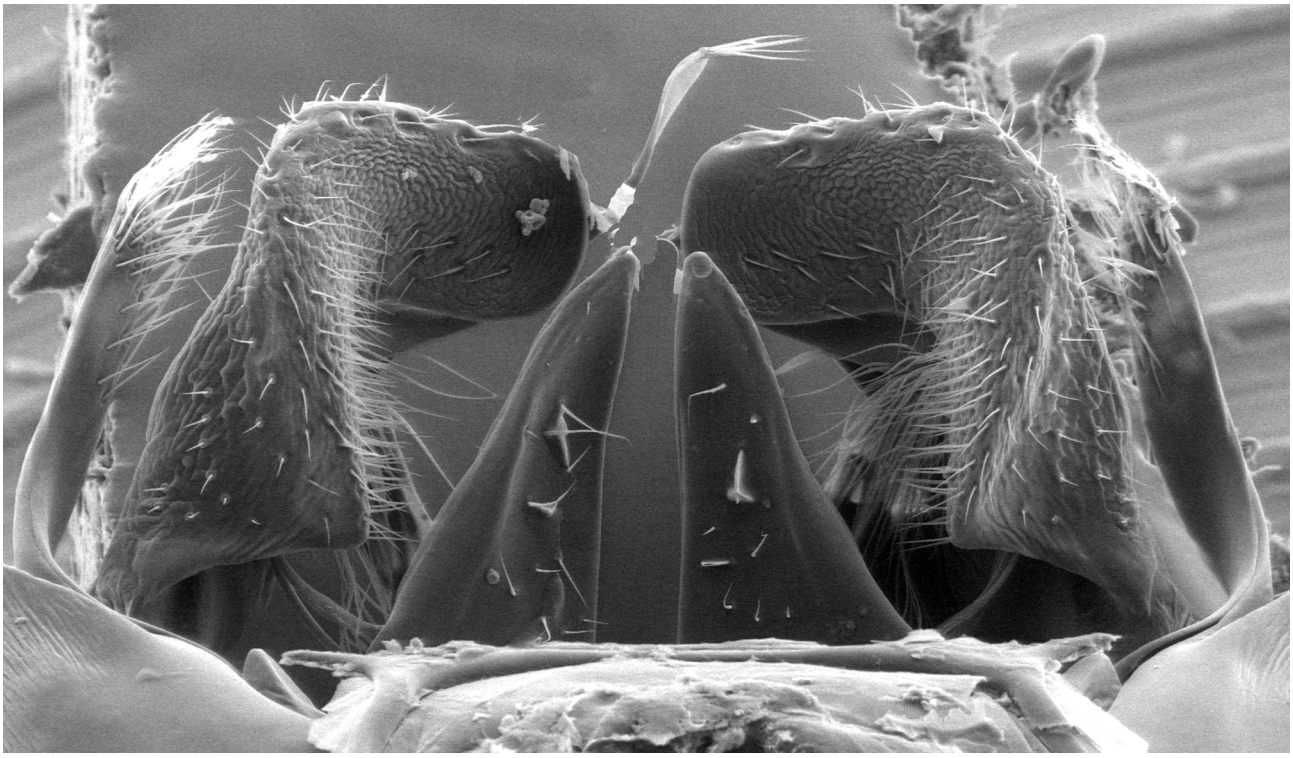

**FIGURE 12.** *Seladonia gemmella* **sp. nov.** (= form B) (Egypt, Sinai, St Katherines), ventral view of the projections of the gonocoxites.

**Description.** Male and female as described for *S. smaragdula* except as follows: underplate of the large projection of male gonocoxite boomerang-shaped, length/width of the distal plate = 1.77 (Figs 11, 12). Small projection of the gonocoxite moderately thin (Fig. 11, 12, 24c). Fourth antennal segment of the male moderately short (length/ width = 1.41).

**Variations.** Specimens from Cyrenaica in Lybia often show more blue green reflexions, the punctation is often finer (Fig. 10), and the body size is smaller (5 mm) than specimens from other regions.

**Holotype.** SPAIN, Almeria, Almerimar, coastal rocky area, 3.VIII.2014, on *Asteriscus maritimus*, 1♂, leg. A. Pauly (RBINS).

**Paratypes** (68 males, 13 females). FRANCE. Hérault, Montpellier, Castelnau, 6.IX.1955, 1♂, leg. H.C. Blöte (RMNHL).

SPAIN. Valencia, Alberique, 25.VII.1969, 1♂ (FSAG).—Alicante, Benidorm, 1.VII.1970, 1♂, *Eryngium campestre*, 16.VII.1970, 1♂, 25.VII.1970, 2♂, 10.X.1971, 1♂, leg. A. Pauly (RBINS).—Almeria, Nijar, Banco las Ninas, Cabo de Gata, 30SWF5657, 220m, 2.X.2008, 1♂, leg. F.J. Ortiz-Sanchez.—Almeria, Cuevas de Almanzora, 30SXG02, 30.IX–6.X.1992, 1♂ (leg. J.E. Belda).—Almeria, El Ejido, 80m, 30SWF1671, 23.VI.2005, 2♂, leg. F.J. Ortiz-Sanchez.—Almeria, La Aldeilla, El Ejido, 30SWF1870, 60m, 21.V.2005, 1♂, leg. F.J. Ortiz-Sanchez.—Almeria, La Mojonera, El Ejido, 30SWF2666, 2.VII.1988, 1♂, leg. F.J. Ortiz-Sanchez.—Almeria, Cuevas de Almanzora, 30SXG02, 7–13.X.1992, 1♂, leg. J.E. Belda, col. F.J. Ortiz-Sanchez.—Almeria, Sierra Alhamilla, 5.VIII.2014, 1♀, leg. A. Pauly (RBINS).—Almeria, Sorbas, 437m, 5.VIII.2014, *Foeniculum vulgare*, 1♀, leg. A. Pauly.—Almeria, Almerimar, 2.VIII.2014, *Asteriscus maritimus*, 6♂ 10♀, leg. A. Pauly (RBINS).—Malaga, Benalmadena, 23.V.1967, 1♂, leg. M.J. & J.P. Duffels (RMNHL).—Melilla, 8.VII.1961, 1♂, *Ziziphus lotus* (FSAG).—Segovia, Riofrio, S. Ildefonso, 1030m, 30TVL0328, 21.VIII.2010, leg. F.J. Ortiz-Sanchez.—Gandia, 66 km S. Valencia, Selfa, 27.VI.1989, 1♂, leg. K. Warncke (OOLM).

MOROCCO. Rabat, 1♂, leg. A. Thery (MNHNP).—Bab Azhar, 14.VII.1968, 1♂ (FSAG).—Haut Atlas, Jebel Ayachi, Mikdane, stream II N of road, 5.VIII.1963, 1♂, leg. A.C. Pont (BMNH).—Tizi-n-Test S., 1900m, 30.VI.1987, 1♂, leg. M. Schwarz.—Tizi-n-Bachkoum, 1700m, 1.VII.1987, 3♂, leg. M. Schwarz.—Haut Atlas, Agaiouar, 1500m, 10.VII.1975, 1♂, leg. J. Gusenleitner (OOLM).—Ain Leuh 10 km S, 1750m, 15.VIII.1988, 4♂, leg. K. Warncke (OOLM).—Tounfitte 24 km W, 1950m, 18.VIII.1988, 1♂, leg. K. Warncke (OOLM).—10 km N. Agadir, 30°31'N 9°38'W, 21.IV.1996, leg. J. Gusenleitner (OOLM).

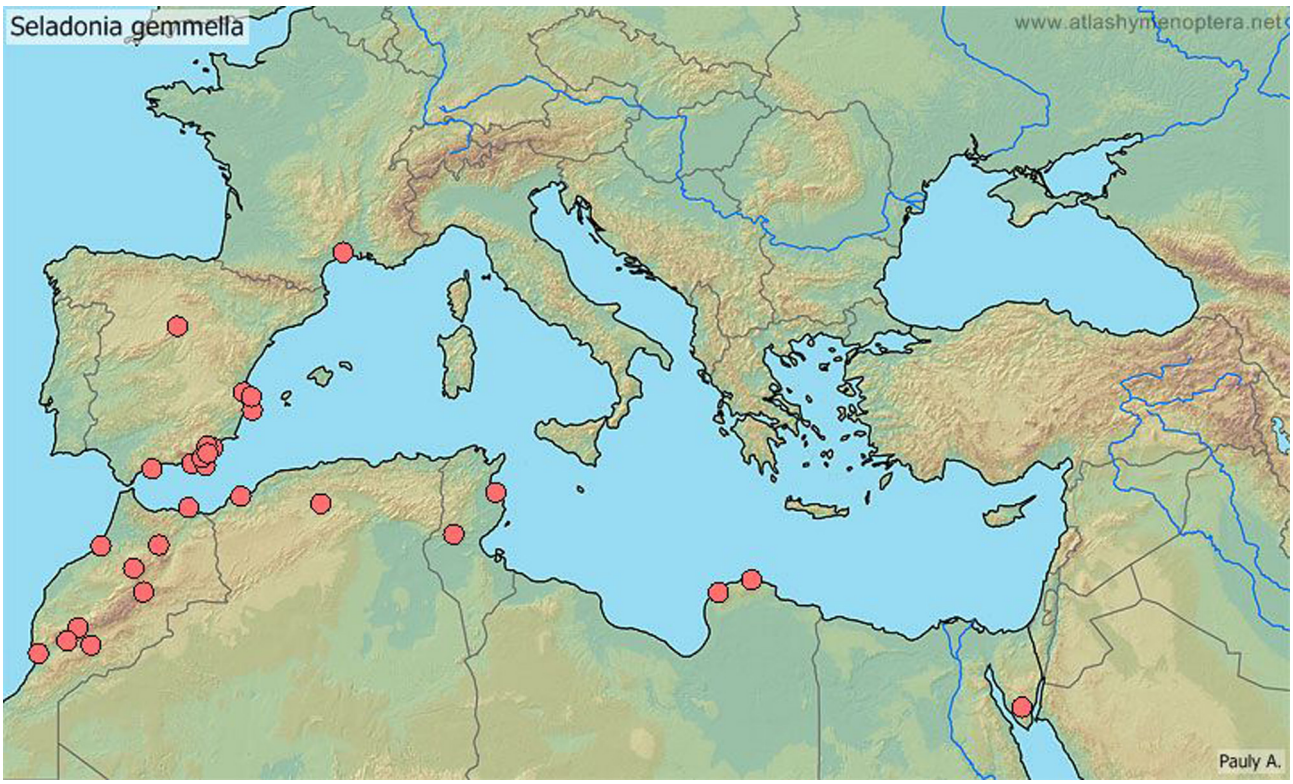


**FIGURE 13.** Geographic distribution of *Seladonia gemmella* **sp. nov.** (males with genitalia form B and barcoded females).

ALGERIA. Alger, Aïn Oussera, 29.V.1924, 1♂ (MNHNP).—Oran, le Petit Lac, 27.VI.1959, 1♂, leg. J. Barbier (MNHNP).—Oran, Misserghim, 18.VII.1959, 1♂, leg. J. Barbier (MNHNP).—Oran, Bou, 19.VII.1959, 1♂, leg. J. Barbier (MNHNP).

TUNISIA. S. Tunisia, Gafsa, "Oasengarten südl", 21.VI.1994, 2♂, leg. & col. Schmid-Egger.—Sousse, 1–9.VIII.1981, 2♂, leg. M. Wolf (OOLM).

LIBYA. CYRENAICA, Apollonia, 1.VIII.1957, 1♂, leg. K.M. Guichard (BMNH).—Cyrenaica, Bersis, W. of Tocra, 26.VII.1957, 1♂, leg. K.M. Guichard (BMNH).

EGYPT. S. Sinai, St Katherines, 28°33'N 33°56'E, V.2013, 4♀, VI.2013, 3♂, 21♀, VII.2013, 7♀, leg. O. Norfolk (UNOT).

**Distribution.** Along the Mediterranean coast from southern France (Montpellier) to southern Spain, in North Africa from Morocco to the Sinai (Fig. 13).

**Visited plants**. *Asteriscus maritimus* Moench (Asteraceae), *Eryngium campestre* L., *Foeniculum vulgare* L. (Apiaceae), *Ziziphus lotus* (L.) Lam (Rhamnaceae).

**Etymology.** The specific epithet is the diminutive of gemma, meaning "gem", and is a reference to the bright green colouration of this small species.

### *Seladonia submediterranea* Pauly sp. nov.

(Figs 14–15, 23c,d, 24e)

*Halictus smaragdulus* Form C in Pauly & Rassel 1982: 144.

**Diagnosis.** The male of *S. submediterranea* differs from that of *S. smaragdula* and *S. phryganica* by the "boomerang-shaped" underplate of the large projection of the gonocoxite (Fig. 14). It differs from *S. orientana* by the longer, not so thick and less pubescent small projection of the gonocoxite (Fig. 14, 24e). From *S. gemmella* it differs by the narrower distal plate of the large projection of the gonocoxite (length/width = 2.46) (Fig. 14).

Females of *S. submediterranea* cannot be distinguished from the other species of the *S. smaragdula* complex by morphological characters. However, female specimens collected in Central Europe belong to this species.

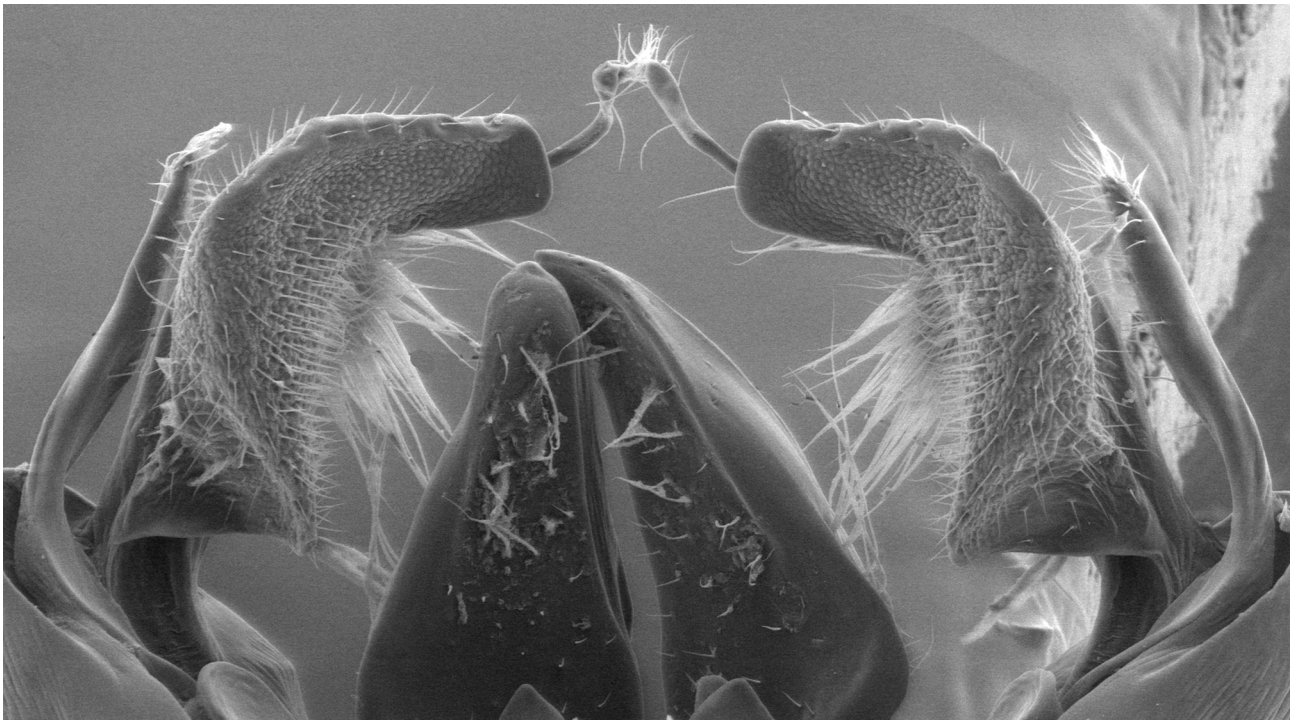

**FIGURE 14.** *Seladonia submediterranea* **sp. nov.**, male holotype (= form C) (France, Deux-Sèvres, Saint-Martin-de-Bernegoue), ventral view of the projections of the gonocoxites.

**Description.** Male and female as described for *S. smaragdula* except as follows: underplate of large projection of male gonocoxite boomerang-shaped, distal part of plate narrow. Small projection moderately thin, as long as large projection, with few setae at apex. Fourth antennal segment of the male moderately short (length/width = 1.32).

**Variations**. In Central Europe the head of both sexes is often shorter and its punctation is stronger than in other regions.

**Holotype.** FRANCE, Deux-Sèvres, Saint Martin-de-Bernegoue, 46°13'N 0°22'W, 55m, 8.VI.2011, *Centaurea cyanus*, 1♂, leg. C. Maffre & O. Rollin (Pol2011.2451) (RBINS).

**Paratypes** (67 males with genitalia dissected, 3 barcoded females from the Mediterranean area, and 67 females identified based on their geographic distribution in Central Europe).

THE NETHERLANDS. Bemelen, "Nekami groeve", 2.VII.1999, 1♀, leg. V. Lefeber (dt Franck van der Meer 2005, rev. AP) (RMNHL).

GERMANY. Sachsen-Anhalt, Wettin, 20.IV.1982, 2♀, 8.VII.1982, 1♂, 1♀ (Ebmer, 1987).—Sachsen-Anhalt, SW Reuden, 51.668°N 12.216°E, 2.VII.2014, 3♀, leg. & col. C. Schmid-Egger, 2♀ (ZSM GBOL09915), 23.VII.2014, 1♀ (ZSM GBOL09916).—Brandenburg, Hohenleipisch, 1994, 1♀ (Dathe et al. 1995).—Hessen, Viernheim, "NSG Glockenbuckel", "Binnendüne", 15.VI.1996, 1♀, 19.VII.1996, 1♀ (Tischendorf 2002).—Hessen, Frankfurt-am-Main, "Güterbahnhof", "sandige Bahnbrache, 1.VIII.1997, 1♂, 2♀, 25.VIII.1998, 1♂, 24.IX.1998, 1♂, 20.X.1998, 1♀, 26.VI.2002, 3♀ (Tischendorf, 2002).—Darmstadt, "US-Truppenübungsplatz", "Flugsandfeld", 22.VI.2002, 1♀ (Tischendorf, 2002).—Hessen, Lorch, 20.VII.2002, 1♀, 16.VIII.2003, 1♂, leg. Tischendorf (Tischendorf & Frommer, 2004).—Rheinland-Pfalz, Wöllstein (Nahegau), 14.VII.1938, 2♀, col. Blüthgen (Blüthgen, 1944).—Rheinland-Pfalz, Nahetal, Schlössbockelheim, 19.VI.1996, 1♀, leg. & col. C. Schmid-Egger, 2♀ (ZSM HYM 01815 & 01816).—Baden-Württemberg, Müllheim, VII.1937, 1♀, leg. H. Leininger (Blüthgen, 1944; Westrich 1989).—Neuenburg, 7.VIII.1927, 1♀ (Westrich 1989).—Karlsruhe, 28.IX.1982, 1♂ (Westrich & Schmidt, 1985).—"Bei der Limburg im Kaiserstuhl" (Blüthgen, 1944).—Baden-Baden (Gauss, 1967).—Baden-Würtemberg, Kaiserstuhl, Vogtsburg, Badberg, 48.08°N 7.67°E, 16.VIII.2008, leg. & col. C. Schmid-Egger.—Baden-Würtemberg, Müllheim, 47.82°N 7.62°E, 13.IV.2014, 1♀, leg. & col. C. Schmid-Egger, 1♀ (ZSM HYM 22010).

AUSTRIA. Burgenland, Neusiedl-am-See, 7–11.VIII.1967, 1♂, leg. Ebmer.

FRANCE. Manche, Carolles, Moulin de Carolles, 15.V.2004, 1♀, leg. & col. A. Livory.—Manche, Champeaux, 12.VIII.2006, *Scilla autumnalis*, 1♀, leg. & col. X. Lair.—Val d'Oise, Guiry-en-Vexin, 8.VIII.2004, 1♀, *Eryngium campestre*, leg. & col. S. Gadoum.—Yvelines, Les Mureaux, 21.VII.1996, 1♀, leg. & col. S. Gadoum.—Yvelines, Guernes, 10.VII.2003, 1♀, leg. & col. S. Gadoum (Gadoum & Pauly, 2006).—Saint-Martin-la-Garenne, 11.VI.2004, 1♀, leg. & col. S. Gadoum.—Essone, Lardy, 1♀, leg. H. Honoré (RBINS).—Val de Marne, Nogent-sur-Marne, bords de la Marne, 11.VII.1900, 1♂, leg. Fleutiaux (MNHNP).—Haut-Rhin, Niedermorschwihr, 21.VII.1938, 1♀ (MZS).—Colmar, 1♀, leg. M. Klein (Blüthgen, 1944).—Haut-Rhin, Colmar, Bollenberg, 22.VIII.1993, 1♂, leg. Stuke, col. C. Schmid-Egger.—Haut-Rhin, 21 km NNW Mulhouse, S. Westhalten, Bolenberg, 47.57°N 07.16°E, 8.VIII.1999, 1♀, leg. & col. Schmid-Egger, 1♀ (ZSM HYM 01817).—Loire Atlantique, La Bernerie-en-Retz, 8.VIII.1887, 1♀, leg. Marmottan (MNHNP).—Loire Atlantique, Montoir-de-Bretagne, Les Lévriers-Les léards, Terminal multi-vrac, 47°19'25"N 2°06'44"W, 28.IX.2012, 1♀, leg. F. Herbrecht (col. X. Lair).—Maine-et-Loire, St Rémy-la-Varenne, 1903, 1♀ (MNHNP).—Maine-et-Loire, Beaulieu-sur-Layon, RNR Pont-Barré, 47,31816°N 0,62277°W, coteau calcaire, 28.VII.2011, 1♀, 5.IX.2011, 2♀, leg. F. Herbrecht (col. Gretia & X. Lair).—Vendée, Longeville, 19.IX.1965, 1♀ (BMNH).—Nièvre, Decize, 13.VIII.1979, 2♀, 5.IX.1979, 1♂, leg. & col. H. Marion (RBINS).—Nièvre, Teinte, Sougy-sur-Loire, 23.VII.1979, 1♀, leg. H. Marion (MNHNP).—Allier, Vichy, 29.V.1874, 1♀, leg. J. Tosquinet (RBINS).—Deux-Sèvres, Vallans, 46°12'N 32°31'W, 49m, 4.VI.2011, *Torilis*/ *Anthriscus*, 1♀ (Pol2011.3297).—Deux-Sèvres, Secondigné-sur-Belle, 46°N10'W 0°20'W, 50m, 29.V.2011, *Torilis* / *Anthriscus*, 1♀, (Pol2011.3279), 30.VI.2011, *Picris echioides*, 1♀ (Pol2011.4436), *Plantago lanceolata*, 1♀ (Pol2011.4446).—Deux-Sèvres, Saint Martin de Bernegoue, 46°13'N 0°22'W, 55m, 8.VI.2011, *Centaurea cyanus*, 1♀, 1♂ (Pol2011.2470 et Pol2011.2451).—Deux-Sèvres, Belleville, 46°8'N 0°29'W, 50–100m, 23.V.2011, *Anthemis arvensis*, 1♀ (Pol2011.2092), 27.VI.2012, *Trifolium repens*, 2♀(Pol2012.1913 et Pol2012.1915), 26.VII.2012, *Ammi majus*, 1♀ (Pol2012.6917), *Daucus carota*, 2♀ (Pol2012.5211, Pol2012.5220).—Deux-Sèvres, Perigne, 46°11'N 0°16'W, 12.VI.2012, *Leucanthemum vulgare*, 1♀ (Pol2012.4703), 1♂ (Pol2012.4896).—Deux-Sèvres, Frontenay-Rohan-Rohan, 46°15'N 0°33'W, 27.VI.2012,

*Trifolium repens*, 2♀ (Pol2012.2758 & Pol2012.2759), 7.VIII.2012, *Daucus carota*, 2♀ (Pol2012.4891 & Pol2012.4892).—Deux-Sèvres, Prissé-la-Charrière, 46°9'N 0°29'W, 50–100m, 27.VI.2011, *Malva sylvestris*, 1♂ (Pol2011.3817), 2.VII.2011, *Malva sylvestris*, 1♀ (Pol2011.5089), 4.VII.2011, *Ammi majus*, 1♀ (Pol2011.5902), 24.VIII.2011, *Ammi majus*, 1♀ (Pol2011.4295), 26.VII.2012, *Crepis-Hieracium* sp., 1♀ (Pol. 2012.6383).—Deux Sèvres, Saint Symphorien, 46°15'N 0°28'W, 50–100m, 18.VII.2012, *Daucus carota*, 2♀ (Pol.2012.6685 et Pol2012.6174).—Deux-Sèvres, Brulain, 46°11'N 0°19'W, 50–100m, 23.VII.2012, *Daucus carota*, 1♀ (Pol2012.6749).—Deux-Sèvres, Granzay, 46°13'N 0°27'W, 50–100m, 25.VII.2012, *Daucus carota*, 1♀ (Pol20125773).—Deux-Sèvres, Fors, 46°14'N 0°25'W, 25.VII.2012, *Centaurea jacea*, 2♀ (Pol2012.6098 et Pol2012.6103).—Deux-Sèvres, Niort, 46°18'N 0°24'W, 47m, 1.VII.2011, *Centaurea jacea*, 1♀ (Pol2011.5549), *Origanum vulgare*, 1♀ (Pol2011.5558).—Deux Sèvres, Marigny, 46°11'N 0°24'W, 64m, 11.VII.2011, *Falcaria vulgaris*, 2♀ (Pol2011.4476 & Pol2011.4482).—Deux-Sèvres, La Foye-Monjault, 46°12'N 0°30'W, 44m, 3.IV.2011, *Torilis*/ *Anthriscus*, 1♀ (Pol2011.3671), all leg. C. Maffre/O. Rollin (INRA, RBINS).—Charente Maritime, Doeuil-sur-le-Mignon, 46°07'N 0°30'W, 50–100m, 28.VI.2012, *Inula helenium*, 1♀ (Pol2012.2839) (INRA).—Landes, Castelsarrazin, 12.VII.1972, 1♂ (FSAG).—Gers, Laymont, L'Espinette, 6.IX.2010, 1♂, leg. D. Genoud.—Gers, Laymont, Le Rumeau, 10.VIII.2010, 1♂, leg. D. Genoud.—Gers, Laymont, Ruisseau de Monès, 6.IX.2010, 1♂, leg. D. Genoud.—Gers, Mongausy, Larroucau, Sensas, 17.VIII.2010, 1♂, leg. D. Genoud.—Haute-Garonne, Casties-Labrande, bord ruisseau de Magnac, 17.VIII.2010, leg. D. Genoud.—Var, Montauroux, 29.V.1970, 1♂, leg. van der Vecht (RMNHL).—Var, Gonfaron, 150m, 30.VII.1991, *Scabiosa atropurpurea*, 1♂, leg. M. Terzo (UMH).—Var, Gonfaron, 150m, 30.VII.1991, *Origanum vulgare*, 1♂, leg. M. Terzo (UMH).—Var, Les Mayons, Bastide d'Aille, 96m, 16.IX.1987, 1♂, leg. P. Rasmont (UMH).—Bouches du Rhône, Mallemort, 16–25.VII.1984, 1♂, leg. H. Wiering (RMNHL).—Bouches du Rhône, Barbegal, 18.VIII.1994, 1♂ (RMNHL).—Pyrénées Orientales, Alenya, Etang de Canet, 1.VII.1994, 2♂, leg. H. & J. E. Wiering (RMNHL).

SPAIN. Huesca, Jaca, Pena de Oroel, 1210m, 2.VIII.1995, *Eryngium campestre*, 4♂, leg. M. Terzo (UMH).—Segovia, Gd Parada, Cerezo de Abajo, 7.VIII.2013, leg F.J. Ortiz-Sanchez.—Avila, Dehesa de la Cogota, 40°31'N 4°40'W, 6.VIII.2013, leg. F.J. Ortiz-Sanchez.—Barcelona, Montseny, 2012, n°MNLG04-72-M6, leg. J. Bosch.—Gerona, Puigcerda, 28.VII.1934, 1♂ (MNHNP).—Sevilla, Ecija, 18.IX.1952, 1♂, leg. B. De Jong et al. (RMNHL).

PORTUGAL. Porto, Leca de Palmeira, 3.VIII.1962, 1♂, low vegetation near seashore, leg. J. Abraham & L. Horacsek (BMNH).

CROATIA. Hvar Island, 10.VI.1962, 2♂, 12.VI.1962, 1♂, 15.VI.1962, 1♂, leg. J. Gusenleitner, 21.VI.1962, 1♂, leg. J. Schmied, col. M. Schwarz.

ROMANIA. Comana Vlasca, 1911, 1♂, leg. A.L. Montandon (MNHNP).—Bucarest, 1♂ (FSAG).

BULGARIA. (SW) Vlahi, 14.VIII.1993, 1♂, leg. M. Halada, col. M. Schwarz.—Prov. Burgas, Mesemvria [42°39'N 27°44'E], 12.VIII.1956, 2♂, leg. W.J. Pulawski, col. M. Schwarz.—Slncev Brjac (Slantchev Briag), 16.VII.1968, 1♂, leg. Kocourek (OOLM).

USSR. Krym, Yalta, 8.X.1985, 1♂, leg. M. Halada (OOLM).

IRAN. Mazdaran Prov., 10 km S. Chaloos, N36.51° E51.33°, 380m, 15.VI.2010, 1♂, leg. Mi Halada (OOLM).—Gilan Prov., Tulkabo near Roodbar, N36.83° E49.66°, 16.VI.2010, 3♂, leg. Mi Halada (OOLM).—Elburs, Damavand-Gebiet, Polur, 2000m, 22.VII.1977, 1♂, leg. J. Gusenleitner (OOLM).

**Material identified** (not included in the type series). ITALY. Sardinia, Macomer, 24.V.1965, leg. S. Nowitzky, col. M. Schwarz.—Sardinia, Cagliari, 10.VII.1959, 1♂, leg. H. Wolff (OOLM).

TURKEY. Ankara, 22.VI.1993, 1♂, leg. K. Denes (OOLM).—Hakkari, 1250m, südl. Beytussebap, 10.VIII.1983, 13 ♂, leg. K. Warncke (col. M. Schwarz), 11♂ (OOLM).—Artvin, Damar near Murgul, 1–3.VII.1997, 1♂, leg. P. Prudek & M. Riha (OOLM).—Bayburt 10 km N, Gümüshane, 1600m, 22.VIII.1991, 1♂, leg. K. Warncke (OOLM).

**Distribution.** Central Europe. It occurs from central Spain to southern Germany and the Danubian valley, to the East in northern Iran (Fig. 15).

**Host plants.** Specimens of this species have been collected on Apiaceae, Asteraceae and some other families of plants: *Ammi majus* L., *Anthriscus* sp., *Daucus carota* L., *Eryngium campestre* L., *Falcaria vulgaris* Bernh., *Torilis* sp. (Apiaceae), *Anthemis arvensis* L., *Centaurea cyanus* L., *Centaurea jacea* L., *Crepis* sp., *Hieracium* sp., *Inula helenium* L., *Leucanthemum vulgare* Lam., *Picris echioides* L. (Asteraceae), *Scabiosa atropurpurea* L. ("Dipsacaceae", now Caprifoliaceae), *Origanum vulgare* L. (Lamiaceae), *Malva sylvestris* L. (Malvaceae), *Trifolium repens* L. (Fabaceae), *Scilla autumnalis* L. (Liliaceae), *Plantago lanceolata* L. (Plantaginaceae).

**Etymology.** The specific epithet refers to the submediterranean distribution of this species.

**Comments**. This species is found in Central Europe. Specimens from Iran have been barcoded and shared the same barcode as the Central European specimens. Identification of specimens from Turkey and Sardinia need to be confirmed by barcoding. Specimens from NE Turkey differ by having a larger "boomerang-shaped" underplate of the large projection of the gonocoxite and they may constitute a subspecies or another cryptic species. They were not been included in the type series.

We were able to examine a few specimens of *S. submediterranea* and *S. orientana* from the large islands of Sardinia and Sicily. Because no fresh specimens were available for barcoding, we tentatively used the morphology of the small projection of the gonocoxite to include the specimens from Sardinia in *S. submediterranea* and one specimen from Sicily in *S. orientana*.

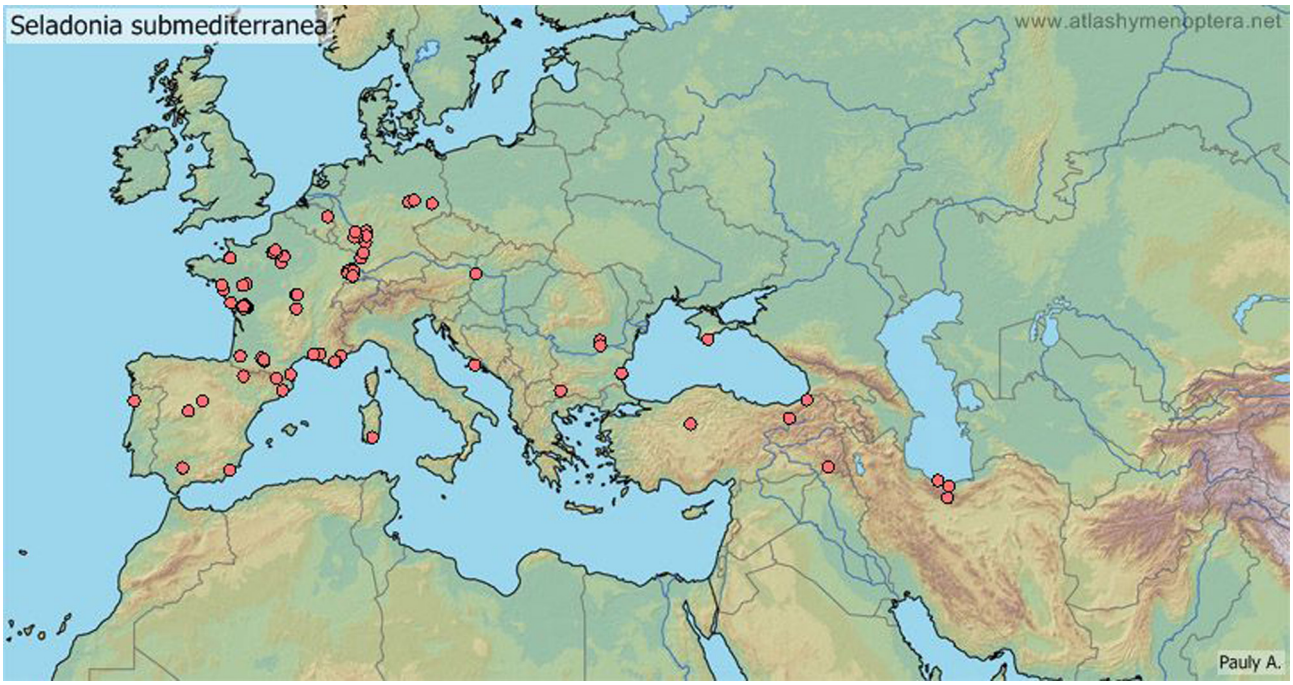


**FIGURE 15.** Geographic distribution of *Seladonia submediterranea* **sp. nov.** (males with genitalia form C, barcoded females from Southern Europe and females from Central Europe).

***Seladonia orientana* Pauly & Devalez sp. nov.**
(Figs 16–17, 23e,f, 24f)

*Halictus smaragdulus* form D in Pauly & Rassell 1982: 144.

**Diagnosis**. The male of *S. orientana* differs from that of *S. smaragdula* and *S. phryganica* by the boomerang-shaped underplate of the large projection of the gonocoxite (Figs 16, 23e,f). It differs from *S. submediterranea* and *S. gemmella* by the thick, short, and more pubescent small projection of the gonocoxite (Figs 16, 24f). The female of *S. orientana* cannot be distinguished from the other species of the *S. smaragdula* complex by morphological characters. Because this species overlaps with all others (except *S. cretella*), the geographic distribution cannot be used to associate the female of this species.

**Description**. Male and female as described for *S. smaragdula* except as follows: underplate of large projection of male gonocoxite boomerang-shaped, distal plate very narrow at apex (length/width from 2.88 to 4.72) (Figs 16, 23e,f). Small projection of gonocoxite thick and short, three quarts as long as large projection, apex with numerous long setae (Fig. 24f). Fourth antennal segment of the male relatively short (length/width = 1.12–1.14).

**Variations**. In populations from Central Asia (Tajikistan, Kazakhstan) the underplate of the large projection is narrower at apex and the small projection is even shorter and thicker than those of the European specimens.

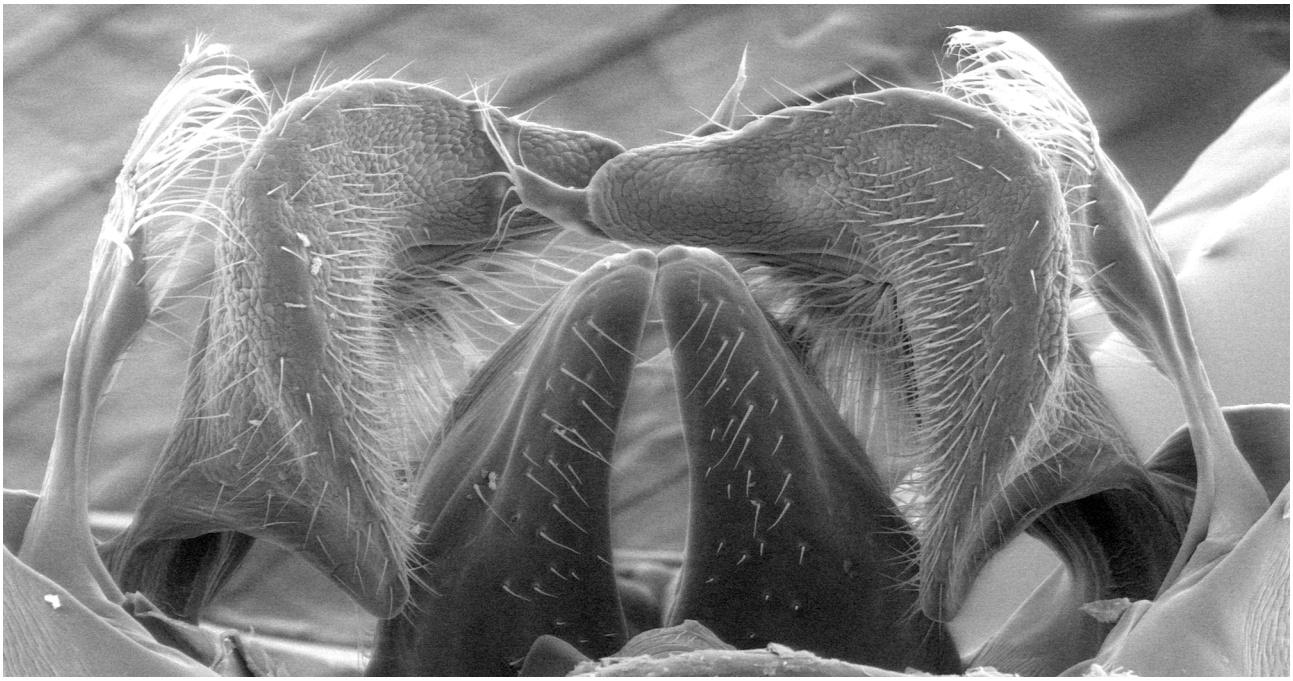

**FIGURE 16.** *Seladonia orientana* **sp. nov.**, male (= form D) (Greece, Samothrace Island, Dafnes), ventral view of the projections of the gonocoxites.

**Holotype**. CROATIA, Ugljan island, Preko, 100m, 22.VII.1989, *Eryngium campestre,* 1♂, leg. R. Wahis (RBINS).

**Paratypes** (61 males, 4 barcoded females). SPAIN. Cadiz, Sendero Torreon, Sierra Grazalema (Benamahoma), 30STF8270, 870m, 8.VII.2011, 1♂, leg. F.J. Ortiz-Sanchez.

ITALY. Valle d'Aosta, 6 km W Aosta, St Pierre, 800m, 16.V.1998, 1♀, leg. C. Schmid-Egger (ZSM).—Valle d'Aosta, St Pierre, 45.716°N 7.235°E, 700m, 20.VII.2012, 2♀, leg. C. Schmid-Egger (ZSM).—Sicily, Enna, Assoro, Sparagio, 348m, *Origanum vulgare*, 1♂, leg. M. Terzo (UMH).

CROATIA. Ugljan island, Preko, 100m, 2.VIII.1970, 1♂, 8.VIII.1970, 1♂, 22.VII.1989, 1♂, leg. R. Wahis (FSAG).—Omis, near Split, 3.IX.1970, 1♂ leg. OWR (BMNH).

GREECE. Makedonia, Edessa, 23.VIII.1965, 2♂, leg. Blommers (RMNHL).—Makedonia, Kastoria, 40°33'N 21°15'E, 760m, 23–25.VII.1963, 1♂ (RMNHL).—Makedonia, Chalkidiki, E and SW Arnaia, 40°30'N 23°36'E, 120–400m, 26–28.VII.1978, 1♂, H. & U. Aspöck et al., col. A. Ebmer.—Central Macedonia, Pieria, Mnt. Olympus, 40.1052N 22.4822E, 16.VIII.2013, *Rubus sp.*, 1♂ (UAEG n°091193), leg. K. Minachilis (UAEG).—Peloponnisos, 2 km N. Dhimitsana, 37°36'N 22°03'E, 900m, 20.VIII.1979, 1♂, leg. E. & J. Hüttinger, col. Ebmer.—Mt Likeo, 1300m, 25.VIII.1990, 1♂, leg. K. Warncke (OOLM).—Thessalia, Portaria, Pelionpass, 39°23'N 23°02'E, 675–825m, 29–31.VII.1963, 1♂ (RMNHL).—Sparta 30 km W, Gorani, 1000m, 27.VIII.1990, 1♂, leg. K. Warncke (OOLM).—Evros, Dadia, 8 km W of Provatonas, 41.0398N 26.1699E, 11–13.VIII.2012, 1♂ (UAEG n°036962), leg. P. Tsalkatis (UAEG). Evros, Dadia, 8 km W of Kila, 40.9819N 26.0643E, 10–12.VIII.2012, 1♂ (UAEG n°034405), leg. P. Tsalkatis (UAEG).—Samothrace, Panagia, 40.4055N 25.5818E, 6.VII.2012, *Eryngium campestre*, 1♂ (UAEG n°044405), 1♀ (UAEG n°044434), leg. M. de Courcy (UAEG).—Samothrace, Dafnes, 40.4151N, 25.5518E, 4–6.VII.2012, *Heliotropium europaeum*, 1♂ (UAEG n°043840), 1♂ (UAEG n°043813), leg. M. de Courcy (UAEG).—Lesvos, Ag. Marina, 39.0633N 26.5843E, 5.X.2014, *Dittrichia viscosa*, 1♂ (UAEG n°124598), leg. J. Devalez (UAEG).—Lesvos, Parakoila, 39.1781N 26.1378E, 5–9.VI.2012, 1♂ (UAEG n°008560), leg. A. Chroni (UAEG).—Lesvos, Mytilene, 39.0816N 26.5754E, 10.IX.2014, *Foeniculum vulgare*, 1♂ (UAEG n°124109), leg. J. Devalez (UAEG).—Lesvos, 3.8 km SSE Agiasos, 39°3'17"N 26°23'50"E, 760m, Chestnut Forest, 8.X.2005, 1♂ (UAEG n°0023702), leg. T. Petanidou (UAEG).—Corfou, 23.VII–4.VIII.1954, 5♂, leg. P.M. Verhoeff (RMNHL).

TURKEY. Constantinople (Istanbul), 1919, 4♂, leg. J. De Gaulle (MNHNP).—Eskisehir, Inönu, 800m, 1.VIII.1991, 2♂, leg. K. Warncke (OOLM).—Ankara 10 km S, 1100m, 26.VIII.1991, 2♂, leg. K. Warncke

(OOLM).—Tarsus, 29–31.V.1965, leg. J. Gusenleitner, col. M. Schwarz.—Konya, N Taskent, 1800m, 6.VIII.1991, 1♂, leg. K. Warncke (OOLM).—Mut, 23.V.1970, 1♂, leg. J. Gusenleitner (OOLM).—Hakkari, 1250m, südl. Beytussebap, 10.VIII.1983, 1♂, leg. K. Warncke (col. M. Schwarz), 4♂ (OOLM).—Hakkari, Beytussebap 22 km S, 1200m, 26.VI.1985, 1♂, leg. E. Schacht (OOLM).—Hakkari, Semdinli, 1350m, 9.VIII.1985, 1♂, leg K. Warncke, col. M. Schwarz.—Adana Province, Feke env., 21–24.VII.2000, 2♂, leg. M. Oboril (OOLM).—Harbie, Antakya, 17.VI.2000, 1♂, leg. M. Halada (OOLM).—Sirnak Prov., 25 km NW Sirnak, 37.67°N 42.31°E, 1600m, 23.VI.2010, 9♂, leg. Mi Halada (OOLM).

KAZAKHSTAN. (Mer.) Georgievka, 43.2°N 75.6°E, 16.VI.1995, 1♂, leg. J. Halada, col. M. Schwarz.—Alma Ata, 35 km zap. Aksaj, 16.VII.1981, 3♂, leg. Kocourek (OOLM).

TAJIKISTAN. Pendzikend 20 km W, Resen Pojom, 29.VI.1981, 3♂, leg. Kocourek (OOLM).

IRAN. Fars, Daria Namak, "steppo presso lago salato", 27 km E Shiraz, 7.VII.1965, 1♂, leg. G. Soika (MNHNP).—Elburs, 50 km S ("90 km strasse") Chalus, 2800m, 26.VII.1977, 2♂, leg. J. Gusenleitner (OOLM).—Elburs, Damavand-Gebiet, Polur, 2000m, 23.VII.1977, 1♂, leg. J. Gusenleitner (OOLM).

**Distribution.** Italy, Greece, Turkey, Iran, Tajikistan, and Kazakhstan. A specimen from Cadiz in Southern Spain bears the same short, small gonostylus and it may represents an isolated population (Fig. 17).

**Visited plants**. Recorded on *Dittrichia viscosa* (L.) Greuter (Asteraceae), *Foeniculum vulgare* L., *Eryngium campestre* L. (Apiaceae), *Heliotropium europaeum* (Boraginaceae) and *Rubus* sp. (Rosaceae).

**Etymology.** The specific epithet refers to the oriental distribution of this species. The more correct Latin adjective "*orientalis*" is already being used.

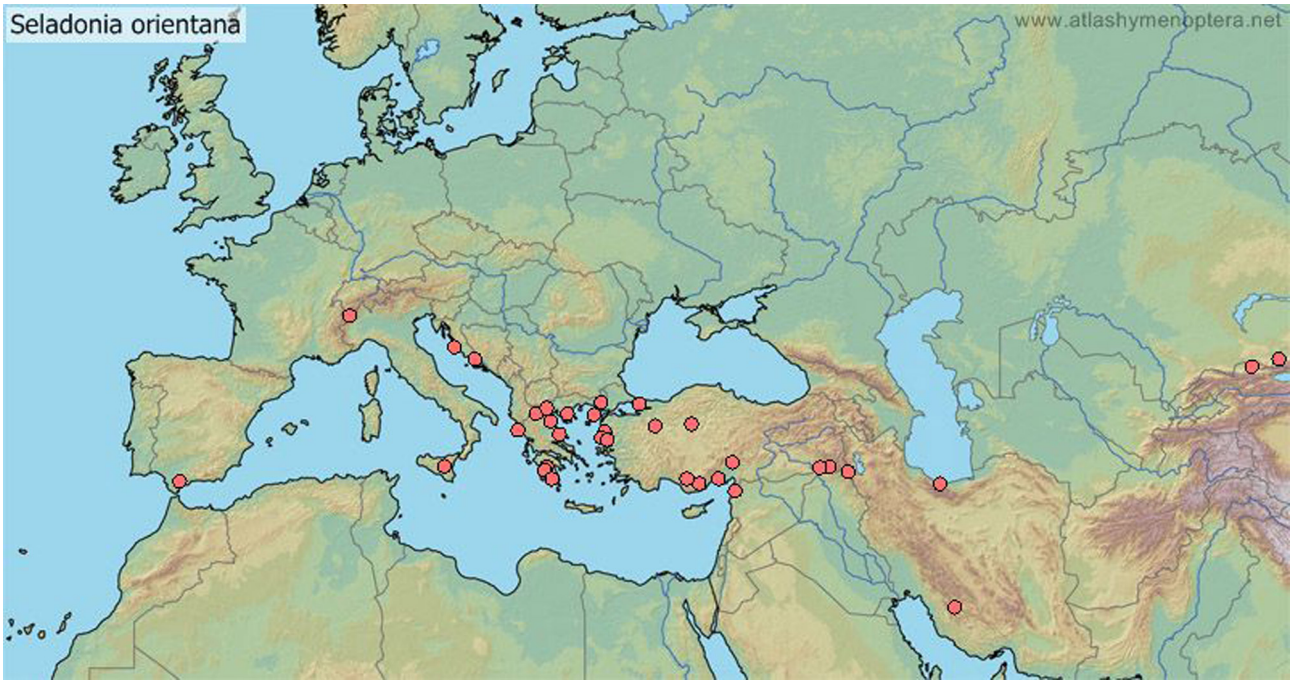


**FIGURE 17.** Geographic distribution of *Seladonia orientana* **sp. nov.** (males with genitalia form D and barcoded females).

### ***Seladonia phryganica*** **Pauly & Devalez sp. nov.**
(Figs 18–19, 22c,d, 24b)

*Halictus smaragdulus* Form E in Pauly & Rassel 1982: 144.

**Diagnosis**. Compared to *S. smaragdula*, the male of *S. phryganica* has a more reduced underplate of the gonocoxite, with its inner side being more concave (Figs 18, 22c,d). Both species are geographically separated; *S. smaragdula* occurs in the West Mediterranean while *S. phryganica* in the East Mediterranean (Figs. 9, 19). The male of *S. phryganica* can be easily separated from the sympatric *S. orientana* by the very thin, small projection of the gonocoxite (Figs 18, 22c,d, 24b). Such a small projection is short and thick in *S. orientana* (Fig. 24f). In Crete

and Karpathos, the male of *S. phryganica* can be separated from that of *S. cretella* by its shorter fourth antennal segment (length/width ranges from 1.05 to 1.17 in *S. phryganica* and from 1.44 to 1.53 in *S. cretella*). The males of *S. gemmella* and *S. submediterranea* can be differentiated by the more boomerang-shaped underplate of the large projection of the gonocoxite. They can be separated also by their geographic distribution, except in Greece and Turkey where *S. submediterranea* **sp. nov.** also occurs.

Females of *S. phryganica* cannot be distinguished from the other species of the *S. smaragdula* complex by morphological characters. Specimens collected on Aegean Islands belong to this species, except on Lesvos where *S. phryganica* is sympatric to *S. orientana*.

**Description**. Male and female as described for *S. smaragdula* except as follows: underplate of large projection of male gonocoxite subtriangular, inner side of plate concave (Figs 18, 22c,d, 24b). Small projection of gonocoxite very thin, with few apical setae (Fig. 24b). Fourth antennal segment of the male short (length/width = 1.05–1.17).

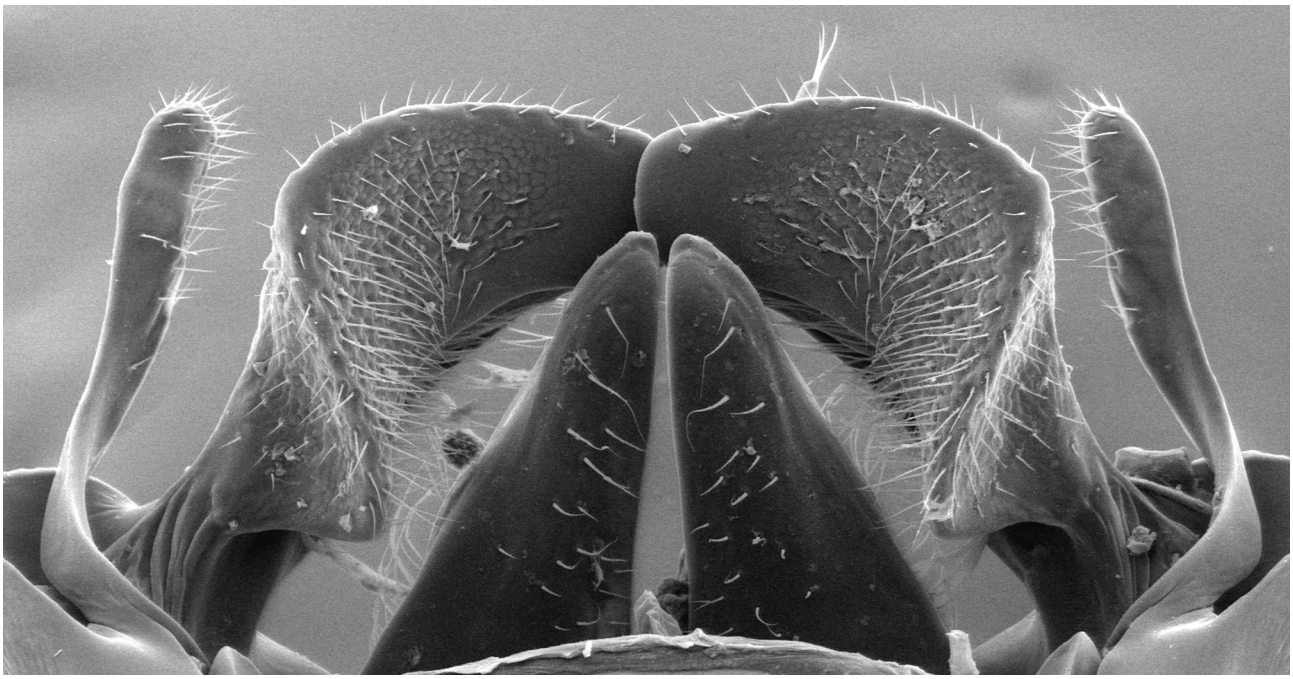

**FIGURE 18.** *Seladonia phryganica* **sp. nov.**, male (= form E) (Greece, Crete, Iraklio). Ventral view of the projections of the gonocoxites.

**Holotype**. GREECE, Attiki, Dafni, 10 km W Athens, 1.VIII.1991, Malaise trap in phrygana, 1♂, leg. Th. Petanidou & G. Priebe (RBINS).

**Paratypes** (75 males, 10 barcoded females). BULGARIA. Prov. Burgos, Mesemvria, 12.VIII.1956, 1♂, leg. W.J. Pulawski, col. M. Schwarz.—Melnik, 16–22.VI.1987, 1♂, leg. J. Halada (OOLM).

GREECE. Attiki, Dafni, 10 km W Athens, Malaise trap in phrygana, 1.VIII.1991, 1♂, 5.VIII.1991, 1♂, 15.VII.1991, 1♂, 16.IX.1991, 2♂, 26.IX.1991, 1♂, 30.IX.1991, 1♂, 27.VII.1992, 1♂, leg. Th. Petanidou & G. Priebe (RMNHL).—Portaria, Pelionpas, 39°23'N 23°02'E, 675–825m, 29–31.VII.1963, 1♂ (RMNHL).—Lakonia, 5 km W Sparti, 26.IX.1962, 1♂ (RMNHL).—Lakonia, 10 km W Sparti, 800–1000m, 28.IX.1962, 1♂ (RMNHL).—Thessalia, Kalambaka, hillside meadow, 17–20.VII.1979, 1♂, leg. M.C. Day et al. (BMNH).—Thessalia, Kastrack, 39°47'N 21°31'E, 320m, 13.VI.1988, 2♂, leg. Vogtenhb (OOLM).—Thessalia, Kalambaka, hillside meadow, 14–20.VII.1979, 2♂, leg. M.C. Day, G.R. Else & D. Morgan (BMNH).—Trikala, 12 km W Kalambaka, 13–14.VI.1988, 1♂, leg. J. Tiefenthaler (OOLM).—Chalkidiki, Sithonia, Sikia, 23.VIII.1978, 3♂, leg. K. Warncke (col. M. Schwarz), 7.IX.1986, 1♂ (OOLM).—Mykene, 24.VII.1971, 1♂, leg. M. Schwarz.—Peloponnese, Alt-Korinth, 1.VI.1984, leg. M. Schwarz.—Evros, Dadia, Lefkimmi, 41.0317N 26.1795E, 11–13.VIII.2012, 1♂ (UAEG n°036781), 1♂ (UAEG n°045537), leg. P. Tsalkatis (UAEG).– Evros, Dadia, 3 km NW of Kila, 40.9957N 26.1226E, 14–16.VII.2012, 1♂ (UAEG n°033070), 1♂ (UAEG n°033959), 20–22.IX.2012, 1♂ (UAEG n°045326), 21–23.IX.2012, 1♂ (UAEG n°046348), 11–13.VIII.2012, 1♂ (UAEG n°038958), 21–23.VIII.2012, 1♂ (UAEG n°046238), leg. P. Tsalkatis (UAEG).—Crete, Iraklion 7 km W, 28.X.1972, 1♂, leg. A.C.

& W.N. Ellis (RMNHL).—Crete, Levka Ori, Xyloscalo, 1200m, 26.VII.1980, Thymus sp., 1♂, leg. A.W. Ebmer.—Crete, Levka Ori, "Kallergi Hütte", 1400–1600m, 29.VII.1980, 1♂, leg. A.W. Ebmer.—Crete, Dikti Oros, Potamies, 200m, 2.VIII.1980, 2♂, leg. A.W. Ebmer.—Crete, Knossos, 23.VII.1980, 1♂, leg. A.W. Ebmer.—Crete, Iraklio Province, Heraklion, 35.3383N 25.1234E, 4.VIII.2013, *Glebionis coronaria*, 1♀ (UAEG n°081083), 1♂ (UAEG n°081084) 1♂ (UAEG n°081085) 1♂ (UAEG n°081086), leg. J. Devalez (UAEG).—Crete, Koumas, Asprouliani, 30 km W. Rethymnon, 4.X.2003, 1♂, leg. E. Scheuchl (col. E. Scheuchl).—Crete, Kolimbari, 30 km W. Chania, 4.X.2001, 1♂, leg. E. Scheuchl (col. E. Scheuchl).—Crete, Maleme, 25 km W Chania, 5.X.2001, 1♂, leg. E. Scheuchl (col. E. Scheuchl).—Karpathos, Avlona, 35.7689N 27.1849E, 8.VI.2012, 1♂ (UAEG n°033722), 1♂ (UAEG n°033857), 1♂ (UAEG n°033763), leg. T. Petanidou (UAEG).—Karpathos, Airport, 35.4309N 27.1502E, 7–9.VI.2012, 1♂ (UAEG n°021558), leg. T. Petanidou (UAEG).—Santorini, Ag. Fanourios Dune, 36.4781N 25.3995E, 8–10.V.2013, 1♂ (UAEG n°081765), 1♂ (UAEG n°081827), 1♂ (UAEG n°081832), 1♂ (UAEG n°081848), 1♂ (UAEG n°081854), 1♂ (UAEG n°081874), 1♂ (UAEG n°081875), leg. T. Petanidou (UAEG).—Santorini, Akrotiri-Faros, 36.3569N 25.3616E, 8–10.VI.2013, 1♂ (UAEG n°085553), leg. T. Petanidou (UAEG).—Anafi, Vagia, 36.363N 25.7438E, 15–17.VI.2013, 1♂ (UAEG n°083654), leg. T. Petanidou (UAEG).—Anafi, Helicodrome, 36.3565N 25.7736E, 15–17.VI.2013, 1♂ (UAEG n°082672), 1♂ (UAEG n°082723), leg. T. Petanidou (UAEG).—Anafi, Zoodohos Pigi, 36.3581N 25.8303E, 16.VI.2013, *Foeniculum vulgare*, 1♀ (UAEG n°086459), leg. T. Petanidou (UAEG).—Naxos, Fragma, 37.132N 25.4398E, 16–18.VI.2012, 1♀ (UAEG n°030851), leg. I. Vavitsas (UAEG).—Syros, Kambos, 37.4949N 24.9148E, 2–4.V.2013, 1♀ (UAEG n°093084), leg. I. Vavitsas (UAEG).—Ios, Archaeological Site of Skarkos, 36.7315N 25.2836E, 10.VIII.2013, 1♂ (UAEG n°081256), leg. T. Petanidou.—Ios, Ag. Theodoti, 36.7538N 25.3252E, 15–17.V.2013, 1♂ (UAEG n°080193), leg. T. Petanidou (UAEG).—Ios, Kambos, 36.7518N 25.2921E, 16.V.2013, *Opopanax hispidus*, 1♂ (UAEG n°087564), leg. T. Petanidou (UAEG).—Ios, Epano Kampos, 36.742N 25.2967E 20.VI.2013, *Vitex agnus-castus*, 1♂ (UAEG n°095888), 1♂ (UAEG n°095896), 1♂ (UAEG n°095905), 1♀ (UAEG n°095879), leg. T. Petanidou (UAEG).—Lesvos, Mytilene, 39.0843N 26.5687E, 3.X.2013, *Dittrichia viscosa*, 1♀ (UAEG n°092353), leg. J. Devalez (UAEG).—Lesvos, Thermi, 39.1814N 26.4939E, 5.VIII.2012, *Capparis spinosa*, 1♂ (UAEG n°0041450), leg. G. Nakas (UAEG).—Chios, Ag. Georgios Sikousis, 38.3084N 26.039E, 25–27.VI.2013, 1♂ (UAEG n°071253), leg. G. Nakas (UAEG).—Pieria, Litochoro, 40.1043N 22.4935E, 9.VIII.2013, *Mentha* sp., 1♂ (UAEG n°081057), leg. J. Devalez (UAEG).—Lesvos, Sigri, 39.2274N 25.8584E, 26–29.V.2012, 1♂ (UAEG n°011055), leg. G. Nakas (UAEG).—Sifnos, Ag. Anna, 36.9692N 24.7058E, 15.VI.2011, 1♀ (UAEG n°095384), leg. E. Papas (UAEG).—Thasos, Potos, 40.613N 24.6195E, 23.V.2012, *Sedum* sp., 1♀ (UAEG n°043556), leg. M. de Courcy (UAEG).—Kea, Poisses, 37.581N 24.281E, 27.VI.2013, *Centaurea spinosa*, 1♀ (UAEG n°086766), leg. T. Petanidou (UAEG).—Iraklia, 2 km S of Livadi, 36.8289N 25.469E, 22.VI.2013, *Thymbra capitata*, 1♀ (UAEG n°089871), leg. J. Gavalas (UAEG).—Attiki, Daphni, 38.0099N 23.6451E, 26.VIII.2013, 1♀ (UAEG n°089878), leg. T. Petanidou (UAEG).—Kyklad, Mykonos, 8.VI.1962, 1♂, leg. M. Schwarz.—Rhodos ("Rodi, Egeo"), V.1939, leg. Dr Meyer (OOLM).

TURKEY. Denizli, 10 km NE Denizli, 37°58'N 29°07'E, 290m, 4.VII.2006, 1♂, leg. M. Halada (OOLM).—Denizli, Isikli Golu, 22.VI.1998, 1♂, leg. J. Halada (OOLM).—Burdur, 5 km NE Yesilova, 37°35'N 29°55'E, 1060m, 6.VII.2006, 1♂, leg. M. Kadlecova (OOLM).—Adana, 30 km SE Catalan, 60m, 24.IX.1991, 1♂, leg. H.V. Oorschot & H. Wiering (RMNHL).—Taurus, Gulek, 1♂, leg. J. Vachal (MNHNP).—Mugla, Koycegiz, 37.0027N 28.7099E, 18.IX.2013, *Drimia maritima*, 1♀ (UAEG n°089907), leg. T. Petanidou (UAEG).—10 km W. Alanya, Konaki, 36.58°N 31.89°E, 1.VIII.2009, 1♂, leg. & col. Schmid-Egger.—Icel, Mersin 3km N, 20.VI.1985, 1♂, leg. & col. M. Schwarz.—Mut, 10.VI.1965, 1♂, leg. & col. M. Schwarz, 19.V.1970, 1♂, leg. J. Gusenleitner (OOLM).—Mut 10 km S, 8.VI.1966, 1♂, leg. H.H.F. Hamann (OOLM).—20 km W Mut, 14.VI.2000, 2♂, leg. M. Halada (OOLM).—Gaziantep, 2 km N Fevzipasa, 600m, 28.IX.1991, 1♂, leg. H.V. Oorschot & H. Wiering (RMNHL).—Gaziantep, 43 km WNW Kilis, Gozkaya, 600m, 29.IX.1991, 1♂, leg. H.V. Oorschot & H. Wiering (RMNHL).

CYPRUS. Moni, 20–21.V.1952, 1♂, leg.G.A. Mavromoustakis (BMNH).—8 km S. Limassol, Akrotiri, near Airbase, 34.60°N 32.97°E, 20.VI.2013, 1♂, leg. & col. C. Schmid-Egger.—8 km N. Pafos, Mavrokolympos Res., 34.85°N 32.40°E, 20.VI.2013, 1♂, leg. & col. C. Schmid-Egger.—Paphos, Kato, Paphos ancient site, 3.V.2003, 2♀, leg. E. Scheuchl (ZSM HYM06052 & HYM06053).—Lemesos, Amathus, Ancient site, 15.IV.2002, 1♀, leg. E. Scheuchl (ZSM HYM06054).—Famagusta, 18.VIII.1998, 1♂, leg. Boness (OOLM).

ISRAEL. Jerusalem, 13.VII, 1♂ (MNHNP).—Bet Guvrim, 3.VI.2012, 2♂, 27.V–3.VI.2012, 9♀, leg. G.

Pisanty (HUJ).—Judean Foothills, Beit Govrin, UTM 36R 679040 3500740, *Heliotropium* sp., 31.V.2010, 1♂, leg. G. Pisanty n°61688 (HUJ).—Judean Foothills, Sha'alvim, UTM 36R 688530 3527290, 7.VI.2010, *Citrullus lanatus*, 1♂, leg. G. Pisanty n°62953 (HUJ).—Central Coastal Plain, En Wered (= En Vered), 29.IV.2013, 1♂, leg. G. Pisanty (HUJ).—Wadi Qilt, Ein-el-Fawwar, 19.V.1991, 3♂, leg. K. Warncke (OOLM).

IRAN. Babolsar, "Kaspi See Niederung", 0m, 14.VII.1977, 1♂, leg. A.W. Ebmer.—Iran, Esfahan, Dehagan Astaneh, 4.VI.2013, leg. Khodarahmi (YASU).—Mazdaran Prov., 10 km S. Chaloos, N36.51° E51.33°, 380m, 15.VI.2010, 1♂, leg. Mi Halada (OOLM).

TAJIKISTAN. Dusambe, 40 km vych Javroc, 24.VI.1981, 1♂, leg. Kocourek (OOLM).

UZBEKISTAN. Tasken (= Tashkent), 40 km Circik (= Tchirtchik, 41.46°N 69.58°E), 4.VII.1982, 3♂, leg. Kocourek, col. M. Schwarz.

**Distribution**. Eastern Mediterranean, from Greece to Israel, Iran, Tadjikistan and Uzbekistan (Fig. 19).

**Visited plants**. The most visited plants by this species in the Greek islands are *Glebionis coronaria* (L.) Cass. *ex* Spach, *Dittrichia viscosa* (L.) Greuter (Asteraceae), *Daucus carota* L., *Eryngium campestre* L. (Apiaceae) and *Thymbra capitata* (L.) Cav. (Lamiaceae).

**Etymology**. The specific epithet refers to the phryganic habitat in which the species is common.

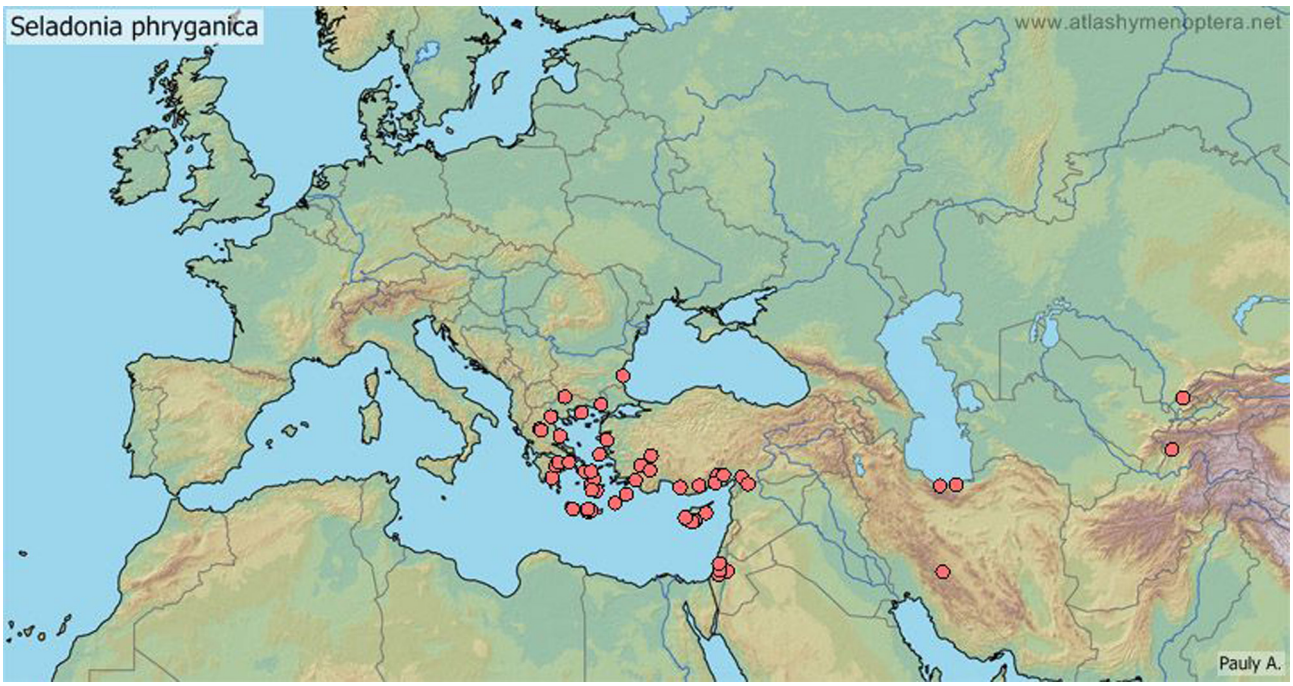


**FIGURE 19.** Geographic distribution of *Seladonia phryganica* **sp. nov.** (males with genitalia form E and barcoded females).

***Seladonia cretella* Pauly & Devalez sp. nov.**
(Figs 20–21)

**Diagnosis**. The underplate of the large projection of the gonocoxite in the male of this species is almost indistinguishable from that of *S. phryganica* and *S. gemmella*. Its shape is somewhat intermediate between those two species (Figs 20c,d). The best character to distinguish *S. cretella* from both species is the long fourth antennal segment (length/width 1.44–1.53 in *S. cretella* vs. 1.05–1.17 in *S. phryganica* and 1.41 in *S. gemmella*; compare Figs 20a and 20b). This species can also be recognized by its geographic distribution, as it is an endemic species to the islands of Karpathos and Crete. On these two islands, the antenna is dark ventrally in *S. cretella* while it is brown yellow throughout in *S. phryganica* (Fig. 20b); the small projection of the gonocoxite is also not as thin as in that of *S. phryganica*.

**Description**. Male and female as described for *S. smaragdula* except as follows: underplate of large projection of male gonocoxite subtriangular to boomerang-shaped (Figs 20c,d). Small projection of gonocoxite moderately thin (Fig. 24d). Fourth antennal segment of the male relatively long (length/width = 1.44–1.53).

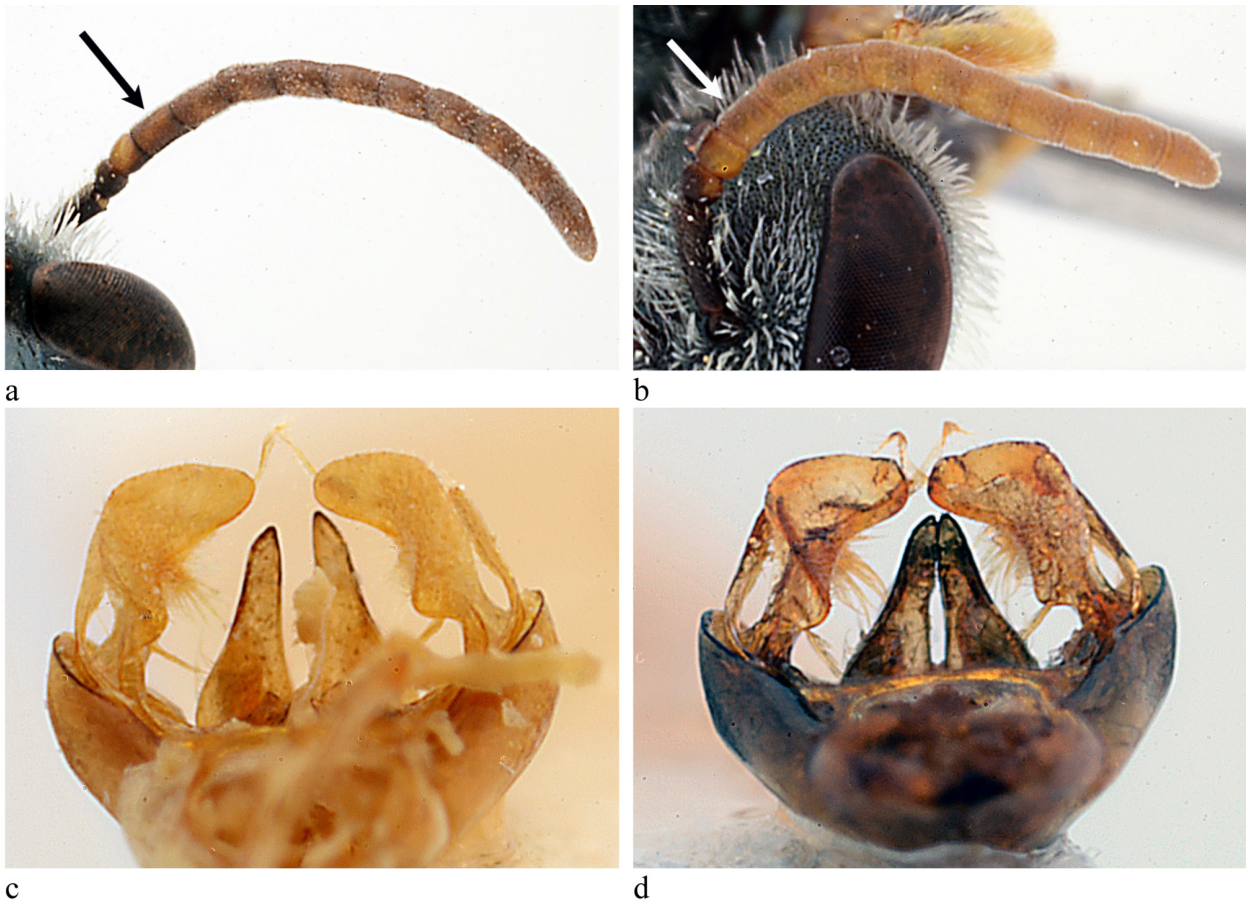


**FIGURE 20.** a, b, male antennae, both from Karpathos; a, *Seladonia cretella*; b, *S. phryganica*; c, d, male genitalia in ventral view of *S. cretella*; c, Crete ; d, Karpathos.

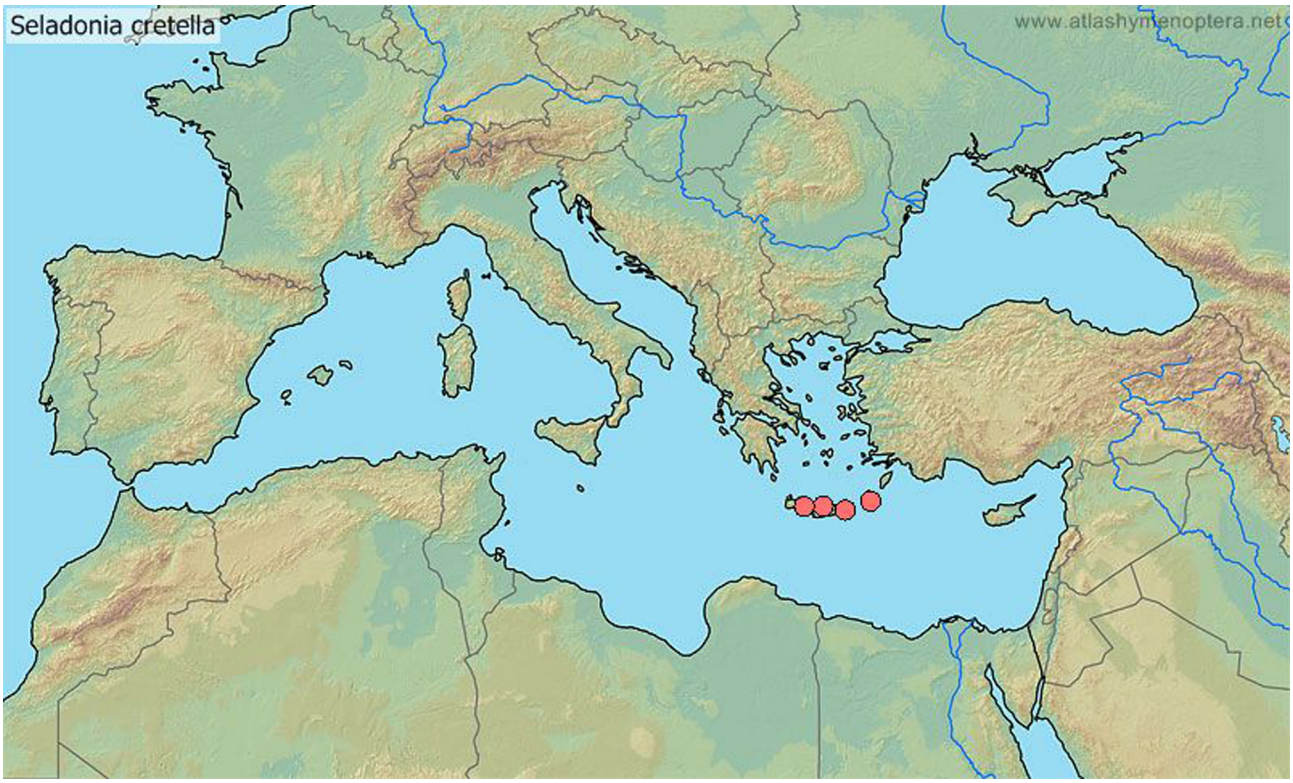


**FIGURE 21.** Geographic distribution of *Seladonia cretella* **sp. nov.**

**Holotype**. GREECE, Crete, Kournas, Asprouliani, 30 km W. Rethymnon, 4.X.2003, 1♂, leg. E. Scheuchl (ZSM).

**Paratypes** (7 males). GREECE, Crete, Sitia, 17–20.V.1963, 2♂, leg. J. Gusenleitner (col. M. Schwarz).—Crete, Heraklion, 25.V.1963, 1♂, leg. J. Gusenleitner (col. M. Schwarz).—Crete, Georgioupolis, Mathes, 30 km W Rethymnon, 10.X.2003, 1♂, leg. E. Scheuchl (col. E. Scheuchl).—Karpathos, Avlona, 35.7689°N 27.1849°E, 8.VI.2012, *Malva sylvestris*, 1♂ UAEG 033704), 1♂ (UAEG 033709), 1♂ (UAEG 033773), leg. T. Petanidou 3494 (UAEG, RBINS).

**Distribution**. Endemic to Crete and Karpathos (Fig. 21).

**Etymology**. The specific epithet is taken from the diminutive of the island "Crete" where the species occurs.

**Comments.** This cryptic species was revealed by its barcode. The specimen from Crete (Asprouliani) barcoded by Schmidt *et al.* (2015) has a barcode positioned at the base of the cluster (*S. gemmella* + *S. submediterranea* + *S. orientana*). Unfortunately, the genitalia of the few collected specimens could not be photographed with a scanning electron microscope for study.

**Variations**. Specimens from Karpathos have antennae dark below while they are brown in the specimens from Crete.

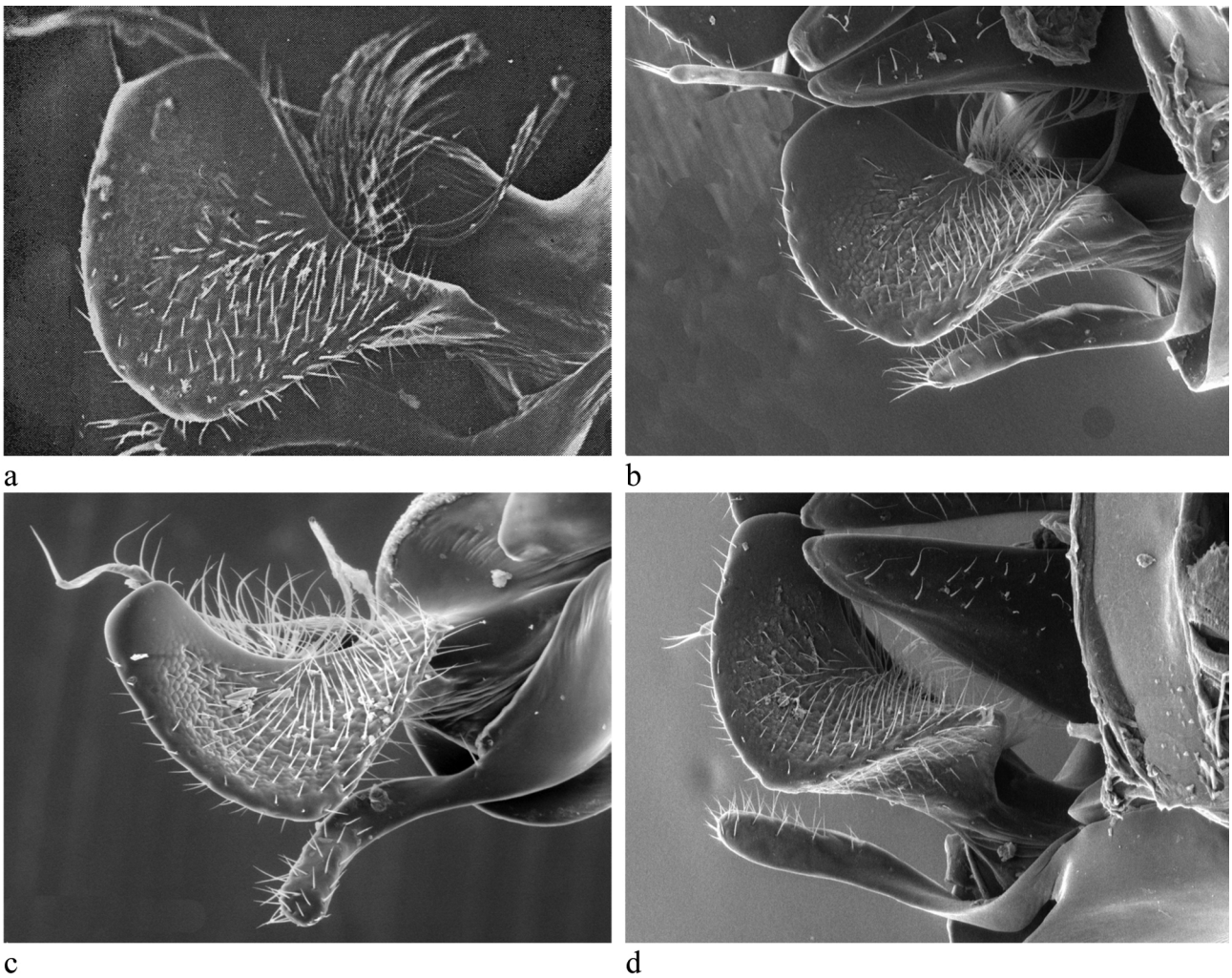


**FIGURE 22.** Comparison between the species of the clade "*S. smaragdula* + *S. phryganica*" in the *S. smaragdula* complex, showing ventral view of the large projection of the gonocoxites; first picture (a) reproduced from Pauly & Rassel (1982), other pictures by Pauly & Cillis; a, *S. smaragdula* (Croatia, Ugljan); b, *S. smaragdula* (France, Porquerolles); c, *S. phryganica* (Greece, Dafni); d, *S. phryganica* (Greece, Crete).

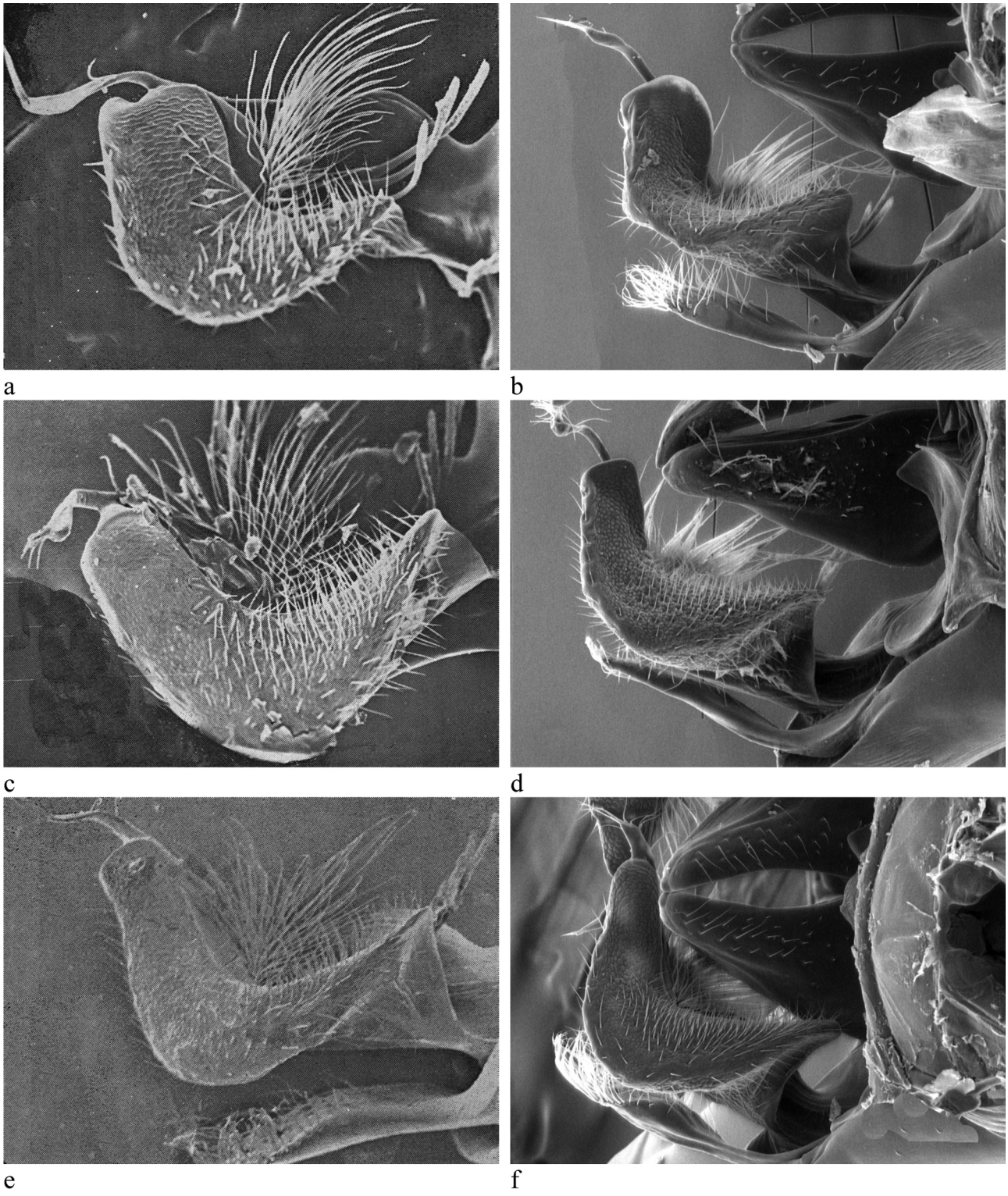


**FIGURE 23.** Ventral view of the large projection of the male gonocoxite of *Seladonia gemmella* **sp. nov.**, *S. submediterranea* **sp. nov.** and *S. orientana* **sp. nov**. Left photographs are reproduced from Pauly & Rassel (1982), at right new photographs by Pauly & Cillis; a, *S. gemmella* (Spain, Alicante); b, *S. gemmella* (Spain, Almeria); c, *S. submediterranea* (Romania, Bucarest); d, *S. submediterranea* (France, Deux-Sèvres); e, *S. orientana* (Croatia, Ugljan); f, *S. orientana* (Greece, Samothrace).

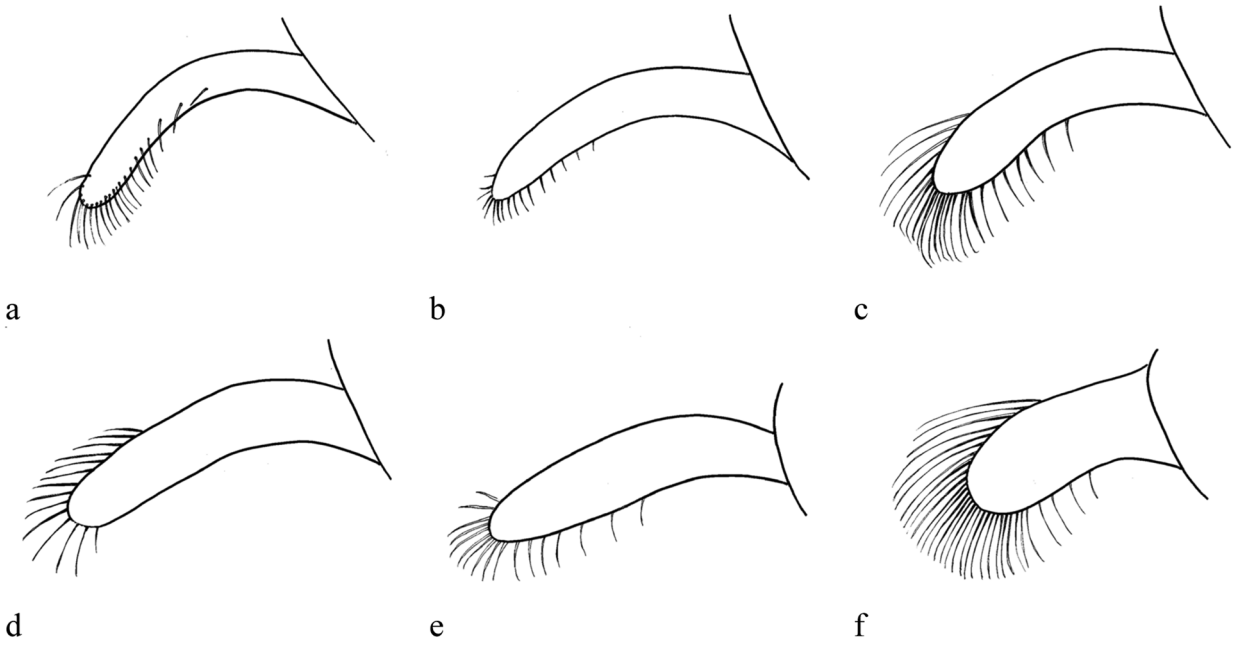


**FIGURE 24.** Contour of the small projection, in lateral view, of the male gonocoxite in the species of the *Seladonia smaragdula* complex; a, *S. smaragdula* (Spain, Almeria); b, *S. phryganica* **sp. nov**. (Greece, Anafi); c, *S. gemmella* **sp. nov**. (Spain, Almeria); d, *S. cretella* **sp. nov**. (Greece, Crete); e, *S. submediterranea* **sp. nov**. (France, Deux-Sèvres); f, *S. orientana* **sp. nov**. (Greece, Lesvos).

### Seladonia nomina dubia

The following two names were proposed based on female specimens and clearly belong to the *S. smaragdula* complex, as they are currently synonymized under *S. smaragdula s. lat*. The types are known and in good shape, but because of their age, the study of molecular characters is assumedly impossible at this point. Males have not been associated with these names, thus their correct identity is uncertain. Until further studies clarify these problems, we have decided to consider both names as nomina dubia (see comments below).

### *Seladonia butea* (Warncke, 1975), nomen dubium

*Halictus buteus* Warncke 1975: 119, ♀. Holotype: 1♀, Turkey, Sile, 5.VIII.1968, leg. K. Warncke (OOLM).

**Comments.** The holotype of *Halictus buteus* is a female of the *S. smaragdula* complex described from Sile, northwestern Turkey. Males of *S. orientana* and *S. submediterranea* occur in the same area and thus they were initially thought as good candidates for an association with this species. In fact, the males identified by Warncke as *S. butea* from some localities in Greece and Turkey actually belong to either *S. orientana* or *S. submediterranea*. However, as the female holotype does not bear specific characters and because no males were collected in the same locality with the type, we decided to recognize *S. butea* as a "nomen dubium" until further studies clarify this issue. The collection of more material from Turkey, including males from the type locality, is needed.

### *Seladonia morinella* (Warncke, 1975), nomen dubium

*Halictus morinellus* Warncke 1975: 118, ♀ ♂. Holotype: 1♀, Turkey, Horasan, Arastal, 3.IX.1973, leg. Warncke (OOLM).

**Comments.** *Halictus morinellus* was described from a small female holotype collected in NE Turkey where both *S. orientana* and *S. submediterranea* occur. The description of the male paratypes is based on specimens from Greece

and Macedonia. These paratypes are actually *S. orientana* and *S. submediterranea*. The correct association of the male of this species is not possible at this point, so we decided to recognize *S. morinella* as a "nomen dubium" until further studies clarify its status. Collecting males from the typical locality is needed.

## Discussion

The morphological recognition of the species described herein is principally based on male genital characters. The results of this morphological approach are corroborated by mitochondrial DNA sequence analyses. The combination of these approaches, plus their sympatry in some regions, revealed the existence of five cryptic new species in *S. smaragdula*, which correspond to the forms described by Pauly & Rassel (1982). This case is similar to the better known complex "*simplex, compressus, langobardicus*" in the genus *Halictus sensu stricto*, where females remain virtually inseparable while the males can be easily separated into more than 20 cryptic species based on the shapes of the mandibles, antennae and genitalia (Pesenko 2004).

The species in the *S. smaragdula* complex can be divided into two major morphological groups based on the male genitalia: one group, consisting of *S. smaragdula* and *S. phryganica*, with a rounded, racquet-shaped underplate of the large projection of the gonocoxite, and a second group comprising the remaining species (*S. gemmella* + *S. submediterranea* + *S. orientana*) with a boomerang-shaped underplate. These observations based on the morphology of the male genitalia are partly supported by our genetic analysis, because the clade grouping *S. smaragdula* and *S. phryganica* is strongly supported in our phylogenetic reconstructions (bootstrap support >93 and posterior probabilities = 1). In contrast, the relationship among the remaining species could not be resolved (Fig. 3).

Two species may occur in the same locality (Table 4). In the case of such sympatric species, more observations are needed to determine if they share the same habitat. For example, in southern Spain, *S. gemmella* is the most commonly observed species in coastal habitats whereas *S. smaragdula* is found at higher altitudes inside the country. On the Aegean Islands in Greece, *S. phryganica* is the most common and widespread species, usually found in phryganic habitats at low altitudes. It is the only species found on islands dominated by phryganic vegetation and without a significant altitudinal gradient. In contrast, *S. orientana* is found at higher altitudes, in habitats dominated by tall shrubs and trees, including riparian habitats along streams; it has not yet been found in the phryganic habitats of the Aegean Islands where *S. phryganica* occurs. More specimens with detailed collecting data are necessary to confirm habitat preference of these species.

**TABLE 4**. Localities with occurrence of two different species of the *Seladonia smaragdula* complex.

| Locality | *S. smaragdula* | *S. gemmella* | *S. submediter-ranea* | *S. orientana* | *S. phryganica* | *S. cretella* |
|---|---|---|---|---|---|---|
| Spain, Pena de Oroel | X | | X | | | |
| Spain, Montseny | X | | X | | | |
| France, Gonfaron | X | | X | | | |
| Croatia, Hvar I. | X | | X | | | |
| Croatia, Ugljan I. | X | | | X | | |
| Greece, Corfou I. | X | | | X | | |
| Greece, Crete | | | | | X | X |
| Greece, Karpathos | | | | | X | X |
| Turkey, Beytussebap | | | X | X | | |
| Iran, Polur | | | X | X | | |
| Morocco, Tizi-n-Test | X | X | | | | |

There are also exclusion zones, where only one species of the *S. smaragdula* complex occurs. For example, *S. smaragdula* occurs in Malta, *S. phryganica* in the Cyclades Islands, *S. phryganica* in Cyprus, *S. phryganica* in Israel, and *S. submediterranea* in Central Europe. Furthermore, *S. smaragdula* and *S. phryganica* seem to have a

vicariant distribution, as *S. smaragdula* is found in the west whereas *S. phryganica* in the east of the Mediterranean region (Figs 9, 19).

An interesting observation concerns the invasion of Australia by a *Seladonia* species, which has been identified morphologically as "*S. smaragdula*" (Gollan *et al*. 2008; Ashcroft *et al.* 2012). We had the opportunity to examine three pictures of the male genitalia from specimens of this continent, as well as sequences of 35 Australian specimens that were provided by Michael Batley, which were compared with those of the species treated in the present work. The COI sequences of the Australian specimens do not match any of these six species of the *S. smaragdula* complex, thus suggesting that they have been misidentified. The closest match in our dataset is with *S. orientalis* (Lepeletier, 1841) from the Reunion island (2% divergence), while morphologically, this Australian species looks very similar to *S. hotoni* (Vachal, 1903), which is described from South Africa. Without a doubt, African specimens of *S. hotoni* should be barcoded to confirm this identity.

The Mediterranean Basin constitute an environment favouring speciation. This area is the second highest biodiversity hotspot for bees with over 2000 recorded species (Kuhlmann 2015). Despite years of taxonomic research on the fauna of this area, many issues remain to be solved and a rich, hidden bee diversity awaits to be discovered, as we have shown here.

## Key to the species of *Seladonia smaragdula* complex

Males

1 Specimens from Crete or Karpathos Islands . . . 6
- Specimens from other areas . . . 2
2 Large projection of the gonocoxite with a rounded racket-shaped or subtriangular underplate, the inner side of the projection not forming a 90° angle . . . 3
- Large projection of the gonocoxite with a boomerang-shaped underplate, the inner side of the projection forming a 90° angle . . . 4
3 Large projection of the gonocoxite with a rounded "racket-shaped" underplate (Figs 22a,b); West Mediterranean (Fig. 9) . . . ***S. smaragdula*** (Vachal, 1895)
- Large projection of the gonocoxite with a subtriangular underplate, the inner side of the plate more concave (Figs 22c,d); East Mediterranean (Fig. 19) . . . ***S. phryganica*** Pauly & Devalez **sp. nov.**
4 Small projection of the gonocoxite thick and with numerous long setae (Fig. 24f); large projection of the gonocoxite with a very narrow underplate (length/width = 2.88 to 4.72) (Figs 23e,f); Northern part of the Mediterranean Basin to Central Asia (Fig. 17) . . . ***S. orientana*** Pauly & Devalez **sp. nov.**
- Small projection of the gonocoxite thin and with few short setae (Figs 24c,e); large projection of the gonocoxite with a less narrow underplate (length/width = 1.77 to 2.46); North Africa, Europe or Central Asia . . . 5
5 Distal part of the underplate of the large projection of the gonocoxite large (length/width = 1.77) (Figs 23a,b); Southern Spain and North Africa to the Sinai in Egypt (Fig. 13) . . . ***S. gemmella*** Pauly **sp. nov.**
- Distal part of the underplate of the large projection of the gonocoxite narrower (length/width = 2.46) (Figs 23c,d); From Spain to Iran, all specimen from Central Europe belong to this species (Fig. 15) . . . ***S. submediterranea*** Pauly **sp. nov.**
6 Antennae dark brown ventrally, fourth flagellomere long (length/width = 1.44–1.53) (Fig. 20a) . . . ***S. cretella*** Pauly & Devalez **sp. nov.**
- Antennae brown yellow ventrally, fourth flagellomere short (length/width = 1.05–1.17) (Fig. 20b) . . . ***S. phryganica*** Pauly & Devalez **sp. nov.**

**Females** (key based on geographical distribution)

1 Central Europe (Fig. 15) . . . ***S. submediterranea*** Pauly **sp. nov.**
- Other areas . . . 2
2 Aegean Islands, Cyprus, Israel (Fig. 19) . . . ***S. phryganica*** Pauly & Devalez **sp. nov.**
- Other areas . . . 3
3 North Africa (Fig. 13) . . . ***S. gemmella*** Pauly **sp. nov.** or ***S. smaragdula*** (Vachal, 1895)
- Other areas . . . 4
4 Crete or Karpathos Islands (Fig. 21) . . . ***Seladonia phryganica*** Pauly & Devalez **sp. nov**. or ***Seladonia cretella*** Pauly & Devalez **sp. nov.**
- Other areas . . . ***S. smaragdula*** (Vachal, 1895), ***S. orientana*** Pauly & Devalez **sp. nov**., ***S. submediterranea*** Pauly **sp. nov.**, ***S. gemmella*** Pauly **sp. nov.** or ***S. phryganica*** Pauly & Devalez **sp. nov.**

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