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Cryptic Diversity Revealed in A Revision of West Palaearctic *Nomiapis* and *Systropha* (Hymenoptera: Halictidae)

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Abstract: Revisionary taxonomic studies of bees from the Old World Mediterranean basin are hindered both by the apparent absence of type material for many taxa and a lack of genetic resources. The discovery of important type materials in combination with the generation of novel DNA barcodes (Cytochrome Oxidase I) has allowed cryptic diversity within the widespread taxa *Nomiapis bispinosa* (Brullé, 1832) and *Systropha planidens* Giraud, 1861 to be clarified. *Nomiapis bispinosa* actually consists of three distinct taxa: *Nomiapis bispinosa* s. str. from Morocco and Iberia to Central Asia, *Nomiapis rufiventris* (Spinola, 1838) **spec. resurr.** from Morocco to Egypt, including Sicily and *Nomiapis paulyi* **spec. nov.** from Portugal and Spain. A lectotype is designated for *Nomia rufiventris* Spinola, 1838. Lectotypes are designated for *Nomia bispinosa* Brullé, 1832 and *Nomia albocincta* Lucas, 1849, and type material for *Nomia perforata* Lucas, 1849 is clarified; both *Nomiapis albocincta* and *Nomiapis perforata* are synonymised **syn. nov.** with *Nomiapis rufiventris*. A lectotype is designated for *Nomia ruficornis* Spinola, 1838, and this taxon is confirmed as a synonym of *Nomiapis bispinosa*. *Systropha planidens* also consists of three distinct taxa: *S. planidens* from Central Europe to Iran and the European part of Russia, *S. grandimargo* Pérez, 1905 **spec. resurr.** from Portugal, Spain, and France, and *S. anatolica* Warncke, 1977 **stat. nov.** from Turkey, Syria, and northern Israel. A lectotype is designated for *Systropha planidens* Giraud, 1861. *Systropha chrysura* Pérez, 1905 is synonymised **syn. nov.** with *S. grandimargo*. These findings illustrate the extent to which our understanding of the taxonomy of Mediterranean bees remains incomplete.

Keywords: taxonomy; solitary bees; Iberian endemic; Mediterranean; barcoding

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1. Introduction

The West Palaearctic biogeographical region is home to the Mediterranean basin, a biodiversity hotspot, particularly for bee species. The bee fauna of this region also has the longest history of study, with many old names available [1–5]. Many of these names were synonymised by later workers [6–12], but sometimes without fully inspecting the type material due to its apparent absence from museum collections. The subsequent re-discovery or re-inspection of type material can demonstrate that those type concepts were incorrect, leading to necessary taxonomic changes [13].

Additionally, the application of genetic barcoding using the cytochrome c oxidase I (COI) region of the mitochondrial genome, along with careful morphological study, has revealed the presence of many cryptic taxa within West Palaearctic bees, typically in the Mediterranean basin [14–17]. In some cases, names are available for cryptic taxa and can be resurrected from synonymy, but in other cases, taxa are simply overlooked and undescribed. Fully resolving taxonomic complexity within the West Palaearctic fauna, therefore, requires the study of type material in combination with morphological and molecular delineation of species. Applying these principles, we investigate two predominantly West Palaearctic bee species that contain taxonomic complexity and have not been fully explored by previous workers. These taxa are *Nomiapis bispinosa* (Brullé, 1832) and *Systropha planidens* Giraud, 1861.

The application of the name *Nomiapis bispinosa* has been confused at multiple levels. Described within a broad concept of *Nomia* Latreille, 1804, subsequent workers have split this genus into many smaller genera, in this case, into the genus *Nomiapis* Cockerell, 1919 [11,18,19]. Recent genetic analysis has confirmed the genus as distinct from *Pseudapis* W.F. Kirby, 1900 [20], and hence it is used here. At the species level, Warncke [8] synonymised many taxa under the name *Nomia unidentata* Olivier, 1811, but Baker [11] subsequently demonstrated that the type of *Nomia unidentata* could not be a *Nomiapis* species, and thus that *Nomiapis bispinosa* was the correct name for this taxon. Despite this clarification, complexity exists, with two nominal 'subspecies' being found together in sympatry in southern Portugal [21]. Though not confused at a generic level, a similar lack of clarity has surrounded *S. planidens* due to apparently lost type material and inconsistency in the literature regarding synonymy with taxa described from Iberia [9,10,22]. This revisionary work aims to clarify the situation for both nominal taxa.

2. Materials & Methods

Specimens of *Nomiapis* and *Systropha* were sampled from Morocco, Portugal, Spain, and France in order to have high taxon coverage of West Mediterranean taxa (Table 1). This included *S. planidens* subspecies *grandimargo* Pérez, 1895 sensu Warncke [9]. For genetic barcoding, a single midleg was removed from pinned specimens and sent to the Canadian Center for DNA barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing. Specimens were sequenced following standardised high-throughput protocols [23]. Both Lep1 and BeeCox1F1 primers were used [24,25] to target the COI-5′ region. Trees for both *Nomiapis* and *Systropha* were supplemented with additional published sequences that were downloaded from Genbank and the Barcode of Life Data System.

Table 1. The scientific names of specimens sampled for genetic analysis with their collection localities and voucher depositories. Specimens are labelled with a yellow label which carries the voucher code. All data are available on BOLD. Acronyms for the collection depositories: Collection Thomas Wood, Mons, Belgium (CTW).

Taxon	Locality	Depository	Collector/Identifier	Voucher Code	BOLD
Nomiapis bispinosa	France: Corsica, Vescovato, Embouchure du Golo	MNHN	R. Le Divelec/R. Le Divelec	BC-LPRCorse 0846	LPRCW640-21
Nomiapis bispinosa	France: Corsica, Vescovato, Embouchure du Golo	MNHN	R. Le Divelec/R. Le Divelec	BC-LPRCorse 0847	LPRCW641-21
Nomiapis bispinosa	France: Arles, Salins de Beauduc	MNHN	R. Le Divelec/R. Le Divelec	BC-RLD-010	HYMFR004-21
Nomiapis bispinosa	Spain: Madrid, Rivas-Vaciamadrid	CTW	T. Wood/T. Wood	TJW_029	WPATW768-22
Nomiapis bispinosa	Spain: Madrid, Rivas-Vaciamadrid	CTW	T. Wood/T. Wood	TJW_030	WPATW769-22
Nomiapis bispinosa	Spain: Madrid, Rivas-Vaciamadrid	CTW	T. Wood/T. Wood	TJW_031	WPATW770-22
Nomiapis diversipes	Spain: Málaga, Parque del Guadalhorce	CTW	T. Wood/T. Wood	TJW_330	WPATW209-21
Nomiapis diversipes	Spain: Murcia, Totana	CTW	T. Wood/T. Wood	TJW_448	WPATW295-21
Nomiapis paulyi **spec. nov.**	Portugal: Guarda, Almeida	CTW	T. Wood/T. Wood	TJW_015	WPATW765-22
Nomiapis paulyi **spec. nov.**	Spain: Ávila, El Losar del Barco	CTW	T. Wood/T. Wood	TJW_018	WPATW766-22
Nomiapis paulyi **spec. nov.**	Spain: Segovia, Segovia	CTW	T. Wood/T. Wood	TJW_028	WPATW767-22
Nomiapis paulyi **spec. nov.**	Spain: Sevilla, Aznalcázar	CTW	T. Wood/T. Wood	TJW_310	WPATW196-21
Nomiapis paulyi **spec. nov.**	Spain: Málaga, Júzcar	CTW	T. Wood/T. Wood	TJW_358	WPATW231-21
Nomiapis paulyi **spec. nov.**	Spain: Segovia, Carbonero el Mayor	CTW	T. Wood/T. Wood	TJW_510	WPATW341-21
Nomiapis rufiventris	Morocco: Drâa-Tafilalet, Ait Ben Yacoub	CTW	T. Wood/T. Wood	TJW_888	WPATW700-22
Nomiapis rufiventris	Morocco: Fès-Meknès, Enjil	CTW	T. Wood/T. Wood	TJW_889	WPATW701-22
Nomiapis rufiventris	Morocco: Fès-Meknès, Aït Ali	CTW	T. Wood/T. Wood	TJW_890	WPATW702-22
Nomiapis rufiventris	Morocco: Fès-Meknès, Aït Ali	CTW	T. Wood/T. Wood	TJW_891	WPATW703-22
Nomiapis rufiventris	Morocco: Fès-Meknès, Aït Ali	CTW	T. Wood/T. Wood	TJW_892	WPATW704-22
Nomiapis rufiventris	Morocco: Khenifra, Sources Oum Rabia	CTW	T. Wood/T. Wood	TJW_893	WPATW705-22
Nomiapis valga	Spain: Granada, Cenes de la Vega	CTW	T. Wood/T. Wood	TJW_410	WPATW269-21
Systropha grandimargo	Spain: Málaga, Benaoján	CTW	T. Wood/T. Wood	TJW_389	WPATW256-21
Systropha grandimargo	Spain: Segovia: Valdeprados	CTW	T. Wood/T. Wood	TJW_508	WPATW339-21
Systropha maroccana	Morocco: Drâa-Tafilalet, Tazenakht	CTW	T. Wood/T. Wood	TJW_897	WPATW709-22
Systropha maroccana	Morocco: Guelmim-Oued Noun, Asrir	CTW	T. Wood/T. Wood	TJW_898	WPATW710-22
Systropha maroccana	Morocco: Drâa-Tafilalet, Agdz	CTW	T. Wood/T. Wood	TJW_899	WPATW711-22
Systropha maroccana	Morocco: Souss-Massa, Anamr	CTW	T. Wood/T. Wood	TJW_901	WPATW713-22

Table 1. *Cont.*

Taxon	Locality	Depository	Collector/Identifier	Voucher Code	BOLD
Systropha maroccana	Morocco: Guelmim-Oued Noun, Bouizakarne	CTW	T. Wood/T. Wood	TJW_902	WPATW714-22
Systropha pici	Morocco: Oriental, Guercif	CTW	T. Wood/T. Wood	TJW_894	WPATW706-22
Systropha pici	Morocco: Oriental, Guercif	CTW	T. Wood/T. Wood	TJW_895	WPATW707-22
Systropha pici	Morocco: Drâa-Tafilalet, Agdz	CTW	T. Wood/T. Wood	TJW_896	WPATW708-22

Sequences were aligned using SeaView [26], and a maximum likelihood analysis was run with 1000 bootstraps. A separate phylogeny was run for *Nomiapis* and *Systropha* separately, with the taxon *Lipotriches flavoviridis* (Cockerell, 1905) used as an outgroup for *Nomiapis* (subfamily Nomiinae) and the taxon *Dufourea halictula* (Nylander, 1852) used as an outgroup for *Systropha* (subfamily Rophitinae). Intra- and interspecific distances were calculated using MEGA-X [27].

For the newly described *Nomiapis* taxon and types from the Spinola collection (MRSN, see below), photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Close-ups were taken with the addition of a Mitutoyo M Plan Apo 10× infinity-corrected objective lens in combination with an Olympus M.Zuiko 2× teleconverter lens, a 10 mm Kenko DG extension tube, and a Meike MK-P-AF3B 10 mm extension tube. Photographs were stacked using Helicon 8.1.1 (HeliconSoft, Kharkiv, Ukraine), and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. For type material from the Paris collection (MNHN, see below) and additional images, photographs were taken with a Canon EOS 6D camera combined with an MP-E 65mm Macro f/2.8 lens and mounted on a semi-automatic Cognisys Rail macro Stack Shot device controlled by Helicon Remote software. The photographs were combined using Helicon Focus 6 software and processed using Adobe Photoshop CS6 (Adobe, San Jose, CA, USA).

Where available, pollen was removed from female *Nomiapis* specimens to determine their pollen foraging niche following the methodology of Wood & Roberts [28]. Dietary classification follows Müller & Kuhlmann [29].

Morphological terminology follows Michener [30]. The abbreviations A, T, and S are used for antennal segments, metasomal terga, and metasomal sterna, respectively. Given the confusion caused by Warncke [8], for brevity, all subsequent mentions of '*Nomia unidentata*' refer to *Nomia unidentata* sensu Warncke [8] nec. Olivier, and to *Nomiapis bispinosa* sensu Baker [11] (e.g., sensu lato).

3. Results

DNA Barcodes and Genetic Analyses

For the genus *Nomiapis*, five taxa were identified (Figure 1). *Nomiapis diversipes* (Latreille, 1806) was recovered as a monophyletic clade with bootstrap support of 84. Iberian specimens and Italian/Austrian specimens have identical sequences within each region, but between region distance was an average of 0.96%, leading to high bootstrap support for each clade (89 and 95, respectively) despite low overall differentiation.

Nomiapis bispinosa s.l. contained three distinct lineages. Material from Morocco and Egypt strongly clustered together, showing an average intraspecific distance of 0.14% (range 0.00–0.38%, Table 2), this clade having bootstrap support of 100. This clade is referable to as *Nomiapis rufiventris* (Spinola, 1838) **sp. resurr.** (see below). Material from Portugal and Spain also strongly clustered together, showing an average intraspecific distance of 0.34% (range 0.00–0.77%), this clade having bootstrap support of 99. This clade represents a previously undescribed species, *Nomiapis paulyi* **spec. nov.** (see below). This new species is separated from *Nomiapis rufiventris* by an average of 3.42% (range 2.87–3.83%). *Nomiapis bispinosa* s. str. formed a monophyletic clade with a lower bootstrap support of 91. This is due to the variation of sequences from specimens from Corsica, which were identical to each other, but which varied by 0.77% from the sequences from Spain and mainland France, which were themselves identical to each other. These two clades within *Nomiapis bispinosa* s. str. have moderate bootstrap support (88 and 61, respectively), though as overall genetic differentiation is low, it is not considered to correspond to a species-specific difference. *Nomiapis bispinosa* s. str. as a whole is separated from *Nomiapis rufiventris* by 2.83% (range 2.49–3.07) and from the new *Nomiapis* species by 2.14% (range 1.72–2.68%). Across all *Nomiapis* species, average interspecific differences were consistently higher (range 3.60–7.27%) than average intraspecific differences (range 0.14–0.57%), and hence a five taxon conclusion was drawn.

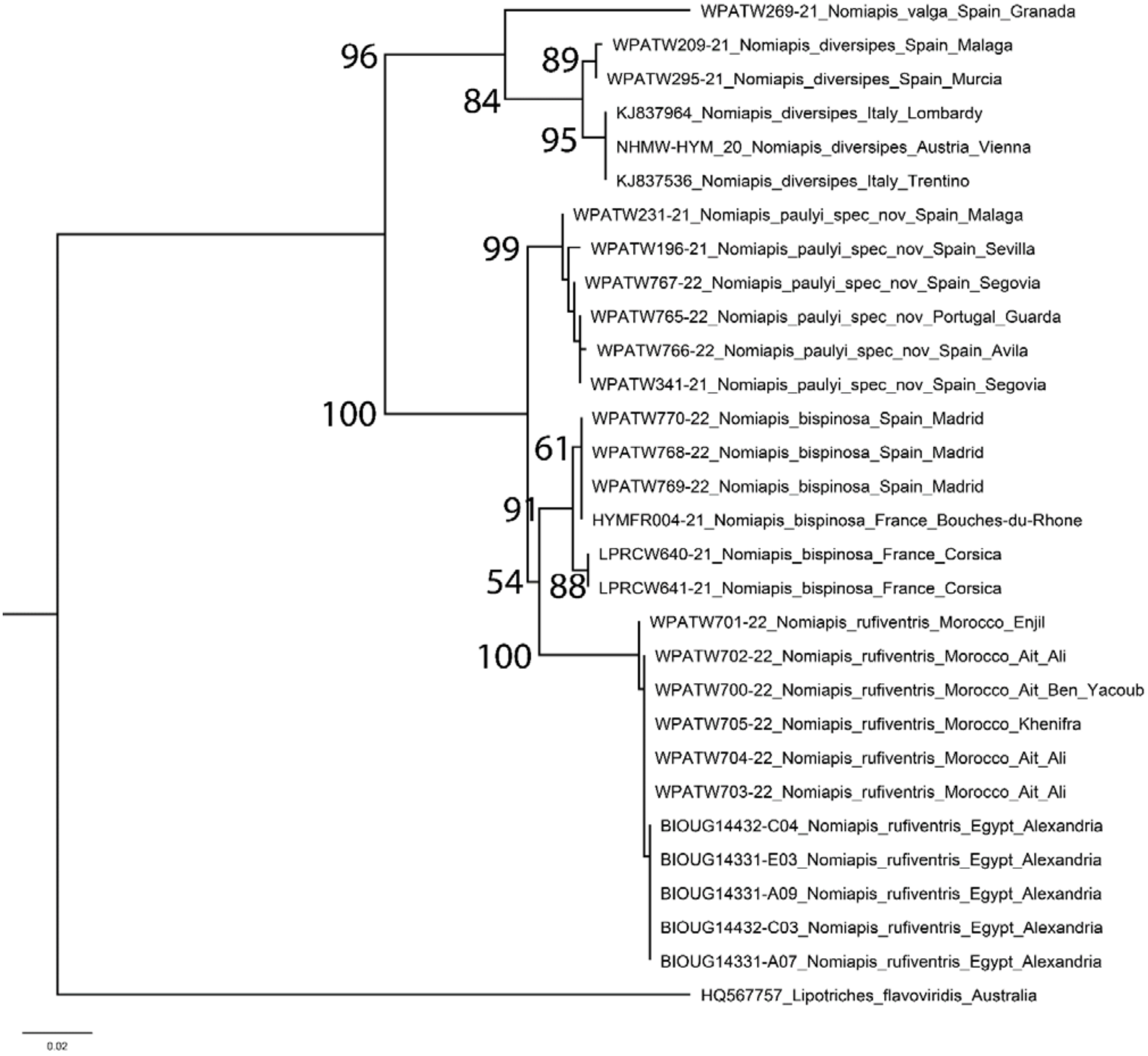

Figure 1. Phylogenetic tree (maximum likelihood) of *Nomiapis* species based on the mitochondrial COI gene with *Lipotriches flavoviridis* (Cockerell, 1905) used as an outgroup. Numbers adjacent to branches represent posterior probabilities (values of <0.5 are omitted).

For the genus *Systropha*, all species were well-resolved, with bootstrap values of 100 for five taxa, including *S. planidens grandimargo* (Figure 2). Intraspecific distances were low, typically less than 2%, but reaching 4.23% in *S. p. grandimargo* (Table 2). However, average interspecific distances between *Systropha* species were very high. The species showing the lowest divergence, *S. p. grandimargo*, had average interspecific distances between 10.27–19.34%, whereas the species showing the greatest distances, *S. pici*, had average interspecific distance between 18.13–22.96%. *Systropha p. grandimargo* was separated from its nearest relative *S. planidens* s. str. by an average of 10.73% (range 10.23–11.18%). It is therefore treated here as a distinct species, *S. grandimargo* **spec. resurr.** Across all *Systropha* species, average interspecific differences were consistently higher (range 16.06–20.22%) than average intraspecific differences (range 0.00–4.23%), and hence a five-taxon conclusion was drawn.

Table 2. Intra- and interspecific COI barcode divergence distances between selected *Nomiapis* and *Systropha* taxa.

Species	Intraspecific Genetic Distance (%)			Interspecific Genetic Distance (%)		
	Min	Max	Average	Min	Max	Average
Nomiapis bispinosa	0.00	0.77	0.41	1.72	7.47	3.60
Nomiapis diversipes	0.00	0.96	0.57	4.60	7.85	6.95
Nomiapis paulyi **spec. nov.**	0.00	0.77	0.34	1.72	8.43	4.01
Nomiapis rufiventris	0.00	0.38	0.14	2.49	7.85	4.64
Nomiapis valga	-	-	-	4.60	8.43	7.27
Systropha curvicornis	0.00	0.30	0.15	15.41	20.85	16.76
Systropha grandimargo	4.23	4.23	4.23	10.27	19.34	16.06
Systropha maroccana	0.00	0.60	0.42	15.41	21.15	17.27
Systropha pici	0.60	2.42	1.81	18.13	22.96	20.22
Systropha planidens	0.00	0.00	0.00	10.27	22.96	16.64

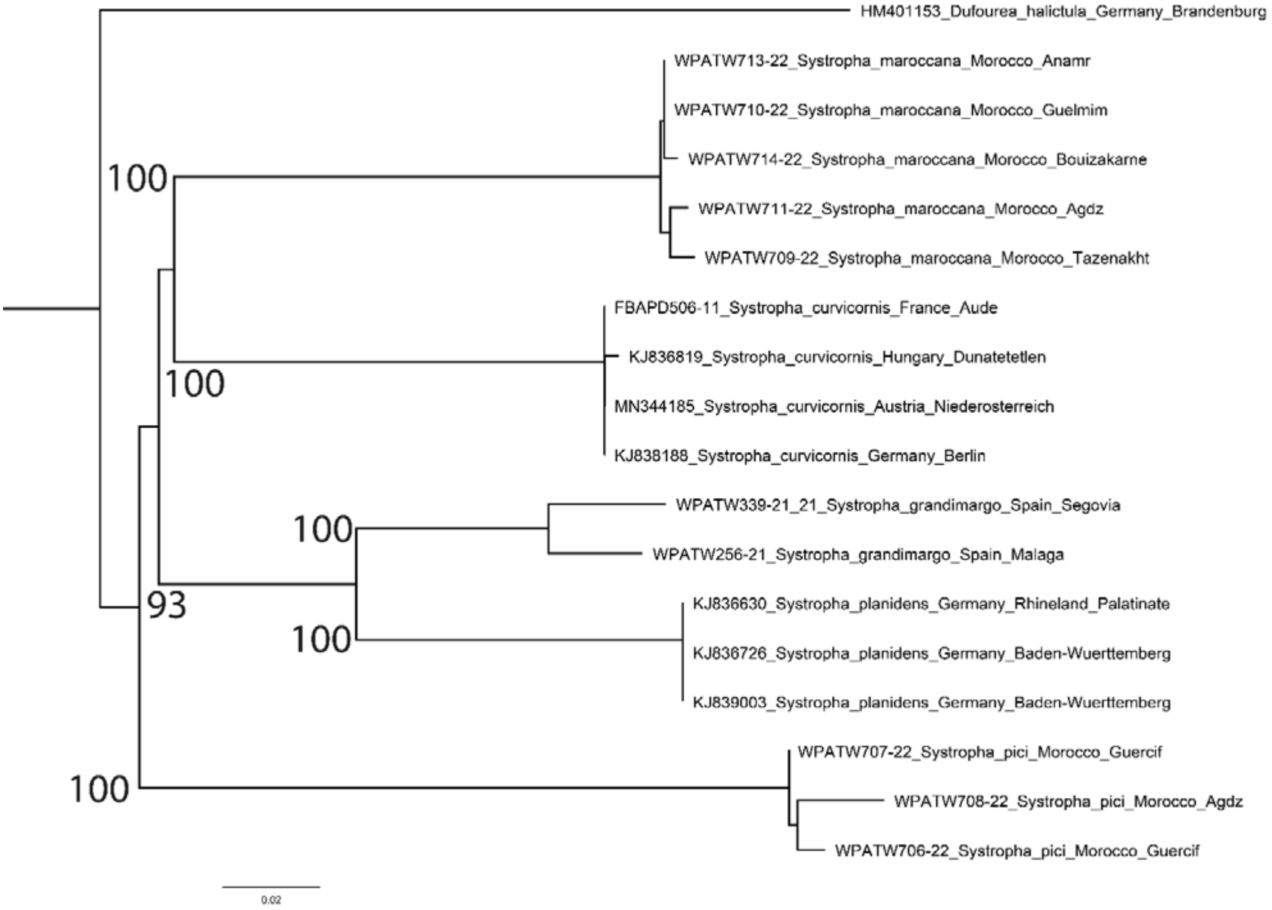

Figure 2. Phylogenetic tree (maximum likelihood) of *Systropha* species based on the mitochondrial COI gene with *Dufourea halictula* (Nylander, 1848) as an outgroup. Numbers adjacent to branches represent posterior probabilities (values of < 0.5 are omitted).

Taxonomic accounts

Genus ***Nomiapis*** Cockerell, 1919

Nomiapis bispinosa (Brullé, 1832)

Nomia bispinosa Brullé, 1832: 348; ♂surroundings of Mistra [Mystras], Greece [MNHN, lectotype by present designation]

Nomia ruficornis Spinola, 1838: 514; ♂Egypt [MRSN, lectotype by present designation]

Nomia aureocincta Costa, 1861: 8; ♂♀San Luca, Calabria Ulteriore, Italy [IEAN, types undesignated, not examined]. Synonymy with *Nomia unidentata* by Warncke [8].

Nomia polita Costa, 1861: 11; ♀Napoli, Italy [exact type location unknown, see Baker [11]]. Synonymy with *Nomia unidentata* by Warncke [8].

Nomia basalis Smith, 1875: 55; ♀. India [NHMUK, holotype, examined]. Synonymy by Baker [11].

Nomia aureocincta var. *turcomanica* Radoszkowski, 1893: 54; ♂♀"*Askhabad ou de ses environs*", Turkmenistan, [IZK, ♀lectotype designated by Astafurova & Pesenko [19]]. Synonymy with *Nomia rufiventris* Spinola, 1838 by Popov (1935), then automatically with *Nomiapis bispinosa* by Baker [11].

Nomia fletcheri Cockerell, 1920: 207; ♀. Peshawar District, Tarnab, India [USNM, holotype, not examined]. Synonymy by Pauly [12].

Nomia basalicincta Cockerell, 1922: 663; nom. nov. pro *Nomia basalis* Smith, 1875.

Type material examined.—Lectotype of *Nomia bispinosa* Brullé (present designation): 767 [species code referring to the original description]//Brullé Morée//Au Mu-séum//*N. bispinosa* Br. 767.//A. PAULY DT 1984 *Nomiapis unidentata* (Olivier)//Lectotype *Nomia bispinosa* Brullé Le Divelec des. 2022//*Nomiapis bispinosa* (Brullé, 1832) ♂Le Divelec det. 2022//MNHN, Paris EY33638 (Figure 3).

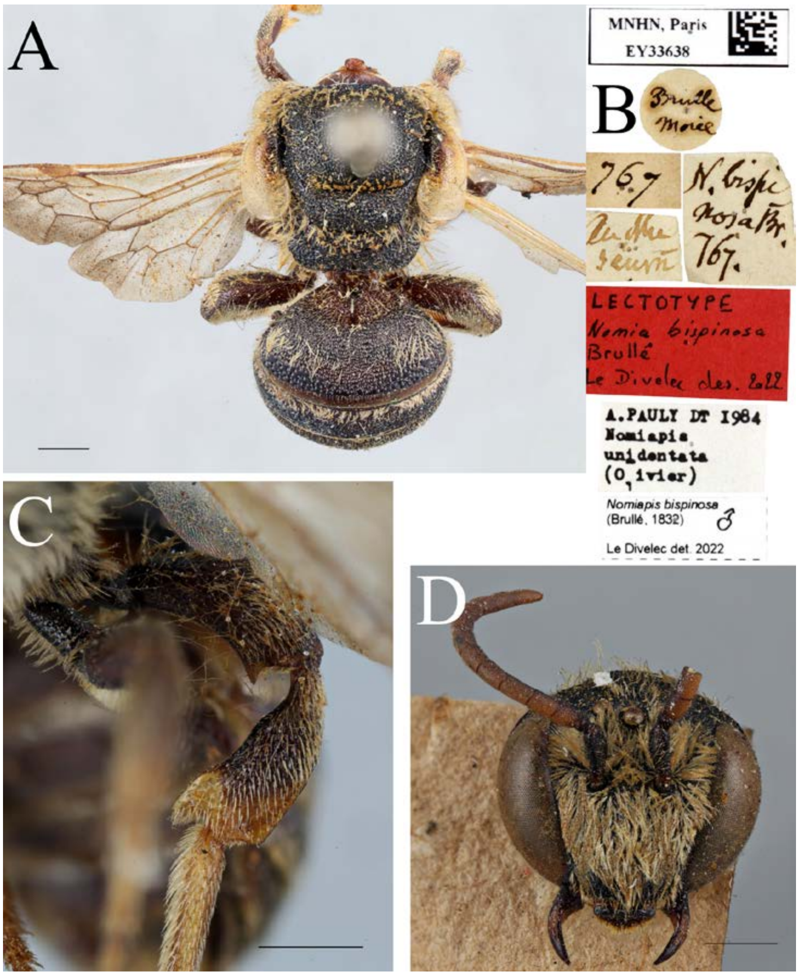

Figure 3. Lectotype specimen of *Nomia bispinosa* Brullé, 1832, male. (**A**) Dorsal view, (**B**) Label details, (**C**) Hind leg, (**D**) Head, frontal view. Scale = 1 mm.

–Lectotype of *Nomia ruficornis* Spinola (present designation): ♂//*Nomia ruficornis* ♂Spinola, 1838 LECTOTYPE des. WOOD 2022//*Nomia ruficornis*, m. ♂, ann. soc. ent. D. Waltl. Egypte (Figure 4).

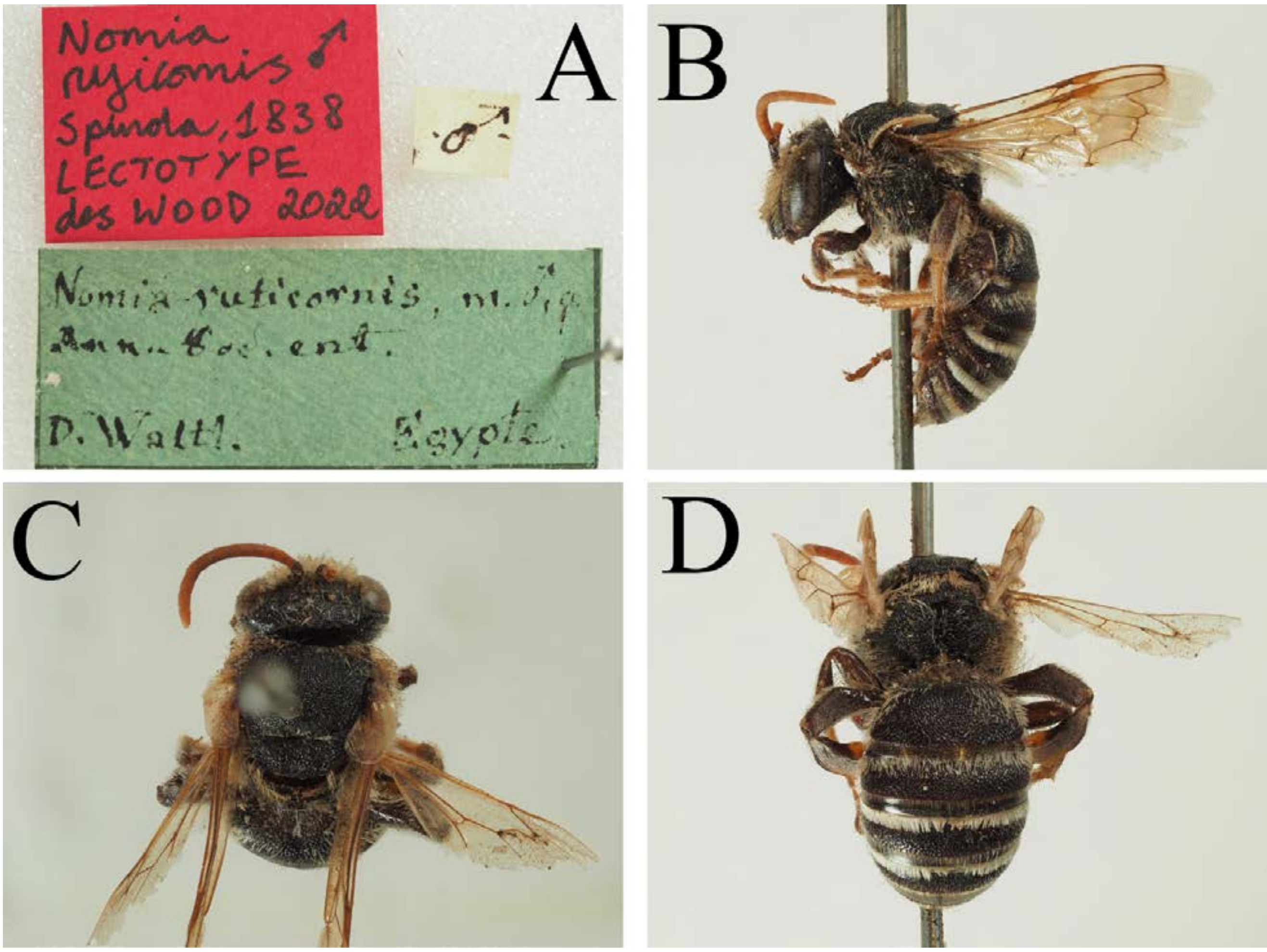

Figure 4. Lectotype specimen of *Nomia ruficornis* Spinola, 1838, male. (**A**) Label details, (**B**) Profile, (**C**) Dorsal view, (**D**) Terga, dorsal view.

Other material examined (illustrative, see Table S1). AFGHANISTAN: 1♂, Herat province, Koshk district, 24.vi.1997, leg. G.G.M. Schulten, RMNH; **BULGARIA:** 1♀, Warna [Varna], 5.viii.1956, leg. W.J. Pulawski, RMNH; **CROATIA:** 1♀, Lussingrande [Veli Lošinj], 24.vii.1924, leg. Dr. Fudakowski, RMNH; **CYPRUS:** 1♂, Akrotiri, SW of Limassol, 25.vi.1971, leg. M.J. & J.P. Duffels, RMNH; **EGYPT:** 1♂, Ghizeh, Reg. du Caire, 15.iv.1958, leg. W.J. Pulawski, RMNH; **FRANCE:** 1♂, 2♀, Pyr. Or., la Barcarès (Lido), 8.viii.1950, leg. P.M.F. Verhoeff, RMNH; **GREECE:** 17♀, Cyclades, Naxos, dunes S. of Naxos (village), 24–26.vii.1975, leg. Ph. Pronk, RMNH; **HUNGARY:** 1♂, Budapest, Mocsáry, RMNH; **IRAN:** 1♀, Mollasani, Ahwaz, 28.ii.1943, MNHN; **ISRAEL:** 1♂, Negev, Bir Reckene [Bir Rekhme, =Be'er Yeruham], 14.vi.1919, leg. Bytinski-Salz, RMNH; **ITALY:** 1♂, Bibione/Adria, 3–15.viii.1969, leg. H. Wolf, RMNH; **KAZAKHSTAN:** 1♂, 1♀, Tschelkar, Grosse-Barsuki, Barbier collection, MNHN; **MALTA:** 1♀, N. Gozo, NW of Zaghra, nr. Ir. Ramla [=Ramla Bay], 30.ix.1980, leg. Ph. Pronk, RMNH; **MOROCCO:** 2♂, Tanger, 1–30.viii.1895, Barbier collection, MNHN; **PORTUGAL:** 1♀, Algarve, Mexilhoeira Grande, 19.viii.2015, leg. J. D'Haeseleer, TJWC; **ROMANIA:** 1♀, Mamaia, 6.vi.1961, K. Bleyl, RMNH; **SERBIA:** 2♀, Deliblato, 23.vii.1886, André collection, MNHN; **SPAIN:** 24♂, 2♀, Almería, El Alquián, 20.v.1960, RMNH; **TURKEY:** 2♂, Pamukale, 15 km N of Denizli, 13.vii.1980, H. v. Oorschot, RMNH; **TURKMENISTAN:** 1♂, Achkhabad, Grosse-Barsuki, 25.v.1916, Barbier collection, MNHN; **UKRAINE:** 1♂, Измаилъская обл [Izmail Oblast] окр г. Килия [district of Kiliya], 11.vi.1951, leg. A. Осыцнюк [A. Osytshnjuk], RMNH.

Remarks. The type material of *Nomiapis bispinosa* was considered to be lost [8,11]. Careful examination of the MNHN collection has resulted in the discovery of one male from the Brullé collection collected during the 'Morée,' which was the Morea expedition [*Expédition de Morée*] by the French army during 1828–1833 to the Peloponnese, which was accompanied by a scientific commission [*Expédition Scientifique de Morée*]. The specimen was labelled as *Nomia bispinosa* by Brullé (code 767). Vachal [31] said he examined the type of *Nomia bispinosa* and, given that most species described by Brullé are single specimens, it is probably a holotype. It is not possible to conclude this from the original description, so the present specimen is designated as the lectotype. *Nomiapis bispinosa* can be separated from its two closely related sister species predominantly by the density of the punctures of the scutum in the female sex and the shape of the pair of raised tubercles on S6 in the male sex, see Table 3.

Table 3. Determination table to morphologically separate members of the *Nomiapis bispinosa* (Brullé, 1832) group. Key characters are highlighted in bold.

Morphological Feature	***Nomiapis bispinosa* (Brullé, 1832)**	***Nomiapis rufiventris* (Spinola, 1838)**	***Nomiapis paulyi* spec. nov.**
Scutum punctation, ♀	**Very coarsely and unevenly punctate** with many large interspaces clearly larger than one puncture diameter, usually greater than two puncture diameters	**Densely and evenly punctate on most of its surface, few interspaces greater than one puncture diameter**; punctation contiguous in the anterior quarter, subcontiguous laterally between parapsidal line and lateral margin of scutum; disc with many interspaces larger than two punctures diameter(except in Egyptian specimens in which scutum punctuation approaches that of *N. bispinosa*)	**More densely and evenly punctate over most of its surface, punctures contiguous in the anterior third** and laterally between parapsidal line and lateral margin of scutum; disc with only a few interspaces greater than two punctures diameters
T1 punctation, ♀	**Punctation is remarkably coarse and dense**, somewhat sparser laterally on the disc but not forming two clear impunctate areas (impunctate areas at most as wide as 2/as long as 5 puncture diameters)	Punctation finer and denser, sparser laterally on the disc with **two distinct impunctate areas** (usually wider than 2/longer than 8–9 puncture diameters)	Punctation is finer and denser, somewhat sparser laterally on the disc but **without two clear impunctate areas** (impunctate areas as wide as 2/as long as 5 punctures diameters)
Disc of T2, ♀	Disc of T2 with at most a pair of inconspicuous impunctate areas	Disc of T2 with a pair of conspicuous long impunctate areas measuring around 1/4th of the width of the tergum in length and around as wide as 3–4 puncture diameters).	Disc of T2 with at most a pair of inconspicuous impunctate areas
Marginal area of T2–3, ♀	**Depression of T2 punctate basally for 1/3rd of its length at most**; depression of T3 is basally punctate with only 3–4 rows of punctures on the transition between the disc and the depression, covering less than 1/3rd of its length	**Depression of T2 punctate basally punctate for $\frac{1}{2}$ of its length at most**; depression of T3 with many rows of punctures covering around 1/3rd of its length	**Depression of T2 punctate basally more than 1/2 of its length (almost 2/3rds)**; depression of T3 with many rows of punctures covering around 1/2 of its length
Sternum 6, ♂	**S6 with a pair of strongly produced tubercles medially**, clearly forming a strong triangular shape	**S6 with a pair of weakly produced tubercles medially**, forming a weak triangle	**S6 with a pair of weakly produced tubercles medially**, forming a weak triangle
Body size, ♂	**Larger**, 10–12 mm	**Smaller**, 7–9 mm	**Smaller**, 7–9 mm
Depression of T2-T3, ♂	**The transition between disc and depression is sharp**, edge almost carina-like; punctation is almost indistinct in dorsal view, punctation restricted to two rows of punctures, so punctation does not extend onto the flat basal part of the depression	**The transition between disc and depression is smoother**, with punctation distinct in dorsal view, with around four rows of punctures that extend on the flat basal part of the depression (covering the basal fifth of the depression)	**The transition between disc and depression is smoother**, with punctation distinct in the dorsal view, with around four rows of punctures (sometimes more) that extend on the flat basal part of the depression (covering at least the basal fifth of the depression)
Tibia 3, ♂	Hind tibia with inner margin usually slightly bisinuate, without notable angle following the basal depression; inner margin apically carinate, but the carina usually does not reach the basal depression	Hind tibia with inner margin comparatively more depressed basally with a subsequent more pronounced angle; inner margin usually crossed over by a sharp carina that runs over up to the basal depression	Hind tibia with inner margin usually slightly bisinuate, without notable angle following the basal depression; inner margin apically carinate, but the carina usually does not reach the basal depression

Spinola [1] published two *Nomia* species based on Egyptian material, citing the French expedition to the country in 1798–1801, "*Exp. d'Eg., loc. cit.*", referring to Savigny [32]. Note that Baker [11] lists the publication of Spinola as 1839, but this is not the position of other authors (e.g., [33]). We follow their position that the year of publication is 1838. *Nomia rufiventris* Spinola, 1838 was described in the female sex and *Nomia ruficornis* Spinola, 1838 was described in the male sex. It was not clear that the two were conspecific, as Gerstäcker [4] used the name *Nomia ruficornis* without mentioning *Nomia rufiventris*. Friese [34] considered that *Nomia rufiventris* might be a reddish female of *Nomia ruficornis* but did not propose a synonymy. Alfken [6] synonymised the two names under *Nomia rufiventris*, but it is unclear if he examined type material.

We examined the Spinola collection in Turin and were able to locate the type material. Standing above the label of *Nomia rufiventris* (individual specimens are unlabelled, and one must refer to the labels pinned within the box itself, see Casolari & Casolari 1980) was a male *Anthidium* specimen. This is clearly a mistake since both the sex and family are incorrect. Standing to the right of the *Nomia rufiventris* label is a label for '*Nomia calceata*,' which is listed (see [35] for an explanation of the numerical numbering system used in the Spinola collection) as a taxon described by Drège, the specimen coming from '*Cap de Bonne-Espérance*' [Cape of Good Hope, South Africa], from the collection of Drège, with nominally zero specimens placed here. However, a single female *Nomiapis* specimen with red metasomal terga labelled 'Egitto?' [Italian for Egypt] was placed here (Figure 5). The name '*Nomia calceata*' is unpublished, and as *Nomiapis* species are unknown from sub-Saharan Africa, this specimen has clearly been misplaced and is, in fact, the type of *Nomia rufiventris*. It is here designated as the lectotype. It may automatically be the holotype, but as Spinola did not indicate how many specimens he examined, this is not clear.

Figure 5. Lectotype specimen of *Nomia rufiventris* Spinola, 1838, female. (**A**) Label details, (**B**) Profile, (**C**) Dorsal view, (**D**) Terga, dorsal view.

Examination of the specimen reveals that it is not conspecific with *Nomiapis bispinosa*, as thought by Warncke ([8], as *Nomia unidentata*) and Baker [11]. The scutal punctation is relatively coarse and sparse, suggesting *Nomiapis bispinosa*, but Egyptian specimens of the North African *Nomiapis* taxon display this character state when compared to material from Morocco and Algeria (see Table 3). Importantly, the punctation of the marginal area of T2 covers $\frac{1}{2}$ of its area (Figure 5D), whereas, in *Nomiapis bispinosa,* the punctures cover only 1/3rd of the marginal area of T2 (Figure 6). The disc of T2 also has two lateral impunctate zones mediolaterally (Figure 5D), which are absent in *Nomiapis bispinosa* (Figure 6). *Nomiapis rufiventris* is, therefore, not conspecific with *Nomiapis bispinosa* and is the valid name for the North African *Nomiapis* taxon (see below). The red terga are not significant, as bee specimens from hot regions often display red colouring that is not expressed in specimens from cooler climes, as can be seen within *Andrena afzeliella* (Kirby, 1802) from Egypt (*Andrena afzeliella* var. *heliopolis* Friese, 1914, [17]). A final note, though the description of *Nomia rufiventris* Spinola [1] mentions that the taxon is illustrated in Savigny [32] on "*pl. 5, Figure 17, ♀*", this illustration displays what appears to be a female *Lipotriches parca* (Kohl, 1906). We believe that this is a misnumbering or typographical error by Spinola, as the lectotype specimen is clearly a *Nomiapis* with large tegulae.

Figure 6. Detailed dorsal view of terga of female *Nomiapis bispinosa* (Brullé, 1832) (France, Arles, Salins de Beauduc).

The type of *Nomia ruficornis* was located in its expected place (Figure 4). This specimen belongs to *Nomiapis bispinosa* due to its comparatively large body size, depression of T3 sharply depressed and with a sharp carina separating it from the tergal disc, and the marginal area with only a single line of very narrow punctures basally. It is also designated as a lectotype, following the same logic as for *Nomia rufiventris*. Therefore, its synonymy with *Nomiapis bispinosa,* as listed by Baker [11], is confirmed to be correct.

One outstanding issue is the identity of *Nomia aureocincta* Costa, 1861. The original description does not allow a clear distinction because the males of *Nomiapis bispinosa* and *Nomiapis rufiventris* are morphologically extremely similar. Both species occur in Sicily and might occur in the neighbouring region of Calabria. Warncke [8] synonymised *Nomia aureocincta* with *Nomia unidentata*, but type revision will be needed to see if *Nomia aureocincta* belongs to *Nomiapis bispinosa* s. str. or to *Nomiapis rufiventris*. We also consider *Nomia polita* Costa, 1861 to be a probable synonym of *Nomiapis bispinosa*, as suggested by Warncke [8]. Baker [11] placed it with doubts among the synonyms of *Nomiapis monstrosa* (Costa, 1861) without any justification except that of the misunderstanding of Warncke [8] regarding the application of the name of *Nomia unidentata*. Astafurova & Pesenko [19] list the taxon as a synonym of *Nomiapis bispinosa*. The description of *Nomia polita* fits *Nomiapis bispinosa* better (hair fringes on T2-4; scutal punctuation sparse), and this taxon is much more common in Italy than *Nomiapis monstrosa* and more likely to be collected around Naples, though this should be confirmed by type examination.

In Iberia, France, and Corsica, *Nomiapis bispinosa* is strongly halophilic, nesting in saline soils, both on the coast and also inland in central Spain on salt steppe ([36], as *Pseudapis monstrosa* (Costa, 1861), misidentification; RLD & TJW *pers. obs.*). It is, therefore, less commonly encountered than *Nomiapis paulyi* (see below), which can be found on a wide range of soil types, from coastal sands to calcareous steppe soil. The distribution and nesting ecology of *Nomiapis bispinosa* s. str. should be carefully studied in light of these taxonomic changes to confirm if this behaviour is consistent across its distribution, though based on material studied here (Figure 7), it does appear to be strongly associated with coastal environments or salt steppe at inland localities. It is parasitised by *Pasites maculatus* Jurine, 1807 (36; RLD & TJW *pers. obs.*). Very few pollen loads were available, but *Nomiapis bispinosa* was observed to collect pollen from *Limonium* (Plumbaginaceae) in Central Spain, reflecting its halophilic distribution, as well as from *Onopordum* (Asteraceae, Table 4). Additional samples will confirm that *Nomiapis bispinosa* is polylectic, as is the case in other *Nomiapis* species.

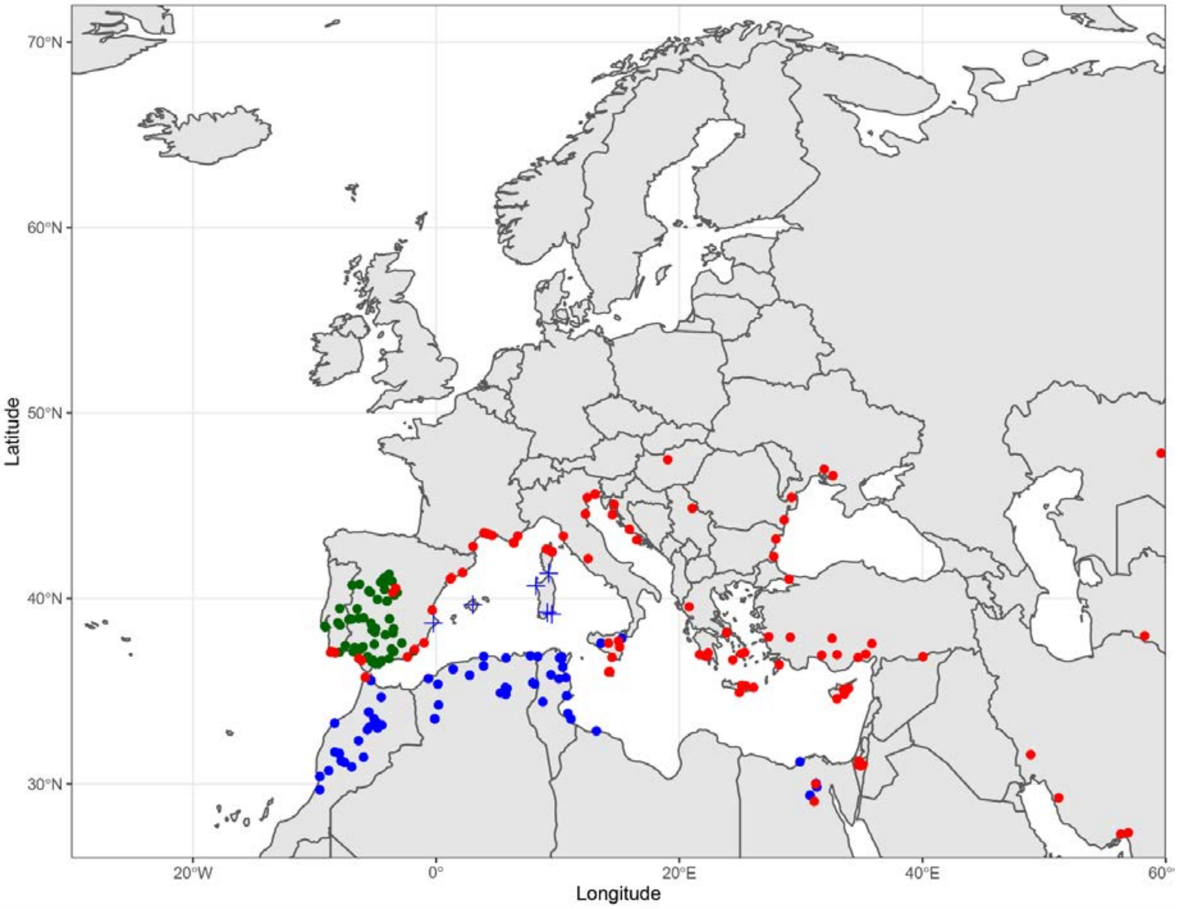

Figure 7. Distribution of taxa within *Nomiapis bispinosa* (Brullé, 1832) s.l.; *Nomiapis bispinosa* s. str. is marked in red, *Nomiapis rufiventris* (Spinola, 1838) is marked in blue, and *Nomiapis paulyi* **spec. nov.** is marked in green. Ambiguous *Nomiapis rufiventris* specimens are marked with a blue cross.

Table 4. Host plant use and diet categories for selected *Nomiapis* species. *N*, number of analysed pollen loads; *n*, number of unique sampling localities. Plant taxa: API, Apiaceae; AST, Asteraceae; BRA, Brassicaceae; CAP, Caprifoliaceae; CON, Convolvulaceae; FAB, Fabaceae; FRA, Frankeniaceae; HYP, Hypericaceae; LAM, Lamiaceae; PLA, Plantaginaceae; PLU, Plumbaginaceae; RAN, Ranunculaceae; ROS, Rosaceae; RUB, Rubiaceae.

Species	*N*	*n*	Result of Microscopic Analysis of Pollen Grains (% of Pollen Grains)	Percentage of Pure Loads of Preferred Host	Percentage of Loads with Preferred Host	Host Range
Nomiapis bispinosa (Brullé, 1832)	3	1	PLU 61.9, AST 38.1	66.7	66.7	Polylectic s. str.
Nomiapis diversipes (Latreille, 1806)	19	14	FAB 35.4, FRA 10.8, ROS 10.8, PLA 9.5, LAM 7.9, AST 7.7, RUB 4.8, CON 4.1, HYP 4.1, RAN 3.2, others 1.8	15.8	63.2	Polylectic s. str.
Nomiapis paulyi **spec. nov.**	11	8	AST 49.5, LAM 14.0, API 11.3, CAP 9.5, BRA 7.9, RUB 2.4, others 5.3	27.2	54.5	Polylectic s. str.

Distribution. In North Africa, we could only confirm its occurrence in Tangier (northern Morocco) and Egypt. The distribution is, therefore, northern Morocco, Iberia, southern France (including Corsica), Italy, southern parts of Central Europe (Hungary, Ukraine), Balkan Peninsula, Turkey, Cyprus, Egypt, Israel (Negev), Iran, the Caucasus to Central Asia, northern India, and north-western China (Figure 7.

Nomiapis rufiventris (Spinola, 1838) **sp. resurr.**

Nomia rufiventris Spinola, 1838: 513; ♀Egypt [MRSN, lectotype by present designation].

Nomia albocincta Lucas, 1849: 187; ♀La Calle, Lac Tonga, Algeria [MNHN, lectotype by present designation] **syn. nov.**

Nomia perforata Lucas, 1849: 185; ♂La Calle, Lac Tonga, Algeria [MNHN] **syn. nov.**

Type material examined.—Lectotype of *Nomia rufiventris* Spinola (present designation): 183//Egitto?//*Nomia rufiventris* ♀Spinola, 1838 LECTOTYPE des. WOOD 2022//*Nomia rufiventris*, ♀m. Ann. Soc. ent. D. Waltl. Egypte (Figure 5).

–Lectotype of *Nomia albocincta* Lucas (present designation): Blue circle [underside with the locality code 1525 referring Lucas's manuscript)//*Nomia albocincta*, Luc. ♀//LECTOTYPE //Lectotype *Nomia albocincta* Lucas Le Divelec des. 2022//*Nomiapis albocincta* (Lucas, 1849) Le Divelec det. 2022//MNHN, Paris EY33640 (Figures 8 and 9).

–Paralectotype of *Nomia albocincta* Lucas: Blue circle [underside with the locality code 1525 referring Lucas's manuscript)//*Nomia albocincta*, Luc.//PARALECTOTYPE//Paralectotype *Nomia albocincta* Lucas Le Divelec des. 2022//*Nomiapis albocincta* (Lucas, 1849) Le Divelec det. 2022.

–Holotype of *Nomia perforata* Lucas: Blue circle [underside with the locality code 1258 referring Lucas's manuscript)//*Nomia armata*, Luc. ♂//*Nomia albocincta*, Lucas est la femelle de la *Nomia armata* Lucas ♂//HOLOTYPE//Holotype *Nomia perforata* Lucas—Le Divelec 2022//*Nomiapis albocincta* (Lucas, 1849) Le Divelec det. 2022//MNHN, Paris EY33639 (Figure 10).

Other material examined (illustrative, see Table S1). ALGERIA: 1♀, La Calle [El Kala], 26.vii.1910, Ferton collection, MNHN; **EGYPT:** 1♀, Cairo, 13.vi.1939, MNHN; **ITALY:** 1♂, Sicily, Pérez collection, MNHN; **LIBYA:** 1♂, Tripolis, OÖLM; **MOROCCO:** 1♂, 4♀, Fès-Meknès, Midelt, R503, W of Aït Ali, Oued Taourda, 1550 m, leg. T.J. Wood, TJWC; **TUNISIA:** 1♂, Djerba, 14.iv.1955, leg. P.M.F. Verhoeff, RMNH.

Unclear material (*Nomiapis* cf. *rufiventris*). FRANCE: 1♀, Corsica, Bonifacio, Cavallo Island, 24.ix.1898, Ferton collection, MNHN; **ITALY:** 1♂, Sardinia, Cagliari, 15–20.vii.1959, leg. H. Wolf, RMNH; 1♀, Sardinia, Villasimius, 1–30.vi.1975, leg. Bouček, RMNH; **SPAIN:** 1♀, Benifato, Alicante, 12.vi.1978, leg. H. Teunissen, RMNH; 2♂, Mallorca, 1–24.vi.1954, leg. Klokke—Moll, RMNH.

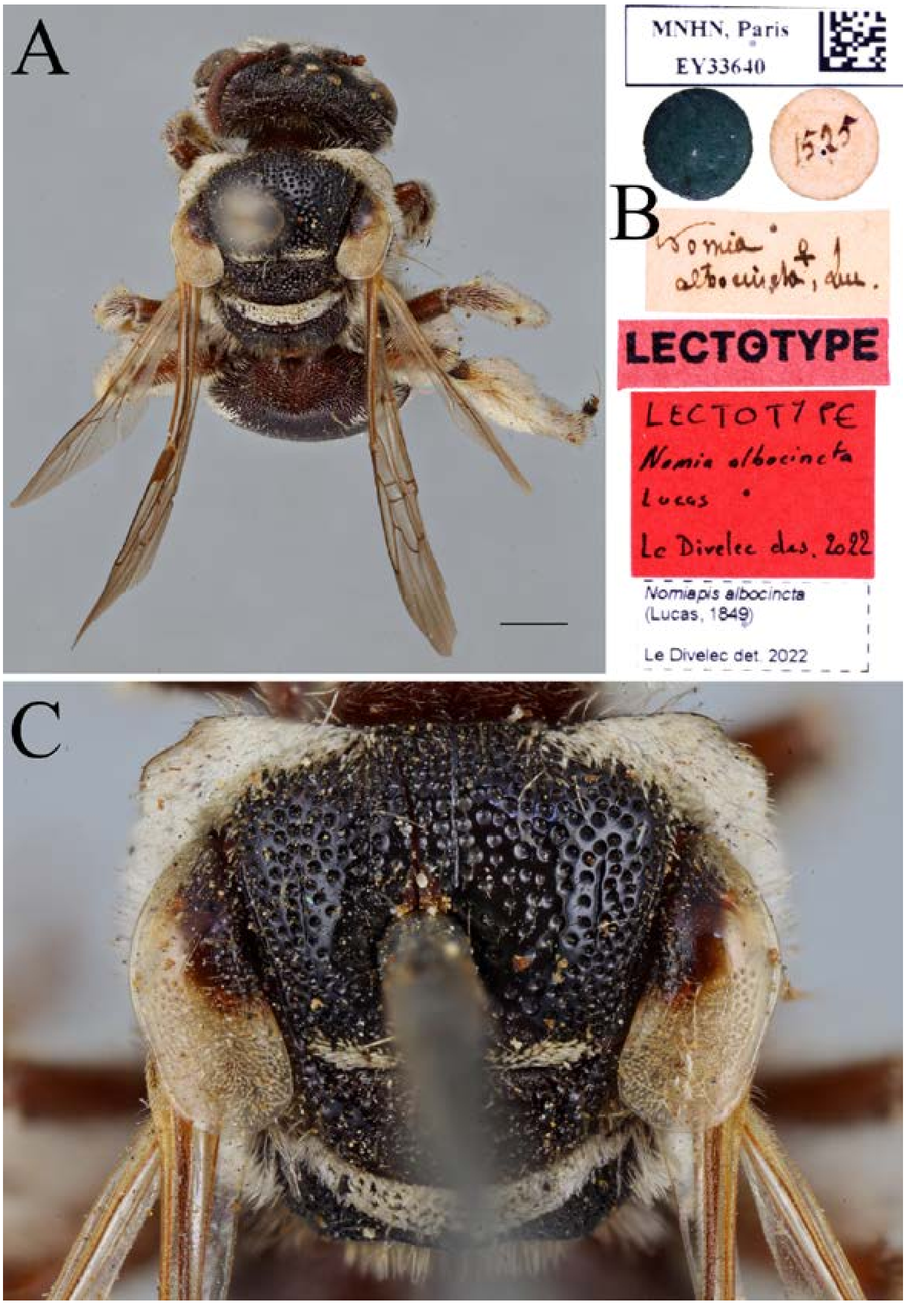

Figure 8. Lectotype specimen of *Nomia albocincta* Lucas, 1849, female. (**A**) Dorsal view, (**B**) Label details, (**C**) Scutum, dorsal view. Scale = 1 mm.

Remarks. Genetic results strongly support a North African taxon from Morocco to Egypt, with this taxon extending north into Sicily based on morphology. As discussed above, the oldest name for this taxon is *Nomiapis rufiventris*. The next oldest names from North Africa come from Lucas [2]. Lucas mentioned four specimens for the three species of *Nomia* described from Algeria, and these remain in his collection. Two specimens are his females of *Nomia albocincta*, one is the holotype of *Nomia flavilabris* Lucas, 1849 which is actually a male of *Ancyla oraniensis* Lepeletier, 1841 and not a female of *Nomia* despite being described as such, and one is a male *Nomiapis* labelled as "*armata* Lucas". *Nomia armata* Lucas was never described. The collecting station code of this specimen is 1258. It is similar to the code used for *Nomia flavilabris* and refers to Lac Tonga in June, according to the unpublished catalogue of Lucas, which is housed at the MNHN. As mentioned by Lucas [2], *Nomia flavilabris* was collected in the same place and at the same time as *Nomia* *perforata*, which was in June 1841, around Lac Tonga. For this reason, we consider the present specimen to be the holotype of *Nomia perforata* which was not properly labelled after its description. The holotype matches the original description and drawings. Vachal [31], who examined the type of *Nomia perforata,* considered it to be the same species as *Nomia albocincta*. Lucas also added a label to this specimen stating that *Nomia armata* Lucas was the male of *Nomia albocincta* Lucas. Examination of the type confirms these statements. Both names are synonymised with *Nomiapis rufiventris*.

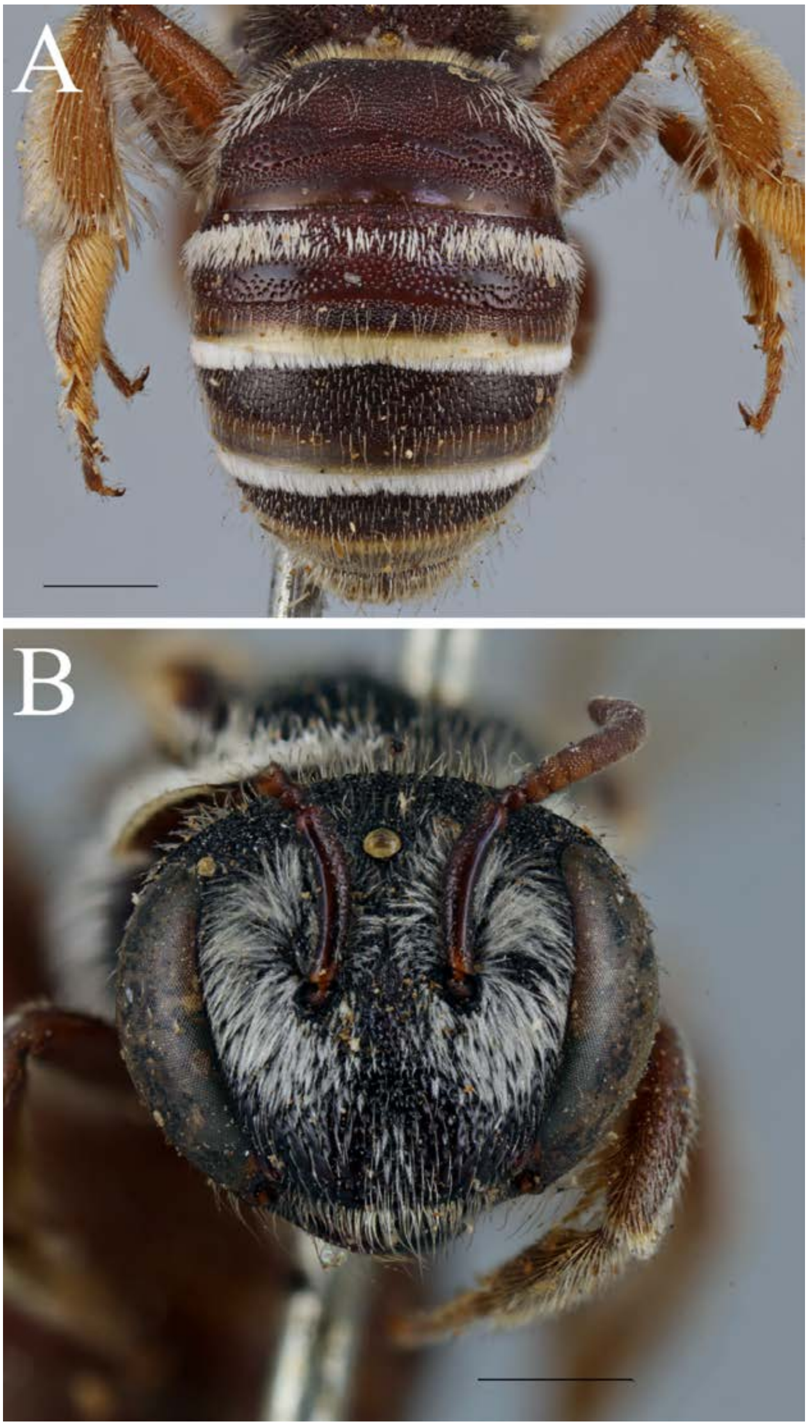

Figure 9. Lectotype specimen of *Nomia albocincta* Lucas, 1849, female. (**A**) Terga detail, (**B**) Face, frontal view. Scale = 1 mm.

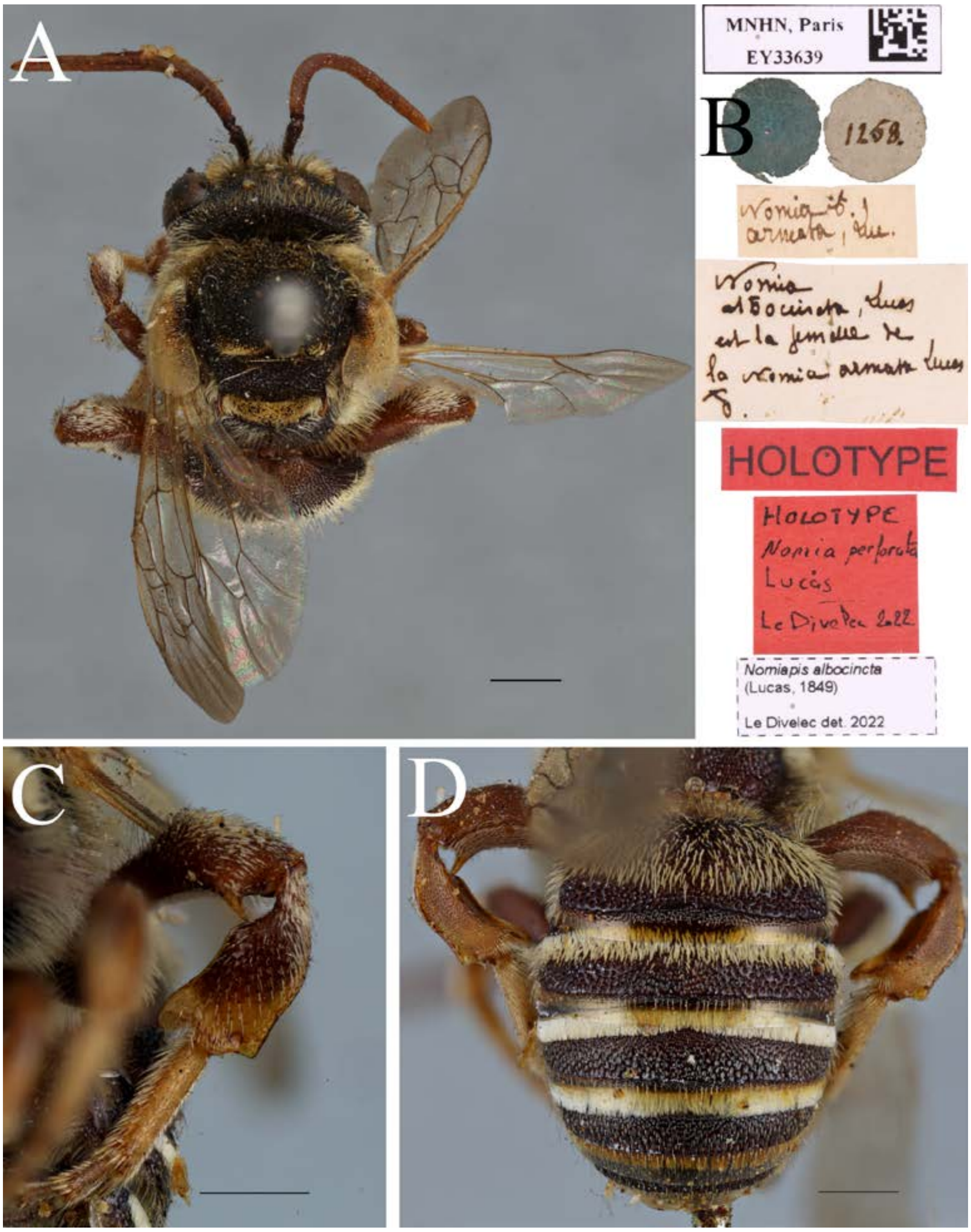

Figure 10. Holotype specimen of *Nomia perforata* Lucas, 1849, female. (**A**) Dorsal view, (**B**) Label details, (**C**) Hind leg, (**D**) Terga, dorsal view. Scale = 1 mm.

Nomiapis rufiventris can be most easily recognised in the female sex by the punctation of the scutum. The punctation is finer and denser than in *Nomiapis bispinosa* but less dense than in *Nomiapis paulyi* (see below). It is, therefore, intermediate between the two. Males can be separated from *Nomiapis bispinosa* by the smaller tubercles of S6, but separation from males of *Nomiapis paulyi* is challenging, and reference is best made to the determination table below (Table 3). As mentioned, female Egyptian *Nomiapis rufiventris* have the punctation of the scutum a little less dense than in specimens from north-western Africa and thus begin to approach the condition in *Nomiapis bispinosa* s. str. However, barcoded specimens from Egypt and Morocco showed almost no genetic differentiation (maximum 0.38%) and hence are considered conspecific.

Specimens from the Balearic Islands (Mallorca), Sardinia (reported as *Pseudapis unidentata albocincta* by [37]), a single female specimen from Corsica, and a single female specimen from eastern Spain (Alicante) have an ambiguous morphology that is closest to *Nomiapis* *rufiventris*, but they could potentially belong to *Nomiapis paulyi*. In the absence of genetic data from these regions, we refrain from a decisive determination and await further genetic work to decisively settle their placement.

Distribution. Morocco, Algeria, Tunisia, Italy (Sicily and southern Italy), Libya, and Egypt (Figure 7). Based on re-examined material (RMNH), records of *Pseudapis* (*Nomiapis*) *unidentata albocincta* from Malta [37] are *Nomiapis bispinosa* (see Table S1). In Europe, *Nomiapis rufiventris* occurs in Sicily. This record is based on two males. The identity of Sicilian material, as well as ambiguous material from the Balearics, Corsica, and Sardinia, should be confirmed in the future by genetic barcodes.

Nomiapis paulyi Wood & Le Divelec, **spec. nov**.

Holotype. SPAIN: 1♀, Segovia, Camino Natural Vía Verde Valle del Eresma, 40.9286° N, −4.1210° W, 18.vii.2019, leg. TJWC, RMNH. Barcoded, reference TJW_028, BOLD WPATW767-22.

Paratypes. PORTUGAL: 1♂, 2♀, Alg. [Algarve] Pr. do Castela [Praia do Castelo], 1–15.vii.1977, leg. P.M.F. Verhoeff, RMNH; 1♂, Alto Alentejo, bij Aquaduct van Elvas, langs N 4, 28.vii.1970, leg. E.N. Kuijper, RMNH; 3♂, 4♀, Alto Alentejo, lands E 4 tuss. Montemor O Novo & Arraiolos, 28.vii.1970, leg. Ph. Pronk, RMNH; 3♂, Evora, 24.vii.1953; leg. P.M.F. Verhoeff, RMNH; 1♂, Gavião, Portall.P., 31.v.1979, leg. H. Teunissen, RMNH; 1♂, Algarve, Santa Bárbara de Nexe, 20.ix.1980, leg. H. Teunissen, RMNH; 2♂, Algarve, Lagos, 3.viii.1968, leg. K. Warncke, OÖLM; 1♂, Algarve, Alcoutim, 24.viii.1968, leg. K. Warncke, OÖLM; **SPAIN:** 1♀, 10 km SW El Escorial, 1200 m, 23.vii.1972, leg. M.J. & J.P. Duffels, RMNH; 1♂, Alcaracejos, Córdoba, 19.vi.1961, leg. J. v. d. Vecht, RMNH; 1♀, Aznalcázar, S of Pinares de Aznalcázar, 21.v.2021, leg. T.J. Wood, TJWC; 7♂, Badajoz, Mérida, 29–30.vi.1968, leg. P.M.F. Verhoeff, RMNH; 1♂, Benalauría, Puerto de Benalauría, 1.vi.2021, leg. G. Ghisbain, G. Ghisbain collection (Mons, Belgium); 1♂, Málaga, Benaoján, 2.viii.1978, leg. R. Leys, RMNH; 1♂, Segovia, Bernuy de Porreros, Fuente de los Caños, 20.vii.2021, leg. T.J. Wood, TJWC; 10♂, 1♀, Cádiz, Jerez de la Frontera, 10.ix.1961, leg. P.M.F. Verhoeff; RMNH; 1♀, Jerez de la Frontera, 1.viii.1964, leg. P.M.F. Verhoeff; RMNH; 2♂, 1♀, Jerez de la Frontera, 15.ix.1965, leg. P.M.F. Verhoeff; RMNH; 1♂, Segovia, Carbonero el Mayor, 2 km SW, Calle las Tejeras to Río Eresma, 18.vii.2021, leg. T.J. Wood, TJWC; 1♀, Segovia, Carbonero el Mayor, 500 m W, Calle las Tejeras, 18.vii.2021, leg. T.J. Wood, TJWC; 1♂, Écija, 18.ix.1952, leg. Bär, Blöte, de Jong, Osse, RMNH; 1♂, El Bosque, Cádiz, 27.vii.1978, leg. R. Leys, RMNH; 1♂, 1♀, Ávila, El Losar del Barco, 2 km N, 17.vii.2020, leg. T.J. Wood, TJWC; 1♂, 3♀, env. Calahonda, betw. Fuengirola-Marbella; 4–9.ix.1975, leg. C. v. Heijningen, RMNH; 5♀, env. La Carolina (Jaén), bridge Rio Guarrizas, 14.vi.1961, leg. Ph. Pronk, J. v. d. Vecht, C. v. Heijningen, RMNH; 1♂, 1♀, Córdoba, Espiel, 19.vi.1961, leg. J. Wiebes & J. v. d. Vecht, RMNH; 1♂, Extremadura, Badajoz, 25.vii.1953, leg. P.M.F. Verhoeff; RMNH; 1♀, Granada, Baños de Zújar, 19.vi.1970, leg. M.C. & G. Kruseman, RMNH; 1♂, Granada, Canales, 22.vii.1978, leg. R. Leys, RMNH; 2♂, 2♀, Granada, Pantano de Cubillas, 27.v-9.vi.1978, leg. R. Leys, RMNH; 1♂, Helechar [Helechal], Badajoz, 20.vi.1961, leg. J. v. d. Vecht, RMNH; 5♀, Jaén, env. of Sta. Elena, 15.vi.1961, leg. C. v. Heijningen, RMNH; 1♂, Málaga, Júzcar, Júzcar to Sendero de la Eras, 29.v.2021, leg. T.J. Wood, TJWC; 1♀, La Aliseda [La Aliseda de Tormes], Ávila, 23.vi.1961, leg. C. v. Heijningen, RMNH; 2♂, Las Correderas (Jaén), 25.v.1958, RMNH; 1♀, Las Correderas (Jaén), 16.vi.1961, leg. J. v. d. Vecht, RMNH; 1♂, Lozoyuela [Lozoyuela-Navas-Sieteiglesias], 10.ix.1952, leg. Bär, Blöte, de Jong, Osse, RMNH; 2♀, Madrid, Chinchón, 6 km N, M-311, 8.vii.2021, leg. T.J. Wood, TJWC; 1♀, Málaga, Benalmádena, 29.v.1962, leg. Jeekel & Wiering, RMNH; 1♂, Málaga, Nerja, 18.ix.1969, leg. C.A.W. & A.M. Jeekel, RMNH; 3♂, Málaga, San Julián 8 km SW of Málaga, 25.v.1962, leg. Jeekel & Wiering, RMNH; 5♂, Málaga, San Pedro de Alcántara, 12–15.v.1960, RMNH; 1♀, Malpartida de Cáceres, 6.vi.1979, leg. H. Teunissen, RMNH; 3♀, Marmolejo, Jaén, 27.v.1979, leg. H. Teunissen, RMNH; 1♂, Martín de Yeltes, Salamanca, 22.vi.1981, leg. H. Teunissen, RMNH; 1♀, Mazagón, Huelva, 22.iv.1985, leg. H. Teunissen, RMNH; 1♀, Medellín, bed of Río Guadiana (Badajoz), 20.vi.1961, leg. J. v. d. Vecht, RMNH; 1♀, Madrid, Pozuelo del Rey, 2 km NW, 10.vii.2021, leg. T.J. Wood, TJWC; 1♂, 2♀, Segovia, Sanchidrián, Esquistos con metarcosas del Precámbrico, 19.vii.2021, leg. T.J. Wood, TJWC; 2♂, 1♀, Sevilla, 29.vii.1950, leg. P.M.F. Verhoeff, RMNH; 3♂, Sevilla, 19.vi.1963, leg. P.M.F. Verhoeff, RMNH; 1♂, Sevilla, Villamanrique [Villamanrique de la Condesa], 8 km SW Pilas, 13.vii.1969, leg. H. Overbeek, RMNH; 1♂, 1♀, Sierra-Morena, El Soldado [Villanueva del Duque], 1.vii.1927, leg. A. Seyrig, MNHN; 1♂, Toledo, 25.vii.1967, leg. P.M.F. Verhoeff, RMNH; 4♂, 1♀, Toledo, 16–18.viii.1967, leg. P.M.F. Verhoeff, RMNH; 2♀, Toledo, 2–3.vii.1968, leg. P.M.F. Verhoeff, RMNH; 1♀, Toledo, 9–10.vi.1968, leg. P.M.F. Verhoeff, RMNH; 2♂, 1♀, Toledo, Alto de Tiendas, 28.v.1995, leg. H. & J.E. Wiering, RMNH; 1♂, Toledo, Talavera de la Reina, 14.ix.1960, leg. H. Wiering, RMNH; 3♂, Villamartín [Cádiz], 30.vii.1950, leg. P.M.F. Verhoeff, RMNH; 2♀, Segovia, Villar del Olmo, 2 km SE, Arroyo de Val, 11.vii.2021, leg. T.J. Wood, TJWC; 1♂, Segovia, Villaseca, Ermita de San Frutos, fields to south and east, 24.vii.2021, leg. T.J. Wood, TJWC; 2♂, 1♀, Huelva, Niebla, 13.viii.1968, leg. K. Warncke, OÖLM;

Diagnosis. *Nomiapis paulyi* can be recognised within *Nomiapis* as being part of the *bispinosa* group in the female sex due to the strongly punctate and dull disc of T1 and the weakly and obscurely punctate disc of T3 that strongly contrasts the discs of T1-2 (Figure 11). In the male sex, it can be recognised by the shape of the hind leg, with a 'normal' hind femur (not grossly enlarged as in other *Nomiapis* species) which has only very short squamous hairs ventrally (shorter than the width of a flagellum) and the hind tibia is compact, with the apex only produced into a short rounded extension ventrally, not grossly enlarged or forming a long extension (Figure 12C).

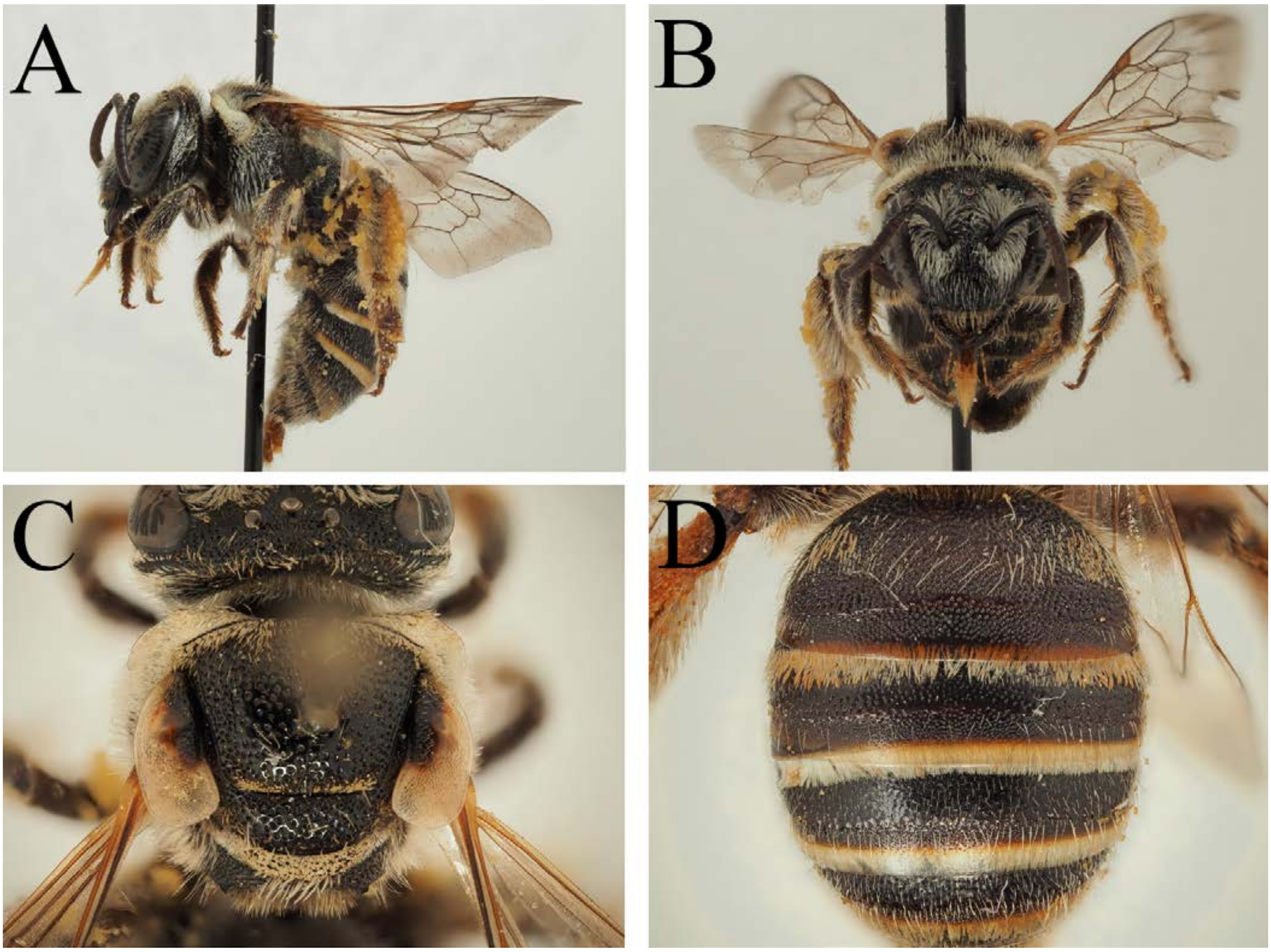

Figure 11. *Nomiapis paulyi* **spec. nov.** female. (**A**) Profile, (**B**) Face, frontal view, (**C**) Scutum, dorsal view, (**D**) Terga, dorsal view.

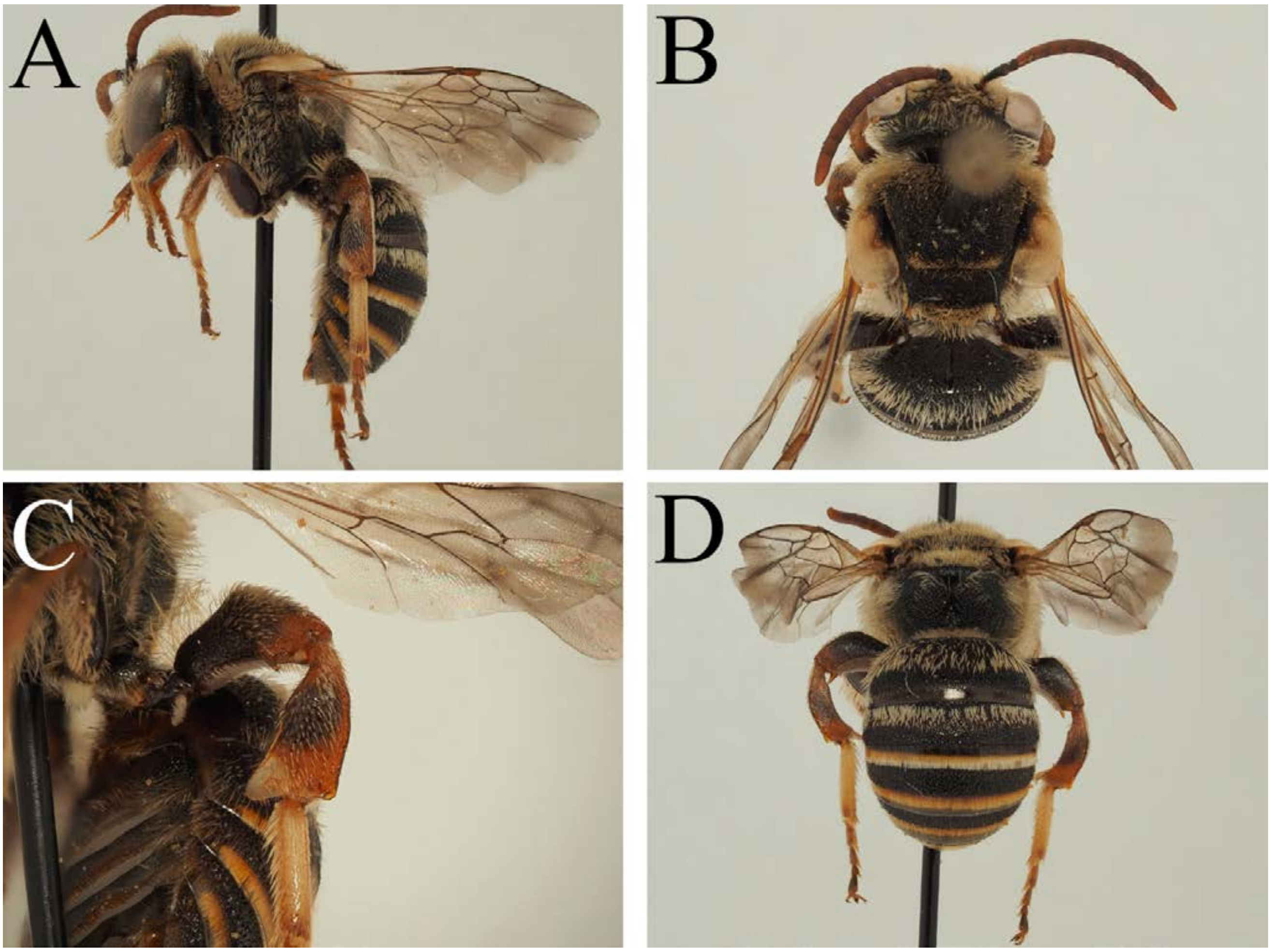

Figure 12. *Nomiapis paulyi* **spec. nov.** male. (**A**) Profile, (**B**) Scutum, dorsal view, (**C**) Hind leg, (**D**) Terga, dorsal view.

The female can be separated from *Nomiapis bispinosa* (alternative character state in parentheses) by the densely punctate scutum with medial punctures separated by 0.5–2 puncture diameters but generally by 1 puncture diameter (scutum irregularly punctate with many large interspaces that are usually greater than 2 puncture diameters medially), and the depression of T2 is punctate basally for more than $\frac{1}{2}$ of its length (depression of T2 punctate basally for at most 1/3rd of its length). Males can be separated from *Nomiapis bispinosa* by the smaller body size of 7–9 mm (10–12 mm), the small and weakly produced pair of tubercles on S6 (Figure 13A; S6 with a pair of strongly produced tubercles, Figure 13B), and the depression of T3 which is weakly differentiated from the disc, with the depression basally possessing around four distinct rows of punctures that extend into the depression itself (depression of T3 strongly differentiated from the disc, the edge of the disc sharp, almost carina-like, the depression of T3 with one to two rows of punctures at most, these almost indistinct, not extending far onto the depression).

The smaller body size places *Nomiapis paulyi* closer to *Nomiapis rufiventris* that, to our knowledge, cannot be found in sympatry. Females can be separated by comparison of the tergal punctures. *Nomiapis paulyi* has T1 without two clear elongate impunctate areas lateromedially on the disc (T1 with two clear elongate impunctate areas lateromedially on the disc), T2 is more densely punctate, without clear elongate impunctate areas lateromedially on the disc (T2 less densely punctate, with two clear elongate impunctate areas lateromedially on the disc), and the medial scutal punctures are denser, typically separated by 1 puncture diameter (medial scutal punctures sparser, typically separated by more than 1 puncture diameter). At the moment, there is no clear character that allows the separation of males of *Nomiapis paulyi* and *Nomiapis rufiventris*. There may be small differences in the structure of the hind tibia, with this being apically broader in *Nomiapis paulyi* and narrower in *Nomiapis rufiventris*. For now, males should be separated on the basis of their non-overlapping range (Figure 7). Table 3 provides full comparative details to allow the separation of members of the *bispinosa* group.

Figure 13. *Nomiapis paulyi* **spec. nov.** male. (**A**) Sterna, ventral view (Spain, Jaén, Las Correderas). *Nomiapis bispinosa* (Brullé, 1832). (**B**) Sterna, ventral view (Spain, Almería, El Alquián).

Description. Female. Body length. 8–9 mm (Figure 11A). **Head.** 1.2 times broader than long (Figure 11B). Clypeus dark, medially with a weak longitudinal impression, densely punctate, punctures separated by 0.5–1 puncture diameter, interspaces shiny, slightly elevated, often joining together to form interconnected longitudinal wrinkles. The paraocular areas and frons have dense white plumose hairs, obscuring the underlying surface. The gena, vertex, and clypeus have longer, sparse, white to brownish hairs. Antennae dark, A3-12 lightened dark brown below, A3 = A4. The vertex is broad, and the ocelloccipital distance equals 2.5 diameters of the lateral ocellus. **Mesosoma.** The scutum is shiny and polished, densely punctate anteriorly and laterally with parapsidal lines and punctures that are almost confluent (Figure 11C). Slightly less densely punctate medially, with punctures separated by 0.5–2 puncture diameters but typically by 1 puncture diameter. The scutellum is densely punctate, with punctures separated by <0.5 puncture diameters, with interspaces weakly shining. The mesepisternum has a strong network of honeycomb-like raised rugosity, underlying surface weakly shining. Honeycomb-like rugosity weakly extending onto dorsolateral parts of propodeum, lateral and posterior faces of propodeum with dense but shallow punctation, puncture separated by 0.5–1 puncture diameters. The scutum anteriorly and posteriorly has a weak hair fringe of dense whitish-yellow hairs, with the metapostnotum entirely covered in dense whitish-yellow hairs; mesepisternum and lateral faces of propodeum with sparser whitish hairs. The tegulae are large, more or less rectangular, equalling the length of the scutum, apically dark brown, laterally and posteriorly yellowish hyaline. The tegulae are impunctate medially at the base of the wings, densely punctate elsewhere, and the punctures are coarsely medially, becoming finer laterally and posteriorly, with punctures confluent. Legs dark, apical tarsal segments lightened dark reddish-brown; general pubescence whitish. The femoral and tibial scopae are composed of uniformly white hairs. The wings are hyaline, with venation and dark orange stigma, and the nervulus is interstitial. **Metasoma.** The T1 with disc densely punctate, with punctures almost confluent medially, becoming slightly sparser laterally, separated by up to 1 puncture diameter. The marginal area of T1 is separated by a narrow, almost impunctate area of 1–2 puncture diameters; the marginal area is densely punctate with 5–6 rows of almost confluent punctures in basal 2/3rds, apical 1/3rd impunctate.

The T2 with disc is irregularly punctate with punctures of different sizes, with punctures becoming stronger and clearer laterally (Figure 11D). The marginal area of T2 is densely punctate over the basal two-thirds with 7–8 rows of small punctures, punctures separated by 0–1 puncture diameters, apical 1/3rd impunctate, hyaline and semi-translucent. The T3 with disc is weakly and obscurely punctate, punctures separated by 1–3 puncture diameters. Marginal area of T3 densely punctate over basal 1/2 with 7–8 rows of small punctures, punctures separated by 0–1 puncture diameters, apical 1/2 impunctate, hyaline and semi-translucent. The lateral corners of T1 and base of T2 with dense, white, adpressed semi-squamous hairs, and these hairs are also present at the base of T3–4, where they are covered by semi-translucent apical margins of T2–3. Marginal areas of T2–4 with very sparse hairs emerging from the junction of marginal area and disc, forming a very weak fringe. The apical fringe of T5 and hairs flanking the pygidial plate are whitish to dark brown. The pygidial plate apically is broadly rounded.

Male. Body length. 7–9 mm. **Head.** 1.2 times broader than long. Clypeus dark, medially densely punctate with punctures confluent, punctures becoming sparser apically, here separated by 1 puncture diameter. The frons, paraocular area, supraclypeal area and clypeus are covered with dense whitish-yellowish plumose hairs. Gena and vertex with sparser light brownish hairs. Scape and pedicel dark, flagellar segments bright orange ventrally, dark red dorsally, A3 = 0.8 × A4. The vertex is broad, and the ocelloccipital distance equals 2.5 diameters of the lateral ocellus. **Mesosoma.** The scutum and scutellum are uniformly densely punctate, with punctures confluent, and the interspaces are dull, lateral corners of the scutellum, each with a small pointed spine. The mesepisternum and propodeum are structurally as in the female. The scutum apically and posteriorly and the metapostnotum has light brown hairs forming a weak fringe, not as strongly produced as in the female. The tegulae are large, more or less rectangular, equalling the length of the scutum, are apically dark brown and laterally and posteriorly yellowish hyaline; entirely densely punctate, with punctures becoming slightly finer laterally and posteriorly. The legs with femorae are dark over the majority of their area and lightened orange apically; the tibiae are predominantly orange with a dark mark medially. The basitarsi are orange with ivory white marks on the outer face, and the remaining tarsal segments are orange, becoming darker apically. The hind femorae are not grossly expanded, apico-ventrally produced into small pointed teeth, ventral face densely covered by white adpressed squamous-flattened hairs. Hind tibiae compact, broad, apico-ventrally produced into a short rounded projection, this projection ivory white. The wings are hyaline, the venation and stigma are dark orange, and the nervulus is interstitial. **Metasoma.** Tergal discs strongly and densely punctate, punctures separated by 0.5–1 puncture diameters. T1 with marginal area densely punctate over basal $\frac{1}{2}$, with 5 rows of confluent punctures. Marginal areas of T2–4 densely punctate over basal 1/3rd with 3–4 rows of confluent punctures, apical 2/3rds lightened hyaline translucent. T1 on the basal part of the disc with long whitish hairs, T2 basally with dense, white, adpressed semi-squamous hairs forming a complete hair band, these hairs present at the base of T3–5 but covered by semi-translucent marginal areas of T2–4.

Etymology. The name is to commend the Belgian entomologist Alain Pauly for his outstanding, detailed, and far-reaching work on bees of the family Halictidae.

Remarks. This is the taxon reported from Portugal and Spain as *Pseudapis unidentata albocincta* by van der Zanden [37] and *Pseudapis bispinosa albocincta* by Wood et al. [21], but which is not conspecific with North African material due to the average 3.42% genetic distance, as well as the morphological differences described above.

Nomiapis paulyi is clearly polylectic, as expected for this genus (Table 4). Nearly half of the pollen was collected from Asteraceae, with almost none collected from Fabaceae. This contrasts with *Nomiapis diversipes* which is also polylectic but which collected some 35% of its pollen from Fabaceae. More study is required to establish if this is a genuine pattern, particularly at sites where the two taxa occur in sympatry. *Nomiapis paulyi* is typically recorded between mid-May and mid-September. Since males can be found in both May and September, the species is clearly at least facultatively bivoltine.

Distribution. Portugal and Spain, though seemingly absent from northern and eastern Iberia (Figure 7).

Genus ***Systropha*** Illiger, 1806

Systropha planidens Giraud, 1861

Systropha planidens Giraud, 1861: 451; ♂♀Austria [MNHN, lectotype by present designation]

Type material examined.—Lectotype of *S. planidens* Giraud (present designation): Autriche//LECTOTYPE//LECTOTYPE—*Systropha planidens* Giraud—Le Divelec des. 2022//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022//MNHN, Paris—EY33648 (Figure 14).

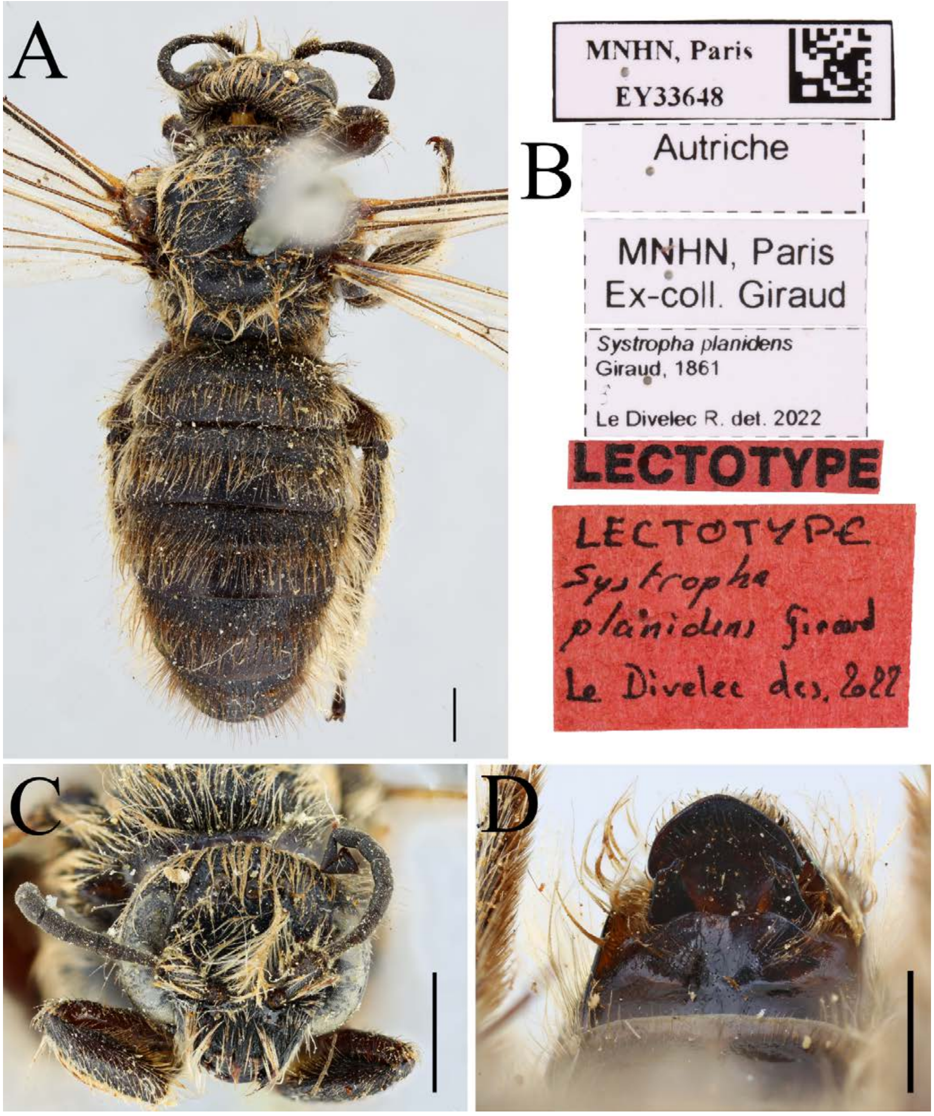

Figure 14. Lectotype specimen of *Systropha planidens* Giraud, 1861, male. (**A**) Dorsal view, (**B**) Label details, (**C**) Face detail, (**D**) Apical sterna, ventral view. Scale = 1 mm.

–Paralectotypes of *S. planidens* Giraud: Autriche//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Autriche//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Autriche//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Autriche//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Autriche//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Blue square label//Bergen-staum.//Autriche—Bergenstaum//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Blue square label//Bergen-staum.//Autriche—Bergenstaum//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha planidens* Giraud, 1861 ♂—Le Divelec det. 2022.—Illegible square label//green rectangular label//hisp. [Hispania]//Espagne [Hisp.]—Dufour L. leg.//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—Espagne [Hisp.]—Dufour L. leg.//PARALECTOTYPE//PARALECTOTYPE—*Systropha planidens* Giraud//MNHN, Paris—Ex-coll. Giraud//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.

Other material examined (illustrative, see Table S1). ARMENIA: 1♀, Arzhakan, 24.vii.1963, leg. G. Soika, OÖLM; **BULGARIA:** 1♂, 30 km SW Svilengrad, 550 m, 21.vi.2008, leg. M. & Z. Halada, OÖLM; **CZECH REPUBLIC:** 2♂, Písek, Pérez Colln., MNHN; **FRANCE:** 2♂, Vogezen, Westhalfen [Westhalten], Zinnköpfe, 1.vii.1951, leg. J. v. Assem, RMNH; **GEORGIA:** 1♀, E of Tianeti, W Akhmeta, 27.vi.2015, leg. M. Snižek, OÖLM; **GERMANY:** 1♂, Würzburg, 1.vii.1876, leg. H. de Vries, RMNH; **GREECE:** 6♂, 1♀, Portaria, 3–4.vi.1971, leg. J. v. d. Vecht & P.M.F. Verhoeff, RMNH; **HUNGARY:** 1♂, 1♀, Budapest, leg. Mocsáry, RMNH; **IRAN:** 1♂, Elburz, Ov Zanak-Ski, 11 km N Ab Ali, 2300 m, 11.vii.1965, leg. G. Soika-Mavromoustakis [G. Soika & G.A. Mavromoustakis], OÖLM; **NORTH MACEDONIA:** 1♂, 2♀, Ohrid, 29.v.1972, leg. H. Teunissen, RMNH; **ROMANIA:** 1♂, Bucharest, Mihai Bravu, 23.vii.1967, leg. G.P. Kruseman, RMNH; **RUSSIA:** 1♀, Sarepta [Volgograd], Vachal Colln., MNHN; **SLOVAKIA:** 1♂, Malý Kamenec, 31.vii.1987, leg. Z. Pádr, OÖLM; **TURKEY:** 2♂, 1♀, Karakurt/Arastal, 12.vi.1977, leg. K. Warncke, OÖLM; **UKRAINE:** 3♂, 2♀, Кировоградская обл. [Kirovogradskaïa], Александрийский р-н. [Oleksandriis'kyi district], Бандуровка [Bandurivka], 12.vii.1953, leg. A. Осычнык [A. Osytshnjuk], RMNH.

Remarks. Giraud [3] described *S. planidens* from multiple countries; "*Je possède des mâles provenant de l'Espagne ... du midi de la France ... et quelques uns que j'ai capturés en Autriche. J'en ai deux ... dans le Musée de Vienne ... d'Amasie [Amasya], dans l'Asie-Mineure*". Baker [10] concluded that the type series was lost, other than the two specimens from Turkey, which are nominally held at the Vienna Museum. He concluded that there "can be no doubt as to the identity of Giraud's Austrian syntypes". Warncke [9] gave the type locality as 'Austria' without locating the type material or designating a lectotype. Given the morphological and genetic evidence supporting the species-specific status of material from Spain and the morphological evidence supporting the specific-specific status of material from Turkey (see below), it is highly likely that Giraud's original type series was polytypic.

The unpublished catalogue of Giraud (see https://science.mnhn.fr/catalogue/ey-bib-giraud2/page/224, accessed 12 October 2022) indicates that his collection contains 10 specimens from Austria and Spain. We could indeed find 10 specimens in his boxes, most of them unlabelled, one with the label "Hisp." for Hispania and two labelled "Bergenstaum," most probably the name of an Austrian entomologist rather than a locality. As expected, Spanish specimens belong to *S. grandimargo*, and Austrian specimens were typical Central European *S. planidens* as diagnosed by Warncke. Syntypes from Turkey housed in Vienna were not examined but could belong to either *S. planidens* or *S. anatolica* (see below for justification of species status). In order to fix the name *S. planidens* definitively on the Central European population, an Austrian specimen is designated as a lectotype (Figure 14), thus preventing the application of this name to Spanish or Turkish syntypic material.

Distribution. France, Germany, Austria, Switzerland, Czech Republic, Poland, Slovakia, Hungary, Romania, Bulgaria, North Macedonia, Greece, Ukraine, Russia, Turkey, Armenia, Georgia, and Iran (see Table S1, Figure 15, [38,39]). The western limit appears to be the Upper Rhine valley. The eastern limit appears to be the Alborz mountains in northern Iran.

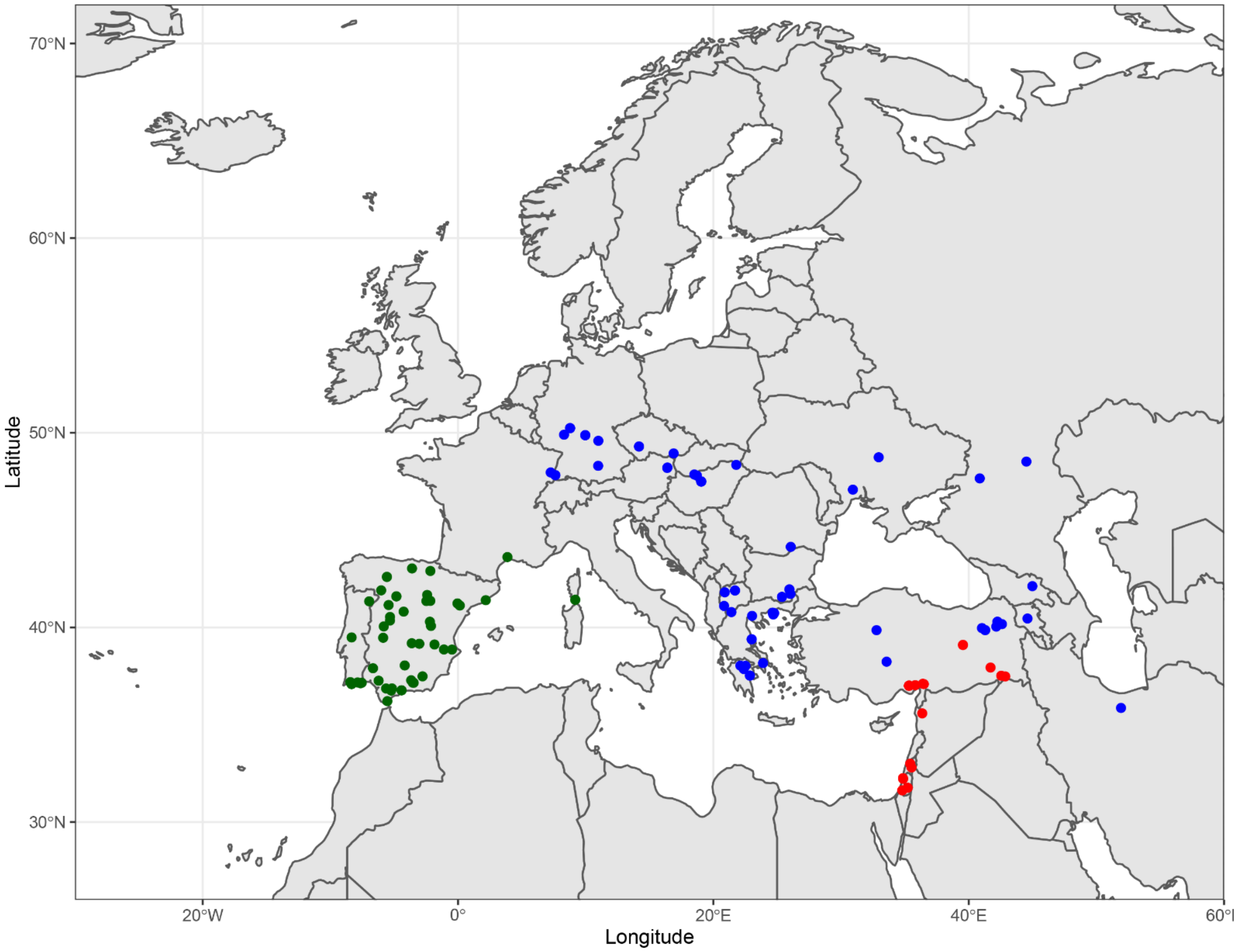

Figure 15. Distribution of taxa within *Systropha planidens* Giraud, 1861 s.l. *Systropha planidens* s. str. is marked in blue, *Systropha grandimargo* Pérez, 1905 is marked in green, and *Systropha anatolica* Warncke, 1977 is marked in red.

Systropha grandimargo Pérez, 1905 **spec. resurr.**

Systropha grandimargo Pérez, 1905: 84; ♂♀Barcelona, Spain [MNHN].

Systropha chrysura Pérez, 1905: 85; ♀Tarragona, Spain [MNHN] **syn. nov.**

Type material examined.—Lectotype of *S. grandimargo* Pérez: green circle [June]//Barcelone//*grandimargo*//MUSEUM PARIS—COLL J.PÉREZ 1915//LECTOTYPE//LECTOTYPE—*Systropha grandimargo* J.P.—Warncke [9] des.//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022//MNHN, Paris—EY33641 (Figure 16).

–Lectotype of *S. chrysura* Pérez: 147//*chrysura* JP//MUSEUM PARIS—COLL J.PÉREZ 1915//LECTOTYPE//LECTOTYPE—*Systropha chrysura* J.P.—Warncke [9] des.//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022//MNHN, Paris—EY33642 (Figure 17).

–Paralectotypes of *S. grandimargo* Pérez: Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022.—blue circle [May]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022. green circle [June]//Barcelne [Barcelone]//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022.—green circle [June]//Barcelne [Barcelone] //MUSEUM PARIS—COLL J.PÉREZ 1915//Barcelone—Espagne—R. Desmier de Chenon

//*Systropha planidens* Gir. ♀—Warncke 74 [identification in 1974]—R. Desmier de Chenon //PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♀—Le Divelec det. 2022.—green circle [June]//Barcelne [Barcelone] //MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone //MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//*grandimargo*//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//La Garriga//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE //*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//La Garriga//MUSEUM PARIS—COLL J.PÉREZ 1915//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022.—green circle [June]//Barcelone//MUSEUM PARIS—COLL J.PÉREZ 1915//Barcelone—Espagne—R. Desmier de Chenon *planidens*//*Systropha planidens* Gir. ♂—Warncke 74 [identification in 1974]—R. Desmier de Chenon//PARALECTOTYPE//*Systropha grandimargo* Pérez, 1905 ♂—Le Divelec det. 2022 [S7–8 and genitalia glued on a separate label].

Other material examined (illustrative, see Table S1). FRANCE: Montpellier, 1♂, Pérez collection, MNHN; Corsica, Bonifacio, 1♂, 1♀, Pérez collection, MNHN; **PORTUGAL:** Algarve, Cacela Velha, 27.iv.2016, 1♂, leg. Wood, det. Wood, TJWC; **SPAIN:** Málaga, Benaoján, Cueva del Hundidero, 3.vi.2021, 1♀, leg. Wood, det. Wood, TJWC.

Remarks. Pérez [5] described *S. grandimargo* from "*divers points de la Catalogne*" without specifying an exact *locus typicus*. Warncke ([9]:96) designated a lectotype from a male specimen from Barcelona (Figure 16) and treated *S. grandimargo* as a subspecies of *S. planidens*. However, Baker [10] rejected this lectotype designation arguing that Warncke 'gave no information identifying any particular specimen'. We disagree with this rejection. The specimen chosen by Warncke is from the Pérez collection, is labelled as being from 'Barcelone' with Pérez's distinctive handwriting and small-style label, and is therefore clearly part of the syntypic series. Thus, the information given by Warncke was sufficient to identify the lectotype in combination with the collection of Pérez, and we accept it as valid.

Pérez [5] described *S. chrysura* from Tarragona from the female sex only. Warncke ([9]:96) designated a female lectotype (Figure 17) and synonymised the taxon with *S. planidens*. It is, however, conspecific with *S. grandimargo*, both morphologically and given that it also comes from the same region of Spain (Catalonia).

In addition to the clear genetic differentiation between Iberian specimens of *S. grandimargo* and *S. planidens* from Central Europe, the two species can be separated morphologically, mostly clearly by the form of the S8 in the male sex. In *S. grandimargo,* S8 is more strongly narrowed medially, the outer margins of the sternal disc are less strongly rounded, and the overall shape is narrower and more rhomboidal (Figure 18B). In *S. planidens* s. str., S8 is broader, the disc resembles a semi-circle, and is not rhombiform (Figure 18A). The full details are given in the identification key below.

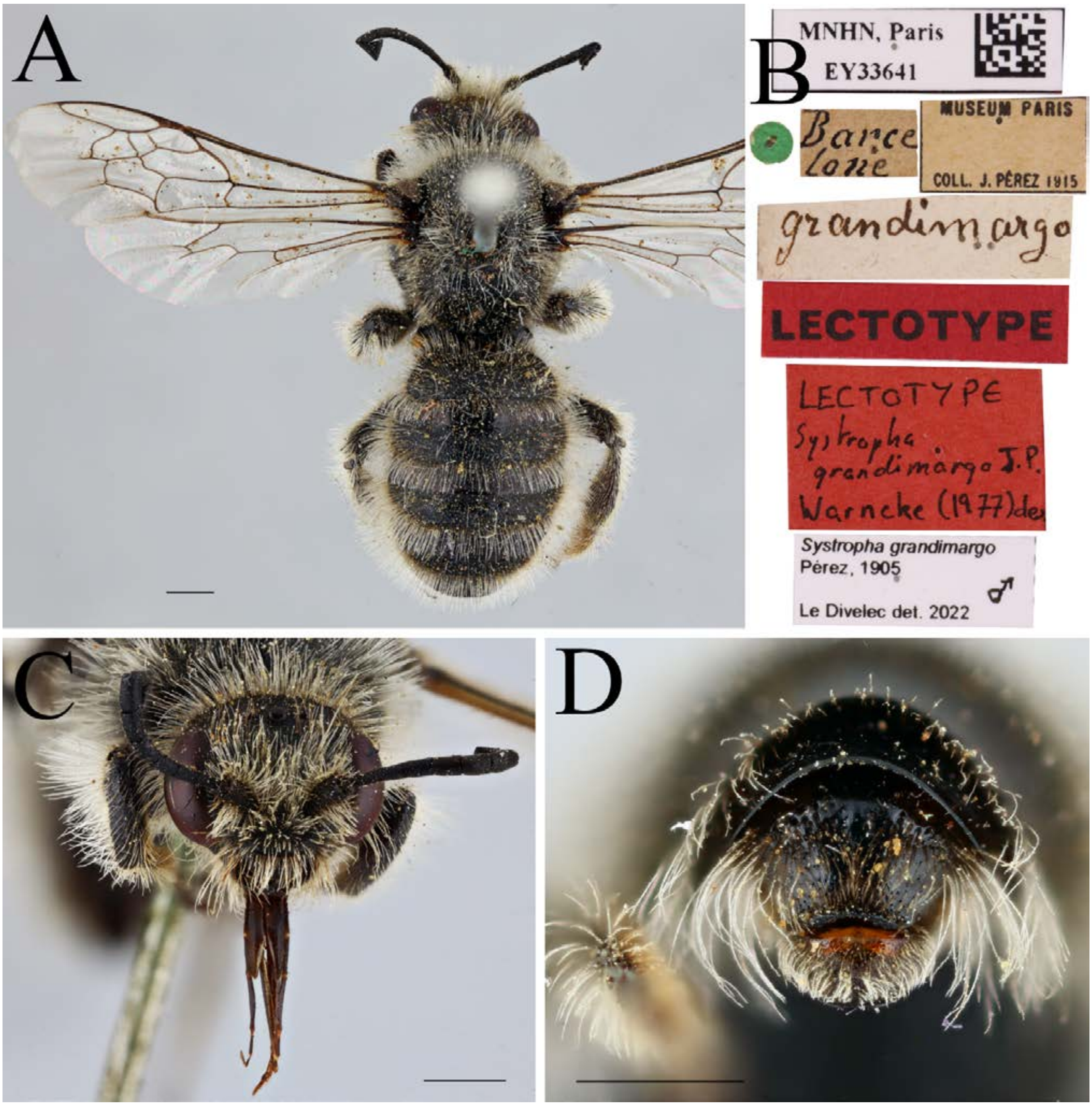

Figure 16. Lectotype specimen of *Systropha grandimargo* Pérez, 1905, male. (**A**) Dorsal view, (**B**) Label details, (**C**) Face detail, (**D**) T7 and apex of S8 detail. Scale = 1 mm.

Though Baker [10] did not follow Warncke [9] in treating *S. grandimargo* as a synonym of *S. planidens* (in contrast to *S. chrysura*), subsequent authors have followed Warncke's position (e.g., [22]). Therefore, we formally treat *S. grandimargo* **spec. resurr.** as a distinct species.

Distribution. Portugal, Spain, France (including Corsica) (Figure 15, [36,38]).

Systropha anatolica Warncke, 1977 **stat. nov**.

Systropha planidens anatolica Warncke, 1977: 96; ♂♀Tunceli, Turkey [OÖLM].

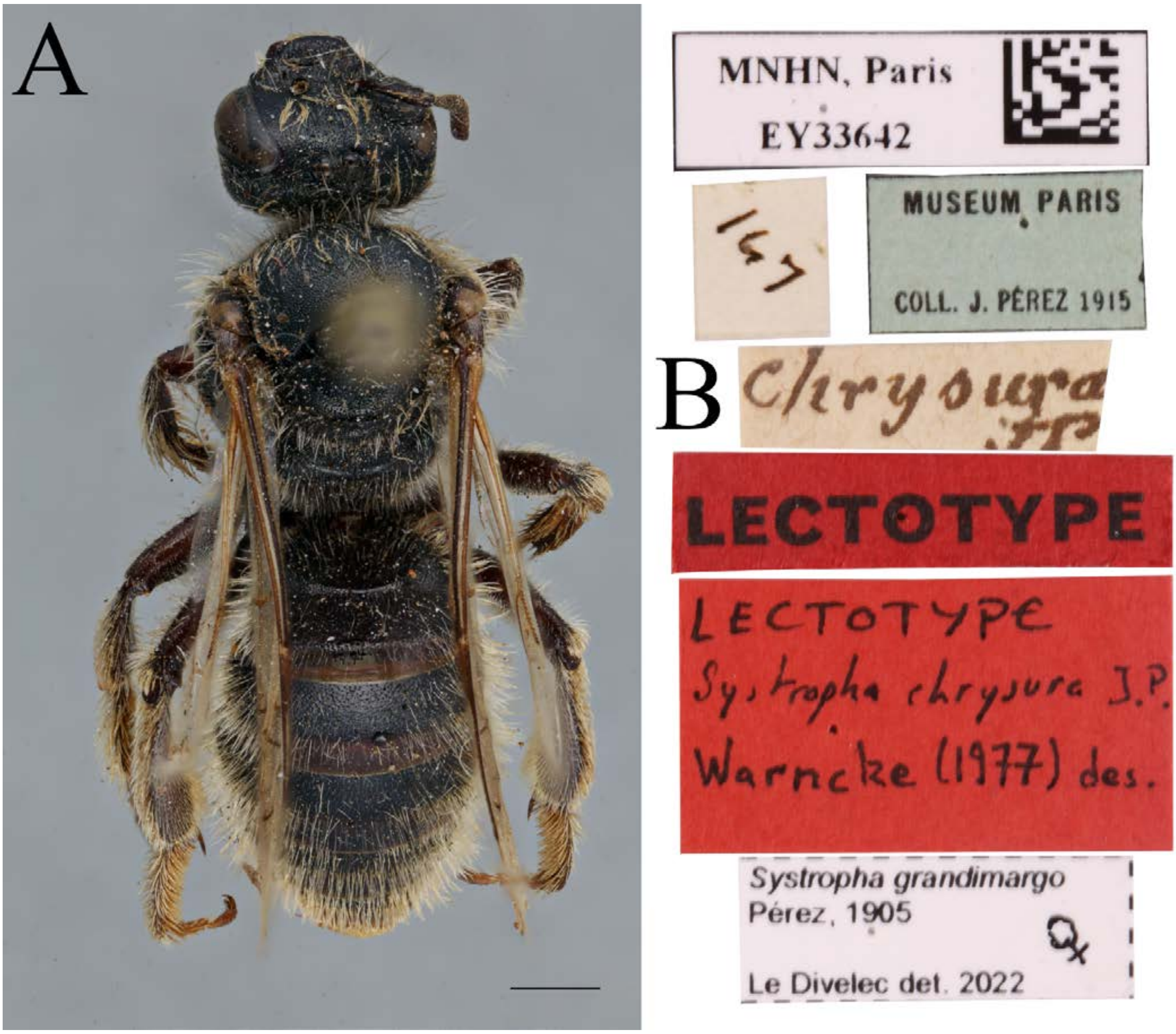

Figure 17. Lectotype specimen of *Systropha chrysura* Pérez, 1905, female. (**A**) Dorsal view, (**B**) Label details. Scale = 1 mm.

Type material examined.—Holotype of *S. p. anatolica* Warncke: Türkei-Tunceli—13-VI-1973—leg. Kl. Warncke//♂//*Systropha planidens* ssp. *anatolica* War—det. Kl. Warncke//Holotypus//coll. K. Warncke—O. O. Landesmuseum—Linz/Austria-cgg. 93.

–Paratype of *S. p. anatolica* Warncke: Türkei-Tunceli—13-VI-1973—leg. Kl. Warncke//♀//*Systropha planidens* ssp. *anatolica* War—det. Kl. Warncke//Para-type//coll. K. Warncke—O. O. Landesmuseum—Linz/Austria-cgg. 93.

Other material examined (illustrative, see Table S1). ISRAEL: 1♂, 1♀, Tiberias, 18–27.v.1967, leg. C.A.W. Jeekel, RMNH; **SYRIA:** 1♂, El Rhab, 52 km NW Hama (Orontes) [Al-Ghab Plain], Syrien, 26.v.1952, leg. E. Schmidt, OÖLM; **TURKEY:** 1♂, East Turkey, Fevzipaşa, 25 km W, 24.v.1959, RMNH.

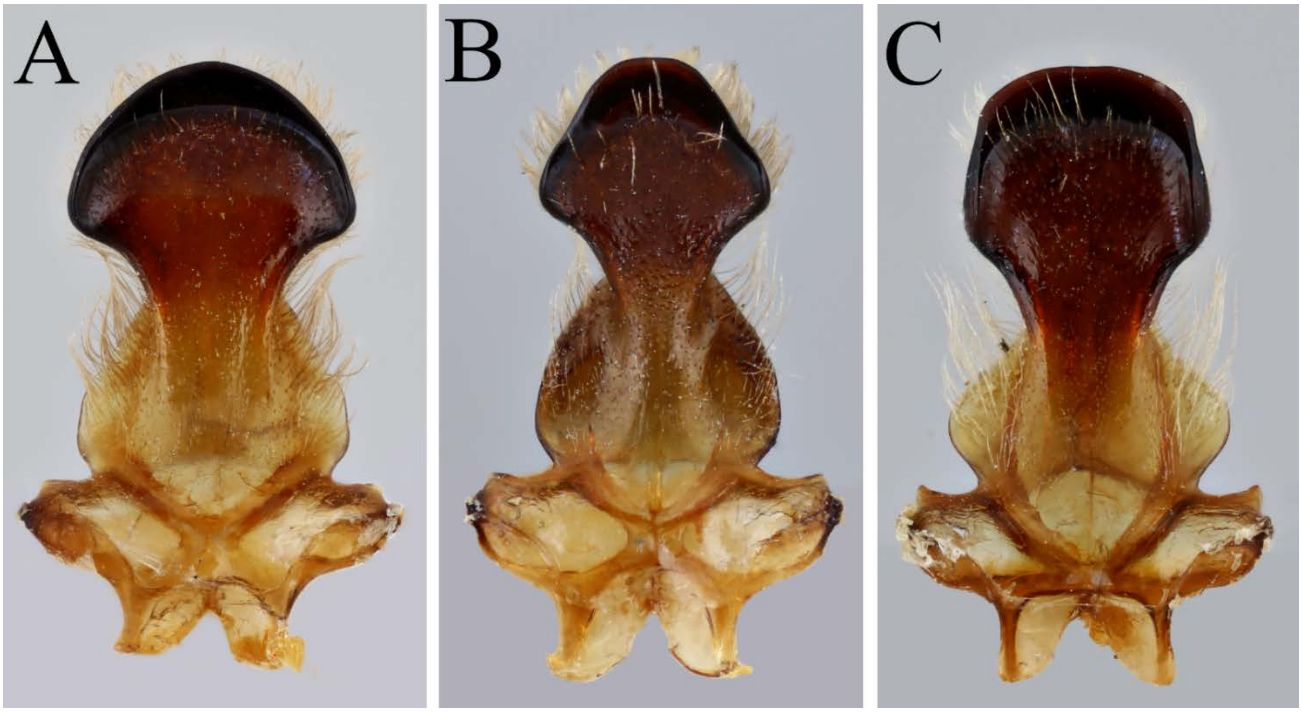

Figure 18. Male S8 for *Systropha* species, ventral view. (**A**) *Systropha planidens* Giraud, 1861. (**B**) *Systropha grandimargo* Pérez, 1905, (**C**) *Systropha anatolica* Warncke, 1977.

Remarks. Warncke [9] described *S. anatolica* as a subspecies of *S. planidens*. Though some authors have followed this viewpoint [22], Baker [10] argued that Warncke's description was inadequate to allow separation from the nominal taxon and that males from Bitlis in Turkey were indistinguishable from males from Greece and Iran. Males of *S. anatolica* are readily separable from *S. planidens* s. str. through a dissection of the hidden sterna (see Figure 18, identification key below). In eastern Turkey, both *S. anatolica* and *S. planidens* can be found, and hence we believe that Baker examined only material of *S. planidens* s. str. Though we do not have any genetic data for *S. anatolica*, given that the differences in the structure of S8 between *S. anatolica* and *S. planidens* s. str. are at least as significant as the differences between *S. grandimargo* and *S. planidens* s. str., we treat it as a valid species.

Distribution. Turkey, Syria, and Israel (see Table S1, Figure 15, [40]).

Identification key for *Systropha* taxa around *S. planidens*

1-♀♂: The second submarginal cell is elongated and longer than it is wide (the third abscissa of the basal vein is slightly shorter than the second submarginal crossvein, Figure 19A). ♀: Terga with double punctation (macro and micro), of which the micropunctation is coarse, dense and unevenly distributed but often aggregating in clumps (particularly visible on T1–2, Figure 19C); this punctation is remarkably dense toward the disc sides where the integument usually is matte over a large area, almost entirely punctate between the macropunctation. Pubescence and therefore appearance darker, hairs of terminal fringe pure black. ♂: Viewed dorsally, the setae on the dorsal surface of S8 are strongly plumose and dense, almost obscuring the underlying integument (Figure 16D). Viewed ventrally, the process of S8 (apical part) is broadly rhomboidal, the apico-lateral margins slightly sinuate and conspicuously converging toward the apex; the basal part of the process of S8 (the "neck") basally constricted, with the lateral margins strongly converging; surface convex, densely and coarsely punctate (Figure 18B) . . . ***grandimargo* Pérez.**

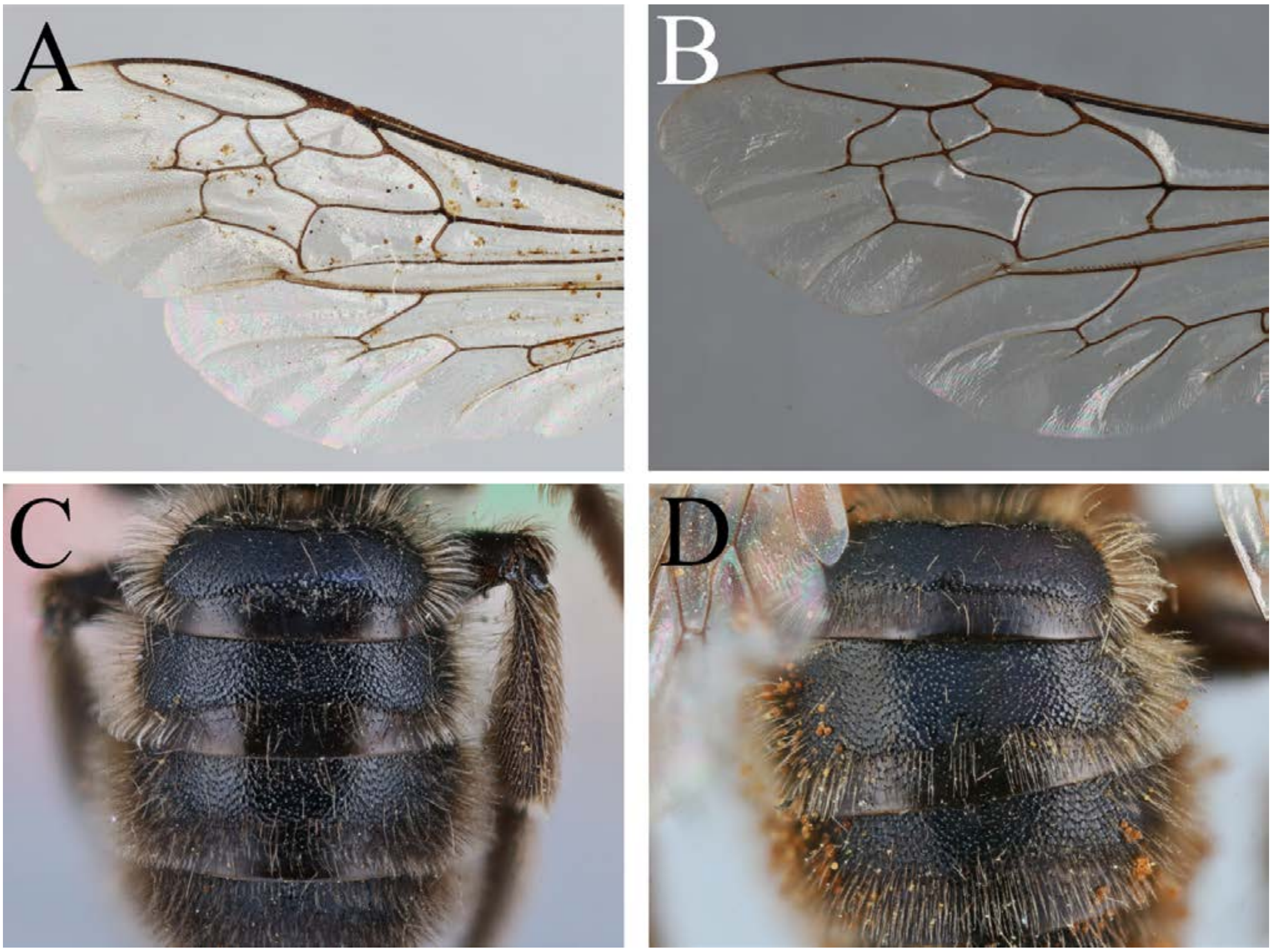

Figure 19. *Systropha grandimargo* Pérez, 1905. (**A**) Forewing, (**C**) Female terga, dorsal view. *Systropha planidens* Giraud, 1861. (**B**) Forewing, (**D**) Female terga, dorsal view.

-♀♂: The second submarginal cell sub-square is wider than it is long (the third abscissa of the basal vein is longer than the second submarginal crossvein, Figure 19B). ♀: The terga have double punctation, compared to which the micropunctation is shallower, finer, and sparser (particularly visible on T1–2, Figure 19D); this punctation is slightly denser on a small lateral part of the discs where the tegument remains shiny and predominantly impunctate between macropunctation. The pubescence and appearance are lighter, with hairs of the terminal fringe coloured dark to light brown, not pure black. ♂: Viewed dorsally, the setae on the dorsal surface of S8 are not strongly plumose, comparatively sparse, and do not obscure the underlying integument. Viewed ventrally, the process of S8 is broadly semi-circular, the apico-lateral margins more or less evenly rounded; the basal part of the process of S8 is not strongly constricted, with the lateral margins only weakly converging; the surface is flat, finely and sparsely punctate (Figure 18A,C) . . . 2.

2-♀: The pilosity of metasoma is usually darker with brown setae on T4–6. The punctation of the frons is comparatively denser and coarser, with many punctures spaced by less than one puncture diameter medially (Figure 20A). ♂: The pilosity of metasomal terga is brown, most clearly on T4–6. Viewed ventrally, the process of S8 is hemispherical, with lateral margins that are clearly evenly rounded. S8 medially (from base to neck) has semi-translucent convex lateral margins, forming a pear shape. Laterally projecting basal part of S8 without a projecting tooth (Figure 18A) . . . ***planidens* Giraud.**

Figure 20. *Systropha planidens* Giraud, 1861. (**A**) Female face, frontal view. *Systropha anatolica* Warncke, 1977. (**B**) Female face, frontal view.

-♀: Pilosity of metasoma light fawn, without dark hairs. Punctation of frons sparser, remarkably sparse dorsomedially where punctures separated by less than one puncture diameter are rare (Figure 20B). ♂: The pilosity of metasomal terga is whitish, at most slightly yellowish at the base of setae. Viewed ventrally, the process of S8 sub-square, lateral margins long, clearly angulate and contrasting truncate apical margin. S8 medially with semi-translucent convex lateral margins of S8, these forming a strong diamond shape. Laterally projecting basal part of S8 with small protruding tooth (Figure 18C) . . . ***anatolica*** **Warncke.**

4. Conclusions

Though revised comparatively recently by previous European workers [8,11], West Palaearctic *Nomiapis* contains cryptic diversity, with a new species recently described from Greece as distinct from the nominally easier-to-identify species *Nomiapis diversipes* [41]. Against this background, the recognition that *Nomiapis bispinosa* s.l. contains cryptic taxa is less surprising, given the recognition of variation in the use of subspecific concepts [8,37].

One outstanding issue relates to the identity of material tentatively identified as *Nomiapis rufiventris* from eastern Spain (Alicante), the Balearic Islands, Corsica, and Sardinia. Female specimens differ slightly from typical *Nomiapis rufiventris* in north-western Africa in their punctation, and given the difficulty in separating males of *Nomiapis rufiventris* and *Nomiapis paulyi*, we do not take a firm position here. Egyptian material of *Nomiapis rufiventris* has scutal punctures that are less dense than in populations from north-western Africa, but the genetic distance is negligible across this range. Genetic barcodes will hopefully conclusively resolve the identity of specimens from these Mediterranean islands. If they do belong to *Nomiapis rufiventris* as we suspect, then this distributional pattern is not without precedent, as other bee taxa can display a distribution of North Africa plus Sicily, Sardinia, and Corsica, such as *Andrena savignyi* Spinola, 1838 and *Andrena rotundata* Pérez, 1895 [42], without also occurring on the Iberian Peninsula.

Compared to the baseline situation of *Nomiapis bispinosa* s.l. and *Systropha planidens* s.l., for the additional four taxa recognised here as valid, names were available for three of them. This suggests that, in this case, the issue at hand is not a lack of taxon description but a lack of revisionary work that was able to fully explore the diversity recognised by previous authors. This is in part because workers on the West Palaearctic fauna are still grappling with the enormous legacy of Klaus Warncke, whose revisionary works were far-reaching but who also often employed very broad species concepts that have resulted in over-lumped taxa (e.g., [17]). Whilst these broad concepts may have been necessary and indeed functional prior to the advent of molecular genetics, as the use of these tools is expanded, many older concepts will have to be revisited as our power to distinguish between closely related taxa increases.

For the molecular results themselves, the interspecific genetic distance values seen for *Systropha* are extremely high, even when compared to genetic distances in other recently delineated bee taxa (e.g., [15,43]). Robust age estimates for every lineage within the family Halictidae are not available, as phylogenies have either not concentrated solely on Halictidae or have not had a sufficiently dense taxon sampling. Danforth et al. [44] estimated a crown age for *Systropha* of around 12 mya, with a stem age of 54 mya, but this is likely to be an overestimate (S. Bossert, *in litt.*), and more recent work gives a stem age of 24 mya for *Systropha* [45]. The same analysis [45] produced a stem age of 34 mya for *Pseudapis* s.l., but only one species within this clade (see [20]) was included. This means that the crown age of *Nomiapis* is almost certainly significantly younger. An upcoming phylogeny with denser sampling produces a stem age of 14 mya (crown age 8 mya) for *Nomiapis* (S. Bossert, *in litt.*), suggesting that *Nomiapis* as a genus is very likely genuinely younger than *Systropha*. It is unclear, however, if the age of each group is in any way related to the observed genetic differences, as these interspecific values can be smaller in older bee genera such as *Schwarzia* (stem age 39 mya, [43]).

Finally, these findings increase the number of known *Systropha* species to 31 [46], seven of which have been described since 1996, and the number of known *Nomiapis* species is either 16 or 17 [11,12,41], depending on the identity of *Nomiapis illepida* (Walker, 1871) from Egypt which has been insufficiently studied due to lost type material [11], and which is likely a synonym of one of the Nomiine bees present in that country. Given that the large interspecific genetic distances observed here within *S. planidens* s.l. are only associated with subtle morphological differences, genetic revision of other *Systropha* taxa is likely to lead to the discovery of additional cryptic diversity within this genus.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14110920/s1, Table S1. Details of examined specimens used for the creation of distribution maps.

Author Contributions: The study was conceived together by both authors; both authors conducted fieldwork for genetic samples, T.J.W. in Iberia and Morocco, R.L.D. in Corsica and mainland France; R.L.D. examined the Paris collection for type material; T.J.W. examined the RMNH, MRSN, and OÖLM collections; both authors wrote the paper together. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

IEAN	Instituto di Entomologia Agraria, Università di Napoli, Naples, Italy
IZK	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland
LPR 2019–2021	La Planète Revisitée (Our Planet Revisited)—Corsica 2019–2021. This was an expedition organised by the MNHN in Corsica for 3 consecutive years. The material will be shared between the MNHN, RLD, and OCIC.
MNHN	Muséum national d'Histoire naturelle, Paris, France
MRSN	Museo Regionale di Scienze Naturali di Torino, Turin, Italy
NHMUK	Naturalis History Museum, London, United Kingdom
OCIC	Observatoire Conservatoire des Insectes de Corse, Corte, Corsica, France.
OÖLM	Oberösterreichisches Landesmuseum, Linz, Austria
RLD	Romain Le Divelec personal collection, Nantes, France
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands
TJWC	Thomas J. Wood personal collection, Mons, Belgium
USNM	Smithsonian National Museum of Natural History, Washington, DC, USA

References

1. Spinola, M. Compte rendu des Hyménoptères recueillis par M. Fischer pendant son voyage en Égypte, et communiqués par M. le Docteur Waltl à Maximilien Spinola. *Ann. Soc. Entomol. Fr.* **1838**, *7*, 437–546.
2. Lucas, P.H. Cinquième Ordre. Les Hyménoptères. In *Exploration Scientifique de l'Algerie Pendant les Années 1840, 1841, 1842 Publié par Ordre du Gouvernment et Avec le Concours d'une Commission Académique. Sciences Physiques, Zoologie*; Histoire Naturelle des Animaux Articulés; Imprimerie Royal: Paris, France, 1849; Volume 3, pp. 141–344.
3. Giraud, J. Fragments entomologiques. I. Description de plusiers Apides nouvelles et observations sur quelques espèces connues. *Verh. Zool. Bot. Ver. Wien* **1861**, *11*, 447–470.
4. Gerstäcker, A. Hymenopterische beiträge. *Stett. Ent. Ztg.* **1872**, *33*, 250–308.
5. Pérez, J. Espèces nouvelles d'Hymenoptera de Catalogne. *Butll. Inst. Catalana Hist. Nat.* **1905**, *5*, 81–88.
6. Alfken, J.D. Beitrag zur Kenntnis der Bienenfauna von Ägypten. (Hym.). *Senckenbergiana* **1926**, *8*, 96–128.
7. Popov, V.V. Contributions to the Bee Fauna of Tajikistan. *Tr. Tajikskoi Basy Akademii Nauk SSSR* **1935**, *5*, 351–408. (In Russian)
8. Warncke, K. Zur Systematik und Verbreitung der Bienengattung *Nomia* Latr. in der Westpalärtis und dem turkestanischen Becken (Hymenoptera: Apoidea). *Reichenbachia* **1976**, *16*, 93–120.
9. Warncke, K. Missione Giordani Soika in Iran 1965. 6. Beitrag zur Bienenfauna des Iran: 2. Die Gattung *Systropha* III. *Boll. Mus. Civ. Stor. Nat. Venezia* **1977**, *28*, 93–97.
10. Baker, D. Notes on some palaearctic and oriental *Systropha*, with descriptions of new species and a key to the species (Hymenoptera: Apoidea: Halictidae). *J. Nat. Hist.* **1996**, *30*, 1527–1547. [CrossRef]
11. Baker, D. On Palaearctic and Oriental species of the genera *Pseudapis* W.F. Kirby, 1900, and *Nomiapis* Cockerell, 1919. *Beitr. Ent.* **2002**, *52*, 1–83.
12. Pauly, A. Classification des Nomiinae de la Région Orientale, de Nouvelle-Guinée et des îles de l'Océan Pacifique (Hymenoptera: Apoidea: Halictidae). *Bull. Inst. R. Sci. Nat. Belg.* **2009**, *79*, 151–229.
13. Le Divelec, R. A taxonomic account on the *Hylaeus gibbus* species-group (Hymenoptera: Apoidea: Colletidae). *Ann. Soc. Entomol. Fr.* **2022**, *58*, 229–249. [CrossRef]
14. Lecocq, T.; Brasero, N.; De Meulemeester, T.; Michez, D.; Dellicour, S.; Lhomme, P.; de Jonghe, R.; Valterová, I.; Urbanová, K.; Rasmont, P. An integrative taxonomic approach to assess the status of Corsican bumblebees: Implications for conservation. *Anim. Conserv.* **2015**, *18*, 236–248. [CrossRef]
15. Pauly, A.; Devallez, J.; Sonet, G.; Nagy, Z.T.; Boevé, J.-L. DNA barcoding and male genital morphology reveal five new cryptic species in the West Palearctic bee *Seladonia smaragdula* (Vachal, 1895) (Hymenoptera: Apoidea: Halictidae). *Zootaxa* **2015**, *4034*, 257–290. [CrossRef]
16. Praz, C.; Müller, A.; Genoud, D. Hidden diversity in European bees: *Andrena amieti* sp. n., a new Alpine bee species related to *Andrena bicolor* (Fabricius, 1775) (Hymenoptera, Apoidea, Andrenidae). *Alp. Entomol.* **2019**, *3*, 11–38. [CrossRef]
17. Praz, C.; Genoud, D.; Vaucher, K.; Bénon, D.; Monks, J.; Wood, T.J. Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): Implications for conservation. *J. Hymenopt. Res.* **2022**, *91*, 375–428. [CrossRef]
18. Pauly, A. Classification des Nomiinae africains (Hymenoptera Apoidea Halictidae). *Mus. R. Afr. Cent. Tervuren Belg. Ann. Sci. Zool.* **1990**, *261*, 1–206.
19. Astafurova, Y.A.; Pesenko, Y.A. Bees of the subfamily Nomiinae (Hymenoptera: Halictidae) in Russia and adjacent countries: An annotated list. *Entomol. Rev.* **2006**, *86*, 74–84. [CrossRef]

20. Bossert, S.; Murray, E.A.; Pauly, A.; Chernyshov, K.; Brady, S.G.; Danforth, B.N. Gene Tree Estimation Error with Ultraconserved Elements: An Empirical Study on *Pseudapis* Bees. *Syst. Biol.* **2020**, *70*, 803–821. [CrossRef]
21. Wood, T.J.; Cross, I.; Baldock, D.W. Updates to the bee fauna of Portugal with the description of three new Iberian *Andrena* species (Hymenoptera: Apoidea: Anthophila). *Zootaxa* **2020**, *4790*, 201–228. [CrossRef] [PubMed]
22. Patiny, S.; Michez, D. Phylogenetic analysis of the *Systropha* Illiger 1806 (Hymenoptera: Apoidea: Halictidae) and description of a new subgenus. *Ann. Soc. Entomol. Fr.* **2006**, *42*, 27–44. [CrossRef]
23. Ivanova, N.V.; Dewaard, J.R.; Hebert, P.D.N. An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Mol. Ecol. Notes* **2006**, *6*, 998–1002. [CrossRef]
24. Hebert, P.D.N.; Penton, E.H.; Burns, J.M.; Janzen, D.H.; Hallwachs, W. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 14812–14817. [CrossRef]
25. Bleidorn, C.; Henze, K. A new primer pair for barcoding of bees (Hymenoptera: Anthophila) without amplifying the orthologous *coxA* gene of *Wolbachia* bacteria. *BMC Res. Notes* **2021**, *14*, 427. [CrossRef]
26. Gouy, M.; Guindon, S.; Gascuel, O. SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Mol. Biol. Evol.* **2010**, *27*, 221–224. [CrossRef]
27. Kumar, S.; Stecher, G.; Li, M.; Knyaz, C.; Tamura, K. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Mol. Biol. Evol.* **2018**, *35*, 1547–1549. [CrossRef]
28. Wood, T.J.; Roberts, S.P.M. Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. *Biol. J. Linn. Soc.* **2018**, *124*, 732–746. [CrossRef]
29. Müller, A.; Kuhlmann, M. Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): The Asteraceae paradox. *Biol. J. Linn. Soc.* **2008**, *95*, 719–733. [CrossRef]
30. Michener, C.D. *The Bees of the World*, 2nd ed.; The Johns Hopkins University Press: Baltimore, MD, USA, 2007; p. 953.
31. Vachal, J. Quelques espèces nouvelles, douteuses ou peu connues du genre *Nomia* Latr. (Hym.). *Misc. Entomol.* **1897**, *5*, 72–75, 87–93.
32. Savigny, J.C. *Description de l'Égypte ou Recueil des Observations et des Recherches qui ont été Faites en Égypte Pendant l'expédition de l'Armée Française, Publié par les Ordres de Sa Majesté l'Empereur Napoléon le Grand*; Tome II, Hyménoptères; Imprimerie Impériale: Paris, France, 1825; pp. 1–7, 10–20.
33. Rosa, P.; Xu, Z.-F. Annotated type catalogue of the Chrysididae (Insecta, Hymenoptera) deposited in the collection of Maximilian Spinola (1780–1857), Turin. *Zookeys* **2015**, *14*, 1–96. [CrossRef]
34. Friese, H. Monographie der Bienengattung *Nomia* (Latr.). *Festschr. Vereins Schlesische Insecktenkunde Breslau* **1897**, 45–84.
35. Casolari, C.; Casolari, M.R. *Collezione Imenotterologica di Massimiliabo Spinola*; Museo Refionale di Scienze Naturali: Torino, Italy, 1980; p. 163.
36. Baldock, D.; Wood, T.J.; Cross, I.; Smit, J. The Bees of Portugal (Hymenoptera: Apoidea: Anthophila). *Entomofauna* **2018**, (Suppl. S22), 1–164.
37. Van der Zanden, G. Einige notizen über die Gattungen *Pseudapis* Kirby 1900 und *Nomia* Latreille 1804 in der Paläarktis. *Linz. Biol. Beitr.* **1997**, *29*, 753–757.
38. Patiny, S.; Pauly, A. *Atlas of the European Bees: Genus Systropha*; STEP Project; Atlas Hymenoptera: Mons, Belgium, 2011; Available online: https://www.zoologie.umh.ac.be/hymenoptera/page.aspx? (accessed on 19 August 2022).
39. Amiet, F.; Müller, A.; Neumeyer, R. Fauna Helvetica 4. Apidae 2. In *Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha*, 2nd ed.; Centre Suisse de Cartographie de la Faune: Neuchâtel, Switzerland, 2014; pp. 1–239.
40. Warncke, K. Die Bienengattung *Systropha* Ill. neu für Israel und Zentralasien. *Linz. Biol. Beitr.* **1992**, *24*, 741–746.
41. Arens, W. *Nomiapis susannae* sp. n., eine neue Bienen-Art aus Griechenland (Hymenoptera, Apoidea: Halictidae). *Mitt. Münch. Ent. Ges.* **2018**, *108*, 103–107.
42. Gusenleitner, F.; Schwarz, M. Weltweite Checkliste der Bienengattung *Andrena* mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, Andrena). *Entomofauna Supplement.* **2002**, *10*, 1–1280.
43. Bossert, S.; Copeland, R.S.; Sless, T.J.L.; Branstetter, M.G.; Gillung, J.P.; Brady, S.G.; Danforth, B.N.; Policarová, J.; Straka, J. Phylogenomic and Morphological Reevaluation of the Bee Tribes Biastini, Neolarrini, and Townsendiellini (Hymenoptera: Apidae) With Description of Three New Species of *Schwarzia*. *Insect Syst. Divers.* **2020**, *4*, 1–29. [CrossRef]
44. Danforth, B.N.; Brady, S.G.; Sipes, S.D.; Pearson, A. Single-Copy Nuclear Genes Recover Cretaceous-Age Divergences in Bees. *Syst. Biol.* **2004**, *53*, 309–326. [CrossRef] [PubMed]
45. Cardinal, S.; Buchmann, S.L.; Russell, A.L. The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution* **2018**, *72*, 590–600. [CrossRef]
46. Bossert, S.; Patiny, S. Description of the previously unknown male of *Systropha* (*Austrosystropha*) *macronasuta* (Hymenoptera: Halictidae: Rophitinae) from Kenya. *J. Melittol.* **2017**, *67*, 1–9. [CrossRef]