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On the status of *Nomiapis valga* (Gerstäcker) and its distribution (Hymenoptera, Halictidae, Nomiinae), with an identification key for European *Nomiapis*

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Abstract

Bees of the subfamily Nomiinae are renowned for their morphological diversity, particularly in the male sex, which often shows enormously modified hind legs and metasomal sterna. This has led to an array of generic and subgeneric classification systems, but nomiine bees also suffer from problems at the species level. This is well-illustrated in the genus *Nomiapis* Cockerell, 1919, which is particularly difficult to delineate in the female sex. One such case involves *Nomiapis valga* (Gerstäcker, 1872), described from southern Spain, which nominally has a fragmented distribution from Spain and southeastern Europe across to Central Asia, and for which type material is lost. New studies show that *N. valga* is actually entirely restricted to Spain, where it is strongly geographically separated from populations ranging from southeastern Europe to Central Asia; these latter populations are best referred to as *Nomiapis caucasica* (Friese, 1897) **sp. resurr.** Type material for *N. caucasica* is definitively located, and a neotype is designated for *N. valga* to fix the concept of this species. Additional support for the species status of *Nomiapis susannae* Arens, 2018, is presented, along with a modern identification key for European *Nomiapis* species. These results highlight the persistent problems with the alpha-level taxonomy of nomiine bees even within well-studied parts of their global range.

Key Words

Cryptic species, lost type, museum collections, neotype, revisionary taxonomy

Introduction

The subfamily Nomiinae contains around 620 species, with its center of diversity in the Afrotropics (Pauly 2009; Ascher and Pickering 2024; Bossert et al. 2025). Members of this subfamily show enormous variation in coloration (with the integument varying from dark to possessing iridescent metallic or enamel sections), pubescence, and morphology, with the male legs often grossly inflated and possessing pointed modifications and squamous hairs. This variation stands in strong contrast to the largest subfamily of Halictidae, Halictinae, most members of which have been described as "morphologically monotonous" (Michener 2007). Due to this morphological variation, traditional delineation of nomiine genera is highly complex, with a lack of consensus in the literature (e.g., Warncke 1976; Pauly 1990, 2009, 2014; Pauly et al. 2001; Baker 2002; Michener 2007). Phylogenomic approaches are beginning to resolve these generic classification issues (Bossert et al. 2021; 2024; 2025), but many challenges remain.

In the West Palaearctic, nomiine bees are represented by only a few lineages; in Europe, for example, only two genera (*Pseudapis* W.F. Kirby, 1900, and *Nomiapis* Cockerell, 1919) are present, with 11 species represented in total (Ghisbain et al. 2023). Although the overall diversity is low, recent studies have shown that West Palaearctic *Nomiapis* were more taxonomically complex than previously thought (Arens 2018; Wood and Le Divelec 2022), with the delineation of cryptic taxa and description of new species. Due to the conspicuous variation present in male morphology (typically the legs and metasomal sterna) and the comparative lack of variation in females, identification of female specimens has caused numerous problems, leading to unrecognized diversity or incorrect geographic ranges based on female records only (Wood and Le Divelec 2022).

The two major modern revisions of the genus *Nomiapis* in its current form (e.g., Bossert et al. 2021) are Warncke (1976) and Baker (2002), after the more dated Friese (1897). Warncke treated *Nomiapis* as a subgenus within a broad genus, *Nomia* Latreille, 1804, and placed some taxa as subspecies of others, e.g., in the combination *Nomia femoralis* ssp. *valga* Gerstäcker, 1872. This revision was strongly criticized by Baker (2002) for its lack of precision, and while Baker's revision clarified the nomenclatural situation for several taxa, it did not fully deal with problems surrounding the *Nomiapis bispinosa* Brullé, 1833 species complex (Wood and Le Divelec 2022), and most pertinently for the present work, did not deal with *N. valga* in detail.

Nomiapis valga was described from southern Spain (Andalusia; Gerstäcker 1872), but the type material is lost (see results), and due to the scarcity of Spanish material in collections, the correctness of this locality has been questioned (Warncke 1976). Van der Zanden (1997) reported material from southern Spain, and Baker (2002) consequently thought said *locus typicus* to be reasonable, having never examined specimens himself. Warncke (1976) also considered the taxon *N. caucasica* (Friese 1897), which was described from the Caucasus, to be conspecific with *N. valga* (as a subspecies), although Baker (2002) treated *N. caucasica* as a synonym of *N. equestris* (Gerstäcker 1872). Impeding our understanding of the correctness of these two hypotheses is the fact that the type material of *N. caucasica* is currently considered lost (Warncke 1976; Baker 2002). A new study of museum collections, modern field collections, and rediscovery of type material in an unexpected location has allowed new light to be shed on these names and the overall distribution of the species *N. valga*.

Methods

Some recently captured *Nomiapis* specimens were sent 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 standardized high-throughput protocols (Ivanova et al. 2006). BeeCox1F1/BeeCox1R2 primers (Bleidorn and Henze 2021) were used to target the COI-5 region. All sequences are published on the Barcode of Life Database (BOLD) (https://portal.boldsystems.org/recordset/DS-NOMSYS).

Using the same primer, additional sequencing was conducted using the Oxford Nanopore GridION sequencer on two FLO-MIN114 flow cells with the SQK-NBD114.24 sequencing kit. The base calling was done with MinKNOW (v24.02.16), the run duration was set to 72 h, and super accuracy base calling was selected. The demultiplexing was performed with Guppy barcoder (v6.5.7). The consensus calling consisted of several steps combined together in a Snakemake (Mölder et al. 2021) pipeline: First, the reads (containing primers at both ends) were filtered by size (>=558, <=758) and quality (>=10), and then reoriented with Cutadapt (v4.5, max error rate 20%, 80% coverage), which also removed flanking sequences. Then consensus sequences were generated using NGSpeciesID v0.3.0 (Sahlin et al. 2021) with Medaka polishing (v2.0.1). A final round of primer sequence trimming was performed with Cutadapt. Following this, multi-fasta files containing consensus sequences were written by using a custom script. Quality control and visualization of the processed FASTQ files were conducted using NanoPlot (De Coster et al. 2018) and MultiQC (Ewels et al. 2016).

Phylogenetic trees were supplemented with additional published sequences that were downloaded from GenBank and the Barcode of Life Data System, as well as including sequences generated from historical specimens from the Naturalis Biodiversity Center collection as part of the Biodiversity Genomics Europe from specimens revised in the framework of this current work (https://portal.boldsystems.org/recordset/DS-BGEMS). Sequences were aligned using MAFFT (Katoh and Standley 2013). Aligned sequences were analyzed in Seaview (Gouy et al. 2010) using a maximum likelihood analysis, which was run with 1000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018). Genetic results are presented first before taxonomic changes are formalized.

Morphological terminology follows Michener (2007), with the exception of the marginal "zones" of the terga, which are referred to as marginal "areas." Unless otherwise stated, all specimens were examined, with determinations validated or corrected as necessary. An identification key is presented for males and females of *Nomiapis* species occurring in Europe to facilitate their identification. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 10X 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 Focus B (HeliconSoft, Ukraine), and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was done in Photoshop Elements (Adobe Systems, USA) to improve lighting to highlight specific characters.

Abbreviations

BBSL-USDA-ARS	Pollinating Insects Research Unit—Dept. Biology, Utah State University, Logan, United States of America
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
OÖLM	Oberösterreichisches Landesmuseum, Linz, Austria
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands
TJWC	Personal collection of Thomas J. Wood, Leiden, the Netherlands
ZMHB	Museum für Naturkunde, Berlin, Germany

Results

Genetics

Genetic sequences were available for nine European *Nomiapis* species, including the first for *N. caucasica*, *N. femoralis* (Pallas, 1773), *N. monstrosa* (Costa, 1861), and *N. susannae* Arens, 2018 (Fig. 1). The central result of Wood and Le Divelec (2022) was reproduced, with three well-supported species in the *bispinosa* group of species, which falls closest to *N. monstrosa*.

The sole sequence of *N. valga* presented by Wood and Le Divelec (2022) is now placed into context by sequences of *N. femoralis* (Czechia and Ukraine), *N. caucasica* (Greece), and additional sequences from southern Spain (Granada). Collectively, these sequences form a clade with bootstrap support of 95, which can be referred to as the *femoralis* group (*Nomia femoralis* sensu lato sensu Warncke). Individually, although only a small number of sequences were available, three distinct subclades were formed corresponding to *N. femoralis* (bootstrap support 82), *N. valga* (bootstrap support 86), and *N. caucasica* (bootstrap support 89). *Nomiapis valga* was separated from *N. caucasica* by an average genetic distance of 2.44% (range 2.43–2.49%) and from *N. femoralis* by an average genetic distance of 5.02% (range 4.54–5.47%). *Nomiapis femoralis* and *N. caucasica* were separated by an average genetic distance of 4.84% (range 4.55–5.13%). Consequently, three distinct clades were observed, and the genetic differences therefore support the morphological and biogeographical differences that are presented below.

Finally, a large clade with bootstrap support of 97 was found containing *Nomiapis diversipes* (Latreille 1806) and *N. susannae*. *Nomiapis diversipes* sequences from Portugal in the west to Kyrgyzstan in the east formed a single monophyletic clade, with *N. susannae* placed as sister to this group. Within the broad *N. diversipes* clade, three subclades were found, namely 1) Armenia and northern Iran, 2) Portugal, Spain, and southern France, and 3) eastern France, Italy, Austria, Bulgaria, Greece, and Kyrgyzstan. *Nomiapis susannae* was separated from all *N. diversipes* sequences by an average genetic distance of 1.86% (range 1.75–2.14%). Within the broad *N. diversipes* clade, average intraspecific genetic distance was 0.68% (range 0.00–1.52%). Although the genetic distance between *N. susannae* and the broad *N. diversipes* clade is small in absolute terms, the minimum separation is greater than the maximum intraspecific distance inside *N. diversipes*, and the barcoded *N. susannae* specimen was captured in sympatry with *N. diversipes* specimens in Eastern Macedonia (around Kavala). The three *N. diversipes* from Kavala had identical sequences and were separated from *N. susannae* by 1.76%. In this context, combined with the observed morphological differences that matched the criteria of Arens (2018), it is appropriate to consider the two taxa distinct at the present time, though further study to clarify the overall range limits of *N. susannae* and identify the unknown female would be beneficial.

***Nomiapis caucasica* (Friese, 1897) sp. resurr.**

Nomia caucasica Friese, 1897: 61, ♂ [Azerbaijan, NHMW, lectotype by present designation] (Fig. 2)

Material examined. **Afghanistan** • 1 ♂; Sarobi [Sarawbi]; 27 May 1951; Rolk leg.; OÖLM; **Armenia** • 1 ♂; pr. Eriwan [Yerevan], Parakar; 10 Jun. 1925; A. Schelkovnikow leg.; OÖLM; **Azerbaijan** • 3 ♂; Araxesthal [near Ordubad]; 1890; Reitter leg.; NHMW (**lectotype** by present designation); **Greece** • 1 ♀; Loutraki; 23 May 1964; M. Schwarz leg.; OÖLM • 1 ♀; Loutraki; 2 Jun. 1964; M. Schwarz leg.; OÖLM • 1 ♂; Loutraki, Golf von Korinth; 23–25 May 1962; M. Schwarz leg.; OÖLM • 1 ♀; Rhodos, Archangelos; 2–14 Jun. 1996; M. Hradský leg.; OÖLM • 1 ♂; Western Macedonia, Anatoliko, 6.3 km E, Church of the Holy Apostles; 1000 m a.s.l.; 15 Jun. 2024; T.J. Wood leg.; RMNH; RMNH.INS.1152625 • 1 ♂; Western Macedonia, Filotas, 3 km N of Antigonos; 600–700 m a.s.l.; 11 Jun. 2024; T.J. Wood leg.; RMNH; RMNH.INS.1152626; **Iran** • 1 ♂; E Iran, Mohammadabad; 1600 m a.s.l.; 3 May 1973; Exp. Nat. Mus. Praha; OÖLM • 1 ♂; Kuhanjan, SE Shiraz/Fars; 16 May 1978; K. Warncke leg.; OÖLM; **Israel** • 1 ♂; 2 km W Massada [Metsada]; 20 Apr. 1990; K. Warncke leg.; OÖLM • 4 ♂; Mizpe Ramon, 12 km W, Zisterne; 21 May 1991; K. Warncke leg.; OÖLM • 4 ♂, 4 ♀; Mizpe Ramon, Borot Lotz; 950 m a.s.l.; 21 May 1991; K. Warncke leg.; OÖLM • 2 ♀; Wadi Abde; 13 May 1966; Bytinski-Salz leg.; OÖLM • 1 ♂; Wadi Ramon; 2 May 1966; Bytinskii-Salz leg.; OÖLM; **Jordan** • 1 ♀; west, Jordan Valley, S. Shuna; 25–26 Apr. 1996; Mi. Halada leg.; OÖLM; **Kazakhstan** • 1 ♂, 1 ♀; centr., Lepsi, 6 km SE; 18 Jun. 1992; M. Halada leg.; OÖLM; **Turkey** • 2 ♀;

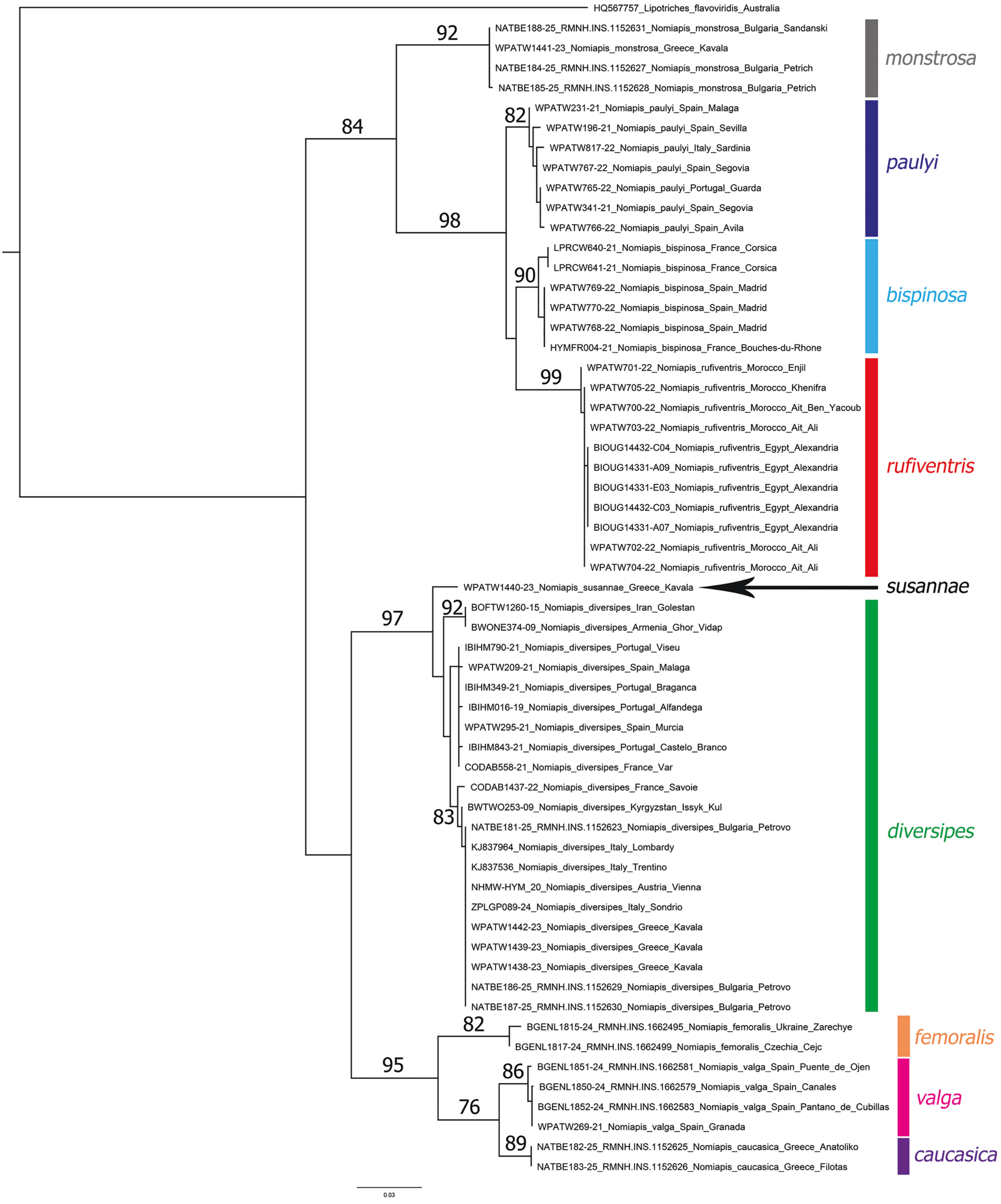

Figure 1. Phylogenetic tree (maximum likelihood) of *Nomiapis* Cockerell, 1919 species based on the mitochondrial COI gene. *Lipotriches flavoviridis* (Cockerell, 1905) is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of < 75 are omitted).

Akseki, Antalya; 1300 m a.s.l.; 3 Aug. 1991; K. Warncke leg.; OÖLM • 1 ♂; Beysehir [Beyşehir]; 13–14 Jun. 1966; H.H.F. Hamann leg.; OÖLM • 1 ♂; Erzurum; 22 Aug. 1967; OÖLM • 1 ♀; Hakkari, Varegös/Mt. Sat; 1750 m a.s.l.; 6 Aug. 1986; K. Warncke leg.; OÖLM • 2 ♀; Malatya, 3 km NW of Darende, st. 126; 1400–1600 m a.s.l.; 31 Jul. 1983; H. v. Oorschot, H. v. d. Brink, H. Wiering leg.; RMNH; RMNH.INS.1662589 • 1 ♀; Malatya; 900 m a.s.l.; 27 Jun. 1984; K. Warncke leg.; OÖLM • 1 ♀; Mut; 7 Jun. 1966; H.H.F. Hamann leg.; OÖLM • 1 ♀; Mut; 26 May 1972; K. Warncke leg.; OÖLM • 1 ♀; Nemrut Dağı, Karadut; 2 Jul. 1993; Mi. Halada leg.; OÖLM • 1 ♀; Nevsehir [Nevşehir], road Göreme-Ürgüp, st. 132; 1000–1100 m a.s.l.; 8 Aug. 1983; H. v. Oorschot, H. v. d. Brink, H. Wiering leg.;

Figure 2. *Nomiapis caucasica* (Friese, 1897) lectotype male (NHMW). **A.** Label details; **B.** Habitus, profile view; **C.** Metasoma, dorsal view; **D.** Apical sterna, ventral view.

RMNH; RMNH.INS.1662591 • 1 ♀; Ulukışla; 19 Jun. 1973; K. Warncke leg.; OÖLM • 1 ♀; Yüksekova/Hakkari; 11 Aug. 1979; K. Warncke leg.; OÖLM; **Turkmenistan** • 1 ♂; Aschabad [Ashgabat]; Ahnger leg.; RMNH; RMNH.INS.1662593 • 2 ♂; Aschabat, 40 km W Firyuza; 6 Jun. 1993; M. Halada leg.; OÖLM • 1 ♀; Кара-Кала, Туркм. [Kara-Kala, Turkmenistan]; 11 Jun. 1953; Крыжановский [Kryzhanovsky] leg.; OÖLM; **Uzbekistan** • 1 ♂; Samarkand - Aman Kutan; 1 Jun. 1919; RMNH; RMNH.INS.1662592; **West Bank** • 1 ♂; Jericho; 3 Apr. 1909; F. Morice leg.; OUMNH • 5 ♂; Jericho, Wadi Qilt; 21 Apr. 1990; K. Warncke leg.; OÖLM • 1 ♂; Shelomzziyon war memorial; 12 Apr. 2000; S.P.M. Roberts leg.; TJWC.

Notes. The location of the type material of *N. caucasica* has been a mystery until now. Friese (1897: 62) wrote, "Im Museum Wien befinden sich 4 ♂ aus dem Kaukasus-Gebeit (Arexesthal 1890)." For inexplicable reasons, Warncke (1976: 113) wrote, "*N. caucasica* FRIESE, 1922, ♂, Kaukasus, Typus. Mus. Berlin, ist *N. femoralis* ssp. *valga!* In seiner Beschreibung kennzeichnete FRIESE dagegen *N. equestris!* Beschreibung und Typus (sowie Paratypen) stimmen nicht überein! Syn. n.!". The "type" specimen in the ZMHB collection is actually a specimen from Sarachs in Turkmenistan, which was identified by Friese (R. Le Divelec, *pers. comm.*), but is clearly of no type value as it does not match the collecting information in the original publication.

That the type of *N. caucasica* clearly should not be in the ZMHB was noted by Baker, who correctly stated that it should be found in the NHMW based on the original publication and who then listed *N. caucasica* as a synonym of *N. equestris*. This synonymy is based on the fact that Friese's description of *N. caucasica* is partially copied from Gerstäcker's description of *N. equestris*, but Baker did not inspect the type material of *N. caucasica* either, and so this synonymy is speculative.

Searches in the NHMW collection in 2024 were not able to retrieve any specimens of *N. caucasica* (D. Zimmermann and R. Le Divelec, *pers. comm.*), but a loan form dated 2 April 1965 was uncovered, this detailing a loan of 38 nomiine specimens to M.A. Diniz at the University of Coimbra (Portugal), including "*Nomia caucasica* ♂ 1 Ex." Searches at the University of Coimbra museum collection as well as communication with Diniz were unable to locate these specimens, including *N. caucasica* (H. Gaspar, *pers. comm.*). This explains why one of the *N. caucasica* specimens was missing from the NHMW collection, but what of the other three?

During searches of the Warncke collection (OÖLM), three specimens were found that had been determined by

Warncke as "*Nomia femoralis* ssp. *valga.*" These had the collecting information "Araxesthal, Reitter 1890" and were labeled by Friese as "*Nomia caucasica.*" Warncke had even added "Para-type" labels, raising the point that he was clearly aware of their type status (Fig. 2A). These three specimens are indisputably the remaining syntypes of *N. caucasica* that had been taken from NHMW by Warncke at an unknown date due to their collecting labels and consistency with Friese's original description. One of them is designated as the lectotype, the type series now having been returned to the NHMW. It is unclear if Warncke took these from the NHMW collection before or after his 1976 publication.

Now that the type material has been definitively located, its identity can be established and the hypotheses of Warncke (conspecific with *valga*) and Baker (conspecific with *equestris*) can be assessed. The specimen is clearly not conspecific with *N. equestris*, as the apical margin of S4 has a deep semi-circular excavation, and the apical margin of S5 is weakly emarginate with two pincer-like, slightly bent digitiform projections (Fig. 2D; the narrowly separated, raised, convex, tongue-like processes of Baker 2002: 57). Moreover, the apical process of the hind tibia is flattened, more-or-less rectangular, and with the apical margin truncate (Fig. 2B). As *N. equestris* males have the hind margin of S4 narrowly incised, S5 with a large circular excavation, and the apical process of the hind tibia narrow and sharply pointed, Baker's hypothesis can be rejected.

Separation from *N. valga* is more challenging. As the lateral margins flanking the emargination of S4 are produced into low-lying posteriorly projecting ridges, it can be separated from *N. femoralis*, which has the lateral margins produced elevated projections with triangular apexes, Warncke's combination of *N. femoralis* ssp. *valga* being rejected by most subsequent workers (Ebmer 1988; Baker 2002; Astafurova and Pesenko 2006). Consultation of a series of specimens from Spain (*N. valga*) and eastern specimens (*N. caucasica*) has allowed discriminative characters to be identified in the male sex:

1. Density of punctures on the disc of T2
2. Punctation of the marginal areas of T2–3
3. Tergal sculpture, including sculpture of marginal areas

The lectotype of *N. caucasica* displays 1) relatively sparse punctures on the disc of T2, with two shining areas mediolaterally that clearly exceed the diameter of a puncture in size (Fig. 2C); 2) the marginal areas of T2–3 have a very narrow row of punctures at their base, these punctures covering <⅕ of the length of the marginal area (Fig. 2C); and 3) the terga have relatively weak microsculpture sculpture and are broadly shining, particularly the marginal areas (Fig. 2C).

In contrast, specimens from Spain display 1) relatively dense punctures on the disc of T2, without impunctate shining areas mediolaterally that clearly exceed the diameter of a puncture in size, at most with slight hints of such an area (Fig. 3C); 2) the marginal areas of T2–3 have 3–4 rows of punctures at their base, these occupying the basal ⅓–⅕ of the marginal areas (Fig. 3C); and 3) the terga have slightly stronger microsculpture and are comparatively more dull, particularly on the marginal areas, which are never polished and shining (Fig. 3C). Finally, the lectotype of *N. caucasica* has the scutellum laterally rounded, whereas specimens of *N. valga* from Spain have the scutellum laterally mucronate, with posteriorly projecting teeth. Baker (2002: 57, couplet 26) considered males of *N. valga* to have the scutellum laterally without posteriorly projecting spines, but he never examined specimens from Spain, which show the spines consistently based on the limited number of specimens examined to date. Specimens from the east are variable, sometimes showing spines and sometimes not; it therefore does not seem to be a stable character in eastern populations, even though it may be stable (always present) in *N. valga*. Overall, these characters taken in combination allow the consistent separation of male *N. caucasica* and *N. valga* regardless of geographic origin, and *N. caucasica* sp. resurr. is returned to species status.

As the type material of *N. valga* is lost, with Friese, Warncke, and Baker unable to locate it in the ZMHB, along with modern searchers (R. Le Divelec, *pers. comm.*), and the clear taxonomic complexity in separating *N. valga* and *N. caucasica*, it is desirable to designate a neotype for *N. valga*. In line with the conditions of article 75.3 (ICZN 1999), this neotype (Fig. 3) is needed to decisively settle the identity of *N. valga*, preserving nomenclatural stability for Iberian populations. The selected specimen is from the province of Granada, which falls within Andalusia, the stated *terra typica* of Gerstäcker. The selected specimen is male, matching the sex in which the species was originally described. This neotype selection allows the name *N. valga* to continue to be applied to Spanish populations. The neotype is deposited in the RMNH collection (unique reference number: RMNH.INS.1662584).

Concerning the distribution of *N. caucasica*, due to historical problems with the species concepts, it is necessary to clarify some points here. Astafurova and Pesenko (2006) list *N. caucasica* as a synonym of *N. valga* following Warncke and give a broad distribution from Spain to Pakistan. This also includes Czechia; this record is outside of the range of *N. valga* sensu Warncke and derives from Van der Zanden (1997). Van der Zanden (1997: 756) reported two males of "*Pseudapis valga*" from Czechia (Čejč), one male from Spain (Granada), one male from Turkmenistan (Ashgabat), and one male from Uzbekistan (Samarkand; reported as collected in 1959 but in reality collected in 1919 based on the label). All specimens are now part of the RMNH collection and were examined; the two males from Czechia are *N. femoralis*, the male from Spain is *N. valga*, and the two males from Turkmenistan and Uzbekistan are *N. caucasica* (full specimen details are found in their respective species entries). This inconsistent identification is unfortunately characteristic of the later work of Van der Zanden (see Baker 2002; Wood and Le Divelec 2022), but the re-examination of material allows for these literature references to be clarified.

Figure 3. *Nomiapis valga* (Gerstäcker, 1872) neotype male (RMNH). **A.** Label details; **B.** Habitus, profile view; **C.** Metasoma, dorsal view; **D.** Hind leg and metasoma, profile view.

Finally, Warncke (1980: 370) reported *N. femoralis* ssp. *valga* from Iran and Afghanistan; specimens from these two records were examined in the OÖLM collection, with them corresponding to *N. caucasica*. Overall, *N. caucasica* can be seen as the eastern counterpart of *N. valga*, which is here restricted in distribution to just Spain (Fig. 4).

Distribution. North Macedonia, Greece (including Samos, Lesbos, and Rhodos), Turkey, Cyprus, Israel and the West Bank, Jordan, Armenia, Azerbaijan, Iran, Kazakhstan, Turkmenistan, Uzbekistan, Tajikistan, Afghanistan, and Pakistan (Warncke 1976; 1980 *partim*, as *Nomia femoralis* ssp. *valga*; Baker 2002 *partim*, as *Nomiapis valga*; Astafurova and Pesenko 2006 *partim*, as *N. valga*; Ebmer 2014 *partim*, as *Pseudapis valga*; Pauly 2015 *partim*, as *N. valga*) (Fig. 4).

Nomiapis femoralis (Pallas, 1773)

Apis femoralis Pallas, 1773: 731, ♂ [Kazakhstan, ZMHB, not examined]

Material examined. Austria • 2 ♂; N.O. Marchfeld, Oberweiden (Sandberge); 7 Jul. 1954; F. Koller leg.; A.W. Ebmer det. 1974; OÖLM • 3 ♂; N.O. Marchfeld, Oberweiden (Sandberge); 21–22 Jul. 1954; F. Koller leg.; A.W. Ebmer det. 1974; OÖLM • 1 ♂, 1 ♀; Ober Weiden, A. i. [Austria Inferior]; [undated]; Mader leg.; M. Schwarz det. 1986; OÖLM • 1 ♂; Oberweiden; 27 Jun. 1931; J. Kloiber leg.; A.W. Ebmer det. 1974; OÖLM • 1 ♀; Oberweiden; 28 Aug. 1949; M. Kocourek leg.; M. Kocourek det.; OÖLM; China • 1 ♂, 1 ♀; Boro Horo mts. [Xinjiang], Jinig [Yining/Gulja], Ining-H-Sein; 27 Jul. 1991; M. Snížek leg.; A. Pauly det. 2008; OÖLM; Czechia • 1 ♀; Čejč - Mor. [Moravia]; 16 Jul. 1939; O. Sustera leg.; RMNH; RMNH.INS.1662494 • 1 ♂; Čejč - Mor. [Moravia]; 27 Jul. 1939; O. Sustera leg.; RMNH; RMNH.INS.1662500 • 1 ♂; Čejč - Mor. [Moravia]; 27 Jul. 1939; V. Zavadil leg.; K. Warncke det.; OÖLM • 1 ♂; Čejč - Mor. [Moravia]; 1 Aug. 1939; O. Sustera leg.; RMNH; RMNH.INS.1662499 • 1 ♂, 1 ♀; Čejč - Mor. [Moravia]; 27 Jul. 1941; V. Zavadil leg.; K. Warncke det.; OÖLM • 1 ♀; Čejč - Mor. [Moravia]; 1–31 Aug. 1958; M. Kocourek leg.; K. Warncke det.; OÖLM; Hungary • 1 ♀; Budapest; 19 Jun. 1927; E. Stöckhert leg.; K. Warncke det.; OÖLM • 1 ♀; Budapest; [undated]; RMNH; RMNH.INS.1662493; Kazakhstan • 1 ♂; Alma Ata, 30 km W, Aksaj; 16 Jul. 1981; M. Kocourek leg.; M. Kocourek det.; OÖLM • 1 ♀; Darbaza, 40 km N Tachkent; 30 May 1994; Ma. Halada leg.; A. Pauly det.; OÖLM • 1 ♀; Džambul [=Taraz] env,

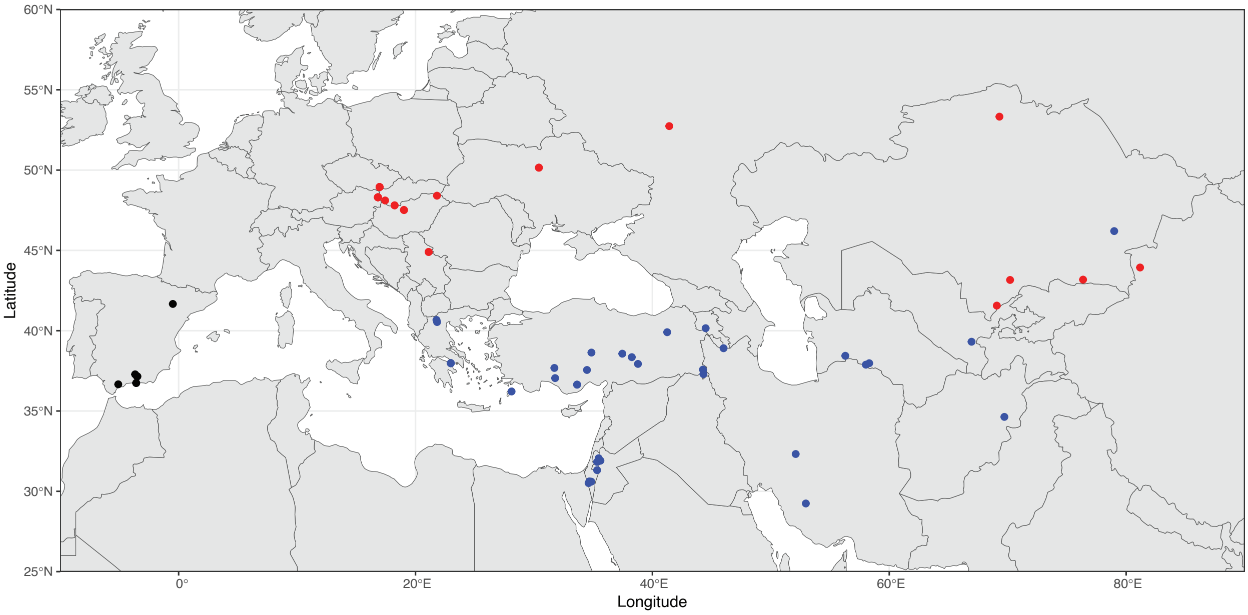

Figure 4. Distribution map based on specimens examined during this study for *Nomiapis valga* (Gerstäcker, 1872) (black circles), *Nomiapis femoralis* (Pallas, 1773) (red circles), and *Nomiapis caucasica* (Friese, 1897) (blue circles). Distributional data presented here are not comprehensive, and additional references in the main text should also be consulted in the context of the revisions to *Nomiapis* species concepts presented here.

Kara Tau, průsmyk [pass] Ujuk; 1000 m a.s.l.; 3 Jun. 1980; Z. Pádr leg.; K. Warncke det.; OÖLM • 1 ♂, 1 ♀; Боровск [Borovsk= Borovoye= Burabay], лес тех Кокчет [Kokchetav] р. Акмол [Akmol]; 2–5 Jul. 1932; В. Попов [V. Popov] leg.; K. Warncke det.; OÖLM; **Russia** • 1 ♂; Tambow [Tambov]; Ф. Моравица [F. Morawitz] leg.; K. Warncke det.; OÖLM; **Serbia** • 1 ♂; Deliblatska Peščara; 2 Aug. 1958; RMNH; RMNH.INS.1662498 • 1 ♂; Deliblatska Pescara [Deliblatska Peščara], Banat - Yoego Slaviě; 12 Jul. 1950; Adamovic leg.; RMNH; RMNH.INS.1662497; **Slovakia** • 1 ♂; Čenkov [Čenkovce]; 1–31 Jul. 1964; M. Kocourek leg.; M. Kocourek det.; OÖLM • 1 ♀; Chotin; 22 Jul. 1962; Z. Pádr leg.; OÖLM • 1 ♂; Chotin; 1–31 Aug. 1962; M. Kocourek leg.; K. Warncke det.; OÖLM • 3 ♂; Somotor; 1–31 Jul. 1952; M. Kocourek leg.; M. Kocourek det.; OÖLM; **Ukraine** • 1 ♂; Киевская Обл [Kiev Oblast], Каневский р-н, о-в Заречье [Zarechye/Zarichchya]; 20 Jun. 1950; А. Осычнюк [A. Osytshnjuk] leg.; RMNH; RMNH.INS.1662495 • 1 ♀; Киевская Обл [Kiev Oblast], Каневский р-н, о-в Заречье [Zarechye/Zarichchya]; 23 Jun. 1950; А. Осычнюк [A. Osytshnjuk] leg.; RMNH; RMNH.INS.1662496.

Notes. The *locus typicus* is "*in deserto ad Iaïkum*," which Astafurova and Pesenko (2006: 78) give as "in a desert on the bank of the Ural River, western Kazakhstan." Revision of material supports the distribution of this species given by Pauly (2015) with the exception of a record from Rhodes; this specimen was determined as "*valga/femoralis* female" by Pauly in 2008 (direct information from the determination label) but seems to have been accidentally encoded and displayed as *N. femoralis*; it is actually referable to *N. caucasica* (see material examined above). *Nomiapis femoralis* is clearly a species of Eurasian steppe and does not descend into the southern Balkans and Turkey, where *N. caucasica* can be found (Fig. 4).

The record from Spain (Barcelona) given by Warncke remains a mystery, as no Spanish specimens in the OÖLM collection could be found. Wood et al. (2020) were able to inspect via photograph (Fig. 5) one of the specimens housed in the BBSL-USDA-ARS collection that was determined to be *Nomiapis monstrosa* but which cannot belong to this species, as the male lacks a digitiform process at the base of the hind tibia. The specimens are of the *valga/caucasica* type due to the sternal morphology (i.e., with curved processes found medially on the 4th sternum), and given the geographic location in Spain, it is considered much more likely that they represent *N. valga* rather than *N. caucasica*, whose closest populations would be in the southern Balkans, some 1,500 km distant. The position is therefore taken that Warncke's (1976) record from Barcelona represents *N. valga*, and *N. femoralis* is excluded from the Spanish fauna.

Finally, based on the limited material examined here, it is important to highlight the clear decline of *N. femoralis* in Europe. Across multiple Central European countries, *N. femoralis* was last recorded in Austria in 1954 (see also Kratschmer et al. 2021), Czechia in 1958 (regionally extinct, Hejda et al. 2017), Serbia in 1958, and Slovenia in 1964. Although the species persists in Hungary, with specimens collected in 2024 (D. Zimmermann, *pers. comm.*), this fits the overall pattern or syndrome of a strong decline of Pannonian or steppic species in Central Europe following agricultural intensification after the Second World War (Hejda et al. 2017; Kratschmer et al. 2021; Wood and Patiny 2025). Whilst this trend is well-established for bumble bees (*Bombus*), taxonomic impediment has limited our understanding of decline in

Figure 5. *Nomiapis valga* (Gerstäcker, 1872) male specimen from Zaragoza, Spain (BBSL740380; BBSL-USDA-ARS); hind leg and metasoma, profile view. Photograph by Skyler Burrows.

European *Nomiapis*; the clarity provided here will hopefully allow a concrete classification of conservation concern to be made.

Finally, Warncke (1976: 111) reports *N. femoralis* ssp. *femoralis* from Croatia (Istria, northern Dalmatia). The location of supporting specimens is unclear. It is not at all clear what these may be, as Istria and Dalmatia have a Mediterranean climate, which does not ecologically match the distributional pattern of *N. femoralis* s. str. Croatia must remain an unconfirmed part of the distribution of *N. femoralis*.

Distribution. Germany, Czechia, Slovakia, Hungary, ?Croatia; Serbia, Romania, Ukraine, Russia (European part, Urals, Western Siberia, Eastern Siberia), Kazakhstan, Turkmenistan, Uzbekistan, Tajikistan, Kyrgyzstan, Mongolia, China (Warncke 1976 as *Nomia femoralis* ssp. *femoralis*; Ebmer 1988; Astafurova and Pesenko 2006; Pauly 2015) (Fig. 4). The specimen reported from Greece (Rhodes) by Baker (2002: 66) is a female and hence is considered to be a misidentification of *N. caucasica*.

Nomiapis valga (Gerstäcker, 1872)

Nomia valga Gerstäcker, 1872: 302, ♂ [Spain: Andalusia, RMNH, neotype by present designation] (Fig. 3)

Material examined. Spain • 1 ♂; Granada, Pantano de Cubillas; 27 May–9 Jun. 1982; R. Leys leg.; RMNH; RMNH.INS.1662584 (**neotype** by present designation) • 2 ♂; Granada, Pantano de Cubillas; 27 May–9 Jun. 1982; R. Leys leg.; RMNH • 1 ♂, 3 ♀; Granada, Canales; 22 Jul. 1978; R. Leys leg.; RMNH; RMNH.INS.1662575 • 1 ♂; Granada, Cenes de la Vega, Sendero del Río Genil; 750 m a.s.l.; 7 Jun. 2021; T.J. Wood leg.; TJWC • 1 ♂, 2 ♀; Granada, Puente de Ojen; 9 Jul. 1985; R. Leys & P. v. d. Hurk leg.; RMNH; RMNH.INS.1662578 • 4 ♂; Granada, Salobreña; 8 May 1983; W. Perraudin leg.; OÖLM • 1 ♀; Granada, Salobreña; 21 May 1983; W. Perraudin leg.; OÖLM • 1 ♂; Zaragoza, 30 km E; 16 Jun. 1974; P.F. Torchio & E. Ase leg.; BBSL740380; BBSL-USDA-ARS (examined by photograph).

Notes. Revision of Spanish material shows that there is a consistent (if infrequently encountered) population in southern Spain, predominantly in the province of Granada but also in Málaga (Pauly 2015); populations in northeastern Spain require investigation, as no records post-1974 are currently available.

Distribution. Spain (Málaga, Granada, Zaragoza, ?Barcelona) (Warncke 1976, as *Nomia femoralis* ssp. *valga*; Pauly 2015 *partim*; *present study*) (Fig. 4).

Identification key for European *Nomiapis*

Wood and Le Divelec (2022) gave characters to allow separation of members of the *bispinosa* group but not a full key, and currently workers are forced to use either the key of Warncke (1976), which has some problems with precision and employs out-of-date species concepts and nomenclature, or the key of Baker (2002), which deals only with males and also uses some out-of-date species concepts. Both of these keys provide valuable information, but their flaws impede access to the genus for inexperienced workers. Therefore, a new key to the 11 species of *Nomiapis* found in Europe is presented. Only European distributions are given within the identification key, not global distributions, for which broader works should be consulted.

The female of *Nomiapis susannae* Arens, 2018, is currently unknown; it is expected to be very similar to the female of *Nomiapis diversipes*, but sex association must be confirmed using genetic techniques. Greater care should be taken with female specimens due to their inherently more difficult identification; association should be made with concurrently active males, when possible. This is a group that benefits greatly from the consultation of confidently determined or barcoded specimens. Supplementary photographs can be seen in Arens (2018) and Wood and Le Divelec (2022); the figures of Warncke (1976) can be consulted with care and an appreciation of their limitations.

1 Antennae with 12 segments; metasoma with 6 segments (females) 2

– Antennae with 13 segments; metasoma with 7 segments (males) 11

2 Tergal margins covered with golden-brown hairbands, these most strongly produced on T3–4 (Fig. 6A) ... Found only in Greece .... *N. equestris* (Gerstäcker)

– Tergal margins without hairbands (Figs 6B, G, H, 7B–D), although hairbands may be present at the base of tergal discs (Fig. 6G), even emerging from beneath the preceding tergum (the margin of which may be translucent), but never occupying the surface of the tergal margin itself 3

3 Ocelloccipital distance 1.5 times the diameter of a lateral ocellus. Scutum very densely punctate, punctures confluent, at most with small and narrow shining interspaces (Fig. 6C). Widespread across Southern and Central Europe, the most commonly encountered European *Nomiapis* .... *N. diversipes* (Latreille)

– Ocelloccipital distance at least 2 times the diameter of a lateral ocellus. Scutum less densely punctate, never with all punctures confluent, at least with some clearly shining interspaces equalling the diameter of a puncture (Fig. 6D–F)............... 4

4 Base of T2 with a strong complete band of short white hairs running across the entire width of the disc (Fig. 6G). Margins of T3–4 translucent and yellowish, with basal hairs of following tergum partially visible............................. 5

– Base of T2 without a hairband, almost without hairs at all. Margins of T3–4 often opaque and non-translucent (Fig. 6B, H), but some specimens can show yellowing or browning of the marginal areas (Fig. 7B–D)....................... 8

5 Anterior margin of scutum (not flattened surface of the dorso-lateral angles of the pronotum) with a dense but weakly developed band of yellowish-white felt-like scales. Clypeus short, 3 times wider than long. Found only in southern European Russia .... *N. fugax* (Morawitz)

– Anterior margin of scutum without a band of felt-like scales, at most with some of the hairs of the pronotal lobes weakly continuing onto the apico-lateral corners of the scutum, not typically forming a complete band (Fig. 6D, E); in *N. paulyi*, sometimes with thin band of hairs appearing to form a weak complete band (Fig. 6F), but this taxon is restricted to the West Mediterranean. Clypeus not so short, around 2 times wider than long (*bispinosa* group)......... 6

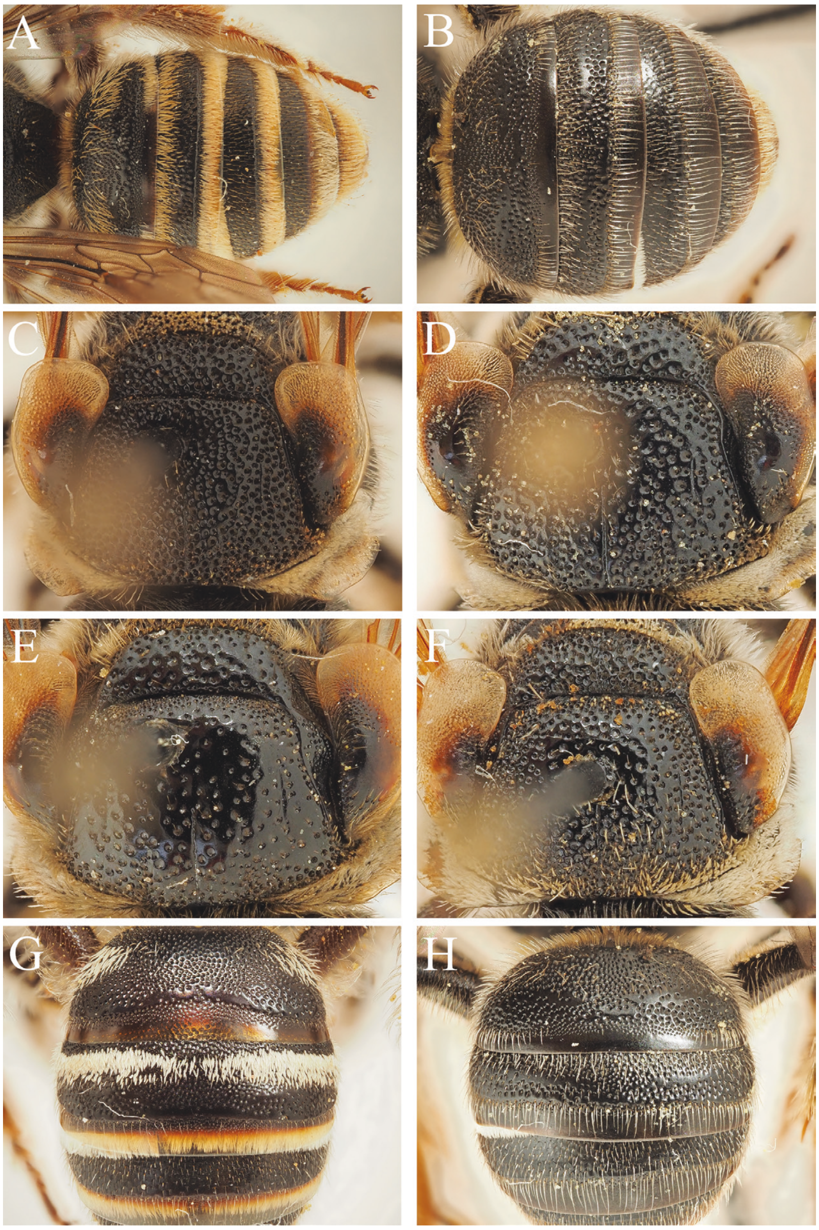

Figure 6. *Nomiapis equestris* (Gerstäcker, 1872) female. **A.** Terga, dorsal view. *Nomiapis monstrosa* (Costa, 1861) female; **B.** Terga, dorsal view; **D.** Scutum and scutellum, dorsal view; **H.** T1–2, dorsal view. *Nomiapis diversipes* (Latreille 1806) female; **C.** Scutum and scutellum, dorsal view. *Nomiapis bispinosa* Brullé, 1833, female; **E.** Scutum and scutellum, dorsal view; **G.** T1–2, dorsal view; *Nomiapis paulyi* Wood & Le Divelec, 2022 female; **F.** Scutum and scutellum, dorsal view.

6 Scutum very coarsely and unevenly punctate with many large interspaces that are clearly larger than one puncture diameter, usually greater than two puncture diameters. T1 with punctation coarse and dense, somewhat sparser laterally on the disc but not forming two clear impunctate areas. Marginal area of T2 punctate basally for at most ⅓ of its length, the marginal area of T3 punctate basally with only 3–4 rows of punctures on the transition between the disc and the marginal area, this covering <⅓ of the length of the marginal area. Distributed across southern Europe in areas with salty soils (coastal habitats, inland saline lagoons, salt steppe) .... *N. bispinosa* (Brullé)

– Scutum densely and evenly punctate, majority of interspaces ≤ 1 puncture diameter. Punctation of T1 finer and denser, but with two distinct impunctate areas mediolaterally. Marginal area of T2 punctate basally for up to ½ its length, marginal area of T3 with many rows of punctures covering up to ⅓ of its length... 7

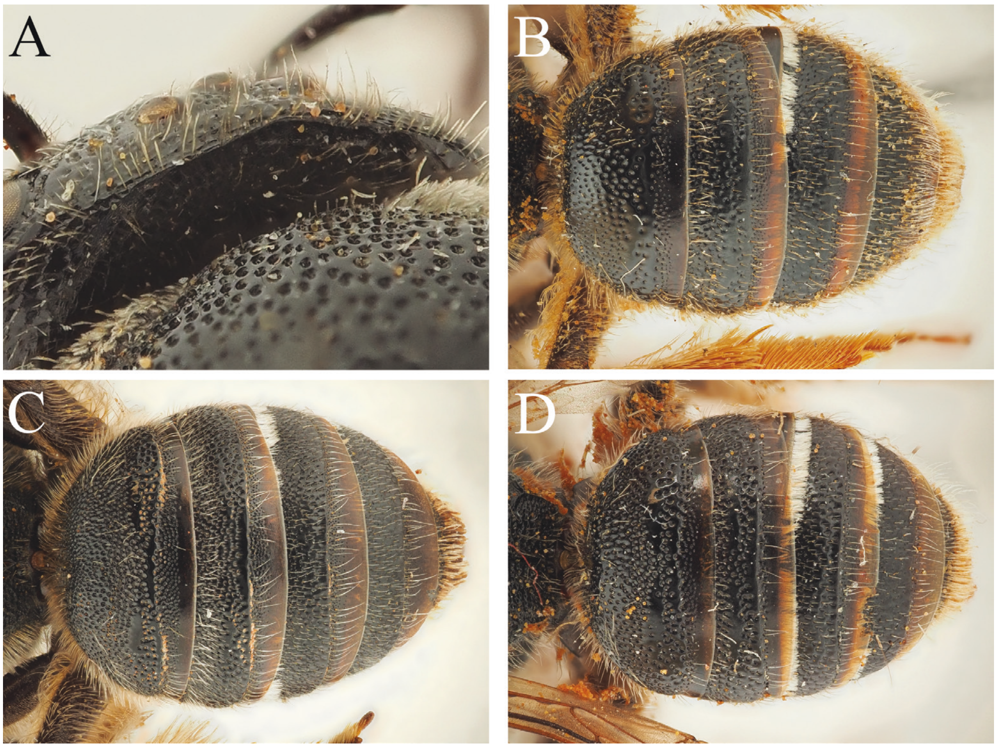

Figure 7. *Nomiapis femoralis* (Pallas, 1773) female. **A.** Vertex, dorsolateral view; **B.** Terga, dorsal view. *Nomiapis valga* (Gerstäcker, 1872) female; **C.** Terga, dorsal view. *Nomiapis caucasica* (Friese, 1897) female; **D.** Terga, dorsal view.

7 Scutum with punctation contiguous in the anterior ¼, subcontiguous laterally between parapsidal line and lateral margin of scutum; disc with many interspaces larger than two puncture diameters. Marginal area of T2 basally punctate for ½ of its length at most; marginal area of T3 with many rows of punctures covering around ⅓ of its length. Disc of T2 with a pair of conspicuous long impunctate areas measuring around ¼ of the width of the tergum in length and around as wide as 3–4 puncture diameters. Found in Italy (Sicily)...*N. rufiventris* (Spinola)

– Scutum with punctation more even, 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 puncture diameters. Marginal area of T2 punctate basally for more than ½ of its length (almost ⅔); marginal area of T3 with many rows of punctures covering around ½ of its length. Disc of T2 with at most a pair of inconspicuous impunctate areas. Found in Iberia, Corsica, and Sardinia.. *N. paulyi* Wood and Le Divelec

8 Head with the posterior margin of the vertex rounded. Found in southern Italy and the Balkan Peninsula .... *N. monstrosa* (Costa)

– Head with the posterior margin of the vertex displaying a sharp carina (Fig. 7A). Widespread (*femoralis*-group)........ 9

9 Disc of T1 strongly polished and shining, mirror-smooth, without any trace of microsculpture (Fig. 7B). Disc of T1 with punctures relatively sparse in basal ½, with punctures separated by one puncture diameter, in ¼ immediately anterior to marginal area with punctures noticeably sparser, separated by 1–4 puncture diameters. Marginal area of T1 with 3–4 poorly defined rows of punctures, interspaces distinct. Found in Pannonian Europe eastwards (Fig. 4) ....*N. femoralis* (Pallas)

– Disc of T1 with fine but distinct microsculpture, never completely smooth and shining (Fig. 7C, D). Disc of T1 with punctures relatively dense, in basal ½ with punctures varying from confluent to separated by 0.5–1 puncture diameter, in ¼ immediately anterior to marginal area with punctures slightly sparser, separated by up to two puncture diameters but typically by < 1 puncture diameter. Marginal area of T1 with punctation variable, but usually with 4–6 rows of punctures separated by ≤ 1 puncture diameter. Found further south (Mediterranean Europe) 10

10 Disc of T1 in basal ½ with punctures extremely dense, separated by < 0.5 puncture diameters, essentially confluent (Fig. 7C). Marginal area of T1 with 5–6 rows of very dense punctures, punctures separated by ≤ 0.5 puncture diameters. Marginal areas of T2–3 with many rows of dense punctures covering their basal ½. Found in Spain (Fig. 4) .... *N. valga* (Gerstäcker)

– Disc of T1 in basal ½ with punctures separated by 0.5–1 puncture diameter (Fig. 7D). Marginal area of T1 with around 4 poorly defined rows of punctures, punctures separated by 0.5–1 puncture diameter. Marginal areas of T2–3 with 1–3 rows of punctures covering only their basal ⅕. Found in southeastern Europe (Fig. 4) .... *N. caucasica* (Friese)

11(1) Mesosoma ventrally without a projecting pair of spines (*bispinosa* group) 12

– Mesosoma ventrally with a pair of strongly projecting spines (Fig. 8A) 14

12 Marginal areas of T2–3 with the transition between the disc and the marginal area sharp, the edge almost carina-like. Punctation of marginal areas indistinct, restricted to 2 rows of punctures in basal part. S6 with a pair of strongly produced tubercles medially, clearly forming a strong triangular shape. Slightly larger, 10–12 mm. Distributed across southern Europe in areas with salty soils (coastal habitats, inland saline lagoons, salt steppe) ..... *N. bispinosa* (Brullé)

– Marginal areas of T2–3 with the transition between the disc and the marginal area relatively smooth. Punctation of marginal areas distinct, comprising around 4 rows of punctures covering at least the basal ⅕ of marginal area. S6 with a pair of weakly produced tubercles medially, forming a weak triangle. Slightly smaller, 7–9 mm. Distributed in the West Mediterranean only, not restricted to salty soils 13

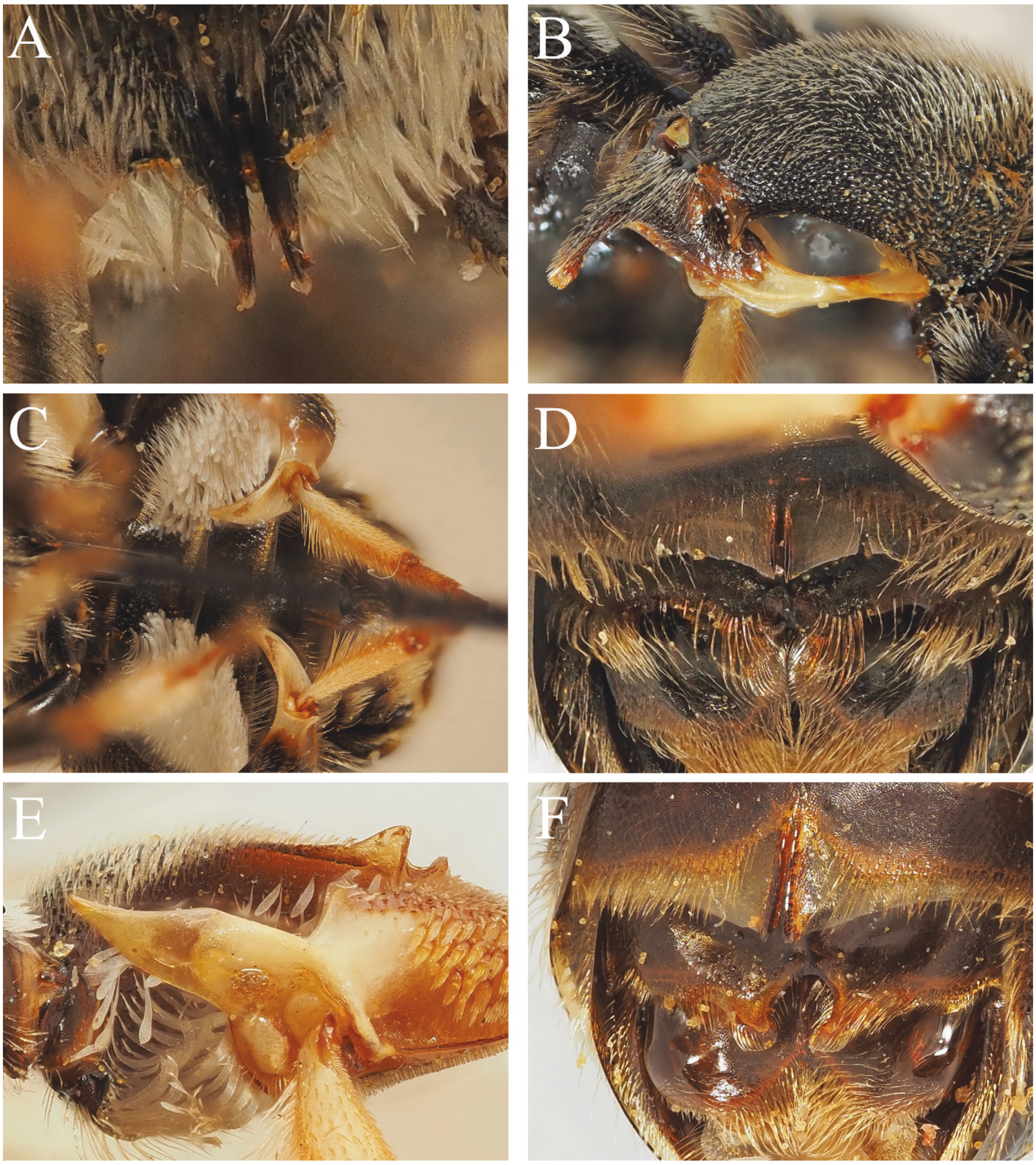

Figure 8. *Nomiapis caucasica* (Friese, 1897) male. **A.** Projecting paired spines on the ventral face of the mesosoma; *Nomiapis monstrosa* (Costa, 1861) male; **B.** Hind leg, femur, and base of tibia, profile view. *Nomiapis diversipes* (Latreille 1806) male; **C.** Hind tibial processes, ventral view; **D.** S4–6, ventral view; *Nomiapis equestris* (Gerstäcker, 1872) male; **E.** Hind tibial process, ventral view; **F.** S4–6, ventral view.

13 Punctures of margins of T2–3 covering basal ⅕ of marginal area. 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. Found in Italy (Sicily) ....*N. rufiventris* (Spinola)*

– Punctures of margins of T2–3 covering slightly more than basal ⅕ of marginal area. 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. Found in Iberia, Corsica, and Sardinia *paulyi* Wood and Le Divelec

14 Base of the hind tibia with a long digitiform projection (Fig. 8B). Found in southern Italy and the Balkan Peninsula ... *N. monstrosa* (Costa)

– Base of the hind tibia rounded or at most slightly angulate, never with a long digitiform projection........................ 15

15 Hind tibia produced into a relatively short and apically pointed process (Fig. 8C, E). S4, with its apical margin either straight or convex (at most very slightly emarginate), with two closely spaced raised longitudinal ridges (Fig. 8D, F)................... 16

– Hind tibia produced into a relatively long, flattened, and more-or-less rectangular shape with a truncate apex (Fig. 9A). S4, with its apical margin either deeply and broadly excavated medially (Figs 2D, 9B) or, if only narrowly incised, without raised longitudinal ridges 18

16 Margin of S5 with deep circular emargination, lateral sides produced into curving digiform projections, almost hyaline, these almost encircling emargination (Fig. 8F). Found only in Greece ....*N. equestris* (Gerstäcker)

– Margin of S5 with small to nondescript emargination, without digiform projections (Fig. 8D) 17

17 S4 medially with raised longitudinal ridges placed very close together, inner margins parallel (Fig. 8D). S5 with median lobes pronounced, comparatively more strongly projecting posteriorly, outer margin therefore somewhat concave. S6 with lateral ridges more strongly developed, standing above the rest of the disc, apically produced into a rounded tooth-like bump. Widespread across Southern and Central Europe, the most commonly encountered European *Nomiapis*..*N. diversipes* (Latreille)

– S4 medially with raised longitudinal ridges with their inner margins diverging apically. S5 with medial lobes weakly produced, only slightly projecting posteriorly, outer margin therefore only weakly concave. S6 with lateral ridges only weakly differentiated from surrounding disc, apically disappearing into underlying sculpture. Currently known only from Greece (Peloponnese, Eastern Macedonia, and Thrace)... *N. susannae* Arens

18 Margin of S4 deeply but narrowly incised, lateral margins only slightly thickened. Margin of S5 with a triangular emargination, without projections internally within this emargination. Found only in southern European Russia .... *N. fugax* (Morawitz)

– Margin of S4 with a deep semi-circular emargination (Figs 2D, 9B), lateral margins with elevated ridges, their surface polished and glabrous. S5 medially with 2 pincer-like, slightly bent digitiform projections (Figs 2D, 9B)................. 19

19 In profile view, lateral margins flanking the emargination of S4 produced elevated projections with triangular to trapezoidal apexes (Fig. 9C). Found in Pannonian Europe eastwards (Fig. 4) ....*N. femoralis* (Pallas)

– In profile view, lateral margins flanking the emargination of S4 produced into low-lying posteriorly-projecting ridges (Figs 2D, 3D, 5, 9D). Found either in Spain or southeastern Europe... 0

20 Disc of T2 uniformly punctate, punctures extending over the entire breadth of the disc, consistently separated by only narrow interspaces with exception of very slightly shining areas mediolaterally, these not exceeding the diameter of a puncture (Fig. 3C). Marginal areas of T2–3 with 3 rows of punctures, these occupying the basal ⅓–⅕ of the marginal areas. In direct comparison, tergal punctation slightly denser and microsculpture slightly stronger, therefore slightly more dull, particularly visible on tergal margins. Scutellum laterally mucronate (Fig. 9E; with two small posteriorly projecting teeth). Found in Spain (Fig. 4)...*N. valga* (Gerstäcker)

– Disc of T2 irregularly punctate, mediolaterally with two shining areas, in size exceeding the diameter of a puncture (Fig. 2C). Marginal areas of T2–3 with 1 row of puncture, sometimes with a very narrow irregular 2nd row composed of very small punctures; punctures occupying <⅕ of the basal part of the marginal areas. In direct comparison, tergal punctation slightly sparser and microsculpture slightly weaker; therefore, slightly more brightly shining, particularly visible on tergal margins. Scutellum mucronate or not (Fig. 9F). Found in southeastern Europe (Fig. 4) ....*N. caucasica* (Friese)

Discussion

The fortunate retrieval of the remaining type material of *N. caucasica* hidden in the Warncke collection has allowed its identity to be decisively settled in opposition to *N. valga*, which is now considered to be endemic to Spain. That the identity and distribution of what is ultimately a small number of species (11 in Europe) could be so confused over time (Friese 1897; Warncke 1976; Van der Zanden 1997; Baker 2002; Wood et al. 2020; Wood and Le Divelec 2022) is testament to the high degree of identification difficulty posed by nomiine bees, particularly in the female sex. The result also continues to reinforce the importance of the Iberian

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* The following two species are more or less impossible to separate in the male sex but can be identified based on the geographic origin and association with females.

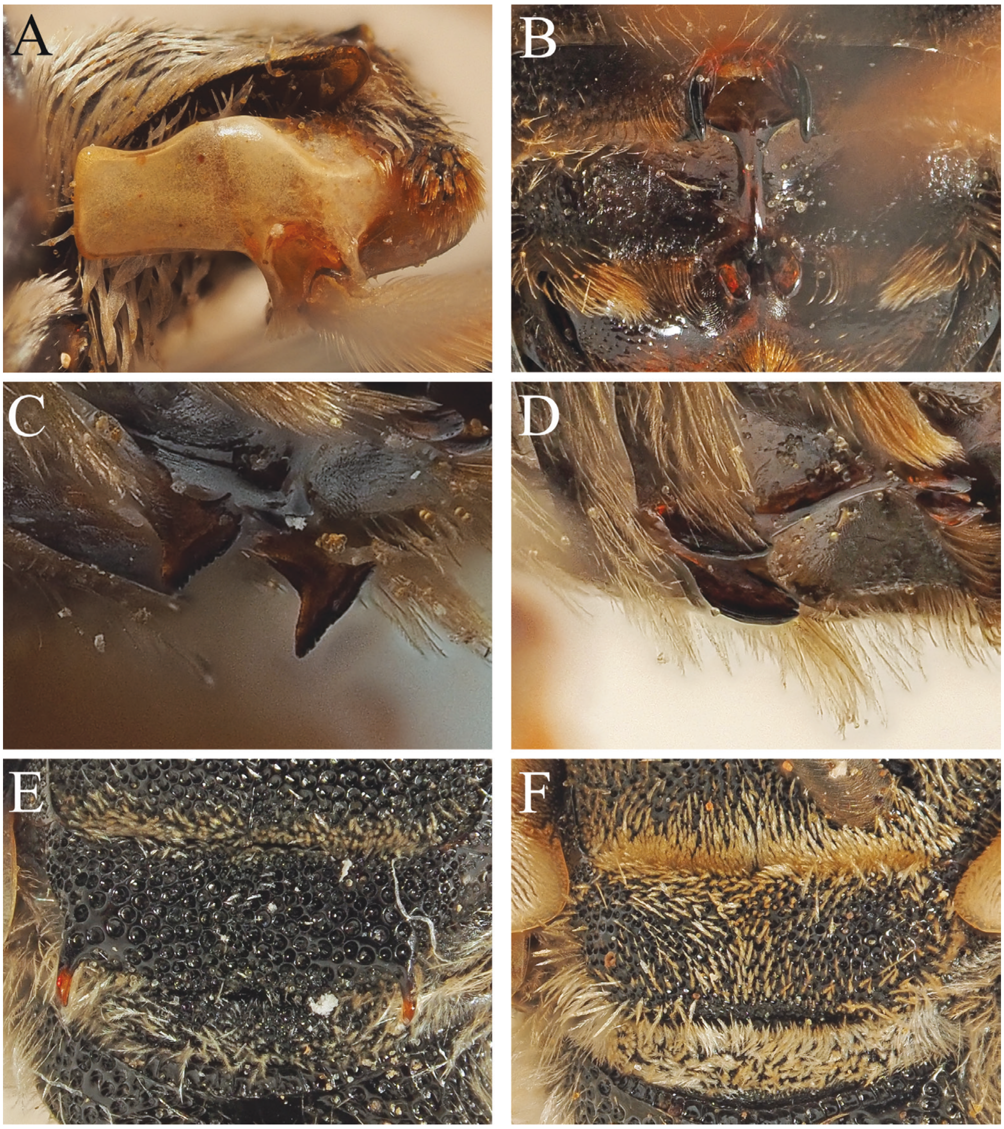

Figure 9. *Nomiapis caucasica* (Friese, 1897) male. **A.** Hind tibial process, ventral view; **F.** Scutellum, dorsal view. *Nomiapis valga* (Gerstäcker, 1872) male; **B.** S4–5, ventral view; **D.** Medial projections of S4, profile view; **E.** Scutellum, dorsal view. *Nomiapis femoralis* (Pallas, 1773) male; **C.** Medial projections of S4, profile view.

Peninsula as a center for endemic bee diversity both globally and within Europe, a pattern repeatedly borne out during the past decade of taxonomic research on bees (Ghisbain et al. 2023).

Concerning the revisionary work presented here, it is fortunate that the type series of *N. caucasica* was male and that the original description of *N. valga* was also made from the male sex. This is not the case in many other groups that pose identification challenges, particularly in the Indo-Malayan region with genera such as *Maculonomia* Wu, 1982, for which some of the oldest names were described from females such as *Maculonomia elegans* (Smith, 1857), *Maculonomia interrupta* (Cameron, 1904), *Maculonomia leucozonata* (Cameron, 1902), and *Maculonomia terminata* (Smith, 1875) (Pauly 2009). Some genera, such as *Reepenia* Friese, 1909, or *Mellitidia* Guérin-Méneville, 1831, have never been properly revised, at least in the modern period (Pauly 2009).

Given the fundamental problems of nomiine nomenclature and species concepts in the European fauna, it is likely that many changes will be needed in the Indo-Malayan region when revisionary opportunities become available, quite apart from the known problems posed by generic delineation and classification (Bossert et al. 2021; 2024; 2025). However, the results presented here also show that *Nomiapis* females can be consistently identified with care, association with males, integration of genetic barcode data, consideration of biogeography, and careful assessment of puncture density and integumental sculpture. This may offer a path towards revision of groups with many taxa described from females, should these groups display similar species-specific variation as that presented here.

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