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Monograph

Molecular Phylogenetics, Phylogenomics, and Phylogeography

A phylogenomic monograph of West-Palearctic *Nomada* (Hymenoptera: Apidae)

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We reconstruct the phylogeny of the most speciose genus of cuckoo bees, genus *Nomada* Scopoli, 1770, using 221 species from throughout its distribution, yet with a strong emphasis on the West Palearctic. For phylogenetic reconstruction, we sequenced ultraconserved elements, allowing robust phylogenetic estimates with both concatenation and coalescent-based methods. By integrating extensive information on *Nomada* host records, we study macroevolutionary patterns of host associations, transitions, and phylogenetic conservatism. Using Bayesian divergence time estimates, we assess the historical biogeography of the genus, focusing on the West Palearctic. Our results show that *Nomada* likely originated in the Eastern Mediterranean and Near Eastern region, and likely expanded its range to a near-global distribution from there. We recovered long-standing phylogenetic conservatism in the host usage of *Nomada* and provided strong statistical evidence for an ancestral host association with *Andrena* and its most recent common ancestor. However, host transitions occurred multiple times independently in the natural history of *Nomada*, and species of the genus are brood parasites in at least 5 genera and 4 different families of bees in the Old World. At last, we systematically revise the taxonomy of the Old World *Nomada* by integrating morphological study with our well-supported phylogenetic estimates. We re-establish the genus *Acanthonomada* Schwarz, 1966, stat. res., as a distinct, second genus in the tribe Nomadini. We recognize 13 subgenera for *Nomada*, 9 of which are described as new: *Afronomada* Straka and Bossert, subgen. nov., *Colliculla* Straka, subgen. nov., *Gestamen* Straka, subgen. nov., *Hungias* Straka, subgen. nov., *Mininomada* Straka, subgen. nov., *Nomacolla* Straka, subgen. nov., *Nomonosa* Straka, subgen. nov., *Plumada* Straka, subgen. nov., and *Profuga* Straka, subgen. nov. Aside from the subgenus *Nomada* s.s., we reinstitute 3 previously synonymized subgenera: *Heminomada* Cockerell, 1902, stat. res., *Holonomada* Robertson, 1903, stat. res., and *Hypochrotaenia* Holmberg, 1886 stat. res. A total of 15 subgeneric names are formally synonymized with the newly established subgeneric concepts.

Key words: ultraconserved elements, phylogenetic reconstruction, brood parasitism, host specialization, Nomadinae

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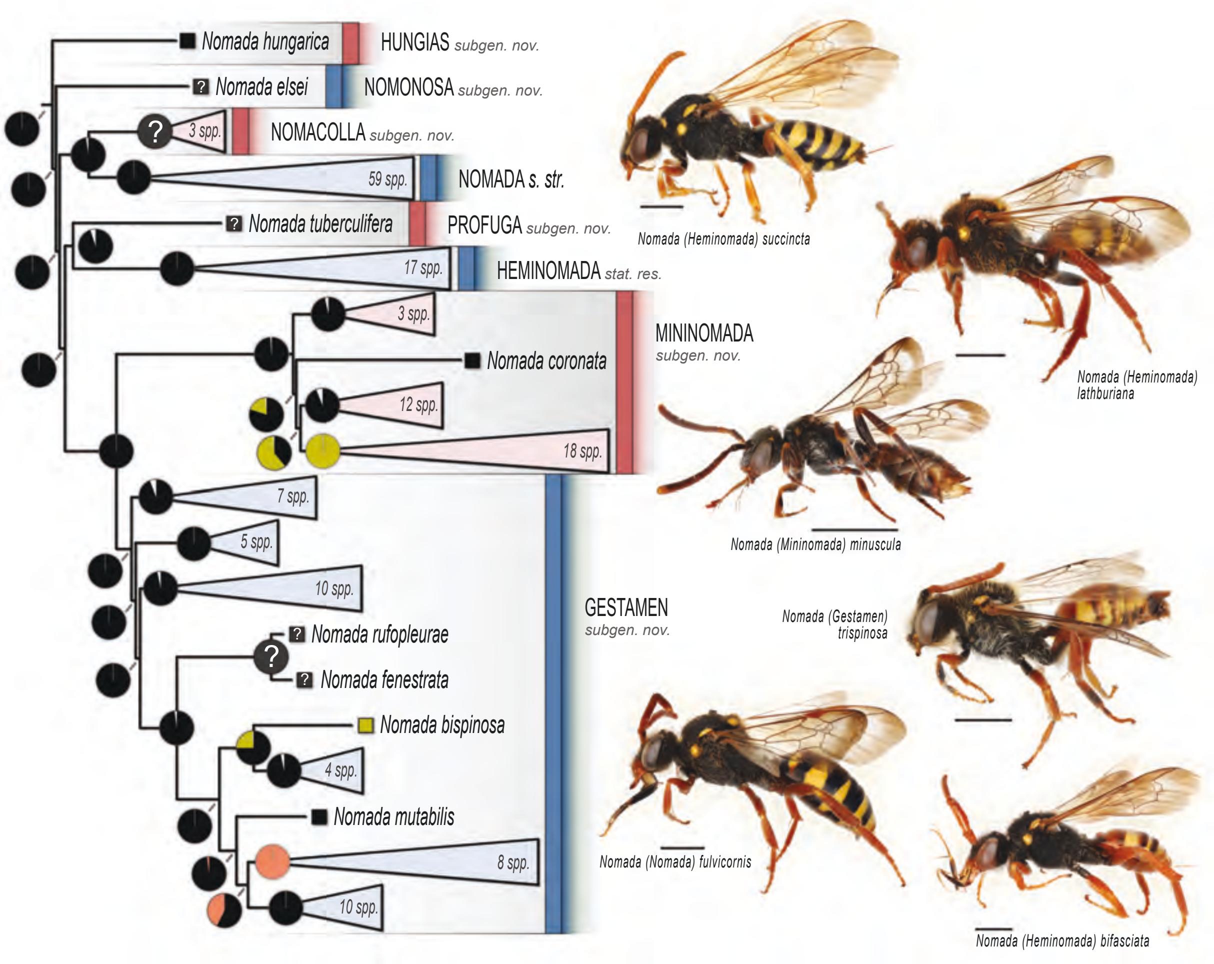
Graphical Abstract



Introduction

Parasitism is a common life history strategy across the Tree of Life (Poulin 2007). Among the various modes of parasitism, a particular strategy involves the stealing of food or other resources from a host by the parasitic animal. This strategy is commonly referred to as brood parasitism (Danforth et al. 2019) and represents a widespread life history trait in many animal groups (Brockmann and Barnard 1979, Hamilton and Dill 2003, Sless et al. 2023), including bees (Michener 2007, Rozen and Kamel 2007). These so-called cuckoo bees represent a substantial fraction of global bee biodiversity: an estimated 12% of the ~20,500 described bee species are considered brood parasitic, and this proportion may be as high as 25% for the family Apidae, the largest of the 7 bee families (Danforth et al. 2019).

In contrast to the solitary and social bees that they parasitize, cuckoo bees do not build their own nests, nor do they collect pollen. Instead, they invade the nests of their host and deposit eggs in the brood cells that hosts have provisioned for their own offspring (Michener 2007, Danforth et al. 2019). If successful, the parasitic larva consumes the brood provisions comprised of pollen and nectar and matures, whereas the host larva dies. In most brood parasitic bees, the first-instar larva is highly modified in comparison to their host counterparts. They are mobile, armed with sharp and elongated mandibles, and usually kill the host larva (Rozen 1991, Alves-dos-Santos et al. 2002), although the adult female carries out this task in certain lineages like *Exaerete* Hoffmannsegg, 1817 (Hymenoptera: Apidae) (Garófalo and Rozen 2001) or *Sphecodes* Latreille, 1804 (Hymenoptera: Halictidae) (Rozen 2000). Strikingly, a brood parasitic lifestyle has evolved multiple times independently in bees and at least 3 times in Apidae alone (Bossert et al. 2019, Policarová et al. 2019), providing an excellent framework to study convergent evolutionary change in light of the shared parasitic life history.

Of the approximately 2,500 described cuckoo bee species, the single genus *Nomada* Scopoli, 1770 (Hymenoptera: Apidae) comprises 761 currently recognized species (Ascher and Pickering 2020). This corresponds to nearly one-third of the global brood-parasitic bee biodiversity and renders *Nomada* the single species-richest genus of brood-parasitic bees in the world. Continuing efforts to discover and describe new species from the West Palearctic region (Schwarz and Smit 2018, 2020, Schwarz et al. 2018, Schwarz et al. 2018, Smit 2018, Schwarz et al. 2019, 2020) and a significantly understudied fauna in North America (Mitchell 1962, Droege et al. 2010, Odanaka et al. 2022) means that the number of total species will inevitably increase in the future, as these regions are thought to harbor the greatest species diversity of *Nomada* globally (Alexander 1994). The genus is less diverse in the Neotropical and Oriental regions (Snelling 1986, Schwarz 1990), and only 14 species are known from sub-Saharan Africa (Eardley and Schwarz 1991, Kuhlmann 2023). A single species, *Nomada australiensis* Perkins, 1912, occurs in Australia (Walker et al. 2020).

The extraordinary species diversity of *Nomada* is particularly fascinating, yet enigmatic, specifically with respect to the pollen-collecting hosts that they exploit. Species of *Nomada* are never closely related to their hosts and do not parasitize other members of their exclusively parasitic subfamily Nomadinae. As far as is known, the majority of *Nomada* species are species-specific parasites on species of *Andrena* Fabricius, 1775 (Hymenoptera: Andrenidae) (Alexander 1991, Smit 2018), which is the second largest genus of bees (>1,600 species) and a rapidly diversifying lineage (Bossert et al. 2022). In Central Europe, where host-parasite associations of *Nomada* are best documented, most species parasitize 1 or 2 species of usually related *Andrena* and mirror the seasonal activity of their hosts, even leading certain *Nomada* species to produce 2 generations if their hosts are bivoltine (Scheuchl 2000, Westrich 2006, Scheuchl and Willner 2016). Beyond their association with *Andrena*, *Nomada* has been reported to exploit hosts in 4 of the 7 bee families, including *Panurgus* Panzer, 1806 (Hymenoptera: Andrenidae), different lineages of *Lasioglossum* Curtis, 1833 (Hymenoptera: Halictidae), *Eucera* Scopoli, 1770 (Hymenoptera: Apidae), and *Melitta* Kirby, 1802 (Hymenoptera: Melittidae) (Smit 2018). Outside of the Palearctic, bees in the genera *Agapostemon* Guérin-Méneville, 1844 and *Lipotriches* Gerstaecker, 1858 (both Hymenoptera: Halictidae), *Exomalopsis* Spinola, 1853 (Hymenoptera: Apidae) (Alexander 1991) and *Redivivoides* Michener, 1981 (Hymenoptera: Melittidae) (Kuhlmann 2023) have been reported to be parasitized by *Nomada* as well.

Despite the rich, sometimes centuries-old documentation of *Nomada* and their hosts, we have a very limited knowledge of the evolution of their host-parasite relationships. Specifically, we do not understand if host usage in *Nomada* is a phylogenetically conserved trait. For example, multiple species of *Nomada* are known to parasitize different species of *Eucera*, *Lasioglossum*, or *Melitta*, yet it is unknown if the *Nomada* species attacking these genera form natural, monophyletic groups according to their host usage. If true, this would indicate only a few genus-level host switches in the evolutionary history of *Nomada*. Limited information is available for the *Lasioglossum*-specific *Nomada*: Lim et al. (2022) suggest that the *Nomada* species that attack *Lasioglossum* are paraphyletic, thus indicating that host switches to *Lasioglossum* have occurred multiple times independently in *Nomada*. Strikingly, comprehensive studies on host usage of *Nomada* are lacking and phylogenetic patterns of host-parasite evolution remain largely unknown. Therefore, understanding the evolution of host-usage in *Nomada* requires the synthesis of 2 components; a sound phylogenetic framework of *Nomada* themselves and detailed documentation of extant host-parasite relationships.

Aside from host-parasite patterns, the lack of robust phylogenetic estimates hampers our ability to evaluate the current taxonomic classification of *Nomada* and previously proposed genus and subgenus concepts. Currently, *Nomada* is considered monophyletic and is usually divided into the 16 species groups established by Alexander (1994) based on cladistic analysis and expanded by Alexander and Schwarz (1994) for the comprehensive global catalog of *Nomada*. A number of subgenera have been used in past studies (i.e., Alexander and Schwarz 1994), but are not recognized by the most recent classifications (Michener 2007, Ascher and Pickering 2020). A recent phylogenomic reassessment of species groups found monophyly for 14 out of the 16 species groups using ultraconserved elements (UCEs) and a broad taxon sampling, albeit by including only a limited number of western Palearctic species (Odanaka et al. 2022). Consequently, the phylogenetic affinities of many other species of *Nomada*, especially those from the West Palearctic, are uncertain and remain in need of integrative, molecular-morphological reevaluation.

At last, a recent treatment of the historical biogeography of *Nomada* suggested a Holarctic origin of the genus, although 2 of the 3 earliest branching lineages occur in the Old World (Odanaka et al. 2022). This includes the single sister lineage to all other *Nomada*, the East Mediterranean-Middle Eastern-endemic *odontophora* group, which consists of 3 described species and was previously considered the separate genus *Acanthonomada* Schwarz, 1966 (Schwarz 1966, Alexander and Schwarz 1994). This spatial pattern mirrors that of the early evolution of Andreninae (Pisanty et al. 2022): *Cubiandrena* Warncke, 1968, the extant sister lineage to all *Andrena* species, comprises 3 currently known species (Wood 2020), and is also endemic to the southern Balkans and the Middle East. These phylogenetic patterns underline the particular significance of the Middle Eastern region for understanding the early evolution of *Nomada* and its hosts. At the same time, the *Nomada* fauna of the Middle East and the Mediterranean Basin is severely understudied, and a comprehensive, phylogeny-guided reassessment is needed to examine the natural history of the West Palaearctic species of *Nomada* and the spatiotemporal origins of its major clades.

In the present study, we develop a densely sampled phylogenetic framework of the West Palearctic Nomadini to address these long-standing questions. Over years of study and fieldwork, we developed an expansive level of taxon sampling, which includes most described species of West Palearctic *Nomada* and several undescribed lineages. Through extensive literature searches, we compiled information on host usage for as many species as possible and synthesized this knowledge in light of a robust, time-calibrated phylogeny based on genomic UCEs. Using Bayesian ancestral state reconstruction, we find evidence for a phylogenetically conserved host usage in *Nomada*, and we discuss the historical biogeography of the genus in the Palearctic realm. At last, we critically evaluate the taxonomic classification of *Nomada* by integrating morphological study with phylogenomic data.

Materials and Methods

Taxon Sampling

Our study includes a total of 221 species of *Nomada*, including a representative of *Acanthonomada* (Supplementary Tables 1 and 2). As outgroup representatives, we used 7 species of Nomadinae from 5 tribes. Outgroup species were selected from tribes closely related to Nomadini according to a recent comprehensive phylogenetic reconstruction of the subfamily Nomadinae (Sless et al. 2022). Identification of *Nomada* species is traditionally difficult, as many species can vary greatly in size, coloration, and morphological features. Nonetheless, we were able to identify 194 out of the 221 included specimens of *Nomada* to species level. Identification of most specimens was carried out by the first author and Maximilian Schwarz, and voucher specimens were deposited in the collection of the first author (Supplementary Table 1). We were unable to determine the remaining 27 included samples to species, likely because they represent undescribed taxa. Our dataset includes all species groups designated by Alexander (1994) and Alexander and Schwarz (1994), except for 4 lineages that are seemingly endemic to North America: (i) the *Nomada* subgenus *Asteronomada* Broemeling, 1988 (= *N. adducta* group), (ii) the subgenus *Pachynomada* Rodeck, 1945 (= *N. vincta* group), (iii) the subgenus *Phelonomada* Snelling, 1986 (= *N. belfragei* group), and (iv) the enigmatic *Nomada rodecki* Mitchell, 1962, an isolated species with unclear phylogenetic status (Alexander 1994). UCE sequence data from 19 Nomadini and all outgroup samples were mined from previously published research (Grab et al. 2019, Gueuning et al. 2020, Sless et al. 2022). Sequence data for a total of 202 specimens were newly generated for the present study. Samples selected for DNA isolation were recently collected (1–20 years old) and were stored either in ethanol or pinned as museum specimens. An overview of the materials used is provided in Supplementary Tables 1 and 2.

Molecular Methods and UCE Data Processing

DNA extractions were carried out using DNeasy Blood & Tissue Kits (Qiagen, Inc.) according to the manufacturer's protocol, including the optional RNAse treatment. DNA extracts were sent either to Daicel Arbor Biosciences (USA) (160 samples) or Rapid Genomics LLC (USA) (42 samples) for commercial UCE target capture and sequencing. Targeted enrichment was carried out using the Hymenoptera v2 probe set (Branstetter et al. 2017), which targets more than 2,500 UCE loci. After sequencing the prepared libraries on Novaseq Illumina platforms, we obtained demultiplexed read data from the sequencing facilities. DNA sequences are available at NCBI (BioProject ID PRJNA846559), and SRA numbers are included in Supplementary Table 1. The quality of the fastq read files was assessed with FastQC (Andrews 2010). We used the program Trimmomatic (Bolger et al. 2014) to trim the remaining adapters of the reads. Subsequently, the reads were reformatted, error corrected, and normalized to a coverage of 200 × using different scripts of the BBTools package (Reformat, Tadpole, and Normalize). For each individual sample, reads were assembled into contigs using SPAdes 3.14.0 (Bankevich et al. 2012) with kmer set from 21 to 121 and the "careful" read correction option. Subsequent processing of contigs was carried out using the PHYLUCE v1.6 pipeline (Faircloth 2016) which implements the software LastZ (Harris 2007) to match the contigs to the UCE probes (using default settings), MAFFT v7 (Katoh and Standley 2013) for sequence alignment, and Gblocks (Talavera and Castresana 2007) for internal trimming of aligned sequences. We used the default parameters for trimming with Gblocks and finalized a concatenated dataset with 80% completeness (1,532 loci). Each individual gene alignment was visualized in Geneious Prime 2021 (https://www.geneious.com) and examined by eye for highly divergent ends of sequences. In a few instances, we manually cropped obvious spurious sequences.

Phylogenetic Reconstruction

Using the concatenated DNA sequence matrix, we carried out maximum likelihood (ML) analysis using the program IQ-TREE v2.1.3 (Minh et al. 2020). We designated partitions by locus and combined UCE subsets with similar substitution rates (-m TESTNEWMERGE) and used the -rclusterf setting at 10 (Chernomor et al. 2016) as implemented in ModelFinder (Kalyaanamoorthy et al. 2017). We carried out 1,000 ultra-fast bootstrap approximations (UFBoot2, Hoang et al. 2018).

To compare the results of our ML analysis with those obtained through Bayesian inference, we used the program PhyloBayes MPI version 1.8 (Lartillot and Philippe 2004) on the entire concatenated 1,532 UCE alignment. Since we used the CAT-GTR model with discrete Γ prior (Lartillot and Philippe 2004), we did not partition the sequence alignment. We ran a total of 4 independent runs, 2 of which progressed for 20,000 cycles and the other 2 for 12,000 cycles. We discarded the first 1,500 trees from each run. Convergence of the Bayesian run identifiers was assessed using Tracer v1.7.1 (Rambaut et al. 2018). Despite our extensive runtime, we needed to accept effective sample size (ESS) values of > 100 for the time and Nmode parameters as marginally converged runs. ESS values for all remaining parameters, including the topology parameter, reached values of > 200.

For conducting a coalescence-based analysis of our dataset, we first calculated individual gene trees for each of the 1,532 UCE alignments. To this end, we calculated 50% majority rule ML trees with 1,000 bootstrap approximations using IQ-Tree and combined the individual tree files in a single text file. The summary analysis under the multispecies coalescent model was conducted in ASTRAL 5.7.7 (Zhang et al. 2018) using default settings.

Divergence Time Estimates

To study the evolutionary history of West Palearctic *Nomada*, we carried out fossil-informed divergence time analyses with Bayesian methods. Since such analyses are computationally challenging for large datasets such as ours, we decided to lower the computational burden by focusing on a particularly well-suited subset of DNA sequence data for divergence time estimation. Recent research suggests improved performance of "tree-like" loci over "clock-like" loci for divergence time analyses when using subsets of UCEs (Chen et al. 2021). The most tree-like loci are those whose gene-tree topology is most similar to that of a preferred species tree, and this similarity is measured by the concordance of shared bipartitions (Smith et al. 2018). Clock-like loci, in turn, are not selected based on the topology of resulting gene trees but instead by their similarity to an ultrametric tree. The latter approach is widely used for dating UCE phylogenies (Branstetter et al. 2021, McFadden et al. 2021, Bossert et al. 2022) but may come with the drawback of comparatively fewer informative sites (Chen et al. 2021). We hence chose to identify the 50 loci with the greatest bipartition concordance with respect to the ML species tree (Figs. 1 and 2), which was based on the 80% completeness matrix. Recent research found that the accuracy of divergence time estimates does increase with an increased amount of data (the addition of more loci does not improve the results; Freitas et al. 2022), which is why we decided on a medium-sized, well-suited set of loci. To this end, we examined the 1,532 individual gene trees and the reference tree and pruned off all outgroups except *Neolarra californica*, which was the outgroup taxon present in more gene trees than any other species. Subsequently, we rooted all trees on *Neolarra*, discarded 42 trees (out of 1,532) that lacked this terminal, and calculated bipartition concordance with SortaDate (Smith et al. 2018). After identifying the 50 most concordant gene trees, we used AMAS (Borowiec 2016) to concatenate their respective alignments and identified the best-fitting partitioning scheme with ModelFinder, as implemented in IQ-Tree. Specifically, we conducted a greedy search (Lanfear et al. 2012) and merged partitions (MF + MERGE), whereby we provided the original locus boundaries as input.

Divergence time estimation was carried out in BEAST (v. 2.6.6; Bouckaert et al. 2019). We designated the 9 previously identified partitions and assigned nucleotide substitution models as found with ModelFinder. We chose estimated frequencies or equal frequencies if the latter was found better fitting in the ModelFinder search. We then applied a Relaxed Log Normal Clock for the clock model and a Yule process for the tree model. Both clock and tree models were linked across partitions and the tree topology was fixed according to the congruent species tree topology found with IQ-Tree, except that we excluded all outgroups other than the closely related *Neolarra californica*. Prior information on absolute ages was included as secondary calibrations, as no *Nomada* fossils are presently available for inclusion as fossil evidence. Only 2 known fossils have been associated with the subfamily Nomadinae: *Protomelecta brevipennis* Cockerell (1908) and *Paleoepeolus micheneri* Dehon, Engel, and Michez (2017). *Protomelecta* may be a melectine bee (tribe Melectini, Apidae), but should be considered an uncertain fossil (Zeuner and Manning 1976). *Paleoepeolus micheneri* was described more recently and with different analytical methods (Dehon et al. 2017), yet has not been universally accepted as a reliable fossil for calibrating nomadine phylogeny (Onuferko et al. 2019). In order to estimate *Nomada* divergence times in light of this uncertainty, we considered ages from 2 separate studies that calculated nomadine divergence times with independent datasets and with each study using only 1 of the 2 previously mentioned fossils: Cardinal et al. (2018)

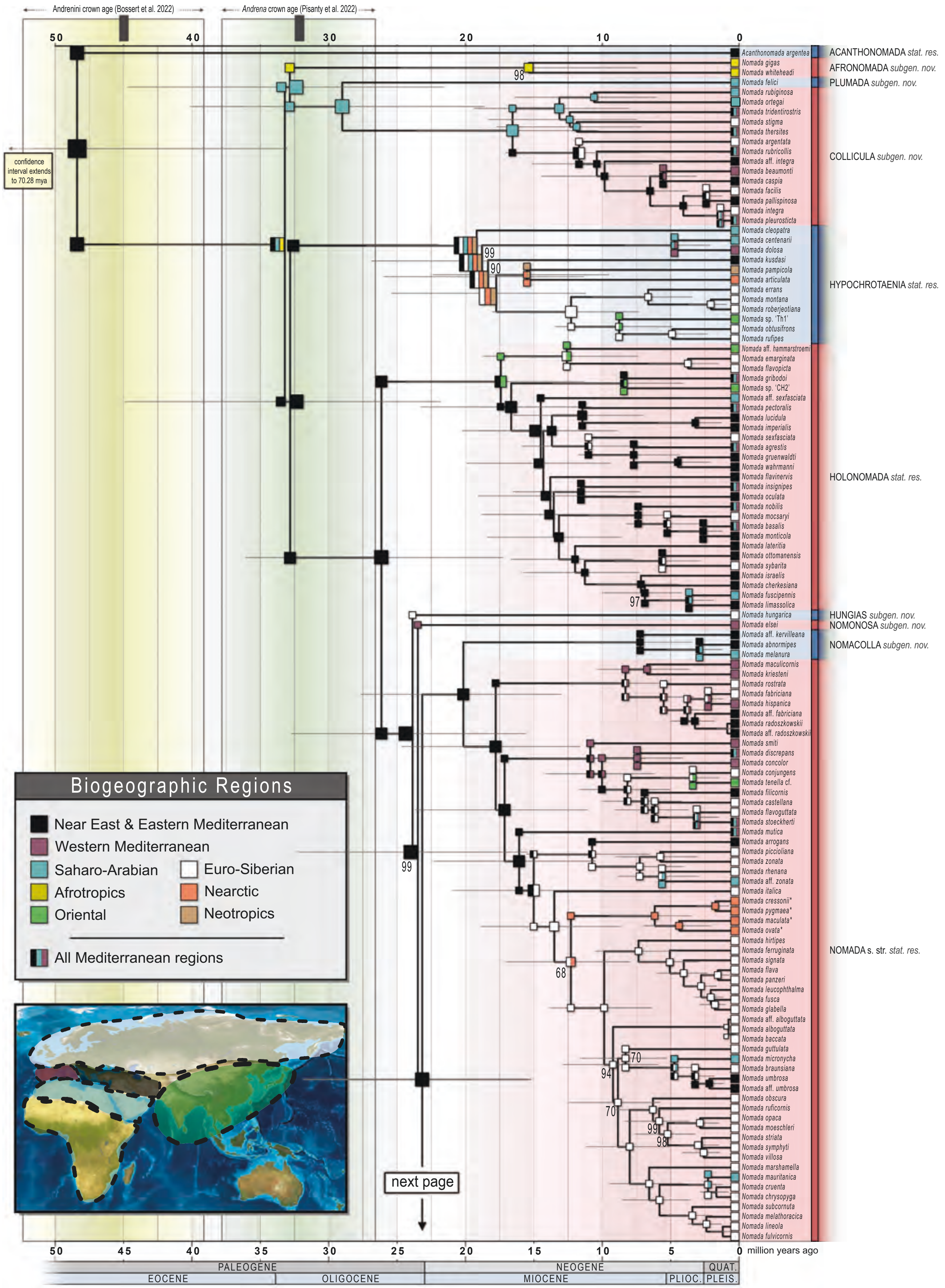


Fig. 1. Fossil-informed chronogram of *Nomada*, with emphasis on species from the Old World (part 1 of 2). The phylogenetic relationships for 221 species of *Nomada* were estimated from 1,532 UCE loci using maximum likelihood (IQ-Tree2). Divergence times are based on the 50 most concordant UCE loci and

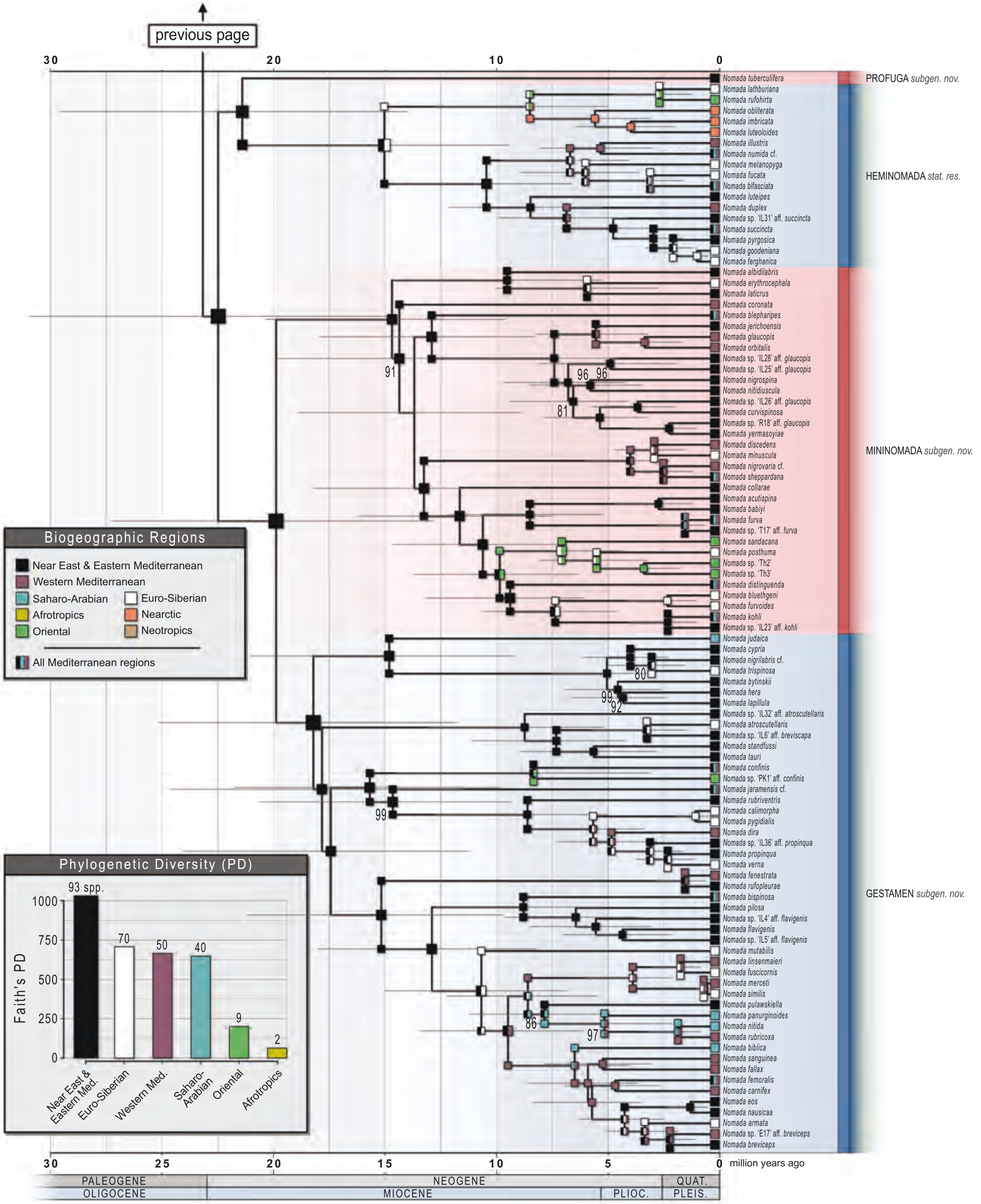


Fig. 2. Fossil-informed chronogram of *Nomada*, with emphasis on species from the Old World (part 2 of 2).

estimated the divergence of *Nomada* and *Neolarra* at 54.2 million years ago (mya) (~42–66 mya, 95% highest posterior density) and included *Protomelecta* as fossil calibration. In contrast, Bossert et al. (2020) used *Paleoepeolus* for calibration and estimated a slightly older age for the same divergence (mean 61.68 mya, with 53.8–70.7 mya 95% HPD). We, therefore, chose to calibrate the root node with

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were estimated with BEAST2. Values next to nodes show ultrafast bootstrap approximations (UFBoot2), which are only shown if values are < 100. Node bars indicate the 95% highest posterior density (HPD) for the estimated divergence times. The historical biogeography of the Old World *Nomada* was estimated with BioGeoBEARS using the DEC model. Node colors indicate the single most likely ancestral range.

a secondary calibration that is intermediate to both studies: using a normal distribution with a mean of 56.3 and σ = 7.5, 95% of the area under the curve falls between 41.5 and 71.0, which effectively covers the entire 95% HPD of both studies. A second secondary calibration was assigned to the split of *Nomada signata* and *Nomada maculata* based on a previous estimate. The mean age of this divergence was found at 20.2 mya (~9–33 mya, 95% HPD; Cardinal et al. 2018), which is why we assigned a normal distribution with a mean of 23.2 and σ = 6, ensuring that 95% of the area under the curve falls between 8.5 and 32.0. Based on these 2 secondary calibrations, our divergence time estimates are not fossil-calibrated, but informed by previous analyses that included fossil information.

We executed 2 separate analyses in BEAST and sampled the parameter space for at least 125,000,000 generations, sampling every 5,000 cycles. Sampling of the Markov chain Monte Carlo was assessed with Tracer (Rambaut et al. 2018) and deemed sufficient once the combined ESS values of all parameters, including the likelihood, posterior, TreeHeight, and the YuleModel, exceeded 200. We combined the tree files with LogCombiner and burn-ins of 10%, and used TreeAnnotator to condense the trees into a maximum clade credibility tree with median node heights.

Historical Biogeography

In order to understand the historical biogeography of *Nomada* in the Old World, we studied the present-day distribution for the included species by combining our own records with those obtained from literature searches (including from the Discover Life database, Ascher and Pickering 2020). The distribution of specimens unassigned to species was narrowly classified based on their collecting locality. Based on these findings, we considered biogeographic regions that correspond to the zoogeographic realms identified by Holt et al. (2013). However, given the present-day distributional patterns of *Nomada*, we decided to apriori separate 4 regions with distinct species assemblages from the Palearctic: we considered the Western Mediterranean and the Middle Eastern region, which includes the Eastern Mediterranean, as separate regions. We also separated northern Africa from both Mediterranean regions, and included it along with the Arabian Peninsula as a Saharo-Arabian region; we recognize the remaining Palearctic as Euro-Siberian. Given the minimal species turnover between the Sino-Japanese and the Oriental realm, we considered them as a single geographic region for our analysis (referred to as the Oriental region). The approximate boundaries of our biogeographic regions are indicated in Fig. 1 (inset). We coded the presence or absence of species according to their present-day distribution (see Figs. 1 and 2) and used the R Package (R Core Team 2021) and BioGeoBEARS (Matzke 2018) to infer the historical biogeography of Old World *Nomada* in a ML framework. We used the DEC model (Ree and Smith 2008) without the + *j* parameter (founder-event speciation, Ree and Sanmartín 2018), did not restrict the combination of areas, and set equal dispersal multipliers between regions.

At last, we contrasted the historical biogeography of *Nomada* with the present-day patterns of species richness and diversity by estimating Faith's phylogenetic diversity (Faith 1992) for each region using the package Picante (Kembel et al. 2010).

Analysis of Host Evolution

Information on the host species usage of the included species of *Nomada* was acquired through extensive literature research (primarily from Kocourek 1966, Alexander 1991, Scheuchl 2000, Smit 2018), personal observation, and data from colleagues (Supplementary Tables 1 and 3). In total, we were able to gather host information for 110 out of 221 species of *Nomada* included in our dataset. Hosts of the outgroup taxa were excluded from the analyses as this would lead to an unbalanced taxon sampling and further overparameterize the analysis. For the same reason, *Cubiandrena* was included in *Andrena* as it is the sister lineage to all *Andrena* (Pisanty et al. 2022). Available data were associated with the phylogram from the PhyloBayes analysis. The ancestral host reconstruction analysis was carried out with BayesTraits V4.0.0 and the multistate analysis, which is available from https://www.evolution.reading.ac.uk (Pagel et al. 2004). BayesTraits relies on Bayesian statistics and takes phylogenetic uncertainty and branch lengths into account. We selected 500 post-burnin trees (approximately every 37th tree) from each of the 4 independent PhyloBayes runs in the analysis (n = 2,000). Ancestral state reconstructions were performed with the reversible jump model with hyperprior settings (the program estimates prior settings from a given distribution). The reversible jump model searches among the possible models of trait evolution (those with the same and different transition rates between character states) and visits these models in proportion to their posterior probabilities (Pagel and Meade 2006). Exponential prior distributions were used with intervals fitted to the values of optimal transition rates from one character state to another. The exponential prior is recommended in the program manual when small values of parameters are more likely than larger ones. The parameter values were set based on preliminary data analysis as follows: HyperPriorAll exp 0 0.4 and RJHP exp 0 1. High number of states and missing data did not allow for BayesTraits ML analysis prior to the Bayesian run to estimate the rates. Hence, we used wide distributions of uniform value settings prior to the final run. The Bayesian analyses were run for 10 million generations and every 1,000th generation was saved. The marginal likelihoods from the stepping-stone analysis were checked between uniform and exponential distribution sets by examining the differences of the runs under their respective model settings. Bayes factors (BFs) were calculated from the marginal likelihoods to quantify the significance of their difference. Approximate run convergence was checked from parameter move acceptance between chains, which ideally is between 20% and 40%. BayesTraits chooses a model of trait evolution and computes the transition rates between character states and the probabilities of character states in each generation. To set the general probability of a particular character state, we computed the mean from all post-burn-in generation values of the probabilities.

Systematics and Nomenclature

For the taxonomic treatments, we present differential diagnosis and a brief diagnostic description for each genus and subgenus of the tribe Nomadini from Africa and the West Palearctic region. Because of this geographic focus, we mention New World taxa only when required for complete listings of synonyms and current name synonymization. The taxonomic descriptions focus primarily on the distinctive morphological characters of the respective taxa. We follow the morphological terminology from Michener (2007) and for specific characters of Nomadini we follow Alexander (1994). For paired structures, we use a singular form in the description. The length of flagellomeres is measured from ventral view. We also present a list of all West Palearctic and African species based on published (Alexander and Schwarz 1994, Ascher and Pickering 2020) and current data. Species of *Nomada*, which we were unable to confidently assign to a subgenus based on the original descriptions or museum specimens, are marked with an asterisk (*) in the list of species. New subgenera are described according to the International Code of Zoological Nomenclature (ICZN 1999) with rather minimalistic division according to morphological characters and the ability to characterize subgenera by morphology. The species group categorization of the genus *Nomada* from Alexander (1994) and Alexander and Schwarz (1994) is mentioned under each subgenus. Newly defined species groups are characterized as smaller groups of species within each subgenus. At last, we present an illustrated identification key to the Old World subgenera of *Nomada* based on morphological characters.

This article and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:5F8166FE-0C60-42D3-8009-FB9B9E467EF4.

Results

Phylogenetic Reconstruction

We successfully generated new UCE sequence data for 202 representatives of the tribe Nomadini, with 1,761 acquired UCE loci on average, spanning from only 25 to 2,334 loci. Only 5 of the newly generated samples and 1 previously published representative comprised fewer than 500 UCE loci (25–277 loci; Supplementary Table 1). These sequence data led to an alignment of 1,532 concatenated loci of 228 taxa, using the 80% completeness threshold. This data matrix is 922,228 bp in length, has 699,324 distinct patterns of which 394,353 are parsimony-informative, and comprises 172,384 singleton and 355,491 constant sites. In total, 22.63% of the sequence alignment is coded as gaps or missing data.

Our sampling is dense for European and West Palaearctic species of *Nomada*. We successfully included 58.9% of all described West Palearctic species (182 of 309) and 71.8% of the described species occurring in Europe (158 of 220). The topology among species is well resolved and strongly supported for the majority of nodes, thereby forming several distinct clades within Nomadini (Figs. 1 and 2, Supplementary Figs. 1–3). All 3 analytical approaches (ML, Bayesian, and Summary analysis) produced highly congruent phylogenies with minor differences for a few, poorly supported nodes (Supplementary Figs. 1–3). This phylogenetic framework serves as the foundation for an integrative reclassification of the tribe: we recognize 2 genera within Nomadini by resurrecting *Acanthonomada* back to genus level (as in Schwarz 1966), and recognize 13 subgenera of *Nomada*, 9 of which are newly described. Interestingly, a few of the included American and Oriental species are nested well within the lineages of subgenera with West Palearctic representatives.

Historical Biogeography

Our results recovered the Near East and the Eastern Mediterranean region as central for the early evolution of *Nomada*. The most recent common ancestor (MRCA) of every major subgenus, which we here consider comprising at least ≥ 15 species in the Palearctic ($n = 9$), was likely present in this region (Figs. 1 and 2). In addition, for 4 out 5 of these subgenera, the MRCA was likely exclusively Near Eastern. A total of 9 out of the 13 subgenera of *Nomada* include the Near East and Eastern Mediterranean as part of their MRCA's ancestral range, and nearly every reconstructed MRCA along the backbone of our phylogeny inhabited this area. The sole sister lineage to all other *Nomada*, *Acanthonomada* (3 described species), is exclusively distributed in the Near Eastern and Eastern Mediterranean region. At last, the significance of this region for the natural history of *Nomada* is strongly reflected by both species richness and phylogenetic diversity: no other Palearctic region harbors a greater number of described species nor a greater phylogenetic diversity than the Middle East and the Eastern Mediterranean (Fig. 2, lower inset).

The analysis of historical biogeography found significant faunal exchange between all Palearctic regions except for sub-Saharan Africa. With the exception of *Collicula* subg. nov., every major subgenus is present in every biogeographic region north of sub-Saharan Africa. To the best of our knowledge, *Collicula* is absent from the Oriental region. A significant number of extant species is concurrently distributed in 3 regions (Figs. 1 and 2), all being present in the 3 Mediterranean regions (Fig. 2, lower inset). Despite the close proximity of the Afrotropics to the species-rich Saharo-Arabian region, the species-richness and phylogenetic diversity of the Afrotropics are the lowest among all assessed regions. Interestingly, however, this region was likely inhabited early in the natural history of *Nomada*. The MRCA of all Palearctic *Nomada* likely had a range that included this area (Fig. 1). Species of *Nomada* that presently occur in Africa are restricted to 2 separate lineages: we associated 8 out of the 10 African *Nomada* (Eardley and Schwarz 1991) with the subgenus *Hypochrotaenia* based on morphology, whereas the remaining 2 comprise the newly described subgenus *Afronomada*. As these lineages are not very closely related, this pattern indicates 2 past separate range expansion events into the Afrotropics region.

The limited number of included *Nomada* species from the New World do not represent a monophyletic group but form 3 separate clades. All 3 lineages are nested within larger clades of Palearctic species (Figs. 1 and 2).

Ancestral State Reconstruction of Hosts

The ancestral host reconstruction analysis in BayesTraits found a Log marginal of −52.441092, which was marginally to significantly higher than the likelihood in our preliminary analyses with uniform variables settings (BFs = 1.7–2.6). According to this reconstruction, the MRCA of the genus *Nomada* was most certainly a parasite of *Andrena* (here understood to include *Cubiandrena*), with a high probability of 99%. However, we found that transitions to different hosts occurred multiple times in the evolutionary history of *Nomada* (Fig. 3). Our results show strong patterns of phylogenetic conservation, indicating at least 8 independent transitions to different hosts. Transitions to exploiting members of the genus *Melitta* as hosts occurred 2 or 3 times independently, and the genus *Lasioglossum* is host to 2 distant lineages of *Nomada*. Conversely, *Nomada* switched from *Andrena* to (i) *Agapostemon* and (ii) *Panurgus* hosts and from *Melitta* to (i) *Redivivoides* and (ii) *Eucera* only once each in their evolutionary history. Transition rates between hosts are generally low (0.3–0.8). Slightly higher rates (1.0–1.2) were calculated for transitions from *Andrena* to *Agapostemon*, *Lasioglossum*, and *Melitta* and for a transition from *Melitta* to *Eucera*.

Systematics

Nomadini Latreille, 1802

Type genus: *Nomada* Scopoli, 1770: 44.

Acanthonomada Schwarz, 1966, status restituted

Schwarz (1966: 383). Type species: *Nomada odontophora* Kohl, 1905, by original designation.

= *Nomada* subgenus *Acanthonomada* (status changed by Warncke 1982).

Diagnosis.

Acanthonomada is an easily recognizable genus. From all representatives of the sister genus *Nomada*, it differs by the robust shape of the head, the labrum being extremely prolonged with a serrated

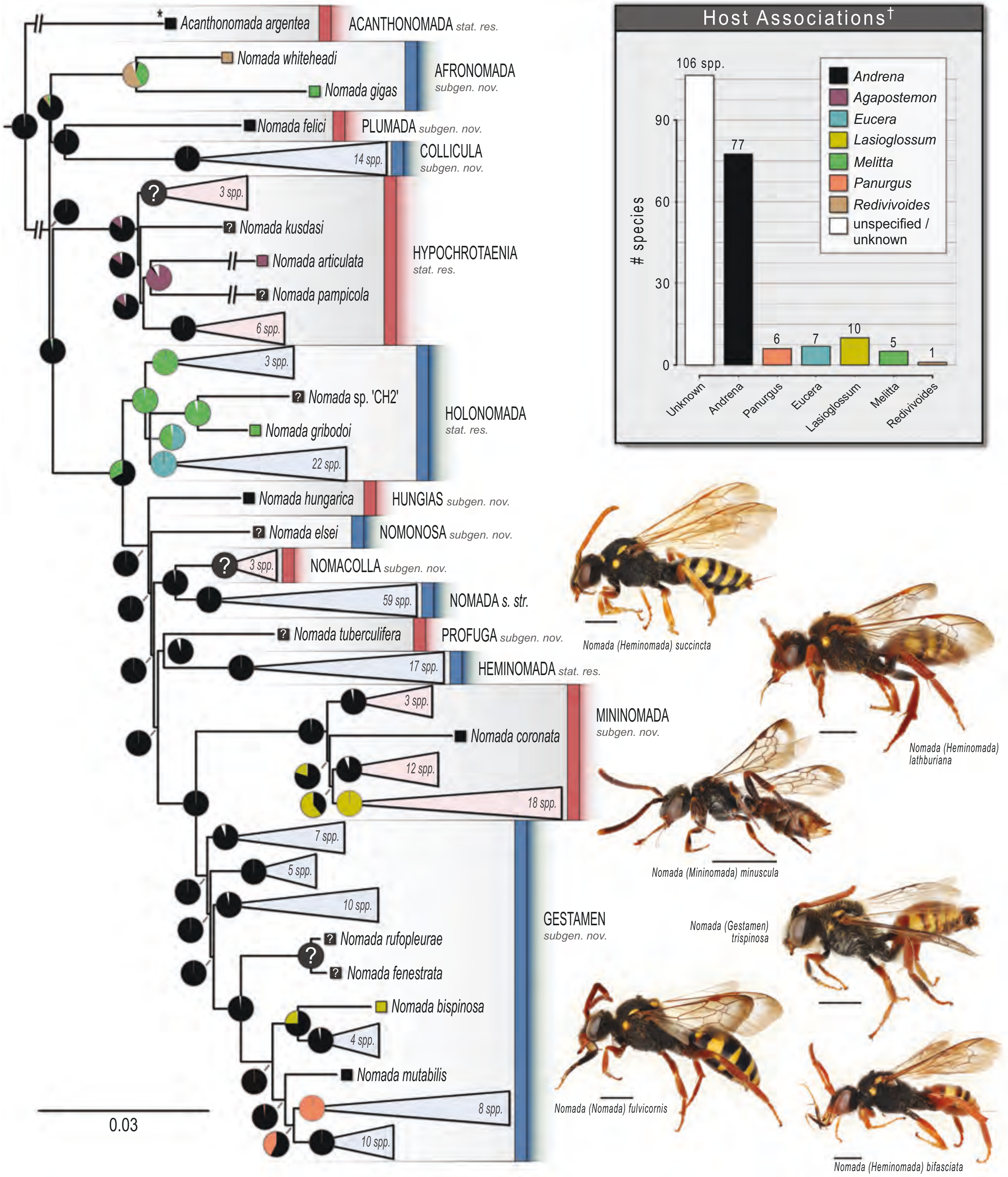

Fig. 3. Host associations of *Nomada*. Pie charts show posterior probabilities of reconstructed hosts, with a focus on West Palearctic species. The shown phylogeny was estimated with PhyloBayes. For visibility, clades with no changes in host associations were collapsed and estimated probabilities for subsequent nodes were at least 93% or higher. Collapsed clades are not proportional to the included species, and the total species numbers are shown in each respective triangle. Host associations are summed up in the inserted bar plot, however, only species outside of the Nearctic and Neotropics are considered (indicated by the asterisk). The left scale bar indicates substitutions per site and scale bars next to specimens show 2 mm in length. The asterisk next to *Acanthonomada* refers to the coding of the host: for simplification, we consider the host *Cubiandrena* as part of *Andrena*, as both these genera are very closely related.

transverse carina in its approximate center, and the propodeal triangle being very small and entirely shiny (Fig. 4b). A clearly defined pseudopygidial area is lacking, instead *Acanthonomada* possesses 2 cuticular teeth (Fig. 4d). The shape of the legs is unique with the coxae being carinate and with 2 ventroapical tooth-like projections on the apex of the metafemora (Fig. 4c). The shape of the mandible, the shape of the thorax, the spines on the outer surface of the metatibiae, and the wing venation (Fig. 4a) all differ from other Nomadini. For figures of all diagnostic characters, see Schwarz (1966).

Description.

Head robust, nearly quadratic with gena enlarged. Female paraocular carina well-developed along eye, reduced in malar area, and not connected to clypeal margin. Labrum prolonged with serrated transversal carina in its approximate center. Mandible simple, with small round expansion directed upward, toward clypeal margin. Base of male mandible with dense and long hair on outer side. Interantennal elevation wide, without carina. Mesosoma dorsoventrally flattened; scutum, scutellum, and postscutellum nearly in 1 elevational level. Propodeal triangle small, nearly rectangular in shape, without basal area, finely microsculptured, and bright shiny. Mid- and metacoxa with distinct lamellate carina on dorsal side. Forefemur thin, with longitudinal carina laterally. Meso- and metafemur short and enlarged, strongly contrasting with weaker-developed forefemora. Meso- and metafemur with 2 teeth ventroapically, 1 on anterior and 1 on posterior side. Meso- and metatibia both short and thick, covered by fine hair laterally, without small tubercles laterally. Spines present dorsally and on the apical margin (4–5) on metatibia. Female tergum V without distinct pseudopygidial area, apicomedially with 2 cuticular teeth. Apical margin of radial cell in forewing rounded and slightly removed from anterior wing margin. Third submarginal cell enlarged, about as long as first submarginal cell. Gonocoxite with rounded inner dorsal lobe and well-developed invagination. Gonostylus simple, narrow finger-shaped with rather short erect hair. Penis valve robust. For a detailed description of the genus *Acanthonomada*, see Schwarz (1966).

Species included.

Acanthonomada argentea Schwarz, 1966
Acanthonomada moricei (Friese 1899), **comb. nov.**
Acanthonomada odontophora (Kohl 1905)

Nomada Scopoli, 1770

Scopoli (1770: 44). Type species: *Apis ruficornis* Linnaeus, 1758, by designation of Curtis (1832: 419).

Diagnosis.

Most species of the tribe Nomadini belong to the genus *Nomada*. *Nomada* can easily be distinguished from *Acanthonomada* by the absence of the prominent characters of the latter. One of the few unique charactersticks of the genus *Nomada* is the form of the outer surface of the metatibia, which is covered by spine-bearing setae throughout (Fig. 8c, e–i). Secondly, tergum 5 bears a well-developed pseudopygidial area (Figs. 4f, 5e, j, and 8a). The head of *Nomada* slightly narrows behind the eyes, the propodeal triangle is larger than in *Acanthonomada* and basally more or less coarsely sculptured (Figs. 4g–i, 5g, 6h, 7a–c, g, h, 8b, and 9b). If the basal area is not coarsely sculptured, then the propodeal triangle is dull. The third submarginal cell is about as large as the second submarginal cell (Fig. 4e). The femur is missing cuticular projections ventroapically and the coxa are less carinate than in *Acanthonomada*.

The genus *Nomada* is further subdivided into subgenera and species groups within subgenera.

Description.

Head short with reduced gena. Female paraocular carina well-developed and connected to clypeal lateral margin (secondarily reduced in some species). Mandible variable, but never with round expansion directed upward toward clypeal margin. Interantennal elevation with longitudinal carina (rarely obtuse). Mesosoma usually convex with scutellum situated above postscutellum and frequently also above scutum. Propodeal triangle with sculptured basal area that is frequently concave, rarely bright shiny in posterior half. Legs simple, without distinct modifications, except enlarged forefemur and excavated metafemur in some species. Metatibia prolonged, covered by tubercules bearing spines (thick setae) on outer surface, apical margin with spines or hair (rarely without). Pseudopygidial area of tergum 5 well-developed, covered by dense white modified flattened setae with velvety appearance. Apical margin of radial cell pointed, only slightly separated from wing margin. Third submarginal cell about as large as second submarginal cell. Shape of gonocoxite and gonostylus very variable. Penis valve weakly built, not robust.

Nomada subgen. *Afronomada* Straka and Bossert, subgen. nov.

Type species: *Nomada gigas* Friese, 1905, designated here.
Nomada gigas species group of Alexander (1994) and Alexander and Schwarz (1994)

Diagnosis.

This subgenus consists of 6 South African species which are quite distinct from all other species of *Nomada*. However, since *N. gigas* is rather distinct from other *Afronomada* subgen. nov. species, we could only establish a few shared morphological features that separate the subgenus *Afronomada* subgen. nov. from the other subgenera. In both species, the labrum is wider than long, with the apical margin thin and serrate, and with a transverse row of teeth in the apical third and a longitudinal carina medially (Fig. 5k). A faint longitudinal carina is present on the clypeus of females as well, at least in the basal half (Fig. 5k). The interantennal elevation is obtuse, with only a fine longitudinal carina (Fig. 5k). This character is only present in a few other species in the subgenus *Hypochrotaenia*. The propodeal triangle resembles that of *Hypochrotaenia*. It is rather finely microsculptured with the basal area straight and with longitudinal ridges, but it can also be finely reticulated, medially narrow with a deep ridge. The posterior part of the propodeal triangle is shiny or slightly shiny. The shape of the pseudopygidial area of tergum 5 is very distinctive: it is poorly developed, consisting of rather unmodified short or long, grey (Fig. 5j) or black setae. Sterna 7 and 8 of the males are distinct in combination with the form of the gonocoxite and the simple plesiomorphic gonostylus.

A detailed description and characterization of particular characters of *N. gigas* is presented by Alexander (1994). The species descriptions can be found in Eardley and Schwarz (1991), Eardley (1993), and Kuhlmann (2023).

Description.

Labrum transverse with apical margin weak and serrate, transverse row of teeth in apical third and longitudinal carina medially. Longitudinal carina distinct also on female clypeus, but can be only faintly distinct in basal half. Interantennal elevation obtuse, with only a fine longitudinal carina. Propodeal triangle rather finely microsculptured with basal area straight and with longitudinal ridges, but can also be finely reticulate, medially narrow and with a deep ridge. Posterior part of propodeal triangle shiny, or slightly shiny. Pseudopygidial plate of tergum 5 poorly developed, consisting of rather unmodified short or long, grey or black hair.

Female pygidial plate narrow or wide, rounded apically without terminal emargination. Male sternum 7 convex, parallel-sided apically. Male sternum 8 slightly narrowed and slightly prolonged apically. Gonocoxite with or without minute invagination and without distinct inner dorsal lobe. Gonostylus simple finger-shaped, with short and sparse hair. Basoventral lobe small with or without tuft of hair. The outstanding characters of *N. gigas* presented in Alexander (1994) are not shared by the second species *Nomada whiteheadi* and are thus not presented in the generic description therein.

Etymology.

The name *Afronomada* combines the biogeographic origin of the subgenus (Africa) and the name of the genus (*Nomada*). The name is feminine.

Species included.

Nomada (Afronomada) erhardti Kuhlmann, 2023
Nomada (Afronomada) gigas Friese, 1905
Nomada (Afronomada) maximiliani Kuhlmann, 2023
Nomada (Afronomada) redivivoides Kuhlmann, 2023
Nomada (Afronomada) roggeveldi Kuhlmann, 2023
Nomada (Afronomada) whiteheadi Eardley and Schwarz, 1991

Nomada subgen. *Collicula* Straka, subgen. nov.

Type species: *Nomada integra* Brullé, 1832, designated here.
Nomada integra species group of Alexander (1994) and Alexander and Schwarz (1994), and *Nomada cinctiventris* species group of Schwarz (1967).

Diagnosis.

This subgenus can be separated into 2 phylogenetic lineages represented by the *N. integra* and *Nomada stigma* species groups. The nov. subgen. *Collicula* can be reasonably well-recognized, however, nearly all characters show some degree of variation and exceptions are common. The labrum is characteristic in shape; it is transverse with a single tooth medially, positioned centrally, or basally. For most species, the labrum is unusually concave between the tooth and the apex, but flat in some species. The mandible of males of *Collicula* are unusually shaped. For most species, the mandible is nearly straight to slightly curved with a distinct tubercle on the outer surface (Fig. 5a). Such mandibular tubercles are absent in any other subgenus. In a few species, the male flagellomeres bear sharp nodules and round knobs on the ventral side (Fig. 5b). The sculpturation of the propodeal triangle is characteristic of the subgenus *Collicula* subgen. nov.: its surface possesses well-developed longitudinal ridges basally and medially, while the rest is unsculptured, or just slightly uniformly microsculptured, and brightly shining (Fig. 4i). The metafemoral base of the males is rather unmodified in most species, but excavated ventrally in *Nomada thersites*. The pseudopygidal plate of tergum 5 with modified hair of the plate transitioning from a densely and finely setose tergal disc, discal setae white (Fig. 4f). The pygidial plate of the males is not or very weakly emarginated apically. The shape of the male terminal sterna, gonocoxites and gonostylus are characteristic: sternum 7 is apically truncated and parallel-sided. The apical projection of sternum 8 is wider than in most subgenera, but distinctly prolonged. The gonostylus is laterally flattened, hooked, and bent downwards, with a hair brush in some species.

The species of *Collicula* subgen. nov. were described in detail in the revision by Schwarz (1967) under the *N. integra* species group (= *N. cinctiventris* species group).

Description.

Body color black and red, pale coloration present only on head of males and missing on metasoma in both sexes. Labrum 1.5 times wider than long, or wider; labrum with 1 tooth medially, positioned centrally, or basally; apical margin thin or thick, frequently crenulated. Labrum concave between the tooth and the apex, but flat in some species. Mandible nearly straight to slightly curved with a tubercle on outer surface. Scapus is thin in most species, if slightly thickened, then with nearly parallel sides. First flagellomere variable in size. Male flagellomeres without modification or with sharp nodules and round knobs on ventral side. Female paraocular carina well-developed. Propodeal triangle intermediate in size in the *N. integra* species group and distinctly larger in *N. stigma* species group; its surface sculptured with well-developed longitudinal ridges basally and medially, the rest is unsculptured, or slightly uniformly microsculptured, and bright shiny. The posterolateral delimitation ridge of the propodeal triangle weak to missing posteriorly; propodeal triangle at the same elevation as lateral propodeal portion, but sometimes impressed anteriorly. The metafemoral base of males rather unmodified in most species, frequently flattened ventrally and carinated posteriorly, and with hair tuft of erect setae present in some species. The metafemur is rarely excavated ventrally (only in *N. thersites*). Apical metatibial spines in females present, variable, short to long, between 4 and 8 spines per row. First metatarsomere of females narrow, unexpanded, slightly flattened laterally. Pseudopygidal plate of tergum 5 transitioning from a densely and finely setose tergal disc, setae on disc white. Female pygidial plate rounded to acute, without apical emargination. Male pygidial plate not or very weakly emarginate apically. Male sternum 7 apically truncate, parallel-sided. Apical projection of male sternum 8 wide, but distinctly prolonged. Gonocoxites variable, frequently with invagination widely opened and inner dorsal lobe angular to pointed in most species, but a few species with relatively deep invagination (*Nomada tridentirostris*). Gonostylus laterally flattened, hooked, bent downward, with a hair brush in some species.

Etymology.

The name *Collicula* refers to the tuberculate mandibles of the male sex. The Latin word colliculus translates to small tubercle. Here the masculine word is transformed to the feminine form and the name *Collicula* is not treated as a Latin word to stabilize the name use.

Species included.

Nomada (Collicula) argentata Herrich-Schäffer, 1839
Nomada (Collicula) beaumonti Schwarz, 1967
Nomada (Collicula) carthaginensis Dusmet y Alonso, 1932
Nomada (Collicula) caspia Morawitz, 1895
Nomada (Collicula) facilis Schwarz, 1967
Nomada (Collicula) glaberrima Schmiedeknecht, 1882
Nomada (Collicula) halophila Wood, 2022
Nomada (Collicula) integra Brullé, 1832
Nomada (Collicula) legoffi Dufrêne, 2021
Nomada (Collicula) ortegai Dusmet y Alonso, 1915
Nomada (Collicula) pallispinosa Schwarz, 1967
Nomada (Collicula) pleurosticta Herrich-Schäffer, 1839
Nomada (Collicula) rubiginosa Pérez, 1884
Nomada (Collicula) rubricollis Schwarz, 1967
Nomada (Collicula) stigma Fabricius, 1804
Nomada (Collicula) thersites Schmiedeknecht, 1882
Nomada (Collicula) tridentirostris Dours, 1873

Nomada subgen. *Gestamen* Straka, subgen. nov.

Type species: *Nomada armata* Herrich-Schäffer, 1839, designated here.

Nomada armata species group, *Nomada fuscicornis* species group, *Nomada trispinosa* species group, and part of the *Nomada ruficornis* species group of Alexander (1994) and Alexander and Schwarz (1994).

Diagnosis.

The species included in the subgenus *Gestamen* subgen. nov. have never been revised as they are defined here. The subgenus *Gestamen* can be subdivided into at least 9 separate phylogenetic lineages represented by the *N. trispinosa*, *Nomada atroscutellaris*, *Nomada calimorpha*, *Nomada fenestrata*, *Nomada bispinosa*, *N. fuscicornis*, and *N. armata* species groups. According to our phylogenetic results, *Nomada judaica* and *Nomada mutabilis* are isolated species in this subgenus. These species groups are quite heterogeneous in their morphology and a straightforward separation of all species of *Gestamen* from other subgenera is problematic. Generally, they possess a similarly shaped propodeal triangle: the convex posterior part is impressed and distinctly reticulate or ridged medially (Fig. 7a–c). The propodeal triangle has paired, gibbous, kidney-shaped areas posterolaterally, with characteristic transverse ridges (sometimes indistinct). The posterolateral delimitation of the propodeal triangle is well-developed by its convex elevation nearly all along the entire lateral margin, with the delimiting ridge distinct or not, but almost always with a secondary impression in place of the ridge. The subgenus is further characterized by a relatively long (longer than wide) first flagellomere; however, if the flagellomere is only as long as wide, then the second flagellomere is short as well. Most species of *Gestamen* have an impressed base of the metafemur with modified hair (Fig. 6d), but this character is also present in the subgenera *Mininomada* subgen. nov. and certain species of *Heminomada*. The pseudopygidial area of tergum 5 consists of 2 types of setae (simple setae basally and modified flat setae apically), although not all representatives clearly share this feature. Certain lineages of *Gestamen* bear a distinctive, oblique facial ridge dorsolaterally close to the compound eye with dense micropunctuation in males (Fig. 7d), as present in the *N. atroscutellaris*, *N. mutabilis*, *N. fuscicornis*, and *N. armata* species groups. However, this unique character is not present in every species within these groups. Particular for *Gestamen* is the great number of apical spines on the metatibia arranged in several rows, as in the *N. fuscicornis* and some specimens of the *N. armata* species groups. All of the above-mentioned characters have more or less frequent exceptions, however, the combination of characters and the below-provided identification key should suffice to distinguish *Gestamen* from the remaining subgenera.

Description.

Labrum 1.3–1.5 × wider than long in most species, except for 1 lineage (*N. fuscicornis* group) with labrum prolonged apically and distinctly longer than wide. Labrum apically pointed with carina along thickened apex in species without labral prolongation; single or multiple teeth present in apical half of the carina, teeth sometimes minute. Labrum can have a unique, large, unsculptured, and shiny base (certain species of the *N. armata* species group). Males of several species (*N. atroscutellaris* species group, *N. mutabilis*, *N. fuscicornis* species group, and *N. armata* species group) bear paired micropunctate oblique facial ridges dorsolaterally on frons. Male scapus can be thin, or slightly thickened in most species, but strongly thickened and rounded in the *N. atroscutellaris* species group. Male first flagellomere longer than wide, rarely shorter (few members of *N. trispinosa* species group, *N. calimorpha* species group, *N. biblica*, and *N. judaica*), about as long as second flagellomere, or slightly shorter or longer; only in a few species of the *N. calimorpha* species group the first flagellomere can be significantly shorter than second flagellomere. Male flagellum not modified in most species, only with small ventral round knobs or emarginations in a few species of the *N. calimorpha* species group, and with distinct longitudinal carina separating sculptured and glabrous areas in the *N. armata* species group, the *N. bispinosa* species group, and *N. mutabilis*. Female paraocular carina well-developed below antennae in all species except in *N. fuscicornis*; presence or absence of female paraocular carina above antennal level is variable within this subgenus and even within species groups, varying from total absence to being well-developed. Propodeal triangle variable, most frequently intermediate in size, covering slightly less than half of propodeal area, its lateral margin straight or concave; basal area coarsely and irregularly sculptured, usually concave, posterior part convex, medially impressed and distinctly reticulate or ridged, posterolaterally with paired gibbous kidney-shaped areas with or without transversal ridges, dull to shiny. Posterolateral delimitation of propodeal triangle well-developed by its convex-shaped elevation nearly all along the lateral margin, delimiting ridge distinct or not, but almost always with impression at its place. Male metafemoral base is generally modified: metafemoral base is flattened to concave with distinct dense patch of posteriorly directed hair, which are longer than in other parts of femur. Frequently additional hair is directed proximally in the impression, with additional long hair on metafemoral sides or throughout the impression. Metafemoral base modification is reduced in certain derived species of the *N. calimorpha* species group and in *N. judaica*. Female apical metatibial spines are well-developed and very variable, but unusually numerous in the *N. fuscicornis* group and several species of the *N. armata* group. Female metatarsomere 1 narrow, unexpanded, slightly laterally flattened. Pseudopygidal plate of tergum 5 consists of 2 types of setae, simple setae basally, and modified flat setae apically; the band of simple basal setae can be very narrow or absent (*N. atroscutellaris* species group). Transition between basal band of simple setae and discal setae is variable, the transition is long in some species or short but distinct in others. Female pygidial plate is rounded to acute, with a small or without apical emargination. Male pygidial plate slightly to strongly emarginate, rarely without emargination. Male sternum 7 apically narrowing. Male sternum 8 narrowed and strongly prolonged apically. Gonocoxite with strong invagination and with a moderately sized inner dorsal lobe. Gonostylus thick, rounded to slightly curved inward, densely hairy with various hair tufts, ventrally bearing hair round; basoventral lobe with narrow basal setal tuft present.

Etymology.

The expression gestamen, which is Latin in origin, refers to ornaments, or carrying a particular object. It refers to the frequently colorful appearance of species of this subgenus and the unusual hair tufts at the base of the male metasoma. It is a neuter.

Species included.

Nomada (*Gestamen*) *abnormispinosa* Schwarz, Smit and Gusenleitner, 2018

Nomada (*Gestamen*) *aeginaica* Schwarz and Smit, 2018

**Nomada* (*Gestamen*) *achaica* Schwarz and Smit, 2020

Nomada (*Gestamen*) *amabilis* Radoszkowski, 1876

**Nomada* (*Gestamen*) *amoenula* Schwarz and Smit, 2018
Nomada (*Gestamen*) *argentipilosa* Schwarz and Smit, 2020
Nomada (*Gestamen*) *armata* Herrich-Schäffer, 1839
Nomada (*Gestamen*) *atroscutellaris* Strand, 1921
Nomada (*Gestamen*) *biblica* Schwarz, Smit and Ockermüller, 2019
Nomada (*Gestamen*) *bispinosa* Mocsáry, 1883
Nomada (*Gestamen*) *bolivari* Dusmet y Alonso, 1913
Nomada (*Gestamen*) *breviceps* Schwarz, Smit and Ockermüller, 2019
Nomada (*Gestamen*) *brevis* Saunders, 1908
Nomada (*Gestamen*) *breviscapa* Schwarz and Smit, 2018
Nomada (*Gestamen*) *bytinskii* Schwarz, Smit and Ockermüller, 2018
Nomada (*Gestamen*) *calimorpha* Schmiedeknecht, 1882
Nomada (*Gestamen*) *carnifex* Mocsáry, 1883
Nomada (*Gestamen*) *cephalotes* Schwarz, Smit and Ockermüller, 2018
Nomada (*Gestamen*) *confinis* Schmiedeknecht, 1882
Nomada (*Gestamen*) *corcyraea* Schmiedeknecht, 1882
Nomada (*Gestamen*) *cypria* Mavromoustakis, 1952
Nomada (*Gestamen*) *dira* Schmiedeknecht, 1882
Nomada (*Gestamen*) *eos* Schmiedeknecht, 1882
Nomada (*Gestamen*) *fallax* Pérez, 1913
Nomada (*Gestamen*) *femoralis* Morawitz, 1869
Nomada (*Gestamen*) *fenestrata* Lepeletier, 1841
Nomada (*Gestamen*) *flavigenis* Schwarz and Standfuss, 2007
Nomada (*Gestamen*) *fuscicornis* Nylander, 1848
Nomada (*Gestamen*) *hera* Schwarz, 1965
Nomada (*Gestamen*) *immaculata* Morawitz, 1874
Nomada (*Gestamen*) *jaramensis* Dusmet y Alonso, 1913
Nomada (*Gestamen*) *judaica* Schwarz and Smit, 2018
Nomada (*Gestamen*) *kocoureki* Schwarz, 1987
Nomada (*Gestamen*) *lapillula* Schwarz and Smit, 2018
Nomada (*Gestamen*) *linsenmaieri* Schwarz, 1974
**Nomada* (*Gestamen*) *marrakechi* Schwarz and Smit, 2020
Nomada (*Gestamen*) *martinschwarzi* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *merceti* Alfken, 1909
Nomada (*Gestamen*) *mutabilis* Morawitz, 1870
Nomada (*Gestamen*) *mutinensis* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Gestamen*) *nausicaa* Schmiedeknecht, 1882
Nomada (*Gestamen*) *nigrilabris* Schwarz and Smit, 2018
Nomada (*Gestamen*) *nitida* Schwarz, 1977
Nomada (*Gestamen*) *panurgina* Morawitz, 1869
Nomada (*Gestamen*) *panurginoides* Saunders, 1908
Nomada (*Gestamen*) *piliventris* Morawitz, 1877
Nomada (*Gestamen*) *pilosa* Schwarz and Gusenleitner, 2017
Nomada (*Gestamen*) *polemediana* Mavromoustakis, 1957
Nomada (*Gestamen*) *polyacantha* Pérez, 1895
**Nomada* (*Gestamen*) *praetiosa* Schwarz and Smit, 2018
Nomada (*Gestamen*) *propinqua* Schmiedeknecht, 1882
Nomada (*Gestamen*) *pruinosa* Pérez, 1895
Nomada (*Gestamen*) *pulawskiella* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *pygidialis* Schwarz, 1981
Nomada (*Gestamen*) *regli* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *rubricornis* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *rubricoxa* Schwarz, 1977
**Nomada* (*Gestamen*) *rubriscuta* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *rubriventris* Schwarz, 1981
Nomada (*Gestamen*) *rufoabdominalis* Schwarz, 1963
Nomada (*Gestamen*) *rufopleurae* Schwarz, 1964, **stat. nov.**
Nomada (*Gestamen*) *sanguinea* Smith, 1854
Nomada (*Gestamen*) *serricornis* Pérez, 1884
Nomada (*Gestamen*) *schulthessi* Schwarz, 1999
Nomada (*Gestamen*) *sicula* Schwarz, 1974
Nomada (*Gestamen*) *similis* Morawitz, 1872
Nomada (*Gestamen*) *standfussi* Schwarz, 2007
Nomada (*Gestamen*) *sternalis* Pérez, 1902
Nomada (*Gestamen*) *subvirescens* Morawitz, 1875
Nomada (*Gestamen*) *tauri* Schwarz, Smit and Ockermüller, 2020
Nomada (*Gestamen*) *transitoria* Schmiedeknecht, 1882
Nomada (*Gestamen*) *trispinosa* Schmiedeknecht, 1882
Nomada (*Gestamen*) *unispinosa* Schwarz, 1981
Nomada (*Gestamen*) *urfaensis* Schwarz, Smit and Ockermüller, 2018
Nomada (*Gestamen*) *verna* Schmiedeknecht, 1882

Nomada subgen. *Heminomada*, Cockerell, 1902, status restituted

Cockerell (1902) in Cockerell and Atkins (1902: 174) (as a subgenus of *Nomada*). Type species: *Nomada obliterata* Cresson, 1863, by original designation.
Nomada bifasciata species group and part of the *N. ruficornis* species group of Alexander (1994) and Alexander and Schwarz (1994).
= *Xanthidium* Robertson, 1903: 174. Type species: *Nomada luteola* Olivier, 1811, by original designation.

Diagnosis.

The subgenus *Heminomada* consists of 4 phylogenetically and morphologically distinct lineages here referred to as the *Nomada lathburiana*, *N. obliterata* (North American), *N. bifasciata*, and *Nomada succincta* species groups. The females of this subgenus can be recognized by the apical metatibial spines that are thick and closely placed together, numbering 2(–3), and distinctly separated from the apical metatibial projection. The base of the metafemur in males is impressed and the metacoxa flattened ventrally with a golden tuft of long and appressed setae (Fig. 6e), while the remaining ventral part of metafemur is nearly glabrous. The ventral area of the metafemur bears very short hair, much shorter than anteriorly or posteriorly on the femur in those species that lack the golden tuft of setae. The propodeal triangle is relatively small and more or less rugose throughout in both sexes of most species (Fig. 7h). The *N. lathburiana* species group is exceptional within the subgenus *Heminomada* and lacks the basoventral metafemoral impression in the male, and the metatibial apical spines are not closely placed together in the female (Fig. 8h). The male gonocoxite and gonostylus are characteristic for this subgenus, but fairly variable in shape.

Description.

Labrum 1.5–2.0 × wider than long; apex thick with incomplete carina close to apical margin and a tooth apicomedilally on the carina. Carina or tooth, or both can be reduced in some species. Longitudinal impunctate area on labrum or faint impunctate carina present medially. Mandible short, normal; rarely slightly prolonged (*N. obliterata* species group). Male scapus slender or slightly thickened. Male first flagellomere slightly to distinctly longer than wide, rarely as long as wide or nearly so (*Nomada ferghanica*, *N. fucata*, and *Nomada pyrgosica*), but frequently shorter than or about as long as fourth antennomere (e.g., slightly longer in *Nomada numida*). Male flagellomeres without modification or rounded knobs, but with pointed nodules ventrally on antennomeres in the *N. lathburiana* species group. Female paraocular carina developed, but not sharp; largely reduced above the level of antennae. Propodeal triangle small, covering about two-fifths of propodeal area, lateral margins concave; sculpture variable, but usually sculptured in all areas with distinctly separated straight basal area with more or less coarse sculptures. Basal area can be distinctly concave in *N. succincta* species group; posterolateral delimitation ridge ill-defined, but usually distinct (sometimes hardly distinct); propodeal triangle at about the same elevational level as the rest of propodeum. Male metafemoral base excavated basally with thick appressed golden setae forming a tuft, similar tuft also on metatrochanters. Metafemoral impression completely missing in the *N. lathburiana* and *N. obliterata* species groups; ventral area of metafemur with either very short hair, much shorter than anteriorly, or posteriorly, or glabrous, with basal hair tuft. Female apical metatibial spines with 2(–3) closely allied short thick spines distinctly separated from apical metatibial projection, however, 3–5 thick short, but separated spines developed in the *N. lathburiana* species group. Female metatarsomere 1 narrow, unexpanded, slightly laterally flattened or not. Pseudopygidial plate of tergum 5 narrow or wide, separated from unmodified and sparse hair on tergal disc. Female pygidial plate rounded, rarely slightly narrowing apically or with small terminal emargination. Male pygidial plate narrow, with deep apical emargination, but without emargination in *N. lathburiana* species group. Male sternum 7 narrowing apically with rounded apex. Male sternum 8 narrowed and slightly prolonged apically. Gonocoxite distinctly dorsoventrally expanded with wide, but deep invagination and a prominent, often sharp inner dorsal lobe. Gonostylus thick and unmodified or thin, apically more or less prolonged and slightly bent downward, densely hairy, or with dense hair tufts. Gonostylus basoventrally with lobe bearing tuft and modified to complex structure. The strongest modification of gonostylus is in *N. fucata* and *N. bifasciata*. Basoventral area of gonostylus with lobe nearly fused with gonocoxite shifted close to mid, or base of gonocoxite.

Species included.

Nomada (*Heminomada*) *accentifera* Pérez, 1895
Nomada (*Heminomada*) *atrohirta* Friese, 1924
Nomada (*Heminomada*) *bifasciata* Olivier, 1811
Nomada (*Heminomada*) *densipunctata* Schwarz and Smit, 2018
Nomada (*Heminomada*) *duplex* Smith, 1854
Nomada (*Heminomada*) *ferghanica* Morawitz, 1875
Nomada (*Heminomada*) *fucata* Panzer, 1798
Nomada (*Heminomada*) *goodeniana* (Kirby, 1802)
Nomada (*Heminomada*) *illustris* Schmiedeknecht, 1882
Nomada (*Heminomada*) *lathburiana* (Kirby, 1802)
Nomada (*Heminomada*) *luteipes* Schwarz and Smit, 2018
Nomada (*Heminomada*) *melanopyga* Schmiedeknecht, 1882
Nomada (*Heminomada*) *nigritula* Schwarz and Smit, 2018
Nomada (*Heminomada*) *nigroflavida* Gribodo, 1894
Nomada (*Heminomada*) *numida* Lepeletier, 1841
Nomada (*Heminomada*) *obscurifrons* Schwarz and Smit, 2018
Nomada (*Heminomada*) *pyrgosica* Schwarz and Smit, 2018
Nomada (*Heminomada*) *rufohirta* Morawitz, 1895
Nomada (*Heminomada*) *siciliensis* Dalla Torre and Friese, 1894
Nomada (*Heminomada*) *succincta* Panzer, 1798

Nomada subgen. *Holonomada* Robertson, 1903, status restituted

Robertson (1903: 174). Type species: *Nomada superba* Cresson, 1863, by original designation.

Nomada superba species group and *Nomada basalis* species group of Alexander (1994) and Alexander and Schwarz (1994).

= *Nomada* (*Laminomada*) Rodeck, 1947: 266 (**syn. nov.**). *Nomada hesperia* Cockerell, 1903.

Diagnosis.

To avoid paraphyly and oversplitting on subgeneric level, we unite the morphologically diverse lineages of the *Nomada flavopicta*, *Nomada gribodoi*, *Nomada sexfasciata*, *Nomada insignipes*, *N. basalis*, and *Nomada cherkesiana* species groups within the subgenus *Holonomada*. Only a few characters are characteristic of all these species groups. The single most distinct character is the strong reduction to the absence of proper spines on the female metatibia (Fig. 5c), although there can be secondary spine-like hair present (Fig. 5d; developed in males as well), which is unique among all *Nomada* species. Most representatives of the *N. flavopicta* and *N. gribodoi* species groups possess no spines or a single pale, but thick spine in an emargination on the apical margin (Fig. 5c). However, some species of the *N. flavopicta* species group can have several rather thick, short spines. In males, sternum 8 is narrowed and strongly prolonged (cf. Fig. 5i), which separates the males of the *N. flavopicta* species group from sometimes similarly looking males of the subgenus *Hypochrotaenia* (Fig. 5h). Additional important characters are the long first flagellomere (Fig. 5f), pygidial plate rounded to broadly rounded in males, and the female pygidial plate, which is without apical emargination. Males can have a characteristically shaped gonocoxite in some species, and females a uniquely modified pseudopygidial plate of tergum 5 (Fig. 5e), however, all these characterstics have several exceptions. Alexander (1994) suggests the presence of an incomplete lateral carina on the procoxa, and a shelf on the inner base of the gonostylus with a few stout melanised setae as characters shared by the species groups here united in the subgenus *Holonomada*. However, our reevaluation found that these characters seem not stable enough to characterize the subgenus sufficiently as they vary greatly.

Description.

Labrum 1.0–1.7 × wider than long; frequently flat, but also with a tooth medially (*N. flavopicta* species group), or with an elevated carina (*N. basalis* species group). Mandible short, widened basally in species with long malar area. Male scapus slender. Male first flagellomere longer than wide; distinctly longer than the second flagellomere, rarely slightly shorter than the second flagellomere. Male flagellomeres frequently with round knobs except in the *N. flavopicta* species group, or with sharp nodules in some species from the *N. basalis* species group. Patches of hair present on flagellomeres ventrally in the *N. basalis* and *N. cherkesiana* species groups. Development of female paraocular carina very variable, well-developed to reduced, but frequently reduced. Propodeal triangle variable in size, most commonly small; sculpture variable, from finely microsculptured with fine transverse ridges basally and longitudinal ridges medially to coarsely sculptured throughout the triangle; posterolateral delimitation ridge ill-defined, but distinct (sometimes hardly distinct); propodeal triangle at about the same elevational level as the rest of propodeum. Male metafemoral base without distinct modification, rarely slightly excavated, but without modified hair patches. Female apical metatibial spines completely missing in the *N. flavopicta* and *N. gribodoi* species groups, the rest of the species possess a large number (usually much more than 10) of thin setiform spines. Female metatarsomere 1 expanded and flattened in numerous species, but not distinctly expanded in the *N. flavopicta* species group and several other species throughout the subgenus. Female pseudopygidial plate of tergum 5 with multiple types of hair basally, centrally, and apically, most commonly formed to a semicircular shape with a few blunt thick (teeth-like) spines at the anterior side of pseudopygidial plate. Plate bears unmodified hair in a patch basally, or a semicircular line. Apical area with flat setae; teeth-like setae are developed only in some species within the *N. insignipes*, *N. basalis*, and *N. cherkesiana* species groups. Pseudopygidial area in the *N. flavopicta* and *N. gribodoi* species groups are rather simple and unmodified. Female and male pygidial plates rounded to broadly rounded in females, without apical emargination. Male sternum 7 apically narrowing, blunt to angulate terminally. Male sternum 8 narrowed, strongly prolonged. Gonocoxite with shallow invagination and round, or with a rectangular-shaped inner dorsal lobe. Invagination fine and distinct, or deep oriented anteriorly with inner dorsal lobe directed posteriorly and sharp in *N. cherkesiana* species group. Gonostylus variable, from relatively simple in the *N. flavopicta* species group to highly modified in the *N. cherkesiana* species group, apically prolonged and curved with various tufts and also with prolonged basoventral lobe bearing hair tuft.

Species included.

Nomada (*Holonomada*) *agrestis* Fabricius, 1787
Nomada (*Holonomada*) *barcelonensis* Cockerell, 1917
Nomada (*Holonomada*) *basalis* Herrich-Schäffer, 1839
Nomada (*Holonomada*) *brevigenis* Schwarz, Smit and Ockermüller, 2019
Nomada (*Holonomada*) *brevispina* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Holonomada*) *coxalis* Morawitz, 1877
Nomada (*Holonomada*) *cretensis* Schulz, 1906
Nomada (*Holonomada*) *cristata* Pérez, 1896
Nomada (*Holonomada*) *dorchini* Schwarz, Smit and Ockermüller, 2019
Nomada (*Holonomada*) *dubia* Eversmann, 1852
Nomada (*Holonomada*) *emarginata* Morawitz, 1877
Nomada (*Holonomada*) *fedtschenkoi* Morawitz, 1875
Nomada (*Holonomada*) *flavinervis* Brullé, 1832
Nomada (*Holonomada*) *flavoorbitalis* Schwarz, Smit & Gusenleitner, 2018
Nomada (*Holonomada*) *flavopicta* (Kirby, 1802)
Nomada (*Holonomada*) *fuscipennis* Lepeletier, 1841
**Nomada* (*Holonomada*) *gredosiana* Schwarz and Gusenleitner, 2013
Nomada (*Holonomada*) *gribodoi* Schmiedeknecht, 1882
Nomada (*Holonomada*) *gruenwaldti* Schwarz, 1979
Nomada (*Holonomada*) *cherkesiana* Mavromoustakis, 1955
Nomada (*Holonomada*) *imperialis* Schmiedeknecht, 1882
**Nomada* (*Holonomada*) *ina* Schwarz and Smit, 2018
Nomada (*Holonomada*) *incisa* Schmiedeknecht, 1882
Nomada (*Holonomada*) *insignipes* Schmiedeknecht, 1882
Nomada (*Holonomada*) *israelis* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Holonomada*) *keroanensis* Pérez, 1895
Nomada (*Holonomada*) *lateritia* Mocsáry, 1883
Nomada (*Holonomada*) *limassolica* Mavromoustakis, 1955
Nomada (*Holonomada*) *lucidula* Schwarz, 1967
Nomada (*Holonomada*) *lutea* Eversmann, 1852
Nomada (*Holonomada*) *melina* Schwarz, Smit and Ockermüller, 2019
Nomada (*Holonomada*) *mideltiaca* Schwarz, Smit and Ockermüller, 2019
Nomada (*Holonomada*) *mocsaryi* Schmiedeknecht, 1882
Nomada (*Holonomada*) *montarco* Álvarez Fidalgo, 2023
Nomada (*Holonomada*) *monticola* Schwarz, Smit and Ockermüller, 2019
Nomada (*Holonomada*) *moravitzii* Radoszkowski, 1876
Nomada (*Holonomada*) *nesiotica* Mavromoustakis, 1958
Nomada (*Holonomada*) *nigrifrons* Schwarz and Smit, 2018
Nomada (*Holonomada*) *nobilis* Herrich-Schäffer, 1839
Nomada (*Holonomada*) *oculata* Friese, 1921
Nomada (*Holonomada*) *ottomanensis* Schwarz and Smit, 2018
Nomada (*Holonomada*) *pectoralis* Morawitz, 1877
Nomada (*Holonomada*) *pesenkoi* Schwarz, 1987
Nomada (*Holonomada*) *pictiscutum* Alfken, 1927
Nomada (*Holonomada*) *podagrica* Gribodo, 1894
Nomada (*Holonomada*) *pseudocoxalis* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Holonomada*) *pulchra* Arnold, 1888
Nomada (*Holonomada*) *quadrifasciata* Schwarz, 1981
Nomada (*Holonomada*) *quinquefasciata* Schwarz, 1981
Nomada (*Holonomada*) *ressli* Schwarz and Smit, 2018
Nomada (*Holonomada*) *rubricosa* Eversmann, 1852
Nomada (*Holonomada*) *sexfasciata* Panzer, 1799
Nomada (*Holonomada*) *simulatrix* Schwarz and Smit, 2018
Nomada (*Holonomada*) *sybarita* Schmiedeknecht, 1882
Nomada (*Holonomada*) *tarsalis* Schwarz and Smit, 2018
Nomada (*Holonomada*) *teunisseni* Schwarz and Smit, 2018
Nomada (*Holonomada*) *unica* Schwarz and Smit, 2018
Nomada (*Holonomada*) *wahrmanni* Schwarz, Smit and Ockermüller, 2019

Nomada subgen. *Hungias* Straka, subgen. nov.

Type species: *Nomada hungarica* Dalla Torre and Friese, 1894, here designed.

Diagnosis.

Hungias subgen. nov. consists of a single, phylogenetically isolated species (Fig. 1). The newly described subgenus *Hungias* is similar to the nominotypical subgenus *Nomada* and *Nomonosa* subgen. nov. in the shape of the very short, bulging first flagellomeres in males (cf. Fig. 6b). *Hungias* further resembles species of the subgenus *Profuga* subgen. nov. in the structure of the labrum (cf. Fig. 6f, g), which has longitudinal and transverse carinae and a tooth. The propodeal triangle is similar to the species of the subgenus *Gestamen* subgen. nov., but it is not elevated over the rest of the propodeal sides (Fig. 8b). Characteristic for *Hungias* is the shape of the pseudopygidial area that is wide and strongly delimited by discal hair (Fig. 8a). *Hungias* subgen. nov. differs from other subgenera only by the combination of the above-mentioned characters.

Description.

Labrum 1.5–1.8× wider than long; transverse carina in the apical third with a tooth centrally, but there are multiple teeth in the transverse carina in some specimens. Longitudinal impunctate area or carina present medially. Mandible short, normally shaped. Male scapus slightly enlarged. Male first flagellomere short, about as wide as long, bulging laterally, distinctly shorter than second flagellomere. Male flagellomeres not distinctly modified, but with felt-like pubescence basally on flagellomeres. Female paraocular carina well-developed throughout its entire length. Propodeal triangle intermediate to small; sculpture rugose basally and medially, forming kidney-shaped areas with less coarse sculpturation.

However, this area is not distinctly elevated above surrounding surface. Posterolateral delimitation of propodeal triangle distinct but weak; propodeal triangle at about the same height as the remaining propodeum. Male metafemoral base not distinctly modified, flattened with short, posteriorly directed hair. Female metatibia apically with 9–13 closely situated, short thick spines in multiple rows and a bristle. Spines situated closely to apical metatibial projection. Female metatarsomere 1 narrow, not distinctly flattened. Pseudopygidial plate of tergum 5 sharply delimited anteriorly, composed of erect hair. Female pygidial plate rounded apically without terminal emargination. Male pygidial plate truncate, or emarginate at an obtuse angle. Male sternum 7 narrowing apically. Male sternum 7 narrowed and prolonged apically. Gonocoxite with distinct invagination and moderate inner dorsal lobe. Gonostylus wide, short, and hairy with small basoventral lobe with tuft.

Etymology.

The name *Hungias* is derived from the area of origin (Hungary, in Latin Hungaria). The word root is combined with -ias suffix. It is masculine.

Species included.

Nomada (*Hungias*) *hungarica* Dalla Torre and Friese, 1894

Nomada subgen. *Hypochrotaenia* Holmberg, 1886, status restituted

Holmberg (1886: 234). Type species: *Hypochrotaenia parvula* Holmberg, 1886, designed by monotypy.

Nomada abyssinica species group, *Nomada elegantula* species group, *Nomada erigeronis* species group, *Nomada roberjeotiana* species group, and *Nomada vegana* species group of Alexander (1994) and Alexander and Schwarz (1994).

= *Nomadita* Mocsáry, 1894: 37 (**syn. nov.**). Type species: *Nomadita montana* Mocsáry, 1894, designed by monotypy.

= *Nomada* (*Micronomada*) Cockerell and Atkins, 1902: 44. Type species: *Nomada modesta* Cresson, 1863, by original designation.

= *Centrias* Robertson, 1903: 174 (**syn. nov.**). Type species: *N. erigeronis* Robertson, 1897, by original designation.

= *Cephen* Robertson, 1903: 174 (**syn. nov.**). Previously synonymized with *Micronomada* (Hurd 1979, Snelling 1986). Type species: *Nomada texana* Cresson, 1872, by original designation.

= *Nomada* (*Nomadula*) Cockerell, 1903: 611 (**syn. nov.**). Previously synonymized with *Centrias* (Snelling 1986). Type species: *Nomada articulata* Smith, 1854, by original designation.

= *Nomadosoma* Rohwer, 1911: 24. Type species: *Pasites pilipes* Cresson, 1865, by original designation.

= *Polybiapis* Cockerell, 1916: 208. Type species: *Polybiapis mimus* Cockerell, 1916, by original designation.

= *Nomada* (*Callinomada*) Rodeck, 1945: 181 (**syn. nov.**). Previously synonymized with *Nomadita* (Broemeling and Moalif 1988). Type species: *Nomada antonita* Cockerell, 1909, by original designation.

= *Hypochrotaenia* (*Alphelonomada*) Snelling, 1986: 9 (**syn. nov.**). Type species: *Nomada cruralis* Moure, 1960, by original designation.

= *Nomada* (*Adamon*) Hirashima and Tadauchi, 2002: 47 (**syn. nov.**). Type species: *Nomada koikensis* Tsuneki, 1973, by original designation.

Diagnosis.

Hypochrotaenia is a very variable subgenus when considering the entire distributional range, including North and South America. However, the morphology of the subgenus is relatively consistent in the Palearctic region and in Africa. It is characterized by the wide labrum bearing a crenate transversal carina in the apical third, a finely sculptured propodeal triangle (Fig. 5g), the female apical metatibial spines which are thick and number 4–8, the shape of the male gonostylus (simple and narrow) and the particularly characteristic male terminalia (Fig. 5h; the only subgenus with a wide sternum 8). Some of these characters are shared with other subgenera, but the combination is unique for *Hypochrotaenia*. Within the subgenus, we can recognize the *Nomada dolosa*, *N. roberjeotiana*, *Nomada rufipes*, and *N. abyssinica* species groups and several stand-alone species in West Palaerctic and Africa. In the New World, the *N. vegana*, *N. erigeronis*, and *N. elegantula* species groups can be recognized within this subgenus.

Description.

Labrum 1.5 × wider than long or wider; modified in the *N. erigeronis* species group; transversal carina located in apical third of labrum, crenate in some species; and apical margin thin. Mandible thin, simple. Male scapus primarily narrow, enlarged tubuliform in the North American *N. erigeronis* species group. Male flagellomeres not modified. Female paraocular carina well-developed, sharp, and connected to clypeal carina; paraocular carina completely reduced in the American *N. vegana* species group. Propodeal triangle intermediate in size, slightly less than half of propodeum; uniformly reticulated, dull, with groove medially, and fine transverse ridges basally and medially, in some species with slightly stronger longitudinal ridges basally; posterolateral delimitation of propodeal triangle with weak to indistinct ridge, transition is smooth, but propodeal triangle slightly impressed posteriorly. Male metafemoral base unmodified, but modified in the North American *N. erigeronis* species group. Female apical metatibial spines well-developed, 4–8, thick, rarely fine, and narrow, sometimes slightly flattened. Female metatarsomere 1 narrow, unexpanded, slightly flattened in a few species, external surface sparsely covered by long semi-erect setae, setae on inner surface long and semierect. Female pseudopygidial plate of tergum 5 consists of flat setae, transitioning from a finely setose tergal disc, discal setae white, and rarely mixed with black setae. Female pygidial plate usually narrowed apically, terminal emargination minute. Male pygidial plate not or just weakly emarginate, rarely distinctly emarginate apically (*N. erigeronis* species group). Male sternum 7 wide, rounded apically. Apical projection of male sternum 8 wide, not prolonged. Gonocoxite without distinct invagination and with or without inner dorsal lobe. Gonostylus narrow, straight, flattened, not distinctly modified (rarely prolonged), and sparsely hairy.

Synonymy.

We formally synonymize the *Nomada* subgenus *Nomadita* and the subgenus *Adamon* with *Nomada* subgenus *Hypochrotaenia*. The reason for synonymizing the subgenus *Nomadita* is based on our phylogenetic results, which include representatives of both *Nomadita* and *Hypochrotaenia*. However, we were unable to include representatives of *Adamon*, but a synonymization is justified based on the original description of the subgenus and the association of *N. koikensis* with the *N. roberjeotina* species group (Hirashima and Tadauchi 2002). The only difference between *Adamon* and other members of *Hypochrotaenia* may be the reduced number of male flagellomeres (12).

Species included.

Nomada (*Hypochrotaenia*) *abyssinica* Meade-Waldo, 1913
Nomada (*Hypochrotaenia*) *africana* Friese, 1911

Nomada (*Hypochrotaenia*) *cordillera* Eardley and Schwarz, 1991
Nomada (*Hypochrotaenia*) *cleopatra* Schwarz, 1989
Nomada (*Hypochrotaenia*) *errans* Lepeletier, 1841
Nomada (*Hypochrotaenia*) *guichardiana* Eardley and Schwarz, 1991
Nomada (*Hypochrotaenia*) *hararensis* Meade-Waldo, 1913
**Nomada* (*Hypochrotaenia*) *kohrowi* Brauns, 1912
Nomada (*Hypochrotaenia*) *kusdasi* Schwarz, 1981
Nomada (*Hypochrotaenia*) *lamellata* Schwarz, 1977
Nomada (*Hypochrotaenia*) *montana* Mocsáry, 1894
Nomada (*Hypochrotaenia*) *obtusifrons* Nylander, 1848
Nomada (*Hypochrotaenia*) *roberjeotiana* Panzer, 1799
Nomada (*Hypochrotaenia*) *rufipes* Fabricius, 1793
Nomada (*Hypochrotaenia*) *sempiterna* Morawitz, 1894
Nomada (*Hypochrotaenia*) *spinicoxa* Schwarz, 1987

Nomada subgen. *Mininomada* Straka, subgen. nov.

Type species: *Nomada sheppardana* Kirby, 1802, here designated.
= *Nomada furva* species group of Alexander (1994) and Alexander and Schwarz (1994).

Diagnosis.

Mininomada subgen. nov. is easily distinguished from other subgenera of *Nomada* by the shape and sculpture of the propodeum, which has the entire propodeal triangle distinctly delimited by a carina (Fig. 4g, h). The labrum of the species included in *Mininomada* is always at least slightly prolonged with a narrowed apex. The male metafemoral base is often excavated basally (not always), and with variously structured patches of dense hair, but at least directed posteriorly. Most species have only 2–3 apical metatibial spines in the female. The male gonostylus is distinctly modified. Most species of *Mininomada* subgen. nov. are small species of less than 8 mm, but a few large species exist (in the *Nomada erythrocephala* species group). We can recognize the *N. erythrocephala*, *Nomada glaucopis*, *N. sheppardana*, *N. furva*, *Nomada posthuma*, and *Nomada kohli* species groups. Several species are rather isolated morphologically and difficult to associate with the species groups presented herein (e.g., *Nomada blepharipes*, *Nomada coronata*, *Nomada collarae*, or *Nomada distinguenda*).

Description.

Labrum distinctly prolonged, 1.4 × wider than long or longer with transversal carina never positioned apically. Transversal carina reduced to teeth in some species, apical margin narrowing apically. Mandible short, normal shape. Male scapus slender. Male first flagellomere variable in size, frequently longer than second flagellomere and rarely shorter than fourth. Male flagellomeres variable, unmodified, but also modified with nodules on ventral site. Female paraocular carina well-developed, often strongly reduced above the level of antennae. Propodeal triangle large in size, appears rectangular-shaped, but with slightly concave lateral margins. Propodeal triangle reaching almost to the base of metasoma; sculpturation coarse, wrinkled and rugose, similarly sculptured in all parts, but also smooth and bright shining in some species with reduced, but distinct coarse sculpture basally. Propodeal triangle posterolaterally distinctly delimited by an elevated carina throughout s, carina reduced very rarely (*Nomada albidilabris*). Male metafemoral base excavated basally or not, but always with a patch of dense hair directed posteriorly; short, proximally directed hairs are present in some species. Apical metatibial spines in female moderate and short, frequently only 2–3, rarely more than 4, an exception is *N. distinguenda* with 5 spines. Female metatarsomere 1 narrow, unexpanded, sometimes slightly flattened. Pseudopygidial plate of tergum 5 ordinarily shaped, not strongly separated from simple hair of tergal disc. Female pygidial plate rather narrow, rounded apically. Male pygidial plate narrow, apically emarginate, sometimes weakly. Male sternum 7 narrowing apically, pointed in some species. Male sternum 8 distinctly narrowed apically, but apical projection is rather short. Gonocoxite of ordinary shape, with distinct invagination and moderately sized inner dorsal lobe. Gonostylus wide, narrowed apically, and bent down and inward, with various patches of hair andbasoventrally projecting hair tuft.

Etymology.

The name *Mininomada* translates to ‘small *Nomada*’. It consists of the prefix mini and the name of the genus. It is a feminine.

Species included.

Nomada (*Mininomada*) *acutispina* Schwarz and Smit, 2018
Nomada (*Mininomada*) *albidilabris* Schwarz and Smit, 2018
Nomada (*Mininomada*) *ashabadensis* Schwarz, 1987
Nomada (*Mininomada*) *babiyi* Schwarz and Standfuss, 2007
Nomada (*Mininomada*) *barbata* Schwarz, Smit and Ockermüller, 2020
Nomada (*Mininomada*) *blepharipes* Schmiedeknecht, 1882
Nomada (*Mininomada*) *bluethgeni* Stoeckhert, 1943
Nomada (*Mininomada*) *bouceki* Kocourek, 1985
Nomada (*Mininomada*) *collarae* Schwarz, 1964
Nomada (*Mininomada*) *connectens* Pérez, 1884
Nomada (*Mininomada*) *coronata* Pérez, 1896
Nomada (*Mininomada*) *crenulata* Schwarz and Smit, 2018
Nomada (*Mininomada*) *curvispinosa* Schwarz, 1981
Nomada (*Mininomada*) *cypricola* Mavromoustakis, 1955
Nomada (*Mininomada*) *diacantha* Schwarz, 1981
Nomada (*Mininomada*) *discedens* Pérez, 1884
Nomada (*Mininomada*) *distinguenda* Morawitz, 1874
Nomada (*Mininomada*) *ebmeri* Schwarz and Smit, 2018
Nomada (*Mininomada*) *erythrocephala* Morawitz, 1870
Nomada (*Mininomada*) *furva* Panzer, 1798
Nomada (*Mininomada*) *furvoides* Stoeckhert, 1944
Nomada (*Mininomada*) *gageae* Schwarz and Smit, 2018
Nomada (*Mininomada*) *glaucopis* Pérez, 1890
Nomada (*Mininomada*) *grandior* Friese, 1921
Nomada (*Mininomada*) *guichardi* Schwarz, 1981
Nomada (*Mininomada*) *gusenleitneri* Schwarz, 1981
Nomada (*Mininomada*) *gusenleitneriella* Schwarz and Smit, 2018
Nomada (*Mininomada*) *gusevi* Schwarz, Smit and Ockermüller, 2020
Nomada (*Mininomada*) *jerichoensis* Schwarz, Smit and Ockermüller, 2019
Nomada (*Mininomada*) *kohli* Schmiedeknecht, 1882
**Nomada* (*Mininomada*) *komarowi* Radoszkowski, 1893
Nomada (*Mininomada*) *laticrus* Mocsáry, 1883
Nomada (*Mininomada*) *magnilabris* Schwarz, Smit and Ockermüller, 2020
Nomada (*Mininomada*) *marginata* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Mininomada*) *mavromoustakisi* Schwarz and Standfuss, 2007
Nomada (*Mininomada*) *minuscula* Noskiewicz, 1930
Nomada (*Mininomada*) *mitteri* Schwarz, Smit and Ockermüller, 2020
Nomada (*Mininomada*) *nigrospina* Schwarz and Smit, 2018

Nomada (*Mininomada*) *nigrovaria* Pérez, 1896
Nomada (*Mininomada*) *nitidiuscula* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Mininomada*) *ockermuelleri* Schwarz and Smit, 2020
Nomada (*Mininomada*) *opaciformis* Schwarz and Smit, 2018
Nomada (*Mininomada*) *oralis* Schwarz, 1981
Nomada (*Mininomada*) *orbitalis* Pérez, 1913
Nomada (*Mininomada*) *ovaliceps* Schwarz, 1981
Nomada (*Mininomada*) *ovalis* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Mininomada*) *pleuripunctata* Schwarz, Smit and Ockermüller, 2020
Nomada (*Mininomada*) *posthuma* Blüthgen, 1949
Nomada (*Mininomada*) *priesneri* Schwarz, 1965
Nomada (*Mininomada*) *pseudoovalis* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Mininomada*) *sheppardana* (Kirby, 1802)
Nomada (*Mininomada*) *scheuchli* Schwarz and Standfuss, 2007
Nomada (*Mininomada*) *triangulata* Schwarz and Smit, 2018
Nomada (*Mininomada*) *yarrowi* Schwarz, 1981
Nomada (*Mininomada*) *yermasoyiae* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Mininomada*) *zwakhalsi* Schwarz, Smit and Gusenleitner, 2018

Nomada subgen. *Nomacolla* Straka, subgen. nov.

Type species: *Nomada kervilleana* Pérez, 1913, here designed.

Diagnosis.

Nomacolla subgen. nov. consists of rather rare species that can be separated into 2 species groups, the *Nomada melanura* and *N. kervilleana* species groups. The groups can be separated by the shape of the labrum. *Nomacolla* subgen. nov. can be separated from other *Nomada* by the very long antennae in the female sex (Fig. 8d) and the uniquely shaped labrum (Fig. 6i, j). A labrum with an elevated apical half seems to be specific only for the *N. kervilleana* species group (Fig. 6i). The procoxa of both sexes usually bears a posteriorly projecting tooth or at least an acute projection, however, this is not strongly developed in all species. The metatibia is characteristically covered with long dense hair on the outer surface that becomes contiguous with the thin and long apical spines that are similar in shape like the tibial setae (Fig. 8e). Similar setae and thin apical spins of metatibia are present in a few species of *Nomada* s. str., such as *Nomada hirtipes*. The subgenus *Nomacolla* differs from the most closely related nominotypic subgenus *Nomada* in the sculpture of the propodeal triangle, which is coarsely sculptured basally and posteromedially (cf. Fig. 7h), and a distinctly longer first flagellomere in both males and females (Figs. 6c and 8d).

Description.

Labrum variable in size, 1.3–1.6 × wider than long; with shallow transverse carina along apical margin with 1–3 teeth in the carina, or apical third of labrum all hump shaped. Mandible short, normal shape. Male scapus slender. Male first flagellomere distinctly longer than wide, slightly bulging laterally in some species, about as long as second flagellomere, or slightly shorter or longer. Male flagellomeres unmodified. Female first flagellomere unusually prolonged, more than 3 × longer than wide; subsequent flagellomere(s) very long as well, about as long as second flagellomere, or slightly shorter. Female paraocular carina well-developed below and above antennal level, but weak on level of antenna. Propodeal triangle moderate in size; distinctly rugose basally, but also posteromedially; posterolaterally delimitating carina ill-defined, distinct or indistinct; propodeal triangle at about the same elevational level as the rest of propodeum. Procoxa of both sexes commonly projecting posteriorly as a tooth, or at least acute, but indistinctly in some species. Male metafemoral base straight; without modified hair patch. Metatibia on the outer surface (especially dorsally) with long hair that posteriorly reaches and becomes contiguous with apical spines. Female apical metatibial spines long, like hairlike bristles, or normal-shaped spines in the number of 6–10. Female metatarsomere 1 narrow, unexpanded, slightly flattened. Pseudopygidial plate of tergum 5 variable among species, usually wide and short, rather well separated from distinctly different hair on tergal disc. Female pygidial plate narrowing posteriorly, apically obtuse, and minutely emarginated. Male pygidial plate with apical emargination. Male sternum 7 narrowing apically. Male sternum 8 narrowed and moderately prolonged apically. Gonocoxite of common type with distinct invagination and moderate inner dorsal lobe. Gonostylus thick and short, densely hairy, basoventrally with more or less distinct projection with hair tuft.

Etymology.

The name *Nomacolla* is derived from the base of the generic name *Nomada* and feminine form of the word *collis* which means small hill, referring to the characteristic hump-shaped labral carina. It is feminine.

Species included.

**Nomada* (*Nomacolla*) *abnormilabris* Schwarz and Smit, 2018
Nomada (*Nomacolla*) *abnormipes* Schwarz and Smit, 2020
Nomada (*Nomacolla*) *barbilabris* Pérez, 1895
Nomada (*Nomacolla*) *flavoscutellata* Schwarz and Smit, 2018
**Nomada* (*Nomacolla*) *gracilicornis* Morawitz, 1894
Nomada (*Nomacolla*) *kervilleana* Pérez, 1913
Nomada (*Nomacolla*) *maxschwarzi* Smit, 2018
Nomada (*Nomacolla*) *melanura* Mocsáry, 1883

Nomada subgen. *Nomada* Scopoli, 1770

Scopoli (1770: 44). Type species: *Apis ruficornis* Linnaeus, 1758, by designation of Curtis (1832: 419).
Nomada ruficornis species group and *Nomada zonata* species group of Alexander (1994) and Alexander and Schwarz (1994).
= *Lamproapis* Cameron, 1902: 419 (**syn. nov.**). Type species: *Lamproapis maculipennis* Cameron, 1902, designated by monotypy.
= *Gnathias* Robertson, 1903: 173 (**syn. nov.**). Type species: *Nomada bella* Cresson, 1863, by original designation.
= *Phor* Robertson, 1903: 174 (**syn. nov.**). Type species: *Nomada integra* Robertson, 1893 = *Nomada integerrima* Dalla-Torre, 1896, by original designation and monotypy.

Diagnosis.

The subgenus *Nomada* can be separated into numerous species groups of related species, namely, *Nomada alboguttata*, *Nomada braunsiana*, *Nomada fabriciana*, *Nomada flavoguttata*, *Nomada fulvicornis*, *Nomada panzeri*, *N. ruficornis* (including *N. striata*), and *N. zonata* species groups. There are multiple species groups in North America. Species of this nominotypic subgenus can be united by several characters. Most diagnostic is the combination of the propodeal shape and sculpture (Fig. 9b), with the short first flagellomere (Fig. 6b). The propodeum possesses a large and wide propodeal triangle with sinuous or convex posterolateral delimiting margin. The basal part of the propodeum is concave with rugose sculpture and the posterior part is rather convex (or straight). The posterior part of the propodeum is distinctly delimited from the basal part and covered by slightly shining microsculpture. Species with rugosity along the medial line of the propodeal triangle are rather rare. The first flagellomere in males is about as long as wide and is bulging laterally in many species (Fig. 6b). It is distinctly shorter than the second flagellomere. Long and thin hairlike female apical metatibial spines can be considered another rather distinct character of the subgenus *Nomada*. It is shared with the sister lineage, the subgenus *Nomacolla* subgen. nov. However, these spines seem to have been secondarily modified into thick and short spines in several species lineages.

Description.

Labrum variable in size, from 1.2 to 1.9 × wider than long; usually with 1–3 teeth, but also without a tooth, very rarely with shallow carina (*Nomada melathoracica*). Mandible short to prolonged, simple, but also often modified with preapical bump, bidentate or blunt apically. Male scapus slender to slightly thickened. Male first flagellomere short to extremely short (frequently as long as wide, or shorter), bulging laterally in many species, distinctly shorter than second flagellomere; in some species, it is distinctly longer than wide, but even in these species the first flagellomere is distinctly shorter than second flagellomere. Male flagellomeres variable, unmodified, but also modified with nodules on ventral site. Female paraocular carina well-developed and above antennal level. Propodeal triangle moderate to large and especially wide; most frequently separated into a basal concave part with rugose sculpture and a convex (or straight) posterior part with uniform microsculpture that is shiny; posterolateral delimitation carina ill-defined, but distinct (sometimes hardly distinct), distinctly sinuate or even convex; and propodeal triangle is at about the same elevational level as the rest of propodeum. Male metafemoral base straight, rarely slightly excavated; without modified hair, but small patch of hair in some species of *N. zonata* species group. Female apical metatibial spines primarily in the form of hairlike thin long bristles in number of 6–10; secondarily short and thick and even reduced to 1 in some species. Female metatarsomere 1 narrow, unexpanded, sometimes slightly flattened. Pseudopygidial plate of tergum 5 very variable among species, commonly well separated from hair on tergal disc, but also nearly contiguous with tergal disc hair; there are wide and short setae types, but frequently also narrow and wide. Female pygidial plate narrowing posteriorly, apically obtuse, straight, or minutely emarginated. Male pygidial plate variable, with or without apical emargination. Male sternum 7 narrowing apically, or parallel-sided apically in some species. Male sternum 8 narrowed and moderately prolonged apically. Gonocoxite of common type with distinct invagination and moderate inner dorsal lobe. Gonostylus thick and short, densely hairy, basoventrally with more or less distinct projection with hair tuft.

Species included.

Nomada (*Nomada*) *alboguttata* Herrich-Schäffer, 1839
Nomada (*Nomada*) *algira* Mocsáry, 1883
Nomada (*Nomada*) *arrogans* Schmiedeknecht, 1882
Nomada (*Nomada*) *baccata* Smith, 1844
Nomada (*Nomada*) *braunsiana* Schmiedeknecht, 1882
Nomada (*Nomada*) *bruneipes* Schwarz, Smit and Ockermüller, 2019
Nomada (*Nomada*) *cadiza* Schwarz and Gusenleitner, 2013
Nomada (*Nomada*) *castellana* Dusmet, 1913
Nomada (*Nomada*) *concolor* Schmiedeknecht, 1882
Nomada (*Nomada*) *conjungens* Herrich-Schäffer, 1839
Nomada (*Nomada*) *cruenta* Smiedeknecht, 1882
Nomada (*Nomada*) *dilleri* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Nomada*) *discrepans* Schmiedeknecht, 1882
Nomada (*Nomada*) *fabriciana* Linné, 1767
Nomada (*Nomada*) *ferruginata* (Linnaeus, 1767)
Nomada (*Nomada*) *filicornis* Schwarz and Smit, 2018
Nomada (*Nomada*) *flava* Panzer, 1798
Nomada (*Nomada*) *flavilabris* Morawitz, 1875
Nomada (*Nomada*) *flavoguttata* (Kirby, 1802)
Nomada (*Nomada*) *fulvicornis* Fabricius, 1793
Nomada (*Nomada*) *fusca* Schwarz, 1986
Nomada (*Nomada*) *glabella* Thomson, 1870
Nomada (*Nomada*) *glabriscuta* Schwarz, Smit and Ockermüller, 2020
Nomada (*Nomada*) *gransassoi* Schwarz, 1986
Nomada (*Nomada*) *guttulata* Schenck, 1861
Nomada (*Nomada*) *hirtipes* Pérez, 1884
Nomada (*Nomada*) *hispanica* Dusmet y Alonso, 1913
Nomada (*Nomada*) *chrysopyga* Morawitz, 1871, **stat. nov.**
Nomada (*Nomada*) *intermediata* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Nomada*) *italica* Dalla Torre and Friese, 1894
Nomada (*Nomada*) *kornosica* Mavromoustakis, 1958
Nomada (*Nomada*) *kriesteni* Schwarz and Gusenleitner, 2013
Nomada (*Nomada*) *leucophthalma* (Kirby, 1802)
Nomada (*Nomada*) *lineola* Panzer, 1798**, stat. nov.**
Nomada (*Nomada*) *litigiosa* Gribodo, 1893
Nomada (*Nomada*) *lobata* Schwarz, Smit and Gusenleitner, 2018
Nomada (*Nomada*) *longipalpis* Schwarz and Smit, 2020
Nomada (*Nomada*) *maculicornis* Pérez, 1884
Nomada (*Nomada*) *mandibularis* Schwarz and Gusenleitner, 2013
Nomada (*Nomada*) *margelanica* Schwarz, 1987
Nomada (*Nomada*) *marshamella* (Kirby, 1802)
Nomada (*Nomada*) *mauritanica* Lepeletier, 1841
Nomada (*Nomada*) *melathoracica* Imhoff, 1834
Nomada (*Nomada*) *micronycha* Pérez, 1902
Nomada (*Nomada*) *moeschleri* Alfken, 1913
Nomada (*Nomada*) *mutica* Morawitz, 1872
Nomada (*Nomada*) *noskiewiczi* Schwarz, 1966
Nomada (*Nomada*) *obscura* Zetterstedt, 1838
Nomada (*Nomada*) *opaca* Alfken, 1913
Nomada (*Nomada*) *panzeri* Lepeletier, 1841
Nomada (*Nomada*) *pastoralis* Schmiedeknecht, 1882
Nomada (*Nomada*) *piccioliana* Magretti, 1883
Nomada (*Nomada*) *platythorax* Schwarz, 1981
Nomada (*Nomada*) *quadriliniata* Schwarz, Smit and Ockermüller, 2020
Nomada (*Nomada*) *radoszkowskii* Łoziński, 1922
Nomada (*Nomada*) *rhenana* Morawitz, 1872
Nomada (*Nomada*) *rostrata* Herrich-Schäffer, 1839
Nomada (*Nomada*) *ruficornis* (Linnaeus, 1758)
Nomada (*Nomada*) *sabulosa* Radoszkowski, 1876
Nomada (*Nomada*) *sarta* Morawitz, 1875
Nomada (*Nomada*) *schmidti* Schwarz, Smit and Ockermüller, 2020
Nomada (*Nomada*) *signata* Jurine, 1807
Nomada (*Nomada*) *smiti* Schwarz, 2018
Nomada (*Nomada*) *stoeckherti* Pittioni, 1951
Nomada (*Nomada*) *striata* Fabricius, 1793
Nomada (*Nomada*) *subcornuta* (Kirby, 1802)
Nomada (*Nomada*) *symphyti* Stoeckhert, 1930
Nomada (*Nomada*) *tenella* Mocsáry, 1883
Nomada (*Nomada*) *trapeziformis* Schmiedeknecht, 1882
Nomada (*Nomada*) *umbrosa* Schmiedeknecht, 1882
Nomada (*Nomada*) *villosa* Thomson, 1870

Nomada (*Nomada*) *warnckei* Schwarz and Smit, 2018
Nomada (*Nomada*) *xanthozona* Schwarz, Smit and Ockermüller, 2020
Nomada (*Nomada*) *zonata* Panzer, 1798

Nomada subgen. *Nomonosa* Straka, subgen. nov.

Type species: *Nomada elsei* Schwarz and Smit, 2018

Diagnosis.

Based on the results of our phylogenetic analysis, the subgenus *Nomonosa* subgen. nov. consists of a single species and no other similar species is known to us. The subgenus *Nomonosa* subgen. nov. is very similar to the nominotypical subgenus *Nomada* and the subgenus *Hungias* subgen. nov. in the short bulging first flagellomere in males (Fig. 6b). It also resembles species from the subgenus *Profuga* subgen. nov. in the structure of the labrum with longitudinal and transverse carinae, but the labrum is distinctly wider than in the aforementioned taxa (Fig. 6f). The propodeal triangle is similar to species of the subgenus *Gestamen* subgen. nov., but it is not elevated above the rest of the propodeal sides (cf. Figs. 7b and 8b). *Nomonosa* subgen. nov. differ from other subgenera primarily by combinations of characters.

Description.

Labrum 1.8–2.0 × wider than long; transverse carina in the apical third with a tooth centrally, sometimes additional small tooth in the transverse carina; with longitudinal impunctate area medially. Mandible short, slightly angulated in the middle of external surface in male. Male scapus is indistinctly enlarged. Male first flagellomere very short, about as wide as long, bulging laterally, distinctly shorter than second flagellomere. Male flagellomeres not distinctly modified, but with carinated unsculptured plates ventrally on flagellomeres. Female paraocular carina well-developed throughout its length. Propodeal triangle intermediate to small; sculpture rugose basally and medially forming kidney-shaped areas with less coarse sculpture, however, this area is not elevated above the surrounding surface; posterolateral delimitation of propodeal triangle distinct, but weak; propodeal triangle at about the same elevational level as the rest of propodeum. Male metafemoral base not distinctly modified, flattened with unmodified hair. Female metatibia apically with 6–7 closely grouped short thick spines and a bristle, spines slightly separated from metatibial apical projection. Female metatarsomere 1 narrow, not distinctly flattened. Female terminal metasomal segments missing in the only described specimen. Male pygidial plate narrowly rounded apically. Male sternum 7 narrowing apically. Male sternum 8 narrowed and prolonged apically. Gonocoxite with distinct invagination and moderate inner dorsal lobe. Gonostylus wide, short, and hairy with small basoventral lobe with tuft.

Etymology.

The name Nomonosa is derived from the base of the generic name *Nomada* and word monos which translates to ‘the only one’. This subgenus is based on a single species. The word is feminized by adding ‘a’ to end. It is feminine.

Species included.

Nomada (*Nomonosa*) *elsei* Schwarz and Smit, 2018

Nomada subgen. *Plumada* Straka, subgen. nov.

Type species: *Nomada felici* Schwarz, 1977.
= *Nomada plumosa* ‘assemblage’ of Alexander and Schwarz (1994).

Diagnosis.

The subgenus *Plumada* subgen. nov. includes only a few species with very similar appearance. The cuticle of the entire metasoma is red in color, contrasting sharply with the dark head and mesosoma. The head and mesosoma are largely covered by long plumose dark erect hair (Fig. 6a). The head and labrum are very wide, the labrum about 2 times wider than long with an arcuate transverse carina and 3 teeth (Fig. 6a). The flagellomeres are short, about as long as wide, but third and second flagellomeres are distinctly longer than wide. The male gonostylus is simple, narrow, and straight with several short hairs.

Description.

Labrum very wide, about 2 × wider than long, or wider; arcuate transverse carina with 3 teeth developed approximately in its center, apical margin fine, and finely serrate. Mandible short, attenuate apically. Male scapus slender. Male first flagellomere longer than wide and longer than second flagellomere. Male flagellomeres unmodified, generally short. Female paraocular carina well-developed, but strongly reduced above the level of antennae. Propodeal triangle moderate in size, short medially and narrow laterally; basal area of propodeal triangle indistinctly concave, coarsely sculptured and posterior part coarsely microsculptured, all dull; posterolateral delimitation carina ill-defined to indistinct, propodeal triangle smoothly transition to lateral area. Male metafemoral base unmodified. Female apical metatibial spines long, thin, numbering 2–10. Female metatarsomere 1 narrow, unexpanded, and slightly flattened. Pseudopygidial plate of tergum 5 not wide, distinctly separated from setae of tergal disc. Female pygidial plate narrowing posteriorly, apically obtuse. Male pygidial plate without apical emargination. Gonocoxite without distinct invagination and with weak inner dorsal lobe. Gonostylus narrow, straight, and sparsely hairy. Head, including labrum, scapus, and mandible and also mesosoma with long erect black or dark brown plumose hair. Whole metasoma red, without yellow markings.

Etymology.

The name Plumada originated from the word pluma (feather) and -ada ending. It refers to the bees’ plumose setae on head and mesosoma. It is feminine.

Species included.

Nomada (*Plumada*) *felici* Schwarz, 1977
Nomada (*Plumada*) *hirticeps* Pérez, 1895
Nomada (*Plumada*) *plumosa* Gribodo, 1894

Nomada subgen. *Profuga* Straka, subgen. nov.

Type species: *Nomada tuberculifera* Schwarz and Smit, 2018.

Diagnosis.

The Nomada subgenus *Profuga* comprises only 3 rare species. The females of this subgenus can be recognized by the 3 or 4 short, more or less closely situated metatibial spines, which are distinctly separated from the small apical metatibial projection (Fig. 8f). The apical metatibial projection is small, short, and acute apically (Fig. 8f). The labrum is of characteristic shape with a transverse carina and a tooth in the middle, and with a faint longitudinal carina joining the tooth (Fig. 6g). The propodeal triangle is relatively small and finely or coarsely rugose, but distinctly uniformly sculptured in most parts (Fig. 6h). The propodeal side is short and possesses plumose appressed or semierect hair; the hair is short to very short (Fig. 6h). The male ventral side of the metafemur is flat, with long erect hair, but possibly not in all species.

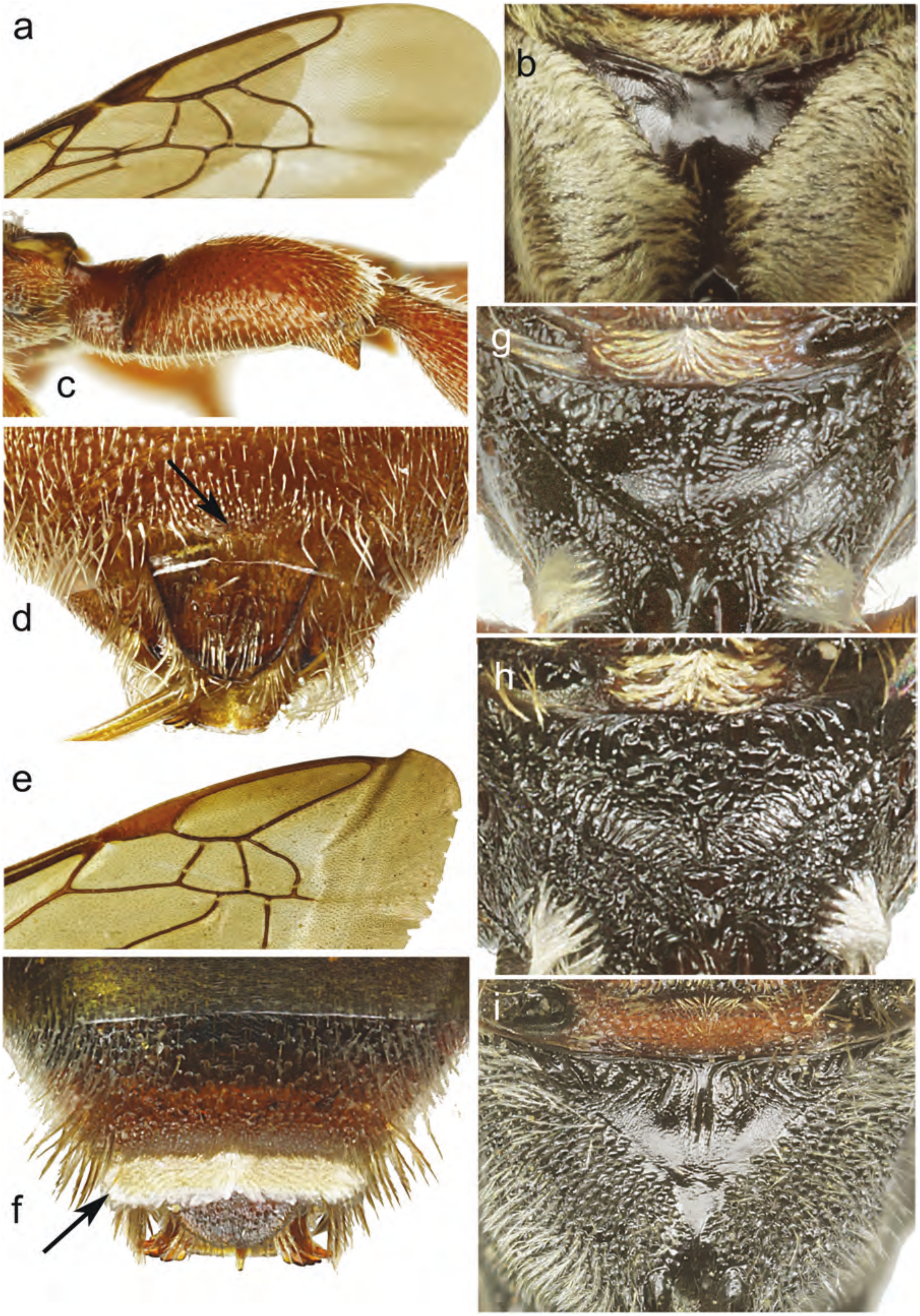

Fig. 4. a) *Acanthonomada argentea*, forewing laterally; b) *A. argentea*, propodeum; c) *A. argentea*, female hind femur; d) *A. argentea*, female tergum 5 and pygidium with an arrow pointing to a cuticle tooth; e) *Nomada* (*Heminomada*) *lathburiana*, forewing laterally; f) *N.* (*Collicula*) *pleurosticta*, female tergum 5 with pseudopygidial plate and pygidium with an arrow pointing to pseudopygidial plate fringe; g) *N.* (*Minimomada*) *sheppardana*, propodeum; h) *N.* (*Mininomada*) aff. *yermasoyiae*, propodeum; i) *N.* (*Collicula*) *pleurosticta*, propodeum.

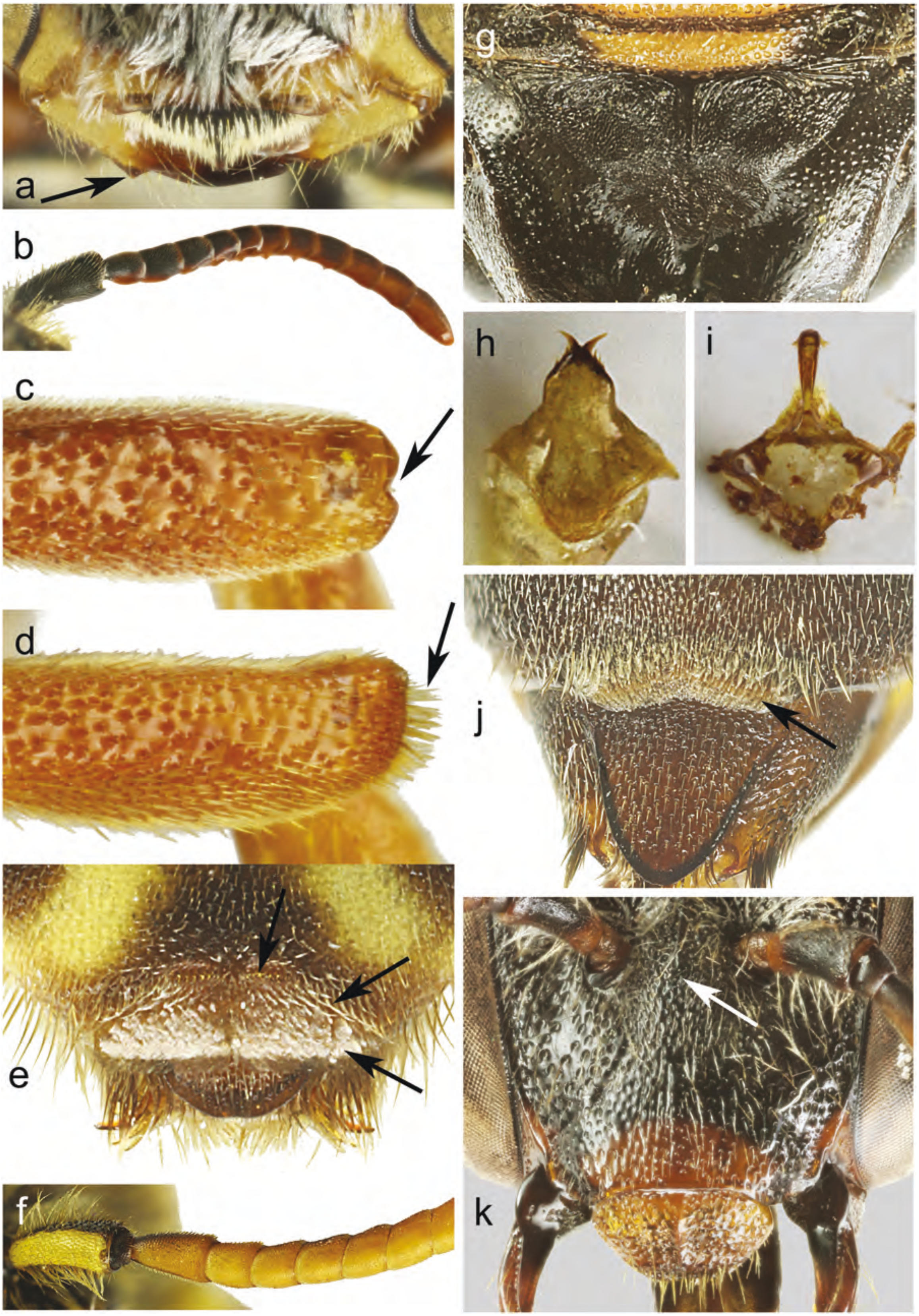

Fig. 5. a) *Nomada* (*Collicula*) *pleurosticta*, lower part of male head with tuberculate mandibles, an arrow pointing to a tubercle; b) *N.* (*Collicula*) *pleurosticta*, male antenna, ventral view; c) *N.* (*Holonomada*) *flavopicta*, female metatibia with a tibial spine at the apex, an arrow pointing to a single spine; d) *N.* (*Holonomada*) *sexfasciata*, female metatibia with tibial spines at the apex, an arrow pointing to a series of hair-like spines; e) *N.* (*Holonomada*) *basalis*, female tergum 5 with semicircular pseudopygidial plate consisting of modified setae, including teeth-like setae, arrows pointing to 3 types of setae; f) *N.* (*Holonomada*) *basalis*, male antenna, ventral view; g) *N.* (*Hypochrotaenia*) *roberjeotiana*, propodeum; h) *N.* (*Hypochrotaenia*) *obtusifrons*, male sternum 8, ventral view; i) *N.* (*Hungias*) *hungarica*, male sternum 8, ventral view; j) *N.* (*Afronomada*) *gigas*, female tergum 5 with poorly developed pseudopygidial plate consisting of unmodified setae pointed by an arror; k) *N.* (*Afronomada*) *gigas*, female labrum, clypeus and supraclypeal area, frontal view, an arrow pointing to a supraclypeal area with a shallow carina.

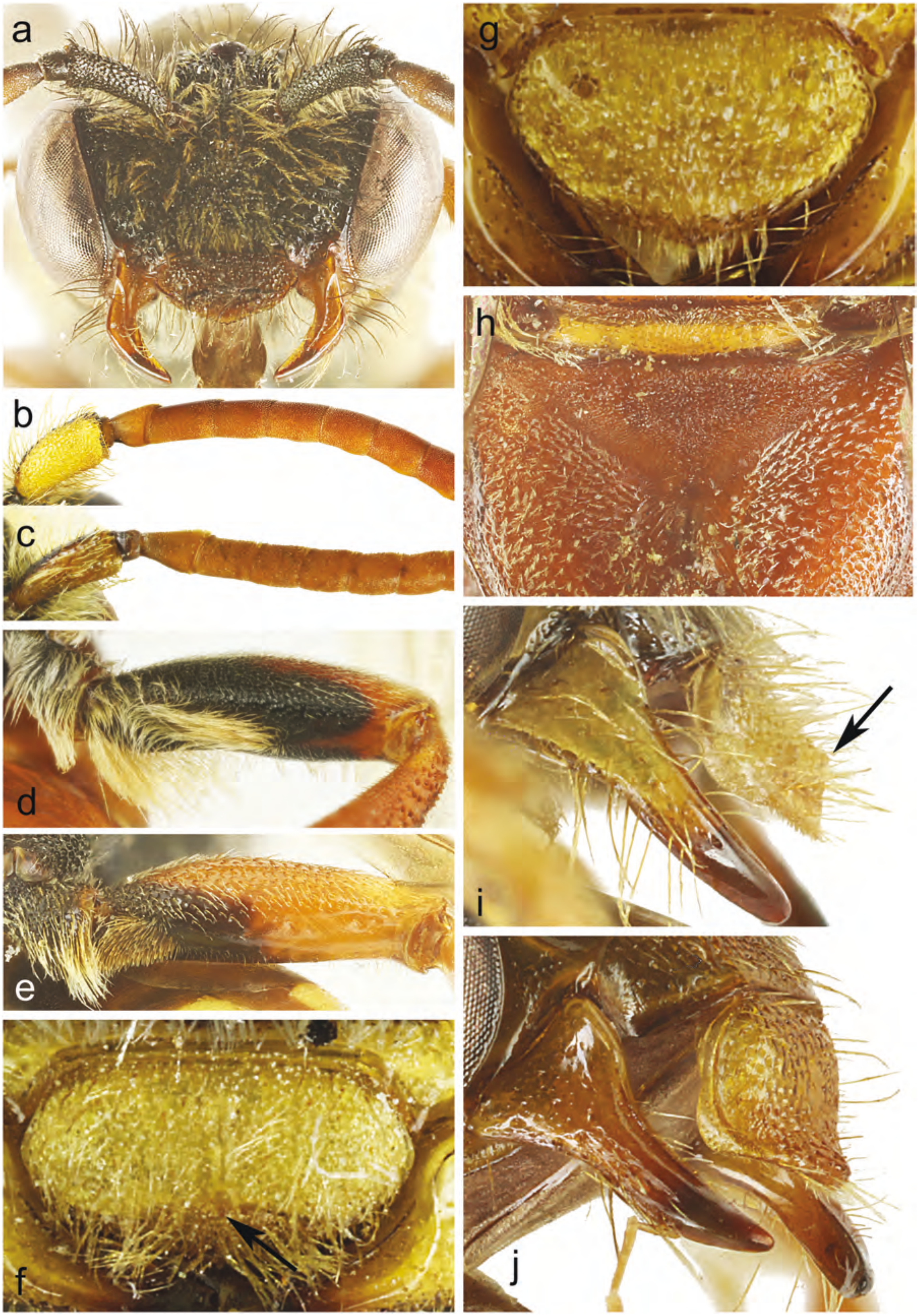

Fig. 6. a) *Nomada* (*Plumada*) *felici*, female head with exposed labrum, frontal view; b) *N.* (*Nomada*) *lineola*, male antenna, ventral view; c) *N.* (*Nomacolla*) *kervilleana*, male antenna, ventral view; d) *N.* (*Gestamen*) *eos*, male hind femur and trochanter with hair tuft, ventral view; e) *N.* (*Heminomada*) *fucata*, male hind femur and trochanter with hair tuft, ventral view; f) *N.* (*Nomonosa*) *elsei*, male labrum, frontal view, arrow pointing to a tooth on joint of medial and transverse carinas; g) *N.* (*Profuga*) *tuberculifera*, female labrum, frontal view; h) *N.* (*Profuga*) *tuberculifera*, propodeum; i) *N.* (*Nomacolla*) *kervilleana*, male labrum, lateral view with and arrow pointing to hump-shaped area of labrum; j) *N.* (*Nomacolla*) *abnormipes*, female labrum, lateral view.

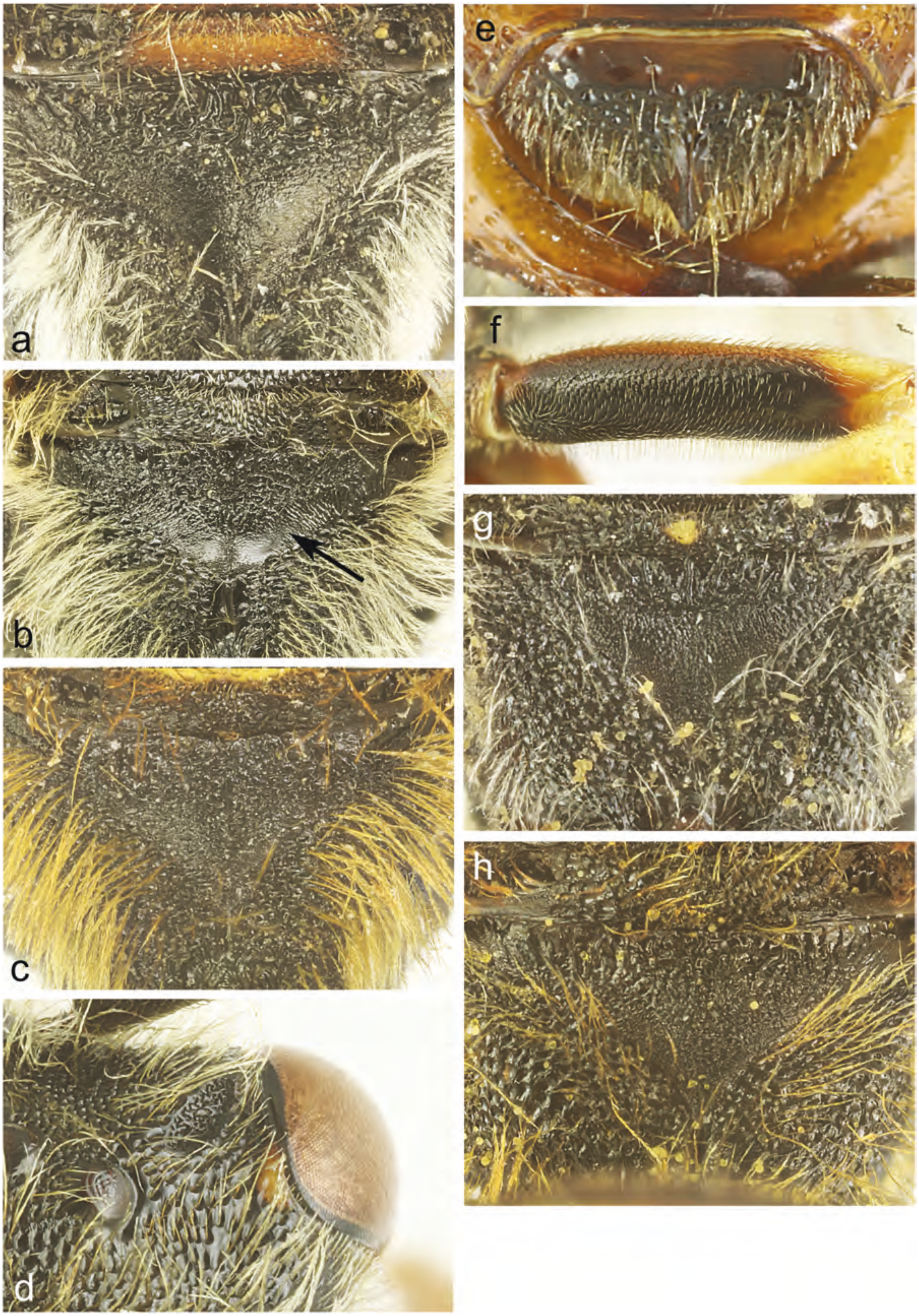

Fig. 7. a) *Nomada* (*Gestamen*) *armata*, propodeum; b) *N.* (*Gestamen*) *eos*, propodeum with an arrow pointing to kidney-shaped area; c) *N.* (*Gestamen*) *propinqua*, propodeum; d) *N.* (*Gestamen*) *eos*, male head ridge; e) *N.* (*Gestamen*) *armata*, labrum, frontal view; f) *N.* (*Heminomada*) *lathburiana*, male hind femur, ventral view; g) *N.* (*Heminomada*) *fucata*, propodeum; h) *N.* (*Heminomada*) *lathburiana*, propodeum.

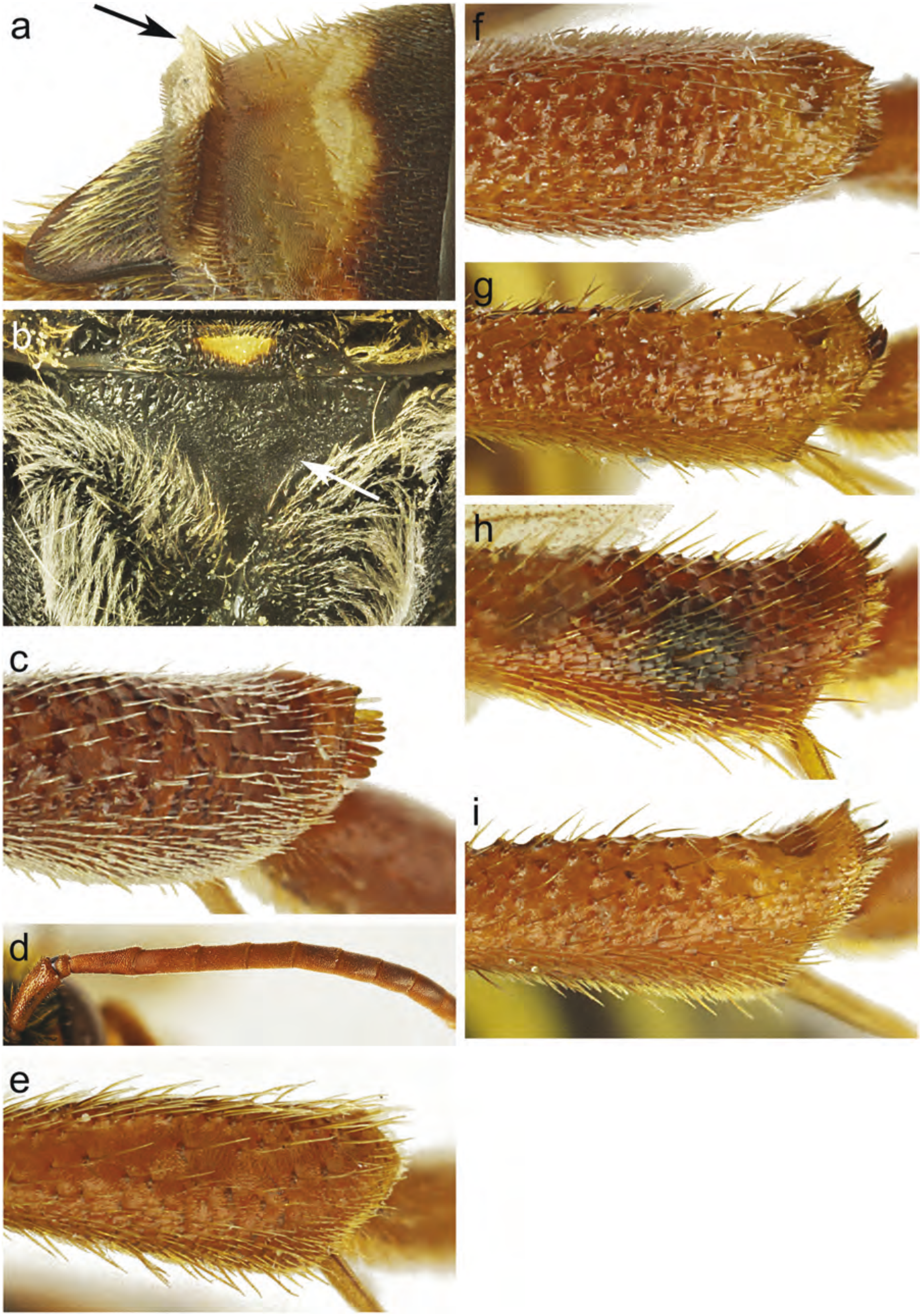

Fig. 8. a) *Nomada* (*Hungias*) *hungarica*, tergum 5 with pseudopygidial plate, dorsolateral view, arrow pointing to erect hair of pseudopygidial area; b) *N.* (*Hungias*) *hungarica*, propodeum with an arrow pointing to kidney-shaped area; c) *N.* (*Hungias*) *hungarica*, female metatibia with tibial spines at the apex; d) *N.* (*Nomacolla*) *abnormipes*, female antenna, ventral view; e) *N.* (*Nomacolla*) *abnormipes*, female metatibia with tibial spines at the apex; f) *N.* (*Profuga*) *tuberculifera*, female metatibia with tibial spines at the apex; g) *N.* (*Heminomada*) *fucata*, female metatibia with tibial spines at the apex; h) *N.* (*Heminomada*) *lathburiana*, female metatibia with tibial spines at the apex; i) *N.* (*Nomada*) *lineola*, female metatibia with tibial spines at the apex.

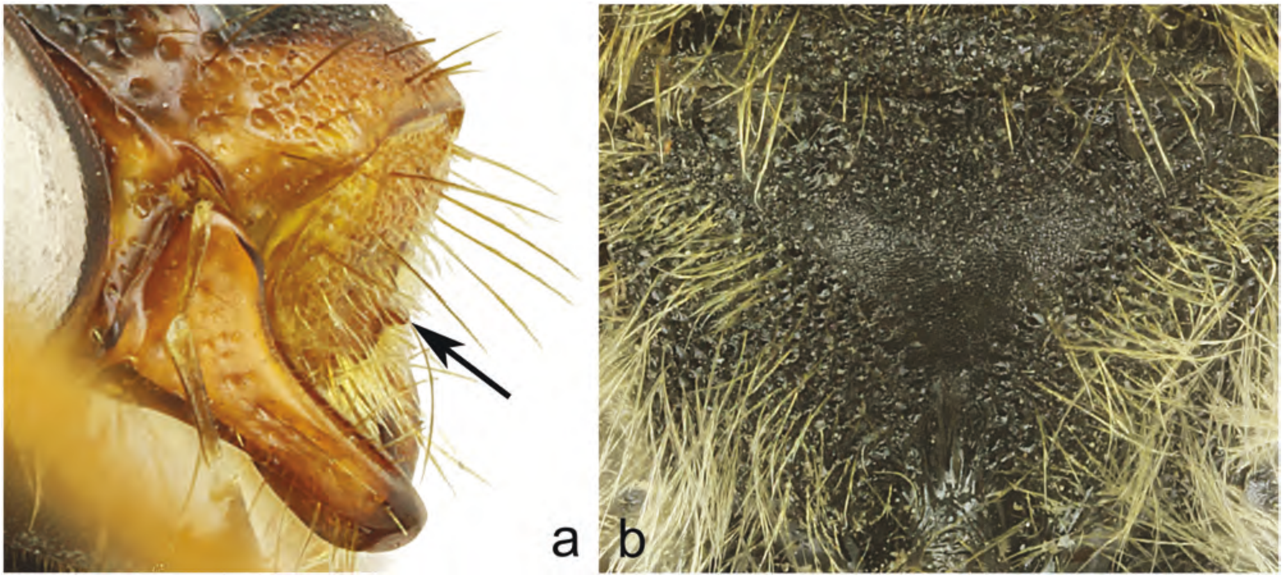

Fig. 9. a) *Nomada* (*Nomada*) *lineola*, female labrum, lateral view, arrow pointing to labral tooth; b) *N.* (*Nomada*) *lineola*, propodeum.

Description.

Labrum 1.5–1.8 × wider than long; apex thick with transverse carina close to apical margin, medially with a tooth in the carina; and ill-defined longitudinal carina present medially and joining the tooth. Mandible short, normal. Male scapus slender. Male first flagellomere slightly shorter than second flagellomere. Male flagellomeres without modification, or with weak tubercules ventrally. Female paraocular carina developed, but not sharp, distinct also above the level of antennae. Propodeal triangle small, very finely rugose (*N. tuberculifera*) to strongly rugose (*Nomada ariasi*) in most parts, except posterolaterally; posterolaterally delimitating ridge ill-defined; and propodeal triangle at about the same elevational level as the rest of propodeum. Propodeal side with plumose hair, short to very short. Male metafemoral base flat to indistinctly emarginated ventrally with long erect hair (*N. tuberculifera*), but with short hair in *N. ariasi*. Female metatibia with 3–4 more or less closely situated short and thick spines, distinctly separated from apical metatibial projection; apical metatibial projection very short, triangular in shape and sharp. Female metatarsomere 1 narrow, unexpanded, and slightly laterally flattened. Pseudopygidial plate of tergum 5 of common shape, separated from unmodified and sparse hair on tergal disc. Female pygidial plate rounded apically. Male pygidial plate narrow, rounded apically.

Etymology.

The name *Profuga* originates from the Latin word profugus which means homeless, banished, but also fugitive or runaway. It is transformed to the feminine form by the ending with 'a'. It refers to its parasitic 'nomadic' lifestyle, but also refers to its rarity. It is feminine.

Species included.

Nomada (*Profuga*) *ariasi* Dusmet y Alonso, 1913
Nomada (*Profuga*) *ibanezi* Dusmet y Alonso, 1915
Nomada (*Profuga*) *tuberculifera* Schwarz and Smit, 2018

Key to the Genera and Subgenera of West Palearctic and African Nomadini

1a. Third submarginal cell enlarged, about as long as first submarginal cell (Fig. 4a). Propodeal triangle small, without basal area, finely microsculptured and clearly shiny (Fig. 4b). Mid- and metacoxa with distinct lamellate carina on dorsal surface. Forefemur thin, with longitudinal carina on outer surface. Meso- and metafemur ventroapically each with 2 teeth arising from a cuticular protrusion, 1 on the anterior and 1 on the posterior side (Fig. 4c). Metatibia short and thick, covered by fine hair laterally and without small tubercules bearing setae on the majority of the outer surface. The dorsal side of male mandible with a small round expansion, directed upward. Female tergum V without distinct pseudopygidial area, nearly glabrous, with 2 small dorsally projecting teeth apicomedially (Fig. 4d). .... genus Acanthonomada Schwarz, 1966

1b. Third submarginal cell about as long as second submarginal cell (Fig. 4e). Propodeal triangle larger, with distinct basal area, shiny or dull (Figs. 4g–i, 5g, 6h, 7a–c, g, h, 8b, and 9b). If without distinct basal area, then it is finely microsculptured and dull. Mid- and metacoxa simple, without lamellate carina on dorsal side. Forefemur without longitudinal carina on outer side. Meso- and metafemur simple, without cuticular protrusion ventroapically (though may be produced into a small projecting point or spine dorsoapically). Metatibia covered with small tubercules bearing setae on the majority of the outer surface. The dorsal side of the mandible even, without expansion. Female tergum V with a distinct pseudopygidial area (Figs. 4f and 5e), which is sometimes reduced but still distinctly hairy. .... 2, genus *Nomada* Scopoli, 1770

2a. Propodeal triangle delimited laterally and posterolaterally by a distinct carina along the entire margin (Fig. 4g, h). .... *Nomada* subgenus *Mininomada* subgen. nov.

2b. Propodeal triangle laterally and posterolaterally rather weakly delineated, with or without distinct ridges, but never with a well-developed and complete carina (Figs. 4i, 5g, 6h, 7a–c, g, h, 8b, and 9b). 3

3a. Propodeum shiny, uniformly finely microsculptured or unsculptured with distinct longitudinal ridges basally (Fig. 4i). Body red and black, without white/yellow markings. Labral tooth located in the basal third, or in the center of the labrum. Outer side of male mandible with a distinct protuberance, or angulated (Fig. 5a; not all species). Male flagellomeres frequently with knobs and pointed nodules ventrally (Fig. 5b; not all species). .... *Nomada* subgenus *Collicula* subgen. nov.

3b. Propodeum dull, basally with or without rugose sculpturation (Figs. 5g, 6h, 7a–c, g, h, 8b, and 9b). Body with or without yellow markings. Labral tooth never in the basal third of the labrum. Outer side of male mandible without protuberance. Male flagellomeres with or without knobs or nodules. 4

4a. Metatibia of both sexes either entirely bare apically, sometimes with 1 tooth located in a medial emargination (Fig. 5c), or with more than 10 hair-like spines (Fig. 5d), never with distinct thick or thin spines. Female pseudopygidial plate modified (not all species), with basal hair simple and apical hair flattened, forming a semicircular area, and the base of the plate with a row of teeth-like setae (Fig. 5e). Male and female pygidial plates rounded apically and rarely slightly emarginate apically. Male first flagellomere longer than wide, distinctly longer than the second flagellomere (Fig. 5f; rarely slightly shorter than the second flagellomere). Male sternum 8 apically narrow and distinctly elongate. .... *Nomada* subgenus *Holonomada* Robertson, 1903

4b. Metatibia apically with 1–10 distinct thick or thin spines (Fig. 8c, e–i); when more spines present, then the spines are short and thick. Female pseudopygidial plate never with teeth-like setae and rarely semicircular in shape. Male and female pygidial plates with or without apical emargination. 5

5a. Propodeal triangle uniformly reticulate to microsculptured, dull, with a groove medially and fine transversal ridges basally and medially (Fig. 5g; sometimes with slightly stronger longitudinal ridges basally); propodeal triangle flat, without strong separation of the basal and posterior areas (Fig. 5g). Multiple apical metatibial spines present, these thick and short and separated from each other. Male apical projection of sternum 8 wide, not prolonged (Fig. 5h). Pseudopygidial plate well-developed. .... *Nomada* subgenus *Hypochrotaenia* Holmberg, 1886

5b. Propodeal triangle frequently separated into basal rugose area (often concave) and posterior microsculptured area (Figs. 7a, b, g, h, 8b, and 9b; flat or convex); some species with propodeal triangle coarsely sculptured throughout (Figs. 6h and 7c). When propodeal triangle flat and finely sculptured, then either apical metatibial spines situated close together and well separated from apical metatibial projection (Fig. 8f, g), or pseudopygidial plate reduced and dark (Fig. 5j). Male apical projection of sternum 8 narrow, more or less prolonged (Fig. 5i). 6

6a. Pseudopygidial plate reduced, consisting of unmodified hair, with very short grey or black hair (Fig. 5j). Labrum and clypeus with more or less distinct longitudinal carina (Fig. 5k; impunctate line). Interantennal hump round, with shallow carina (Fig. 5k). South Africa. .... *Nomada* subgenus *Afronomada* subgen. nov.

6b. Pseudopygidial plate well-developed, consisting of flattened white setae (Fig. 4f). Clypeus without longitudinal carina. Labrum with, or without longitudinal carina. Interantennal hump longitudinal, with crest-like carina. North Africa, Asia and Europe. 7

7a. Labrum more than twice as wide as long (Fig. 6a). Labrum, mandible, frons, scapus, scutum, scutellum, and mesopleuron with long erect black hair (Fig. 6a). Male gonocoxite without distinct invagination. Gonostylus thin, finger-like, with hair on apex. .... *Nomada* subgenus *Plumada* subgen. nov.

7b. Labrum less than twice as wide as long. Body not covered with long, erect black hair. Male gonocoxite with or without invagination. Gonostylus thick or variously modified, covered with hair, or with hair tufts. 8

8a. Males. 9

8b. Females. 15

9a. Flagellomere 1 distinctly shorter than flagellomere 2 and only about as long as wide (Fig. 6b). Flagellomere 1 bulging laterally (Fig. 6b; not all species). Flagellomere 2 among the longest flagellomeres (Fig. 6b). Base of metafemur ventrally without appressed tuft of variously directed hair. Metafemur rarely impressed ventrally. 10

9b. Flagellomere 1 usually equally long as flagellomere 2, or just slightly shorter or longer (Fig. 6c). Flagellomere 1 straight laterally in most species (Fig. 6c). Flagellomere 2 variable. Base of metafemur ventrally with or without appressed tuft of hair, hair directed posteriorly, obliquely, and proximally (Fig. 6d, e). Metafemur frequently impressed ventrally. In case when flagellomere 1 is about as long as wide and shorter than flagellomere 2, then the appressed tuft of hair of metafemur is well-developed. 12

10a. Labrum without longitudinal carina, but with 1 tooth medially, or 3 teeth arranged in a triangle. Transverse carina not developed. Mandible simple or bidentate. Species-rich subgenus distributed throughout the Northern Hemisphere. .... *Nomada* subgenus *Nomada* Scopoli, 1770

10b. Labrum with weak longitudinal carina and transverse carina close to labral apex, bearing a distinct tooth medially (Fig. 6f). Mandible simple. Two isolated species from Central Europe or the Western Mediterranean. 11

11a. Labrum 1.5–1.8 × as wide as long. A single species from West Palearctic. .... *Nomada hungarica*, subgenus *Hungias* subgen. nov.

11b. Labrum 1.8–2.0 × as wide as long (Fig. 6f). A single isolated species from the Western Mediterranean. .... *Nomada* subgenus *Nomonosa* subgen. nov.

12a. Labrum with transverse carina and central tooth, and with faint longitudinal medial carina joining the tooth (Fig. 6g). Propodeal triangle relatively small and flat, finely or coarsely rugose, but uniformly sculptured in most parts (Fig. 6h). Ventral side of metafemur flat, with long erect hair in some species. .... *Nomada* subgenus *Profuga* subgen. nov.

12b. Labrum without transverse carina and faint longitudinal medial carina. Ventral side of metafemur flat with long erect hair. Propodeum separated into a rugose anterior part and a less sculptured posterior part. Propodeum shape more or less convex. 13

13a. Labrum hump-shaped over entire apical half (Fig. 6i), or flat without a tooth (Fig. 6j; sometimes with shallow apical transverse carina). Procoxa projecting posteriorly as a thin tooth, or at least acute; although tooth indistinct in some species. Ventral side of metafemur flat, or slightly excavated, with long erect hair. ....*Nomada* subgenus *Nomacolla* subgen. nov.

13b. Labrum never hump-shaped, frequently with or without a tooth. Procoxa obtuse, rarely with a short tooth. Ventral side of metafemur variable, but frequently with appressed hair basoventrally. 14

14a. Hair tuft on metafemoral venter present (as in Fig. 6d) or not, but never golden and frequently indistinct on trochanters. Ventral area of metafemur with partially long hair on ventral part in species with poorly developed tuft. Basal area of propodeal triangle coarsely irregularly sculptured, usually concave, posterior part of propodeal triangle convex, medially impressed, and distinctly reticulate or ridged, posterolaterally with paired gibbous kidney-shaped areas and with or without transversal ridges, dull to shiny (Fig. 7a–c). Posterolateral delimitation of propodeal triangle well-developed by a convex elevation of the propodeal triangle nearly all along the lateral margin, propodeal triangle elevated above the rest of propodeum. Delimitating ridge of propodeal triangle distinct or not, but almost always with impression at its place. Oblique facial ridge (fovea) with minute punctures present on frons (Fig. 7d; not all species). Aside from any characters above, if the specimen has a conspicuous, large, and shiny unsculptured plate on the base of labrum (Fig. 7e), then follow this couplet. .... *Nomada* subgenus *Gestamen* subgen. nov.

14b. Metafemoral hair tuft usually present and consisting of short golden appressed hair, located on the impressed ventral part of metafemur and joining hair on metatrochanter (Fig. 6e). Entire ventral area of metafemur covered with very short hair, much shorter than anteriorly, or posteriorly on the femur in species with missing golden tuft (Fig. 7f). Propodeal triangle usually sculptured over entire surface, basal area of propodeal triangle with more or less coarse sculptures (Fig. 7g, h). The shape of the basal area of propodeal triangle can be distinctly concave or straight. Propodeal triangle approximately on same elevational level as the remaining propodeum, posterolateral delimitation ridge of propodeal triangle ill-defined, but most often distinct (sometimes hardly distinct). Oblique facial ridge (fovea) never developed. ....*Nomada* subgenus *Heminomada* Cockerell, 1902

15a. Posterolateral delimitation of propodeal triangle well-developed by convex elevation of propodeal triangle along nearly all of its lateral margin, propodeal triangle elevated above the rest of propodeum. Delimitating ridge of propodeal triangle distinct or not, but almost always with impression at its place. Propodeal triangle basally and medially irregularly reticulate, rugose or transversally ridged; in addition, medially longitudinally impressed, leading to sculpturation appearing as paired gibbous, kidney-shaped areas posterolaterally, and with or without transversal ridges that can be dull or shiny (Fig. 7a–c). Independent from any characters mentioned above, if the specimen has a conspicuous, large and shiny unsculptured plate at the base of the labrum (Fig. 7e), then follow this couplet (Fig. 7e). .... *Nomada* subgenus *Gestamen* subgen. nov.

15b. Propodeal triangle at about the same elevational level as the remaining propodeum. Delimitating ridge of propodeal triangle distinct or not, without distinct impression in its place. Propodeal triangle separated into basal concave area and posterior convex area, with basal area coarsely rugose and posterior area with fine sculpturation. Rarely, the propodeal triangle is flat or uniformly convex with relatively uniform sculpture (fine or rugose). When kidney-shaped areas posterolaterally on propodeal triangle are present, then they are not distinctly elevated over the rest of propodeum. 16

16a. Pseudopygidial area of tergum 5 broad, clearly separated from tergal disc, consisting of erect setae (Fig. 8a). Size of propodeal triangle intermediate to small, coarsely sculptured basally and medially; kidney-shaped areas present posterolaterally (Fig. 8b). Between 9 and 13 apical metatibial spines present, short and thick, grouped together in multiple rows (Fig. 8c). A single isolated species from the Western Palearctic. ....*Nomada* subgenus *Hungias* subgen. nov.

16b. Pseudopygidial area of tergum 5 variable in size, but never clearly separated from tergal disc and formed by appressed to semierect setae (unknown in *Nomonosa* subgen. nov.). Propodeal triangle separated into a basal and a posterior area, both of which are similarly sculptured. Metatibial apical spines less numerous. 17

17a. Antennae very long, flagellomeres 4–9 about twice as long as wide and flagellomeres 1–3 and 10 nearly 3 times longer than wide (Fig. 8d). Labrum nearly flat without a tooth, typically with hump-shaped, elevated apical half (Fig. 6i), but also without (Fig. 6j). Procoxa commonly projecting posteriorly as a tooth, or at least acute, although indistinct in some species. Metatibia with long hair on outer surface, which become contiguous with the thin and long apical spines that are similar in shape to tibial setae (Fig. 8e). Propodeal triangle coarsely sculptured basally and posteromedially. ....*Nomada* subgenus *Nomacolla* subgen. nov.

17b. Antennae usually shorter. Combination of characters different. 18

18a. Labrum with transverse carina and with tooth placed medially, and with faint longitudinal medial carina joining the tooth (Fig. 6f, g). Metatibia with 3–6 thick, straight apical spines distinctly separated from apical tibial projection (Fig. 8f). 19

18b. Labrum with or without a tooth, typically without a transverse carina; transverse carina developed very rarely, but if so, then metatibial apical spines not distinctly separated from apical projection (Fig. 8h, i). 20

19a. Labrum 1.5–1.8 × as wide as long (Fig. 6g). Metatibia with 3–4 thick and very short apical spines that are distinctly separated from the apical tibial projection (Fig. 8f). Propodeum covered by short appressed, or semierect plumose hair (Fig. 6h). ....
.... *Nomada* subgenus *Profuga* subgen. nov.

19b. Labrum 1.8–2.0 × as wide as long (Fig. 6f). Metatibia with (5–)6 thick apical spines of usual length. Propodeum with longer, rather simple hair forming an erect, or semierect tuft. .... *Nomada* subgenus *Nomonosa* subgen. nov

20a. Metatibial apical spines commonly only 2–3 (but rarely up to 6), short and thick, grouped together, and clearly separated from metatibial apical projection (Fig. 8g). If metatibial apical spines separated and more numerous (Fig. 8h), then labral tooth positioned apicomedially and mesosoma largely covered by long erect red hair (Fig. 7h). Propodeal triangle intermediate to small, flat or consisting of basal and posterior parts, more or less coarsely sculptured in all parts (Fig. 7g, h). ....
.... *Nomada* subgenus *Heminomada* Cockerell, 1902

20b. Metatibial apical spines usually more numerous (4–10), at least slightly separated from each other and less distinctly separated from metatibial apical projection (Fig. 8i). Labrum with 1 or multiple teeth (Fig. 9a), but never with single apicomedially positioned tooth in combination with long erect hair on body. Propodeal triangle intermediate to large, consisting of a concave basal area and a flat posterior area, basal area coarsely sculptured whereas posterior area usually with distinctly finer sculpturation (Fig. 9b). .... *Nomada* subgenus *Nomada* Scopoli, 1770

Discussion

The Phylogeny of Nomadini

In the present study, we developed a densely sampled, robust phylogeny of *Nomada* using a geographically and taxonomically broad taxon sampling from throughout the Palearctic region, with a particular focus on the West Palearctic. We used 3 different approaches to reconstruct the phylogeny, namely Bayesian and Maximum Likelihood analyses of the concatenated UCE sequence matrix, as well as gene tree summary analysis under the multispecies coalescent model (MSC). All 3 approaches recovered highly congruent phylogenetic trees, which unambiguously found our newly established subgenera as monophyletic groups (Figs. 1 and 2, Supplementary Figs. 1–3). The backbones of our phylogenetic trees are topologically identical and generally well to fully supported. However, the ASTRAL gene tree summary analysis found lower confidence for a number of shallower divergence events (Supplementary Fig. 3). In addition, certain *Nomada* species with low sequencing success were resolved slightly differently in the ASTRAL phylogeny in comparison to the 2 concatenation approaches. For example, the phylogenetic placements of *N. panurginoides* (25 recovered loci), *N. italica* (34 loci), or *Nomada* sp. ‘PK1’ aff. *confinis* (39 loci) are congruently resolved in the ML and Bayesian analyses but differ in the ASTRAL phylogeny. Large numbers of entirely absent gene loci can bias summary analysis under the MSC (Xi et al. 2016, Gatesy et al. 2019) and gene trees from fragmented individual loci tend to be less accurate, thereby decreasing the accuracy of summary trees (Hosner et al. 2016, Sayyari et al. 2017, Bossert et al. 2021). In cases of extensive gene tree estimation error, concatenation approaches can produce more accurate species trees (Molloy and Warnow 2018), which is why we consider the placement of these samples in the concatenation trees as more reliable. However, these samples are outliers: our average UCE capture exceeds 1,700 loci per sample, providing a large number of individual gene trees for coalescent-based analysis, which, in our case, is largely congruent with the concatenation approaches.

Across phylogenetic methods, the phylogeny of Nomadini is characterized by an initial bifurcation that separates the tribe into 2 clades of very uneven size. The species previously known as the *Nomada odontophora* group (Fig. 1), which we here circumscribe as consisting of only 3 species, are the sister group to all remaining *Nomada*, which exceeds 750 described species worldwide. The same pattern was recovered by the global *Nomada* treatment of Odanaka et al. (2022), despite different taxon sampling for both lineages, showing consistent support for this finding (Supplementary Fig. 5). Interestingly, our phylogenetic results align with Schwarz’s (1966) opinion that the *Nomada odontophora* group should be considered a separate genus, *Acanthonomada*. While cladistic analyses of the *Nomada* species groups found the *odontophora* group to be likely a derived lineage within *Nomada* (Alexander 1991, 1994), we found a series of strong morphological characteristics that separates *Acanthonomada* (=*Nomada odontophora* group) from the remaining *Nomada*, justifying its recognition as a separate genus (see also Pittioni 1952). Additional support for this taxonomic change lies in host use by these bees: *Acanthonomada argentea* is a parasite of *Cubiandrena cubiceps* (Friese 1914) (Schwarz 1966; as *Andrena cubiceps*), presenting a case of congruent host-parasite phylogeny. *Cubiandrena*, which also comprise just 3 described species (Wood 2020), is the sole sister group to all remaining *Andrena* and was recently validated as deserving generic rank (Dubitzky et al. 2010, Pisanty et al. 2022). *Andrena*, in turn, is the primary host of the remaining *Nomada*, forming a remarkable pattern of host-parasite relationships. Given the morphologically distinct features and the particular host use of *Acanthonomada*, we consider the recognition of this genus, which is formalized above, as the most appropriate taxonomic action.

By integrating phylogenomics with extensive morphological study, we establish a subgeneric classification of *Nomada* that consists of natural groups yet retains diagnosability for the individual subgenera. While easily recognizable as a genus, species of *Nomada* are notoriously difficult to identify and classify, largely due to the great variability in size and morphological structures (see the keys in Mitchell 1962, Smit 2018). In addition, a large number of seemingly isolated species with uncertain phylogenetic affinities impeded the establishment of robust supraspecific classifications. We rectify this situation by dividing the West Palearctic and African *Nomada* into 13 subgenera, 7 of which are newly defined and described herein. All newly described subgenera are exclusively Old World, however, 4 large subgenera are Holarctic in distribution.

While we took the rich North American fauna of *Nomada* into account, our study does not allow us to adequately circumscribe a global subgeneric classification, yet it serves as a comprehensive framework for future research. For example, 3 exclusively American lineages included in the phylogeny of Odanaka et al. (2022) that are not present in our study deserve subgeneric status (*vincta*, *adducta*, and *belfragei* groups; Supplementary Fig. 5) and all these lineages possess available subgeneric names (*Pachynomada* Rodeck 1945, *Asteronomada* Broemeling 1988, and *Phelonomada* Snelling 1986). At least one other lineage, the extremely rare, monotypic *N. rodecki*, may present another subgenus (Alexander and Schwarz 1994). In comparison to the study of Odanaka et al. (2022) and the current study (Supplementary Fig. 5), only a densely sampled combined dataset of Nearctic and Palearctic *Nomada* will allow the completion of a sound global revision concerning the subgeneric boundaries for the genus.

Comparison to Previous Phylogenetic Studies

Our new phylogeny of *Nomada* can be discussed with respect to both previous cladistic-morphological studies (Alexander 1991, 1994), as well as with recent phylogenomic work (Odanaka et al. 2022). Comparable with the present study, Odanaka et al. (2022) used UCEs to establish the phylogenetic relationships of a broad set of *Nomada* species. However, given their global scope, the representation of *Nomada* from the West Palearctic is sparser than in our study, while we include less representation from the Nearctic. Given these different sampling regimes, the phylogenies are not entirely comparable, yet general patterns are shared: accounting for the reciprocal lack of included lineages, the phylogenies are entirely congruent on the higher, subgeneric, or species group level (Supplementary Fig. 5).

This shows that our new understanding of *Nomada* phylogeny is robust regarding the different sampling and analytical approaches.

Comparing our results to the morphology-based phylogenies of Alexander (1991, 1994) is challenging because of their ambiguous results, yet there are remarkable patterns of similarity. The basal polytomy of the strict consensus tree of Alexander (1994) comprises 8 branches, 7 of which relate to the subgenera *Afronomada*, *Collicula*, and *Hypochrotaenia* as established in the present study. Strikingly, these 3 subgenera comprise 3 of the 4 earliest branching subgenera of our study (Figs. 1–3). Comparable findings are found for the relationships of specific species groups: Alexander's (1994) *Nomada basalis* group makes the *N. superba* group paraphyletic, as in our and Odanaka et al.'s (2022) phylogeny, rendering the newly restituted subgenus *Holonomada* a natural group. Alexander (1994) found no unique, derived character (=autapomorphy) that characterizes the species-rich and morphologically diverse *Nomada ruficornis* group and suggested that the group is paraphyletic. In line with this, Odanaka et al. (2022) recovered a polyphyletic *N. ruficornis* group because of 2 separate clades that did not form a monophyletic lineage. Using our dense sampling of Palearctic *Nomada*, we were able to include the majority of the West Palearctic species of the *N. ruficornis* group (as listed by Alexander and Schwarz, 1994), allowing to explicitly test the association of individual species. We found the polyphyly of the *N. ruficornis* group to be more extensive than previously thought, as we recovered species spread across 7 of the newly established subgenera, thereby underlining the highly artificial nature of this species group in its previous sense. Our revisionary classification settles these issues for the West Palearctic species.

At last, the species listed by Alexander and Schwarz (1994) for the *roberjeotiana* group were not recovered as monophyletic. The *N. erigeronis* and *N. vegana* groups of Alexander and Schwarz (1994) are found to be related inner groups of the *N. roberjeotiana* group defined by these authors. A particular case concerns *N. whiteheadi*, a species tentatively assigned to the *roberjeotiana* group by Alexander and Schwarz (1994) and marked with a questionmark in their study to indicate uncertainty. In line with Odanaka et al. (2022), we found this species to be distantly related to the *roberjeotiana* group and as sister species to *N. gigas*. In the present study, we circumscribe these 2 derived species as the new subgenus *Afronomada* (Fig. 1).

Morphological Delineation of Subgenera

We revise the taxonomy of the Palearctic *Nomada* by placing our extensive morphological study in a phylogenomic context. By only considering well-supported natural lineages, we strive to establish a rank-based taxonomy of monophyletic groups that are recognizable using morphological characters. Like Alexander (1994), we found that the 'extent and quality' of the morphological evidence varies among groups, rendering certain subgenera harder to recognize than others. However, for the vast majority of species, a subgeneric association can be reliably achieved using the newly developed identification key for the subgenera of *Nomada*. Below we discuss the diagnosability of the individual subgenera and highlight potential problematic characters.

The subgenera *Afronomada*, *Plumada*, *Collicula*, and, for the most part, *Mininomada* are well-recognizable groups with distinct morphological features. These subgenera have clear diagnoses and are easily separated in the identification key. The 3 subgenera *Hungias*, *Nomonosa*, and *Profuga* consist of either single or very few species, which are all rare. While we tried to avoid recognizing exceedingly small subgenera, the isolated phylogenetic positions of these lineages required the circumscription of new subgenera. Consequently, the diagnostic characterization of these subgenera is rather simple and based on either single species (subgenera *Hungias* and *Nomonosa*) or just 3 rare species (*Profuga*). In light of these small species numbers, the subgeneric concepts for these lineages are valid given currently known species but may need to be expanded if new species of these groups are discovered.

The subgenera *Holonomada* and *Heminomada* include morphologically very distinctive species with rather plesiomorphic characters as well as derived species with obvious outstanding morphological autapomorphies. By unifying the *N. flavopicta* and the similar *N. gribodoi* species groups with the *N. basalis* and *N. cherkesiana* species groups in the subgenus *Holonomada*, we recognize a morphologically heterogenous lineage that has significant variability in the shape of the head, coxa, metatibial spines, pseudopygidial plate and especially in the structure of the male gonostylus. A similar situation concerns the subgenus *Heminomada* as defined herein: the *N. lathburiana* and *N. bifasciata* species groups are both morphologically distinct from each other and well-recognizable. However, separating these lineages into separate subgenera is inadvisable from a phylogenetic perspective for 2 reasons. First, the clade includes species that have previously been placed into species groups outside of the *N. bifasciata* group like *N. lathburiana* and *N. luteoloides*, which were considered part of the *N. ruficornis* group (Alexander and Schwarz 1994). These species would not clearly fit a narrowly defined subgenus for the *N. bifasciata* species group. Second, species around *N. luteoloides* and similarly also *N. lathburiana* share morphological characters with species of the *N. bifasciata* group. Given their phylogeny, we consider it best to define a broad subgenus *Heminomada*, which includes species from the North American *N. luteoloides*, *N. lathburiana*, and *N. bifasciata* species groups.

The morphological variation within the subgenera *Nomada* s. str. and *Gestamen* is significantly smaller than in the subgenera *Holonomada* and *Heminomada*. However, we were unable to find a single unique character that is unanimously present in every species, or at least in the vast majority of species, for both *Nomada* s. str. and *Gestamen*. Nonetheless, there are morphological features that we deem characteristic because they are rather representative and present in most species. For *Nomada* s. str., the shape of the antennae, especially the relative length of the first flagellomere in males, is decisive for delineating the subgenus. Species of the subgenus *Gestamen* have a characteristically impressed metafemur in males, which is covered by a distinct patch of setae. However, this feature is not present in every single species of *Gestamen* and further occurs outside of this subgenus. Visible in nearly all species of the sister lineage, the subgenus *Mininomada*, and many species of the subgenus *Heminomada*, we conclude that this character was present in the MRCA of *Gestamen*, *Profuga*, *Mininomada*, and *Heminomada*, and was subsequently lost multiple times in descendant lineages, including certain clades of *Gestamen*.

At last, we highlight the propodeum as a morphological structure of great, if not greatest, significance for delineating subgenera and species groups of *Nomada*. However, while shape and surface sculpturing of this structure are highly informative, the nuanced differences between groups are challenging to clearly express and integrate into differential diagnoses and descriptions. In addition, even greatly magnified photographs with high resolution do not always suffice to capture the three-dimensional aspects of the structure, subtle delineating carinae, or the exact relative dimensions of the propodeal triangle. We see great promise in the application of modern imaging technologies, including micro-CT, to better capture the three-dimensional aspects of the propodeum and inform the subgeneric delineation for *Nomada*. Until such technologies become broadly available, we recommend our newly developed identification key as a reliable approach to associate species of Palearctic *Nomada* with subgenera, while noting that a very small percentage of specimens, primarily those showing exceptional degrees of variation, may not key out beyond reasonable doubt.

Historical Biogeography of Nomadini in the Palearctic

Our densely sampled phylogenetic framework allowed us to comprehensively investigate historical biogeographic patterns for the Palearctic species of Nomadini (Figs. 1 and 2). Therefore, our results need to be understood in conjunction with a recent global analysis of *Nomada*: Odanaka and colleagues (2022) reconstructed the phylogeny of 142 species of *Nomada* sampled from across the globe, and estimated ancestral ranges for the MRCA of nearly all species groups. As such, their study on the historical biogeography of *Nomada* establishes routes of dispersal on a global level, but examines patterns at a higher, coarser scale. The present study is a fine-scale analysis of the Palearctic *Nomada*, which is reflected by our dense taxon sampling for this region. For example, we recognize the distinctly different species assemblages of Saharo-Arabia, Euro-Siberia, the Near East and Eastern Mediterranean, and the Western Mediterranean, and hence consider them as separate regions. With the exception of the southern part of the Arabian Peninsula, Odanaka et al. (2022) recognized all aforementioned regions as a single area. Conversely, the present study largely lacks representation of *Nomada* from the New World and is hence insufficient to address range expansions outside of the Old World, or discuss biogeographic patterns for species groups not present in our data. This is reflected by a few unrealistically widespread reconstructed biogeographic distributions, especially for the MRCA of *Hypochrotaenia*: we found this ancestor to be nearly global in distribution, likely because we lack the fine-scale resolution of this subgenus from the New World. The focus and strength of our study lies in the unparalleled sampling of Palearctic *Nomada*, which allows a fine-scale reconstruction of the evolutionary processes that contributed to the present-day distribution of the tribe for this region.

Our results convey that the historical biogeography of the Palearctic *Nomada* is characterized by frequent range expansions, as well as by both sympatric and allopatric cladogenesis. Within most of the major lineages, we recovered different patterns of sympatric cladogenesis. In some instances, such as for the subgenera *Nomada* s. str. or *Collicula*, we recovered sympatric cladogenesis following dispersal. This means that we recovered lineages that likely speciated following dispersal into an area that the MRCA did not previously occupy. *Nomada* s. str., for example, significantly diversified after a range expansion from the Near East and Eastern Mediterranean into the Euro-Siberian region around 15 mya. Interestingly, both the aforementioned subgenera are seemingly exclusively parasitic on *Andrena*. This suggests scenarios in which individual species of *Nomada* dispersed into a previously unoccupied area and subsequently radiated along a newly available fauna of *Andrena* hosts. Conversely, we recovered a wealth of cladogenesis without indication of changes in the biogeographic range. In species-rich clades like *Mininomada*, *Gestamen*, and *Holonomada*, their respective MRCAs were likely present in the Near East and Eastern Mediterranean, where these lineages likely speciated in narrow sympatry (Figs. 1 and 2). Strikingly, these are subgenera for which we recovered a greater breadth in hosts (Fig. 3): all 3 of these genera attack at least 1 additional genus other than *Andrena*. This indicates that for these lineages, speciation was likely not associated with biogeographic change, but may have been associated with an expanded host range.

Our results show allopatry as a major driver of cladogenesis in *Nomada*. Across the phylogeny, we found clades whose MRCAs were recovered inhabiting ranges of 2 or more areas, which subsequently speciated into descendent lineages present in only a subset of the once widespread ancestral range. For nearly all pairs of sister species that occur in 2 separate areas, vicariance was recovered as the most probable process explaining their disjunct distribution. The most common allopatric pattern was recovered for MRCAs being present in both the Near Eastern and the Euro-Siberian range, with subsequent splits into species of restricted range in the daughter lineages: this pattern of allopatry can be found in every major subgenus and suggests that both areas provide similarly suitable environments for *Nomada*. Similarly, a once widespread distribution in the Near East, Western Mediterranean, and the Euro-Siberian ranges was recovered for *Nomada* s. str., *Heminomada*, and *Gestamen*, with subsequent cladogenesis of species inheriting narrower ranges. These frequent faunal expansions are contrasted by the depauperate fauna of African *Nomada*, which is ancient but species-poor. Reasons for this pattern remain to be tested but may lie in the species-poor *Andrena* fauna of Africa and the different climatic conditions.

The Spatial Origin of Nomadini

Our biogeographic analysis found the combined Near East and the Eastern Mediterranean region as the spatial origin of Nomadini. This finding is intuitive because of the early branching patterns in our phylogeny: the single sister group to all *Nomada*, *Acanthonomada*, is restricted to this region, and the MRCA of nearly all major lineages inhabited this range. In addition, the distribution of its host lineage supports this pattern. *Cubiandrena*, the single known host lineage of *Acanthonomada*, is the sister group to all *Andrena* and is also endemic to the Eastern Mediterranean and the Middle East (Wood 2020, Pisanty et al. 2022). However, our data lack appropriate representation from the Nearctic and are hence insufficient to ultimately conclude an ancestral range. Conversely, Odanaka and colleagues (2022) analyzed a global representation of *Nomada* and found a near-certain shared Nearctic + Palearctic spatial origin of Nomadini. This pattern can be explained by the phylogenetic position of the *Nomada vincta* species group, a lineage lacking in the present study, which branched early in the evolution of the genus and is the sister group to the remaining *Nomada* (Odanaka et al. 2022), but not *Acanthonomada*. However, we argue that this range is unrealistically large and likely an artifact of the biogeographic coding and the DEC model. The DEC model is known to produce unrealistically wide ranges when founder event speciation is not considered (Matzke 2014). To the best of our knowledge, no single extant native bee species is concurrently distributed in both the Nearctic and the Middle East, rendering such an ancestral distribution unlikely. However, this exact ancestral range is frequently reconstructed when using the DEC model and biogeographic coding that assigns continental-scale areas and was also recovered as the likely ancestral range for the MRCA of *Andrena* and Andrenini (Bossert et al. 2022, Pisanty et al. 2022). Given the phylogenetically uniquely diverse *Nomada* in the Near Eastern and Eastern Mediterranean region and the position of *Acanthonomada*, we hypothesize that Nomadini originated in this region, and suggest that future research with denser taxon sampling, finer-scaled assignment of biogeographic regions, and rigorous model testing may decisively clarify the spatial origin of *Nomada* and Nomadini.

Evolution of Host Association

Given the extensive historical literature on *Nomada* from Central Europe (Smith 1855, Schmiedeknecht 1882, Alexander 1991, Smit 2018), the West Palearctic *Nomada* and their host associations are better understood than *Nomada* from other parts of the world. This renders the West Palearctic a preferred biogeographic region of study, since we can compile a comparatively dense dataset of host records. Nonetheless, our analysis found that this information is far from complete: synthesizing a thorough review of the literature with our own observations, we were able to associate host species for 107 of the 211 included West Palearctic and African species. This shows that host information is unavailable for about half of all species (= 49.3%; Fig. 3, inset). Naturally, the evidence for some host-parasite associations is less certain than for others, and alternative host records may be discovered in the future. In addition, many of the West Palearctic species that we were unable to include here tend to be rarely collected and are frequently lacking reliable host information, thus aggravating the fragmented knowledge of *Nomada* hosts. Nonetheless, this estimate compares favorably to the now 32-year-old estimate of Alexander (1991), which concluded that host information was available for less than 10% of *Nomada* species globally.

Despite these significant gaps in host records, our analysis of *Nomada* host associations uncovered broad, general patterns of host usage in the genus. Generally, *Nomada* shows strong evolutionary host constancy at a generic level [not in relation to host constancy (Habermannová et al. 2013) and flower constancy (Waser 1986) that are on the intraspecific level and mean limited switches of a single individual when searching host or flower]. Specifically, we found that switches to different host genera are relatively rare (Fig. 3, Supplementary Fig. 4). Our results unambiguously show that the most likely ancestral host of *Nomada* were bees that gave rise to present-day *Andrena*. Species of *Andrena* are by far the most widely parasitized hosts of today's West Palearctic *Andrena* (Fig. 3, inset) and globally (Alexander 1991). In addition, the reconstructed ancestral states along the entire phylogenetic backbone of *Nomada* found this lineage as the most likely ancestral host. Notably, our results provide the first comparative-phylogenetic evidence for this ancient host-parasite relationship: while close host-parasite relationships of *Nomada* and *Andrena* have been described for more than a century (Smith 1855) and *Andrena* may appear as an obvious ancestral host of *Nomada*, previous research did not corroborate this hypothesis. Based on a cladistic-morphological phylogeny of *Nomada*, Alexander (1991) mapped known host records onto his tree but found no unambiguous ancestral state. He recovered *Nomada gigas*, a South African endemic which parasitizes *Melitta*, as a sister group to the remaining *Nomada*. In turn, this phylogenetic pattern does not provide equivocal support for *Andrena* as an ancestral host. Interestingly, we found *Nomada gigas* as part of a relatively early branching clade (Figs. 1–3, Odanaka et al. 2022), a lineage that we here circumscribe as the new subgenus *Afronomada*. However, our Bayesian ancestral state reconstruction strongly supports a scenario in which the MRCA of this lineage switched from an ancestral *Andrena* host to a melittid host. As *Andrena* is presently species-poor and generally rare in sub-Saharan Africa, the MRCA of *Afronomada* may have expanded the distributional range of *Nomada* by transitioning to a locally more abundant host lineage in Africa.

Another prominent example of host switching in *Nomada* occurred in the MRCA of the *Nomada fuscicornis* group. The MRCA of this species group likely transitioned from *Andrena* to a host that gave rise to present-day *Panurgus* (Fig. 3, Supplementary Fig. 4). Consequently, all *Nomada* species of this clade for which host records are available to attack *Panurgus*, though predominantly different species. This strongly indicates that this *Nomada* clade diversified along this novel lineage of hosts. Similarly, we found 2 instances of host transitions from *Andrena* to *Lasioglossum*. Within the new subgenus *Mininomada*, we recovered a species-rich clade of *Lasioglossum* parasites, whose MRCA likely transitioned from *Andrena* to *Lasioglossum* in the mid-Miocene (Fig. 3, Supplementary Fig. 4). Like their hosts, species of this clade are comparatively small in body size. Harrison's rule (Harrison 1915), which predicts a roughly proportional body size of host and parasites, was recently shown to be valid for the subfamily Nomadinae at large (Lim et al. 2022), and *Mininomada* follows this pattern as well. In line with this, earlier branching lineages within *Mininomada* are of larger body size and are associated with *Andrena* (Smit 2018). An additional instance of parasitism of *Lasioglossum* may be restricted to the single species *Nomada bispinosa* in the subgenus *Gestamen*, and this transition could have occurred more recently (0–8 mya). However, this host association is uncertain and requires verification (Scheuchl 2000). In contrast, Lim et al.'s (2022) phylogeny suggests a very probable, independent transition to Halictidae: 2 closely related species, *Nomada aswensis* Tsuneki (1973) and *Nomada kaguya* Hirashima (1953), were reported to parasitize *Lasioglossum* and *Lipotriches* respectively (Mitai and Tadauchi 2007). Though these species were reported to be part of the *Nomada ruficornis* group (Alexander and Schwarz 1994), they obviously belong to the *N. armata* group according to phylogenetic position (Lim et al. 2022). According to morphological characters described and figured by Mitai and Tadauchi (2007), they may have a closer relationship with *N. bispinosa*. Based on this combined evidence, we assume 2 rather than 3 independent transitions to Halictidae (mainly *Lasioglossum*) hosts in the Old World, but additional transitions could be recovered with new data on host-parasite association of *Nomada* at large, especially considering the suggested association with *Halictus* reported for North American species of *N. ruficornis* group (Alexander 1991).

Interesting patterns of evolutionary host constancy can be found for the subgenus *Holonomada*, which contains all known *Eucera* parasites within *Nomada* (Fig. 3, Supplementary Fig. 4). Aside from *Afronomada*, this is the only subgenus for which we recovered an ancestral host other than *Andrena*. Within this subgenus, we recovered an early branching clade of *Melitta* parasites and a clade of *Eucera* parasites. However, a single species parasitizing *Melitta*, *Nomada gribodoi*, renders the *Melitta* parasite clades paraphyletic, thereby rendering the ancestral state reconstruction of this node unequivocal. In any case, an MRCA of the *Eucera*-parasite clade within *Holonomada* very likely transitioned from a *Melitta* host to an *Eucera* host, thereby presenting the sole recovered case of a host transition from a genus other than *Andrena*. Interestingly, *Holonomada* is a Holarctic subgenus and host associations from the Nearctic are available for both *Eucera* and *Andrena* (Alexander 1991). This underlines the association of *Holonomada* and *Eucera*, but also shows that our current picture is incomplete: future research that includes *Nomada* species and host records from across the Holarctic is needed to fully understand the host transitions in this subgenus. This would further allow to establish if North American *Holonomada* may have reversed back to *Andrena*, and to confidently identify the likely ancestral host of the MRCA of this subgenus.

Additional taxonomic sampling from the Nearctic is also necessary to establish the early host associations of the subgenus *Hypochrotaenia*. Like *Holonomada*, this subgenus is widely distributed in the Old and New World, yet our sampling does not incorporate sufficient host records from the Nearctic. One species of *Hypochrotaenia*, *N. articulata*, is well-established as a parasite of the halictid genus *Agapostemon* (Eickwort 1980). Species of the *Nomada modesta* group, which have previously been included in a *Hypochrotaenia* genus concept (Snelling 1986), have been recorded as parasites of distantly related lineages including the New World genus *Exomalopsis* (Raw 1977, Parker 1984, Rozen and Snelling 1986) and *Nomia* (Rozen 1966, Bohart 1970). The inclusion of these *Nomada* in an expanded phylogeny, as well as adding more host associations from the Holarctic, is needed to better understand the host evolution in this subgenus.

In conclusion, the present study represents significant progress towards a comprehensive understanding of host-parasite evolution in *Nomada*. We integrated robust phylogenomic estimates with carefully reviewed literature on *Nomada* hosts from the West Palearctic and uncovered clear phylogenetic patterns within the genus. Nonetheless, our knowledge gaps of reliably identified host-parasite associations remain significant and hamper our ability to characterize the host usage for many lineages of *Nomada*. Even after hundreds of years of study, fieldwork and observations of *Nomada in situ* remain key to understanding their intriguing natural history.

Supplementary material

Supplementary material is available at *Insect Systematics and Diversity* online.

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Author contributions

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Data availability

Supporting data, which were generated over the course of this study (DNA alignments, tree files, and various input files for analyses), was deposited in the Dryad Digital Repository (doi: 10.5061/dryad.51c59zwdq). Unassembled DNA sequence data are available at NCBI under BioProject ID PRJNA846559.

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