JHR 89: 183–210 (2022)
doi: 10.3897/jhr.89.72083
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

An unexpected new genus of panurgine bees (Hymenoptera, Andrenidae) from Europe discovered after phylogenomic analysis

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Academic editor: Michael Ohl | Received 24 July 2021 | Accepted 19 January 2022 | Published 28 February 2022

http://zoobank.org/EBFE14E0-B8CF-40DB-A143-9595D77F1D8C

Citation: Wood TJ, Patiny S, Bossert S (2022) An unexpected new genus of panurgine bees (Hymenoptera, Andrenidae) from Europe discovered after phylogenomic analysis. Journal of Hymenoptera Research 89: 183–210. https://doi.org/10.3897/jhr.89.72083

Abstract

Establishing a higher classification of bees based on morphology alone can fail to capture evolutionary relationships when morphological characters either vary very little between distantly related groups, or conversely vary greatly between closely related species. This problem is well represented in the subfamily Panurginae, for which a recent global revision based on phylogenomic data unexpectedly revealed that two Old World species previously placed in *Camptopoeum* Spinola and *Flavipanurgus* Warncke, are in fact most closely related to each other, and together form a sister group relationship to the remaining *Flavipanurgus* and *Panurgus* Panzer combined. To rectify this situation, we here establish an expanded phylogenomic data set of Old World Panurgini and re-assess generic and subgeneric concepts for the tribe. To solve the paraphyly of *Camptopoeum* and *Flavipanurgus*, we establish the new genus *Halopanurgus* **gen. nov.** containing the species *H. baldocki* (Wood & Cross), **comb. nov.** and *H. fuzetus* (Patiny), **comb. nov.**, both of which are restricted to coastal sands, saltmarshes, and inland saline lagoons in the extreme south of Portugal and south-west of Spain. Re-evaluation of four recently used subgenera in *Panurgus* strongly supports a simplified classification of two subgenera; *Pachycephalopanurgus* Patiny, **stat. rev.** including *Micropanurgus* Patiny **syn. nov.**, and *Panurgus* s. str. including *Euryvalvus* Patiny. *Pachycephalopanurgus* species seem to be oligoleges of Asteroideae (Asteraceae), whereas *Panurgus* s. str. may be oligoleges of Cichorieae (Asteraceae). Our findings reinforce the challenges of establishing a phylogenetically sound classification of Panurginae using morphology alone and illustrate that even in well-studied regions like Europe unrecognised genera can persist in underexplored corners of the continent.

Keywords
Asteraceae, halophile, Iberian endemic species, solitary bees, taxonomy

Introduction

The bee fauna of Europe boasts the longest history of study, and as such has a relatively stable system of taxonomic classification. Depending on taxonomic interpretation, 73 bee genera are known from Europe (Rasmont et al. 2017) when taking a broad approach to *Eucera* (including *Cubitalia*, *Synhalonia*, *Tetralonia*, and *Tetraloniella*; Dorchin et al. 2018) and considering *Halictus* to consist of *Halictus* s. str. and its sister group *Seladonia*, the latter including *Vestitohalictus* (Danforth et al. 1999). As a measure of this stability, only six valid genera have been described for the European bee fauna since 1955, specifically the species-poor lineages *Clavipanurgus*, *Flavipanurgus*, and *Simpanurgus* (Warncke 1972), *Hofferia* and *Stenoheriades* (Tkalců 1984), and *Chiasmognathus* (Engel 2006) (Fig. 1). In contrast, some 20 genera have been described for the broader West Palaearctic region during this time.

Key to maintaining stable bee genera for the future is the use of large-scale molecular revisions to re-evaluate lineages where generic boundaries are ambiguous due to morphological intergradation (Dorchin et al. 2018), or conversely where a great deal of morphological variation has led to a proliferation of described genera that are paraphyletic (Litman et al. 2016). Integrating phylogenomic datasets with traditional morphological study allows the reciprocal illumination of morphological features in light of molecular evidence, and greatly facilitates the systematic identification of synapomorphies and homologous characters for diagnostic purposes (Bossert et al. 2020). The classification of the Panurginae presents aspects of these problems, and delineating the phylogenetic relationships between the different genera has proved challenging for several decades. This has led to numerous tribal classification schemes, as well as disagreement as to what constitutes a genus in some cases (Patiny 2001; Ascher 2004; Engel 2005; Michener 2007; Ascher and Engel 2017). For example, Engel (2005) places the Melitturgini sensu Patiny (1999a) within the Panurgini and distinct from the Meliturgulini, whereas Michener (2007) places both together in Melitturgini, and Michener (2007) takes a broad approach to *Panurgus*, including both *Flavipanurgus* and *Simpanurgus* as subgenera. Treatment of the tribe Panurgini has been particularly problematic, with some interpretations including a limited number of Old World taxa (Patiny 2001), or conversely including all Old World and even some New World taxa (Ascher 2004).

The lack of resolution from morphological analyses has recently been addressed through a phylogenomic approach using Ultraconserved Elements (UCEs; Bossert et al. 2022). An important finding of that study is that the Old World Panurginae are not a monophyletic group. The tribe Melitturgini, comprising only *Camptopoeum* and *Melitturga*, is well-separated from all other Old World genera which can be placed in

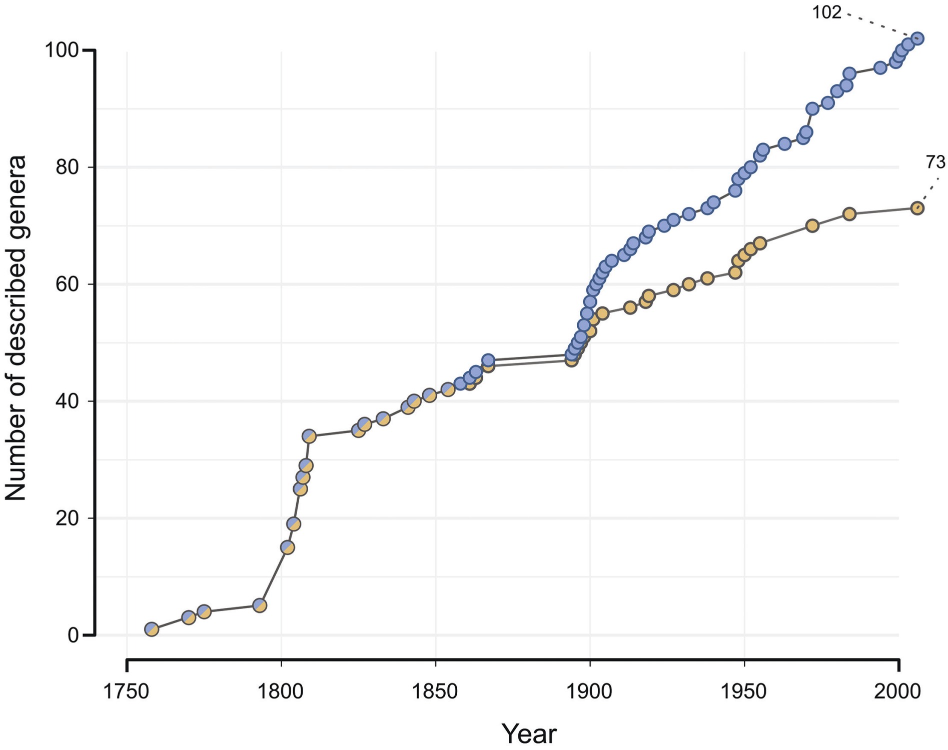


Figure 1. Cumulative number of valid bee genera by year of description for Europe (as defined by Rasmont et al. 2017) (yellow dots) and the wider West Palaearctic region (blue dots). The recognition of genera follows Rasmont et al. (2017) with modifications as defined in the introduction.

a single large tribe, the Panurgini. Sister group to the Panurgini is the endemic North American lineage Perditini, and both these lineages are sister group to Melitturgini: Melitturgini + (Perditini + Panurgini). The Melitturgini likely diverged from the lineage that gave rise to the present-day Panurgini and Perditini 46.1 million years ago (95% highest posterior density 36.8-56.1 mya, Bossert et al. 2022), shortly after their most recent common ancestor (MRCA) colonised the Palaearctic. Both Panurgini and Perditini descend from this MRCA, indicating that Panurginae only geodispersed to the Old World a single time (Bossert et al. 2022). Another surprising finding is that one species described as *Camptopoeum* (*Camptopoeum*) *baldocki* Wood & Cross, 2017 on the basis of its seemingly distinctively long glossa (Wood and Cross 2017, the glossa itself being elongate, not possessing the elongate labial palp morphology used in the division between long-tongued and short-tongued bees, see Michener (2007)) is not actually part of the lineage forming *Camptopeum* and *Melitturga* (the Melitturgini), but instead is more closely related to the genera *Flavipanurgus* and *Panurgus*. Specifically, this species forms a sister group relationship with *Flavipanurgus fuzetus* Patiny, 1999, which has a short glossa consistent with other members of this genus (Patiny 1999b), but its placement together with *C. baldocki* renders *Flavipanurgus* paraphyletic.

Given this paraphyly, the main objectives of the current work are therefore to reassess the diagnosability of *Flavipanurgus* and *Panurgus*, re-evaluate the current usage of subgenera for *Panurgus*, and identify morphological criteria to allow for recognition of these different lineages. Considering morphological, molecular, and ecological aspects, we describe the new genus *Halopanurgus* gen. nov. to ensure that all genera are strictly monophyletic. We also take the opportunity to discuss the relationships between the different West Mediterranean genera of Panurgini, as this region is clearly a particular centre of their Old World diversity, and lastly we propose a simplified subgeneric classification for the genus *Panurgus*.

Methodology

Molecular methods

To better understand the phylogenetic relationships of *Panurgus* and its currently used subgenera, as well as of *Flavipanurgus*, and *Halopanurgus* gen. nov., we assembled a taxon-dense sampling of Old World Panurginae. We obtained DNA sequence data from a recently published phylogeny of Andrenidae (Bossert et al. 2022) and enriched these data with additional samples for our group of interest. Specifically, we included all *Panurgus*, *Flavipanurgus* and "*Camptopoeum baldocki*" from Bossert et al. (2022), as well as three representatives for both of the closely related tribes Melitturgini and Perditini. Additionally, we included one representative for each of the three clades of Panurgini outside of our group of interest that were identified in Bossert et al. (2022), and chose *Neffapis longilingua* as our most distant outgroup. We combined this publicly available UCE sequence data with nine newly analysed samples for *Panurgus* and *Flavipanurgus*. We generated new sequence data for eight species of *Panurgus*, including four new samples of the previously underrepresented subgenus *Pachycephalopanurgus*. This ensures the representation of six out of seven described species of this subgenus sensu Patiny (1999c), both known species of the subgenus *Euryvalvus*, one of the three species of the subgenus *Micropanurgus* sensu Patiny (2002), and 10 out of the 22 species of *Panurgus* s. str. Lastly, we included UCE sequence data of *Flavipanurgus venustus* (Erichson, 1835), ensuring representation of five out of the seven currently recognised species of *Flavipanurgus*. Our taxon sampling totals 35 species. NCBI SRA accession numbers, collection localities and voucher depositories can be found in Table 1.

The molecular lab procedures for UCE sequencing of the nine newly analysed samples are detailed in Bossert et al. (2022), including library preparation, enrichment, and sequencing, since the newly presented data was generated jointly with this previous dataset. All newly analysed samples were enriched with the enhanced principal Hymenoptera bait set (Branstetter et al. 2017). Bioinformatic processing of these data follows the workflow detailed in Bossert et al. (2022), including the same programs and parameters for demultiplexing and sequence assembly (using SPAdes v. 3.13; Bankevich et al. 2012). After combining the new sequence data with the previously

Table 1. The scientific names of the included species with their collection localities and voucher depositories. NCBI SRA IDs marked with an asterisk (*) indicate samples that are newly published. Most voucher specimens are labelled with a green coloured label which carries the voucher code. UCE assemblies of the newly generated sequence are available on the FighShare repository associated with this article (10.6084/m9.figshare.15033552). Acronyms for the collection depositories: Cornell Univ. Insect Collection (CUIC); Collection Silas Bossert (CSB); University of Mons-Hainaut, Mons, Belgium (UMH); Collection Thomas Wood, Mons, Belgium (CTW).

Taxon	Locality	Voucher depository	Collector / Identifier	Voucher Code	SRA
Camptopoeum (*Camptopoeum*) *frontale*	Turkey: Agr I, Gögoglu	UMH	P. Rasmont / D. Michez	BND-1981	SRR16232743
Camptopoeum (*Camptopoeum*) *negevense*	Israel: S Negev, 13 km N Shizzafon Jct.	n/a	from Ascher (2004)	Camp 41	SRR16232742
Clavipanurgus desertus	Morocco: S. Anezal	CSB	Michez & Patiny / Michez & Patiny	BND-1982	SRR16232741
Flavipanurgus flavus	Portugal: Algarve, Aljezur	CTW	T. J. Wood / T. J. Wood	BND-2119	SRR16232720
Flavipanurgus ibericus	Portugal: Alentejo, Mértola	CSB	I. C. Cross / T. J. Wood	BND-2117	SRR16232718
Flavipanurgus kastiliensis	Portugal: Pardelhas, Vila Real	CTW	T. J. Wood / T. J. Wood	BND-2118	SRR16232717
Flavipanurgus venustus	Spain: Doñana	UMH	F.P. Molina / D. Michez	BND-1926	SRR17049175
Halopanurgus baldocki	Portugal: Algarve, Cacela Velha	CSB	T. J. Wood / T. J. Wood	BND-1923	SRR16232744
Halopanurgus fuzetus	Portugal: Algarve, Cacela Velha	CTW	T. J. Wood / T. J. Wood	BND-2120	SRR16232719
Macrotera (*Macroterella*) *mortuaria*	USA: NV, Clark Co., Sacatone Wash	BBSL	T. Griswold / T. Griswold	BND-2005	SRR16232673
Melitturga (*Melitturga*) *clavicornis*	France: Hérault, Causse de la Selle	n/a	from Ascher (2004)	Mecl 73	SRR16232665
Meliturgula (*Meliturgula*) *scriptifrons*	South Africa: Limpopo, 77 km S Ellisras	CUIC	B.N.D. / B.N.D. #CUIC code: 04-22	BND-1037	SRR16232644
Neffapis longilingua	Chile: Coquimbo Region, Vicuña	RPSP	L.Packer / L. Packer	BBX-694	SRR16232638
Panurgus (*Pachycephalopanurgus*) *acutus*	Morocco/SW: 15 km NE Agadir	CSB	C. Schmid-Egger / S. Patiny	BND-1952	SRR16232763
Panurgus (*Pachycephalopanurgus*) *calceatus*	Morocco: Errachidia-Erfoud	UMH	Michez & Patiny / Michez & Patiny	BND-1931	SRR17049183
Panurgus (*Pachycephalopanurgus*) *canescens*	Spain: Sierra Nevada	UMH	J. Ortiz-Sánchez / S. Patiny	BND-1932	SSR17049182
Panurgus (*Pachycephalopanurgus*) *convergens*	Morocco: Anezal	UMH	Michez & Patiny / Michez & Patiny	BND-1933	SSR17049181
Panurgus (*Pachycephalopanurgus*) *farinosus*	Morocco: Marrakech	UMH	Michez & Patiny / Michez & Patiny	BND-1936	SSR17049180
Panurgus (*Pachycephalopanurgus*) *nigriscopus*	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1938	SRR16232758
Panurgus (*Pachycephalopanurgus*) *rungsii*	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1943	SRR16232737
Panurgus (*Panurgus*) *avarus*	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1929	SRR16232762
Panurgus (*Panurgus*) *banksianus*	France: Pyrénées-Or. Eyne, cabane météo	UMH	D. Michez / D. Michez	BND-1930	SRR16232761
Panurgus (*Panurgus*) *calcaratus*	Spain: Province of Almería	UMH	J. Ortiz-Sánchez / S. Patiny	BND-514	SSR17049179

Taxon	Locality	Voucher depository	Collector / Identifier	Voucher Code	SRA
Panurgus (*Panurgus*) *cephalotes*	Portugal: Trás-os-montes, Espinhosela	CTW	T. J. Wood / T. J. Wood	BND-1985	SSR17049178
Panurgus (*Panurgus*) *dentatus*	Morocco: Drâa-Tafilalet, Imider	UMH	Michez & Patiny / Michez & Patiny	BND-1934	SSR17049177
Panurgus (*Panurgus*) *dentipes*	France: Marseilles, Campus Luminy	UMH	D. Michez / D. Michez	BND-1935	SRR16232760
Panurgus (*Panurgus*) *maroccanus*	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1937	SRR16232759
Panurgus (*Panurgus*) *niloticus*	Morocco: Drâa-Tafilalet, Ouarzazate	UMH	Michez & Patiny / Michez & Patiny	BND-1939	SRR16232757
Panurgus (*Panurgus*) *perezi*	Portugal: Trás-os-montes, Vila Real	CTW	T. J. Wood / T. J. Wood	BND-1940	SSR17049176
Panurgus (*Panurgus*) *pici*	Morocco: Drâa-Tafilalet, Ouarzazate	UMH	Michez & Patiny / Michez & Patiny	BND-1941	SRR16232740
Panurgus (*Panurgus*) *pyropygus*	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1942	SRR16232738
Panurgus (*Panurgus*) *siculus*	Malta: Southeastern District, Għaxaq	UMH	Michez & Balzan / D. Michez	BND-1944	SRR16232736
Perdita (Hesperoperdita) trisignata	USA: California	n/a	from Ascher (2004)	PeHe 77	SRR16232659
Perdita (Pygoperdita) californica	USA: CA, Contra Costa Co., Donner Cyn.	n/a	B. Danforth / n. a.	BND-518	SRR16232713
Plesiopanurgus (Zizopanurgus) zizus	Morocco: Drâa-Tafilalet, Ouarzazate	CSB	Michez & Patiny / Michez & Patiny	BND-1945	SRR16232657

published assemblies, we used the Phyluce pipeline (v. 1.7.1; Faircloth 2016) to search the assemblies for UCE sequences (with min-coverage and min-identity parameters of 80), aligned the data with MAFFT and the L-INS-i mode (v. 7.130b; Katoh and Standley 2013), and trimmed the alignments with Gblocks (Castresana 2000) and adjusted parameters (– b1 0.5, – b2 0.5625, – b3 10, – b4 5). We additionally processed the alignments with Spruceup (Borowiec 2019) and generated a concatenated sequence matrix of 80%, meaning that every individual UCE locus is represented by at least 28 taxa.

We estimated phylogenetic relationships with the maximum likelihood implementation IQ-Tree (v. 2.1.3; Minh et al. 2020). Substitution models were assigned after combining partitions of similar substitution patterns using the greedy search strategy (Lanfear et al. 2012). To ease the computational burden, we used the relaxed hierarchical clustering method (Lanfear et al. 2014) at 50% (– rcluster 50). Model selection was carried out with Modelfinder (Kalyaanamoorthy et al. 2017) and support was assessed with 1,000 ultrafast bootstrap approximations (UFBoot2; Hoang et al. 2018).

Newly generated SPAdes assemblies, the concatenated alignment, tree files, and the input files used to generate the phylogeny are deposited in a FigShare online repository associated with this article (10.6084/m9.figshare.15033552). Unprocessed Illumina sequence reads generated for this study are deposited in the NCBI Sequence Read Archive (SRA) under BioProject PRJNA783908 or under the individual identifiers listed in Table 1.

Pollen analysis

Pollen was removed from *Panurgus* species whose pollen preferences have not previously been quantified to assess their pollen preferences following the methodology of Wood & Roberts (2018). The size of pollen loads on individual bees was estimated, ranging from a full load to a one-eighth load. Pollen grains were removed from the scopa using an entomological pin and transferred to a drop of water on a microscope slide. Grains were left to absorb water for a few minutes and then the slides were gently heated to allow evaporation. Molten glycerine jelly stained with fuchsin was added, and the slide was sealed with a coverslip. The percentage of the load composed of different plant taxa was estimated along three randomly selected lines across the cover slip at a magnification of ×400. The percentage of the load was estimated by the relative area of the slide occupied by each plant species, rather than the absolute number of grains. Pollen species representing < 2% of the load were excluded from further analysis because their presence might have arisen from contamination. The percentages of pollen collected were multiplied by the overall size of each load to give a final weighting i.e., a taxon comprising 50% of a ¾ full pollen load would receive a weight of 37.5, whereas a taxon with 100% of a full (1/1) pollen load would receive a weight of 100.0. Pollen loads were identified to the lowest taxonomic level possible using a reference collection assembled during the project, in most cases to subfamily. Host range (dietary specialisation) was characterised following the criteria of Müller and Kuhlmann (2008).

Terminology and imaging

Morphological terminology follows Michener (2007). Michener (2007) was also used as the baseline for taxonomic changes to the subgeneric classification of *Panurgus*, and generic and subgeneric synonymy was adapted from this work. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Close-ups were taken with the addition of a Mitutoyo M Plan Apo 10× infinity corrected objective lens in combination with an Olympus M.Zuiko 2× teleconverter lens, a 10 mm Kenko DG extension tube, and a Meike MK-P-AF3B 10 mm extension tube. Photographs were stacked using Zerene Stacker 1.04 (Zerene Systems, USA) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) to improve lighting to highlight specific characters.

Results

Molecular phylogeny

Combining the newly presented UCE sequences of *Panurgus* with previously published data led to a concatenated sequence alignment of 1,289,627 DNA nucleotides and 35 species. The maximum likelihood analysis with IQ-Tree produced a highly supported phylogeny that resolves the phylogenetic relationships among the examined genera and specifically of the subgenera of *Panurgus* (Fig. 2). Only the single node involving *Panurgus dentatus* Friese, 1901, *P. pici* Pérez, 1895, *P. avarus* Warncke, 1972, and *P. niloticus* Warncke, 1972 received a comparatively low bootstrap value of 53. This means that while this particular placement should be interpreted cautiously, the remaining phylogenetic relationships were resolved with high confidence. The phylogeny is congruent with the previous ML and Bayesian phylogenies of Panurgini in Bossert et al. (2022): even though the present tree includes an additional eight taxa of *Panurgus*, it is otherwise topologically identical to these previous estimates. While similar phylogenies can be expected given the shared data between these two studies, the present nucleotide matrix is nearly twice as long as the more strictly trimmed alignment of Bossert et al. (2022; 595,217 nucleotides).

Our phylogeny shows that *Flavipanurgus* in its previous sense, i.e., including "*Flavipanurgus*" *fuzetus*, is not a monophyletic group (Fig. 2). This species is not more closely related to the remaining *Flavipanurgus* than to *Panurgus*. Instead, it forms a sister group relationship with "*Camptopoeum*" *baldocki*, a lineage previously thought to be part of the genus *Camptopoeum* (Wood and Cross 2017). Recent phylogenomic analyses of the higher-level relationships of Panurginae found *Camptopoeum* to be most closely related to *Melitturga*, and hence not part of the clade investigated in the present study (Bossert et al. 2022). This means that "*Camptopoeum*" *baldocki* renders *Camptopoeum* paraphyletic, requiring taxonomic change. To rectify the paraphyly of both *Camptopoeum* and *Flavipanurgus*, we establish the new genus *Halopanurgus* gen. nov. that unites both "*Flavipanurgus*" *fuzetus* and "*Camptopoeum*" *baldocki* into one genus and ensures monophyly of both *Flavipanurgus* and *Camptopoeum*.

The presented molecular-phylogenetic relationships allow us to illuminate the subgeneric concepts of *Panurgus* with the four subgenera *Euryvalvus*, *Micropanurgus*, *Panurgus*, and *Pachycephalopanurgus* as established by Patiny (1999c). We found the subgenus *Euryvalvus* with its two species *P. banksianus* and *P. pyropygus* to be nested within the largest subgenus *Panurgus* s. str., and the included representative of the morphologically derived *Micropanurgus* renders *Pachycephalopanurgus* paraphyletic. Re-evaluating the morphological characters of these lineages in light of phylogeny, particularly of the highly informative male genitalia, we found that a simplified classification of *Panurgus* with an expanded *Panurgus* s. str. (including *Euryvalvus*) and *Pachycephalopanurgus* (including *Micropanurgus*) is most appropriate (1) to maintain readily diagnosable subgenera, (2) to ensure monophyletic groupings, and (3) to reflect the antiquity of the respective lineages. The taxonomic changes are formalised below.

Taxonomy

Tribe Panurgini Leach, 1815

Halopanurgus Wood, Patiny & Bossert, gen. nov.

http://zoobank.org/D0AEA39D-BF99-406A-A439-38721C79E825

Type species. *Camptopoeum baldocki* Wood & Cross, 2017

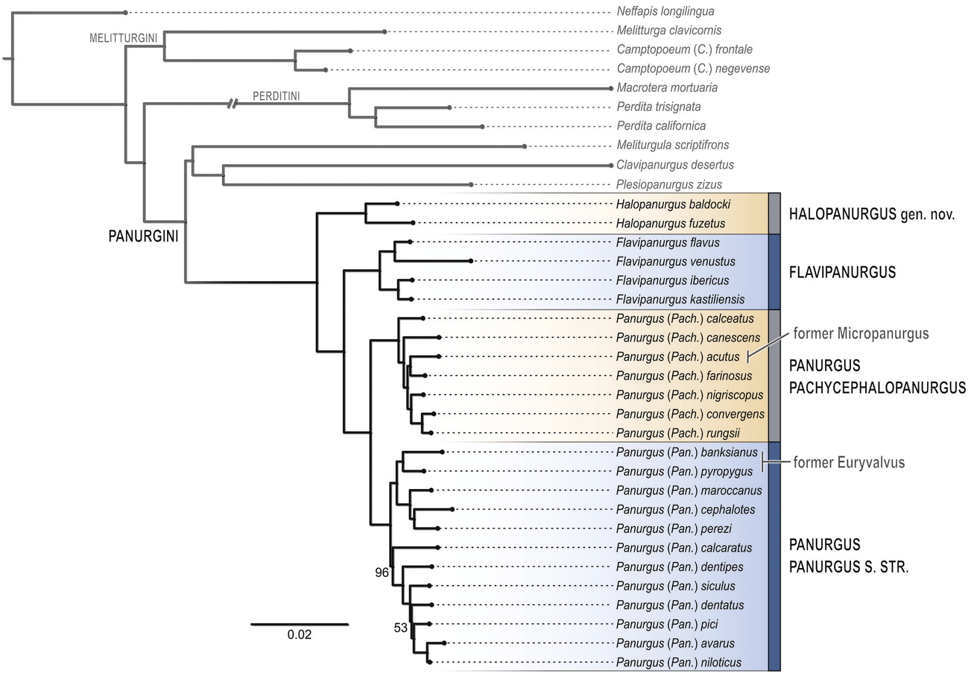


Figure 2. Maximum Likelihood phylogeny of *Panurgus*, *Flavipanurgus*, and the newly described genus *Halopanurgus* gen. nov., based on 2,055 ultraconserved elements. Taxonomic names reflect the nomenclatural changes proposed in this study. Node support corresponds to 100 ultrafast bootstrap support values unless indicated otherwise.

Diagnosis. *Halopanurgus* can be recognised as a panurgine because of its black body with yellow maculations on the head, mesosoma, and metasoma, its small size (4–5 mm), its two submarginal cells, apically truncate marginal cell, poorly developed femoral scopa, two subantennal sutures, and weak facial fovea, these shining, hairless. It is best diagnosed with reference to other similar small, yellow-marked genera with two submarginal cells, as broad characters like those used for tribal classification by Michener (2007) are not universally applicable and are not supported by the new phylogeny (Bossert et al. 2022).

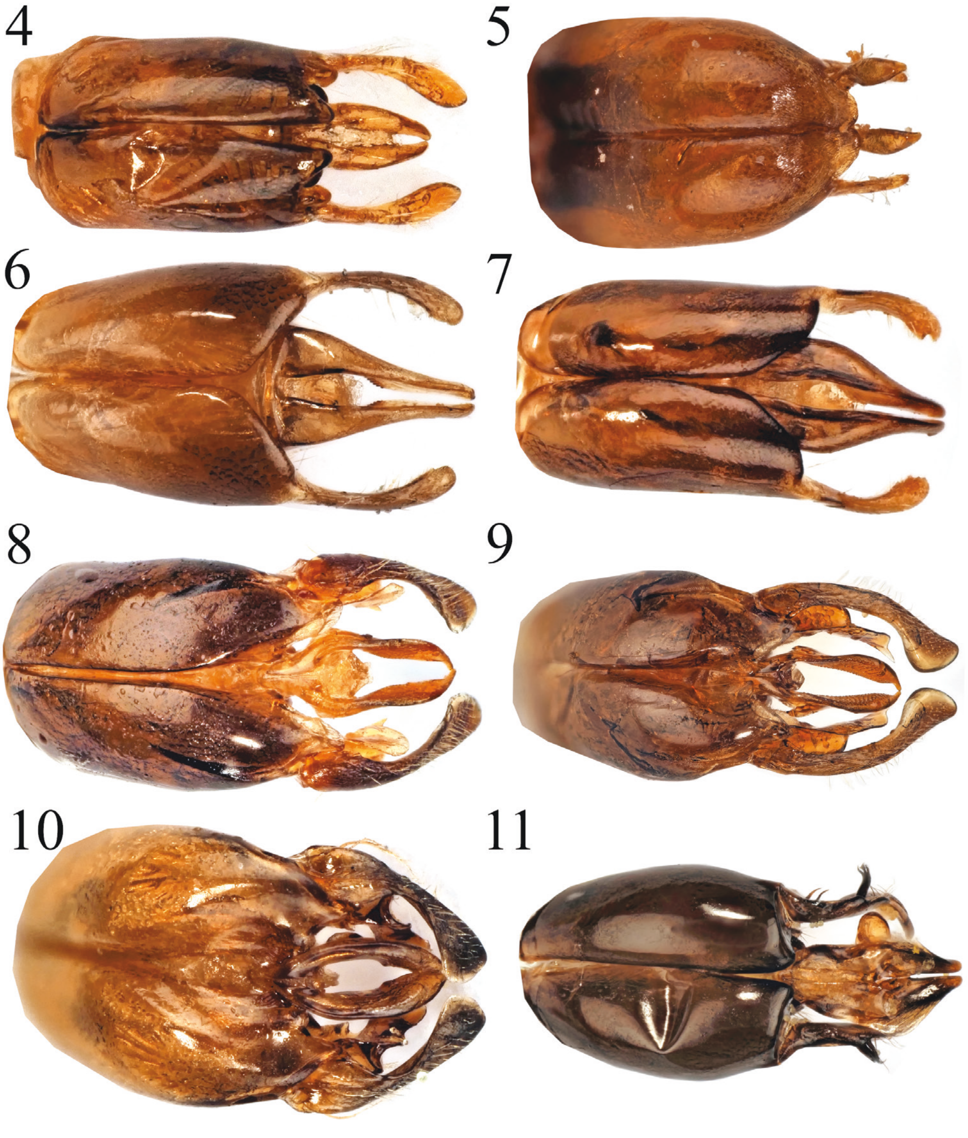
Halopanurgus can be confused with *Camptopoeum* because of the similar structure of the male S7 and genital capsule. *Camptopoeum* has S7 as broad as long or slightly longer than broad, almost parallel sided, and with a broad apical notch (Fig. 14), and the genital capsule is parallel sided, with simple gonostyli and penis valves (Figs 6–7). In *Halopanurgus* S7 is broader, but still apically notched (Fig. 12) and the gonocoxae are produced into strong triangular points apically (Figs 3–4). In *Camptopoeum* no such points are present; the inner margin of the gonocoxae is clearly smooth and inwardly curved (in both subgenera *Camptopoeum* s. str. and *Epimethea*, Figs 6–7).

Separation from *Flavipanurgus* is simple in the male sex, as *Flavipanurgus* has S7 clearly broader than long, and deeply excavated apicomedially (Figs 15–16). The genital capsule is also different with the gonocoxae lacking apical points and the gonostyli

Figure 3. Male genital capsule of *Halopanurgus baldocki*, with arrow indicating the apical part of the gonocoxa which is produced into a strong triangular point.

are flattened, apically widened, and spatulate (Figs 8–10, 31–32). In the female sex, separation is easy for *H. baldocki* because of its very long glossa (clearly longer than the length of the face, Figs 29–29, the first segment of the labial palpus exceeding the length of segments 2–4 together), but in *H. fuzetus* the length of the glossa cannot be used as the glossa is very short (clearly shorter than the length of the face, Fig. 22), with the first labial palpus not exceeding the length of segments 2–4 together. Instead, the puncturing of the face must be used, with punctures fine and weak in *Halopanurgus*, subtle, not strongly contrasting with the underlying integument. In *Flavipanurgus*, the face is strongly and clearly punctate, punctures clearly visible against the integument. This difference is most clearly seen on the frons (compare Figs 22–23).

Halopanurgus can be rapidly separated from *Simpanurgus* because it lacks distinctively flattened fore tarsi and clavate antennae (Figs 26–27), and from *Avpanurgus* because of its 'Y' shaped S7 (Fig. 13) and the genital capsule is very different, lacking the greatly expanded gonocoxae that cover almost the entire dorsal surface (Fig. 5). Note, both *Simpanurgus* and *Avpanurgus* are known only from the male sex, so diagnosis in females is not currently possible. As no genetic sequences are available for *Simpanurgus* or *Avpanurgus* their broader placement is uncertain. As *Simpanurgus* may be more closely related to *Flavipanurgus* than to *Halopanurgus*, description of the latter at a subgeneric



Figures 4–11. Panurgine male genitalia **4** *Halopanurgus baldocki* **5** *Avpanurgus flavofasciatus* **6** *Camptopoeum* (*Camptopoeum*) *frontale* **7** *Camptopoeum* (*Epimethea*) *variegatum* **8** *Flavipanurgus flavus* **9** *Flavipanurgus venustus* **10** *Flavipanurgus kastiliensis* **11** *Panurgus* (*Panurgus*) *calcaratus*.

level would necessitate taking a firm position on all these genera. Given this uncertainty, *Halopanurgus* is described as a genus; future studies may revise the status of these genera when suitable evidence becomes available. Lastly, *Halopanurgus* can be separated from *Panurgus* by the presence of yellow markings on the body; these are never present in *Panurgus*. Moreover, the scopae of *Halopanurgus* species are composed of simple hairs, lacking the branched hairs which are conspicuously present in *Panurgus* species.

Description. Small (4–5 mm) black bees with extensive yellow maculations on head, mesosoma, and metasoma; pronotal lobe, metanotum, and at least some parts of terga always yellow marked, otherwise variable. Male with at least clypeus always yellow, centrally with two small black maculations (Fig. 20). Head broader than long, compound eyes with inner margins parallel. Subantennal sutures essentially straight, outer suture only weakly arched outwards. Facial fovea narrow, slightly narrower than width of lateral ocellus, hairless, equalling length of scape. Ocelloccipital distance short, subequal to width of lateral ocellus.

Face with fine and weak punctures, not strongly contrasting underlying integument (Figs 20, 22). Process of labrum square, as long as wide. Mesoscutum with scattered, fine, and short white hairs; mesepisternum and propodeum with slightly longer white hairs, equally scattered and fine. Forewing with stigma longer than wide, not parallel sided, inner margin weakly curved; two submarginal cells, first submarginal cell longer than second; first recurrent vein entering second submarginal cell; marginal cell apically truncate. Hind tibial spurs unmodified, straight. Basitibial plate present, oval, margins slightly raised; tibial scopa with simple hairs. Tarsal claws with minute inner tooth. Genital capsule simple, gonocoxae apically produced into posteriorly projecting points (Figs 3–4, see also illustrations in Wood and Cross 2017).

Etymology. The name is a combination of the prefix *Halo-* (Greek for salt) with the genus name *Panurgus* because of the pronounced affinity for saline soils shown by the two constituent species, both being restricted to saltmarshes, coastal sands, and inland saline lagoons (Wood & Cross 2017; Cross & Wood 2018; Fidalgo 2021; TJW unpublished data). The gender is masculine.

Included species. *Halopanurgus baldocki* (Wood and Cross, 2017) comb. nov. (Figs 28–29, Spain and Portugal, see Fidalgo 2021) and *Halopanurgus fuzetus* (Patiny, 1999) comb. nov. (Fig. 30, Spain and Portugal).

Flavipanurgus Warncke, 1972

Flavipanurgus Warncke, 1972: 69. Type species: *Panurgus flavus* Friese, 1897

Remarks. No genetic samples were available for *F. granadensis* (Warncke, 1987) or *F. merceti* (Vachal, 1910). However, examination of males of these two species shows that they clearly belong in *Flavipanurgus*: S7 is deeply excavated apicomedially, and the genital capsule has the gonocoxae lacking apical points along with flattened and apically spatulate gonostyli (Figs 31–32).

Included species. Six species, *Flavipanurgus flavus* (Friese, 1897), *Flavipanurgus granadensis* (Warncke, 1987), *Flavipanurgus ibericus* (Warncke, 1972), *Flavipanurgus kastiliensis* (Warncke, 1987), *Flavipanurgus merceti* (Vachal, 1910), and *Flavipanurgus venustus* (Erichson, 1835).

Figures 12–19. Panurgine male sternum seven **12** *Halopanurgus baldocki* **13** *Avpanurgus flavofasciatus* **14** *Camptopoeum* (*Epimethea*) *variegatum* **15** *Flavipanurgus flavus* **16** *Flavipanurgus kastiliensis* **17** *Panurgus* (*Panurgus*) *calcaratus* **18** *Panurgus* (*Panurgus*) *dentipes* **19** *Panurgus* (*Pachycephalopanurgus*) *farinosus*.

Panurgus Panzer, 1806

Panurgus subgenus *Panurgus* s. str. Panzer, 1806

Panurgus Panzer, 1806: 209. Type species: *Andrena lobata* Panzer, 1799 = *Apis calcarata* Scopoli, 1763

Eriops Klug, 1807: 207, 227. Type species: *Andrena lobata* Panzer, 1799 = *Apis calcarata* Scopoli, 1763, monobasic.

Eryops Latreille, 1811: 716, unjustified emendation of *Eriops* Klug, 1807

Panurgus (*Euryvalvus*) Patiny, 1999c: 316. Type species: *Apis banksiana* Kirby, 1802, by original designation.

Diagnosis. The subgenus can be separated from *Pachycephalopanurgus* by the shape of the male S7 which is always broad, approximately as long as wide, and never strongly apicomedially excavated (Figs 17–18, 45–46). There may be very weak excavations, emarginations, or convexities in the apical margin (e.g. Fig. 45), but the lateral corners are never extended into long, apically produced projections (contrast Figs 19, 47–48). Genital capsule usually with gonostyli robust with strong lateral tuft of clumped hairs that diverges laterally at the midpoint of each gonostylus (Figs 11, 33–36). However, in the former group *Euryvalvus* the genital capsule is strongly divergent, lacking robust gonostyli with a strong lateral hair tuft (Figs 37–38). These can be recognised by their black, pill-like volsellae which are visible dorsally, their gonostyli which are flattened in the vertical plane, and by their S7, which as in other *Panurgus* s. str. is broad and lacks long, apically produced and extended projections (Fig. 46). Female *Panurgus* s. str. specimens cannot be consistently separated from those of *Pachycephalopanurgus*.

Included species. All *Panurgus* species previously placed in *Panurgus* s. str. and *Euryvalvus* (Patiny 1999c) and subsequent works; the 24 species are detailed in Table 2.

Panurgus subgenus *Pachycephalopanurgus* Patiny, 1999, stat. rev.

Panurgus (*Pachycephalopanurgus*) Patiny, 1999c: 316. Type species: *Panurgus rungsii* Benoist, 1937, by original designation.

Panurgus (*Stenostylus*) Patiny, 1999c: 317. [not *Stenostylus* Pilsbury, 1898]. Type species: *Panurgus ovatulus* Warncke, 1972, by original designation syn. nov.

Panurgus (*Micropanurgus*) Patiny, in Ascher and Patiny 2002: 140. Replacement name for *Stenostylus* Patiny. Type species: *Panurgus ovatulus* Warncke, 1972, autobasic and by original designation syn. nov.

Diagnosis. The subgenus can be separated from *Panurgus* s. str. by the shape of the male S7 which has the lateral corners strongly produced into long, apical projections, these bearing a short tuft of hairs laterally (Figs 19, 47–48). S7 therefore appears to be deeply excavated. Genital capsule with gonostyli slender, the majority of species (7 out

Figures 20–27. Panurgine faces **20** *Halopanurgus baldocki* comb. nov. male **21** *Avpanurgus flavofasciatus* male **22** *Halopanurgus fuzetus* comb. nov. female **23** *Flavipanurgus granadensis* female **24** *Flavipanurgus kastiliensis* male **25** *Simpanurgus phyllopodus* male, including **26** male antennae and **27** male fore tarsi.

Table 2. Revised subgeneric classification system for the genus *Panurgus*, with all globally known species.

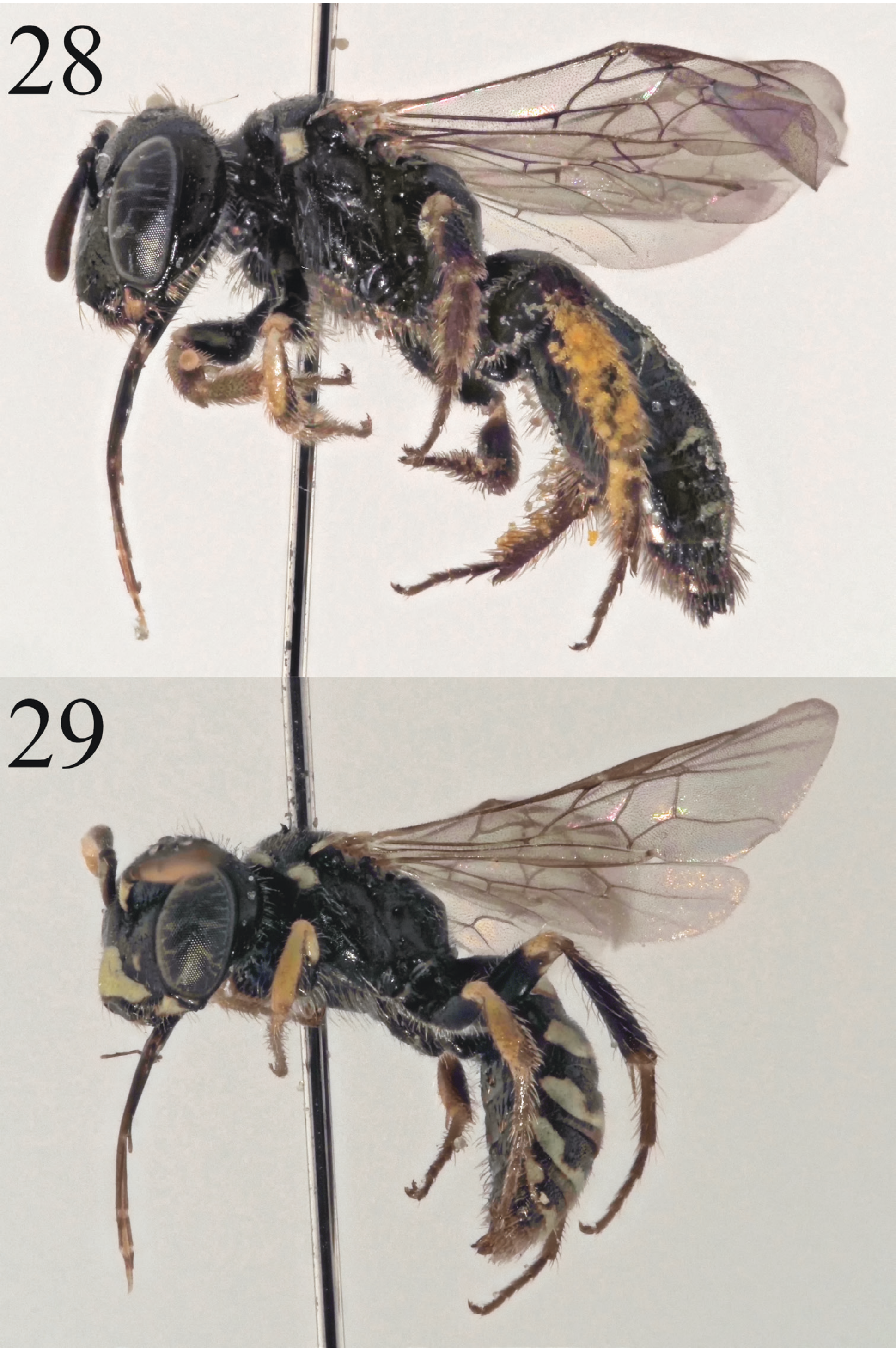
Subgenus *Panurgus* s. str. Panzer, 1806	**Subgenus *Pachycephalopanurgus* Patiny, 1999 stat. rev.**
Panurgus afghanensis Warncke, 1972	*Panurgus acutus* Patiny, 2002
Panurgus avarus Warncke, 1972	*Panurgus calceatus* Pérez, 1895
Panurgus banksianus (Kirby, 1802)	*Panurgus canescens* Latreille, 1811
Panurgus buteus Warncke, 1972	*Panurgus convergens* Pérez, 1895
Panurgus calcaratus (Scopoli, 1763)	*Panurgus farinosus* Warncke, 1972
Panurgus canarius Warncke, 1972	*Panurgus meridionalis* Patiny, Ortiz & Michez, 2005
Panurgus cephalotes Latreille, 1811	*Panurgus minor* Warncke, 1972
Panurgus corsicus Warncke, 1972	*Panurgus nigriscopus* Pérez, 1895
Panurgus cyrenaikensis Warncke, 1972	*Panurgus ovatulus* Warncke, 1972
Panurgus dargius Warncke, 1972	*Panurgus rungsii* Benoist, 1937
Panurgus dentatus Friese, 1901	
Panurgus dentipes Latreille, 1811	
Panurgus intermedius Rozen, 1971	
Panurgus maroccanus Pérez, 1895	
Panurgus niloticus Warncke, 1972	
Panurgus oblitus Warncke, 1972	
Panurgus perezi Saunders, 1882	
Panurgus pici Pérez, 1895	
Panurgus platymerus Pérez, 1895	
Panurgus posticus Warncke, 1972	
Panurgus pyropygus Friese, 1901	
Panurgus siculus Morawitz, 1872	
Panurgus sidensis Warncke, 1987	
Panurgus vachali Pérez, 1895	

of 10) with a clear lamelliform projection that diverges at the midpoint of each gonostylus (Figs 39–42, 44). However, in the former group *Micropanurgus* (three species), this lamelliform projection is greatly reduced and inconspicuous (Fig. 43). Gonocoxae always with strongly projecting points. Female *Pachycephalopanurgus* specimens cannot be consistently separated from *Panurgus* s. str.

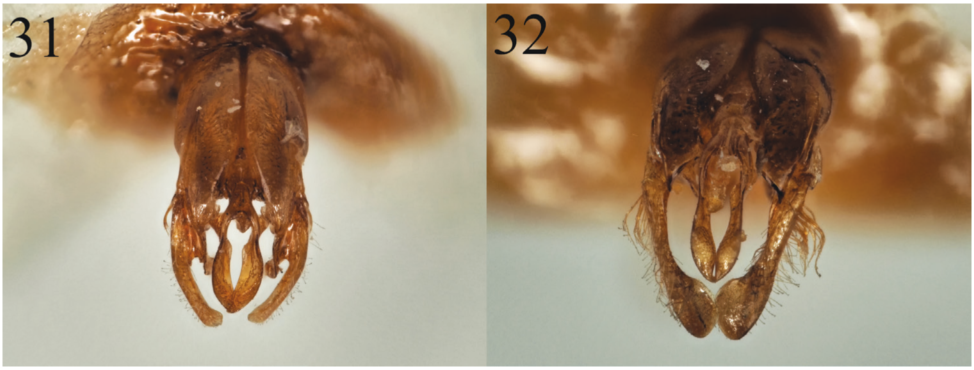
Included species. All *Panurgus* species previously placed in *Pachycephalopanurgus* and *Micropanurgus* (Patiny 1999c; Ascher and Patiny 2002; Patiny 2002); the 10 species are detailed in Table 2.

Genera closely related to *Panurgus*

Compared to the baseline of Michener (2007), these changes result in the elevation of *Flavipanurgus* and *Simpanurgus* from subgenera of *Panurgus*, and the re-establishment of two subgenera within *Panurgus*, *Panurgus* s. str. and *Pachycephalopanurgus*. The description of the genus *Halopanurgus* and the reorganisation of genera within panurgine tribes means that it is necessary to write a new key to facilitate their identification. Within the scope of this paper, we provide a key to the genera closely related to *Panurgus*, specifically the five genera, *Avpanurgus*, *Flavipanurgus*, *Halopanurgus*, *Simpanurgus*, and *Panurgus*. As *Avpanurgus flavofasciatus* (Warncke, 1972)



Figures 28–29. *Halopanurgus baldocki* comb. nov. profile **28** female **29** male.



Figures 31–32. *Flavipanurgus* male genitalia **31** *Flavipanurgus granadensis* **32** *Flavipanurgus merceti*.

and *Simpanurgus phyllopodus* (Warncke, 1972) are known only from the type series (comprised entirely of males), no samples were available for genetic analysis and they are therefore absent from the tree of Bossert et al. (2022). However, we retain these species in this group of related genera because of male genital morphology and for biogeographic reasons, as all genera are restricted, to or show a centre of diversity (greatest number of genera and extant taxa), in the West Mediterranean region. Specifically, the genital capsule of *Simpanurgus* resembles that of *Flavipanurgus* in its gonocoxae which lack apical points, their inner margin rounded; in its large penis valves, the blades of which are flattened in the vertical plane; and there are also similarities in the structure of S7 which is broader than long and deeply excavated medially with a tiny apicomedial tooth (see Warncke 1972, compare Figs 8–10, 15–16, 31–32, S7 of *S. phyllopodus* very similar to *F. kastiliensis*). In *Avpanurgus*, the gonostyli and penis valves are thin and delicate and have similarities with those of *Halopanurgus*, but the gonocoxae are grossly enlarged (Fig. 5). The shape of S7 is also similar, generally as long as broad, and with an apicomedial notch, though this is much more strongly pronounced, with a narrow basal stem (Fig. 13). The face is similar, being less extensively punctured (Figs 20–23) and with less yellow maculation than in *Flavipanurgus* and *Simpanurgus* (Figs 20–21, 24–25).

Key to the genera closely related to *Panurgus*

1 Male S7 with extremely narrow stem, medially with apical projection that is deeply notched, forming a 'Y' shape, apical breadth greater than length (Fig. 13). Gonocoxae grossly enlarged, covering entire dorsal surface of capsule, only apexes of gonostyli and penis valves extend beyond its apical extent (Fig. 5).. ***Avpanurgus* Warncke**

– Male S7 narrow or broad, notched or not, but never with a 'Y' shaped apical projection (Figs 12, 15–19, 45–48). Gonocoxae not grossly enlarged, base of both gonostyli and penis valves visible in dorsal view................................. **2**

2 Male antennae clavate, clearly broadened apically (Fig. 26). Fore tarsi with all segments strongly expanded and flattened (Fig. 27). Male S7 medially excavated .... ***Simpanurgus* Warncke**

– Male antennae not clavate, apical segments not noticeably broader than basal segments (e.g. Figs 20, 24). Fore tarsi normal, not noticeably expanded or flattened. Male S7 medially excavated or not **3**

3 Male S7 comparatively narrow, slightly broader than long, medially notched (Fig. 12). Genitalia with gonocoxae apically produced into strong points (Figs 3–4). Body black with yellow markings. Face with reduced punctation, punctures fine, superficial, not strongly standing out from underlying integument (Figs 20, 22). Tongue over twice the length of face or not (Figs 28–30) .... ***Halopanurgus* gen. nov.**

– Male S7 broad, much broader than long, strongly excavated medially or not, but not narrowly notched (Figs 15–19). Genitalia with gonocoxae either without apical points (Figs 8–10, 31–32, 37–38), or if with apical points (Figs 11, 33–36, 39–44), then body black, never with yellow markings. Face with clear punctation (Fig. 23). Tongue never over twice as long as face...... **4**

4 Body with yellow markings (except female of *F. flavus* (Friese, 1897)). Scopal hairs simple, not spiralled. Genitalia with gonocoxae lacking apical points, inner margin rounded, gonostyli flattened in lateral plane, spatulate (Figs 8–10, 31–32)... ***Flavipanurgus* Warncke**

– Body never with yellow markings. Scopal hairs distinctively and minutely spiralled. Genitalia with gonocoxae usually with apical points (Figs 11, 33–36, 39–44), if absent then gonostyli flattened in vertical plane, never in lateral plane and never spatulate (Figs 37–38) ....***Panurgus* Panzer**

Pollen preferences

A total of 93 pollen loads were analysed from nine *Panurgus* species (Table 3). All pollen was collected from Asteraceae, which is why we assume all species to be oligolectic or suspect them to be oligolectic where sample sizes were too low to be confident. *Panurgus* (*Panurgus*) showed a strong association with the subfamily Cichorioideae, whereas *P.* (*Pachycephalopanurgus*) showed a strong association with the subfamily Asteroideae, though confidence in the strength of this relationship is limited by the very low sample sizes available for North African species.

Discussion

As demonstrated at a global scale (Pisanty et al. 2021; Bossert et al. 2022), the use of ultraconserved elements for phylogenetic analysis has considerably improved our understanding on the evolutionary relationships of andrenid bees, including the subfamily

Figures 33–38. *Panurgus* (*Panurgus* s. str.) male genitalia **33** *Panurgus cephalotes* **34** *Panurgus dentipes* **35** *Panurgus maroccanus* **36** *Panurgus perezi* **37** *Panurgus banksianus* **38** *Panurgus pyropygus*.

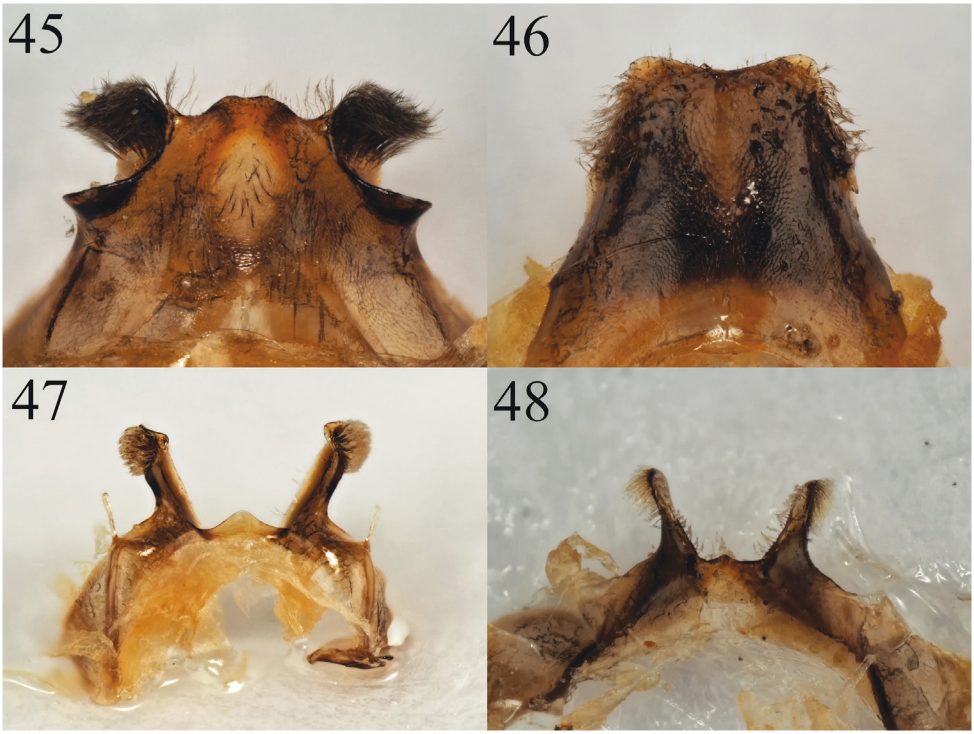
Panurginae. In the case of the Panurginae, the reciprocal analysis of morphological characters given our robust molecular phylogeny revealed that certain morphological features used to characterise genera of Old World Panurginae have been overvalued in the past and have incorrectly resulted in the association of *Halopanurgus baldocki* with the genus *Camptopoeum*.

Albeit separated by ~50 million years of divergence time (Bossert et al. 2022), certain species of Panurgini and Melitturgini share remarkably similar morphological features, leading authors to conclude close phylogenetic relationships until very recently. The most pertinent example is *Camptopoeum*, which was included with the two-celled members of the Panurgini by Michener (2007). *Halopanurgus baldocki* was described as a *Camptopoeum* (*Camptopoeum*) because of the elongate tongue, in which the first segment of the labial palpus is about as long as the second to fourth segments taken together. Indeed, based only on tongue morphology, *H. baldocki* is more similar to *Camptopoeum* (*Camptopoeum*) than it is to its sister species *Halopanurgus fuzetus*,

Figures 39–44. *Panurgus* (*Pachycephalopanurgus*) male genitalia **39** *Panurgus calceatus* **40** *Panurgus canescens* **41** *Panurgus convergens* **42** *Panurgus farinosus* **43** *Panurgus minor* **44** *Panurgus rungsii*.

and more similar to *Camptopoeum* (*Camptopoeum*) than to *Camptopoeum* (*Epimethea*), which have very short glossa. Tongue length within Old World panurgines is therefore clearly homoplasious.

This confusion that arose from misleading tongue morphology serves as a cautionary tale into panurgine classification. Tongue length can clearly be a labile morphological character and is not necessarily suitable for diagnosing suprageneric taxa (Danforth et al. 2019). Bee mouthparts represent a particularly intuitive example of a morphological structure facing selective pressure. All bee species examined in this study exhibit some degree of host plant specialization and most seem to be true oligoleges. It is expected that tongue length varies among species in respect to their host plant, and the appearance of bee species with physically long tongues within the short-tongued bee families such as Andrenidae (e.g. Shimizu et al. 2014), Colletidae (e.g. Laroca et al. 1989; Rozen and Wyman 2015), and Halictidae (e.g. Burger 2020) is well established, usually being associated with particular floral shapes that necessitate morphological adaptation to access particular resources. In the case of *H. baldocki*, their long tongues are used to access the



Figures 45–48. Sternum 7 for members of the former four subgenera of *Panurgus* **45** *Panurgus* (*Panurgus*) *cephalotes* **46** *Panurgus* (*Euryvalvus*) *banksianus* **47** *Panurgus* (*Pachycephalopanurgus*) *canescens* **48** *Panurgus* (*Micropanurgus*) *ovatulus*.

nectaries of its host *Frankenia laevis* (Frankeniaceae) which are found at the base of a tubular corolla, necessitating a long tongue for a bee of only 4 mm in length (Wood and Cross 2017). *Halopanurgus fuzetus* in turn visits species of *Spergularia* (Caryophyllaceae, Wood and Cross 2017), which have an open floral structure, and therefore do not require a long tongue to access the nectaries despite their equally small body size. The ~7.5 million years of divergence time between the two *Halopanurgus* species (Bossert et al. 2022) was sufficient to allow their tongue morphologies to diverge, and it is intuitive that they represent adaptations towards nectar uptake from different host plants. This mirrors the situation in *Camptopoeum* (*Camptopoeum*) and *Camptopoeum* (*Epimethea*), which based on the very limited number of species whose foraging niches are well understood are specialists of *Centaurea* (Asteraceae) and Apiaceae, respectively (Friese 1926, TJW unpublished data). Like *Frankenia*, *Centaurea* flowers have individual florets in which nectar is found at the bottom of a tubular corolla, whereas in the Apiaceae used by *Camptopoeum* (*Epimethea*) species, the floral structure is open and does not require a long tongue to access nectaries.

Against this context, the description of new panurgine genera from the Arabian Peninsula and Central Asia (Engel et al. 2019) based primarily on tongue morphology raises interesting questions. Placing close to *Flavomeliturgula* Patiny (now within a broad Panurgini, Bossert et al. 2022; Meliturgulina sensu Engel et al. 2019), the genus

Belliturgula Engel (Saudi Arabia) is diagnosed predominantly on the basis of tongue characters combined with body colouration (Engel et al. 2019), and the genus *Khuzimelissa* Engel (Iran and Pakistan) is diagnosed mainly on the basis of tongue characters and additionally on the shape of the outer antennal sulcus. Both genera are monotypic, and were described from female material only, with no male specimens known. Given the labile nature of tongue length within Panurginae, and the lack of male material that was crucial for morphologically confirming differences between the genera in the present study, it is difficult to assess the status of these genera and the relationships between the species related to *Flavomeliturgula* with confidence.

From a biogeographical perspective, the genera closely related to *Panurgus* that have been confidently placed through genetic analysis (Bossert et al. 2022) show a West Mediterranean distribution, restricted to Iberia (*Halopanurgus* and *Flavipanurgus*) or with particular diversity in the western Maghreb (*Panurgus*; Patiny and Gaspar 2000; Patiny 2001; Lhomme et al. 2020). The only known collecting localities for *Avpanurgus* and *Simpanurgus* being in Algeria and Spain, respectively (Warncke 1972; Patiny 2001), means that they align with this overall pattern; the centres of diversity for other Panurgini clades are located further east, such as Asia (taxa related to *Panurginus*), and the Middle East to sub-Saharan Africa (taxa related to *Meliturgula* and *Mermiglossa*), and also for *Camptopoeum* whose centre of diversity is the Middle East (Patiny 2001). Though the placement of *Avpanurgus* and *Simpanurgus* in the group of genera related to *Panurgus* requires additional molecular investigation and confirmation, it forms the basis of a suitable hypothesis should fresh specimens become available.

A further line of evidence that can help inform our understanding of panurgine groups are their pollen preferences. Though the division of *Panurgus* into two subgenera is justified on the basis of the strong molecular and morphological evidence in the male sex, this division between *Panurgus* s. str. and *Pachycephalopanurgus* may also be reflected in their use of Asteraceae pollen. All known *Panurgus* species are oligoleges of Asteraceae, but *Panurgus* s. str. are specialists of the subfamily Cichorioideae (Table 3, see Münster-Swendsen 1970; Westrich 1989 for *P. calcaratus*, *P. banksianus*, and *P. dentipes*; Rozen 1971 for *P. maroccanus*, *P. intermedius*, *P. pici*), whereas *Pachycephalopanurgus* appear to be specialists of the subfamily Asteroideae (Table 3, see Cross 2020 for *P. meridionalis*). Clearly, a much greater sampling effort is needed for North African *Pachycephalopanurgus* species, but a nominal specialisation on Asteroideae forms the basis of a testable hypothesis. Why these two lineages of *Panurgus* seem to divide their efforts between these two lineages of Asteraceae is unclear, but a proposed mechanism is related to their pollen-collecting behaviour. Specifically, when foraging on *Astericus* (Asteroideae), *Pachycephalopanurgus* species focus on the non-ligulate disc florets and sweep pollen into their scopae whilst rapidly pulsing and moving their metasoma, a technique that seems unlikely to be effective in the Cichorioideae where only ligulate florets are present (Cross 2020). More broadly, with their spiralled scopal hairs and specialisation on Asteraceae, *Panurgus* appear to represent another independent lineage of bees that have converged on carrying their pollen dry (Portman and Tepedino 2017), in contrast to their closest relatives *Flavipanurgus* and *Halopanurgus* which carry their pollen moistened by nectar (Wood and Cross 2017; Cross and Wood 2018).

Table 3. Host plant spectrum and inferred category of host use in *Panurgus* species. *n* total number of pollen loads, *N* number of pollen loads from different localities. Plant taxa AST, Asteraceae.

Species	*n*	*N*	Results of microscopic analysis of pollen grains (% pollen grains)	% Pure loads of preferred host	% Loads with preferred host	Host range
P. (*Panurgus*)						
Panurgus cephalotes	28	15	AST (Cichorioideae) 98.9, AST (Asteroideae) 1.1	100.0	100.0	Broadly oligolectic (Asteraceae, Cichorioideae)
Panurgus maroccanus	14	5	AST (Cichorioideae) 91.1, AST (Asteroideae) 9.9	100.0	100.0	Possibly broadly oligolectic (Asteraceae, Cichorioideae)
Panurgus perezi	23	14	AST (Cichorioideae) 100.0	100.0	100.0	Broadly oligolectic (Asteraceae, Cichorioideae)
P. (*Pachycephalopanurgus*)						
Panurgus calceatus	10	2	AST (Asteroideae) 65.9, AST (Cichorioideae) 26.0, AST (Carduoideae) 8.1	100.0	100.0	Broadly oligolectic (Asteraceae)
Panurgus canescens	12	8	AST (Asteroideae) 100.0	100.0	100.0	Broadly oligolectic (Asteraceae, Asteroideae)
Panurgus convergens	2	2	AST (Asteroideae) 100.0	100.0	100.0	Possibly broadly oligolectic (Asteraceae, Asteroideae)
Panurgus nigriscopus	1	1	AST (Asteroideae) 100.0	100.0	100.0	Possibly broadly oligolectic (Asteraceae, Asteroideae)
Panurgus ovatulus	1	1	AST (Asteroideae) 100.0	100.0	100.0	Possibly broadly oligolectic (Asteraceae, Asteroideae)
Panurgus rungsii	2	2	AST (Asteroideae) 94.0, AST (Carduoideae) 6.0	100.0	100.0	Possibly broadly oligolectic (Asteraceae, Asteroideae)

Acknowledgements

Our thanks go to Esther Ockermüller and Martin Schwarz for access to the Warncke Collection, loan of material, and hospitality at Linz, and to Ian Cross for access to his personal collection. We also thank Pierre Rasmont for substantial assistance with photography. TJW is supported by an F.R.S.-FNRS fellowship "Chargé de recherches". This work was supported by NSF grant DEB-2127744 and a Peter Buck fellowship to SB. The authors thank Laurence Packer, Zachary Portman, and an anonymous reviewer for comments that substantially improved the manuscript.

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