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Evolutionary associations among pollen scopa structure, floral breadth and eusociality in Halictidae (Hymenoptera: Apoidea)

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The biological traits associated with the origin of social behaviour remain a fundamental question in evolutionary biology. Among bees, the family Halictidae provides a particularly valuable system for addressing this question, as it represents the only bee family outside Apidae in which eusociality has evolved. Yet, the ecological and morphological factors underlying these transitions remain poorly understood. To investigate the evolutionary relationships among scopa type, floral breadth and eusociality, we conducted a comparative analysis using a multilocus phylogeny reconstructed from 207 species. Ancestral state reconstructions indicate that the posteriorly caged scopa evolved multiple times from an ancestral straight form, most prominently within Halictini and closely related tribes. Comparative analyses indicate a consistently positive but transformation- and clade-sensitive association between posteriorly caged scopa and recorded floral breadth, whereas eusocial taxa show a more robust association with broader recorded floral breadth. Together, these findings suggest non-random phylogenetic associations among pollen-transport morphology, floral breadth and sociality in Halictidae, while indicating that these relationships do not follow a single causal pathway.

1. Introduction

Morphological traits and ecological or behavioural roles frequently undergo correlated evolution across animal lineages [1,2], and bees (Anthophila) provide some of the most compelling examples of such integration [3]. Classic instances of morphology/ecology coevolution in bees include the correspondence between proboscis morphology and floral morphology [4,5], and the association of mandibular form with nesting materials [6]. Key behaviours of bees such as pollen foraging, host plant specialization and diverse life history strategies are closely associated with pollen-transport morphology, which can influence the efficiency of floral resource exploitation [7,8].

A notable example is the Apidae, in which the corbicula has been interpreted as a key functional innovation that dramatically increased the efficiency and stability of pollen transport [9], establishing a morphological foundation closely associated with the subsequent evolution of complex eusociality in corbiculate bees [10,11]. Whether morphological and ecological factors are associated with social evolution in other bee families, however, remains poorly understood. This gap is especially pronounced in Halictidae, which represents the only bee family outside Apidae with inferred origins

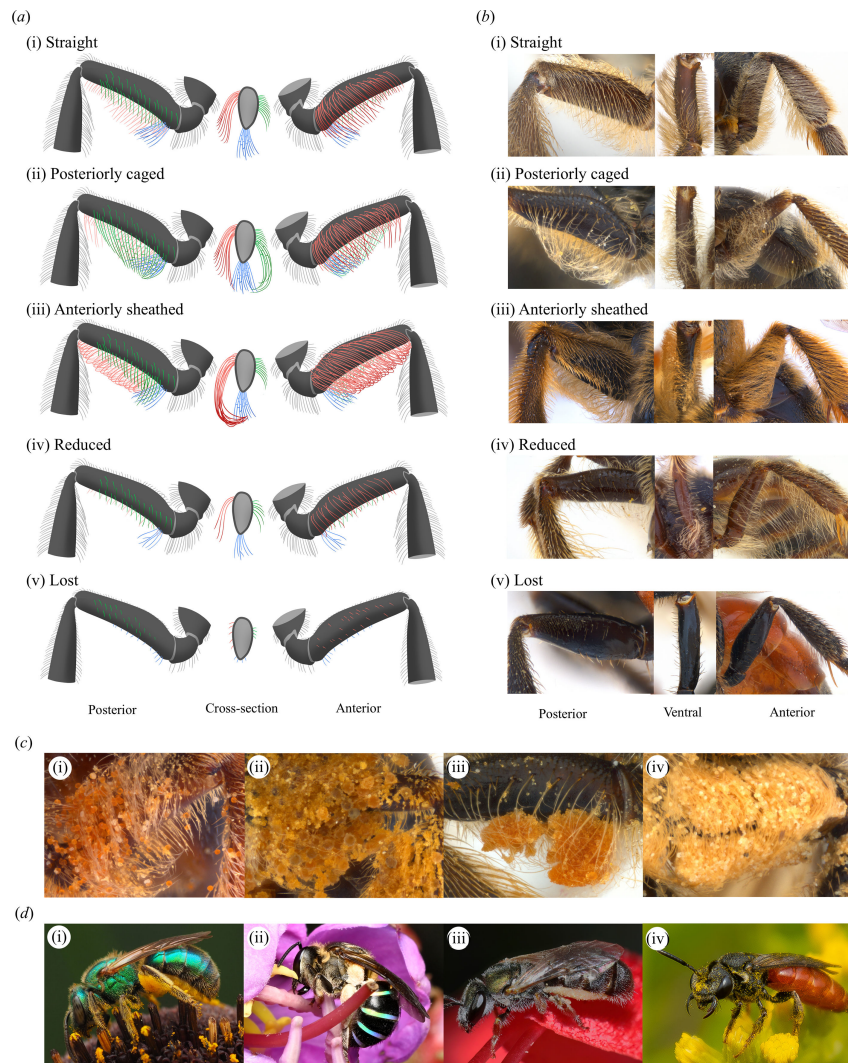


Figure 1. Femoral scopa types of Halictidae. Five femoral scopa types recognized in Halictidae: illustrated by schematic diagrams (a), photographs of preserved specimens (b), photographs of pollen-laden femora (c), and ecological photographs of foraging bees (d). (a) Schematic diagrams showing scopal hair orientation on the femur for each type. Colours indicate hair region: red, anterior hairs; green, posterior hairs; blue, ventral hairs. Three views are shown per type: posterior (left), cross-section (middle) and anterior (right). (b) Photographs of preserved specimens illustrating each scopa type: (i) *Gnathonomia thoracica* (straight), (ii) *Lasioglossum* (*Sphecodogastra*) *vulsum* (posteriorly caged), (iii) *Maculonomia apicalis* (anteriorly sheathed), (iv) *Lipotriches* (*Rhopalomesella*) *yasumatsui* (reduced), (v) *Sphecodes scabricollis* (lost). Three views are shown per type: posterior (left), ventral (middle), and anterior (right). (c) Photographs of pollen-laden femora: (i) *Nomia mandschurica* (straight, anterior view), (ii) *Lasioglossum* (*Sphecodogastra*) *affine* (posteriorly caged, anterior view), (iii) *Lasioglossum* (*Leuchalictus*) *upinense* (posteriorly caged, posterior view), (iv) *Curvinomia iridescens* (anteriorly sheathed, anterior view). (d) Ecological photographs of bees during natural foraging: (i) *Augochlorella aurata* (posteriorly caged), (ii) *Curvinomia strigata* (anteriorly sheathed), (iii) *Lasioglossum* (*Homalictus*) *urbanum* (reduced), (iv) *Sphecodes albilabris* (lost). Photo credits for figure 1d: (i) Thilina Hettiarachchi, (ii) Tim Wing Yam, (iii) Laurence Sanders and (iv) votinceva-elena.

of eusociality and exhibits wide variation in social organization across the family [12]. Halictid bees exhibit striking diversity both in pollen-collecting structures and in pollen host use, ranging from extreme oligolecty to broad polylecty [3,13]. Importantly, it remains unclear whether morphological transitions in pollen-collecting structures are associated with ecological expansions in floral breadth, or whether broader floral use itself covaries with the evolution of eusociality.

A key morphological feature in Halictidae is the hind femoral scopa, which exhibits considerable diversity yet has received limited macroevolutionary analysis. Across bees, scopal structures show clear phylogenetic patterns [3,14,15] and documented morphology–function correlations within clades [7,16], but their evolutionary consequences at macroevolutionary scales are seldom tested. In Halictidae, the femoral scopa exhibits several distinct morphological forms, ranging from complete loss or reduction to straight, uncurved hairs, and to posteriorly caged or (more rarely) anteriorly sheathed scopa types (figure 1). These forms are characterized by the development and orientation of the anterior and posterior scopal fringes that border the ventral femoral surface. Such structural differences may influence how pollen grains of different sizes and shapes are collected and retained, potentially affecting the range of floral hosts from which pollen can be effectively carried [16].

Although pollen loads collected directly from bee specimens provide the most direct evidence of individual foraging choices, pollen composition varies dramatically across time and space within the same species, limiting comprehensive data collection across diverse taxa at macroevolutionary scales [17–19]. To address this limitation, we supplemented pollen-load records with direct floral visitation observations, which capture broader ecological contact patterns, including males, non-foraging visits and nectar collection. We therefore use compiled floral association records to infer broad, macroevolutionary patterns of resource

use. While these records represent less direct measures of resource breadth than specimen pollen loads, they provide substantially improved geographical and temporal coverage, enabling macroevolutionary comparative analysis across Halictidae [20].

Floral breadth itself is an ecologically consequential trait [21]. Although many bees show phylogenetically conserved oligolectic foraging, repeated evolutionary shifts towards more generalized resource use have been reported across multiple lineages [22,23], with such expansions implicated in enhancing population stability and behavioural flexibility [24–26]. For social insects, access to diverse, temporally reliable resources can buffer colonies against fluctuations in pollen availability, relaxing energetic constraints of overlapping generations and cooperative brood care [27–29]. Despite this conceptual plausibility, the relationship between floral breadth and the evolution of sociality has rarely been tested in a phylogenetic comparative framework, especially in groups such as Halictidae where social organization varies from solitary to facultatively or primitively eusocial.

Testing these questions requires a phylogeny that supports repeated comparisons across scopa morphology, recorded floral breadth, and sociality. Although phylogenomic datasets based on ultraconserved elements (UCEs) can provide deep resolution, available sampling remains limited for many halictid genera and subgenera, constraining species-rich comparative analyses. We therefore assembled a multilocus Sanger framework with broad taxon coverage across Halictidae [30–33].

Using this phylogeny together with compiled floral association records and comparative data on scopa morphology and social behaviour, we address two questions: (i) whether transitions among femoral scopa types (straight, posteriorly caged, anteriorly sheathed, reduced and lost) are associated with differences in floral breadth, and (ii) whether floral breadth is associated with eusociality across taxa. By examining these dimensions jointly, we evaluate whether femoral scopa architecture is associated with ecological breadth, and whether ecological breadth covaries with eusociality within Halictidae.

2. Methods

(a) Taxon sampling, sequencing and phylogenetic analyses

We sampled 215 taxa for phylogenetic inference: 207 Halictidae species as ingroup taxa, representing all subfamilies and tribes, and 8 non-halictid outgroup taxa from other bee families (e.g. Apidae, Colletidae). Sequences were obtained from GenBank and from newly generated sequences. Background classification follows Ascher & Pickering, with *Seladonia* treated following Pesenko and Nomiinae following Pauly where these better matched our phylogenetic results [34–36]. Total genomic DNA was extracted using DNeasy Blood & Tissue kit (Qiagen). Five genes were selected: cytochrome *c* oxidase subunit I (COI, barcode region), 28S, elongation factor-1 alpha (EF-1 α), long-wavelength rhodopsin (LwRh) and *Wingless* (*wg*). Polymerase chain reaction (PCR) products were purified and sequenced (Bionics). Sequence alignment was performed in MAFFT v. 7 [37]; ambiguously aligned intron regions were identified by visual inspection and excluded. The aligned sequences were combined in SequenceMatrix v. 1.8 [38], yielding a 3669 bp alignment, including introns.

Phylogenetic analyses were performed using Bayesian inference (BI; MrBayes v. 3.2.7) [39] and maximum likelihood (ML; IQ-TREE v. 2.2.2.6) [40]. The dataset was partitioned by gene and codon position. For MrBayes, best-fit substitution models were selected using PartitionFinder v. 2.1.1 [41], Markov chain Monte Carlo (MCMC) chains were run until convergence (average s.d. of split frequencies, ASDSF <0.01), totalling 34 870 000 generations (25% burn-in, sampling every 1000 generations). Runs were combined after confirming convergence. For ML, model selection used ModelFinder [42] with partition merging and branch support was assessed via 1000 ultrafast bootstrap [43] replicates and 1000 Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT) replicates [44].

(b) Operational taxon definition and dataset assembly

For comparative analyses, species-level records were aggregated into genus/subgenus-level operational taxa to reflect recognized taxonomy, phylogenetic non-monophyly and scopa-type heterogeneity within genera. Details of operational-taxon delimitation are provided in electronic supplementary material, S1. After excluding operational taxa lacking either femoral scopa data or floral records, the comparative dataset comprised 83 operational taxa. Ancestral state reconstruction used the 207-species ingroup tree obtained by removing the 8 non-halictid outgroups from the 215-taxon topology. For visualization of floral breadth patterns, this tree was pruned to 88 operational taxa with floral records; phylogenetic comparative analyses were performed on the 83-taxon subset. The species-level and operational-taxon trait datasets used in these analyses are provided in electronic supplementary material, S4.

(c) Morphological and ecological data collection

(i) Femoral scopa types

Pollen scopa morphology was collected from specimens, coded at the species level based on direct observations (pinned specimens or quality photographs) and, where available, corroborated using additional congeneric or consubgeneric specimens within the same lineage. Among the 207 halictid species included in the phylogenetic analysis, scopa morphology was scored for 166 species (80.2%) based on direct observations. For 30 species (14.5%) lacking direct scopa observations, scopa types were inferred based on concordance with scopa types observed in other directly scored species from the same lineage that were also represented in the phylogeny. Although scopa type can vary within some subgenera (e.g. *Sphecodogastra*), inferred taxa in our

dataset were supported by matching scopa types among directly examined close relatives within the same genus/subgenus. The remaining 11 species (5.3%) lacked sufficient information for fixed scopa assignment; these species were not used in summaries requiring fixed scopa states but were retained as unresolved tips in ancestral state reconstruction. In the comparative dataset ($n = 83$ operational taxa), 9 taxa (10.8%) were inferred based on this approach. The femoral scopa was selected for analysis because it exhibits clear morphological differentiation and represents the primary scopal structure in most halictid taxa. The femoral scopa was classified into five distinct types (figure 1a,b).

- *Straight type*: femoral scopal hairs are not fully enclosing the ventral femoral surface (not caged). Anterior hairs are dense and long ($\geq$ femoral height) and directed downward (straight, not distinctly curled); posterior hairs are dense but vary in length across taxa and are directed downward.
- *Posteriorly caged type*: the posterior scopal hairs are sparse but very long ($>$ femoral height) and arranged in a longitudinal row, curling down to meet the anterior fringe and ventral scopal hairs ventrally, forming a closed cage around the ventral femoral surface ('caged').
- *Anteriorly sheathed type*: the anterior scopal hairs are very long ($>$ femoral height) and curled down (partly covering the femoral ventral surface), whereas posterior hairs remain dense but short ($\leq$ femoral height) and directed downward, resulting in an open (partly closed) cage.
- *Reduced type*: characterized by sparse and/or short scopal hairs (often patchy) on both anterior and posterior surfaces, i.e. reduced compared with close relatives (lower density and/or patchy distribution). The specific features of reduction vary among lineages: hair length is shortened in *Systropha*, density is decreased in *Lipotriches*, and both length and density are reduced in *Homalictus*, reflecting independent evolutionary modifications rather than a single derived morphology.
- *Lost type*: scopal hairs are absent or vestigial and thus no longer function as a pollen-transport structure.

The straight type category as defined here is operationally broad and encompasses inter-lineage variation in scopal hair distribution and density. For example, some Augochlorini taxa (e.g. *Augochloropsis tupacamaru*) exhibit well developed ventral femoral setae with reduced posterior fringes, whereas some Rophitinae taxa (e.g. *Dufourea novaeangliae*) show more prominent tibial scopae than femoral scopae; however, because hair density and relative length are continuous traits that vary with specimen condition and photographic angle, we did not attempt quantitative scoring of these features and instead applied a conservative definition based on the presence and orientation of curved hair fringes.

(ii) Floral associations and eusociality

Floral breadth (FB) of the 88 operational taxa was quantified as the number of plant families compiled from floral association records (literature and institutional datasets), which include pollen-load studies and direct visitation observations. Records were compiled from primary literature, institutional datasets and online biodiversity platforms (including citizen-science repositories), and standardized to plant-family counts for each operational taxon. Because this metric is derived from heterogeneous literature and online datasets with uneven coverage, it inherently reflects both true ecological breadth and taxonomic research effort. Sampling-effort corrections (e.g. rarefaction or publication-count offsets) were considered but not implemented, because available proxies for research effort are themselves highly heterogeneous across regions and taxa and could introduce artefactual structure into the data. We therefore treat floral breadth as a coarse proxy for ecological niche breadth rather than a precise measure of pollen diet. Species-level floral data were aggregated to match operational taxa definitions. Plant taxa were verified against *Plants of the world online* [45]. Eusociality traits for the 83 operational taxa were classified into three categories: eusocial (taxa containing polymorphic, facultative and seasonally eusocial species); non-eusocial (taxa for which eusociality has not been documented); parasitic (cleptoparasitic).

(d) Phylogenetic comparative analyses

(i) Ancestral state reconstructions, phylogenetic signal and clustering of traits

Ancestral state reconstruction was conducted using stochastic character mapping (make.simmap) with an all-rates-different (ARD) model fitted via fitMk [46,47]. Analyses were performed in R using ape (v. 5.8.1), phytools (v. 2.5.2) and GEIGER (v. 2.0.11) [47–49]. The dataset included all 207 ingroup taxa. Species with observed or inferred scopa assignments were coded to one of five states, and the 11 uncertain species were treated as tips with equal prior probabilities across the five scopa states. Stochastic mapping (make.simmap, 1000 simulations) was used to sample the posterior distribution of ancestral states; posterior probabilities were summarized across simulations and visualized using phytools, based on the MrBayes topology.

Phylogenetic clustering of scopa types was evaluated using Fritz & Purvis's D -statistic, implemented in the caper package [50,51]. Because D is defined for binary traits, each scopa type was coded separately as presence/absence across operational taxa, and D was estimated for each type in turn. The D -statistic tests whether a binary trait is randomly distributed ($D = 1$), follows Brownian motion expectations ($D = 0$), or shows stronger clustering ($D < 0$). Phylogenetic signal in floral breadth was evaluated using Blomberg's K and Pagel's λ , implemented in the phytools and ape packages in R [52,53]. Statistical support was assessed via randomization tests (for K) and likelihood-ratio tests against $\lambda = 0$ (for Pagel's λ). Pagel's λ for floral breadth was estimated by maximum likelihood and tested against $\lambda = 0$; in phylogenetic generalized least squares (PGLS), λ was re-estimated by maximum likelihood within each fitted model to parameterize residual phylogenetic covariance [54]. Phylogenetic tree visualization was performed in R using ggtree (v. 3.2.1) and ggplot2 (v. 4.0) [55,56].

(ii) Testing trait associations and evolutionary regime shifts

PGLS regression was performed to test associations between scopa type and floral breadth, and floral breadth and eusociality using the caper package. Pagel's λ was estimated by maximum likelihood within each PGLS model to account for phylogenetic non-independence in the residual error structure [53,54]. As a sensitivity analysis, we also refitted each model with Pagel's λ fixed at 1.0 (Brownian-motion error structure) and compared parameter estimates with those from the ML- λ models. The dataset included 83 genus/subgenus-level operational taxa. For scopa type, we used five-state coding (F5: straight, posteriorly caged, anteriorly sheathed, reduced, lost) with treatment contrasts and the straight type as the reference baseline, allowing each scopa type's independent association with floral breadth to be tested. Alternative aggregated coding schemes (F2–F4; electronic supplementary material, table S1) were evaluated for robustness. Floral breadth was analysed under three transformations (raw, log, square-root); log-transformation (natural-log; $\ln(\text{FB} + 1)$) was primary as it minimizes skewness for count data spanning 1–142 families and prevents high-breadth outliers from dominating.

Floral breadth evolution across scopa types was analysed using the OUwie package (v. 2.16) in R, fitting Ornstein–Uhlenbeck (OU) models that allow floral breadth to evolve towards estimated trait optima (θ) that may differ among scopa types [57,58]. This approach tests whether floral breadth is better described by models allowing different evolutionary optima among scopa regimes than by models with a single shared optimum. The dataset included 83 genus/subgenus-level operational taxa, with taxa categorized into five scopa types (straight, posteriorly caged, anteriorly sheathed, reduced, lost). Multiple OU models were compared, including: OU1 (single evolutionary optimum), OUM (different optima by regime) and OUMV (different optima and variance by regime). Model selection was performed using the corrected Akaike information criterion (AICc). Analysis was repeated under alternative coding schemes (F2–F5) to assess robustness. Because OUwie regime-specific parameter estimation requires adequate sample sizes per regime, and three scopa types had very small samples (anteriorly sheathed $n = 2$, reduced $n = 5$, lost $n = 2$), we treated the binary coding scheme F2A (posteriorly caged versus non-posteriorly caged) as primary for regime-shift models. Five-state coding (F5) and intermediate schemes (F3, F4) were evaluated as robustness checks, but these fine-grained schemes yielded single-optimum models or unstable parameter estimates for rare regimes owing to limited statistical power.

We tested correlated evolution between posteriorly caged scopa and eusociality using Pagel's test, comparing dependent versus independent models by likelihood-ratio tests [59].

All primary analyses were repeated across multiple data transformations (raw, log and square-root) and alternative model codings; full details are provided in the electronic supplementary material. Primary PGLS and OUwie analyses were conducted on the maximum clade credibility (MCC) tree from the BI. Sensitivity to phylogenetic uncertainty was assessed by repeating PGLS across 1000 posterior trees (500 per run, 25% burn-in) and OUwie across 100 posterior trees under the F2A coding scheme. Clade-exclusion analyses were performed by removing Augochlorini or Halictini from each posterior tree before re-running PGLS.

3. Results

(a) Ecological and morphological data acquisition

(i) Floral breadth of Halictidae

Across all compiled records, Halictidae taxa were recorded visiting plants spanning 49 orders and 236 families overall. At the subfamily level, most Rophitinae taxa were recorded from fewer than 15 plant families, whereas generally Nomiinae and Nomiodinae taxa were recorded from approximately 20–50 families. Within Halictinae, several taxa exceeded 100 recorded plant families (e.g. *Augochlora*, *Agapostemon*, *Halictus*, *Lasioglossum*). Electronic supplementary material, S5 summarizes the floral breadth data of Halictidae (88 operational taxa), quantified as the number of recorded plant families per bee taxon (with counts of plant genera and orders also provided). Figure 2 shows the bee taxon $\times$ plant-family visitation matrix, with each cell indicating the number of recorded plant genera within that plant family for each bee taxon. Across Halictidae, Asteraceae and Fabaceae were the most broadly recorded plant families, each recording 70 of 88 operational taxa, followed by Lamiaceae (63 taxa); all three families are species-rich and geographically widespread [45], consistent with patterns reported for other bee groups [19].

(ii) Femoral scopa morphology of Halictidae

The posteriorly caged type occurred primarily within the Halictini *sensu lato* clade (i.e. Thrinchostomini, Caenohalictini, Sphecodini, Halictini *sensu stricto*) and several Augochlorini lineages. The anteriorly sheathed type was restricted to Nomiinae (*Curvinomia* and *Maculonomia*). The reduced type occurred in lineages such as *Systropha*, some subgenera of *Lipotriches* and *Lasioglossum*, and the lost type was recorded only in parasitic taxa (e.g. *Sphecodes*, *Parathrinchostoma*, and *Megalopta* formerly placed in *Noctoraptor*).

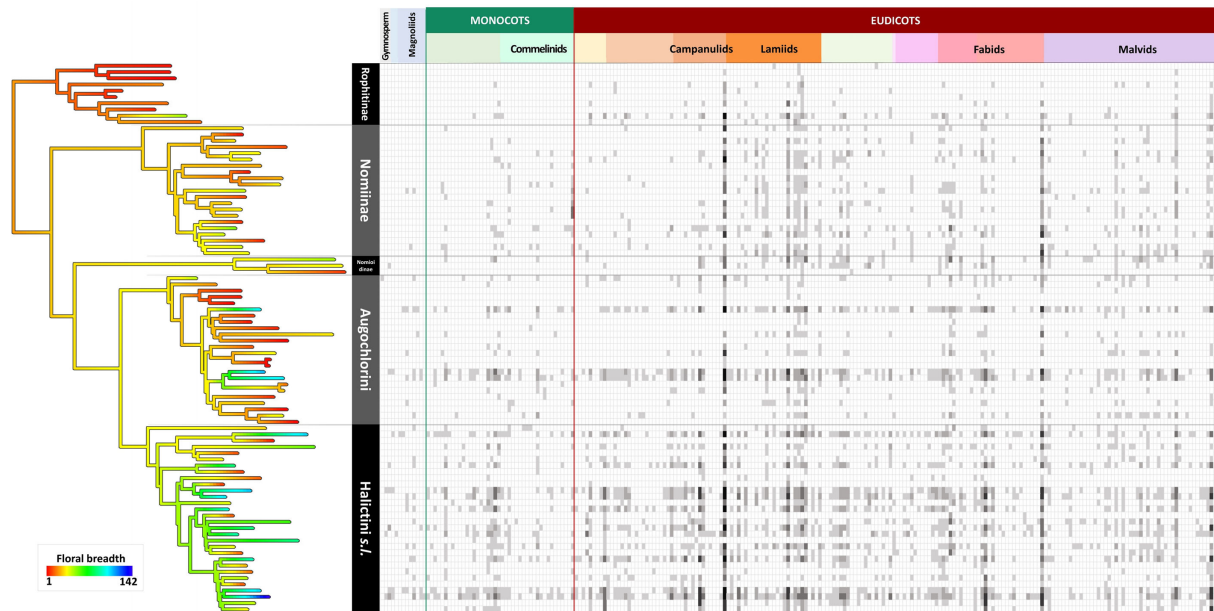


Figure 2. Plant-family visitation matrix across Halictidae. Heatmap of plant-family visitation records for Halictidae operational taxa. Columns are plant families ordered by major plant clades; rows are bee taxa ordered by phylogeny. Cell shading indicates the number of recorded plant genera per taxon–family combination, scaled in five bins: light grey (1–3 genera), medium grey (4–10 genera), dark grey (11–30 genera), darker grey (31–100 genera) and black (>100 genera). White cells indicate no recorded visits. The phylogeny on the left is coloured by floral breadth (scale 1–142 plant families).

(b) Phylogenetic analyses

The ML and BI tree topologies were mostly congruent, with a few incongruent shallow nodes (figure 3, red branches). Halictidae, its four subfamilies, and all 12 tribes were strongly supported as monophyletic groups, with relationships among subfamilies consistent with previous studies and generally well supported across inference methods. Most of the weakly supported nodes were inter- or intrageneric relationships (figure 3, reddish circles at nodes). Most of the genera were recovered as monophyletic, with a few exceptions: *Austronomia*, *Rhinocorynura*, *Ruizantheda* and *Thrinchostoma*.

(c) Phylogenetic comparative analyses

(i) Ancestral state reconstructions, phylogenetic signal and clustering of traits

The straight (S) type was inferred as the ancestral state at the root node (posterior probability = 0.994). This type was distributed throughout basal nodes in Rophitinae, Nominiinae, and basal Nomiinae and basal Augochlorini (Halictinae). The posteriorly caged (P) type was inferred with high support at multiple internal nodes across the tree. Stochastic character mapping under an ARD model recovered a mean of 3.27 independent S→P transitions (electronic supplementary material, table S11). These transitions included two within Augochlorini, at the most recent common ancestor (MRCA) of *Augochlora* and *Augochlora* (node A in figure 4) and at the MRCA of *Rhinocorynura*, *Rhettomia* and *Corynurella* (node B in figure 4), and one in the sister clade to Augochlorini. No reversals from the posteriorly caged type back to the straight type were observed (electronic supplementary material, table S11). The anteriorly sheathed type evolved in the lineage leading to *Maculonomia* (node C in figure 4) and *Curvinomia* (node D in figure 4). The reduced and lost types were inferred on multiple branches of the phylogeny. The reconstructed character states at internal nodes are shown in figure 4, with pie charts indicating the relative probabilities of alternative states.

For the log-transformed dataset, floral breadth showed non-zero phylogenetic signal (Blomberg's $K = 0.402$, $p = 0.001$; Pagel's $\hat{\lambda} = 0.401$, $p = 0.001$; $n = 83$ taxa) and phylogenetic clustering analysis indicated that scopa types are non-randomly distributed across the Halictidae phylogeny (electronic supplementary material, table S2). At the genus/subgenus (operational-taxon) level ($n = 83$), the straight type showed strong clustering ($D = -0.673$, $p < 0.001$), as did the posteriorly caged type ($D = -0.857$, $p < 0.001$) and the lost type ($D = -2.903$, $p = 0.003$). By contrast, the anteriorly sheathed ($D = -0.643$, $p = 0.067$) and reduced type ($D = 0.355$, $p = 0.074$) showed weaker evidence of clustering. Species-level analyses ($n = 196/207$) showed stronger clustering across states, including the anteriorly sheathed and reduced types.

(ii) Phylogenetic generalized least squares and OUwie results

In PGLS with log-transformed floral breadth, the coefficient for the posteriorly caged type relative to the straight type was positive but not significant ($\beta = 0.565$, $p = 0.130$; Pagel's $\hat{\lambda} = 0.257$; table 1). Under raw and square-root transformations, the posteriorly caged coefficient was positive and significant (raw: $\beta = 32.847$, $p < 0.001$, $\hat{\lambda} < 0.001$; square-root: $\beta = 2.484$, $p < 0.001$, $\hat{\lambda} < 0.001$; electronic supplementary material, table S3), whereas the corresponding posteriorly caged type contrasts became

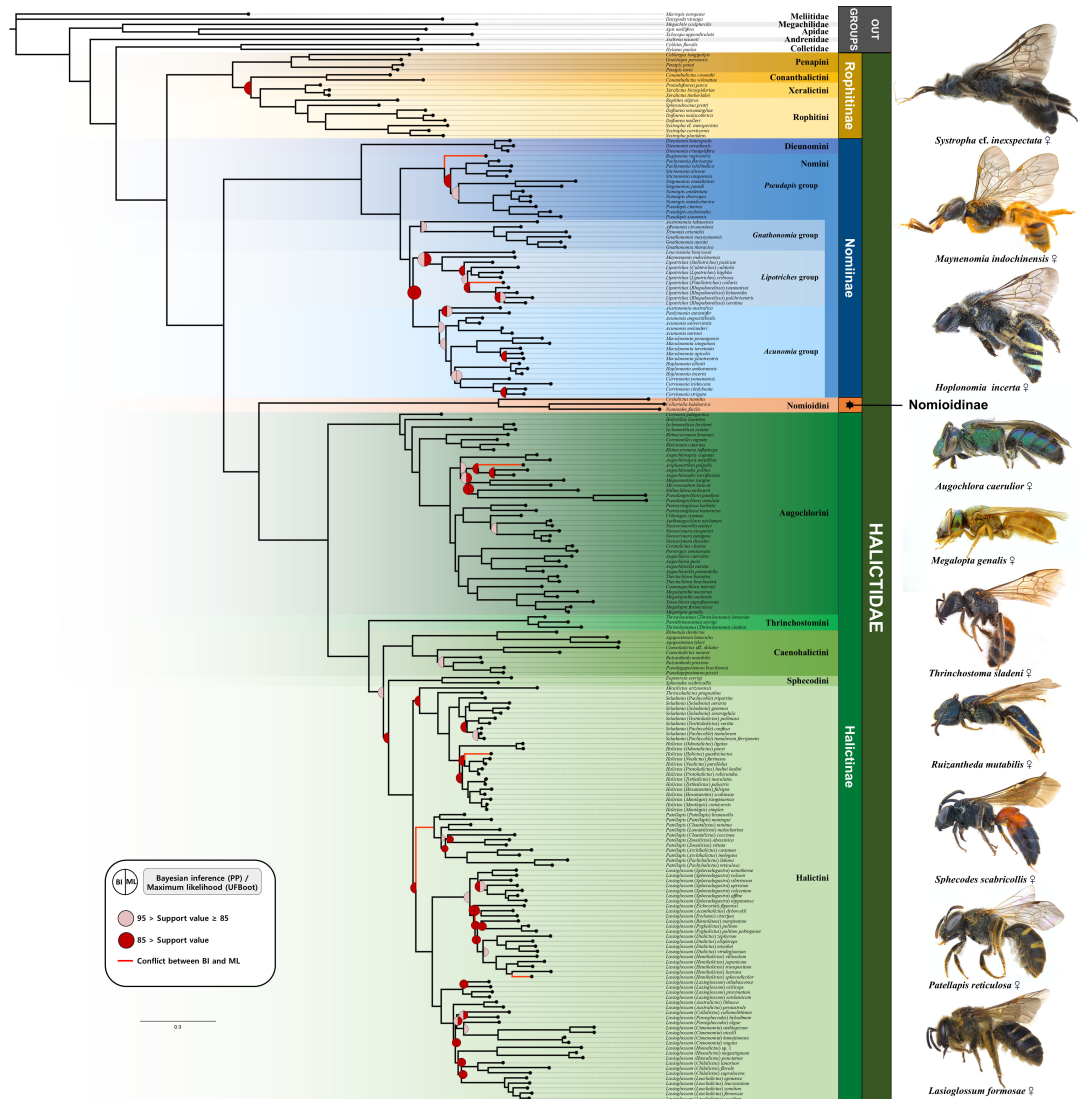


Figure 3. Main phylogeny of Halictidae with support. Concatenated five-gene phylogeny of Halictidae (207 taxa, ingroup) inferred using Bayesian inference (BI) and maximum likelihood (ML) (COI, EF-1 α , *wg*, LwRh, 28S; 3669 bp). Node support is shown by split symbols (left: Bayesian posterior probability; right: ML ultrafast bootstrap), coloured by support category (light pink: 85–94; red: <85). Branches highlighted in red indicate topological disagreement between BI and ML; nodes with high support in both analyses are left unmarked.

non-significant when λ was fixed at 1.0 ($p > 0.05$), indicating sensitivity to assumptions about residual phylogenetic covariance. Other scopa types (anteriorly sheathed, reduced and lost) showed no significant associations under any transformation ($p > 0.05$). Posterior-tree analyses confirmed a consistently positive posteriorly caged type coefficient across all 1000 trees, but significance was transformation-dependent: all trees yielded $p < 0.05$ under raw and square-root transformations, whereas none did under log-transformation. The signal for the posteriorly caged type is primarily concentrated in Halictini: removing Halictini eliminated significance entirely under log and square-root transformations (0/1000 trees) and substantially reduced it under raw transformation (650/1000). By contrast, removing Augochlorini increased the frequency of significant log-scale posteriorly caged type contrasts (168/1000 trees); raw and square-root significance was unchanged (1000/1000 trees).

PGLS indicated a significant difference in floral breadth between lifestyle categories. Eusocial taxa showed significantly higher log-transformed floral breadth than non-eusocial taxa ($\beta = 1.203$, $p < 0.001$; Pagel's $\hat{\lambda} = 0.457$, $n = 12$ eusocial, 69 non-eusocial, 2 parasitic; table 1). In terms of raw plant-family counts, eusocial taxa averaged 78.7 families (range = 1–142), whereas non-eusocial taxa averaged 27.6 (range = 1–110). Unlike the scopa–floral breadth association, this lifestyle effect was robust across transformations, posterior-tree analyses and clade-exclusion datasets, with all successfully fitted posterior-tree models yielding significant positive eusociality coefficients. In our dataset, 75% of eusocial taxa (9/12) possessed the posteriorly caged type scopa (electronic supplementary material, table S10). Results for all coding schemes (F2–F5) and PGLS analyses under the three data transformations (raw, log and square-root) are provided in electronic supplementary material, tables S3–S6.

Under the primary log-transformed F2A coding scheme, the two-regime OUM model was best supported (Akaike weight, AICw = 0.754; table 2). The estimated optimum floral breadth was higher in the posteriorly caged-type (P) regime than in the non-P regime ($\theta_P = 3.63$ versus $\theta_{\text{non-P}} = 2.73$). Posterior-tree analyses supported higher optima for the posteriorly caged type-containing regime in 100% of trees under both log and square-root transformations, with OUM or OUMV models best-supported in the majority of posterior trees (100/100 under log; 100/100 under square-root). Raw-scale analyses were excluded from biological inference owing to boundary optima far exceeding observed values, a pattern consistent across both

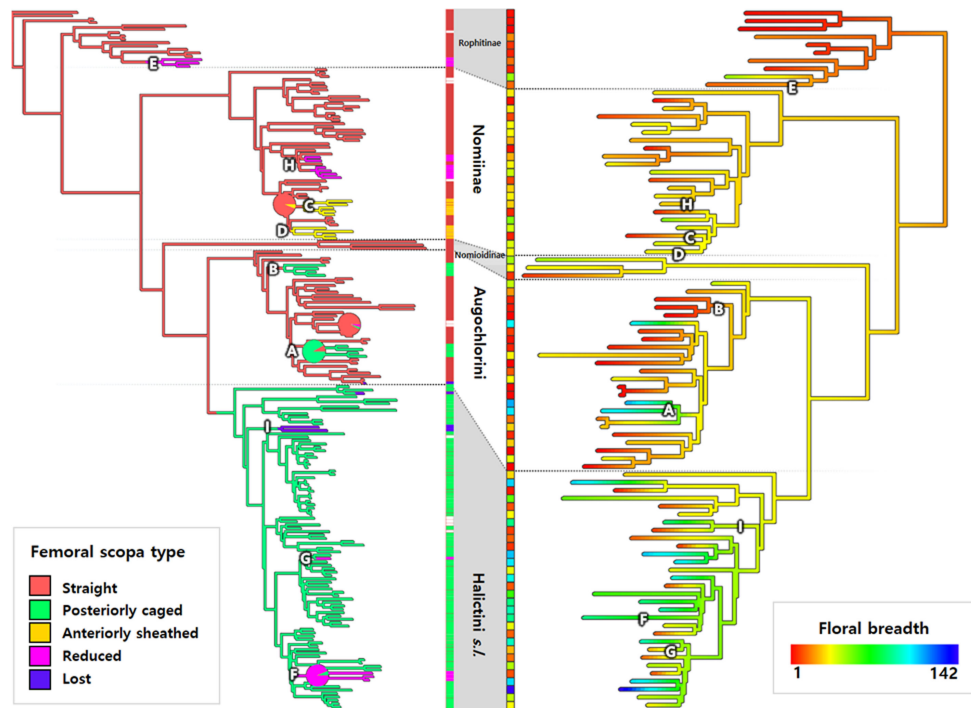


Figure 4. Femoral scopa evolution and floral breadth. Femoral scopa types and floral breadth mapped onto the pruned comparative tree. Left, ancestral state reconstruction of femoral scopa type (node pies are shown only for nodes with maximum marginal probability <0.95). Right, the corresponding tree with tips coloured by floral breadth (number of recorded plant families; scale 1–142). Labels A–I denote focal internal nodes referenced in the text. The central band indicates the subfamily- and tribe-level affiliation of taxa.

Table 1. Primary phylogenetic generalized least squares (PGLS) results for associations of log-transformed floral breadth with (A) femoral scopa type and (B) lifestyle. PGLS models were fitted on the genus-/subgenus-level phylogeny ($n = 83$) with Pagel's λ estimated by maximum likelihood, ML ($\lambda = \text{ML}$). (A) Results for femoral scopa morphology (F5 coding) using treatment contrasts with the straight type ($n = 44$) as the reference. (B) Results for lifestyle using treatment contrasts with non-eusocial ($n = 69$) as the reference. FB, floral breadth; s.e., standard error; $\hat{\lambda}$ = Pagel's λ . Full PGLS results for raw and square-root transformations, alternative coding schemes and sensitivity analyses are provided in electronic supplementary material, tables S3–S6.

predictor type	predictor	no. taxa	estimate	s.e.	t-value	p-value	$\hat{\lambda}$
(A) femoral scopa	posteriorly caged	30	0.565	0.369	1.530	0.130	0.257
	anteriorly sheathed	2	−0.308	0.801	−0.385	0.702	
	reduced	5	0.368	0.514	0.716	0.476	
	lost	2	0.404	0.832	0.486	0.628	
(B) lifestyle	eusocial	12	1.203	0.333	3.617	<0.001	0.457
	parasitic	2	0.187	0.759	0.246	0.806	

MCC and posterior trees. Robustness results across alternative transformations and coding schemes (F2–F5) are summarized in electronic supplementary material, tables S8 and S9; full model sets are in electronic supplementary material, S3.

(iii) Pagel's test results

Pagel's test supported non-independence between the posteriorly caged type and eusociality (likelihood ratio (LR) = 9.968, $p = 0.041$), with similar results when parasitic taxa were excluded (LR = 9.677, $p = 0.046$). Results for all PGLS and Pagel's tests are provided in electronic supplementary material, table S7.

4. Discussion

Our study identifies non-random phylogenetic associations among femoral scopa type, floral breadth and sociality across Halictidae. Using a densely sampled phylogenetic framework that recovers the expected higher-level structure of the family, we evaluated associations among femoral scopa type, floral breadth and social behaviour within a shared evolutionary history. These associations suggest that pollen-transport morphology and floral breadth are linked to the evolutionary distribution of eusociality in this family without resolving causal direction.

Table 2. Primary OUwie model comparison for log-transformed floral breadth under the binary F2A scopa coding scheme shown for the all-rates-different (ARD) transition model (primary analysis). Models are ranked by AICc. logLik, log-likelihood; AICc, Akaike information criterion corrected for small sample size; Δ AICc, difference in AICc relative to the best-ranked model; AICw, Akaike weight; α , strength of attraction towards the optimum; σ^2 , evolutionary-rate parameter; θ , trait optimum; n.a., not applicable; FB, floral breadth; P, posteriorly caged; non-P, non-posteriorly caged (i.e. straight, anteriorly sheathed, reduced or lost). Parameters are on the $\ln(\text{FB} + 1)$ scale. For BM1 and OU1, a single optimum is assumed ($\theta_{\text{non-P}} = \theta_{\text{P}}$). Full results across transition models, transformations and coding schemes are provided in electronic supplementary material, tables S8 and S9.

model	rank	logLik	AICc	Δ AICc	AICw	α	$\sigma^2_{\text{non-P}}$	σ^2_{P}	$\theta_{\text{non-P}}$	θ_{P}
OUM	1	−148.764	310.63	0.000	0.754	3.958	9.296	9.296	2.729	3.627
OUMV	2	−149.296	314.086	3.452	0.134	2.683	6.384	6.470	2.722	3.752
OU1	3	−151.860	314.499	3.866	0.109	2.028	5.889	5.889	2.976	2.976
BM1	4	−158.384	325.281	14.647	0.000	n.a.	3.207	3.207	2.530	2.530

(a) Evolutionary associations among eusociality, floral breadth and pollen scopa morphology

PGLS and OUwie analyses were directionally consistent in associating posteriorly caged scopa with higher floral breadth (tables 1 and 2), but the PGLS signal varied in significance among transformations and was concentrated largely in Halictini, suggesting that the detected pattern reflects a limited number of evolutionary transitions rather than a broadly distributed association. We interpret this pattern as consistent with functional differences among scopal architectures that may influence how effectively pollen from diverse floral hosts can be collected and retained. Although our floral breadth measure is derived from visitation records rather than pollen-load analyses, recent work suggests that visitation data can provide an informative, though imperfect, proxy for dietary breadth in bees [20].

Transformation-dependent significance may reflect both uneven sampling of floral records and compression of high floral-breadth values on the log scale. Nevertheless, the posteriorly caged coefficient remained positive across posterior trees and transformations, supporting a consistent directional tendency rather than a uniformly significant effect. Based on specimen observations, the cage-like enclosure formed by relatively sparse, elongate posterior hairs and flexible anterior hairs appears to create an internal cavity capable of accommodating pollen grains of varying sizes and shapes (figure 1c(ii,iii)), suggesting that this architecture may provide structural features that facilitate handling and retention of diverse pollen types. Compared with denser scopal arrays which may impose tighter packing constraints [7] (figure 1c(i,iv)), this loosely caged structure could plausibly stabilize pollen loads across a wider range of grain morphologies, potentially reducing handling constraints when foraging across diverse floral hosts [16].

By contrast, other scopa types showed no detectable association with recorded floral breadth in our dataset. Limited sample sizes likely reduce power for some rare types, but these morphologies may also reflect alternative ecological strategies rather than generalized foraging. For example, the anteriorly sheathed type, occurring in taxa that also possess additional propodeal scopae (figure 1d(ii)), may represent a strategy focused on increasing pollen load capacity rather than expanding floral breadth. The reduced type often coincides with shifts in pollen-transport strategy (figure 1d(iii)) or specialization, and the lost type is tightly associated with cleptoparasitism (figure 1d(iv)). Together, these patterns suggest that null associations for these states could reflect a combination of ecological divergence and limited statistical power.

Eusocial taxa showed broader floral breadth in our dataset, paralleling broader patterns in social bee lineages, where eusocial taxa exhibit elevated rates of dietary generalization relative to non-eusocial relatives [19]. In Halictidae, this eusociality–floral breadth relationship co-occurs with scopa type: discrete-trait analyses supported non-independence between the posteriorly caged type and eusociality (electronic supplementary material, table S7). These phylogenetic associations, however, do not by themselves establish a causal pathway: several non-eusocial taxa within the posteriorly caged-rich lineages, such as *Agapostemon* and non-eusocial subgenera of *Lasioglossum*, show floral breadths comparable to or greater than eusocial congeners. This suggests that broader floral use may be permissive rather than sufficient for social transitions, and that additional ecological or genetic factors were likely required. Notably, unlike the scopa–floral breadth association, this eusociality effect was unaffected by clade composition or data transformation, suggesting it reflects a broadly distributed pattern across Halictidae rather than a lineage-specific signal.

The association between eusociality and floral breadth should therefore be interpreted as phylogenetic covariance rather than evidence for a single causal pathway: both broad host-plant use and posteriorly caged scopa tend to occur in lineages where pollen-transport morphology may have reduced constraints on exploiting diverse pollen sources. A broadly analogous, though non-homologous, pattern is seen in eusocial corbiculate bees (Apini, Bombini and Meliponini), where specialized pollen-carrying structures evolved before the major eusocial lineages and are associated with diverse floral foraging [10,11]. Similarly, in our dataset, 75% of eusocial halictid taxa possess the posteriorly caged scopa, which evolved repeatedly from the ancestral straight type. While causal direction remains unresolved, this interpretation is consistent with the idea that broader floral use could help meet colony-level resource demands in Halictidae.

Eusocial colonies require reliable acquisition of pollen and nectar to sustain multiple nestmates and overlapping generations [29]. Because floral resources are spatially and temporally heterogeneous, and bees forage within restricted distances from their nests, the ability to exploit a wide range of flowering plants may allow colonies to maintain more stable resource intake, buffering against seasonal and spatial fluctuations in availability. In Halictidae, the repeated occurrence of posteriorly caged scopa in lineages with higher recorded floral breadth is consistent with this generalist-capacity hypothesis and may, together

with broader floral use, have made it easier for some lineages to meet the resource demands associated with colony-level provisioning.

However, this pattern is not deterministic. Some eusocial taxa, such as *Augochloropsis* and *Megalopta*, retain the straight type, while many posteriorly caged taxa remain non-eusocial. These exceptions indicate that while the posteriorly caged type and broad floral breadth may have provided permissive conditions for the evolution of eusociality, additional factors, such as behavioural flexibility, environmental opportunities or genetic architecture, are likely required for eusocial evolution to proceed.

Several lineages with reduced or lost femoral scopae retain floral breadth records comparable to posteriorly caged-type relatives, suggesting breadth may be maintained independently of scopa elaboration once established. Cleptoparasitic lineages with the lost type, such as *Sphecodes*, are nested within Halictini *sensu lato* and often exploit phylogenetically close halictine hosts, including *Halictus* and *Lasioglossum* [32]. Their broad floral association records may therefore partly reflect host-associated ecological contexts used by closely related host lineages, rather than a direct association between lost femoral scopa and broad resource use. Overall, these results suggest that variation in floral breadth and the diversity of social systems in Halictidae reflect multiple interacting factors rather than a simple linear pathway.

(b) Patterns of floral breadth and evolutionary conservatism of scopa

The subfamily Rophitinae has often been described as a clade in which most species are oligolectic, exhibiting narrow host ranges [30]. Subfamily-level contrasts in floral breadth (figure 2; electronic supplementary material, S5) broadly match these natural history expectations, with Rophitinae tending towards narrower breadth than other subfamilies. Consistent with phylogenetic signal in floral breadth, closely related halictid lineages often resemble one another in breadth. Although uneven research effort can influence absolute breadth estimates, the alignment of these broad subfamily-level contrasts with well established natural history suggests that sampling alone may not fully account for the observed patterns. Within Rophitinae, breadth is generally narrow, yet some derived genera show broader floral breadth than basal taxa; for example, *Dufourea* was recorded visiting many plant families and includes the only known polylectic species within this subfamily (*Dufourea paradoxa*) [60]. Similar within-subfamily variation is also observed in Nomiinae and Halictinae.

The inferred transitions between scopa types are directionally asymmetric (figure 4). Together with the clade-level retention of posteriorly caged and lost types, these results suggest limited reversals once derived scopa states arise. Consistent with the clustering results, scopa type is largely conserved within clades. This structural conservatism appears to reflect phylogenetic history more strongly than body size or other ecological correlates: *Lasioglossum dybowskii* and *Lasioglossum politum pekingense*, which differ by fourfold in body length, share identical scopa types [61,62], suggesting that scopa type is transmitted within lineages largely independently of size-related constraints. However, this conservatism is occasionally modified in specific ecological contexts: (i) shifts to abdominal pollen transport (*Systropha*, node E and *Homalictus*, node F in figure 4), where pollen is carried primarily on abdominal scopa rather than the hind femur; (ii) shifts towards narrow host specialization (oligolecty) (e.g. *Lasioglossum (Sphecodogastra) sensu stricto*; Onagraceae specialist; node G in figure 4) and *Lipotriches (Rhopalomelissa)*; Poaceae specialist; node H in figure 4), which may favour more efficient foraging on a narrow set of floral hosts over broad generalism [63,64]; and (iii) parasitism (e.g. the cleptoparasitic genus *Sphecodes* (node I in figure 4), whose females lay eggs in the nests of other bee species and rely on host-provisioned pollen), in which females do not collect and transport pollen.

The contrast between species-level and genus/subgenus-level clustering patterns further reflects this conservatism: scopa type is broadly shared within genera and subgenera, such that the stronger clustering signal at species level likely reflects within-lineage retention rather than independent acquisition at fine scales. Transitions among derived states are rare, and when they do occur, they tend to coincide with major ecological reorganizations, as with the lost type in cleptoparasites and the reduced type in lineages shifted to abdominal pollen transport, suggesting that ecological context reinforces state stability once a derived morphology is established. Against this background of general conservatism, the repeated origins of posteriorly caged scopa from the ancestral straight state, including in Halictini *sensu lato* and Augochlorini, are particularly notable. Although the statistical signal is concentrated largely in Halictini, this repeated association with broader recorded floral breadth suggests a candidate morphology–ecology link that warrants functional testing.

Among these secondary modifications, reduction of the femoral scopa is particularly heterogeneous. The reduced type encompasses multiple lineage-specific forms of hair reduction (see Methods) and is therefore best interpreted as a composite state rather than a single derived morphology. Our reconstructions suggest that reductions arose repeatedly from different ancestral scopa types, indicating convergent outcomes reached via multiple evolutionary pathways. Even so, reductions primarily involve the reduction of hair elaboration (length and/or density), whereas the spatial placement and overall orientation of the hair fields tend to track the inferred ancestral condition (e.g. straight versus posteriorly caged). This pattern may indicate that the spatial placement of scopal hair fields is more conserved than hair length or density.

Ethics. This study used insect specimens. Ethical approval was not required. No fieldwork permits were required.

Data accessibility. Data and code supporting this article are available from Zenodo [65]. DNA sequence data are deposited in GenBank; accession numbers are provided in electronic supplementary material, S2. Electronic supplementary material, S1–S5 are available online [66].

Declaration of AI use. We used AI tools to assist with language editing, organization of literature references, clarification of statistical methods, and troubleshooting and refinement of R code. All AI-assisted outputs were reviewed and verified by the authors, who take full responsibility for the integrity of the reported analyses.

Authors' contributions. S.H.J.: conceptualization, data curation, formal analysis, software, investigation, methodology, visualization, resources, writing—original draft, writing—review and editing; S.H.L.: project administration, methodology, visualization, writing—original draft, writing—review and editing; M.S.O.: methodology, validation, writing—review and editing; M.H.L.: methodology, validation, writing—review and

editing; R.B.G.: resources, writing—review and editing; S.W.L.: funding acquisition, project administration, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

- Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- Wainwright PC. 2007 Functional versus morphological diversity in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **38**, 381–401. (doi:10.1146/annurev.ecolsys.38.091206.095706)
- Michener CD. 2007 *The bees of the world*, 2nd edn. Baltimore, MD: Johns Hopkins University Press.
- Rodríguez-Gironés MA, Llandres AL. 2008 Resource competition triggers the co-evolution of long tongues and deep corolla tubes. *PLoS One* **3**, e2992. (doi:10.1371/journal.pone.0002992)
- Shimizu A *et al.* 2014 Fine-tuned bee–flower coevolutionary state hidden within multiple pollination interactions. *Scient. Rep.* **4**, 3988. (doi:10.1038/srep03988)
- Flores-Prado L, Pinto CF, Rojas A, Fontúrbel FE. 2014 Strong selection on mandible and nest features in a carpenter bee that nests in two sympatric host plants. *Ecol. Evol.* **4**, 1820–1827. (doi:10.1002/ece3.995)
- Thorp RW. 1979 Structural, behavioural, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. MO Bot. Gard.* **66**, 788. (doi:10.2307/2398919)
- Alves-dos-Santos I. 2009 Cleptoparasite bees, with emphasis on the oilbees hosts. *Acta Biol. Colomb.* **14**, 107–114.
- Michener CD, Winston ML, Jander R. 1978 Pollen manipulation and related activities and structures in bees of the family Apidae. *Univ. Kans. Sci. Bull.* **51**, 575–601. (doi:10.5962/bhl.part.17249)
- Cardinal S, Danforth BN. 2011 The antiquity and evolutionary history of social behavior in bees. *PLoS One* **6**, e21086. (doi:10.1371/journal.pone.0021086)
- Martins AC, Melo GAR, Renner SS. 2014 The corbiculate bees arose from New World oil-collecting bees: implications for the origin of pollen baskets. *Mol. Phylogenet. Evol.* **80**, 88–94. (doi:10.1016/j.ympev.2014.07.003)
- Danforth BN, Minckley RL, Neff JL. 2019 Bee phylogeny, bee diversity, and the distinction between solitary and social bees. In *The solitary bees: biology, evolution, conservation*, pp. 6–36, 2nd edn. Princeton, NJ: Princeton University Press. (doi:10.1515/9780691189321-003)
- Dar SA *et al.* 2025 Solitary bees as vital bioindicators: a comprehensive review of the diversity, decline, and conservation imperatives of the Halictidae family. *Entomol. Res.* **55**, e70047. (doi:10.1111/1748-5967.70047)
- Michener CD, McGinley RJ, Danforth BN. 1994 *The bee genera of North and Central America (Hymenoptera: Apoidea)*. Washington, DC: Smithsonian Institution Press.
- Gonzalez VH, Griswold T, Praz CJ, Danforth BN. 2012 Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. *Syst. Entomol.* **37**, 261–286. (doi:10.1111/j.1365-3113.2012.00620.x)
- Portman ZM, Tepedino VJ. 2017 Convergent evolution of pollen transport mode in two distantly related bee genera (Hymenoptera: Andrenidae and Melittidae). *Apidologie* **48**, 461–472. (doi:10.1007/s13592-016-0489-8)
- Smith AR, López Quintero JJ, Moreno Patiño JE, Roubik DW, Wcislo WT. 2012 Pollen use by *Megalopta* sweat bees in relation to resource availability in a tropical forest. *Ecol. Entomol.* **37**, 309–317. (doi:10.1111/j.1365-2311.2012.01367.x)
- Wray JC, Elle E. 2016 Pollen preferences of two species of *Andrena* in British Columbia's oak-savannah ecosystem. *J. Entomol. Soc. Br. Columbia* **113**, 39–48.
- Wood TJ, Müller A, Praz C, Michez D. 2023 Elevated rates of dietary generalization in eusocial lineages of the secondarily herbivorous bees. *BMC Ecol. Evol.* **23**, 67. (doi:10.1186/s12862-023-02175-1)
- Smith C, Bachelder N, Russell AL, Morales V, Mosher AR, Seltnmann KC. 2025 Pollen specialist bee species are accurately predicted from visitation, occurrence and phylogenetic data. *Oecologia* **207**, 13. (doi:10.1007/s00442-024-05653-5)
- Bommarco R, Biesmeijer JC, Meyer B, Potts SG, Pöyry J, Roberts SPM, Steffan-Dewenter I, Ockinger E. 2010 Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B* **277**, 2075–2082. (doi:10.1098/rspb.2009.2221)
- Michez D, Patiny S, Rasmont P, Timmermann K, Vereecken NJ. 2008 Phylogeny and host-plant evolution in Melittidae s.l. (Hymenoptera: Apoidea). *Apidologie* **39**, 146–162. (doi:10.1051/apido:2007048)
- Sedivy C, Praz CJ, Müller A, Widmer A, Dorn S. 2008 Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees. *Evolution* **62**, 2487–2507. (doi:10.1111/j.1558-5646.2008.00465.x)
- Fontaine C, Collin CL, Dajoz I. 2008 Generalist foraging of pollinators: diet expansion at high density. *J. Ecol.* **96**, 1002–1010. (doi:10.1111/j.1365-2745.2008.01405.x)
- Kleijn D, Raemakers I. 2008 A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* **89**, 1811–1823. (doi:10.1890/07-1275.1)
- Wood TJ, Roberts SPM. 2017 An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. *Biol. Conserv.* **215**, 72–80. (doi:10.1016/j.biocon.2017.09.009)
- Kaluza BF, Wallace HM, Heard TA, Minden V, Klein AM, Leonhardt SD. 2018 Social bees are fitter in more biodiverse environments. *Scient. Rep.* **8**, 12353. (doi:10.1038/s41598-018-30126-0)
- Wood TJ *et al.* 2021 Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. *J. Anim. Ecol.* **90**, 2421–2430. (doi:10.1111/1365-2656.13553)
- Devkota K, Dos Santos CF, Souza-Santos PD, Ramos JD, Otesbelgue A, Mishra BP, Almeida EAB, Blochtein B. 2024 Pollen diet diversity across bee lineages varies with lifestyle rather than colony size. *J. Insect Sci.* **24**, 1. (doi:10.1093/jisesa/ieae023)
- Patiny S, Michez D, Danforth BN. 2008 Phylogenetic relationships and host-plant evolution within the basal clade of Halictidae (Hymenoptera, Apoidea). *Cladistics* **24**, 255–269. (doi:10.1111/j.1096-0031.2007.00182.x)

31. Gibbs J, Brady SG, Kanda K, Danforth BN. 2012 Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). *Mol. Phylogenet. Evol.* **65**, 926–939. (doi:10.1016/j.ympev.2012.08.013)
32. Habermannová J, Bogusch P, Straka J. 2013 Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: Sphecoides). *PLoS One* **8**, e64537. (doi:10.1371/journal.pone.0064537)
33. Gonçalves RB. 2016 A molecular and morphological phylogeny of the extant Augochlorini (Hymenoptera, Apoidea) with comments on implications for biogeography. *Syst. Entomol.* **41**, 430–440. (doi:10.1111/syen.12166)
34. Ascher JS, Pickering J. 2025 *Discover Life bee species guide and world checklist* (Hymenoptera: Apoidea: Anthophila). See https://www.discoverlife.org/mp/20q?guide=Apoidea_species.
35. Pesenko YA. 2006 Contributions to the halictid fauna of the eastern Palaearctic Region: genus *Seladonia* Robertson (Hymenoptera: Halictidae, Halictinae). *ESAKIA* **46**, 53–82. (doi:10.5109/2861)
36. Pauly A. 2009 Classification des Nomiinae de la Région Orientale, de Nouvelle-Guinée et des îles de l'Océan Pacifique (Hymenoptera: Apoidea: Halictidae). *Bull. Inst. R. Sci. Nat. Belg. Entomol* **79**, 151–229. Classification of the Nomiinae of the Oriental Region, New Guinea and the islands of the Pacific Ocean (Hymenoptera: Apoidea: Halictidae) [In French].
37. Katoh K, Standley DM. 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780. (doi:10.1093/molbev/mst010)
38. Vaidya G, Lohman DJ, Meier R. 2011 SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* **27**, 171–180. (doi:10.1111/j.1096-0031.2010.00329.x)
39. Ronquist F *et al.* 2012 MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **61**, 539–542. (doi:10.1093/sysbio/sys029)
40. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. 2020 IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* **37**, 1530–1534. (doi:10.1093/molbev/msaa015)
41. Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2017 PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Biol. Evol.* **34**, 772–773. (doi:10.1093/molbev/msw260)
42. Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermini LS. 2017 ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* **14**, 587–589. (doi:10.1038/nmeth.4285)
43. Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018 UFBoot2: improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* **35**, 518–522. (doi:10.1093/molbev/msx281)
44. Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010 New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Syst. Biol.* **59**, 307–321. (doi:10.1093/sysbio/syq010)
45. Royal Botanic Gardens, Kew. 2025 *Plants of the world online*. See <http://www.plantsoftheworldonline.org/>.
46. Bollback JP. 2006 SIMMAP: stochastic character mapping of discrete traits on phylogenies. *BMC Bioinform.* **7**, 88. (doi:10.1186/1471-2105-7-88)
47. Revell LJ. 2024 phytools 2.0: An updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* **12**, e16505. (doi:10.7717/peerj.16505)
48. Paradis E, Schliep K. 2019 ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/bioinformatics/bty633)
49. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 GELGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131. (doi:10.1093/bioinformatics/btm538)
50. Fritz SA, Purvis A. 2010 Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042–1051. (doi:10.1111/j.1523-1739.2010.01455.x)
51. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2025 *caper: Comparative analyses of phylogenetics and evolution in R*, v. 1.0.4. Vienna, Austria: R Foundation for Statistical Computing.
52. Blomberg SP, Garland Jr T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution (N Y)* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)
53. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
54. Freckleton RP, Harvey PH, Pagel M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)
55. Yu G, Smith DK, Zhu H, Guan Y, Lam TY. 2017 ggtree: An R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol. Evol.* **8**, 28–36. (doi:10.1111/2041-210X.12628)
56. Wickham H. 2016 *ggplot2: Elegant graphics for data analysis*. Cham, Switzerland: Springer. (doi:10.1007/978-3-319-24277-4)
57. Beaulieu JM, Jhwueng DC, Boettiger C, O'Meara BC. 2012 Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* **66**, 2369–2383. (doi:10.1111/j.1558-5646.2012.01619.x)
58. Hansen TF. 1997 Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**, 1341–1351. (doi:10.1111/j.1558-5646.1997.tb01457.x)
59. Pagel M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**, 37–45. (doi:10.1098/rspb.1994.0006)
60. Müller A. 2018 Pollen host selection by predominantly alpine bee species of the genera *Andrena*, *Panurginus*, *Dufourea*, *Megachile*, *Hoplitis* and *Osmia* (Hymenoptera, Apoidea). *Alp. Entomol.* **2**, 101–113. (doi:10.3897/alpento.2.29250)
61. Murao R, Lee H, Tadauchi O. 2014 *Lasioglossum* (*Acanthalictus*) *dybowski* (Hymenoptera, Halictidae) newly recorded from South Korea, with a checklist of the genus *Lasioglossum* in Korean Peninsula. *J. Hymenopt. Res* **38**, 141–153. (doi:10.3897/jhr.38.7572)
62. Blüthgen P. 1925 Beiträge zur Kenntnis der Bienengattung *Halictus* Latr. II. *Arch. Naturgesch. A* **90**, 86–136. Contributions to the knowledge of the bee genus *Halictus* Latreille. II [In German].
63. McGinley RJ. 2003 Studies of Halictinae (Apoidea: Halictidae), II: revision of *Sphecodogastra* Ashmead, floral specialists of Onagraceae. *Smithson. Contrib. Zool.* **610**, 1–55. (doi:10.5479/si.00810282.610)
64. Pauly A. 2014 Les abeilles des Graminées ou *Lipotriches* Gerstaecker, 1858, *sensu stricto* (Hymenoptera: Apoidea: Halictidae: Nomiinae) de l'Afrique subsaharienne. *Belg. J. Entomol* **20**, 1–393. The Bees of Grasses or *Lipotriches* Gerstaecker, 1858, *sensu stricto* (Hymenoptera: Apoidea: Halictidae: Nomiinae) of sub-Saharan Africa [In French].
65. Jung S, Lee S, Oh M, Lee M, Gonçalves RB, Lee S. 2026 Data and code for: Evolutionary associations among pollen scopa structure, floral breadth, and eusociality in Halictidae (Hymenoptera: Apoidea) [Data set]. Zenodo. (doi:10.5281/zenodo.20543816)
66. Lee S, Jung S, Lee S, Oh M, Lee M, Gonçalves RB. 2026 . Supplementary Material from: Evolutionary Associations among Pollen Scopa Structure, Floral Breadth, and Eusociality in Halictidae (Hymenoptera: Apoidea). Figshare <https://doi.org/10.6084/m9.figshare.c.8572287>