The Impact of Molecular Data on Our Understanding of Bee Phylogeny and Evolution

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Abstract

Our understanding of bee phylogeny has improved over the past fifteen years
as a result of new data, primarily nucleotide sequence data, and new methods,
primarily model-based methods of phylogeny reconstruction. Phylogenetic
studies based on single or, more commonly, multilocus data sets have helped
resolve the placement of bees within the superfamily Apoidea; the relation-
ships among the seven families of bees; and the relationships among bee
subfamilies, tribes, genera, and species. In addition, molecular phylogenies
have played an important role in inferring evolutionary patterns and pro-
cesses in bees. Phylogenies have provided the comparative framework for
understanding the evolution of host-plant associations and pollen special-
ization, the evolution of social behavior, and the evolution of parasitism.
In this paper, we present an overview of significant discoveries in bee phy-
logeny based primarily on the application of molecular data. We review the
phylogenetic hypotheses family-by-family and then describe how the new
phylogenetic insights have altered our understanding of bee biology.

INTRODUCTION

The phylogeny used in developing a classification is a hypothesis. With new characters or additional taxa, phylogeny often changes. Its great merit is that one can explain how it was developed, but it is always a hypothesis subject to challenge, perhaps to change.

Charles Michener (65)

Sister group(s): two groups or lineages that are closer to each other than to any other species or clade in the group

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Bees are arguably the most important group of angiosperm-pollinating insects. They arose in the early to mid-Cretaceous approximately 140 to 110 Mya (million years ago), roughly coincident with the origins and early diversification of flowering plants. Bees, comprising nearly 20,000 described species (8), and angiosperms, comprising over 250,000 described species (100), represent one of the most successful (and fascinating) coevolutionary partnerships on earth. Bees are also of enormous economic importance. They are the most important wild and managed agricultural pollinators, and an estimated one-third of the human diet is derived from fruits, vegetables, and nuts that rely on animal-mediated, primarily bee, pollination (46).

Because of their importance in both basic and applied research, it is essential that we have a clear understanding of bee biodiversity, phylogeny, evolution, and diversification. Over the past 15 years our understanding of bee phylogeny and evolution has improved dramatically, due largely to the increased availability of molecular (especially single-copy, nuclear gene) data and improved methods of phylogenetic analysis, including maximum-likelihood (42) and Bayesian (43) methods. In addition, molecular phylogenies, in combination with fossil data, can now be used to generate "fossil-calibrated" phylogenies by using model-based, relaxed-clock methods (31). Molecular studies have revised our understanding of the sister group to the bees (70, 75), family-level relationships in bees (29), evolution and antiquity of eusociality (11, 17), parasitism (19, 37, 99), and host-plant evolution (84, 96). Detailed, multigene phylogenies now exist for most bee families, subfamilies, and many tribes. It is therefore timely to summarize the major insights derived from more than a decade of molecular research on bee phylogeny.

PHYLOGENY

In the sections below, we review recent findings on bee phylogeny, starting with the placement of bees within the superfamily Apoidea, the family-level phylogeny of bees, and the relationships

COMMONLY USED GENES IN BEE (AND WASP) PHYLOGENY

The number of genes used to reconstruct bee phylogeny has expanded dramatically over the past 15 years. Early studies (14, 21, 47) tended to focus on mitochondrial genes because they are easy to amplify. Mitochondrial genes, such as 16S, *cytB*, and COI and/or COII, continue to be widely used in bee phylogeny (**Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**), but these genes tend to have their greatest utility at lower taxonomic levels (52). Nuclear ribosomal genes (18S and 28S) have been used in a variety of studies (**Supplemental Table 1**). However, ribosomal genes pose serious challenges because they are difficult to align unambiguously. Nuclear protein-coding genes provide an ideal source of data for higher-level studies because coding regions can be aligned unambiguously across a broad range of organisms (75). One of the most widely used protein-coding genes is the F2 copy of elongation factor-1α (EF-1α F2), which has been used in over 30 published bee studies (**Supplemental Table 1**). The availability of the complete honey bee genome (41) and a number of published bee transcriptomes (108) provides an opportunity for researchers to expand the range of protein-coding genes used in bee phylogeny.

▶ Supplemental Material

within the bee families to the level of tribe (see **Supplemental Figure 1** for a graphical summary of bee phylogeny to the tribal level). We focus on how molecular data have altered our understanding of bee phylogeny based on previous, primarily morphological, studies.

Phylogeny of Apoidea and the Sister Group to the Bees

Bees clearly arise from within a paraphyletic group of hunting wasps collectively referred to as spheciform wasps (64), sphecoid wasps (79), or apoid wasps (59); hence, bees are essentially "vegetarian wasps." The apoid wasps, including the families Heterogynaidae, Ampulicidae, Crabronidae, and Sphecidae, together with the bees comprise the Hymenoptera superfamily Apoidea. Where exactly bees arise from within the apoid wasps is not clear. Morphological studies (1, 59, 79) have mostly supported placement of bees as sister to the family Crabronidae. However, alternative topologies were obtained in all these studies and monophyly of Crabronidae was not universally supported.

Recent molecular studies (70, 75), based on limited taxon sampling for apoid wasps and a limited sampling of genes, have suggested that bees arise from within Crabronidae, thus rendering Crabronidae paraphyletic. The precise placement of bees within Crabronidae remains unclear.

Relationships Among the Bee Families

The extant bees (Hymenoptera: Apoidea: Anthophila) are currently classified into 7 widely recognized families (64) and 25 subfamilies. Bees are clearly a monophyletic group based on both morphological data [Michener (64) provides a complete list of morphological synapomorphies] and molecular data (26, 29, 70, 75). Most bee families are consistently recovered as monophyletic in both morphological and molecular studies. However, monophyly of the family Melittidae remains unclear (**Figure 1**). Both molecular and morphological studies have supported the monophyly of the long-tongued bees (Apidae and Megachilidae), but the short-tongued bees (Andrenidae, Colletidae, Halictidae, Melittidae, and Stenotritidae) are most likely a paraphyletic group (2, 29).

Molecular data have provided new insights into bee family-level phylogeny. Although Colletidae has traditionally been viewed as the most basal bee family (i.e., the family sister to the remaining bee families) on the basis of morphological studies (2, 33, 64), molecular studies have largely supported a root node near (or within) Melittidae (**Figure 1**). Studies that support a Melittidae basal hypothesis include those based on multilocus nuclear genes analyzed by parsimony and Bayesian methods (26, 29), combined multilocus nuclear genes plus morphology analyzed by parsimony methods (29), studies of unique introns in elongation factor-1α (EF-1α) (9), and most recently, studies based on gene duplication in EF-1α (10). None of the molecular studies have supported a root node of bees near Colletidae, even though colletids share a similar, but possibly convergently evolved, glossal morphology with apoid wasps.

Melittidae

Melittidae (**Figure 2**), one of the smallest bee families, includes roughly 200 described species in 3 subfamilies (Meganomiinae, Melittinae, and Dasypodainae), 4 tribes, and 15 extant genera (66). Melittid bees occur in semixeric, Mediterranean, and temperate areas of the Old and New World. The family is absent from Australia and South America. The area of greatest melittid phylodiversity is southern Africa, where all three subfamilies occur (63). Melittids are fascinating bees because the vast majority of species are narrow host-plant specialists (reviewed in Reference 67). Oil collecting, otherwise a relatively uncommon behavior in bees, has arisen multiple times in Melittinae (66).

Melittidae has been a problematic group from the perspective of phylogeny. Early phylogenetic studies based on combined data sets of both adult and larval morphology (2, 63) failed to identify any single morphological synapomorphy for the family, suggesting that melittids may be a paraphyletic

Paraphyletic:
describes a group comprising some, but not all, of the descendants of a single common ancestor; same as artificial group

Monophyletic:
describes a group comprising a common ancestor and all of its descendants; same as natural group or clade

Root node:
basal-most node of a tree or clade of interest; the position of this node determines the oldest sister-group relationship in the clade being analyzed
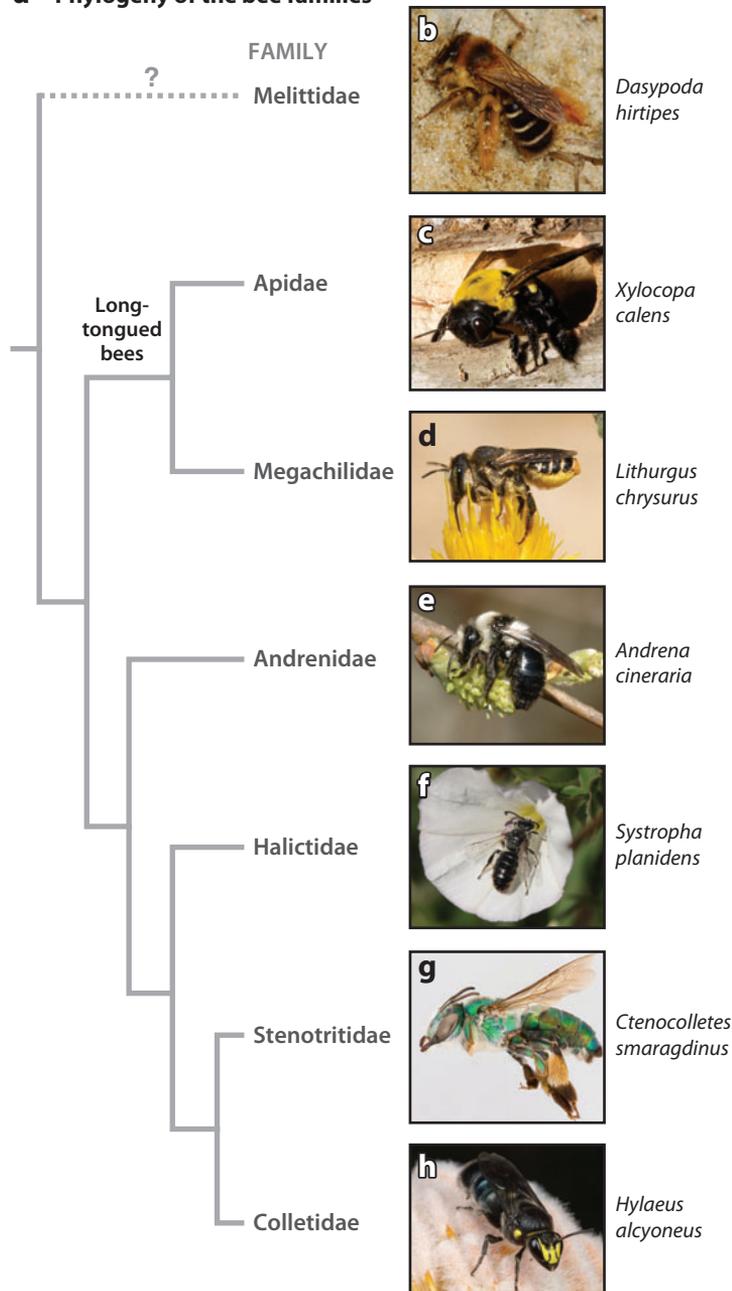
a Phylogeny of the bee families

Figure 1

(*a*) Family-level phylogeny of bees based on a variety of sources (9, 10, 26, 29). (*b*) *Dasypoda hirtipes*, female (credit: Nicolas Vereecken). (*c*) *Xylocopa calens*, female (credit: Nicolas Vereecken). (*d*) *Lithurgus chrysurus*, female (credit: Nicolas Vereecken). (*e*) *Andrena cineraria*, female (credit: James K. Lindsey). (*f*) *Systropha planidens*, male (credit: Alain Cipière). (*g*) *Ctenocolletes smaragdinus*, female (credit: Laurence Packer, York University: Bee Tribes of the World photographic project). (*h*) *Hylaeus alcyoneus*, female (credit and copyright: Bernhard Jacobi).
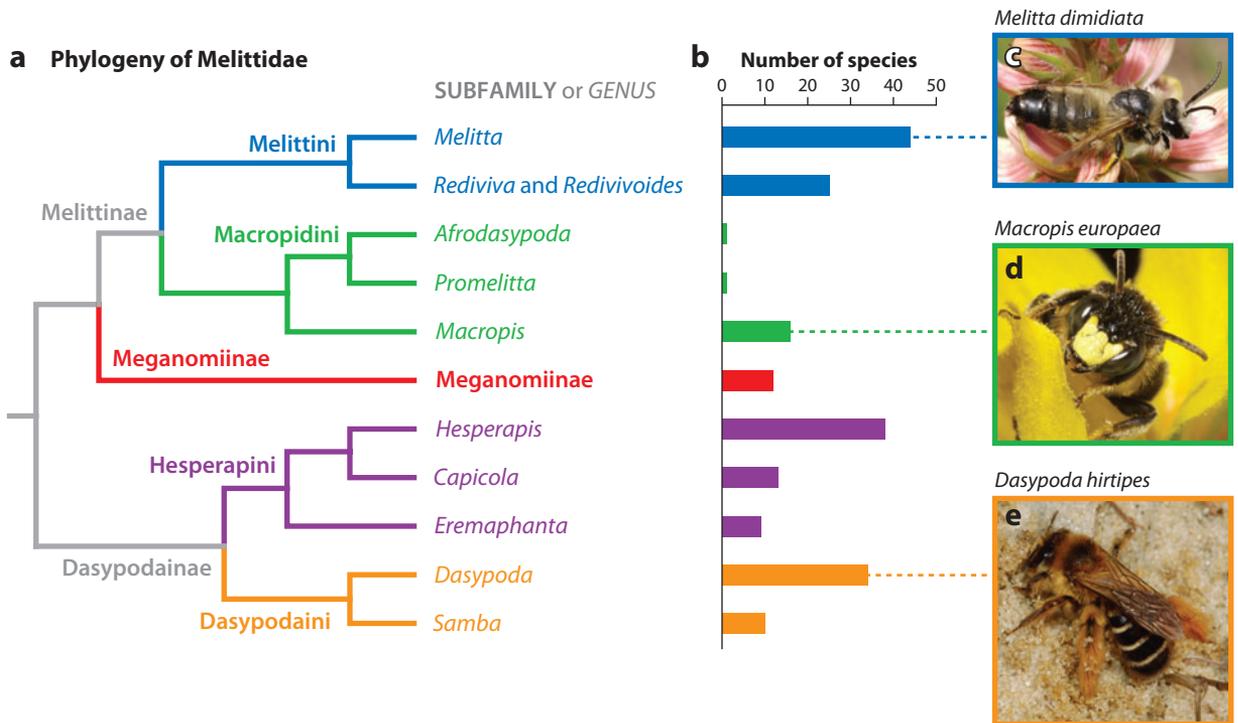
Figure 2

(*a*) Phylogeny of the subfamilies, tribes, and genera of Melittidae (66). (*b*) Histogram showing the number of described species (8, 66) for each group. (*c*) *Melitta dimidiata*, male (credit: Nicolas Vereecken). (*d*) *Macropis europaea*, male (credit: Nicolas Vereecken). (*e*) *Dasypoda hirtipes*, female (credit: Nicolas Vereecken).

group. Subsequent studies based exclusively on molecular data or on combined molecular and morphological data (26, 29, 66) obtained inconsistent or weakly supported results. Monophyly of Melittidae remains uncertain (**Figure 1**).

Although each of the currently recognized subfamilies of Melittidae (Meganomiinae, Melittinae, and Dasypodainae) is clearly monophyletic, the tribal limits, the placement of certain genera, and the relationships among tribes had not been clearly resolved exclusively on the basis of morphology (64). Michez et al. (66) analyzed phylogenetic relationships at the generic and tribal levels using 5 nuclear genes and 68 morphological characters and established the phylogenetic relationships among melittid genera, tribes, and subfamilies (**Figure 2**).

Apidae

Apidae (**Figure 3**) is the largest family of bees, with over 5,700 described species (8). Apid bees are widespread but their greatest diversity is in the Neotropical and Oriental regions, where they compose a large proportion of bee species. Apidae, which includes the most important managed pollinator, the honey bee (*Apis mellifera*), is an enormously diverse group with varied life histories. Many species are ground nesting (e.g., Emphorini, Eucerini), but some species nest in wood (e.g., some Xylocopini and *Tetrapedia*) or stems (e.g., Ceratinini and Allodapini) or construct nests from plant resins (e.g., Euglossini and Meliponini). Both primitive (e.g., Allodapini and Bombini) and advanced (e.g., Meliponini and Apini) eusociality occurs in Apidae. The family includes a large

Primitive eusociality: a eusocial colony in which queens and workers are distinguished primarily based on size alone
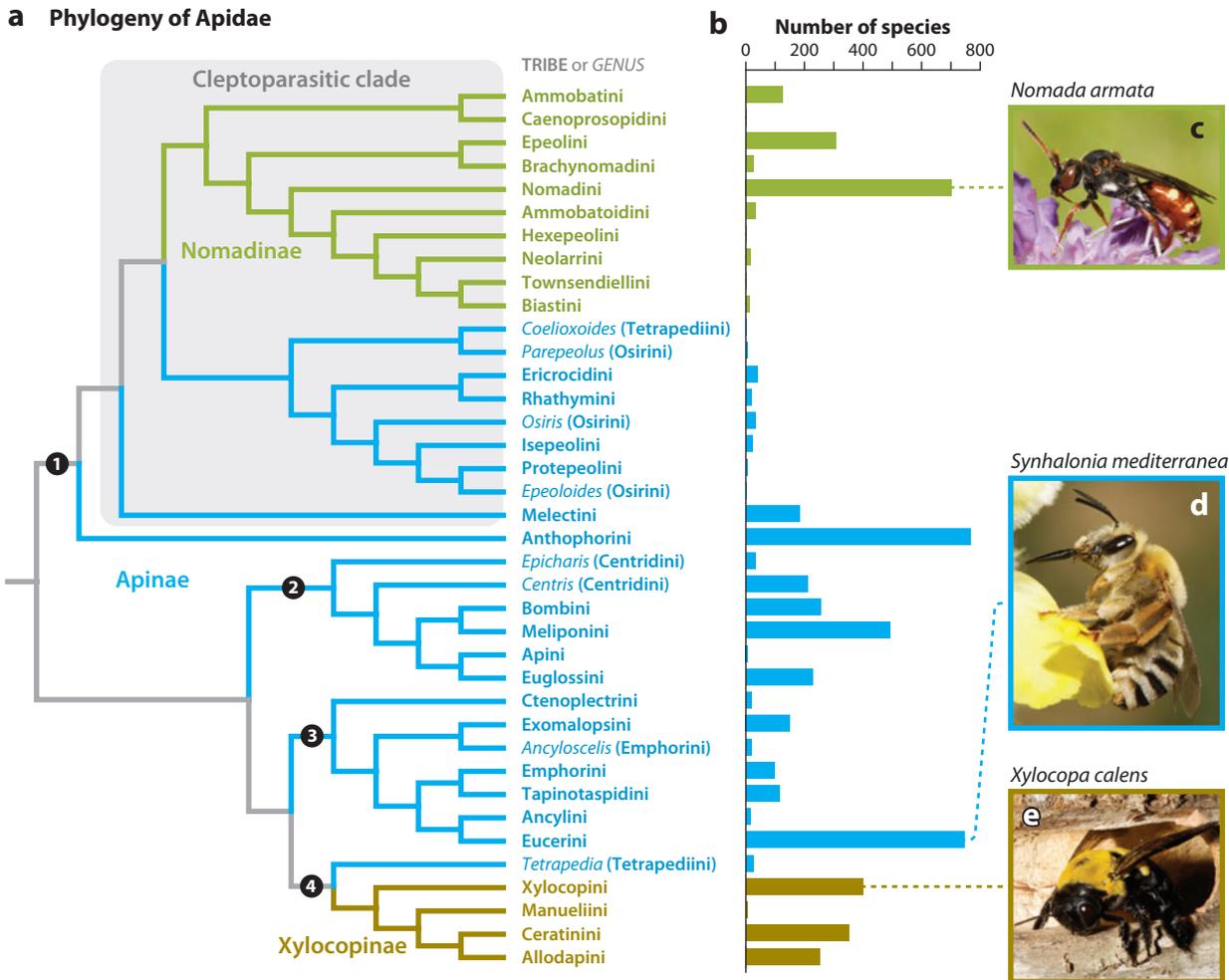
a   Phylogeny of Apidae

b Number of species

c *Nomada armata*

d *Synhalonia mediterranea*

e *Xylocopa calens*

Figure 3

(*a*) Phylogeny of the subfamilies, tribes, and genera of Apidae (19). (*b*) Histogram showing the number of described species (8) for each group. (*c*) *Nomada armata*, female (credit: Nicolas Vereecken). (*d*) *Synhalonia mediterranea*, female (credit: Nicolas Vereecken). (*e*) *Xylocopa calens*, female (credit: Nicolas Vereecken). Node labels are as follows: 1, Anthophorini + cleptoparasitic clade; 2, corbiculate tribes arising from a paraphyletic Centridini; 3, Ctenoplectrini + Silveira's "eucerine line"; 4, *Tetrapedia* + Xylocopinae.

proportion (∼30%) of cleptoparasitic species (Nomadinae, many tribes of Apinae) as well as social parasites (e.g., Bombini and Allodapini). The family also includes several groups of oil-collecting bees (mostly in Centridini, Ctenoplectrini, Tetrapediini, and Exomalopsini) (12).

Presently, Apidae is classified into 3 subfamilies (Apinae, Xylocopinae, and Nomadinae) (**Figure 3**), 34 extant tribes, and 209 genera (8). Roig-Alsina & Michener (85) analyzed the relationships among the subfamilies and tribes of Apidae on the basis of larval and adult morphology. The topologies obtained varied widely depending on the subset of taxa and characters included. Their preferred tree recovered the following relationships among subfamilies: (Xylocopinae + (Nomadinae + Apinae)) (85). However, the phylogenetic positions of the cleptoparasitic taxa were not well resolved, and the authors suspected that some of the morphological characters

Social parasite:
female social parasites take over the nest (and adult workforce) of a host species by excluding or killing the host queen

had convergently evolved in the parasitic taxa. Straka & Bogusch (102) subsequently reanalyzed relationships within Apidae using only larval characters for a subset of the taxa. Their analysis suggested close relationships among many of the cleptoparasitic Apinae; however, the tree had low branch support and did not recover a monophyletic Apidae. To resolve subfamily and tribal relationships within Apidae independent of morphological convergence due to a parasitic lifestyle, Cardinal et al. (19) analyzed a multigene molecular data set. They recovered monophyly of Xylocopinae and Nomadinae, but Apinae was clearly paraphyletic (**Figure 3**). Relationships among the four xylocopine tribes have differed among studies owing to variable placement of Manueliini. Some studies based on morphological (85, 89) and molecular data (35) recover Manueliini + (Xylocopini + (Allodapini + Ceratinini)), whereas other studies based on morphological (33, 85) and molecular data (19) recover Xylocopini + (Manueliini + (Allodapini + Ceratinini)). We consider the latter topology to be more likely. Recent studies of genus- and species-level relationships within the xylocopine tribes were based on combined nuclear and mitochondrial sequence data. Relationships within Xylocopini were analyzed by Leys et al. (51) and within Ceratinini by Rehan et al. (83), and numerous studies of Allodapini have been conducted by Schwarz and colleagues (reviewed in Reference 105). The xylocopine tribes have been the focus of numerous biogeographical analyses (20, 36, 92) as well as numerous studies focused on understanding the evolutionary history of sociality, especially in Allodapini (reviewed in References 94, 105) (see Social Behavior, below).
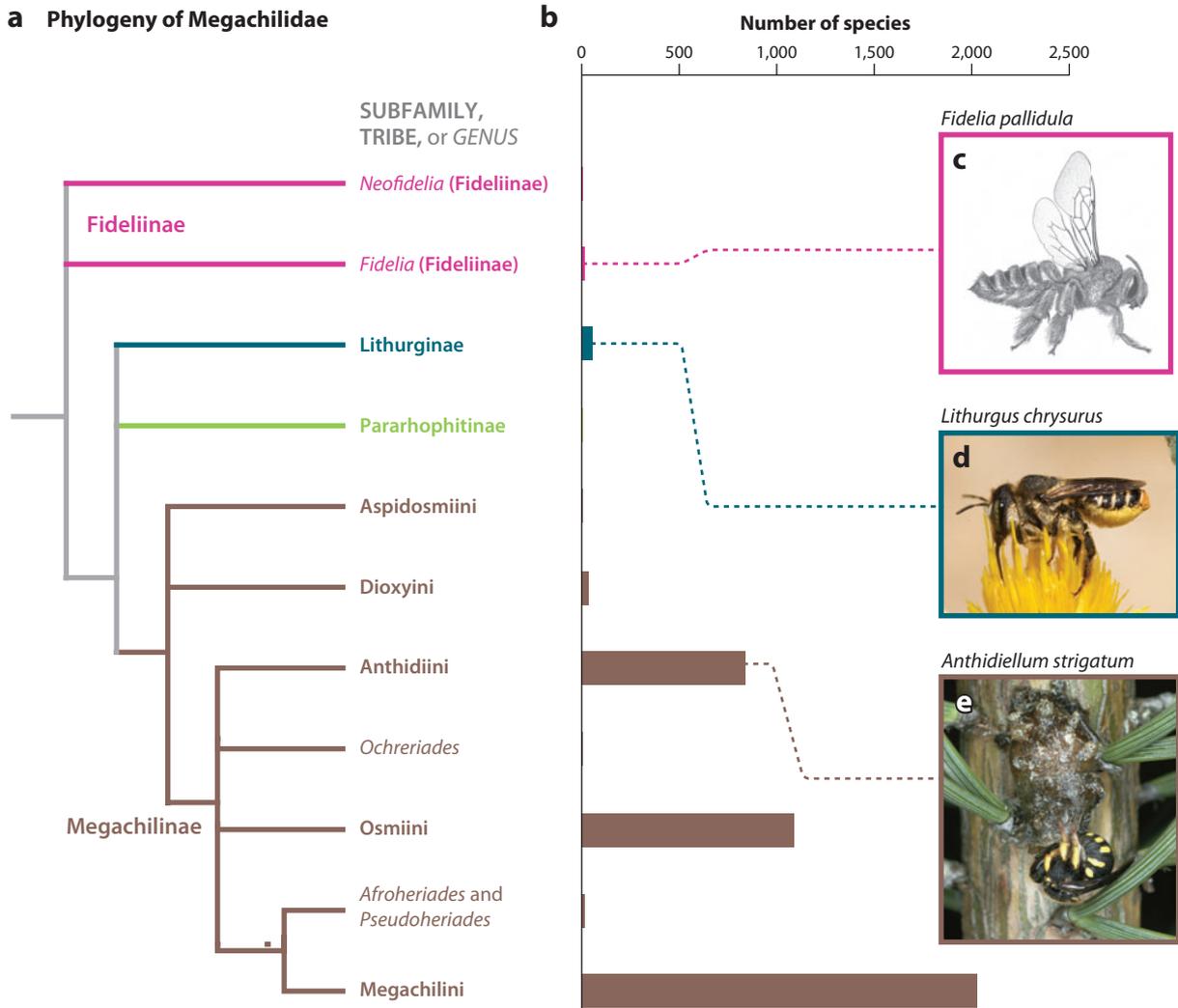
The molecular phylogenetic analysis of Cardinal et al. (19) strongly supports paraphyly of Apinae with respect to Nomadinae and Xylocopinae. All the strictly cleptoparasitic apine tribes (Ericrocidini, Rhathymini, Isepeolini, Protepeolini, Osirini, and Melectini) plus *Coelioxoides* formed a monophyletic group with the cleptoparasitic Nomadinae (referred to as the cleptoparasitic clade; **Figure 3**). The cell-provisioning Anthophorini was sister to the cleptoparasitic clade (node 1, **Figure 3**). The remaining apids formed three major lineages: a monophyletic group referred to as corbiculate Apidae (Euglossini, Bombini, Meliponini, and Apini) arising from a paraphyletic Centridini (node 2, **Figure 3**), Silveira's (97) eucerine line sister to Ctenoplectrini (node 3, **Figure 3**), and Xylocopinae sister to *Tetrapedia* (node 4, **Figure 3**).

Relationships among the four corbiculate tribes (Euglossini, Bombini, Meliponini, and Apini) have been highly controversial because of the implications they have for our understanding of the evolution of eusociality. As reviewed by Cardinal & Packer (18), most morphological, behavioral, and some combined morphological and molecular analyses support the phylogeny proposed by Michener (60): (Euglossini + (Bombini + (Apini + Meliponini))). Most molecular studies have supported a sister-group relationship between Bombini and Meliponini, often with high bootstrap support, but with variable placement of Apini and Euglossini. Analyses of two large molecular data sets (19, 45) strongly support the topology ((Bombini + Meliponini) + (Apini + Euglossini)), as in **Figure 3**. Comprehensive molecular phylogenies have been published for all four corbiculate tribes: Apini (80), Euglossini (81), Bombini (15, 39), and Meliponini (82).

Megachilidae

The long-tongued bee family Megachilidae (**Figure 4**) includes over 4,000 described species (8), all of them solitary or communal. Megachilids are abundant in most ecosystems, from arid habitats to tropical forests. Most of them are noteworthy for including foreign material in their nests, such as leaf discs (leafcutting bees, genus *Megachile*), resin (resin bees, tribe Anthidiini), or mud (mason bees, tribe Osmiini). Some megachilids are readily attracted to trap nests, which has made them important model organisms for investigating pollen digestion and bee-flower relationships (78, 95, 107).

a Phylogeny of Megachilidae

b

Number of species

SUBFAMILY,
TRIBE, or GENUS

Neofidelia (**Fideliinae**)

Fideliinae

Fidelia (**Fideliinae**)

Lithurginae

Pararhophitinae

Aspidosmiini

Dioxyini

Anthidiini

Ochreriades

Megachilinae   Osmiini

Afroheriades and
Pseudoheriades

Megachilini

Fidelia pallidula

Lithurgus chrysurus

Anthidiellum strigatum

Figure 4

(*a*) Phylogeny of the subfamilies, tribes, and genera of Megachilidae (53). (*b*) Histogram showing the number of described species (8)
for each group. (*c*) *Fidelia pallidula*, female (credit: Frances Fawcett). (*d*) *Lithurgus chrysurus*, female (credit: Nicolas Vereecken).
(*e*) *Anthidiellum strigatum*; female closing a resin cell (credit: Albert Krebs).

Megachilidae has traditionally been divided into two morphologically and behaviorally distinct
subfamilies, Fideliinae and Megachilinae (64, 85). The subfamily Fideliinae includes two species-
poor lineages whose phylogenetic affinities have long remained unclear: Fideliini and the small
genus *Pararhophites*. The subfamily Megachilinae includes the vast majority of megachilid tribes
and genera.

The phylogenetic relationships among different lineages of Megachilidae have only recently
been investigated using molecular markers. Litman et al. (53) presented a comprehensive fossil-
calibrated phylogeny of Megachilidae, including all tribes and many genera. This study confirmed
the monophyly of the family but found Fideliinae to be paraphyletic. Both lineages of the tribe

Fideliini, the African genus *Fidelia* and the South American genus *Neofidelia*, appeared as an unresolved polytomy at the base of Megachilidae; furthermore, the genus *Pararhophites* appeared more closely related to Lithurginae and Megachilinae than to Fideliini. The results of this study thus suggest the recognition of four subfamilies, Fideliinae, Lithurginae, Pararhophitinae and Megachilinae, as proposed by some authors (e.g., 34) and in agreement with a recent phylogeny inferred from morphological characters (38).

The study by Litman et al. (53) further demonstrated that the shared morphological and biological traits of Fideliini are plesiomorphies within Megachilidae. Fossil calibration of the phylogeny suggests that this group is of Gondwanan origin and has survived in the deserts of South America and Africa since the separation of these continents over 100 Mya.

Pararhophitinae, Lithurginae, and Megachilinae (sensu 38) form a monophyletic group, but the relationships among these lineages are weakly supported (53). Whereas Pararhophitinae and Lithurginae include a single tribe each, the subfamily Megachilinae is extremely diverse and includes the speciose tribes Anthidiini, Osmiini, and Megachilini, as well as the cleptoparasitic tribe Dioxyini. The peculiar, southern African genus *Aspidosmia*, originally included in Anthidiini (64), appears as the sister group to all other megachiline tribes except Dioxyini (53), a placement in agreement with morphological studies (38). *Aspidosmia* has recently been transferred to its own tribe, Aspidosmiini (38).

It has long been suspected that Osmiini is a paraphyletic group from which Megachilini arose (64). A detailed phylogenetic study of this tribe revealed that the core osmiine genera formed a monophyletic group, but that four species-poor genera, *Afroheriades*, *Noteriades*, *Ochreriades*, and *Pseudoheriades*, did not appear closely related to the Osmiini (76). Gonzalez et al. (38) transferred *Noteriades* to Megachilini, but the placement of the other three genera remains unresolved.

Andrenidae

Andrenidae (**Figure 5**) is a large family of over 2,900 described species (8) in 3 subfamilies and 8 currently recognized tribes (6). Andrenidae is a widely distributed family (excluding Australia), with greatest diversity in arid western North America, South America, and the Palearctic. All species are solitary, ground-nesting bees. Many andrenid bees have narrow host-plant preferences. The subfamily Andreninae consists of several small genera, all of which are oligolectic, and one very large and widely distributed genus (*Andrena*) that includes a mix of host-plant specialists and a smaller number of host-plant generalists (50).

The subfamily Panurginae includes an even higher proportion of oligolectic species. Nearly one-half (635 species) (8) of these are in the North American genus *Perdita*, which consists almost entirely of narrow host-plant specialists on an enormous diversity of plant families (48). The remaining subfamily, Oxaeinae, includes 21 species of large, fast-flying bees that show a strong preference for flowers with poricidal anthers, such as Solanaceae, some Fabaceae, and Melastomataceae.

Andrenidae has been a challenging group from the perspective of phylogeny. The number of recognized subfamilies has varied from two or three (2) to five (33). The subfamily Oxaeinae has been recognized as a distinct family (Oxaeidae) in the past, but studies based on morphological (2) and molecular (26, 29, 88) data place Oxaeinae within Andrenidae. Ascher (6) provided the first (and most recent) combined analysis of morphological and molecular data and established the topology shown in **Figure 5**. Andrenidae provides an ideal group for understanding the evolution of host-plant associations in bees (49, 50), but the group has largely been overlooked by bee molecular systematists.
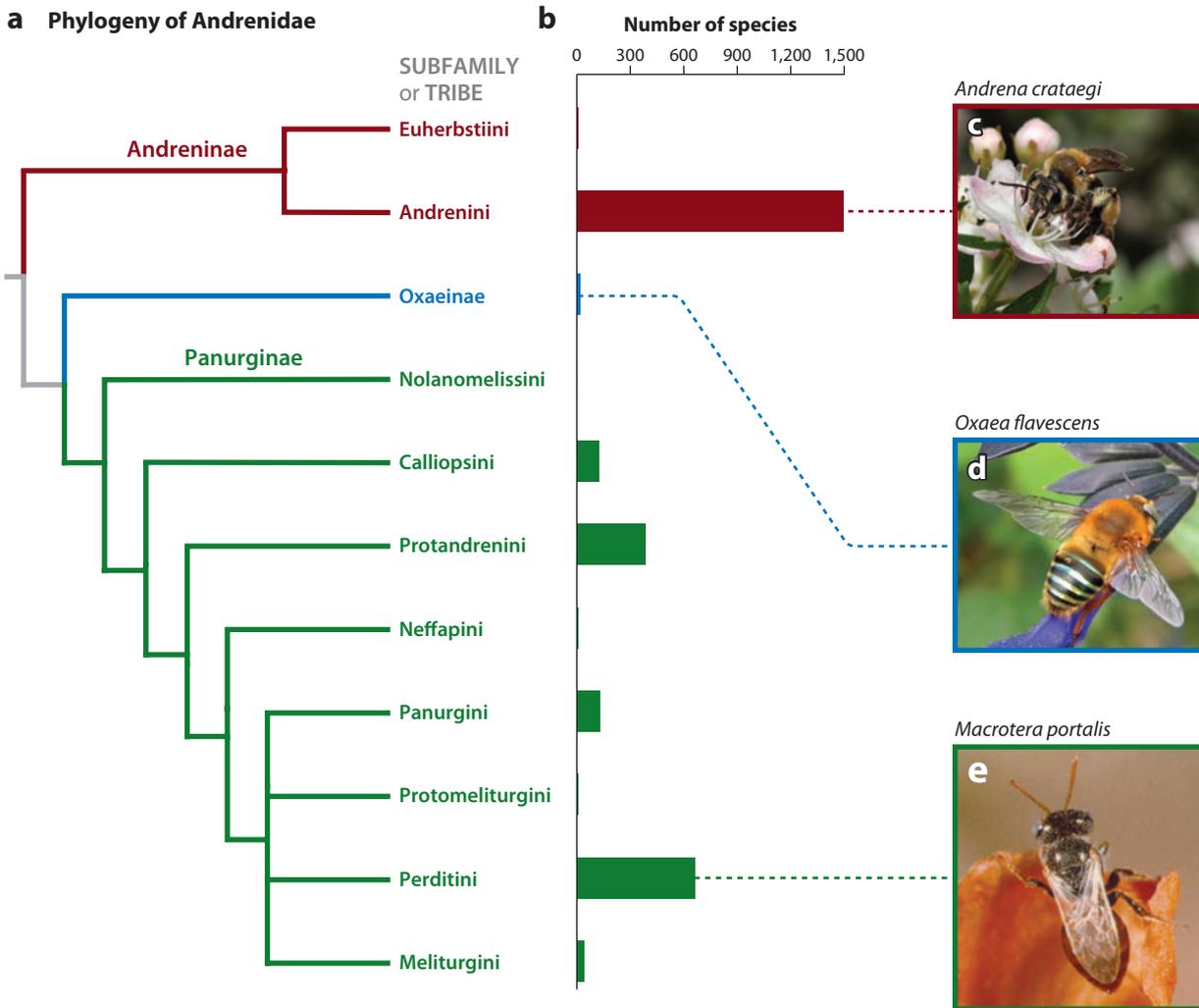
a Phylogeny of Andrenidae

b Number of species

Figure 5

(*a*) Phylogeny of the subfamilies and tribes of Andrenidae (6, 29, 88). (*b*) Histogram showing the number of described species (8) for each group. (*c*) *Andrena crataegi*, female (credit: Phil Huntley-Franck). (*d*) *Oxaea flavescens*, male (credit: Christiane Terra de Lisboa). (*e*) *Macrotera portalis*, male (credit: Bryan Danforth).

Halictidae

Eusocial: a group of females occupying the same nest in which there is cooperative brood care, reproductive division of labor, and overlap of generations
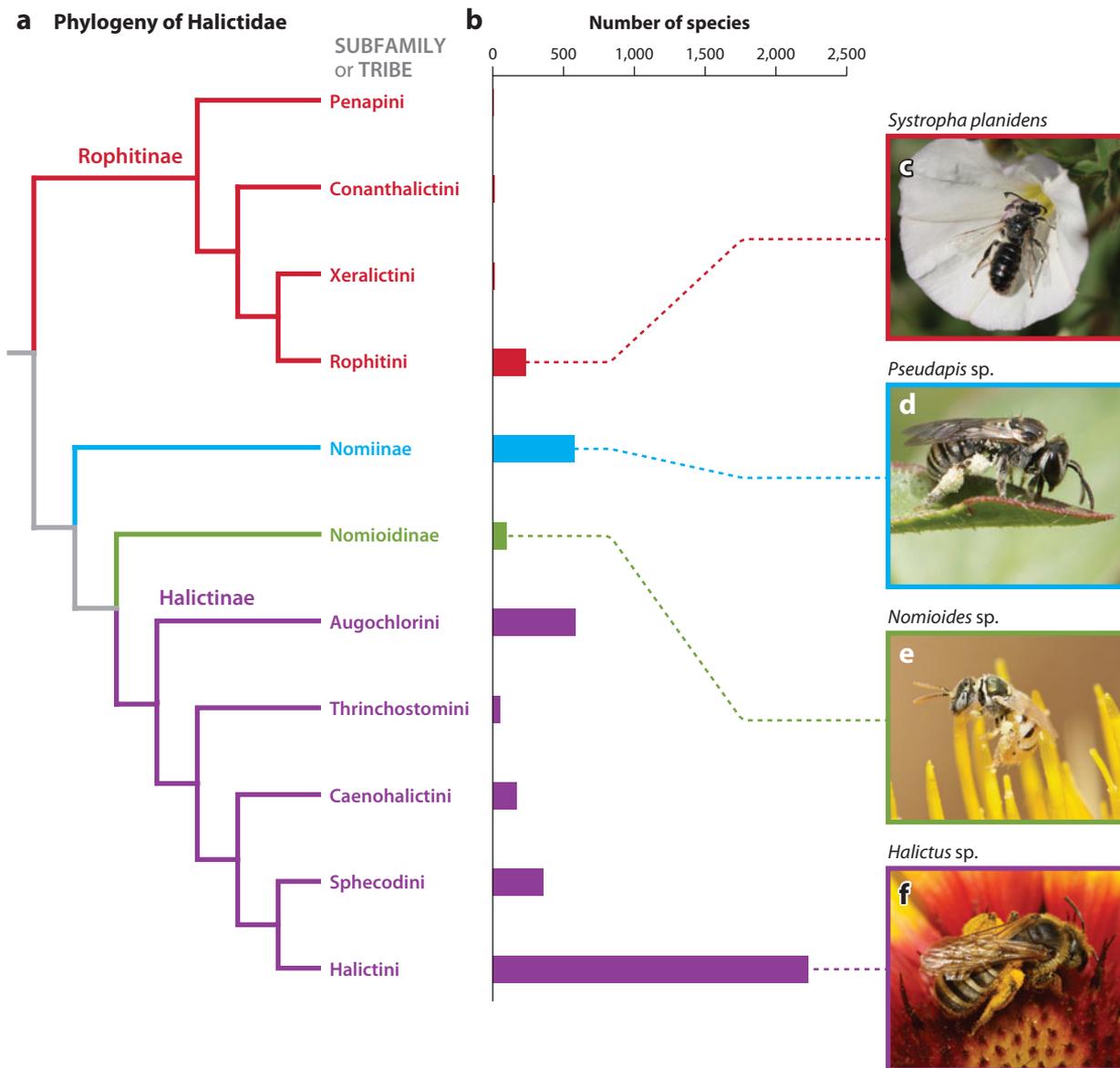
Halictidae (**Figure 6**) is the second largest family of bees with over 4,300 described species (8) in 4 subfamilies and 9 tribes. The family is distributed on all continents except Antarctica and composes between 20% and 60% of the bee species in faunal surveys in North America, Eurasia, and South America (see Reference 25). Whereas most halictid bees are host-plant generalists, the subfamily Rophitinae includes primarily host-plant specialists. Halictidae includes numerous lineages of cleptoparasitic and socially parasitic bees, and parasitism is estimated to have arisen at least 12 times within Halictinae (37). Halictids are perhaps best known for their diverse social behaviors, which include solitary, communal, semisocial, and eusocial associations among adult females (reviewed in Reference 93).

a Phylogeny of Halictidae

b Number of species

Figure 6

(*a*) Phylogeny of the subfamilies and tribes of Halictidae (11, 23, 25). (*b*) Histogram showing the number of described species (8) for each group. (*c*) *Systropha planidens*, male (credit: Alain Cipière). (*d*) *Pseudapis* sp., female (credit: Nicolas Vereecken). (*e*) *Nomioides* sp., female (credit: Nicolas Vereecken). (*f*) *Halictus* sp., female (credit: Nicolas Vereecken).

At the subfamily level, morphological studies (74) and molecular studies (23, 25) have provided congruent results (**Figure 6**). Phylogeny of the subfamily Rophitinae was recently analyzed using a combined data set of morphological characters and three protein-coding nuclear genes (72). The subfamilies Nomioidinae and Nomiinae have been largely unstudied from the perspective of molecular phylogeny. Most molecular phylogenetic work on halictids has focused on the cosmopolitan subfamily Halictinae (**Figure 6**).

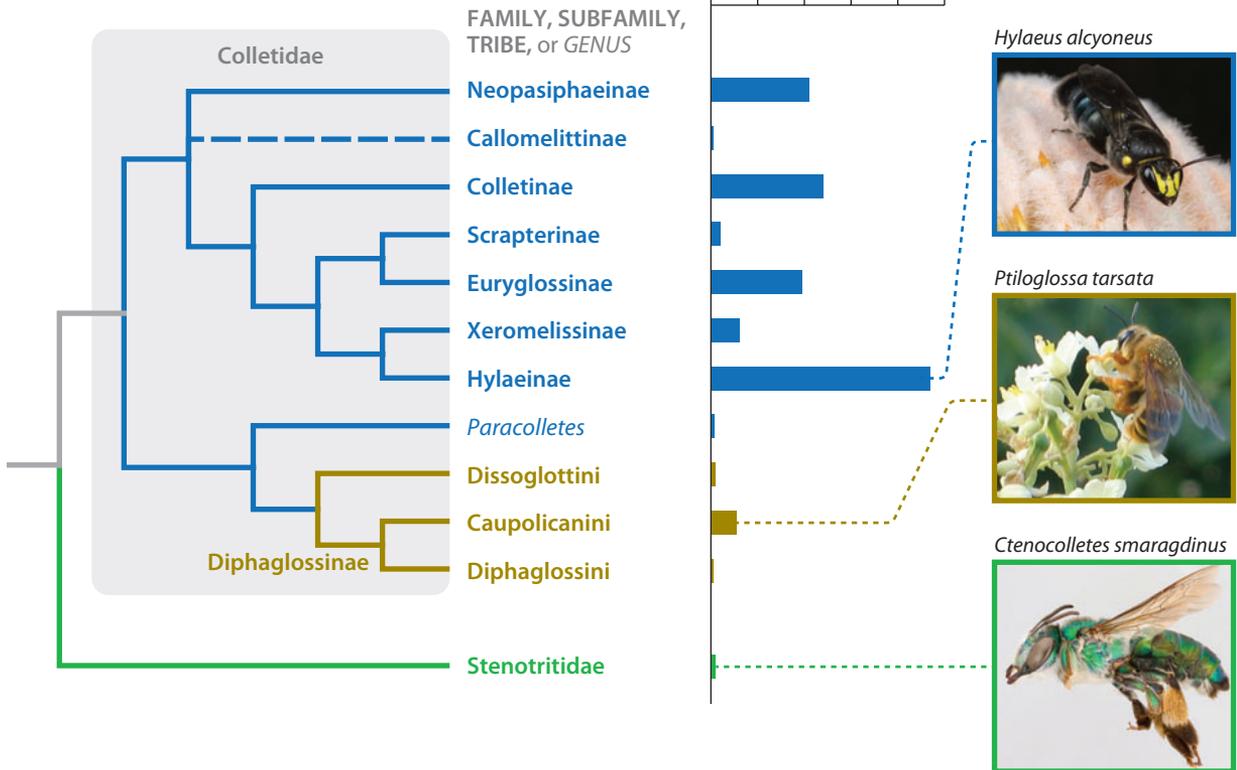**a   Phylogeny of Colletidae and Stenotritidae**

b   Number of species

FAMILY, SUBFAMILY, TRIBE, or GENUS

Colletidae

- Neopasiphaeinae
- Callomelittinae
- Colletinae
- Scrapterinae
- Euryglossinae
- Xeromelissinae
- Hylaeinae
- *Paracolletes*
- Dissoglottini
- Caupolicanini
- Diphaglossini

Diphaglossinae

Stenotritidae

Hylaeus alcyoneus

Ptiloglossa tarsata

Ctenocolletes smaragdinus

Figure 7

(*a*) Phylogeny of the subfamilies, tribes, and genera of Colletidae and Stenotritidae (4, 5). (*b*) Histogram showing the number of described species (8) for each group. (*c*) *Hylaeus alcyoneus*, female (credit and copyright: Bernhard Jacobi). (*d*) *Ptiloglossa tarsata*, female (credit: Eduardo Almeida). (*e*) *Ctenocolletes smaragdinus*, female (credit: Laurence Packer, York University: Bee Tribes of the World photographic project).

Halictinae is an enormous group (including nearly 3,400 described species) (8) that includes all the eusocial and cleptoparasitic lineages of Halictidae. The group is clearly monophyletic. Whereas previous morphological studies (32, 61, 62) failed to resolve tribal relationships in Halictinae, recent molecular studies have supported monophyly of five, clearly defined tribes: Augochlorini, Thrinchostomini, Caenohalictini, Sphecodini, and Halictini sensu stricto (11, 23, 25) (**Figure 6**). Most molecular work has focused on the two tribes that include eusocial species: Augochlorini (104) and Halictini (11, 23, 25). Within Halictini, molecular studies have focused on subgenus- and species-level relationships within two predominantly eusocial genera: *Halictus* (28) and *Lasioglossum* (21, 24, 27, 37). Such studies have provided important insights into the antiquity and evolution of social and parasitic behaviors (see sections Social Behavior and Evolution of Parasitic Lifestyles, below).

Stenotritidae

Stenotritidae (**Figure 7**), including just 21 described species (8) in two genera (*Stenotritus* and *Ctenocolletes*), is an enigmatic group of endemic Australian bees. All species are large,

ground-nesting, fast-flying, solitary bees collected primarily on flowers of the family Myrtaceae. The phylogenetic affinities of Stenotritidae have been obscure. Previous morphological studies have obtained conflicting results about the placement of Stenotritidae. This family has been hypothesized to be (*a*) the sister group to the andrenid subfamily Oxaeinae (2), (*b*) the sister group to all other bees (2), (*c*) the sister group to the Colletidae (2), (*d*) a group arising within the colletids [on the basis of larval data (58) and adult morphological data (2)]. Molecular studies have strongly supported a sister-group relationship between Colletidae and Stenotritidae (4, 5, 26, 29) (**Figure 7**).

Colletidae

The family Colletidae (**Figure 7**) includes more than 2,500 described species (8), with highest diversity in the southern continents (although two colletid genera are widely distributed: *Colletes* and *Hylaeus)*. Colletid bees are diverse, ranging from small, slender, relatively hairless bees to large, robust, hairy bees. Most colletid females carry pollen either externally in a hindleg scopa, or internally in the crop (subfamilies Euryglossinae, Hylaeinae, and few Neopasiphaeinae).

Morphological, behavioral, and a wealth of molecular data have established colletid monophyly. The bifid glossa possessed by all female (and most male) colletid bees was once considered a plesiomorphic trait indicating affinity of Colletidae to apoid wasps. Molecular studies have strongly supported the hypothesis, originally proposed by Perkins (73) and later by McGinley (57), that the bifid glossa of Colletidae is a derived trait associated with the application of a unique cellophane-like polyester coating to the cell and burrow walls in Colletidae (reviewed in Reference 3). Molecular phylogenetic studies have universally supported monophyly of Colletidae (4, 5, 26, 29). Further support for colletid monophyly comes from a unique, derived intron in the F1 copy of EF-1α in all colletids (9).

Our understanding of colletid phylogeny at the subfamily, tribe, and genus levels has changed dramatically as a result of new DNA sequence data. Almeida & Danforth's (4) examination of the higher-level relationships among subfamilies and tribes of Colletidae was based on four nuclear genes and broad taxon sampling. Their multigene results implied significant changes in colletid phylogeny: (*a*) the genus *Paracolletes* is sister to the Diphaglossinae; (*b*) the genus *Scrapter*, traditionally placed in the Paracolletini, represents a distinct clade (Scrapterinae) sister to Euryglossinae (see also 7); (*c*) the genus *Callomelitta*, traditionally placed within Paracolletini, is a distinct lineage of uncertain affinity now classified as Callomellittinae; and (*d*) the subfamily Colletinae is reduced to a small clade including *Colletes* plus three closely related South American genera (*Hemicotelles*, *Rhynchocolletes*, and *Xanthocotelles*). The remaining genera of "Paracolletini" are now designated Neopasiphaeinae (5).

NEW INSIGHTS INTO BEE EVOLUTION

Phylogenies have played an important role in the analysis of evolutionary patterns and processes in bees. Phylogenies have been used in the context of host-plant evolution and the evolution of social behavior and parasitism. We review some of the most interesting results obtained from recent molecular phylogenetic studies.

Host-Plant Associations

Virtually all bees rely entirely on flowering plant products, including nectar, pollen, and floral oils, for larval and adult nutrition [the sole known exception to this rule involves three species of stingless bees in the genus *Trigona* that rely on carrion as a protein source (13)]. As in all phytophagous

insects, bees show enormous variation in the range of host plants visited. Oligolecty is present in all bee families but is predominant in certain lineages (e.g., Dasypodainae, Melittinae, Andreninae, Panurginae, Scrapterinae, Rophitinae, Fideliinae, Emphorini, Eucerini) and almost entirely absent from others (e.g., Xylocopinae as well as most social lineages). See References 16, 30, 68, 71, and 106 for excellent reviews of host-plant use in bees.

While polylecty was long held as the primitive state in bees (reviewed in Reference 69), a number of studies have suggested oligolecty is the ancestral state. Müller (69) mapped oligolecty and polylecty onto a phylogeny of western Palearctic Anthidiini based on morphological characters. He detected four clear transitions from oligolecty to polylecty but no unequivocal switches in the other direction, suggesting that oligolecty might be a primitive condition in bees. Considering bee phylogeny as a whole, evidence suggests that oligolecty is the primitive condition in bees. The family-level phylogeny of bees places Melittidae, especially the subfamily Dasypodainae, close to the root of the bees (29). Melittidae is highly host-plant-specific (67) and its placement near the base of the tree supports Müller's hypothesis of an oligolectic ancestor for bees.

A number of studies have used molecular phylogenies to reconstruct the dynamics of host-plant evolution in bees. On the basis of a molecular phylogeny of Megachilidae, Litman et al. (53) inferred that oligolecty was the primitive condition for the family. In particular, the megachilid subfamily Fideliinae (sensu 38) includes mostly oligolectic or narrowly polylectic species. Likewise, Patiny et al. (72) inferred that the common ancestor of the halictid subfamily Rophitinae was most likely oligolectic with an ancestral specialization on the plant families Boraginaceae and Hydrophyllaceae. Larkin et al. (50) inferred that the common ancestor of *Andrena* was most likely oligolectic.

At the species level, phylogenies have been used to infer the details of host-switching in bees and to identify transitions between oligolecty and polylecty. Sipes & Tepedino (98) traced the evolution of floral association in the genus *Diadasia* (Apidae), which specializes on a variety of distantly related host-plant families (Malvaceae, Onagraceae, Cactaceae, Convolvulaceae, and Asteraceae). They inferred that the ancestor of the genus probably specialized on flowers of the family Malvaceae, and detected several transitions from oligolecty to polylecty as well as shifts from polylecty to oligolecty. In *Diadasia*, most speciation events were not associated with host shifts, and bees using the same hosts generally formed monophyletic groups. Host-switches among distantly related plant families in *Diadasia* seem to result from similarity in floral and/or pollen morphology.

Sedivy et al. (96) constructed a worldwide phylogeny of the genus *Chelostoma* (Megachilidae). As in the case of *Diadasia*, oligolecty was the primitive condition for the genus, with two independent origins of polylecty. Overall, host-shifts were rare, so that all species specialized on a given host formed monophyletic groups. The two polylectic species, clearly derived from oligolectic ancestors, appeared to have broadened their diets by incorporating novel hosts that were also utilized by closely related (oligolectic) species, consistent with patterns observed in other herbivorous insects (44). This observation, coupled with evidence from physiological data on larval performance (78), led the authors to conclude that bees were strongly constrained in their host choices (96). These constraints may relate to the physiological capabilities of bee larvae (78), to host recognition or neurological constraints (77), or to the inability of bees to process flowers with differing floral architecture (53, 69).

Social Behavior

Most bee species are solitary. Based on our current understanding of bee family-level relationships, this is clearly the primitive state in bees. Most apoid wasps are solitary [the sole known exception is the genus *Microstigmus* in the Pemphredoninae (56, 86)]. Sociality, in various forms,

Oligolecty: describes a species that collects pollen from just one plant family; a host-plant specialist

Polylecty: describes a species that collects pollen from a variety of (usually distantly related) plant families; a host-plant generalist

occurs in many bee groups. Communal nesting is widespread in bees, occurring in a number of families, including Melittidae, Halictidae, Andrenidae, Apidae, and Megachilidae. More elaborate forms of sociality such as temporary associations between females of two generations or temporary division of labor during the active breeding season, such that some females serve as guards and others serve as foragers (and egg layers), have been reported in Apidae (Xylocopini, Ceratinini, Allodapini, Euglossini) (17) and Colletidae (Hylaeinae) (101). The form of sociality that has received the most attention from behavioral ecologists is eusociality. Eusociality, as defined here, is limited to a small number of lineages within Apidae (Allodapini, corbiculates) and Halictidae (some genera of Augochlorini and two genera of Halictini: *Lasioglossum* and *Halictus*). We estimate that approximately 10% of bee species are eusocial.

Phylogenetic studies have played an important role in our understanding of the evolution of eusociality in bees. Phylogenies combined with mapping of known behavioral phenotypes, either by parsimony or likelihood-based methods, have provided important insights into the number of distinct origins of eusociality in bees (17, 21, 22, 24, 28, 103) and the evolutionary progression of behavioral states that give rise to eusociality (17, 91, 94). In Halictidae, phylogenetic studies have established that there are relatively few origins of eusociality (as many as four and as few as two), but that eusocial lineages have repeatedly given rise to secondarily solitary descendants (21, 22, 24, 28). In Apidae, eusociality appears to have evolved once in the allodapines (93) and once in the corbiculate Apidae. Using a large molecular data set for the family Apidae and model-based ancestral state reconstruction methods, Cardinal & Danforth (17) inferred that the four corbiculate tribes shared a primitively eusocial common ancestor. Furthermore, their results suggest that stingless and honey bees evolved advanced eusociality independently, and that the solitary/communal behavior found within orchid bees is derived secondarily from eusociality. In retrospect, Cameron's (14) report of dual origins of advanced eusocial behavior in corbiculates based on just a single mitochondrial gene now looks remarkably prescient.

Fossil-calibrated phylogenies combined with mapping of behavioral phenotypes and ancestral state reconstructions have been used to estimate the antiquity of eusociality in Halictidae (11) and Apidae (17), and we now have a comprehensive understanding of the timeline of eusocial origins in bees (17). Origins of eusociality in bees span a wide range, from as recent as 21 Mya (12–29 Mya) in eusocial Halictidae to as ancient as 53 Mya (41–65 Mya) in eusocial allodapines and 87 Mya (78–95 Mya) in corbiculate Apidae (17). These dates indicate that eusocial complexity within bees is roughly correlated with age, such that more ancient lineages (corbiculates) show more complex social organization than do the more recent groups (allodapines and halictines). Furthermore, the more recent eusocial halictid lineages are also more prone to showing reversals from eusociality to solitary nesting, suggesting that eusociality in halictids is evolutionary labile, compared with the advanced eusocial lineages of Apidae.

Evolution of Parasitic Lifestyles

Some bees do not build or provision their own nests with nectar and pollen for their offspring. Instead, they are parasites of other bees. Most parasitic bees can be classified into two main groups, cleptoparasites and social parasites. Phylogenetic analyses show that these two forms of parasitism are evolutionarily unrelated.

Cleptoparasitism is found within many lineages of bees and we estimate that 12% of bees and as many as 30% of Apidae are cleptoparasites. There is much evidence to suggest that, in certain lineages, cleptoparasites arise frequently from their (closely related) hosts. Examples in which cleptoparasites attack closely related host species can be found in Colletidae (Hylaeinae) (54, 55), Halictidae (Halictini, Augochlorini) (25, 37, 64, 104), Megachilidae (Megachilini, Osmiini, Anthidiini)

Communal nesting: multiple, reproductively active females of the same generation share a common nest with no evidence of reproductive division of labor or cooperative brood care

Advanced eusociality: a eusocial colony in which there are fixed morphological differences between queens and workers such that queens lack structures needed to collect and manipulate pollen

Cleptoparasite: brood parasites in which an adult female enters the nest of a pollen-collecting host and lays an egg either in a closed or open (partially provisioned) brood cell

(64), and Apidae (Euglossini, Ctenoplectrini) (19, 90). A comprehensive analysis of apid phylogeny (19), however, indicates that cleptoparasitism has evolved far fewer times than was previously estimated (87), and that most of the cleptoparasitic Apinae are unrelated to their pollen-collecting hosts (the cleptoparasitic clade in **Figure 3**). On the basis of a fossil-calibrated phylogenetic analysis, this large, cleptoparasitic apid clade is estimated to have evolved 95 Mya (87–103 Mya) (19). Model-based ancestral state reconstruction in Apidae supports the assumption that cleptoparasitism is an irreversible trait (i.e., nest-making bees cannot evolve from a cleptoparasitic ancestor) despite the antiquity of the cleptoparasitic clade (**Figure 3**). Large, ancient obligately cleptoparasitic clades also exist in Megachilidae [Dioxyini, 30–70 Mya (53)] and Halictidae [Sphecodini, 25–50 Mya (23)].

Social parasitism is much more taxonomically restricted than cleptoparasitism. Social parasites, by definition, only parasitize eusocial hosts, thus restricting the range of potential hosts to eusocial Halictidae and Apidae. Phylogenetic studies have shown that social parasites are often closely related to their hosts (in the same tribe or genus) (15, 37, 39, 40, 99). Social parasitism has evolved repeatedly in bumble bees (15, 40). In allodapine bees 7.9% of described species are social parasites (99) and social parasitism is estimated to have arisen at least 11 times (105). Social parasitism is estimated to have arisen repeatedly in Halictinae (in tribes Halictini, Augochlorini, and Sphecodini) (37).

SUMMARY POINTS

1. Molecular data have substantially changed our understanding of family-level relationships in bees. Melittidae, rather than Colletidae, appears to be the sister group to the remaining bees, but questions remain about precise location of the root node.

2. Molecular data have helped resolve the phylogeny of a number of enigmatic bee groups, including the placement of Stenotritidae, relationships among the genera of "Paracolletinae," phylogenetic affinities of Scrapterinae (Colletidae), relationships among genera and tribes of Melittidae, relationships among megachilid subfamilies and tribes, relationships among parasitic groups of Apidae, and relationships and antiquity of the four corbiculate tribes.

3. Molecular phylogenies, combined with mapping of host-plant range and associations, have improved our understanding of host-plant evolution in bees. Specialization appears to be the primitive state for many bee groups, with multiple origins of polylecty from within oligolectic groups. Patterns of host-plant associations in bees appear to be determined largely by floral or pollen morphology (and possibly chemistry), rather than host-plant phylogeny.

4. Eusociality appears to have arisen relatively rarely in bees, and numerous reversals to solitary or communal nesting have been identified, especially in Halictidae. We now have a clear understanding of the temporal origins of eusocial bee lineages, and social complexity in bees appears to be related to clade antiquity.

5. Cleptoparasitism appears to have had multiple origins in Halictidae and Megachilidae, and in most cases, cleptoparasites are closely related to their hosts. In contrast, cleptoparasitism has arisen just four times in Apidae. In this family, an ancient cleptoparasitic clade includes most of the apine cleptoparasites plus Nomadinae.

6. Molecular phylogenies, combined with fossil data and relaxed clock dating methods, have improved our understanding of the origins of major bee groups and have provided important insights into the temporal diversification of bees.

FUTURE ISSUES

1. Increased use of next-generation sequencing of bee transcriptomes and genomes will rapidly expand the number of genes and data sets used for bee and wasp phylogeny.

2. New molecular data suggest that bees arise from a paraphyletic Crabronidae, but the precise sister group to the bees remains unclear. Future studies should include broader taxon sampling across the apoid wasps in order to identify the sister group to the bees.

3. The root node of bees remains elusive. Future studies should examine the impact of expanded gene and taxon sampling (especially for apoid wasps) on the placement of the root node of bees.

4. A global analysis of bee historical biogeography based on a well-resolved family-level phylogeny of bees has not yet been conducted.

5. The limited fossil record of bees makes it difficult to put a point estimate on the antiquity of bees. A comprehensive, fossil-calibrated phylogeny spanning all bee families has yet to be conducted.

6. Andrenidae remains one of the most poorly understood groups in terms of molecular phylogeny. Relatively few molecular studies have analyzed relationships within subfamilies, tribes, and genera of Andrenidae.

7. The evolutionary implications of "key innovations" on patterns of bee diversification have been examined only to a limited extent. Future studies should focus on identifying phenotypic traits that alter bee diversification rates.

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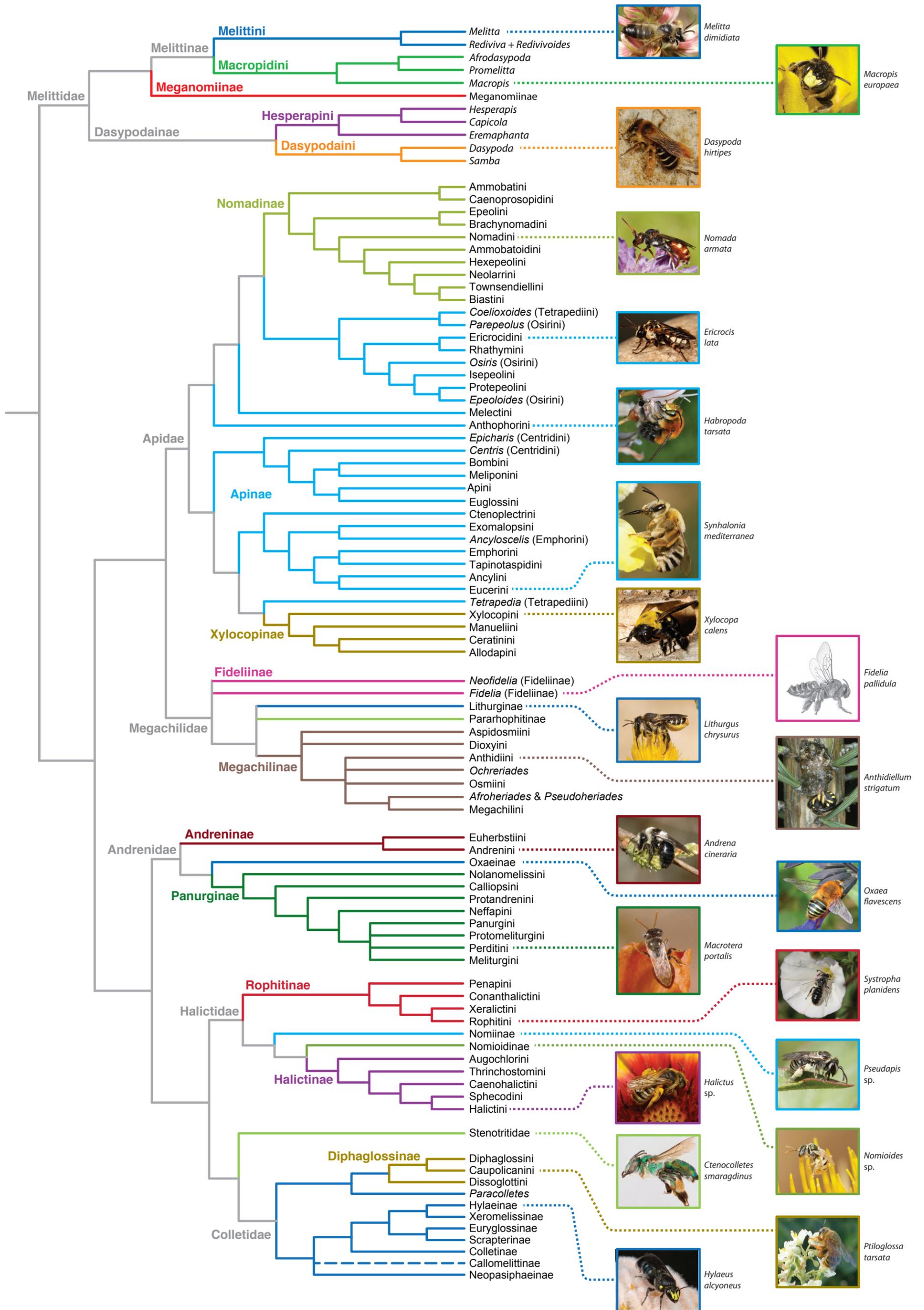
Bee phylogeny

Supplemental Figure 1 Summary phylogeny of the bees to the family, subfamily, and tribal levels. Photo credits: *Melitta dimidiata*, male (credit: Nicolas Vereecken); *Macropis europaea*, male (credit: Nicolas Vereecken); *Dasypoda hirtipes*, female (credit: Nicolas Vereecken); *Nomada armata*, female (credit: Nicolas Vereecken); *Ericrocis lata*, female (credit: Nicholas Richter); *Habropoda tarsata*, males (credit: Jelle Devalez); *Synhalonia mediterranea*, female (credit: Nicolas Vereecken); *Xylocopa calens*, female (credit: Nicolas Vereecken); *Fidelia pallidula*, female (credit: Frances Fawcett); *Lithurgus chrysurus*, female (credit: Nicolas Vereecken); *Anthidiellum strigatum*; female (credit: Albert Krebs); *Andrena cineraria*, female (credit: James Lindsey); *Oxaea flavescens*, male (credit: Christiane Terra de Lisboa); *Macrotera portalis*, male (credit: Bryan Danforth); *Systropha planidens*, male (credit: Alain Cipière); *Pseudapis* sp., male (credit: Nicolas Vereecken); *Nomioides* sp., female (credit: Nicolas Vereecken); *Halictus* sp., female (credit: Nicolas Vereecken); *Ctenocolletes smaragdinus*, female (credit: Laurence Packer); *Ptiloglossa tarsata*, female (credit: Eduardo Almeida); *Hylaeus alcyoneus*, female (credit: Bernhard Jacobi).