

Social Behavior and Nest Architecture of Nomiine Bees (Hymenoptera: Halictidae; Nomiinae)

WILLIAM T. WCISLO¹

Smithsonian Tropical Research Institute, Apartado 2072, Balboa,
República de Panamá

MICHAEL S. ENGEL

Department of Entomology, Cornell University, Ithaca New York 14853-0999

ABSTRACT: To facilitate future comparative studies among halictid bees, we review social behavior and nest architecture for 21 species of Nomiinae (Halictidae). Nothing is known of the biology of the vast majority of named species. Approximately half of the species consist of solitary bees, and half consist of females which live within social groups. Social organization varies among species, but there is insufficient information to assess whether it also varies within species. All nomiines nest in the ground, and nest architecture is variable within the subfamily. Architectural characters may provide some useful information for taxonomic and systematic purposes.

As readers of this *Festschrift* know, George Eickwort was fascinated with the evolution of sweat bees (Hymenoptera: Halictinae), and he always emphasized the value of comparative studies. In this spirit we compiled the scattered information on social behavior and nest architecture for halictid bees in the subfamily Nomiinae. This information will facilitate comparisons with the subfamilies Rophitinae (Eickwort et al., 1986; Rozen, 1993) and Halictinae (reviews of social behavior: Michener, 1974, 1990; Wcislo, in press a; Yanega, in press; Danforth and Eickwort, in press. Reviews of nest architecture: Sakagami and Michener, 1962; Eickwort and Sakagami, 1979). Secondly, we hope to draw more attention to an extremely large and diverse group of bees that is of considerable biological interest in its own right. The group has economic potential as well, since one species (*Nomia melanderi*) has been used in agricultural systems (Richards 1993; Wichelns et al. 1992). We focus on female behavior, including nest architecture. Male courtship behavior and some aspects of male morphology are reviewed elsewhere (Wcislo and Buchmann, 1995; Wcislo, 1995).

Nomiine bees constitute a relatively small part of the Nearctic bee fauna (Cockrell, 1910), with only 20 species in the New World (Moure and Hurd, 1987) placed in two genera (Michener et al., 1994). In the Old World, however, nomiines are extremely diverse, especially in Africa (Pauly, 1990), Australia (Cardale, 1993), and Asia (Hirashima, 1961). There are numerous genera and subgenera, but there has been no attempt at a revision of the entire subfamily.

Social Behavior

The better known nomiine bees in the New World (e.g., *Nomia melanderi*) are solitary, but most species have not been studied. Many reports are anecdotal, or are based on small numbers of nests, so conclusions are tentative. We present information as if it characterizes *species*, but the dearth of information means that

¹ Present address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 U.S.A.

we do not know if this typological approach is justified (for discussion, see Wcislo, in press b). Nevertheless, the available data challenge the assumption that nomiines are mostly "solitary" bees (Table 1). Bees in 11 species are exclusively or nearly always solitary (e.g., *Dieunomia heteropoda* was tallied as a solitary bee, despite the fact that two nests each had two provisioning females), and 9 species have nests with multiple females. Based on available information, social behavior is as common as solitary behavior in nomiines.

Since few detailed studies are available, it is not feasible to further characterize the kinds of social behavior seen in various colonies of different species. Bees such as *Nomia tetrasonata* or *Afronomia sjostedti* are apparently communal, as inferred from the fact that the mature females in a nest had developed ovaries and were mated (Wcislo, 1993; Michener, 1969). *Nomia capitata* in India might represent a more hierarchical society, with reproductive and non-reproductive individuals (Batra, 1966), although further studies are needed to confirm this categorization. Most multi-female associations in Nomiinae involve very few bees per nest, although up to 12 cohabiting females are known in *N. capitata* (Batra, 1966), and up to 20 in *N. tetrasonata* (Wcislo, 1993).

Some nomiines (e.g., *N. (Leuconomia) candida*, *Afronomia sjostedti*) have nests isolated from nearest neighbors by vast distances (Michener, 1969), whereas others (e.g., *Nomia melanderi*, *Dieunomia triangulifera*) nest in dense aggregations (e.g., Cross and Bohart, 1960; Minckley et al., 1994). Different species show different degrees of philopatry based on behavioral data, but only one study investigated population structure using electrophoretic data. Schweiger et al. (1994) showed that different populations of *Dieunomia triangulifera* were not genetically differentiated, although they examined only eight putative loci.

As with other halictines, those species with social behavior (e.g., *N. oxybeloides* and *N. tetrasonata*) utilize pollen from a wide variety of plants (polylecty). In contrast, solitary nomiines such as *D. triangulifera* or *D. heteropoda* are oligolectic (Cross, 1958; Hurd et al. 1980), but this is not true of all solitary species (e.g., *N. melanderi* is polylectic) (Johansen et al. 1978).

Nest Architecture

Nest architecture has been reviewed for the Halictinae by Sakagami and Michener (1962), for Augochlorini by Eickwort and Sakagami (1979), and for Rophitinae by Rozen (1993). Wcislo (1993) reviewed some nest architectural characters which support the decision by Michener et al. (1994) to recognize two genera of North American nomiines, *Dieunomia* and *Nomia*. At higher taxonomic levels, however, comparisons among the different lineages of Halictidae have been hampered by the fact that the information on nest architecture of Nomiinae is scattered (see Rozen, 1993). A further difficulty is that not all authors are equally attentive to reporting the fine details of nest structure (Appendices 1 and 2).

Representative features of nest architecture for 21 nomiine species (Table 2) are illustrated in Figs. 1 to 3, and are tabulated in Appendix 2. All known nomiines nest in the soil, often in more or less flat ground, although observations of *N. punctulata* nesting in both vertical banks and horizontal ground (Hirashima, 1961) suggest some flexibility in nest-site selection.

The nest entrances of some nomiines are an extended turret or "chimney." These constructions may be vertical as in some *Rhopalomelissa* (Fig. 1a, b) or as

Table 1. Comparative information on social behavior of female nomiine bees.

Taxon	Locality of population	Social behavior (no. nests excavated)	Reference
<i>Dieunomia triangulifera</i>	Lawrence, Kansas	Solitary (~35)	Cross and Bohart, 1960
<i>D. triangulifera</i>	Topaz, Utah	Solitary (~35)	Cross and Bohart, 1960
<i>D. triangulifera</i>	Eudora, Kansas	Solitary (>50)	WTW, pers. obs.
<i>D. triangulifera</i>	St. Louis, Missouri	Solitary (?)	Rau, 1929
<i>D. heteropoda</i>	near Notom, Utah	Solitary (9)	Parker et al., 1986
<i>D. heteropoda</i>	West Turkey Creek, Arizona	Solitary ¹ (15)	Wcislo, 1993
<i>D. nevadensis</i>	Lawrence, Kansas	Solitary (18)	Kerfoot, 1964
<i>Hoplonomia punctulata</i>	Kasii and Wajiro, Japan	Solitary (?) ²	Hirashima, 1961
<i>Rhopalomelissa esakii</i>	Kashii, Japan	Solitary (16)	Hirashima, 1961
<i>R. yasumatsui</i>	Wajiro, Japan	Solitary (?)	Hirashima, 1961
<i>Rhopalomelissa</i> sp.	Cameroon	Solitary (8)	Michener, 1969
<i>Nomia melanderi</i>	Pacific Northwest (USA)	Solitary (?) ³	Johansen et al., 1978
<i>Nomia tetrazonata</i>	near Sasabe, Arizona	Communal (12)	Wcislo, 1993
<i>Austronomia australica</i>	Cabboboonee State Forest, Victoria, Australia	Communal, possible semisocial (>50)	Rayment, 1956; Vogel and Kukuk, 1994; Ku- kuk, pers. comm.; WTW, pers. obs.
<i>Nomia ruficornis</i>	Lido de Venise	? (1?)	Soika, 1932
<i>Nomia capitata</i>	Punjab, India	Multi-female (semi- social?) (4)	Batra, 1966
<i>Pseudapis oxybeloides</i>	Punjab, India	Multi-female (com- munal?) (2)	Batra, 1966
<i>Pseudapis diversipes</i>	Pakistan	Multi-female? ⁴ (3)	Rozen, 1986
<i>Nomia nasicana</i>	Punjab, India	Solitary? ⁵ (3)	Batra, 1966
<i>Nomia unidentata</i>	Egypt	Solitary? (?)	Rashad et al., 1979
<i>Nomia nortoni</i>	Texas	Multi-female? ⁶ (?) ⁷	Parks, 1928
<i>Nomia (Leuconomia)</i> <i>candida</i>	Cameroon	Multi-female (paraso- cial or communal) (1)	Michener, 1969
<i>Afronomia sjostedti</i>	Natal	Communal (1)	Michener, 1969
<i>Hoplonomia pulchribal-</i> <i>teata</i>	Papua New Guinea	Solitary (?) ⁸	Michener, 1964

¹ Each of two nests were provisioned by two females.² Observations are based on "a number of nests."³ The number of nests excavated is not given, but this species has been used widely in agricultural systems, and there are no reports of social behavior.⁴ One of three nests excavated by the author had three adult females present; no females were present in the other nests at the time of excavation.⁵ Only one nest was excavated, and it contained 3 non-provisioning females; Batra suggested the females may have been overwintering together.⁶ The author stated that "more than one female inhabited a burrow."⁷ Observations are based on "several" nests.⁸ The number of nests excavated was not given, but there were "several dozen" in the aggregation.

Table 2. Species in the Nomiinae whose nest architecture has been studied. Taxonomy follows Michener et al. (1994) and Pauly (1990); abbreviations are used in Appendix 2.

Taxon	References
<i>Acunomia</i> (sensu, Pauly, 1990) [= <i>Nomia</i> of Michener et al., 1994]	
<i>melanderi</i> Cockerell (Nm)	Johansen et al., 1978; Ribble, 1965; Stephen et al., 1969
<i>nortoni</i> Cresson (Nn)	High, 1921; Parks, 1928
<i>tetrazonata</i> Cockerell (Nt)	Wcislo, 1993
<i>Afromomia</i>	
<i>sjostedti</i> (Friese) (As)	Michener, 1969
[= <i>N. hypochrysea</i> (Cockerell)]	
<i>Austronomia</i>	
<i>australiana</i> Smith (Aa)	Rayment, 1956; P. Kukuk, pers. comm.; Wcislo, pers. obs.
<i>Dieunomia</i>	
<i>heteropoda</i> (Smith) (Dh)	Blair, 1935; Cross and Bohart, 1960; Parker et al., 1986; Wcislo, 1993
<i>nevadensis</i> Cockerell (Dn)	Cockerell, 1934; Cross and Bohart, 1960; Kerfoot, 1964
<i>triangulifera</i> (Vachal) (Dt)	Rau, 1929; Cross and Bohart, 1960; Wcislo, unpubl. data
<i>Holonomia</i>	
<i>pulchribalteata</i> (Cameron) (Hl)	Michener, 1964
<i>punctulata</i> (Dalla Torre) (Hp)	Masuda, 1943; Hirashima, 1961
<i>Leuconomia</i>	
<i>candida</i> Smith (Lc)	Michener, 1969
<i>Pseudapis</i>	
<i>diversipes</i> (Latreille) (Pd)	Rozen, 1986
<i>oxybeloides</i> (Smith) (Po)	Batra, 1966
<i>Rhopalomelissa</i> (= <i>Lipotriches</i> sensu Pauly, 1990)	
<i>esakii</i> Hirashima (Re)	Hirashima, 1961
<i>halictella</i> (Cockerell) (Rh)	Rayment, 1956
<i>ruficornis</i> (Spinola) (Rr)	Gutbier, 1915; Soika, 1932
<i>yasumatsui</i> Hirashima (Ry)	Hirashima, 1961
<i>Nomia</i> # 1 (C. D. Michener) (R1)	Michener, 1969
<i>Nomia</i> [incertae sedis]	
<i>capitata</i> Smith (Nc)	Batra, 1966
<i>nasicana</i> Cockerell (nn)	Batra, 1966
<i>unidentata</i> Oliver (Nu)	Rashad et al., 1979

illustrated for *Austronomia australica* (Fig. 1c) by Rayment (1956). [P.F. Kukuk (pers. comm.), however, has never seen turrets in over 500 nests at several aggregations of *A. australica*.] The nest entrance of *Nomia melanderi* is a vertical extension of the main burrow, comprised of compacted soil, which is surrounded by a tumulus (Fig. 1d). In other taxa, such as *Dieunomia triangulifera* and *D. heteropoda*, there is a more or less horizontal tube, perpendicular to the main vertical burrow, and it is surrounded by a mound of excavated soil ("tumulus") (Figs. 1e, 2a, b). The nest entrances of many nomiine bees are not noticeably constricted, unlike those of many halictine nests, which have a nest entrance

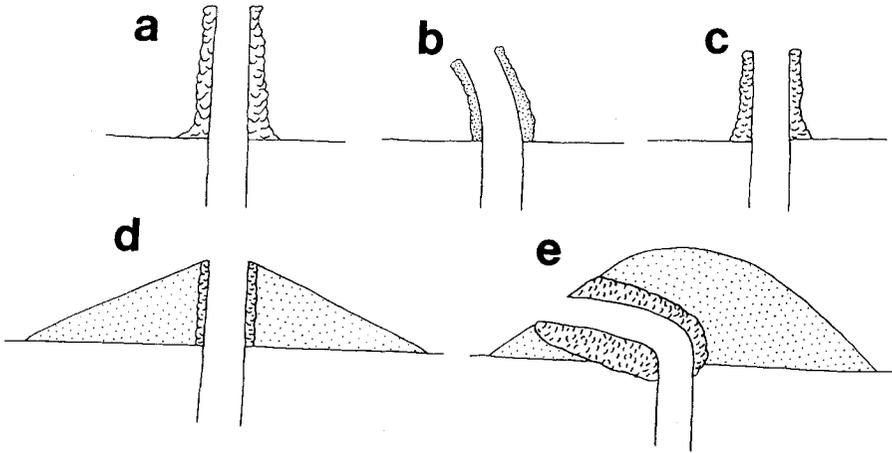


Fig. 1. Nest turrets. a) *Rhopalomelissa esakii*, redrawn from Hirashima 1961; b) *Rhopalomelissa ruficornis*, redrawn from Soika 1932; c) *Austronomia australica*, redrawn from Rayment 1956 [Kukuk (pers. comm.) has never seen such turrets for what is believed to be the same species—see text]; d) *Nomia melanderi*, redrawn from Stephen et al. 1969; e) *Dieunomia triangulifera*, redrawn from Stephen et al. 1969.

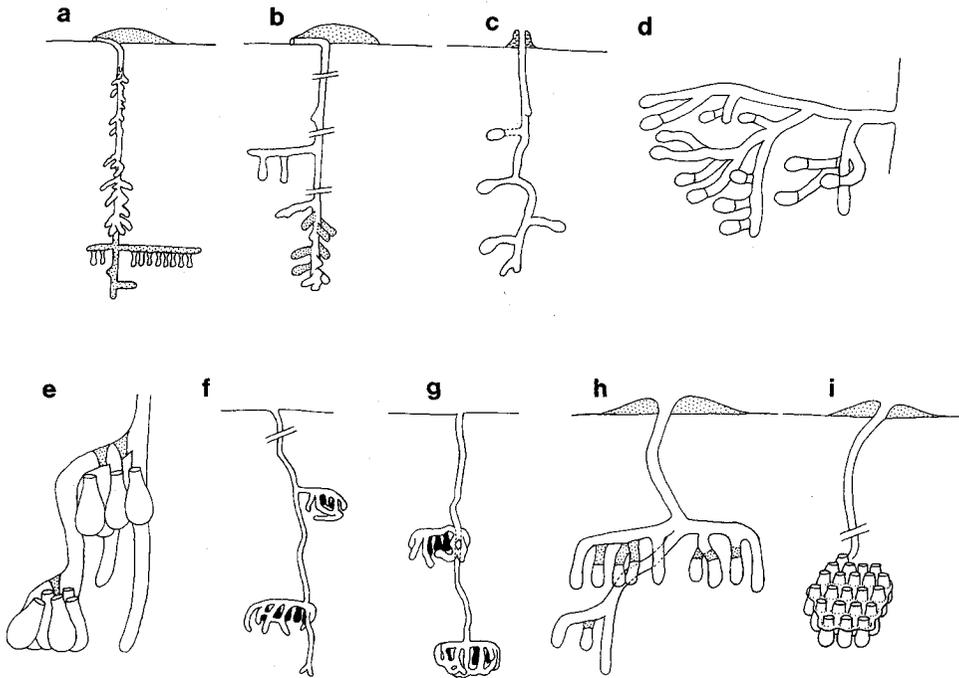


Fig. 2. Nest structure. a) *Dieunomia triangulifera*, redrawn from Cross and Bohart, 1960; b) *Dieunomia heteropoda*, redrawn from Cross and Bohart 1960; c) *Rhopalomelissa esakii*, redrawn from Hirashima, 1961; d) *Afronomia sjostedti*, redrawn from Michener, 1969; e) *Austronomia australica*, redrawn from Rayment, 1956 [Kukuk (pers. comm.) writes that this drawing is not accurate, and that the nest architecture is more similar to that shown in Figs. 2g or 2h]; f) *Nomia capitata*, redrawn from Batra 1966; g) *Nomia oxybeloides*, redrawn from Batra 1966; h) *Hoplonomia pulchribalteata*, redrawn from Michener 1964; i) *Nomia unidentata*, redrawn from Rashad et al. 1979.

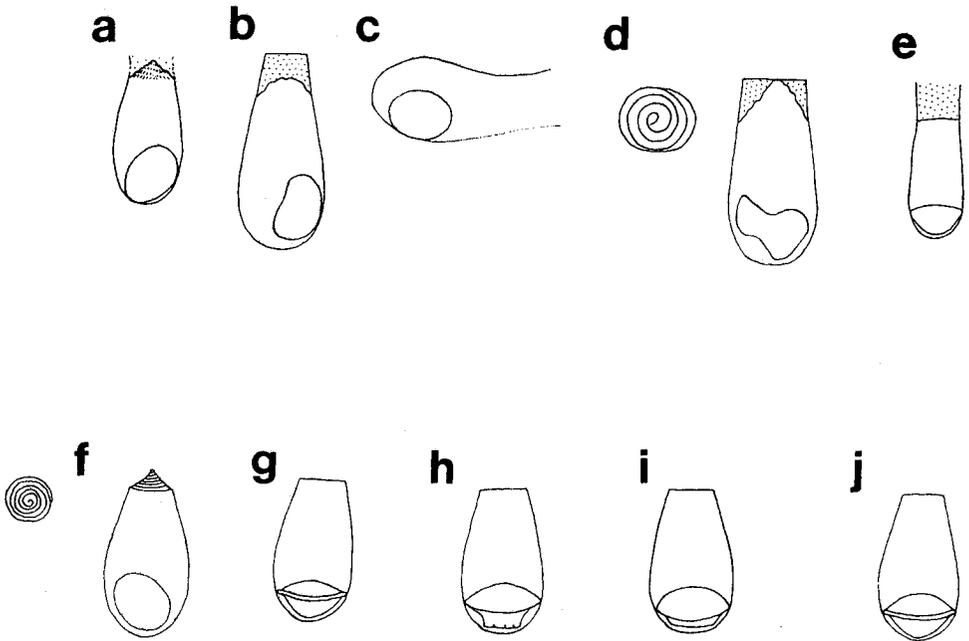


Fig. 3. Cell structure and pollen mass shapes. a) *Pseudapis diversipes*, redrawn from Rozen 1986; b) *Nomia oxybeloides*, redrawn from Batra 1966; c) *Afromomia sjostedti*, redrawn from Michener 1969; d) *Nomia unidentata*, redrawn from Rashad et al. 1979; e) *Hoplonomia pulchribalteata*, redrawn from Michener 1964; f) *Nomia melanderi*, redrawn from Stephen et al. 1969; g) *Dieunomia triangulifera*, redrawn from Stephen et al. 1969; h) *Dieunomia nevadensis arizonensis*, redrawn from Stephen et al. 1969; i) *Dieunomia nevadensis bakeri*, redrawn from Stephen et al. 1969; j) *Dieunomia heteropoda*, redrawn from Stephen et al. 1969.

narrowed to approximately the width of the bee's head (Sakagami and Michener, 1962).

The main tunnel is vertical in most taxa (Fig. 2a–c, f, g), or nearly vertical (Fig. 2h, i), although it is sub-horizontal in *Afromomia* (Fig. 2d). The main tunnel branches, with each branch then leading to individual cells (Fig. 2d), a row of cells (Fig. 2a, b), or to a cluster of cells (Fig. 2e–g, i). In all taxa except *Afromomia* and *Nomia unidentata*, the main tunnel continues beyond the depth of the cells. Many nomiines orient their cells in a vertical direction (i.e., perpendicular to the soil surface) (Appendix 2) (e.g., Fig. 2a, b), but in *Afromomia* (Fig. 2d) and *Rhopalomelissa* (Fig. 2c) they are horizontal or subhorizontal, as they are in many halictines (Sakagami and Michener, 1962). Another major difference is that halictine cells are usually bilaterally symmetrical, being slightly flattened on the lower surface. In contrast, the cells of most of the known nomiines are radially symmetrical (Fig. 3a, b, d–j). *Hoplonomia punctulata* may be exceptional in having bilaterally symmetrical cells, and the illustration of *Afromomia* (Fig. 3c) appears to indicate that cells are bilaterally symmetrical.

The shape and orientation of the pollen mass provides important characters (Fig. 3). For example, in all known *Dieunomia* the pollen mass has a rimmed, oval- to mushroom-shape, with additional species-specific modifications, or even intraspecific differences (Fig. 3h–i). In most other nomiines the pollen mass has

a slightly flattened, nearly spherical shape (Fig. 3a–c, f). The pollen mass illustrated for *Nomia unidentata* (Fig. 3d) is very irregular, and it would be useful to confirm this shape with additional studies. In some nomiines the pollen mass is snugly situated in the bottom of the cell (e.g., Fig. 3f–j), but in *Pseudapis* (Fig. 3a) and some *Nomia* (e.g., Fig. 3b), the pollen mass is tilted on end.

The pattern of fecal deposition *in situ* by the last larval instar may provide useful systematic characters, but this information has not been adequately described for many of the taxa. In two of the known *Dieunomia*, fecal deposits are cylindrical, whereas in other nomiines (e.g., *Acunomia*) feces are deposited as flattened bands.

Discussion

The ethological characters summarized here provide a wealth of systematic data, but information is not available for enough taxa to be of much value in phylogenetic studies. A few comparative comments highlight similarities and differences from bees in the other halictid subfamilies. The social behavior of nomiine bees spans the same range as seen in the better studied sweat bees (Halictinae), ranging from solitary behavior, to communal and possibly hierarchical social groups (e.g., Kukuk, 1990; Vogel and Kukuk, 1994). Solitary females of one species (*Nomia melanderi*) even open cells that are infested by fungi and compactly fill these cells with soil, which reduces fungal sporulation and contamination of other cells (Batra and Bohart, 1969). There are no known parasitic nomiine or rophitine bees, unlike the Halictinae (see Wcislo, *in press a*).

The diversity of nomiine nest architecture is also apparently as rich as that of halictine bees. Females of all species construct nests; Wcislo (1993) pointed out that Moure and Hurd (1987) incorrectly stated that females of *Dieunomia heteropoda* re-use wasp burrows. In contrast to most halictine bees, the cells of nomiines usually have their long axis vertical with respect to the soil surface, and they rarely situate their nests in vertical earthen banks. Cells in nomiines are sometimes re-used (50% of species for which information is available), while cell re-use is uncommon in halictines (reviewed in Wcislo, *in press a*; Sakagami and Michener, 1962). Nests of most halictines and nomiines have blind tunnels which extend below the depths of the cells, but these blind tunnels are not present in the rophitines (Eickwort et al., 1986).

The lactone composition of the Dufour's glands secretions (which are used to line cells) differs among the 3 halictid subfamilies (Duffield et al., 1982, 1984). Available evidence shows that halictines and nomiines apply the lactones in a similar manner (Batra, 1970). In general, cell walls of nomiine and halictine bees are water repellent and often shiny, while those of rophitine bees are thinner, more or less water absorbent, and dull (Rozen, 1993).

Data on nomiine nesting behavior are fragmentary, and clearly much more work needs to be done. A fitting tribute to George Eickwort will be to start filling the huge gaps in our knowledge of these interesting bees.

Acknowledgments

We are thankful to J. G. Rozen, Jr., P. F. Kukuk, and two anonymous reviewers for helpful comments on the manuscript; to Donna Conlon for preparing the illustrations; and to Byron Alexander and Bryan Danforth for handling editorial

matters relating to this manuscript. WTW was supported with general research funds from the Smithsonian Tropical Research Institute.

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Appendix 1. Description of nest architectural characters scored for nomiine taxa. ? = information not known or ambiguous in original publications.

- A Turret or nest chimney present?¹ 1 = yes; 2 = no
- B Maximum depth of nest? 1 = <100 cm; 2 = <50 cm
- C Orientation of main axis of nest cell: 1 = vertical; 2 = horizontal; 3 = intermediate
- D Cell shape: 1 = radially symmetric; 2 = bilaterally symmetric
- E Cell lining present? 1 = yes; 2 = no
- F Arrangement of cells in nest: 1 = even spacing along lateral tunnels; 2 = cells clustered but no cavity; 3 = cells clustered within an excavated cavity; 4 = cells scattered at end of lateral tunnels; 5 = cells nearly sessile, attached to main tunnel
- G Cell attached with lateral tunnels? 1 = no; 2 = yes; 3 = variable
- H Interior face of plug with spiral? 1 = yes; 2 = no
- I Shape of pollen mass: 1 = ovoid saucer-shape; 2 = slightly flattened sphere; 3 = slightly flattened rectangle
- J Pollen mass orientation: 1 = snug in bottom of cell; 2 = tilted on edge
- K Pollen mass coated with secretion? 1 = no; 2 = yes
- L Shape of fecal deposit: 1 = cylindrical, sausage-shaped; 2 = flattened strip
- M Location of fecal deposits: 1 = restricted to basal quarter of cell; 2 = restricted to basal third of cell
- N Orientation of main tunnel: 1 = vertical; 2 = horizontal
- O Main tunnel branches? 0 = none; 1 = horizontal; 2 = subvertical; 3 = vertical
- P Pollen utilization: 1 = restricted to one family; 2 = polylectic
- Q Nest entrance plugged when female(s) leave nest? 1 = yes; 2 = no
- R Cells are re-used? 1 = no; 2 = yes
- S Orientation of nesting site: 1 = horizontal ground; 2 = vertical ground (bank)

¹ Iwata (1976) distinguishes between a "turret" and a "chimney" in that chimneys are added onto the nest tunnel, while turrets are continuations of the nest tunnel itself. For most taxa, behavioral data are lacking and this distinction cannot be made at present.

Appendix 2. Matrix for nest architectural characters for nomiine bees. The full names for the taxa can be found in Table 2.

	Dt	Dh	Dn	Nm	Nn	Nt	Pd	Po	Aa	Hp	Hl	Re	Rh	Rr	Ry	Rl	Lc	As	Nu	Nc	nn
A	1	1	1	2	2	2	2	2	2	2	2	1	1	1	2	2	1	2	1	2	2
B	1	1	1	2	2	2	2	2	?	2	2	1	1	1	1	1	2	2	?	2	?
C	1	1	1	1	1	3	1	1	3	3	3	2	2	1	2	3	3	3	1	1	2
D	1	1	1	1	1	1	1	1	1	?	1	?	?	?	?	?	?	?	1	1	2
E	1	1	1	1	1	1	1	1	?	1	1	?	?	?	1	?	1	1	?	?	?
F	1	1	1	3	3	2	2	3	3	3	4	5	5	2	5	5	4	4	3	2	?
G	3	1	1	1	1	1	1	1	1	3	3	2	2	?	2	2	2	2	1	1	?
H	1	1	1	1	1	1	1	1	?	1	1	?	?	?	?	?	?	?	1	?	?
I	1	1	1	2	2	2	2	2	?	?	?	3	3	3	3	3	2	2	?	2	?
J	1	1	1	1	1	1/2	2	2	?	1	1	1	1	1	1	1	1	1	?	?	?
K	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L	1	1	1	2	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M	1	1	1	2	2	2	1	2	?	?	2	?	?	?	?	?	?	?	?	?	?
N	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
O	1	1	1	?	0	2	2	0	0	?	3	0	0	0	0	0	0	3	0	1	?
P ¹	1	1	2	2	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Q	1	1	1	2	2	2	2	2	2	2	2	1	1	1	1	1	2	2	?	2	?
R	1	1	1	1	1	1	2	2	1	2	?	2	2	2	2	2	?	1	?	?	?
S	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2

¹ Since most species are not well studied, it is impossible to know whether apparent pollen specialization is an artifact of limited information.