

Substrates and Materials Used for Nesting by North American *Osmia* Bees (Hymenoptera: Apiformes: Megachilidae)

JAMES H. CANE,¹ TERRY GRISWOLD, AND FRANK D. PARKER

USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, UT 84322-5310

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ABSTRACT Nesting substrates and construction materials are compared for 65 of North America's 139 described native species of *Osmia* bees. Most accounts report *Osmia* bees nesting in preexisting cavities in dead wood or pithy stems such as elderberry (*Sambucus* spp.), with cell partitions and plugs made from a pulp of finely masticated leaf tissue. Mud is widely used by species constructing free-form clumps of nest cells against stone surfaces. Some *Osmia* bees adopt abandoned nests of other Hymenoptera, particularly those of mud dauber wasps (*Sceliphron* spp.) and larger ground-nesting bees (e.g., *Anthophora* spp.). Reports of subterranean nesting by *Osmia* species are uncommon but possibly under-represent the habit, because subterranean nests are obscure and likely to be scattered. Ground- or surface-nesting habits are suspected for species that are absent from intensive trap-nesting programs in their native ranges but that otherwise have been commonly taken at flowers. The range of nesting habits and materials of European species are largely comparable, although records indicate that far more European species may nest in empty snail shells.

KEY WORDS Apoidea, bees, trap-nest, nest

The nesting habits of bees in the Megachilidae collectively show more variety than any other bee family. Typically, linear nests are built in various substrates, including soil, in cracks amid soil or rock, under or on rock surfaces, on stems, in pithy stems or galls, in nests of other bees and wasps, in snail shells, and in preexisting tunnels left in wood by the larvae of wood-boring beetles. Nest cells are partitioned, capped and sometimes lined with exogenous materials, such as cut or masticated leaves, leaf hairs, mud, resin, or pebbles, sometimes in combination (O'Toole and Raw 1991). A species' cephalic morphology often indicates preferred nest-building material. Thus, *Osmia* mason bees have facial horns used to polish mud partition surfaces (Torchio 1989), whereas mandibles of congenics have mandibular biting surfaces to chew leaf mastic (Williams and Goodell 2000). The mandibles of leaf-cutting *Megachile* bees have beveled cutting edges. So-called "carder bees" (*Anthidium* spp.) have a rake of fine mandibular teeth to glean plant hairs (Michener and Fraser 1978), and species that collect resin have sparse facial hair. In contrast, the morphologies of megachilid bees hold few clues as to preferred nesting substrates; such information accumulates incrementally as bee biologists find and describe nests.

This review was motivated by a need to know the nesting habits of American *Osmia* species needed for managed pollination, both in traditional crops (e.g.,

Cane 2005b) as well as for wildflowers being farmed for habitat restoration seed (e.g., Cane 2005a). To protect or enhance pollination services of native bees in crops and plant communities, knowledge of the bee species' nesting habits can be essential. If an effective pollinator is numerically inadequate, one may need to foster expanding populations by assuring adequate nesting resources through informed habitat management practices. Species of *Osmia* that nest underground or on rock surfaces are unlikely to be managed for agricultural purposes. However, cavity-nesters can be provided with artificial or natural nesting substrates. Only a few cavity-nesting species of two megachilid genera, *Osmia* and *Megachile*, are being sustainably managed thus far (e.g., Bosch and Kemp 2001), but these are the two nonsocial bee genera that are most likely to contribute additional species of managed agricultural pollinators (Strickler and Cane 2003). Recognizing cavity-nesting species among pollinator guilds will help guide strategies for pollinator management. The purpose of this study was to compile and interpret both published and unpublished nesting records from among the 139 described species of *Osmia* bees native to North America (Table 1).

Materials and Methods

Most of the *Osmia* nesting records reported here were drawn from primary sources in the published literature beginning in the mid-19th century. Euro-

¹ Corresponding author, e-mail: jcane@biology.usu.edu.

Table 1. Known nesting substrates and exogenous nest construction materials used by *Osmia* species native to North America

<i>Osmia</i> subgenus and species ^a	Nesting substrate ^b	Nest plug, partition ^c	Details of nesting ^d	Reference
<i>Acanthosmioides</i> 8/23				
<i>integra</i> Cresson	Soil, surface?	L, M?	Linear in sand or clustered mud cells under rock?	Hicks 1926 as <i>O. novomexicana</i> ; Sugden 1985; Gordon 2003
<i>kenoyeri</i> Cockerell	Soil	M+F	Shallow linear nest dug in sandy loam	Rust and Osgood 1993
<i>lanei</i> Sandhouse	Soil	L	Shallow subterranean, also reuses nest burrows	C. Otto and M. Mesler, unpublished data
<i>longula</i> Cresson	Surface	M	Single nest clump on side of stone	Parker 1975
<i>nifoata</i> Cockerell	Soil	L	Shallow subterranean	Fulton and Bergen 1935
<i>nigrifrons</i> Cresson	Surface, stem	M	Clustered in culvert, or underground, or in stem nests	Hicks 1926; Rust et al. 1974
<i>nigrobarbata</i> Cockerell	Soil	L	Shallow subterranean, ± linear	Rozen and Favreau 1967
<i>unca</i> Michener	Soil, nests	M+L	Shallow subterranean, also reuses nest burrows	Stephen et al. 1969
<i>Cephalosmia</i> 5/5				
<i>californica</i> Cresson	Wood, stem	M+L	Ball of leaf pulp rolled in mud	Levin 1966; Rust 1974; Torchio 1989
<i>grinnelli</i> Cockerell	Wood	L		Parker 1985b
<i>marginipennis</i> Cresson	Surface	M+L	Clusters in cracks of outcrops	Parker 1980
<i>montana</i> Cresson	Wood, stem	L		Rust 1974; Torchio 1989
<i>subaustralis</i> Cockerell	Wood	L	Beetle burrow, nest block	Rust 1974; F. D. Parker, unpublished data
<i>Diceratosmia</i> 3/5				
<i>botitena</i> Cresson	Shell		Snail shells	F. D. Parker, unpublished data
<i>conjuncta</i> Cresson	Shell	L	Snail shells	Rau 1937
<i>subfasciata</i> Cresson	Wood, shell	L+S	Beetle burrows, snail, ball of leaf pulp rolled in sand	Linsley 1946; Mitchell 1962; Krombein 1967; Neff and Simpson 1992
<i>Euthosmia</i> 1/1				
<i>glauca</i> Fowler	Nests, stem, wood	M+W	<i>Sceliphron</i> wasp nests, stem cell cap with pith chips	Linsley and MacSwain 1941 as <i>O. exilis</i> ; Rust and Clement 1972;
<i>Helicosmia</i> 4/4				
<i>chalybea</i> Smith	Wood	L	Other bees' nests in clay banks Trap nested in wood blocks in Mississippi	Frankie et al. 1998 B. Sampson, unpublished data
<i>coloradensis</i> Cresson	Wood, stem	L		Rust 1974; Hawkins 1975
<i>georgica</i> Cresson	Wood	L	Also in burrows in Jeffrey pine cone	Hartman 1944; Krombein 1967; Hawkins 1975
<i>texana</i> Cresson	Nests, wood, stem	L	Primarily <i>Anthophora</i> bee nests in clay banks	Hicks 1926; Mickel 1928; Rau 1937; Hobbs et al. 1961; Rust 1974; Hawkins 1975; Tepedino and Frohlich 1984
<i>Melanosmia</i> 40/93				
<i>aglaia</i> Sandhouse	Wood	L	In wooden nest blocks for <i>Megachile rotundata</i> (F.)	Cane 2005b
<i>albiventris</i> Cresson	Wood	L	Pebbles in terminal cell and cap	Rau 1937; Medler 1967; Jenkins and Matthews 2004
<i>albolateralis</i>	Stem	L	Single nest	F. D. Parker, unpublished data
<i>atriventris</i> Cresson	Bark, stem, wood	L		Graenicher 1906; Fye 1965; Horn and Hanula 2004
<i>atrocyanea</i> Cockerell	Wood	L		F. D. Parker, unpublished data
<i>bakeri</i> Sandhouse	Wood, stem	L+M	Leaf pulp smeared with mud	Rust 1987; Frankie et al. 1998; J. H. Cane and M. Weber, unpublished data
<i>bruneri</i> Cockerell	Wood, stem, nests	L+W	<i>Sceliphron</i> nests, soil banks and sand as <i>O. bennettiae</i>	Hicks 1926; Frohlich 1983; F. D. Parker, unpublished data
<i>bucephala</i> Cresson	Wood	L+W	Wood chips from cavity interior added to leaf pulp	Packard 1868; Krombein 1967
<i>cahuila</i> Cooper	Bark	B	Single nest between bark and wood of stump	Cooper 1993; J. H. Cane unpublished data
<i>clarescens</i> Cockerell	Wood, nest	L, S	<i>Sceliphron</i> nests	T. C. Griswold and R. R. Snelling, unpublished data
<i>cobaltina</i> Cresson	Stem	L		F. D. Parker, unpublished data
<i>cordata</i> Robertson	Nests, wood	L	<i>Sceliphron</i> , <i>Trypoxylon</i> , <i>Melitoma</i> , <i>Anthophora</i> nests	Rau 1937;
<i>crassa</i> Rust & Bohart	Stem	L		Rust and Bohart 1986
<i>cyarella</i> Cockerell	Wood, stem			Frohlich et al. 1988; F. D. Parker, unpublished data
<i>densa</i> Cockerell	Wood	L(+F?)	Beetle burrows	Linsley and MacSwain 1951
<i>dolerosa</i> Sandhouse	Wood		Two bees from single nest block	T. Criswold, unpublished data
<i>gabrielis</i> Cockerell	Wood	M		F. D. Parker, unpublished data

Table 1. Continued

<i>Osmia</i> subgenus and species ^a	Nesting substrate ^b	Nest plug, partition ^c	Details of nesting ^d	Reference
<i>gaudiosa</i> Cockerell	Wood, stem	L		Krombein 1967; F. D. Parker, unpublished data
<i>indeprensata</i> Sandhouse	Wood, stem	L		Rust 1987
<i>inermis</i> Zetterstedt	Surface	L	Clusters under rocks	Zetterstedt 1840; Smith 1851 misidentified as <i>O. parietina</i> ; Priesner 1981; Westrich 1989; Else and Edwards 1996
<i>iris</i> Cockerell & Titus	Wood	L+S	Sand grains imbedded in leaf pulp	F. D. Parker, unpublished data
<i>kincaidii</i> Cockerell	Wood, stem	L		Parker and Bohart 1966; Rust 1987; Frohlich et al. 1988
<i>laeta</i> Sandhouse	Stem	L		F. D. Parker, unpublished data
<i>liogastra</i> Cockerell	Soil			P. F. Torchio, unpublished data
<i>marginata</i> Michener	Stem	L	Stem-traps	Parker and Bohart 1966; Tepedino and Parker 1983
<i>neocyanopoda</i> Rust & Bohart	Stem	L	Stem-traps	Rust and Bohart 1986
<i>nigriventris</i> Zetterstedt	Wood		Also pine bark, old stumps	Westrich 1989
<i>penstemonis</i> Cockerell	Stem	L		F. D. Parker, unpublished data
<i>pikei</i> Cockerell	Wood, stem	M		Parker and Bohart 1966; Cripps and Rust 1985
<i>proxima</i> Cresson	Wood, stem	L		Fye 1965; Medler 1967
<i>pumila</i> Cresson	Wood, stem	L	Rose stem	Graenicher 1906; Krombein 1967; Medler 1967; Johnson 1986
<i>pusilla</i> Cresson	Wood, stem	L		F. D. Parker, unpublished data
<i>rostrata</i> Sandhouse	Wood		Date palm logs	R. R. Snelling, unpublished data
<i>sanrafaelae</i> Parker	Wood, soil	L	Clusters in cracks in soil bank	Parker 1985a, 1985c
<i>sanctarosae</i> Cockerell	Stem		Single nest from elderberry	L. Stange, unpublished data
<i>sculleni</i> Sandhouse	Stem	L	Single nest in stem-trap	Parker and Tepedino 1982
<i>simillima</i> Smith	Gall, wood	M	Clusters in oak-apple galls <i>Amphibolips</i> spp.	Packard 1868; Graenicher 1906; Scott 1993
<i>tanneri</i> Sandhouse	Surface, soil	M	Clusters beneath surface stones	Parker 1975; Tepedino and Boyce 1979; Torchio 1984
<i>tersula</i> Cockerell	Wood, stem	L		Medler 1967; Sheffield et al. 2003
<i>tristella</i> Cockerell	Wood, stem			F. D. Parker, unpublished data
<i>Mystacosmia</i> 1/1				
<i>memoris</i> Sandhouse	Nests, stem	L(+R?)	Soil burrows of <i>Diadasia</i> bees	Bohart 1955 as <i>O. seclusa</i> Sandhouse; Rust and Clement 1972
<i>Osmia</i> 2/2				
<i>lignaria</i> Say	Wood, nests	M	Also crevices, mud or paper nests of wasps, and ground nests of bees, <i>Xylocopa</i> nests	Rau 1926, 1937; Hicks 1934; Balduf 1962; Levin 1966; Krombein 1967; Medler 1967; Rust 1974; Torchio 1989
<i>ribifloris</i> Cockerell	Wood, nests	L	<i>Sceliphron</i> nests, nest blocks	Rust 1986; Krombein 1967; J. H. Cane, unpublished data
<i>Trichinosmia</i> 1/1				
<i>latisulcata</i> Michener	Wood, stem	G+S+L		Parker 1984; Frankie et al. 1998

^a The fraction of described native North American *Osmia* species with known nesting habits is given for each subgenus.

^b The substrates wood and stem refer to drilled holes in wood blocks or pithy stems, or their natural counterparts. Surface nests are affixed to a hard surface, typically stone. Soil indicates a subterranean nest. Nests refers to use of abandoned subterranean or surface nests of other wasps or bees.

^c Codes for nesting construction materials (cell partitions and caps, occasionally cell walls) are as follows: F, plant fiber; G, gravel; L, leaf pulp or mastic; M, mud; R, resin; S, sand; and W, wood or pith chips. A plus sign indicates that the two to three nest-building materials are used together, whereas a comma between nest materials indicates that different investigators reported use of different materials.

^d Nest cells of *Osmia* bees are typically arrayed in a linear series, but where noted, they can be clustered in an irregular mass.

pean nesting records were included for several Holarctic species, although the several Eurasian *Osmia* records adventive in North America (Cane 2003) were not considered (e.g., *Osmia caerulea* L.). We also excluded species classified as *Hoplitis* sensu Michener (2000), although some European taxonomists include these species in *Osmia*. A number of

additional unpublished nesting records were compiled from the extensive trap-nesting programs run by scientists at the USDA-ARS Bee Biology and Systematics Laboratory (BBSL) in Logan, UT. These efforts focused on California and the U.S. Intermountain West, particularly northern Utah, over the past 50 yr. These records are accompanied by curated collection

vouchers in the BBSL collection, pinned with the specimen's natal cocoon. Multiple published reports were included in our literature survey, except for brief notes for otherwise intensively studied species. Author's names of *Osmia* species are provided in Table 1.

Results and Discussion

Our compilation identified nesting records for 65 of the 139 described *Osmia* species of North America, including first reports for 16 species (Table 1). Pre-existing above-ground cavities (wood, pithy stems, snail shells, and *Sceliphron* nests) were the sole nesting substrates reported for 48 (73%) of the species (Fig. 1). No doubt this large fraction partly reflects the ease and efficacy of trap-nesting most of these species. In contrast, experience, patience and luck are required for discovering subterranean *Osmia* nests, especially if a species does not nest gregariously. Species of the subgenus *Acanthosmioides* depart from the more typical nesting habit; the seven American species with nesting records all build surface nests or excavate soil nests (Fig. 1, 4). Only one *Acanthosmioides*, *O. nigrifrons*, sometimes occupies trap-nests as well. A few American *Osmia* species occupy abandoned subterranean nests of other bee species, especially species of *Anthophora* (Fig. 1, 2), although the habit has only been commonly reported for *O. texana*. If reusing nests of other Hymenoptera, American *Osmia* typically adopt the above-ground nests of mud-daubing wasps, particularly *Sceliphron* or *Trypoxylon* ($n = 6$) (Table 1; Fig. 1, 3). Again, reuse of these nests may be more commonly reported because such wasp nests are more often found and studied than comparable nests of other wasp genera. Collectively, the records for North American *Osmia* represent a substantial fraction of the world's fauna of 318 described species of *Osmia sensu stricto* (Michener 2000).

Nests of nearly all North American *Osmia* are produced in a preexisting cavity discovered by the nesting female (Table 1). The exception again comprises the eight species of the North American subgenus *Acanthosmioides* with nesting records, all of which construct their nests de novo (Table 1; Fig. 1, 4 and 5). *Acanthosmioides* nests are either free-form mud nests clumped against a hard substrate, typically rock, or a linear shallow subterranean nest tunnel apparently excavated by the nesting female (C. Otto and M. Mesler, personal communication). Building a nest de novo presumably frees these species to occupy habitats lacking the deadwood or pithy stems required by other *Osmia* species, such as the beach dunes, desert basins, and agricultural landscapes thus far reported (Table 1). Species of *Acanthosmioides* also may be freed from competition with similar-sized megachilids for the finite numbers of preexisting cavities available in a given habitat, albeit for an unspecified cost of time invested in constructing an entire nest. As with other ground-nesting bees, female *Acanthosmioides* are freed to consistently make nest cells of optimal size for their offspring, rather than accommodating the dimensions of an existing cavity.

For most North American *Osmia* bees (84%), masticated leaf pulp was reported as the primary material used to partition and cap nest cells (Table 1). The pulp is sometimes admixed with sand, wood or pith chips, or plant fibers (Fig. 1, 1, 2, 3, and 5). Some species blend mud and mastic in construction; observers report that the female bee rolls each ball of mastic in sand or mud before returning it to the nest, rather than collecting alternating loads of soil and mastic (Torchio 1989, Neff and Simpson 1992). We found scattered sand grains imbedded in all leaf pulp partitions of *O. iridis*. This was not previously noted, so the habit may be more common than currently reported, because it was only evident with microscopic examination. Mud is an uncommon nesting material for North American *Osmia* species. Only five cavity-nesting species use mud to partition and cap their nest cells (Table 1; Fig. 1, 6); four other species build surface nests of mud (Fig. 1, 4). Sometimes one or more mud-foragers will extend a tunnel underground to access suitable mud, giving the false impression of subterranean communal nesting. This erroneous observation can be easily corrected by intercepting departing individuals to note mud pellets. We remain ignorant of the relative adaptive trade-offs in bees' use of mud versus masticated leaf to seal nests against parasites and predators as well as the comparative effort needed to acquire and manipulate the two materials.

For several reasons, we are confident in all but a few of the nesting records compiled in Table 1. In the BBSL collections, all but one of the trap-nesting records are represented by >10 specimens, even among the species lacking published nesting accounts. For example, *O. penstemonis* and *O. cobaltina* are each represented by >60 specimens that had been reared from stem nests. In Table 1, we have noted the minority of cases for which our nesting insights come from only one or two specimens or a single reported nest. In one rare case, *O. dolerosa*, the two specimens reared from a single trap-nest are paratypes from the species' original description (Sandhouse 1939).

For a very few *Osmia* species, a peculiar combination of nesting habits reported by different authors warrants cautious interpretation. Hicks' (1926) brief report of mud surface nests for *O. integra* contrasts with a more recent and thoroughly documented report for subterranean sand nests lined with masticated leaf pulp for this species (Gordon 2003). No other reported *Osmia* species is known to have such divergent nesting habits. The taxonomist determining Hicks' specimens (T.D.A. Cockerell) was unaware of the daunting diversity of western *Osmia* species that would be described in the ensuing 80 yr, including synonymy of his name for this species (*O. novomexicana*) with *O. integra*. The location of Hicks' voucher specimens, if they exist, is unknown, so Cockerell's identification cannot be verified. Nearly all of the other published nesting records in Table 1 are authored by, or acknowledge identifications by, competent *Osmia* taxonomists. Specimens for the unpublished records likewise have recent authoritative identifications. Those few confusing cases for which

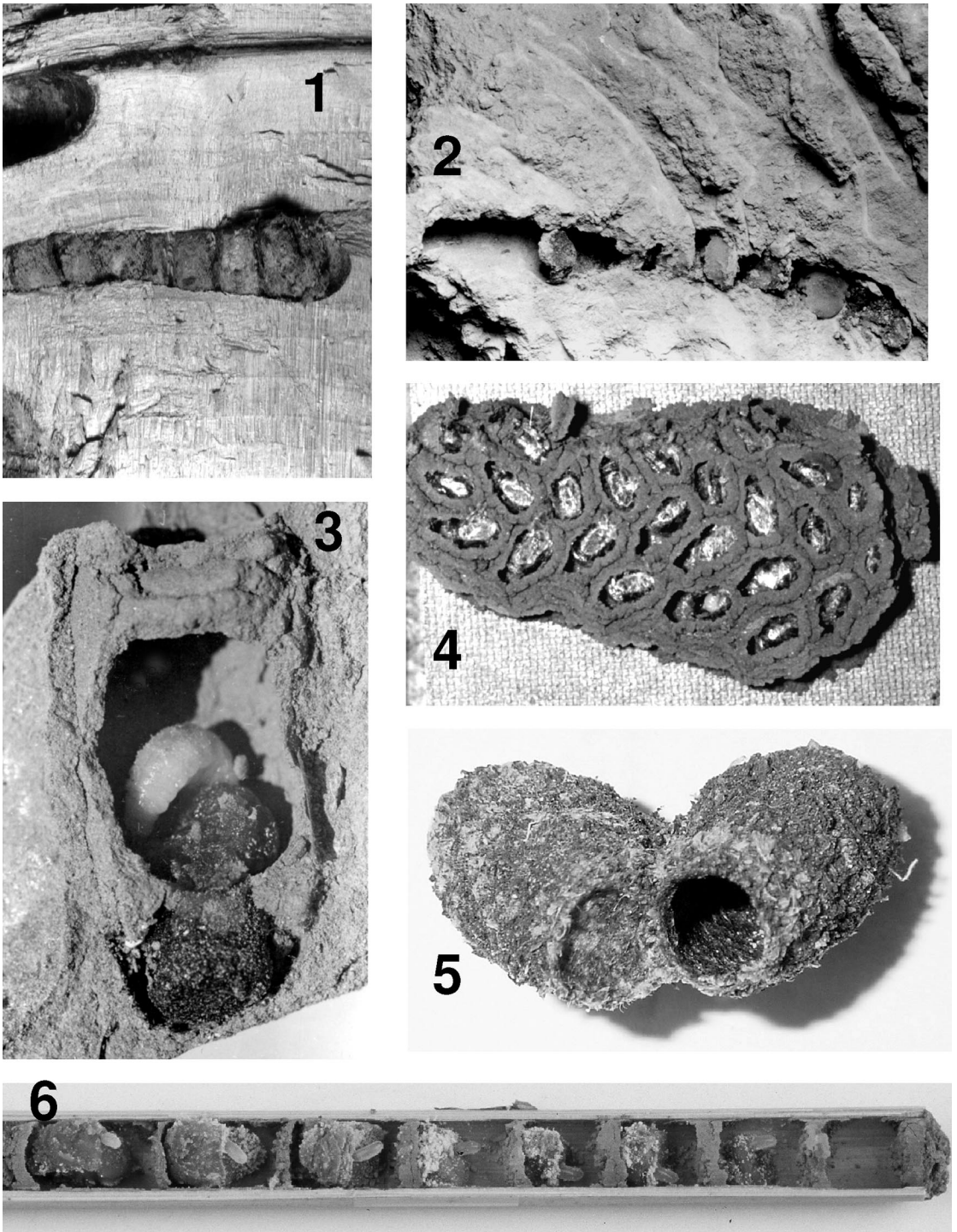


Fig. 1. Nests of various American *Osmia* species representing the diverse major nesting substrates that they use (photographer's name in parentheses). (1) Nest of *O. californica* built in a tunnel bored through maple by a cerambycid beetle larva (Bill Nye). (2) Abandoned nest of *Anthophora occidentalis* Cresson occupied by cells of *O. texana* (Bill Nye). (3) Nest of an *Osmia* sp. in an old nest cell of a *Sceliphron* wasp (Bill Nye). (4) Surface nest of *O. nigrifrons* with clumped nest cells made of mud (Bill Nye). (5) Subterranean soil nest of an *Osmia* sp. whose two nest cells were constructed and capped with masticated leaf pulp (Jim Cane). (6) Linear nest of *O. lignaria* built in a hollow reed with partitions and cap made of mud (Jordi Bosch).

we lack confidence or replication in nesting reports should be considered tentative and, for older records, possibly erroneous.

We remain ignorant of nesting habits for about half of the American *Osmia* species. We suspect that a disproportionate number of these species will be surface- or ground-nesters for two reasons. First, surface or soil nesting substrates predominate for all eight species of subgenus *Acanthosmioides* with nesting records (Table 1); 15 more North American species of this subgenus lack nesting records. Second, otherwise common species that are absent from extensive trap-nesting programs within their native geographic ranges probably nest in other substrates. Entomologists at the BBSL have trap-nested intensively for years in Cache Valley and its surrounding mountains in northern Utah and southern Idaho. Four species of *Osmia* (*Melanosmia*) that have repeatedly been collected at flowers in Cache Valley have never been found in trap-nests: *O. bella* Cresson, *O. brevis* Cresson, *O. paradisiaca* Sandhouse, and *O. trevoris* Cockerell. Similarly, *O. (M.) cerasi* Cockerell and *O. (M.) titusi* Cockerell were absent from an intensive block and stem trapping effort where these two species occur in the San Rafael Desert of central Utah. Ground-nesting species may predominate in such scrub deserts, where cavity-nesting opportunities are rare.

The California species, *O. laeta*, is useful to illustrate the assertion that a ground-nesting habit can be suspected for those species that are otherwise common in collections but absent from intensive local block and stem-trapping efforts. Uncommon *Osmia* species may be absent from trap-nest surveys merely because they are rare (e.g., *O. sequoiae* Michener). However, there are >1,000 pinned specimens of *O. laeta* in the collections at the BBSL alone. Most were netted at flowers. Males and females have been taken in 20 counties from throughout California, beginning in 1933. Repeated programs of trap-nesting with blocks and stick nests in several of these California counties have yielded other similar-sized *Osmia* species, but *O. laeta* has never been reported from trap-nests, and it has only once been reared from a stem-nest (Table 1). The typical nesting habit *O. laeta* awaits discovery of more nests, which are likely to be subterranean.

Some states and regions are more likely than others to yield new cavity-nesting records. California remains under-sampled, given the state's sheer size, the diversity of habitats and flora, distinct seasonality, and rich *Osmia* fauna. The case of *O. laeta* in California remains enigmatic. For another California example, *O. aglaia* was not previously reported from trap-nests, but hundreds of nests of this Pacific coast species were obtained from drilled nest blocks and are now being propagated for pollination of cultivated bramble fruit (Cane 2005b).

Comparable surprises await trap-nesting in other regions. In southern Mississippi, for example, the nesting habits of southeastern *O. chalybea* were previously unknown, but nests were obtained recently in large numbers from drilled nest blocks (Blair Sampson, per-

sonal communication). Last, additional nesting records are expected from collections containing specimens that have been reared from trap-nests, but represent undescribed but recognizable species of western *Osmia*, or unidentified material that is difficult to reliably discern. Surmounting these taxonomic impediments will extend the list of nesting habits for North American *Osmia* species.

In general, habits of the Eurasian *Osmia* fauna (mostly Europe and Japan) are comparable with those of North America (Maeta 1978; Westrich 1989; O'Toole and Raw 1991; Banaszak and Romasenko 1998). European studies began earlier, but European nesting records are complicated by taxonomic synonymies that have not yet been disentangled. Maeta (1978) lists 39 species with complete nest habit records, whereas Banaszak and Romasenko (1998) list 24 of Europe's 51 species. As with the American fauna, just one European species uses plant galls, and a few more make free-standing nests (using either mud or leaf mastic) or adopt abandoned nests of *Anthophora* bees and *Sceliphron* wasps. Snail shells are used, sometimes exclusively, by nine to 17 European species and one of Japan's five species, in contrast with the three uncommon North America *Osmia* species using snail shells. Fewer European and Japanese species reportedly nest in wood tunnels, perhaps reflective of less intensive trap-nesting efforts there. As for North America, most European *Osmia* bees plug and partition with leaf mastic, except for most species of subgenus *Osmia*, which use mud, including three of Japan's five *Osmia* species.

Comparative knowledge of the nesting habits of *Osmia* bees can be used to generate phylogenetic and evolutionary hypotheses for the genus (Eickwort et al. 1981; Frohlich 1983; Bosch et al. 2001). A few subgenera of North American *Osmia* use the same distinctive nesting substrate. For example, snail shells are used by all three species of the American subgenus *Diceratosmia* that have nesting records but by no other North American *Osmia* species (Table 1). Several species of the Eurasian subgenus *Pyrosmia* also nest in snail shells (O'Toole and Raw 1991). Michener (2000) noted that the "two subgenera [*Diceratosmia* and *Pyrosmia*] could well be united," suggesting common ancestry. However, the habit of nesting in snail shells is known for at least seven other Eurasian *Osmia* species that represent other subgenera (Maeta 1978; Westrich 1989; O'Toole and Raw 1991; Banaszak and Romasenko 1998), some of which further conceal their snail shell nests beneath pine needles or grass straw. Such an unusual habit seems unlikely to be plesiomorphic, but it may reflect either independent origins converging on snail shell nesting, or faulty taxonomic constructs for the subgenera.

Conversely, species of the large subgenus *Melanosmia* are mostly wood and stem nesters; however, a few Nearctic species have been taken from ground nests (*O. liogastra*) or both surface and subterranean nests (*O. tanneri*) (Table 1) with parallel examples in the Palearctic fauna (Michener 2000). These exceptional species represent a diversity of nesting habits within

this large and unwieldy subgenus. Eickwort et al. (1981) argued that ground-nesting might be the ancestral habit among bees of the Megachilidae (Megachilinae sensu Michener (2000) exclusive of ancestral Lithurgini), with multiple independent origins of the cavity-nesting habit. If true for *Osmia*, then the scattered reports of ground-nesting habits are readily explicable phylogenetically. Recognizing the vacillating history of classification for *Melanosmia* (Michener 2000), the current subgeneric bounds of *Osmia* are clearly not stable, so independent ancestry for these divergent nesting habits also remains possible.

What are the adaptive trade-offs for different nesting materials used by *Osmia*, specifically the use of leaf mastic versus mud for cell partitions and nest closures? Do species that use mastic rolled in sand or mud represent a primitive unspecialized state, an intermediate evolutionary stage, or a derived behavior? Within the subgenus *Osmia*, at least, mud use is considered to be a derived trait (Bosch et al. 2001). Our compilation reveals that species of *Osmia* collectively offer an unusual opportunity to conveniently evaluate these questions, perhaps only rivaled by the genus *Hoplitis* (table 2 in Eickwort et al. 1981). Replicated functional comparisons are possible (Williams and Goodell 2000), because most subgenera have both mud- and mastic-building species (Table 1).

Presumably, the primary function of both cell partitions and nest caps is physical deterrence of predatory and parasitic insects that would destroy bee progeny. Do both materials equally resist penetration or circumvention? Does the addition of sand grains to mastic (e.g., *O. californica* or *O. subfasciata*) strengthen the partition or render it more abrasive to the mandibles of would-be antagonists? The capability and method for breaching or circumventing these defenses varies with the antagonist. For example, larvae of *Trichodes* checkered beetles (Cleridae) tear through partitions with apparent ease, decimating the contents of entire nests. Cleptoparasitic *Dioxys* bees can penetrate leaf mastic of *Osmia* to lay eggs in completed cells (Rozen and Favreau 1967). In contrast, the smaller nest parasitoids enter completed nest cells only through cracks and crevasses in the substrate, cap or partitions (Bosch and Kemp 2001). Is mud or mastic more prone to cracking over time, or more easily compromised by water? Are they equally gas permeable and does it matter? Mud and mastic differ in availability and distribution across habitats and perhaps seasons, and should require different search strategies and sensory capabilities. But where both materials are readily available nearby, *O. lignaria* and *O. ribifloris* expend equivalent effort collecting and using mud and mastic, respectively (Rust 1993). These two early spring species are closely related, similar in size, and with broadly overlapping ranges. Most species use mastic, but does leaf choice influence construction or function of partitions and closures, or does mastic use reflect ease of acquisition? Comparable experimental studies of adaptive trade-offs in nest attributes between closely related species of *Osmia* should yield

insights of ecological and evolutionary interest, sometimes with practical application for agricultural or conservation management.

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