

Colletidae nesting biology (Hymenoptera: Apoidea)*

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Abstract – Colletidae are unique among bees for certain aspects of their nesting biology. In this review, attributes of colletid nesting are evaluated and discussed in light of a novel phylogenetic hypothesis for the family. Some predictions made about evolution of certain traits, such as the cocoon-spinning behavior of Diphaglossinae, are confronted with phylogenetic evidence. The cellophane-like cell lining of Colletidae is a synapomorphy of this bee family, formed by polyester and characterized for being thick and strong, waterproof, and insoluble in different solvents. Historical developments towards the understanding of nature of the cell lining applied by colletids are summarized along with an account of diversity of some aspects of nesting of these bees.

bee / nest / Colletidae / Stenotritidae / Dufour's gland

1. OVERVIEW

Nests are essential for the reproductive success of bees because they shelter the brood, providing essential conditions for development of immatures. The majority of bee species are solitary (Michener, 2000; Danforth, 2007) and most of them excavate a burrow containing brood cells in a substrate, usually soil. Construction of brood cells is particularly important and a generalized sequence of steps when setting up cell walls comprise (Michener, 2000: 20): (1) lining the surface with a smooth earthen layer, (2) tamping the cell surface smooth with the pygidial plate, and (3) applying a secreted film of wax-like or cellophane-like material to the earthen surface. The earthen layer and the secreted lining are likely synapomorphies of the bee clade, as indicated by their absence in lineages of Hymenoptera closely related to bees (Michener, 2000).

Colletid bees have been long known for the special brood cell lining, which is commonly described as “cellophane-like” (e.g. Benoist, 1942; Cane, 1983; Michener, 2000). This cell lining is commonly interpreted as a synapomorphy of the family (Rozen, 1984; Michener, 2000). Colletidae are also unique among bees for their mouthpart morphology, in which the glossa is broad, truncate, bilobed or bifid, and generally short (Fig. 1). Mouthparts of colletid bees have been considered to represent the most primitive morphology among bees, because the bifid glossa is shared with apoid wasps (Apoidea: Ampulicidae, Crabronidae, Heterogynaidae, and Sphecidae). These wasps comprise the most closely related lineages to bees (Melo, 1999). Mouthpart morphology and brood cell lining are linked to one another in Colletidae because the female paints the lining precursors onto the nest wall using her broadly bifid brush-like glossa (Perkins, 1912; McGinley, 1980; Michener and Brooks, 1984; Michener, 1992, 2000).

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So much is known about colletid nest architecture that a comprehensive treatment of

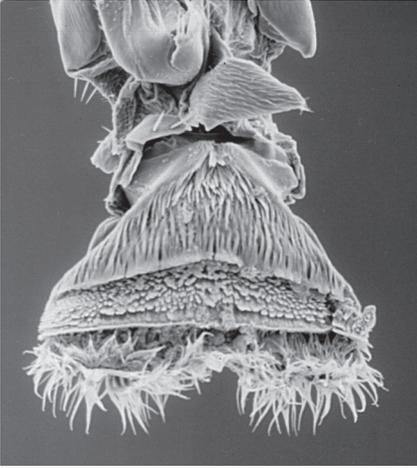


Figure 1. Bilobed brush-like glossa of *Hylaeus basalisis* (Smith) (SEM photo, University of Kansas, by Robert W. Brooks; courtesy of Charles D. Michener).

this topic would not be as satisfactory as the primary literature dealing with it (e.g. Claude-Joseph, 1926; Malyshev, 1927, 1968; Benoist, 1942; Janvier, 1933; Rayment, 1935, 1948; Michener and Lange, 1957; Michener, 1960, 2002; Eickwort, 1967; Rozen and Michener, 1968; Houston, 1969; Sakagami and Zucchi, 1978; Batra, 1980; Roubik and Michener, 1984; Rozen, 1984; Torchio, 1984; Torchio and Burwell, 1987; Torchio et al., 1988; Maynard and Burwell, 1994; Mader, 1999; Michener and Rozen, 1999; Spessa et al., 2000; Packer, 2004). Malyshev (1935, 1968) and Michener (1964, 2000) presented very useful partial summaries of nest architecture in Colletidae, as well as of other bee families.

The goal of this paper is to explore some aspects of the nesting biology of Colletidae. The topic to receive the most extensive treatment will be the brood cell lining of colletid nests. The evolution of cocoon-spinning habit, social behavior, and parasitism are also reviewed.

1.1. Bee phylogeny and Colletidae

The history of early diversification of bees and the relationships among its major lineages have long been filled with uncertainty; virtually every bee family has been

considered a candidate for the first lineage in bee diversification (Michener, 2000: 83–87; Danforth et al., 2006b). Resemblance between colletid mouthpart morphology and that of apoid wasps has been taken as evidence that Colletidae are an early diverging branch of bees (the sister to the rest of the bees). As relationships between Colletidae and other bee families still is a contentious topic, primitiveness of mouthpart morphology remains questionable, as new sources of evidence are added to the debate (Alexander and Michener, 1995; Danforth et al., 2006a, b). Additional plesiomorphic morphological characters reinforce the hypothesis that Colletidae could be the earliest-diverging branch of the bee phylogeny, the living sister clade to all other bees (Michener and Brooks, 1984; Michener, 2000). Michener's monograph (1944) became a landmark in the context of contemporary ideas about bee evolution and classification. In that article, Michener presented evidence for the recognition of Colletidae, in particular Paracolletinae, as the group with the most plesiomorphies among bees, strongly suggesting its primitiveness. Furthermore, Colletidae are primarily distributed in austral continents (Australia, temperate South America, and South Africa), with the exception of two widespread genera: *Colletes* and *Hylaeus*. This disjunct distribution suggests antiquity, which could be explained by origin of this family in Gondwanaland during the Cretaceous.

The study by Alexander and Michener (1995) cast doubts in regard to the monophyly of Colletidae. However, a wealth of evidences from various sources currently supports colletid monophyly (e.g. Michener and Brooks, 1984; Michener, 2000: 127; Brady and Danforth, 2004; Danforth et al., 2006a, b; Almeida, 2007). Part of this evidence comes from the unique cell lining found in nests of colletid bees, which is discussed in detail in the sections below.

1.2. Phylogenetic relationships within Colletidae

A phylogenetic study of Colletidae, which included 122 colletid species representing

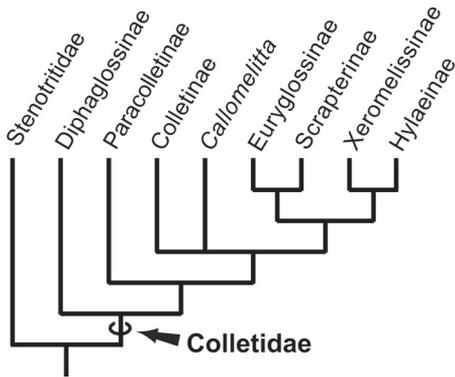


Figure 2. Summary of the phylogenetic relationships among the main lineages of Colletidae and Stenotritidae. Results based on the combined analysis of four nuclear protein-coding genes: EF-1 α , LW-rhodopsin, *wingless* and 28S rRNA (Almeida, 2007).

all of its recognized subfamilies and tribes, was conducted using molecular data from four nuclear gene loci: elongation factor-1 α (F2 copy), *wingless*, long-wavelength (LW) opsin, and 28S rRNA (Almeida, 2007). Results of Almeida (2007) are summarized in Figure 2. Some important results to be highlighted here were: (1) the removal of the only African endemic genus, *Scapter*, from Colletinae and placement in a new subfamily, Scapterinae (as proposed by Melo and Gonçalves, 2005; see also Ascher and Engel in Engel, 2005); (2) the recognition of Colletinae *s.str.* (i.e. *Colletes* and related South American genera) and Paracolletinae as independent taxa (Silveira et al., 2002; Engel, 2005; Melo and Gonçalves, 2005); (3) *Callomelitta*, if kept as part of Paracolletinae, renders the latter paraphyletic. Therefore, *Callomelitta* is not treated here as part of any of the existing subfamilies. Additional taxonomic adjustments are to be undertaken later.

The present article will also take into account available data for Stenotritidae, the closest extant relatives of colletid bees (Danforth et al., 2006a, b; Almeida, 2007). Stenotritidae comprise 21 described species, all distributed in Australia. Throughout history of bee classification, these enigmatic bees have been grouped with various other bee taxa.

Most commonly, Stenotritidae were regarded as either part of or closely related to Andrenidae (Oxaeinae) or Colletidae (particularly Diphaglossinae and Paracolletinae). Currently, though, enough evidence invalidates hypotheses in which Stenotritidae are nested within Colletidae, derived from biological studies (e.g. Houston and Thorp, 1984), comparative morphology (McGinley, 1980), and phylogenetic hypotheses based on morphology (Alexander and Michener, 1995) and on molecular data (Danforth et al., 2006a, b; Almeida, 2007). Most recent studies have placed Stenotritidae as sister to Colletidae (e.g. Alexander and Michener, 1995 [implied weights analysis of their “Series II” characters]; Danforth et al., 2006a, b; Almeida, 2007).

2. NESTING BIOLOGY AND EVOLUTION

2.1. Nest substrates

Colletidae can be divided into two large groups based on substrate used for nesting. The first includes soil nesters and encompasses all Diphaglossinae (e.g. Roubik and Michener, 1984; Rozen, 1984), Paracolletinae (e.g. Michener and Lange, 1957; Michener, 1960, 1964; Maynard and Burwell, 1994), and Scapterinae (Rozen and Michener, 1968), and most Colletinae (e.g. Michener and Lange, 1957; Batra, 1980; Mader, 1999; Michener, 2000). Those subfamilies include mostly hairy and generally robust bees. All species of Stenotritidae studied so far also nest in the ground (Houston and Thorp, 1984; Houston, 1975, 1984, 1987).

The second group includes species reported to nest inside stems, soft wood, pre-existing cavities, as well as in soil. Included in this group are the species of *Callomelitta* (Rayment, 1935), Hylaeinae, Euryglossinae, and Xeromelissinae. These bees are, on average, smaller, and less hairy. The species of Euryglossinae and Hylaeinae lack an external pollen-carrying scopa because females transport pollen internally.

Most species of Colletinae are ground nesters, but at least one South American

species nests in pithy stems instead: *Colletes rubicola* Benoist (Benoist, 1942). Many but not all species of *Colletes* have a quite peculiar nest architecture compared to other ground-nesting bees of their and other families – the lateral burrows of some *Colletes* species are subdivided into series of cells (Michener, 2000: 130, and references therein; for an account of the diversity of nest architectures of seven South American species of *Colletes*, see Claude-Joseph, 1926: 125–139). In contrast, lateral burrows of typical soil-nesting bee end in a single cell (Michener, 1964, 2000).

The linear cell arrangement observed in *Colletes* nests (Fig. 3a) resembles that of stem-nesting bees (Fig. 3c). Moreover, *Colletes* have reduced basitibial and pygidial plates, two generally well-developed morphological structures in soil-nesting bees (Batra, 1980: 525; Radchenko and Pesenko, 1996). These morphological characters plus the nest architecture (in addition to the known case of stem-nesting behavior) suggest the possibility that extant species of *Colletes* descended from a stem-nesting ancestor. Regrettably, nest information is not available for *Hemicotelles*, *Mourecotelles*, and *Xanthocotelles*, the three basal-most lineages of Colletinae (Almeida, 2007).

Nests of Xeromelissinae are generally built in holes in hollow stems or beetle burrows in wood or stems, but some recently described species are ground nesters (Michener and Rozen, 1999; Packer, 2004). All species of *Chilicola* whose nesting behavior has been studied were found to nest in woody substrates, i.e. stems, abandoned beetle burrows, etc. (Packer, 2004: 818–819, and references therein). Claude-Joseph (1926) described nests of *Chilicola inermis* (Friese) in hollow bamboo stems and of *Chilicola friesei* (Ducke) occupying abandoned stem nests of *Manuelia* (Apidae). Eickwort (1967) studied nests of *Chilicola ashmeadi* (Crawford) and Michener (2002) described nests of *Chilicola espeleticola* Michener and *Chilicola styliiventris* (Friese). Stem-nests of *Chilimelissa* generally follow the same plan as that of *Chilicola* (Michener, 1995). Michener (1995: 33) pointed out that, in general, xeromelissine nests do not differ conspicuously

from those of *Hylaeus*. This is quite significant given a well-supported sister-group relationship between Xeromelissinae and Hylaeinae (Fig. 2). Ground-nesting species were more recently documented for this subfamily: *Geodiscelis megacephala* Michener and Rozen, *Chilimelissa australis* Toro and Moldenke (Michener and Rozen, 1999; Packer, 2004), and probably also *G. longicephala* Packer (as suggested by morphological adaptations of bees of this species for sand nesting – Packer, 2005).

Houston's (1969) observations of various nests of Euryglossinae species illustrate the diversity of nesting habits for these bees. Some groups were found to nest in the ground (*Euryglossasp.*, *Euryglossula chalcosoma* (Cockerell), and *Brachyhesma perlutea* (Cockerell)), whereas others nest in wood (*Euryglossina hypochroma* Cockerell, *Euryglossina pulchra* Exley, *Pachyprosopis haematostoma* Cockerell, and *Pachyprosopis indicans* Cockerell). *Euhesma fasciatella* (Cockerell) and *Euryglossa ephippiata* Smith also nest in the soil (Rayment, 1935, 1948, respectively).

Hylaeinae seem to include mostly stem-nesting species (Michener, 2000), but some species use abandoned nests of other insects, pre-existing cavities, volcanic rock, and earth banks (Rayment, 1935; Sakagami and Zucchi, 1978; Michener, 2000; Daly and Magnacca, 2003). Examples of stem-nesting species include *Amphylaeus* (Spessa et al., 2000) and *Meroglossa* (Michener, 1960). *Hylaeus* (*Nesoprosopis*) includes both soil- and stem-nesters (Daly and Magnacca, 2003).

Michener (1964) compared nesting substrates used by different groups of bees and concluded that soil nesting is probably a plesiomorphic character state for bee nesting. It seems that soil nesting is the ancestral condition for the clade formed by Colletidae and Stenotritidae, given the soil-nesting behavior of Stenotritidae, Diphaglossinae, and Paracolletinae, and the phylogenetic relationships within this group (Fig. 2).

Callomelitta perpicta Cockerell nests in decaying wood, as reported by Rayment (1935: 97); unfortunately he neither illustrated nor described in detail the architecture of this bee's nests. The phylogenetic placement



Figure 3. Cellophane-like cell lining of Colletidae. (a) Linear array of nest cells of *Colletes* sp. (Arizona, USA) in a single polyester tubular membrane (picture by James H. Cane). (b) Brood cell of *Colletes validus* Cresson filled with provision and an egg (picture by James H. Cane). (c) Prepupae of *Hylaeus mesillae* (Cockerell) viewed through the nest cell lining (picture by William Nye, USDA-ARS Bee Biology and Systematics Lab; courtesy of James H. Cane).

of *Callomelitta* is not completely understood (Fig. 3), but this genus is part of clade comprised of Colletinae, Euryglossinae, Hylaeinae, Scapterinae, and Xeromelissinae. It is possible that the common ancestor of this clade was a stem-nesting bee, and multiple reversals to soil nesting (and to rotten wood) would then have taken place during the diversification of the group.

2.2. Brood cell lining

The application a waterproof lining on the brood cells wall is a synapomorphy of bees and is probably associated with the pollen-feeding habits of bees (Michener, 1964, 2000). The origin of this behavior and the secretion of the lining by bee's glands are associated with one another, as no species of apoid wasps was reported to do it (Hefetz et al., 1979; Espelie et al., 1992). The glandular lipoidal secretion is sometimes replaced by oils collected in flowers, as in the case of species of *Centris* (Apidae) (Vinson et al., 1997) or *Macropis*

(Melittidae) (Cane et al., 1983a), and a few bees do not line their cells at all (e.g. *Hesperapis* and *Dasyпода*: Melittidae) (Rozen, 1987; Michener, 2000). The importance of cell lining certainly has to do with reduction of water exchange between the brood cells and the environment (Michener, 1964, 2000; May, 1972; Cane, 1983), and it may also be resistant to fungal hyphae (Albans et al., 1980). Prior to lining the brood cells, some bees apply a mandibular gland secretion that is very effective both for fungistasis as well as for bacteriostasis (Cane et al., 1983b).

Populations of certain species of *Colletes*, e.g. *C. halophilus* Verhoeff, are often flooded while overwintering but the cells are completely waterproof because of the lining along the cell walls and a flap that seals the opening (Albans et al., 1980). In some other species of colletid and stenotritid bees, the main problem may be desiccation, and a waterproof lining should work just as well.

Colletidae, in particular *Colletes* spp., became well known for the apparently unique

lining of their nest cell walls. As early as 1742, Réaumur perceived the uncommon nature of this cell lining and described the multi-layered silky membrane of colletid brood cells (Batra, 1980). Colletid bees (and most other ground-nesting bees) generally apply a waterproof lining to their brood cells but not to the nest tunnels. Nonetheless, the hylaeine *Meroglossa torrida* (Smith) can line the entire cavity of a twig with cellophane-like material, and this lining can even extend outside the nest entrance (Michener, 1960).

Cell linings of *Colletes* are insoluble in either aqueous or organic solvents, and are not degraded by either acidic or basic hydrolysis (Hefetz et al., 1979). Jakobi (1964) tried 11 different solvents on nest cell linings of diverse bees: *Colletes* was unique in that lining was not soluble in chloroform, but was soluble in pyridin (unlike halictids and apids, among others). Colletid bees employ their brush-like glossa as the main tool for applying the secretion (e.g. Janvier, 1933; Malyshev, 1968; Batra, 1980).

By the end of the 1970's, behavioral and morphological evidence suggested that the cell-lining secretion was produced by the female Dufour's gland, associated with the sting apparatus (e.g. Batra, 1964, 1966, 1970; Lello, 1971). The Dufour's gland is a blind sac that empties its secretions into the base of the sting (Fig. 4; e.g. Lello 1971; Batra, 1980; Cane, 1981; Duffield et al., 1984). This gland can be very large in bees that actively secrete and it may represent up to 10% of the live weight of a *Colletes* bee (Duffield et al., 1984) and it may occupy 20–50% of the abdominal cavity of a *Colletes* (Batra, 1980). Dufour's gland functions in Hymenoptera are diverse, and include defense and alarm pheromones, trail pheromone, host marking and discrimination, and sexual attraction (Hefetz et al., 1978). Cane (1983: 658) provides a helpful historical account of research dealing with Dufour's gland and its secretions. Lello conducted comparative studies of the Dufour's gland in many groups of bees (Lello, 1971 [for Colletidae], other papers by Lello cited in Lello, 1976; see also Duffield et al., 1984: 403–414 for an anatomical and functional review of this gland in bees).

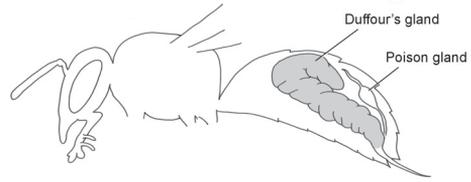


Figure 4. Position of the Dufour's gland and the poison sac in a female *Colletes* (redrawn from Batra, 1980: Fig. 11).

Hefetz et al. (1979) compared their chemical nature of the contents of the Dufour's glands and nest cell lining of three species of *Colletes*. The main chemicals found in both the gland secretion and the lining were macrocyclic ω -lactones, hydrocarbons, and aldehydes. Macrocyclic ω -lactones are the precursors of lipid polyester of the nest cell lining, the latter being composed of ω -hydroxy acid units (Hefetz et al., 1979; Cane, 1981). Although the detection of macrocyclic lactones inside the Dufour's gland of *Colletes* had already been accomplished by Bergström (1974), the comparative chemical analysis of nest cell lining and gland secretion of the same bee species, side-by-side, was only attained later (Hefetz et al., 1979; Albans et al., 1980). The membrane made of natural high molecular weight polyesters found in *Colletes* spp. was referred to as "laminester" (Hefetz et al., 1979).

At a period when important progress was made on the chemical nature of the Dufour's gland contents and cell lining of colletid bees, Batra (1980) conducted a detailed study of the nesting biology of three species of *Colletes*. She described the process of cell lining application by *Colletes* spp. and substantiated the evidence of the Dufour's gland chief role in secreting the lining liquid (Batra, 1980). According to her, the process consists of two phases: "(1) imbibing the Dufour's gland secretion from the partly exerted sting; and (2) regurgitating the secretion while licking the cell" (Batra, 1980: 525). The ingestion of the secretion by the female bee happens very rapidly (0.3–0.5 s) when she "somersaults or reverses her position in the cell" (Batra, 1980: 525). Albans et al. (1980) and Torchio et al. (1988) also reported the deposition of a droplet of liquid from the tip of the metasoma. When the

bee applied the secretion to the cell wall, “the liquid dried and rapidly formed a continuous membrane”, but it failed to dry and remained soluble in organic solvents when experimentally applied to a glass plate (Albans et al., 1980). To explain this fact, Albans et al. (1980: 559) hypothesized that “[p]olymerization of the Dufour’s gland secretion may be mediated by an enzyme, which is probably secreted by the thoracic salivary glands”; but the chemical nature of the polymerization has not yet been completely understood.

Batra (1980) and Torchio et al. (1988) give different accounts for the process of deposition of secretions by the female *Colletes*. According to Batra, salivary and Dufour’s secretions are mixed in the crop (p. 525). According to Torchio et al. (1988: 608), these two secretions are separately applied onto the cell wall and the polymerization occurs after the bee coats the nest surface with the Dufour’s gland secretion on the top of a previously applied layer of salivary secretion. In Torchio et al.’s words: “[t]he (presumable) salivary liquid is applied sparingly but during long periods of time, whereas the (presumable) Dufour’s gland liquid is deposited in larger quantities but infrequently... the primary purpose of somersaulting usually followed extended periods of salivary deposition when those liquids began solidifying directly on the mouthparts before they were deposited on the nest wall... salivary material deposited by *Colletes* carries enzymes that open and then cross-esterfy the lactones produced in the Dufour’s gland into the polyester layers found in *Colletes* cell linings. These enzymes apparently remain active well after salivary liquids harden and, as a consequence, Dufour’s gland liquids solidify only after contact with the salivary coating” (Torchio et al., 1988: 622).

In addition to the investigation of nesting behavior of *Colletes* spp., Batra (1980) also compared X-ray and infrared characteristics of nest cell linings of *Colletes* and *Hylaeus*. She concluded that they were only superficially similar, because nest membranes of *Hylaeus* appeared to be constituted by silk (Batra, 1980: 521; see also Torchio, 1984). Duffield et al. (1980) studied the Dufour’s gland secretion of *Hylaeus modestus* Say and

discovered the presence of macrocyclic lactones. Later, Espelie et al. (1992) found that the nest cell lining of *Hylaeus leptocephalus* Morawitz consists of a mixture of a lipid polyester and silk protein. Chemical analyses of the cell linings of *H. leptocephalus* indicated that these bees use the same Dufour’s gland secretion as the other colletids, but it is complemented with silk (Espelie et al., 1992). Interestingly, Torchio (1984) did not observe *Hylaeus* to curl to acquire Dufour’s secretion while in the nest.

The difference in the relative sizes of the Dufour’s gland and the thoracic salivary gland between *Colletes* and *Hylaeus* is noticeable for the species studied by Batra (1980: Fig. 11). The silk filaments produced by *Hylaeus* are secreted by the salivary gland (also known as the labial gland – e.g. Duffield et al., 1984) and its hypertrophy, as compared to that in *Colletes*, is compensated for by a not so-well developed Dufour’s gland. Silk production is observed in a diverse array of Hymenoptera (e.g. members of Chalcidoidea, Vespoidea, Apoidea: Melo, 1997 and references therein). *Hylaeus* species generally live inside stems and that the production of Dufour’s gland secretion seems to be more closely associated with earthen nests. The shift to stem nesting may be related to silk secretion (Cane, 1983).

In Stenotritidae, cells are coated with a thin, waterproof membrane much like a plastic film that is not readily separable from the earthen wall (Houston, 1984; Houston and Thorp, 1984: 164–165); the membrane was insoluble in organic solvents did not appear to be fibrous nor silky, and did not melt when heated. This lining was hypothesized by Houston (1984) to be made of polyester, as in Colletidae. No chemical analyses of either the stenotritid Dufour’s gland secretions nor their cell lining have been undertaken. So far, Colletidae are the only bees known to have representative taxa whose brood cell walls are coated with polyester derived from macrocyclic lactones.

Rozen (1984) noticed that there is a physical difference between the lining of Diphaglossinae and of the remaining groups of Colletidae. In the Diphaglossinae (as well as in Stenotritidae), it is thinner, more fragile, and closely connected to the substrate; in all other

colletid bees it is loosely attached to the substrate (Rozen and Favreau, 1968; Roubik and Michener, 1984; Rozen, 1984; Michener and Rozen, 1999). As Rozen (1984: 26) portrayed it: “[t]his lining seems to be homologous with that of the cells of other colletid subfamilies, and probably is applied with the specialized glossae characteristic of all colletid bees. However, there are no air spaces between the lining and the cell wall nor are its layers separated by air spaces and fibrous strands, as seems to be typical of *Colletes*, *Scapter*, *Hylaeinae*, and *Xeromelissinae* [multi-layered lining was first described for *Colletes compactus* Cresson by Rozen and Favreau, 1968]. The lining of diphaglossine cells therefore lacks the glistening, reflective appearance of these other colletids and much more closely resembles the “varnished” cell surface of other families with a conspicuous, nonwaxlike lining”.

2.3. Mouthparts and nesting

Apoid wasps and bees that possess a short and truncate glossa face limitations in the extent to which they can reach flower bases when collecting nectar (Krenn et al., 2005). Limitations can be overcome in a number of colletid bees by modification of different mouthpart structures. There are no cases, however, of a greatly elongate glossa in Colletidae (e.g. Michener, 2000; Krenn et al., 2005). Diphaglossinae and some taxa of Paracolletinae (*Glossopasiphae*, *Lonchopria* [*Porterapis*], and *Tetraglossula*) are peculiar for their elongate lateral glossal expansions (Michener, 2000), and some species may have a basally longer glossa (e.g. *Leioproctus capitus* species group – Houston, 1990), but it is never as extreme as in the case of Apidae and Megachilidae. Colletid mouthpart evolution apparently occurred under a constraint for a short and blunt glossa (Fig. 1), which is largely associated with painting the secreted linings onto the inner walls of the cells (McGinley, 1980; Michener, 1992, 2000; Krenn et al., 2005). Indeed, comparisons of the glossa of cleptoparasitic bees (which never build nests) and pollen-collecting bees showed a simpler

morphology for the former, indicating that nest construction imposes selective pressures on glossal morphology (Michener and Brooks, 1984). The role of colletid glossal morphology for nest cell construction has long been appreciated (e.g. Kirby, 1802).

Colletid bees fold their glossa longitudinally in repose and, depending on the shape of the glossal lobes, the glossa may resemble a pointed glossa, which may even have a valve for the bees. Claude-Joseph (1926: Fig. 25, p. 146) illustrated a folded glossa of *Cadegualla occidentalis* (Haliday). If there are morphological constraints to maintain the broad colletid glossa to function for the application of the nest lining, they may prevent the lobes from being abnormally long.

Batra (1972) studied halictids and apids when lining their cells and called attention to the use those bees make of their pygidial plate and penicillus. *Colletes* lack a penicillus and, instead, use their brush-like glossa to apply the cell lining (Batra, 1980).

2.4. Provisions

Most bees provision their brood cells with a mixture of pollen and nectar. The pollen content of the food mass, relative to the amount of nectar, determines the consistency of the mixture. Michener (1964) suggested that semi-solid provisions reduce the contact between the food ball and the cell wall, thus reducing points of contact with the nest wall and risk of fungal colonization. Firm provision has been considered a plesiomorphy for bees (Radchenko and Pesenko, 1996), and most groups of bees (with the exception of Colletidae) predominantly have firm food masses. Stenotritids, for example, make a solid smooth and moist uncoated pollen loaf of characteristic shape (Houston, 1984; Houston and Thorp, 1984).

Colletidae are known for producing more liquid provisions than most other bees. A reasonable assumption to make is that fluid provisions can only be found in nests of which brood cells are lined with a waterproof membrane (like those of colletids), because liquid food masses would not be well preserved in

a chamber whose surface were permeable. As Albans et al. (1980: 562) put it: “female colletids are freed from the labor of shaping their pollen stores”.

Most colletid subfamilies have provisions that vary from liquid to semi-liquid: Colletinae (e.g. Claude-Joseph, 1926; Malyshev, 1927; Michener and Lange, 1957; Batra, 1980); Diphaglossinae (Janvier, 1933; Roberts, 1971; Roubik and Michener, 1984; Rozen, 1984; Torchio and Burwell, 1987), Euryglossinae (Rayment, 1935: 27 – described provisions of *Euhesma fasciatella* (Cockerell) as “pudding”; Michener, 1960; Houston, 1969), Hylaeinae (Michener, 1960; Sakagami and Zucchi, 1978; Torchio, 1984), Xeromelissinae (Claude-Joseph, 1926; Eickwort, 1967; Michener and Rozen, 1999; Packer, 2004). Paracolletinae is the only subfamily for which semi-solid provisions are reported (Michener and Lange, 1957; Michener, 1960). However, Janvier (1933: Fig. 47, p. 328) described nests of *Perditomorpha tristis* (Spinola) and based on his account of the provisions and the illustration of the nest, provisions of this species appear to be semi-liquid and viscous. In *Scrapper*, the consistency of the provisions was found to be intermediate between a semi-solid pollen ball (typical of Paracolletinae), and a semi-liquid mass as in most other colletids (Rozen and Michener, 1968).

Roberts (1971) wondered how provisions of the diphaglossine *Ptiloglossa guinnae* Roberts could have small amount of pollen and still contain a high-enough protein content to be nutritious to the immatures. According to Roberts (1971: 287), it is possible that yeast found fermenting the provisions might, in a situation like that, substitute the ordinary protein source of bees (pollen).

2.5. Cocoon spinning

Cocoon spinning is considered to be a plesiomorphic characteristic among bees (Rozen, 1984; Radchenko and Pesenko, 1996; Michener, 2000). Stenotritid larvae do not spin a cocoon (Houston, 1984; Houston and Thorp, 1984) and, among Colletidae, Diphaglossinae are the only known examples of cocoon-spinning bees. Rozen (1984) interpreted the presence/absence of this behavior

in extant groups of bees as the result of multiple independent losses the cocoon-spinning behavior during bee evolution. A parsimonious interpretation for the absence of cocoon spinning in all colletids except Diphaglossinae would be its single loss in a group formed by all subfamilies except Diphaglossinae (Rozen, 1984), which makes sense in light of the phylogenetic hypothesis shown in Figure 2.

Brood cells have their opening sealed by an operculum, which might serve for the same purpose as the leathery cocoon wall, i.e. protection against predators and nest parasites (Rozen, 1984). In Diphaglossinae, cells have a closure made of soil. The operculum is the top of the cocoon (made of silk) that presumably permits exchange of gases and at the same time might serve to exclude parasites (Rozen, 1984).

Michener and Lange (1957) reported having found a cocoon-spinning species of *Colletes*, but this must have been an erroneous observation because Michener (2000: 128) stated that Diphaglossinae are the only colletids that retained this behavior.

2.6. Sociality

No species of Colletidae are known to be eusocial (*sensu* Crespi and Yanega, 1995). The great majority of the species are solitary, as are most of the short-tongued bees. All the Andrenidae, Melittidae, Stenotritidae, and Rophitinae (Halictidae) are solitary. Eusociality, among short-tongued bees, evolved three independent times in Halictidae, a phenomenon restricted to the subfamily Halictinae (Brady et al., 2006).

For Stenotritidae and Colletidae, it is common to observe nest aggregations, but communal nests and primitive levels of sociality are remarkably uncommon. Sakagami and Zucchi (1978) first reported on a possibly social species of Colletidae. *Hylaeus (Hylaeopsis) tricolor* (Schrottky) was found reusing nests of apoid and vespid wasps in Brazil (Sakagami and Zucchi, 1978). There were more females in the nests studied than cells being provisioned, which along with other biological characteristics allowed Sakagami and Zucchi to propose that *Hylaeus tricolor* is

facultatively quasisocial (following the classification by Michener, 1974). Females of *Meroglossa* spp. (Hylaeinae) may co-exist in a nest for sometime, but Michener (1960) found no strong evidence for cooperation among them.

The second possibly parasocial colletid species was reported by Spessa et al. (2000). The authors found sub-tropical populations of *Amphylaeus morosus* (Smith) in Australia to have multiple females sharing a nest. However it was not clear whether division of labor takes place. Relatedness between females sharing a nest was too low to suggest kin selection, and ovary differentiation was not noticeable (Spessa et al., 2000). K. Hogendoorn (unpublished, *in litt.*) studied two-female nests and observed labor division in which one female assumed reproductive position. Egg laying would then be suppressed on the second female unless the first did not return to the nest. Parasitism and nest reutilization may constitute the main selective pressures for nest sharing (Spessa et al., 2000).

2.7. Cleptoparasitism

About 20% of all bee species are cleptoparasites (cuckoo bees): instead of building their own nests, these bees lay eggs in brood cells built by other bees (Michener, 2000; Danforth, 2007). Cleptoparasitism is estimated to have arisen over 25 independent times in bees and much of the diversity of cleptoparasites is concentrated in Apidae, Megachilidae, and Halictidae (Danforth, 2007). As for Colletidae, only five species of *Hylaeus* (*Nesoprosopis*) from Hawaii are presumably cleptoparasites, based on circumstantial evidence (Daly and Magnacca, 2003), whose hosts are other species of Hawaiian *H.* (*Nesoprosopis*). All other Colletidae and all species of Stenotritidae are free-living, but many serve as hosts of bees of various tribes of Nomadinae and Isepeolini (e.g. Rozen and Michener, 1968; Rozen, 1984; Michener, 2000), as well as other Hymenoptera (e.g. Gasteruptionidae, Mutillidae).

2.8. Concluding remarks

Various topics discussed in this review appear to make sense when taking into consid-

eration the phylogenetic relationships within Colletidae, as illustrated in Figure 5. In light of our knowledge, the polyester cell lining was present in the common ancestor of colletid bees, a subsequent modification having happened in the clade formed by all colletids except Diphaglossinae. Cocoon-spinning was lost once, and a single transition from semi-liquid to firm provisions happened in the evolution of Colletidae (Fig. 5). Hylaeinae are known to add silk to their cellophane-like cell lining (Fig. 5), but future studies may indicate that this trait is more widely distributed if it is found to occur in other colletid lineages. Further research is needed to understand the evolution of nesting substrate preference in the clade comprising *Callomelitta*, Colletinae, Euryglossinae, Hylaeinae, Scapterinae, and Xeromelissinae. It is possible that the shift from soil-nesting to wood-nesting (especially in stem) happened once (Fig. 5), followed by multiple reversals to soil nesting, but this is not yet clear. Uncertainty about the evolution of nest substrate preference will hopefully be dissipated as nesting habits are described for more taxa and phylogenetic relationships within colletid subfamilies are studied.

Detailed accounts were made for various aspects of nesting behavior *Colletes*, *Hylaeus*, and Diphaglossinae (e.g. Batra, 1980; Rozen, 1984; Torchio, 1984; Torchio et al., 1988). However, Xeromelissinae, Euryglossinae, and Paracolletinae remain largely unexplored, and no information exists about nests of Dissoglottini (Diphaglossinae). Very important chemical studies were conducted with various lineages of Colletidae, most prominently of *Colletes* and *Hylaeus*. The Australian groups of Colletidae (Euryglossinae, Australian Paracolletinae; various endemic lineages of Hylaeinae), Xeromelissinae, and Stenotritidae remain completely unexplored chemically. Additionally, research of the chemical nature of the cell lining was conducted for a small proportion of taxa for which the Dufour's gland secretion was studied.

As indicated in Cane (1983), the production of macrocyclic lactones to line nesting cells is not restricted to the Colletidae. Many of the same molecules are possessed by representative species of the Halictidae (Halictinae and

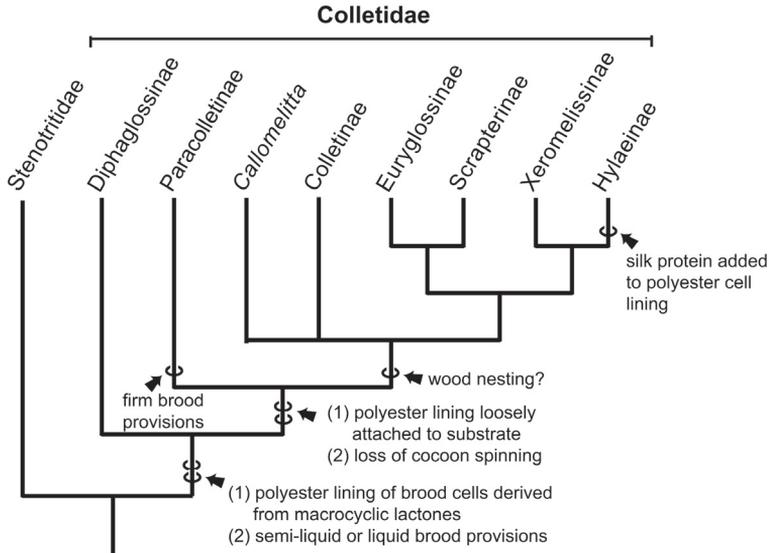


Figure 5. Phylogenetic relationships within Colletidae as a framework to understand the evolution of nesting behavior (see text for details). The transition from soil to wood nesting, if properly represented in this figure, was followed by multiple reversals to soil nesting in Colletinae, Euryglossinae, Hylaeinae, Scapterinae, and Xeromelissinae (see Sects. 2.1 and 2.7 for further discussion).

Nomiinae) and Andrenidae (Oxaeinae), although they are uncommon molecules among eukaryotes. Cell linings of these groups very much resemble those of the Diphaglossinae. The difference with *Colletes* and others seems to lie with either (1) how the presumed polymerase enzyme works on the macrocyclic lactones, or (2) how the forming polymers are extruded and stretched by the glossa (in the same way that various plastics, such as polyethylene, take on different physical characteristics depending on how they are extruded). These features constitute the derived evolutionary characteristics of colletid sub-groups, and not the lactones themselves. It also points to a rewarding direction for future research. Chemical analyses of the cell linings of Diphaglossinae and Stenotritidae would greatly contribute for elucidating possible differences in their chemical nature as compared to other lineages of Colletidae.

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Biologie de la nidification chez les Colletidae (Hymenoptera : Apoidea).

Colletidae / Stenotritidae / glande de Dufour / nid / abeille

Zusammenfassung – Nestbiologie der Colletidae (Hymenoptera: Apoidea). In vielen Aspekten ihrer Nestbiologie nehmen die Colletidae eine Sonderstellung innerhalb der Bienen ein. In diesem Übersichtsartikel werden Aspekte der Nestweise der Colletidae unter Gesichtspunkten neuer phylogenetischer Hypothesen für diese Familie diskutiert. Einige Vorhersagen zur Evolution verschiedener Merkmale, wie z.B. das Kokospinnverhalten der Diphaglossinae, wird in Bezug gesetzt zu phylogenetischen Befunden. Die Cellophan-ähnliche Auskleidung der Brutzelle der Colletidae stellte eine Synapomorphie für diese Bienenfamilie dar. Diese Auskleidung ist eine dicke, starke Polyestermembran, die wasserfest und auch in verschiedenen Lösungsmitteln unlöslich ist. Ältere Ansichten zum Verständnis der Natur dieser Zellauskleidung der Colletidae und zur Diversität einiger Aspekte der Nestweise finden sich in dieser Arbeit zusammengestellt. Colletidae sind beispielsweise einzigartig in Hinsicht auf die Verproviantierung der Brutzellen, die im allgemeinen aus einer halb bis ganz flüssigen Futtermasse besteht, im Unterschied zu den festen Pollenbällen, wie sie bei den meisten Bienen zu finden sind. Ausserdem gibt es bei den Colletidae einige Fälle von sozialem und kleptoparasitischem Verhalten, die hier ebenfalls diskutiert werden.

Biene / Nest / Colletidae / Stenotritidae / Dufourdrüse

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