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The Evolution of Parasitism Among Bees

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OF PARASITISM
AMONG BEES

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FORTY-FIRST HONOR LECTURE
SPRING 1970
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George E. Bohart was selected by the committee to deliver the Annual Faculty Honor Lecture in the Natural Sciences. On behalf of the members of the Association we are happy to present Dr. Bohart's paper.

THE EVOLUTION OF PARASITISM AMONG BEES

Committee on Faculty Honor Lecture
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Figure 1. Family tree of the bees (Apoidea) showing the derivation of parasitic lines (in red).
THE EVOLUTION OF PARASITISM AMONG BEES

George E. Bohart

Before discussing parasitic bees, I will present a rough outline of the biology of "ordinary" or non-parasitic bees. The superfamily Apoidea (bees) includes perhaps 25,000 or 30,000 species divided into nine families by recent authorities (Stephen, Bohart, Torchio, 1969). A common biological thread holding this vast assemblage together is the provision by adults of pollen and nectar for their young. Only in the honey bees (the genus *Apis* which includes four species) are the larvae fed primarily on a different substance (a secretion of the pharyngeal glands), and even this is derived from pollen and honey eaten by the adults.

Most bees are solitary in that each female provides for her own offspring without help from other adults. However, many species are gregarious and may construct hundreds or even thousands of nests in small areas. The social species (perhaps 10 percent of the total) range from those with small nests containing only two or three adults to ones whose nests contain many thousands [like the honey bees and some stingless bees (Meliponini)]. Most bees construct burrows and cells in the soil, but many others nest in small (usually tubular) cavities such as hollow stems, beetle holes, and small rock pockets. Bees in the family Apidae nest in larger cavities such as rodent burrows, caves, and boxes. Nearly all bees construct individual brood cells in which they store a supply of pollen and honey. They then lay an egg on the provision and seal the cell. A much smaller number (including honey bees and bumble bees) feed their larvae progressively (at least in part).

Figure 1 presents a family tree of the bees, indicating the basic lines of descent as a frame of reference for the ensuing discussion. It also shows where the separate lines of parasitic bees are believed to have arisen.

SURVEY OF PARASITIC BEES

Approximately 15 percent of the 4,000 to 5,000 species of bees in America north of Mexico are parasitic. If the same ratio holds in
other parts of the world, there should be a total of about 3,700 parasitic species. All are parasitic on other bees and have a life style known as clepto- or cuckoo parasitism. Like the cuckoo bird, the parasitic bee lays her egg in the host nest and her immature offspring usually destroy the host's helpless young and then consume the food placed in the nest by the unsuspecting mother. Thus it is that parasitic bees, like their non-parasitic sisters, provide their young with a diet of pollen and honey even though they do not gather it themselves.

Although parasitic bees prey exclusively on other bees, and most of them in essentially the same manner, they provide fascinating insights into the evolution of parasitism and the morphological parallelism resulting from a common life style. Their diversity is apparent from the many higher taxa involved. Of the nine families of bees, four are known to include parasitic species. Of the 115 genera of bees in America north of Mexico, 30 are exclusively parasitic. A few, such as *Paralictus* in North America and *Inquilina* in Australia, are doubtfully separate from their host genera and two non-parasitic genera, *Bombus* and *Alloclapula*, include one or more apparently parasitic species. Figure 1 indicates that there have been at least 16 separate derivations of parasitic bees from non-parasitic ancestors.

An interesting feature of parasitic bees, and one that sheds light on their origin, is the close taxonomic relationship that many of them bear to their hosts (Wheeler, 1919). Although Nomadinae, the largest, most diverse, and presumably the most ancient group of parasitic bees, has extended its host range to include all of the major bee families, nearly all of the other phyletic lines of parasitic bees attack hosts in their own family, and usually in their own subfamily or tribe. As noted previously, a few have not yet achieved clear-cut generic distinction from their hosts. Behavior suggesting the several pathways through which parasitism has developed is exhibited by a number of non-parasitic bees.

**HONEY BEES (APIS)**

Robbery of stores from other nests is a behavioral pattern commonly found in the social forms of the family Apidae (honey bees, stingless bees, and bumble bees (*Bombus*)). The common honey bee (*Apis mellifera* L.) is a notorious robber of honey from other honey
bee colonies and occasionally from other apid species. It usually robs during periods of poor natural forage, and sometimes populous colonies completely “rob-out” the stores of weaker ones, leaving them to starve. Fighting usually occurs at the entrances of invaded nests and lasts until the guard bees are killed or greatly reduced in number.

Some recent attention has been focused on *Apis mellifera capensis*, a South African race of honey bees noted for its ability to produce workers and queens from unfertilized eggs laid by workers. In other races, such eggs almost invariably develop into males (drones). As early as 1929, beekeepers observed that many workers of *A. m. capensis* habitually invaded colonies of other races and laid eggs destined to become workers. This often seemed to “demoralize” the queen, causing her to stop laying and eventually be superseded by a queen developed from a worker-laid egg (Lundie, 1929). Since *A. m. capensis* did not exist alongside other races until beekeepers bought European races in, it appears that this method of taking over another colony is opportunistic and has little evolutionary significance except perhaps to show how a unique trait, such as the ability of workers to lay female eggs, could eventually lead to obligatory parasitism.

**STINGLESS BEES (MELIPONINAE)**

Stingless bees (a large assemblage of tropical species) carry pillage to the extent of stealing pollen and nest-building materials as well as honey. Pillaging individuals usually try to rob from any colonies in the vicinity, regardless of species. According to Moure, Nogueiro-Neto and Kerr (1958), robbing is usually initiated by faulty orientation. Returning bees, finding themselves in the wrong hive, load up and leave with honey. They then establish a scent trail between the two hives, and systematic robbing begins. Fighting is often vigorous, with high mortality on both sides, but sometimes the invaders are not molested. Strangely enough, weaker colonies sometimes rob from stronger ones, or two colonies may rob from each other at the same time, while the role of dominance between them may reverse itself over a period of time.

It is not surprising that such well established facultative robbing behavior among the stingless bees has led to the development of species that depend on pillaging. The genus *Lestrimelitta*, including two Neotropical and one Ethiopian species, is an obligatory robber, apparently unable to obtain food stores directly from flowers. The
principal Neotropical species, *Lestrimelitta limao* (F. Smith), usually confines its attack to two subgenera of stingless bees, and the African species, *L. cubiceps* (Friese), attacks only one host species. (Portugal-Araújo, 1958). The robbing behavior of these obligatory parasites resembles that of the facultative thieves in many ways but differs in a few important details. Once the *Lestrimelitta* have invaded a host nest, they kill or drive off the defending guards and establish their own guards to prevent defending bees from reentering. Another feature, well known in the case of *L. limao*, is the rapid domination of victim by the invaders. Apparently they accomplish this by overwhelming the colony odor of the robbed hive with their own lime-like mandibular gland secretion. It is apparent that *Lestrimelitta*, since it retains the nesting function, is not a true “cuckoo,” but it certainly merits designation as an obligatory cleptoparasite. An interesting postscript to the story of *Lestrimelitta* is that its colonies are not immune to robbery, and even destruction, by some of the other species of stingless bees (Moure, Nogueira-Neto, Kerr, 1958).

*Lestrimelitta* is probably less distinct from its nearest relatives in the genus *Trigona* than some of the *Trigona* are from each other. Actually, the subgenera of *Trigona* are so distinctive that they are often given generic status. The absence of a pollen transporting corbiculum on the tibia is *Lestrimelitta’s* most distinctive characteristic. This first led investigators to suspect that its robbing habit was obligatory (Michener, 1946). Apparently, the genus developed as an obligatory robber rather early in the evolution of the stingless bees, as indicated by its occurrence in the tropics of both hemispheres. It is also possible that the African species had a separate origin from the American ones and, hence, should be placed in a different genus.

Robbing of stores is not the only motive for depredations by the stingless bees. Reproductive swarms, looking for a place in which to nest, often invade active colonies and attempt to dispossess them. In some cases the larvae of the invaded colony are spared and eventually develop into workers in the new colony. *Lestrimelitta* swarms engage in this form of warfare, but apparently so do some of the facultative thieves.

**BUMBLE BEES (BOMBUS AND PSITHYRUS)**

Dispossession of another queen’s nest is a more prominent feature of bumble bees than it is of stingless bees. Bumble bees do not
divide their colonies by swarming. Consequently, it is the queens, looking for a place to found new nests in the spring, who attempt to dispossess queens from nests already started (Plath, 1934). Several species are notorious for this behavior. Colonies of *Bombus terrestris* Linn. in the Old World and those of its close relative in the New World, *Bombus occidentalis* Greene, often contain several dead queens of the same species, mute evidence of struggles for possession of the nests. Contrary to the usual concepts of struggle over territory, the invader often wins. For example, in 1954 I succeeded in inducing a queen of *Bombus huntii* Greene to found a nest in the greenhouse, only to have her killed and her young brood taken over by another queen. I had scarcely marked the new queen before she in turn was killed and dispossessed by another. It was soon discovered that queens were more interested in taking over an established nest than they were in founding their own. In most cases such take-overs are infraspecific, but they also occur between different species with similar nest habitat requirements.

In the Far North (Elsmere Land) *Bombus hyperborius* Schonherr habitually takes over the nests of *Bombus polaris* Curtis. In the short Arctic summer *B. polaris* normally has time to produce only one brood of workers before it is time to raise queens. When the *hyperborius* queen takes over the nest, all of her young are raised as queens by the *polaris* workers. Consequently, *hyperborius* workers are not produced and pollen collectors are never seen (Milliron and Oliver, 1966). In northern Europe, workers of *hyperboreus* have been reported, indicating that the parasitic habit is not completely obligatory there. However, it is possible that in areas with a longer season, workers develop and function alongside the remaining host workers. The scarcity of *hyperboreus* workers in Europe has led some investigators to mistakenly believe this species lacks a worker caste because it is solitary (Friese, 1923). The parasitic habit, although well developed, must be of recent origin, since no morphological adaptations for a parasitic existence have been developed.

It is easy to imagine how the freebooting piracy carried on by bumble bees has led to the form of parasitism practised by the guest bumble bees, *Psithyrus*. Although members of this genus are obviously bumble bees, they have lost their pollen-transporting corbiculae and acquired a heavily armored, downcurved abdomen provided with an unusually long sting (Figure 2). The hibernated female emerges late in the spring and usually invades a bumble bee colony after the latter has already produced two or more generations of workers.
Figure 2. A guest bumble bee (*Psithyrus insularis* F. Smith), showing downcurved abdomen, long sting, and absence of corbiculum on hind tibia.

Figure 3. *Sphecodes arvensiformis* Cockerell leaving nest of *Halictus farinosus* Smith.

Figure 4. Nest of *Osmia lignaria* Say superseded by *Osmia californica* Cresson. Cells from bottom to top with increasing amounts of plugging materials and pollen brought in by the *californica* but with *lignaria* eggs. Top cell provided entirely by *californica* except for some pollen gathered by *lignaria*.

Figure 5. Ventral view of female *Coelioxys texana* Cresson, showing attenuate abdomen, heavy sculpturing, unobtrusive legs, and absence of abdominal pollen brush.

Figure 6. Cocoon of *Coelioxys moesta* Cresson, showing head capsule of second stage larva incorporated in cocoon fabric.

Figure 7. Adult female of *Stelis* (undescribed species), showing sparse pubescence and absence of pollen brush on abdominal venter.

Figure 8. Two cells of *Osmia californica* (Megachilini). Upper cell occupied by *Stelis montana* Cresson cocoon covered with elongate fecal pellets (typical of *Stelis*) and corpse of a third stage *Osmia* larva.

Figure 9. Cocoon of *Stelis* (undescribed species), showing nipple and highly polished interior typical of anthidine bees. The well chitinized head capsule is often found in parasitic bee larvae.

Figure 10. *Xeromelecta californica* Cresson (Melectini) entering entrance turret of *Anthophora occidentalis* Cresson (see also cover photo).
She is usually attacked by the host workers when she enters the nest and is sometimes ejected or stung to death. However, the fighting usually dies down after several hours. In most cases the *Psithyrus* intimidates the queen bumble bee by her presence and apparently lives amicably with the workers after she acquires the colony odor (Plath, 1922).

Several days after the parasite enters the nest, the host queen stops laying eggs and loses interest in her brood, even though she may live out a normal life span. During this period the *Psithyrus* tears open the host brood cells. Subsequently, the host workers discard the larvae from these cells, as they always do when larvae become exposed. The parasite then builds egg cells from spare wax in the nest (her own wax glands are degenerate) and fastens them to cocoons in the normal bumble bee fashion (Plath, 1922). When her eggs hatch, the larvae are fed so generously by the workers that the resulting adults are “queen-sized.”

Species of *Psithyrus* appear to be specific on only a few species of hosts. Presumably, they either do not care to stay in a nest of the wrong species or they are never accepted therein. Furthermore, some species of bumble bees quickly eject any species of *Psithyrus* that enter their nests. It is apparent that the offensive weapons and defensive armor of *Psithyrus* are not entirely for purposes of forcing entry. It has been observed that they are sometimes called into service when a parasite enters a nest already occupied by another parasite. In this case, the *Psithyrus* acts like a searching queen bumble bee by attempting to kill any reproductive of her own species that she finds in an established nest. *Psithyrus* has the unusual habit of entering honey bee hives, presumably to take nectar, although the possibility that the hive is mistaken for a bumble bee colony cannot be ruled out. In any event, a fierce fight ensues in which many honey bee workers, and usually the *Psithyrus*, are killed (Plath, 1927).

**EUGLOSSINE BEES**

Of the four tribes in the family Apidae, only the Euglossini, a group of large neotropical bees, is solitary. Euglossines, aside from being solitary, resemble bumble bees in many details of nest construction and life history. The genus *Eulaema* is parasitized by a beautiful metallic green and blue euglossine, *Exaraetae*. Although this parasite is superficially different from *Eulaema* by virtue of its
brilliant coloring and nearly bare surface, its close relationship is evidenced by a peculiar pouch on the hind tibia which males of both genera use for collecting and transporting orchid perfume to attract females. The host of Aglae, another parasitic euglossine, is unknown, but it may be another euglossine, Eufriesia. Unfortunately, little is known of the biology of these parasites, although it can be speculated that their habits are probably intermediate between those of Psithyrus and the parasites of solitary bees in other families.

ALLODOPINE BEES

In the family Apidae we have considered the transition from non-parasitic to facultatively parasitic to obligatorily parasitic behavior. It was noted that the clearly parasitic genera, although closely related to their host genera, have lost their pollen transporting apparatus and (Psithyrus and Exaraetaceae, at least) show several other structural modifications for a parasitic existence. Several related groups of parasitic bees which show early stages of divergence from their non-parasitic relatives are found in the tribe Allodapini. These small, semi-social carpenter bees are peculiar in not making separate cells for their larvae. Usually the nest foundress with one or more of her daughters occupies a hollow stem or thorn in the midst of a communal nursery.

In this small group of genera, it appears that parasitism has arisen no fewer than three times since each of the parasitic groups is closely related to its respective host genus (Michener, 1966). Two presumably parasitic Australian species, Allodapula associata Michener and A. praeumentiosa Michener retain pollen transporting scopal hairs on the tibia and cannot be distinguished generically from their hosts. The only biological evidence to support the parasitic nature of A. associata is its discovery on four occasions in the nests of a non-parasitic species, A. unicolor Smith. A. praeumentiosa is thought to be parasitic on the basis of its morphological resemblance to A. associata. Some of the morphological similarities may represent modifications for a parasitic existence, but further evidence is needed.

Another allodapine genus, Exoneura, has a single known bee parasite, Inquilina excavata Cockerell, an Australian species. Although described in 1922, it was not until 1961 that Michener recognized its parasitic nature and placed it in a separate genus. However, he stated that generic or subgeneric ranking would be about equally logical. Inquilina was taken repeatedly from the nests of a single
species of *Exoneura*, but otherwise its parasitic habits are unknown. It differs from the various species of *Exoneura* in many characters, but those obviously associated with its status as a parasite include the greatly shortened scopal hairs on the hind tibia and the feeble development of the basitibial plate. The latter is a sort of "kneecap" used by bees for maneuvering about in tunnels.

The third parasitic allodapine group is *Eucondylops*, based on a single South African species (Brauns, 1902). Although little is known of its parasitic habits, it is reported to be the most divergent of the parasitic allodapines, with complete absence of pollen-transporting scopal hairs and reduced wing venation.

**HALICTINE BEES**

The third principal group of social bees comprises most of the subfamily Halictinae (family Halictidae). This is a very large group of soil burrowing bees, most of which form small colonies. As in the bumble bees, nests of most of the social forms are founded by an overwintered adult female whose earlier progeny are workers and whose later progeny are males and overwintering females (queens).

Incipient parasitism in the Halictinae is illustrated by *Halictus scabiosae* (Rossi) in Europe. Although this species usually constructs, provisions, and lays eggs in its own nests, Knerer and Plateaux-Quenu (1967) found that it often invades the nests of another halictine, *Evylaeus marginatus* (Brulle). For several days the invading queen lives in association with the *Evylaeus* and eventually drives out or kills the original proprietress and takes over the nest, building and provisioning cells in the usual manner. These authors also found an *Evylaeus* cell in which the egg appeared to be that of *H. scabiosae*. It is easy to imagine how, by emphasizing egg-laying in the *Evylaeus* cells, *H. scabiosae* could evolve into a cleptoparasite with habits almost identical to those I am about to describe.

Within the Halictinae, obligatory parasitism has arisen at least three times. The largest and best known parasitic genus is *Sphecodes*. The females have many characters which set them apart from non-parasitic forms, but the males are sometimes difficult to distinguish from *Evylaeus*, one of the non-parasitic genera. Characters of the females associated with their parasitic behavior include absence of pollen-transporting hair, general lack of pilosity, thick, heavily sculptured body surface, poorly developed basitibial plates, and absence of a pseudopygidium (an abdominal structure most halictines use to shape and tamp the nest burrows).
Sphecodes biology (Ferton, 1898, Bluthgen, 1923) is rather unique in that the parasite usually enters the host nest by force to destroy the host eggs and young larvae, and replace them with eggs of her own. She usually kills the adult host or hosts and remains in the nest most of the time for 1 to 3 days. During this period in a colonial nest of Halictus she can place eggs on five or six cells. Presumably, she opens each cell in turn, eats the egg or very young larva already there, replaces it with an egg of her own, and reseals the cell. The adult female often spends days investigating nest entrances and making quick inspection trips inside, but not carrying through with an act of parasitism (Figure 3). This deliberate behavior combined with the absence of obvious evidence that anything is amiss in a parasitized nest led many earlier investigators (Morice, 1901; Friese, 1923) to wonder whether Sphecodes was parasitic at all.

The larval Sphecodes, since it has no host to destroy and no siblings to battle, looks like a normal halictine. The Sphecodes life history is similar to that of other halictines in that the mated female overwinters, sometimes in the hibernating burrow of her host. The host range of Sphecodes is somewhat in doubt. The overwhelming majority of records are in the parent subfamily Halictinae. However, there is an authentic case of parasitism in the Andrenidae (genus Melitturga) and several probable records in other andrenid genera (Panurginus and Andrena, for example). Sphecodes' problem in extending its host range probably lies in its inherited synchronization with the halictine life history. The andrenids, which are apparently occasionally utilized as hosts, often nest alongside the more "normal" halictine hosts. However, they are strictly solitary, usually have but one generation per year (in contrast to two or more in most halictines), and overwinter as mature larvae. Rozen (1965a) found that all females of Sphecodes albilabris (Kirby) captured at the nesting site of their host Melitturga clavicornis (Latreille) were extremely worn in contrast to the fresh condition of the host females. This evidence of poor synchronization suggests that Melitturga was merely a supplementary or "accidental" host.

Paralictus, like Sphecodes, is a halictine bee parasitic on halictines. It is closely related to its host, Dialictus, sometimes being placed in the same genus. Except for a minor, and not always consistent difference in wing venation, the male cannot be distinguished from Dialictus. It would be interesting to compare its parasitic behavior with that of Sphecodes, which is obviously a more ancient form, but no careful studies have been made.
Temnosoma is a brilliant green parasitic halictine found in Mexico and Central America. Its hard, heavily sculptured body surface in both sexes indicates a rather long period of evolution. Its wing venation, which lacks a bend in the basal vein (a distinguishing feature of all other halictines), also suggests an early origin, perhaps from an extinct progenitor of the halictines. If so, its resemblance to its brilliant green hosts is probably mimetic in origin.

PARASITIC MEGACHILIDAE

The family Megachilidae includes a large assemblage of bees that rarely dig burrows of their own but use a wide assortment of materials such as leaves, resin fibers, mud, etc., with which to build brood cells and accessory structures. Behavior suggesting a step on the road to parasitism was observed in a nest of Osmia lignaria Say (Bohart, 1955). An unrelated species, Osmia californica Cresson, began using the lignaria nest, contributing some of its own distinctive mud to the first cell, both mud and pollen to the next two cells, and finally a complete cell of its own with a characteristically concealed egg (Figure 4). The sequence of events was obvious because of the different kinds of mud, pollen, and egg deposition involved. Similar supercedures taking place between members of the same species would be more difficult to observe. It seems possible that similar tendencies toward either intra- or interspecific nest competition could eventually lead to true parasitic behavior.

COELIOXYS (MEGACHILINI)

Parasitism has arisen at least three times in the Megachilidae. The best known parasitic genus, Coelioxys, with rare exceptions, attacks Megachile, another genus in the same tribe. However, Coelioxys is obviously a parasite of long standing since in all stages it differs strikingly from its host. The adult, presumably for defense against its host, has an exceptionally heavy armor and its appendages tend to fit into crevices in its body wall. It also has an elongate, pointed abdomen, an obvious modification for inserting eggs into the sealed host cell (Figure 5). The egg, shaped like a horseshoe nail, is usually laid in hidden places in the cell (Iwata, 1939), but in some species it is placed against that of the host on top of the pollen mass (Ferton, 1897). The first stage larva has large, sharp mandibles, but the second is even more modified, with enormous, sickle-shaped
mandibles. Both stages are much more mobile than the highly sedentary host larvae.

Although it has usually been assumed that the impressive mandibles and mobility of the first and second stage larvae are adaptations for destroying eggs or young larvae of the host, observations in the cells indicate that the first stage larva feeds only on pollen. In some species the first stage remains attached to the oviposition site (Iwata, 1939), and in others it migrates to the surface of the pollen (Medler and Koerber, 1958). The sharp mandibles may be used to destroy other Coelioxys larvae (several eggs are often laid in the same cell). Also, in those species that lay their egg next to the host, the first stage larva probably punctures the host egg. The second stage larva of the species studied by Iwata punctures the host larva with its mandibles, but the one studied by Medler and Koerber merely churns up the pollen near the host, eventually causing it to die. The third and final larval stages, which feed peacefully on the pollen without competition from host or other cell-mates, have the usual short, broad mandibles of pollen-feeding larvae. The mature larva spins a cocoon similar to, but coarser than, that of its host. Head capsules of the early larval instars, as well as those of deceased competitors, are often incorporated in the cocoon fabric (Figure 6).

Although Coelioxys nearly always confines its attacks to Megachile (sensu latum), a species was reared in England by Richards (1949) from cells of Anthophora furcata Kirby in decayed logs also utilized by Megachile. Since the same species of Coelioxys was reared from the Megachile, it appears that the Anthophora was parasitized “by mistake.” Although such “accidental” expansions of host range are not commonly observed among parasitic bees, they indicate how an obligatory change of host could evolve. Rozen (1969) reared a Coelioxys from an Anthophora cell in a road bank in Africa. Since he found no Megachile in the same bank, it appears that this relationship was more than “accidental.”

PARASITIC ANTHIDIINIES

Anthidiini is the only other megachilid tribe known to have parasitic representatives. The two parasitic groups (Dioxyx and the Stelis complex) apparently arose independently from non-parasitic forms. Both groups are parasites of other megachilids, with the exception of a Stelis (subgenus Odontostelis) that parasitizes Euglossa, a tropical apid (Bennett, 1966). Although the parasitic anthidiines include several genera and have a wider natural host range than do Coelioxys,
they are apparently of more recent origin since they have not diverged as far structurally from their non-parasitic parent stock.

*Dioxys* lays its eggs on or near that of its host on top of the pollen mass. In cells under observation by Rozen and Favreau (1967), the *Dioxys* egg, which looked much like that of its host (*Osmia*), hatched first, and the larva used its unusually sharp mandibles to kill the host egg. However, it was observed that the first three larval instars had sharp mandibles and were very active, indicating that their attack on the host may sometimes be delayed for several days. No more than one egg was ever found in a single cell, thus indicating that the sharp mandibles were used primarily against the host rather than competing parasites. The fourth (final) stage larva has two mandibular teeth separated by a cusp and otherwise resembles that of a non-parasitic form. A peculiarity of the genus in all larval stages is its unusually long antenna, but the significance of this is not clear (Rozen, 1967). After consuming the host’s pollen, the mature *Dioxys* larva spins a cocoon similar to that of other anthidiine bees.

Most species of *Stelis* (Figure 7) have a similar biology to that of *Dioxys*. The egg is often buried in the host’s food mass and the larva usually molts at least once before attacking the partially grown host larva (Figure 8). The mandibles of most species, being unidentate and quite sharp in the early larval stages, are obviously adapted for destroying the host egg or larva. They are not unusually large, however, and in general there is little to distinguish *Stelis* larvae from those of other anthidiines (Rozen, 1966a). The mature larvae spin a strong, finely constructed cocoon with a large nipple at the exterior end and a polished interior (Figure 9).

Although the parasitic anthidiines are generally conservative in their host range and uniform in their biology, the subgenus *Odontostelis* has gone far afield to parasitize *Euglossa* and its biology is correspondingly divergent (Bennett, 1966). The female parasite enters the *Euglossa* nest cavity and opens the cells, removing and stinging the host eggs or larvae as they are encountered. She then lays an egg on the food mass and reseals the cell, using the resinous nesting material gathered by the host. When the parasite encounters the parent *Euglossa* in the nest, she seizes it and attempts to sting it while the *Euglossa*, though more formidable armed, attempts to escape. The host larvae, which are not removed from the cells for later oviposition by the parasite, are destroyed through the cell walls, presumably by stinging. The early larvae of *Odontostelis* are nearly sedentary and have mandibles quite similar to those of non-parasitic anthi-
diines. Mobility and weaponry are obviously of no use when only one egg is placed in the cell and the host has been removed.

*Odontostelis* is biologically much more similar to *Sphecodes* than it is to other parasitic megachilids. It is difficult to see how its biology could have departed so far from the relatively stereotyped *Stelis* pattern and also how the larvae could have retrogressed to a non-parasitic type. It seems more logical to postulate that *Odontostelis* developed independently from a non-parasitic anthidiine. If this postulate is correct, the ancestor of *Odontostelis* must have been similar enough to the one from which *Stelis* developed for the adults to have been mistakenly placed in the same genus. Furthermore, for *Odontostelis* to develop its original parasitism by attacking an unrelated bee like *Euglossa* would provide an interesting departure from "Muller's law," as discussed by Wheeler (1919), which states that parasitism in aculeate Hymenoptera arises from the same stock as the original host. Most cases of parasitic bees attacking hosts unrelated to themselves can be explained as specialization occurring long after the parasitic habit had been acquired.

**MELECTINE AND ERICROCINE BEES**

Most of the species and genera of parasitic bees belong to the family Anthophoridae. There are two major groups, Nomadinae and two tribes related to each other, *Melectini* and *Ericocini*. A third tribe, *Protepeolini*, is usually considered to belong to Nomadinae but, as indicated later, it is probably an independently derived group.

The *Melectini* and *Ericocini* are often considered to be a single tribe under the former name. However, Rozen (1969a) believes that they were independently derived, *Ericocini* from a centridine stock and *Melectini* from a pre-anthophorine stock. Since centrines are the hosts of ericrocines and anthophorines are the hosts of melectines, a diphylectic origin of the two parasitic tribes would preserve "Muller's law." *Rathymus*, a South American genus of parasitic bees was accorded tribal rank by Rozen but since it appears to have had a common origin with the ericrocines, it is included with them in this discussion.

The melectines (in the broad sense) enter the host burrow (Figure 10 and cover photo), break into the cap of their host cells after they are sealed, insert the tip of their abdomen through the small
Figure 11. Cell of *Anthophora peritomae* Cockerell with *Zacosmia maculata* Cresson (Melectini) egg suspended from cap. Host egg is on food below.

Figure 12. *Anthophora peritomae*, inner view of cell cap showing empty *Zacosmia* egg membrane and off-center, plugged scar made by *Zacosmia*.

Figure 13. First stage *Zacosmia maculata* larva leaving egg membrane.

Figure 14. First stage *Xeromelecta californica* larva attacking *Anthophora occidentalis* egg (host egg in unnatural position on cell cap).

Figure 15. Second stage larva of *Zacosmia maculata* after disposing of *Anthophora peritomae* egg (host membrane at left).

Figure 16. Cocoon of *Xeromelecta californica* in cell of *Anthophora occidentalis* (*Anthophora* does not spin a cocoon).

Figure 17. Overwintering larva of *Xeromelecta californica* in its cocoon in cell of *Anthophora occidentalis*.

Figure 18. *Triepeolus* sp. (Nomadinae) taking nectar from sunflower (*Helianthus* sp.).

Figure 19. *Triepeolus concavus* Cresson. Egg in lower wall of cell of *Svastra obliqua* (Say) (host egg on food mass above).
hole effected and deposit one or two eggs on the remaining inner surface of the cap (Figure 11) or from the zone where the cap and lateral cell walls join (Torchio and Youssef, 1968). The adult bee then patches the cap with mud (Figure 12). This habit led most investigators to conclude that melectines laid their eggs before the cap was constructed (Porter, 1951). The first stage larvae crawl down to the pollen mass and attack the host egg with their sharp, but only moderately elongate, mandibles (Figures 13, 14). When the host food is liquid on top, as it usually is in anthophorine cells, the larva appears to extend its ventral surface and contract its dorsal surface until it becomes somewhat boat-shaped. The remaining three larval stages are relatively similar to those of other anthophorine and centridine bees (Figure 15). The mature larva spins a fibrous cocoon caked with the waxy cell lining of its host (Figure 16), and overwinters therein as a somewhat leathery prepupa (Figure 17), in contrast to the naked and very flaccid prepupa of the anthophorines.

**NOMADINE BEES**

The Nomadinae includes a large number of tribes, most of which are too poorly known for a tribe-by-tribe accounting. Michener (1944) considered many of the tribes to be independently derived from non-parasitic anthophorids. Perhaps they have been kept in one group more for the sake of convenience and lack of knowledge about their ancestry than from features held in common. However, in spite of the great diversity in adult morphology and wide range of hosts, they hold several biological features in common and their immature stages are quite similar in appearance (Rozen, 1966).

The adults range in size from species larger than honey bees (many *Tripeolus*) to ones among the smallest of bees (Neolarra). They share (in common with nearly all parasitic bees) the absence of any pollen-transporting apparatus and of a pronounced basitibial plate (the “kneecap” used for working in burrows). The flattened, scale-like pubescence (Figure 17), common to many parasitic bees, is especially well developed among many nomadines.

All genera whose biologies are known, enter the cell while it is still open and insert their egg in the wall of the cell (Figure 19). Often, only the flush anterior end (operculum) of the egg can be seen on the inner cell wall, but sometimes (as in *Nomada*) the egg is only partially “toenailed” into the wall. To escape from the egg chorion, the first stage larva pushes away the operculum (Figure 20),
a method of hatching quite different from that of any other bee. The larva then mounts the host egg and destroys it (Figure 21), usually continuing to feed on it until midway through the second stage (Figure 23).

The first stage larvae of all genera whose biologies are known have long, curved, sharp mandibles (Figure 22), although these are better developed in some groups (Epeolini) than others (Nomadini, etc.) The later larval stages have short but sharply pointed mandibles with a poorly developed second tooth, if any. The mature larvae do not spin a cocoon and after defecating, they develop a very rigid body wall and have unusually prominent spiracles (Figure 24).

The most interesting diversity in the biology of the Nomadinae is in the manner in which the eggs are inserted in the cells. Some (for example, Triepeolus) are completely buried and at right angles to the cell wall (Bohart, 1966); some are only thrust into the wall part way and at an angle (Nomada) (Linsley and MacSwain, 1955), some are doubled over in the cell wall (Oreopasites) (J. G. Rozen, Jr., in lit), and some are placed in the wall almost parallel to it with the anterior end toward the cell cap (Pseudodichroa) (Rozen and Michener, 1968). Epeolus, which lays eggs in Colletes cells, which are composed of two cellophane-like layers, places its egg between the two layers, with the anterior end exposed and directed toward the cell cap (Rozen, 1968). Females of most nomadine genera have distinctive structures (externally and internally) at the end of the abdomen for specific methods of egg laying in specific types of cells.

Nomada, the largest genus of parasitic bees, has over 100 species in North America. It also has the largest host range. Most of the species attack members of the large genus Andrena (Andrenidae), but others have become adopted to members of such diverse families as Melittidae (Dasypoda), Halictidae (Nomia, Figure 25, Halictus), and Anthophoridae (Eucera). Another large genus, Triepeolus, has extended its host range from the usual host tribe Eucerini (an anthophorid) to include a few non-eucerine anthophorids and several genera in other families (Ptiloglossa in Colletidae, Protoxaea in Oxaeidae, and Nomia in Halictidae. Although one species of Nomia is clearly a host of Triepeolus (E. A. Cross, in lit), another appears to be an “accidental” host as indicated by the following observation. In central Utah a species of Triepeolus was reared from several nests of Melissodes, which is one of the principal host genera for this genus of parasite. Two Triepeolus of the same species were taken from
Figure 20. *Triepeolus dacotensis*. Anterior end of egg membrane showing operculum pushed open by emerging larva.

Figure 21. *Oreopasites* sp. (Nomadinae). First stage larva feeding on egg of *Nomadopsis scutellaris* Fowler.

Figure 22. *Triepeolus dacotensis*. First stage larva from cell of *Anthophora occidentalis*.

Figure 23. *Oreopasites* sp. Second stage larva finishing its meal on the egg of *Nomadopsis scutellaris*.

Figure 24. *Triepeolus dacotensis*. Overwintering larva in host cell (note absence of cocoon, prominent spiracles, and rigid body characteristic of mature nomadine larvae).

Figure 25. Overwintering larva of *Nomada suavis* Cresson beside that of its host, *Nomia melanderi* Cockerell.

Figure 26. Overwintering larva of *Isepeolus* sp. in its cocoon from cell of *Colletes*.

Figure 27. *Triepeolus dacotensis*. Overwintering larva attacked by parasitic bee fly larva (*Anthrax limatulus* Say).

Figure 28. *Triepeolus* sp. sleeping on sweetclover stem (note mandibles grasping stem).
over 5,000 cells of *Nomia melanderi* examined from nests surrounding those of the *Melissodes*.

**PROTEPEOLINE BEES**

One tribe of parasitic anthoporids, the *Protepeolini*, differs quite strongly from the true nomadines in characters of the mature larvae and in having a cocoon-spinning habit (Figure 26). One of its genera, *Isepeolus*, is a parasite of the colletid subfamily, Colletinae, but the host for the other genus, *Protepeolus*, is unknown. Although most of the details in the biology of this group are unknown (Michener, 1957), it seems wise at present to merely consider it as a separately derived parasitic tribe of Anthophoridae.

**GENERAL COMMENTS**

Although parasitic bees cause the destruction of their host's brood, the adult hosts are rarely seen attacking or expelling them from the nest. Aggressive social forms like bumble bees and stingless bees actively defend their nests, and subsocial forms like halictines and allodapines often employ nest guards to block the entrance with their abdomen. Solitary bees commonly plug their nests and conceal the entrances, but they usually ignore the parasites when they encounter them, or merely push them aside. However, Thorp (1969) observed an *Anthophora* repeatedly attacking a *Melecta* that was starting to dig into her recently completed nest.

Bees are subject to many parasites besides cuckoo bees. Some of these are cleptoparasites, like sapygid wasps, but others feed primarily on the host tissues. Parasitic bees, being somewhat related to their hosts and occupying the same nests, are subject to the same parasites in most instances (Fig. 27). Most bees are parasitized by only one species of cuckoo bee in a single locality, but *Anthophora occidentalis* in Cache Valley, Utah, is parasitized by both *Triepeolus dacotensis* Stevens, and *Xeromelecta californica* Cresson (Esmaeli, 1963). Even more unusual is the occurrence in Idaho of two species of *Triepeolus* as more or less equally abundant parasites of *Melissodes tepida* Cresson (David Triplett, *in litt*).

Although cuckoo bees do not provision nests and nearly all of them have lost pollen-transporting structures, they visit flowers, like any other bee, to satisfy their nutritional requirements. However, the
females spent most of their time searching for host nests and are thus relatively poor pollinators. The habits of male cuckoo bees are essentially the same as those of other male bees. Cuckoo bees of both sexes, being essentially homeless, often sleep in the open in the manner of males and the newly emerged females of other bees (Figure 28).

SUMMARY

Parasitic bees are exclusively parasitic on other bees. They are referred to as clepto- or cuckoo parasites in reference to their habit of placing eggs in the host nest. Most species parasitic on solitary bees lay their eggs either before or after the cell is sealed, but without destroying the host egg. Before feeding on the food in the cell, the parasitic larva then dispatches the host egg or young larva and any eggs or young larvae of other parasites. *Sphecodes* (parasitic primarily on halictines) and *Odontostelis* (parasitic on euglossines) destroy the host eggs or young larvae before ovipositing. *Psithyrus*, parasitic on bumble bees, demoralizes the host queen and lays eggs which are reared by the host workers. Several parasitic genera of small carpenter bees (Allodapini) apparently function in a similar manner in the nests of their allodapine hosts, although the details are not well known. *Lestrimelitta*, a parasite of stingless bees, robs food stores and building materials from its host species, often taking over the host nest in the process. It retains its nesting habits and thus should be thought of as an obligatory robber rather than a true "cuckoo."

About 15 percent of the 4,000 to 5,000 species of bees in North America are parasitic. By extrapolation of this ratio, there should be about 3,500 parasitic species in the world. These are distributed among four of the nine families of bees. Morphological evidence indicates that existing parasitic lines were derived at least 16 times from non-parasitic ancestors. Since nearly all of these phyletic lines parasitize other bees in the subfamily from which they were derived, it appears that parasitism among bees has arisen by the genetic fixation of a tendency on the part of certain individuals of a population to take advantage of other members of the same species (or in rare instances, of related species). The older and more diverse phyletic lines have considerably extended their host ranges. For example, the most diverse group, Nomadinae, parasitizes many genera included in six families.
Host specificity is strongly developed among parasitic bees. The few known instances of species attacking more than a few related host species probably represent "accidental" occurrences rather than fixed "promiscuous" behavior. Parasitic genera usually attack only one host genus or a few closely related ones. *Nomada* and *Triepeolus* are outstanding exceptions.

Physical characteristics shared by many or most parasitic bees (depending upon the characteristic) include (1) absence of scopa or corbiculum, (2) reduced pilosity, (3) scale-like pubescence on some part of the body, (4) reduction or absence of basitibial plate, (5) apical attenuation and specialization of abdomen, (6) strong, carinate, coarsely punctate exoskeleton, (7) bright or contrasting color pattern, (8) large (or at least unusually sharp) mandibles in one or more early larval instars, (9) unusual mobility of early larval instars.
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