Bees of Northwestern America: *AGAPOSTEMON*

(Hymenoptera: Halictidae)

Technical Bulletin 125

AGRICULTURAL EXPERIMENT STATION
Oregon State University
Corvallis, Oregon

June 1973

Contents

AUTHOR: Radclyffe B. Roberts is a research associate in entomology, Department of Entomology, Oregon State University.

Bees of Northwestern America: *Agapostemon* (Hymenoptera:Halictidae)

RADCLYFFE B. ROBERTS

ABSTRACT

Diagnoses, synonymies, range maps, and an illustrated key are provided for the six species of *Agapostemon* found in the Northwest: *A. angelicus*, *A. coloradinus*, *A. femoratus*, *A. melliventris*, *A. texanus*, and *A. virescens*. Adults of both sexes of *A. virescens* share a nest. Peculiar linearly paired male-female cells in nests of *A. virescens* link *Agapostemon* with certain South American Halictinae.

Key words: Bees, *Agapostemon*, synonymy, key, Pacific Northwest, biology.

Introduction

The genus *Agapostemon*, like all of the bright green Halictidae, is restricted to the Western Hemisphere occurring from southern Canada to Paraguay. Closely related to *Paragapostemon*, *Ruizantheda*, and other neotropical genera, *Agapostemon* is the only member of the group to occur north of Mexico. In a recent revision (Roberts, 1970) of the 43 species of *Agapostemon*, 12 species were reported from the United States, six of which are present in the Northwest.[1]

Until very recently the biology of the genus *Agapostemon* was unknown but for some incidental notes in the literature. Eickwort and Eickwort (1969) reported on the biology of the neotropical species, *Agapostemon nasutus* Smith. Roberts (1969) reported on the biologies of the North American *A. radiatus*, *A. splendens*, and *A. texanus* and summarized the biologies of other species insofar as known. Each of these papers contains more detailed information than can be presented here.

Generic Diagnosis

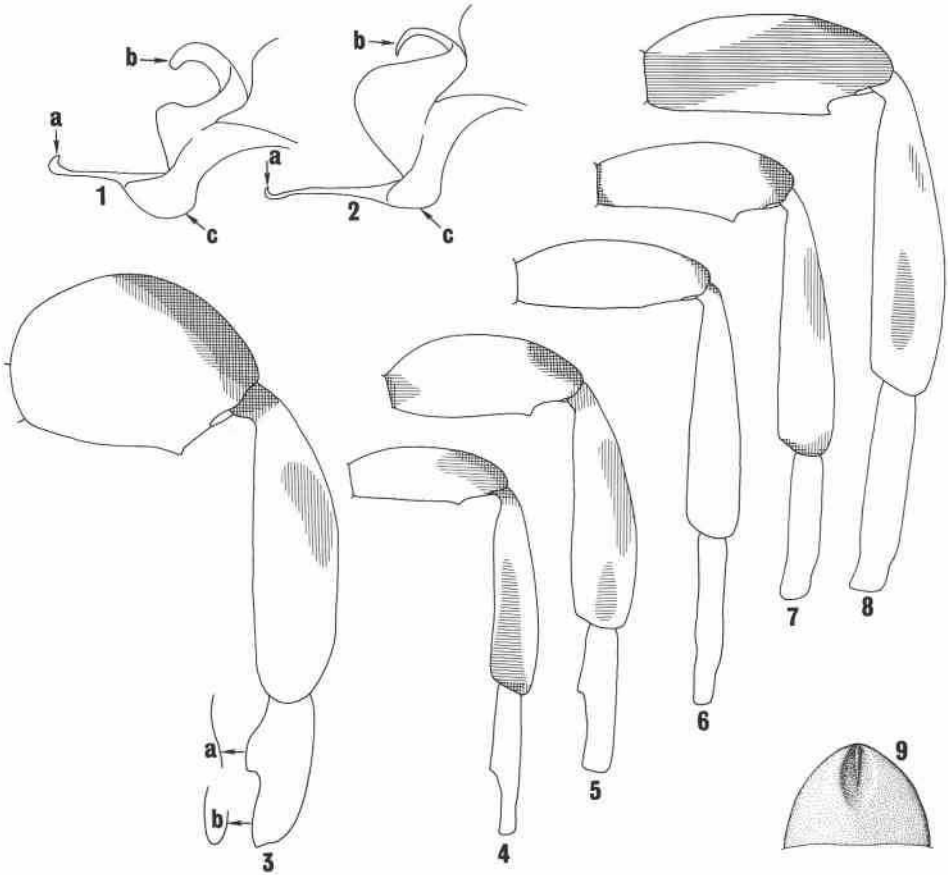
The bees of the genus *Agapostemon* are easily distinguished from other North American bees by (1) a distinct carina around the posterior surface of the propodeum (Fig. 12), (2) four tarsal segments on the hind legs of males,[2] and (3) the combination of bright metallic green or

[1] Here defined as Oregon, Idaho, Washington, British Columbia, Yukon, and Alaska.

[2] There are five segments (believed to be subdivisions of a single primitive tarsal segment) in most bee tarsi, but the basal pair of tarsal segments are fused on the hind leg of *Agapostemon* males.

blue head and thorax with a black, or amber, or black and yellow metasoma. All North American *Agapostemon* possess one or more of these features, any of which is sufficient to distinguish them from all other North American bees.

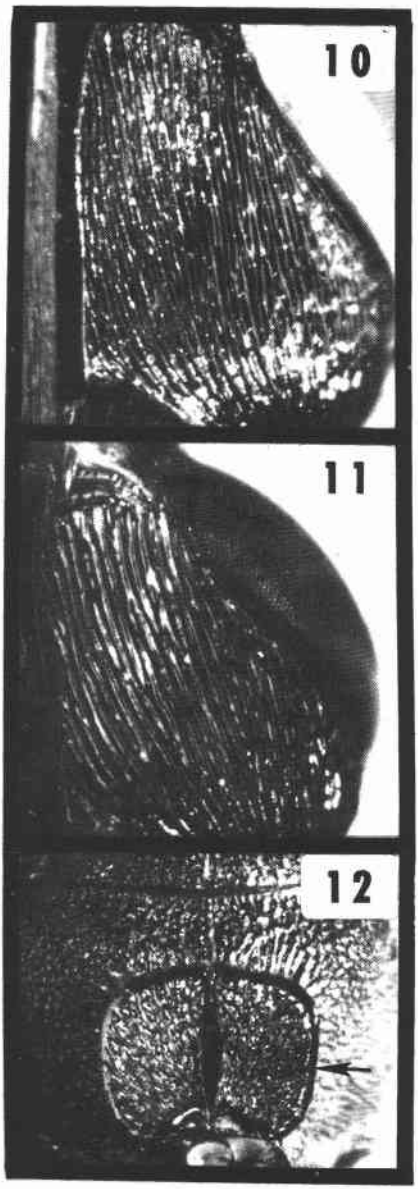
Some of the neotropical Halictidae have a color pattern similar to that of *Agapostemon* and the males have four tarsal segments, but unlike *Agapostemon* they have conspicuously hairy eyes.

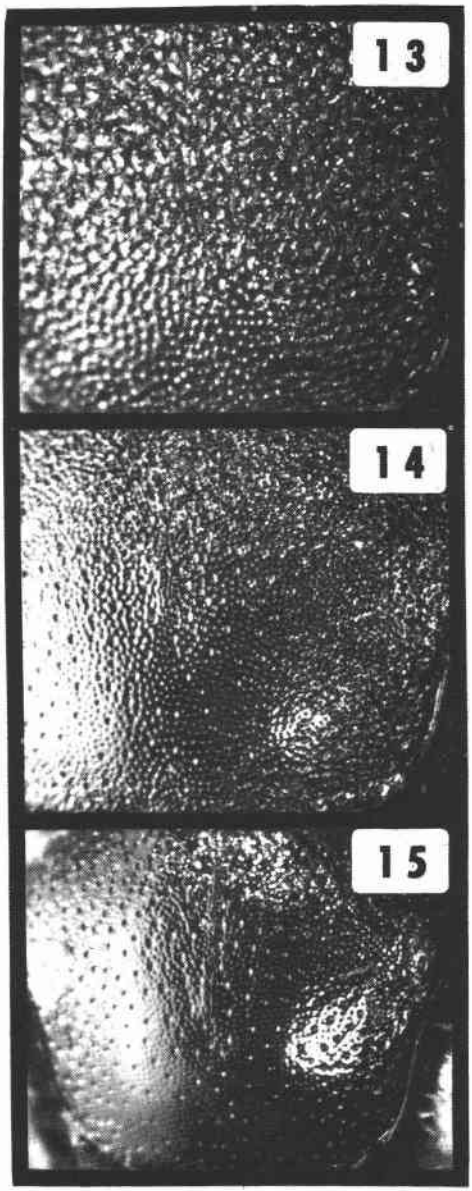


Figures 1-2. Male gonostylus with apical stylus (a), basal stylus (b), and base of apical stylus (c): (1) *A. angelicus;* (2) *A. texanus.*

Figures 3-8. Male hind femora, tibiae, and basitarsi (yellow with brown or black on anterior surfaces indicated by vertical hatching and on posterior surfaces by horizontal hatching): (3) *A. femoratus* with front and side views of basal ridge (a) and apical groove (b) of basitarsus; (4) *A. angelicus;* (5) *A. texanus;* (6) *A. melliventris;* (7) *A. virescens;* (8) *A. coloradinus.*

Figure 9. *A. virescens* male, last visible sternite.





Figures 10-11. Postero-ventral view of female gena: (10) *A. coloradinus* with fine ridges; (11) *A. virescens* with coarse ridges.

Figure 12. *A. texanus* female with carina (arrow) around posterior surface of propodeum (posterior view).

Figures 13-15. Sculpturing of female mesoscutum (dorsal view): (13) *A. femoratus* (rugose); (14, 15) *A. texanus* or *A. angelicus* with small punctures deep (Fig. 14) and small punctures shallow (Fig. 15).

Key to Species of *Agapostemon* in the Northwest

1. Female: 10 flagellar segments; hind leg with scopa, metasoma green, black, or amber 2

   Male: 11 flagellar segments; hind leg without scopa; metasoma with black and yellow bands 6

2. (1) Metasomal terga bright metallic green to blue, like head and thorax 3

   Metasomal terga black or amber, unlike metallic head and thorax 4

3. (2) Scutum coarsely punctate or rugose, punctures of uniform size and without shiny interspaces (Fig. 13) ..... *femoratus*

   Scutum with numerous fine punctures interspersed with fewer larger and deeper punctures (Fig. 14); punctation sometimes so fine as to leave scutum shiny (Fig. 15) .... *texanus* and *angelicus*[3]

4. (2) Clypeus with transverse apical or subapical yellow band; metasoma honey-color, rarely black ..... *melliventris*

   Clypeus metallic with apical region dark brown or black; metasoma always black 5

5. (4) Genal ridges coarse (2-3 per 0.25 mm) (Fig. 11); mandible usually yellow basally ..... *virescens*

   Genal ridges fine (5-6 per 0.25 mm) (Fig. 10); mandible amber, brown, or black basally ..... *coloradinus*

6. (1) First metasomal tergum with anterior face yellow or pale amber; hind leg (Fig. 6) slender and yellow with brown or black restricted to apex of femur and base of tibia ..... *melliventris*

   First metasomal tergum with anterior face brown or black basally; hind leg often swollen and usually with brown or black stripe longitudinally on tibia 7

7. (6) Metasoma with last two visible sterna (fifth and sixth) dark brown or black, without yellow markings; metasomal sterna 2-4 with yellow lacking or restricted to basal margins 8

[3] The females of *A. texanus* and *A. angelicus* cannot be reliably separated on the basis of their morphology; however, females occurring well outside the range of *A. angelicus* males are probably *A. texanus* (see map, Fig. 18).

Metasoma with extensive yellow markings on last two visible sterna (fifth and sixth) as well as on sterna 2-4 9

8. (7) Hind femur lacking brown or black stripe on posterior surface (Fig. 7) ..... *virescens*

Hind femur with conspicuous brown or black stripe on most or all of posterior surface (Fig. 8) ..... *coloradinus*

9. (7) Hind femur subglobose; hind tarsus with enlarged basal segment bearing conspicuous basal ridge and broad apical groove (Fig 3); posterior metasomal terga lacking metallic tints ..... *femoratus*

Hind femur longer than broad; hind tarsus with slender basal segment bearing inconspicuous basal ridge and apical groove; posterior metasomal terga with metallic tints laterally 10

10. (9) Hind tibia with brown or black longitudinal stripe on posterior surface but never on anterior surface (Fig. 4); apical stylus of gonostylus with base inflated (Fig. 1c) ..... *angelicus*

Hind tibia with brown or black longitudinal stripe anteriorly (Fig. 5), but if lacking, then longitudinal stripe on posterior surface also absent; apical stylus of gonostylus with base not inflated (Fig. 2c) ..... *texanus*

Agapostemon angelicus Cockerell, 1924

Diagnosis. The male of this species has a bright metallic green head and thorax; the metasoma is black and yellow banded, with metallic tints apically. The male of *A. angelicus* may be distinguished from males of *A. coloradinus* and *A. virescens* by the presence of yellow on its last two visible sterna (fifth and sixth), from males of *A. melliventris* by the presence of an apical black stripe on the posterior surface of its hind tibia (Figs. 4, 6), and from males of *A. texanus* and *A. femoratus* by the lack of a medial brown or black stripe on the anterior surface of its hind tibia (Figs. 3-5). *Agapostemon texanus* may lack the anterior tibial stripe, but such specimens also lack the posterior stripe present in *A. angelicus*.

The female of *A. angelicus* has a bright metallic green head, thorax, and metasoma. It may be distinguished from females of most other species by the presence of two sizes of punctures on its scutum (Figs. 14-15). The females of *A. texanus* are similarly colored and also have two sizes of scutal punctures. Thus, females of *A. texanus* and *A. angelicus* cannot be distinguished by morphological features.

Distribution. Although common only in the arid regions of the southwestern United States and northern Mexico, males of *A. angelicus* have been found as far north as west-central North Dakota, as far south as northern Durango (Mexico), as far east as central Iowa, and as far west as southwestern California (Fig. 18).

In the Northwest *A. angelicus* has been collected only in northern Utah, southeastern Oregon, and in the Snake River Valley of Idaho. It may also occur in northern Nevada.

This species ranges from below sea level in Death Valley, California, to 12,000 feet (3,658 m) on Mt. Evans, Colorado, where timberline is 11,700 feet. The recorded altitudinal range of this species surpasses that of almost all other North American bees.

In the southern portion of its range (Arizona) males of this species have been collected from April through November. Further north in Kansas males of *A. angelicus* have been collected from June through October.

Biology. Little is known of the biology of this species, but it is probably similar to the biology of its close relative, *A. texanus*. *Agapostemon angelicus* has been observed (Linsley, 1962) sleeping on the dried flower heads of a clump of *Heterotheca subaxillaris* (Compositae) in southeastern Arizona. Numerous males and occasional females were seen on these plants on 26 of 28 consecutive nights. The females always slept alone, but the males tolerated each other's presence and as many as six could be seen crowded onto one flower head. Grasping the plant with their legs, the males slept with their bodies extended, wings folded, and antennae held forward and pressed together or only slightly divergent. The author has observed the males of this species sleeping atop sunflowers (*Helianthus* sp.) in a pasture in eastern Colorado, in a manner similar to that noted by Linsley (1962). Both flowers and bees were covered with a heavy dew. As the morning was cold, the bees did not dry off and fly until about nine o'clock.

This species, like most bees, normally forages from about 9 a.m. to noon when the weather is warm and sunny. However, it is obvious that the females are able to adapt their foraging period to the availability of a locally abundant pollen source. *Agapostemon angelicus* females have been reported (Linsley and Hurd, 1959) gathering pollen from the afternoon-flowering *Mentzelia pumila* (Loasaceae) at sunset (5:40 p.m.). The same species has been reported (Linsley, 1960) collecting pollen from the matinal flowering *Curcurbita foetidissima* at 5:35 a.m. when the air temperature was 52-54° F (11.1-12.2° C) and a heavy overcast was threatening rain.

Agapostemon coloradinus (Vachal), 1903

Synonymy: *Agapostemon coloradensis* Crawford, 1901.

Diagnosis. The male of this species has a bright metallic blue or green head and thorax and a metasoma banded with pale yellow and black. It is the only species of *Agapostemon* in the Northwest with a long brown or black streak longitudinally on the posterior surface of the hind femur (Fig. 8).

The female has a bright metallic blue or green head and thorax and a black metasoma banded with short, dense, white hair. It may be distinguished from the similarly colored *A. virescens* and *A. melliventris* by its brown wings, finer genal carinae (Figs. 10, 11), and larger size.

Distribution. The rarest of the North American representatives of this genus, *A. coloradinus* is found principally in the southern Rocky Mountains and adjacent plains of Colorado and Utah. In all probability it also occurs in southern Idaho and southwestern Oregon.

Biology. Females have been seen gathering pollen from *Opuntia*, but they probably take pollen from many other plants. Nothing is known of the nests of this species.

Agapostemon femoratus Crawford, 1901

Synonymy: *Agapostemon californicus* Crawford, 1901 (females only).

Diagnosis. The male of this species has a bright metallic green head and thorax, and a metasoma banded with black and yellow. The male of *A. femoratus* may be distinguished from males of other *Agapostemon* species by its conspicuously swollen hind legs and the large basal ridge and apical groove on the basal segment of the hind tarsus (Fig. 3).

The female of *A. femoratus* is bright metallic green on the head, thorax, and metasoma. It may be distinguished from similarly colored females of other species occurring in the Northwest by its coarsely rugose (instead of punctate) scutum (Fig. 13).

Distribution. This is the most common species of *Agapostemon* in the Northwest. It occurs as far north as Chilcotin, British Columbia; as far south as San Vicente, Baja California; and as far east as Williston, North Dakota (Fig. 16). In the northern part of its range (Washington) females have been collected from April through October and males from June through October. In California, south of Los Angeles, females have been collected from February through November, and males in March and from May through November. This species also has great altitudinal range,

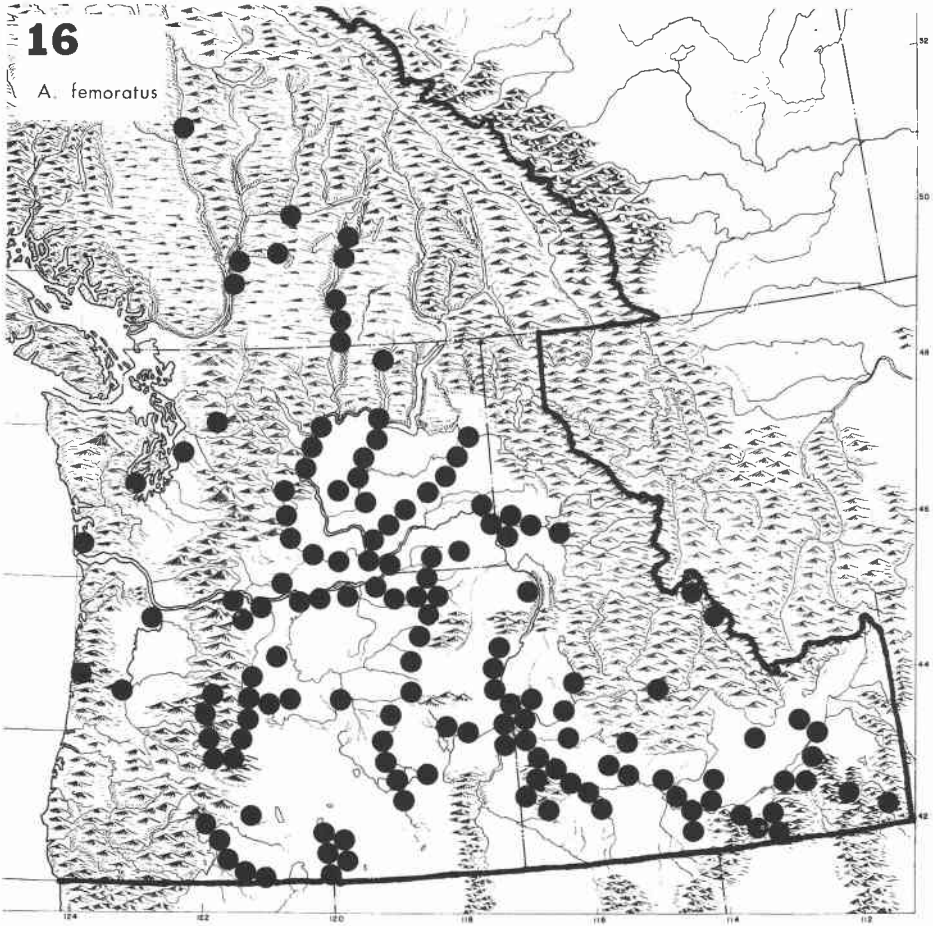


Figure 16. *A. femoratus* distribution in Idaho, Oregon, Washington, and British Columbia.

being found from sea level to 10,150 feet (3,094 m) in Mono County, California, and 8,600 feet (2,541 m) in Lake County, Oregon.

Biology. Little is known of the biology of this common species. Bohart (1950) observed both sexes of *A. femoratus* (reported as *A. cockerelli*) around fermenting watermelons in Davis, California. He observed copulation between males and females of *A. femoratus*, an act that took approximately 10 seconds. He also noted that males of *A. femoratus* frequently attempted to mate with females of *Halictus ligatus*, *H. farinosus*, and *H. rubicundus*.

Linsley (1946) reports that *A. femoratus* (given as *A. cockerelli*), "nests very deeply in hard soil, far below the level of cultivation."

Agapostemon melliventris Cresson, 1874

Synonymy: *Agapostemon fasciatus* Crawford, 1901; *Halictus* (*Agapostemon*) *plurifasciatus* Vachal, 1903; *Agapostemon digueti* Cockerell, 1924.

Diagnosis. The male of this species has a bright metallic green head and thorax, and a yellow metasoma with narrow black bands. It may be distinguished from males of other species found in the Northwest by the restriction of brown or black to narrow subapical bands on its metasomal terga.

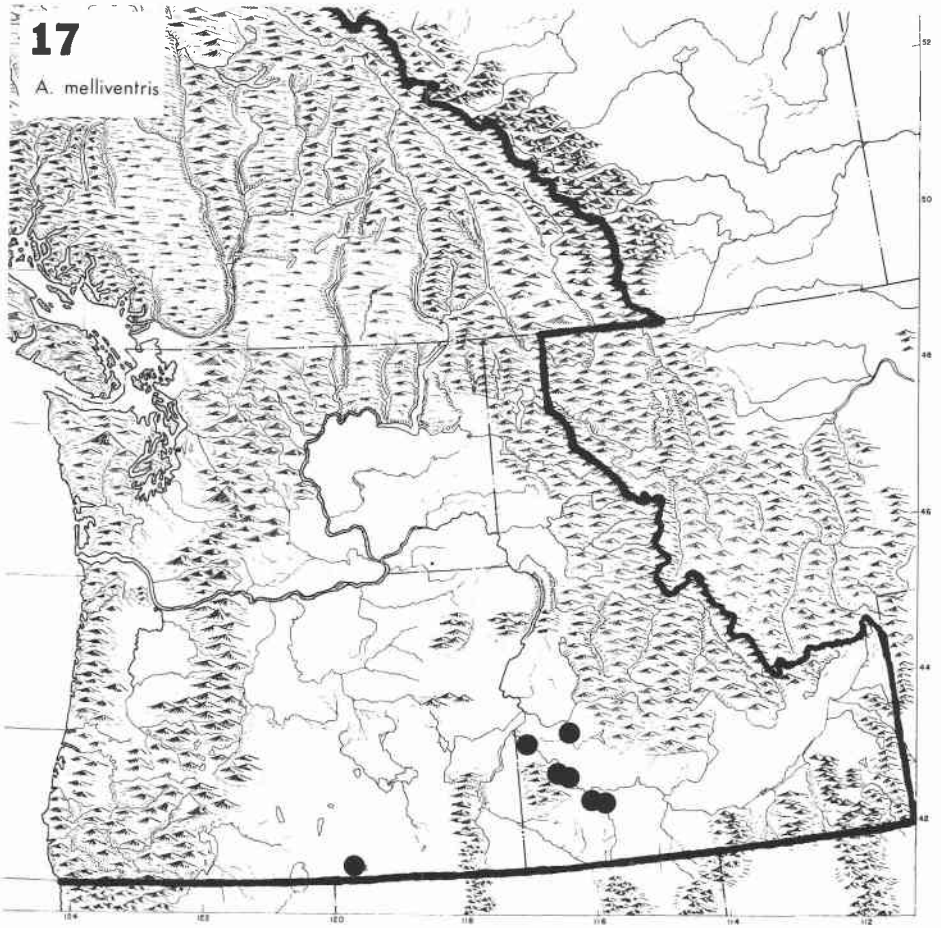


Figure 17. *A. melliventris* distribution in Idaho, Oregon, Washington, and British Columbia.

The female of *A. melliventris* has a bright metallic green head and a honey-colored metasoma banded with short, dense, white hair. In some populations, the female metasoma is black instead of honey-color, but this variant has not yet been found in the Northwest. The female of *A. melliventris* may be distinguished from females of other species in this region by the presence of a yellow band on the apical margin of its clypeus. In addition, it is the only species in the Northwest whose females have a honey-colored metasoma.

Distribution. This species is most abundant in the arid southwestern United States and northern Mexico. However, it ranges as far east as eastern Kansas and as far north as northern Montana. In the Northwest it has been found in southeastern Oregon and in the Snake River Valley of Idaho (Fig. 17).

Biology. Little is known of the habits of these bees. Linsley (1946) notes that in the alfalfa-growing regions of California *A. melliventris* "nests deep in the soil, below the level of cultivation."

Agapostemon texanus Cresson, 1872

Synonymy: *Agapostemon texanus subtilior* Cockerell, 1898; *Agapostemon borealis* Crawford, 1901; *Agapostemon californicus* Crawford, 1901; *Halictus (Agapostemon) brachycerus* Vachal, 1903; *Agapostemon texanus iowensis* Cockerell, 1910; *Agapostemon proscriptus* Cockerell, 1912; *Agapostemon joseanus* Friese, 1916; *Agapostemon sulfuripes* Friese, 1916; *Agapostemon cyanozonus* Cockerell, 1924; *Agapostemon proscriptellus* Cockerell, 1924; *Agapostemon texanus vandykei* Cockerell, 1925; *Agapostemon californicus psammobius* Cockerell, 1937; *Agapostemon angelicus idahoensis* Michener, 1937; *Agapostemon californicus clementinus* Cockerell, 1937.

Diagnosis. The male of *A. texanus* has a bright metallic green or blue head and thorax, and a black and yellow banded metasoma with metallic tints on the apical terga. The male of this species may be distinguished from males of *A. virescens* and *A. coloradinus* by the metallic tints on its apical metasomal terga and the presence of yellow on its last two visible sterna (fifth and sixth), from *A. melliventris* by the dark brown or black on the anterior face of its first metasomal tergum, from *A. femoratus* by the inconspicuous basal ridge and apical groove on the basal segment of its hind tarsus, and from *A. angelicus* by the presence of an anterior stripe on its hind tibia or the absence of both anterior and posterior stripes on its hind tibia.

The female of *A. texanus* has a bright metallic green or blue head, thorax, and metasoma. It may be distinguished from the females of most similarly colored species by the presence of two sizes of punctures on its scutum. The females of *A. texanus* cannot be distinguished from the similarly sculptured *A. angelicus*.

Distribution. The range of *A. texanus* (Fig. 18) is far greater than that of any other species in the genus. It is found from southern Canada (52 degrees N) to central Costa Rica (10 degrees N) and from Cape Cod,

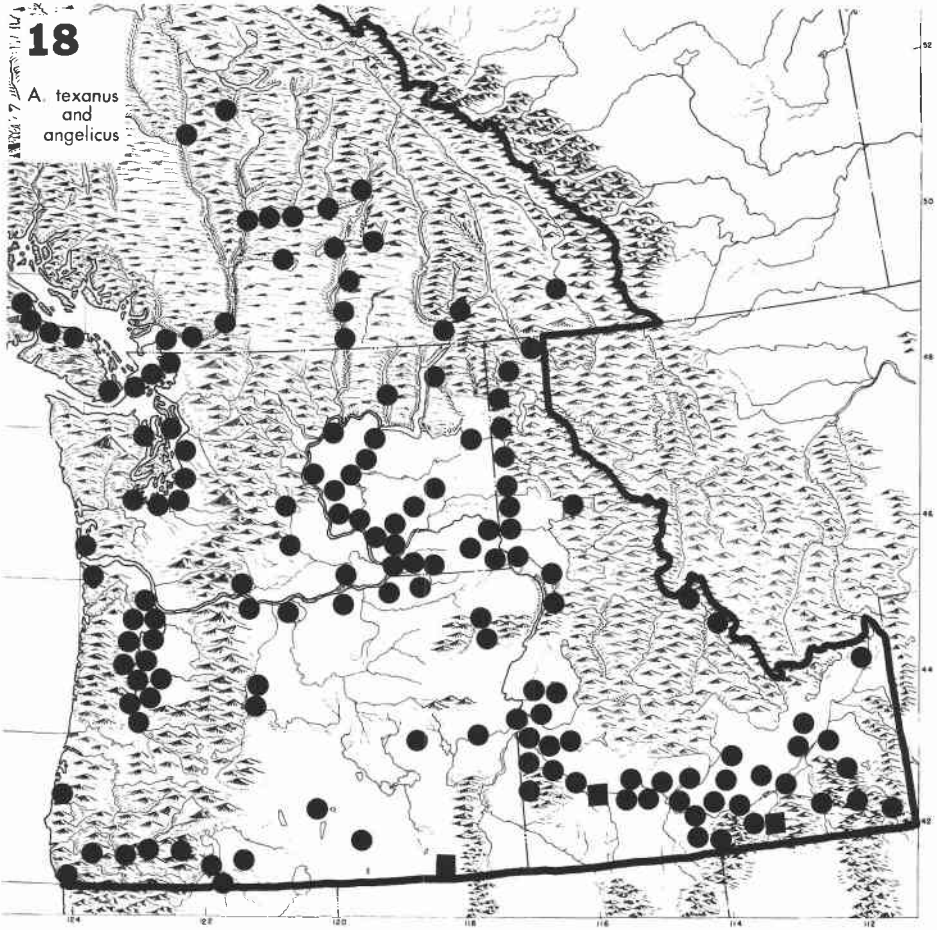


Figure 18. *A. texanus* and *A. angelicus* distribution in Idaho, Oregon, Washington, and British Columbia. Circles represent males of *A. texanus* and females of *A. texanus* or *A. angelicus*. Squares represent males of *A. angelicus*.

Massachusetts (70 degrees W) to Vancouver Island, Canada (125 degrees W). This species is most abundant near the western coast of the United States and is fairly abundant west of the Mississippi River excepting the arid Southwest; it is uncommon in the southwest, east of the Mississippi River, in Mexico, and in Central America. *Agapostemon texanus* occurs from sea level on the Atlantic, Gulf, and Pacific coasts to about 8,000 feet (2,438 m) in the Sierra Nevada of California. At the northern limits of its range (British Columbia) females of *A. texanus* have been collected from May through October and males from July through October. In Kansas, females have been collected from April through October and males in April (very rare) and June through October (Fig. 22); in Arizona, females have been collected from February through November and males in July and August; and in Mexico, females[4] have been collected from February through October and also in December, and males in April and from June through September.

Biology. The biology of this species is relatively well known (Roberts, 1969) and is discussed in the summary of the biology of *Agapostemon*.

Agapostemon virescens (Fabricius), 1775

Synonymy: *Andrena virescens* Fabricius, 1775; *Andrena nigricornis* Fabricius, 1793; *Halictus dimidiatus* Lepeletier, 1841; *Halictus tricolor* Lepeletier, 1841; *Agapostemon bicolor* Robertson, 1893.

Diagnosis. The male of this species has a bright metallic green head and thorax, and a metasoma banded with black and yellow. It may be distinguished from males of *A. coloradinus* by the absence of a long brown or black streak on the posterior surface of its hind femur. The male of *A. virescens* may be distinguished from those of *A. femoratus*, *A. melliventris*, *A. texanus*, and *A. angelicus* by the depression and medial ridge on the apical half of its last visible (sixth) metasomal sternum (Fig. 9).

The female of this species has a bright metallic green head and thorax, and a black metasoma banded with short, dense, white hair. The female of *A. virescens* may be distinguished from females of *A. coloradinus* by its hyaline wings, coarse genal striae (2-3 per 0.25 mm) (Figs. 10, 11) and largely yellow mandibles. It may be distinguished from those females of *A. melliventris* having black metasoma by the lack of yellow on its clypeus.

[4] Females from Kansas, Arizona, and Mexico include the indistinguishable females of *A. angelicus*.

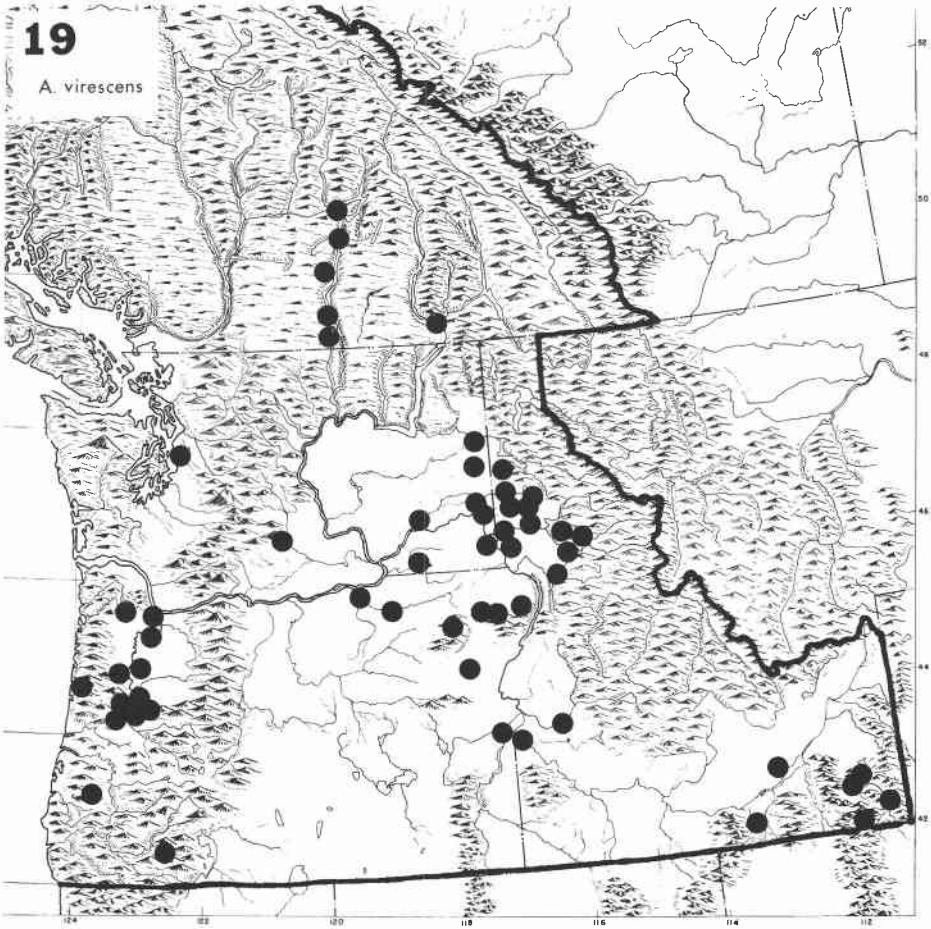


Figure 19. *A. virescens* distribution in Idaho, Oregon, Washington, and British Columbia.

Distribution. This species is common in the northern United States and southern Canada where it occurs from coast to coast (Fig. 19). It occurs as far south as the Gulf Coast but is rare in that region.

Biology. Little has been published on the biology of this species. Felt (1928) reported a large nesting aggregation of *A. virescens* (given as *Halictus virescens*) damaging a lawn in Catskill, New York. W. P. Stephen (pers. comm.) has seen a nesting aggregation in a lawn in Corvallis, Oregon, and D. H. Janzen (pers. comm.) reports numerous nests in a field

near Eugene, Oregon. Thus, it seems that *A. virescens* is usually, if not always, aggregatory in its nesting habits.

G. C. Eickwort, W. E. LaBerge, and W. P. Stephen (pers. comm.) also have observed more than one female per nest. In addition to multiple occupancy of a single burrow, W. P. Stephen reports that *A. virescens* females, which seemed to be in a state of diapause, shared their burrow with bees of the parasitic genus *Sphecodes* which also seemed to be in diapause.

On August 5-7 a nest of *A. virescens* was observed and excavated by the author in Moscow, Idaho (Fig. 20). According to Dr. W. F. Barr, in whose garden the nests were situated, there had been a small aggregation of active nests earlier in the summer but by August 5 only two nests were still open.

One day was spent observing the nest entrances. In late morning and early afternoon two males and two females left each burrow, returning from one to three hours later. During their absence other females occasionally appeared in the burrow entrances. Their action could hardly be considered "guarding" because the slightest movement, even the passage of a butterfly, was enough to cause their disappearance for as long as an hour. In no other species of *Agapostemon* are males known to return to occupied burrows once they have emerged.

Plateaux-Quénu (1959) reports that females of *Lasioglossum marginatum* (given as *Halictus marginatus*) occupy their own nests during the spring. During the summer the nest entrances are closed but in the fall males emerge from the nests, forage, and return to the nests to mate with the females. The males then die but the females overwinter in the nests. Perhaps a similar phenomenon occurs in *A. virescens*.

Before excavation, the burrows were filled with plastic.[5] The result was a tough, permanent, transparent replica of the burrow system. In these respects, the use of plastic is far more satisfactory than the commonly employed plaster of Paris method.

One of the two active *A. virescens* nests had no tumulus or turret but the other had a small turret 4 mm high with walls 3 mm thick. This turret probably was the consolidated remnant of a much larger tumulus which had been destroyed by wind. The branched main burrow was 7.0± .8 mm in diameter and the laterals (not illustrated) were about 5.3 mm. There was no discernible constriction of the nest entrance, but some of the branch burrows were slightly constricted where they joined the main burrow. Owing to the complexity of the nest and its proximity to other nests, it was nearly impossible to trace the earth-filled laterals back to the main

[5] Polyester resin available from Taylor and Art Plastics, Inc., Oakland, California 94606.

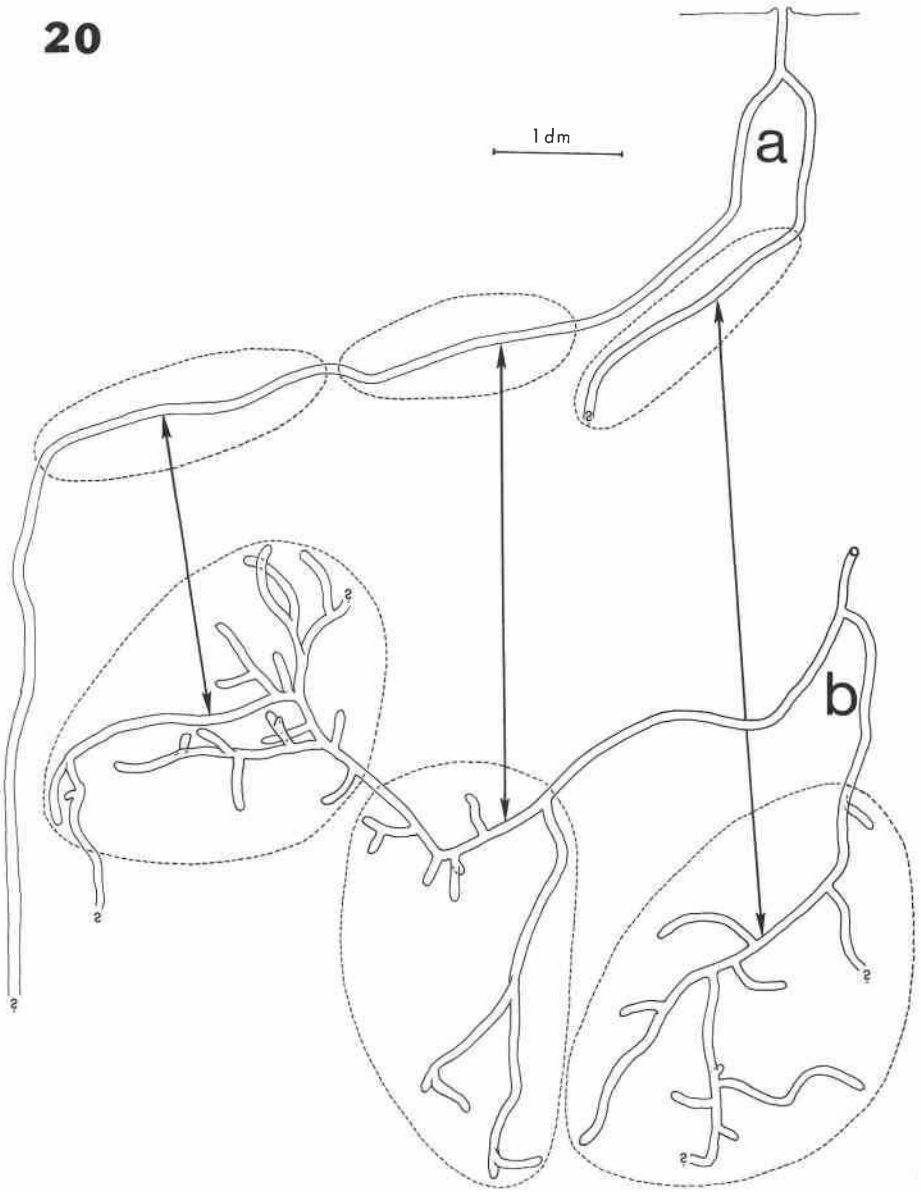


Figure 20. *A. virescens* nest with side (a) and top (b) views of main galleries. For clarity, clusters of branching galleries illustrated in section b are omitted in section a. A question mark at the open end of a gallery indicates that the gallery continued but was lost in the course of excavation. (Not shown are 100 or more lateral burrows which terminated in from one to three cells and extended horizontally for several centimeters from the main galleries.)

burrows, but most of the cells were several centimeters from the main burrows. Thus it seems that in the construction of laterals much longer than the lengths of the cells, *A. virescens* is similar to other species of *Agapostemon.*

During excavation, numerous adults were found in a state of torpor in their natal cells. In other *Agapostemon* species the adults emerge from their natal cells within 48 hours after their final molt. Many cells were uncovered in the course of excavation and the contents of 158 were preserved—69 were female pupae and adults, 57 male pupae and adults, and 32 were late instar larvae or prepupae.

Especially noteworthy was the occurrence of linear pairs of cells at the ends of many of the laterals. In each of the 12 pairs examined (many others were accidentally destroyed in the course of excavation), the distal cell always contained a female and the proximal cell a male. One lateral contained two male cells and a distal female cell. Related genera such as *Ruizantheda* (but never the genera allied to *Halictus or Augochlora*) construct long strings of linearly arranged cells. Daly and Wille (in Sakagami and Michener, 1962), describe a nest of *A. nasutus* in which only linear pairs of cells were found. As in *A. virescens,* the distal cell always contained a female and the proximal cell a male. In extensive observations of *A. nasutus,* Eickwort and Eickwort did not find such linear pairs of cells. Perhaps the construction of cell pairs is facultative in *A. nasutus* as it seems to be in *A. virescens.*

But for the paired cells and the presence of males, the *A. virescens* nest excavated was similar to those of *A. nasutus* described by Eickwort and Eickwort (1969) in that it had many main branches occupied by many bees. As none of the *A. virescens* females were reproductively active at the time the nest was excavated, it was not determined whether this species is social or, more likely, merely communal like *A. nasutus.*

Biology

The following composite of *Agapostemon* biologies is based principally on studies of *A. nasutus* (Eickwort and Eickwort, 1969), *A. radiatus, A. splendens,* and *A. texanus* (Roberts, 1969).

Nest site

Members of the genus *Agapostemon* are soil nesters. Some species such as *A. nasutus* have only been observed nesting in banks while others such as *A. virescens* are only known to nest in horizontal surfaces. *Agapostemon radiatus, A. splendens,* and *A. texanus* are known to nest both in vertical banks and horizontal surfaces. Most species nest in loam, but

A. splendens prefers to nest in sand. In fact, the distribution of *A. splendens* seems to be limited by the availability of sand.

Females of *A. radiatus*, *A. splendens*, and *A. texanus* searching for a nest site engage in a slow wavering flight a few centimeters from the soil surface. They alight frequently and are especially attracted to small shadows or dark spots. As a result their nests are frequently initiated under pebbles or leaves or in pre-existing cracks or holes in the soil. This habit of concealing the entrance makes the nests of these species especially difficult to find in the field.

Some species such as *A. texanus* appear to be solitary, whereas others such as *A. virescens* and *A. nasutus* have only been reported as nesting in aggregations. Still others, such as *A. radiatus*, have been reported both as solitary and aggregatory nesters.

Nest architecture

A nest of *Agapostemon* in a horizontal surface accumulates a tumulus (mound of soil) at the entrance. The size of the tumulus is dependent upon the extent of nest excavation, but the tumulus is commonly dispersed by wind or rain. If allowed to accumulate undisturbed, the tumulus of *A. radiatus*, *A. splendens*, or *A. texanus* is a symmetrical cratered cone 3-5 cm in diameter and 1-3 cm high. The nest entrance is in the center of the cone and is normally open during the day when the occupant is foraging. The nest entrance is usually blocked with soil pushed up from below in the late afternoon or early evening, and remains closed until the female initiates foraging the next morning.

Sakagami and Michener (1962) claim that "Constriction of the entrance is a seemingly universal, or at least predominant, character of the halictine nests." However, none of the species of *Agapostemon* are known to form a nest entrance noticeably narrower than the diameter of the main burrow. Eickwort and Eickwort (1969) claim that *A. nasutus* (Sakagami and Michener, 1962) and *A. radiatus* (LaBerge and Ribble, 1966) are reported in the literature as forming distinctly constricted nest entrances. The author's examination of the references cited did not reveal any statements to that effect. Apparently, the absence of a constricted nest entrance sets *Agapostemon* apart from other genera in the Halictinae.

A typical nest of a solitary *Agapostemon* species is shown in Figure 21. It consists of a nearly vertical burrow with six to fourteen subhorizontal laterals, each terminating in a single cell. There is no definite vertical sequence of construction of lateral burrows. The occasional deepening of the vertical burrow results in a downward trend in lateral construction, but new laterals are often constructed above old laterals. The vertical burrow may be 20 to 150 cm deep and the laterals are from 5 to 20 cm long.

21

Nest of AGAPOSTEMON TEXANUS Cresson

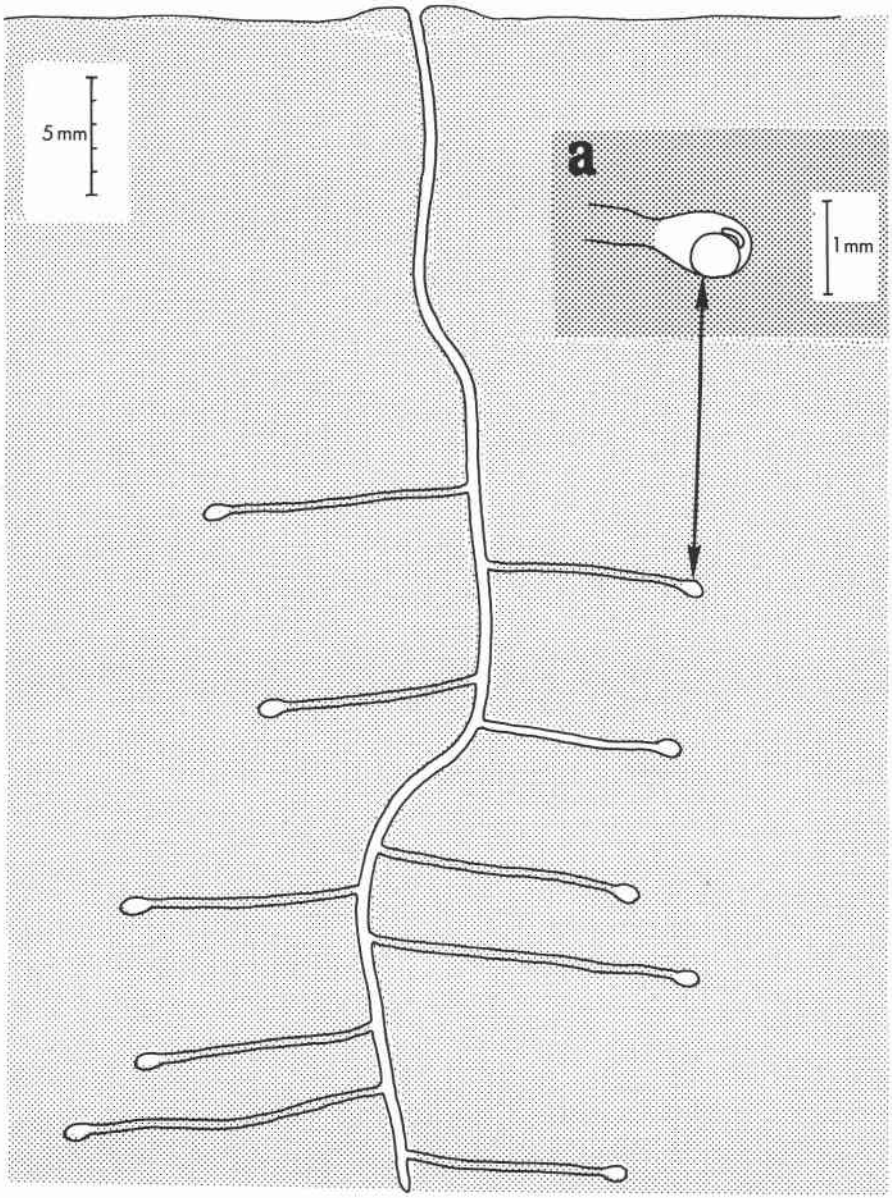


Figure 21. *A. texanus* nest, typical of solitary species of *Agapostemon*. All lateral burrows except the one under construction are filled with soil. Inset (a) shows cell with pollen ball and egg.

The vertical burrow is about 4 mm in diameter and is just wide enough to enable the female to turn around. The female is unable to turn in the slightly narrower laterals.

Each lateral is normally many times the length of its single terminal cell. This characteristic of *Agapostemon* nests is unique among North American genera of the Halictinae. In the other North American genera in the Halictinae the cells occur in clusters and/or are located immediately adjacent to the vertical burrow. The South American Halictinae closely related to *Agapostemon* dig long laterals but construct two or more linearly arranged cells at the terminus of each lateral. Sakagami and Michener (1962) reported nests of *A. nasutus* with a pair of cells at the terminus of each lateral, but extensive studies of this species by Eickwort and Eickwort (1969) revealed only a single cell at the terminus of each lateral. *Agapostemon virescens* often constructs pairs of cells with the most distal containing a female and the proximal a male.

Only one lateral is open at a time because upon completion of a cell, the lateral is packed tightly with soil. Filled laterals are nearly indistinguishable from the surrounding soil, so one must be especially careful to find each lateral and its associated cell when excavating these nests.

The cells are radially symmetrical and about 7 by 11 mm (Fig. 21). The entrance is slightly constricted and the interior of the cell is lined with a salivary secretion. This secretion dries to form a fragile film on the cell walls. After oviposition and immediately before cell closure the female adds a secretion from her anal region to the cell entrance.

Sakagami and Michener (1962) report that the Halictinae characteristically line their cells with pulverized substrate. "Cells that are excavated in the substrate (soil or rotting wood) are often if not always roughed out by the bees to a size somewhat larger than that of the finished cells. Fine soil or clay is used, often to a thickness of a millimeter or more in large cells, to make a beautifully smoothed cell lining." Extensive observations revealed that *A. radiatus, A. texanus,* and *A. splendens* do not line their cells (Roberts, 1969), and there is no evidence of cell lining in other species of *Agapostemon.*

According to the modified Iwata system (Stephen et al., 1969) the nests of *A. radiatus, A. splendens,* and *A. texanus* are classified as Od $(LCh)^n$ and the branched nests of *A. nasutus* are classified as Od $(L'(LCh)^n)^m$. The nests of *A. nasutus* are similar to those of *A. texanus* except the nest entrance is in a vertical bank. The excavating females of *A. nasutus* angle sharply downward after penetrating the bank and construct subhorizontal laterals and cells like those of *A. texanus.* Probably as a result of communal behavior, the main burrow of *A. nasutus* may

branch as many as four times and there are more laterals and cells per nest than in *A. texanus*.

Life history

The seasonal cycle of *Agapostemon* can be inferred from both label data and observations on the duration of the immature stages. The life cycle of *A. texanus* in the central United States is summarized in Figure 22.

The fall-spring generation overwinters as fertilized females and, as evidenced by a few males collected in early spring, about 0.1 percent of the fall-spring generation males survive the winter. The fall-spring females emerge from their underground hibernacula in the early spring. They begin feeding and nesting, and by the time the first cells are constructed the females have attained full ovarian development. After four or five weeks of nesting activity the fall-spring females die.

The period of subimaginal development is about 33 days at 28° C (Fig. 23). No *Agapostemon* can be found in the field until early summer when the first of the summer generation begins to emerge. The summer generation consists almost entirely of females, the diploid product of fertilized eggs. These bees begin nesting immediately but, owing to the shortage of males, a large number of females are not fertilized. As a result, the summer generation females lay many unfertilized eggs which develop into haploid males.

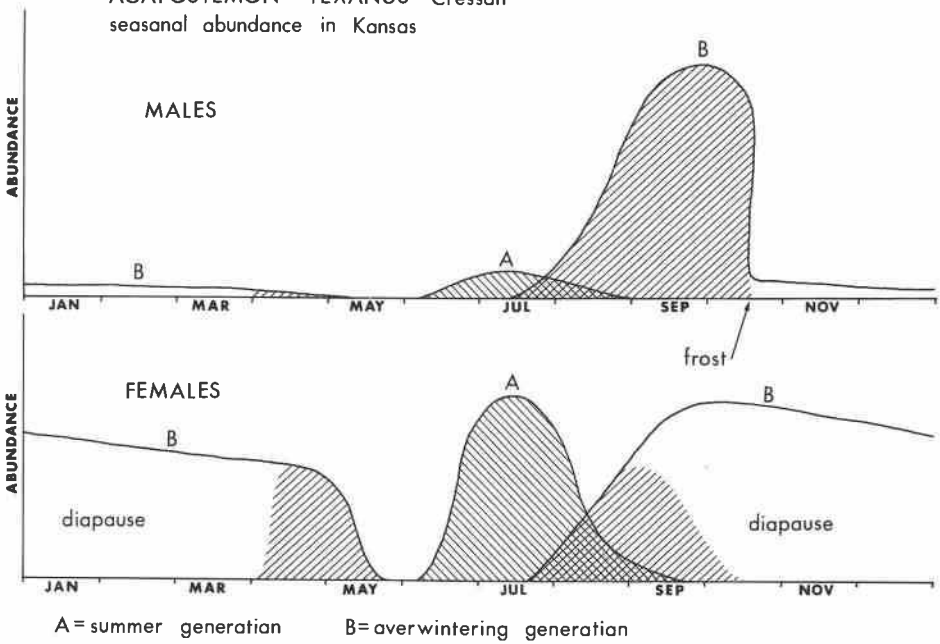
In the late summer the fall-spring generation of bees begins to emerge. For the reasons just given, a large proportion of this generation is male. These males spend all their time at flowers, where they sometimes concentrate in great numbers. The fall-spring females visit the flowers upon emergence, where they feed and are inseminated by the abundant males. Upon accumulation of fat reserves, the females enter their subterranean hibernacula (often old nests) where they spend the winter. Nearly all the males are killed by the hard frosts of late fall. It is not known whether the few males found the following spring overwinter as larvae, pupae, or adults.

Foraging

Females of *Agapostemon* are found at almost any time of day on almost any flower physically available to them. They will gather the very fine pollen of *Solanum* (Solanaceae) as well as the large spiny grains of *Opuntia* (Cactaceae), *Sida* (Malvaceae), and *Cucurbita* (Cucurbitaceae). The females usually gather most of their pollen from about 9 a.m. until noon, but in the hot, arid southwestern United States they have been recorded flying at sunset (Linsley and Hurd, 1959). In the same region

22

AGAPOSTEMON TEXANUS Cressan
seasonal abundance in Kansas



A = summer generation B = overwintering generation

23

Development of AGAPOSTEMON TEXANUS Cressan in nest

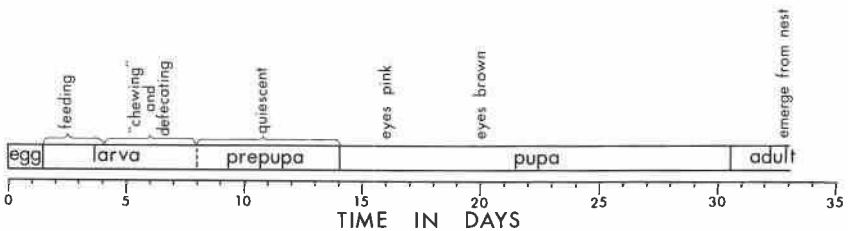


Figure 22. Graphs of relative seasonal abundance of adult males and females of *A. texanus*. Hatched areas indicate periods of adult activity; unhatched areas of curves indicate periods of adult diapause or quiescence.

Figure 23. Graph of subimaginal development of *A. texanus*.

A. melliventris has been reported visiting *Datura* (Solanaceae) at 4:56 a.m. when it was so dark a flashlight was used to examine the flowers (Linsley, 1960).

Eickwort and Eickwort (1969) reported that 96 percent of the pollen gathered by a population of *A. nasutus* was from *Sida rhombifolia* and *S. acuta* (Malvaceae), the availability of other flowers notwithstanding. As *A. nasutus* has been observed gathering pollen from many plant species in diverse families, the authors concluded that their population was exhibiting a strong constancy to *Sida* but probably was not restricted to this pollen source (not oligolectic).

Parasites and predators

There are no records of parasites or predators which are specific to *Agapostemon*. Crab spiders (Thomisidae), ambush bugs (Phymatidae), philanthine wasps (Sphecidae), and robber flies (Asilidae) have all been observed preying on *Agapostemon*.

Eickwort and Eickwort (1969) report that the fly, *Zodion americanum* (Conopidae), was abundant in the vicinity of the nests of *A. nasutus* and attacked the female bees as they returned to their nests. The conopid larvae were later found in the metasoma of some of the bees. The authors also observed the fly, *Phalacrotophora halictorum* (Phoridae), at the nest site. Female flies were seen entering the nests of *A. nasutus* but only three of 250 cells examined contained the fly larvae. A mite, *Parapygmephorus* sp. (Pyemotidae), was "omnipresent" in the nests of these bees but seemingly did not adversely affect the bees. Mites are often present on pinned specimens of *Agapostemon*, but it is not known whether the mites show any specificity for the bees.

The triungulin larvae of blister beetles (Meloidae) are common on adults of *Agapostemon*, and the author has found the coarctate larva of a blister beetle in a cell of *Agapostemon texanus*. Strepsipterans, common parasites of the Halictinae, were conspicuously absent from the more than 50,000 specimens of *Agapostemon* examined.

The parasitic bee *Sphecodes* has been reported (Stephen et al., 1969) sharing the hibernacula of *A. virescens* females. It seems likely that this parasite of halictine bees attacks *Agapostemon*.

Intraspecific interaction

As mentioned earlier, some species of *Agapostemon* nest in aggregations but none are known to be social, semisocial, or quasisocial (Michener, 1969). However, *A. nasutus*, an aggregatory species, is known to be communal in the sense that several females may inhabit a single burrow, although each builds cells, provisions them, and oviposits independent of the activities of others. In *A. virescens*, also an aggregatory species, more

than one female will occupy a burrow, so it is reasonable to assume that this species is communal also. *Agapostemon radiatus, A. splendens,* and A. *texanus* females are solitary and will not allow another bee to share their nests once they have begun to construct cells. However, diapausing females seem to prefer to share a common hibernaculum.

Interestingly, there is a strong positive correlation between the tendency to nest in aggregations and the tendency to occupy communal nests (*A. nasutus* and *A. virescens*). Those species known to be strictly solitary (e.g., *A. texanus*) are not known to have communal nests.

Literature Cited

Bohart, G. E. 1950. Observations on the mating habits of halictid bees. Pan-Pacific Ent., *26*:34-35.

Eickwort, G. C., and K. R. Eickwort. 1969. Aspects of the biology of Costa Rican halictine bees, I. *Agapostemon nasutus* (Hymenoptera: Halictidae). Jour. Kansas Ent. Soc., *42*:421-452.

Felt, E. P. 1928. Observations and notes on injurious and other insects of New York state. New York State Mus. Bull., *274*:145-176.

LaBerge, W. E., and D. W. Ribble. 1966. The nests and larvae of two species of *Agapostemon* (Hymenoptera:Halictidae). Jour. Kansas Ent. Soc., *39*:467-472.

Linsley, E. G. 1946. Insect pollinators of alfalfa in California. Jour. Econ. Ent., *39*:18-29.

Linsley, E. G. 1960. Observations on some matinal bees at flowers of *Cucurbita, Ipomoea* and *Datura* in desert areas of New Mexico and southeastern Arizona. Jour. New York Ent. Soc., *68*:13-20.

Linsley, E. G. 1962. Sleeping aggregations of aculeate Hymenoptera-II. Ann. Ent. Soc. Amer., *55*:148-164.

Linsley, E. G., and P. D. Hurd. 1959. Ethological observations on some bees of southeastern Arizona and New Mexico (Hymenoptera:Apoidea). Entomol. News, *70*:63-68.

Michener, C. D. 1969. Comparative social behavior of bees. Ann. Rev. Entomol., *14*:299-342.

Plateaux-Quénu, C. 1959. Un nouveau type de société d'insectes: *Halictus marginatus* Brullé (Hymenoptera, Apoidea). Année Biologique, 35:325-444.

Roberts, R. B. 1969. Biology of the bee genus *Agapostemon* (Hymenoptera:Halictidae). Univ. Kansas Sci. Bull., *48*:689-719.

Roberts, R. B. 1972. Revision of the bee genus *Agapostemon* (Hymenoptera:Halictidae). Univ. Kansas Sci. Bull., *49*(9):437-590.

Sakagami, S., and C. D. Michener. 1962. *The Nest Architecture of the Sweat Bees.* Univ. Kansas Press, Lawrence.

Stephen, W. P., G. E. Bohart, and P. F. Torchio. 1969. *The Biology and External Morphology of Bees with a Synopsis of the Genera of Northwestern America.* Agric. Expt. Sta., Oregon State Univ., Corvallis.