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Observations on the nests of Costa Rican Halictus with taxonomic notes on Neotropical species (Hymenoptera: Halictidae)

by

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This paper consists of descriptions of nests of the two species of Costa Rican burrowing bees of the genus *Halictus* (subgenus *Seladonia), H. hesperus* and *H. lutescens,* together with taxonomic observations on the three neotropical species of the subgenus. The observations on *H. hesperus* were mostly made from February 25 to March 20, 1954. Data on *H. lutescens* were gathered from June 23 to 26, 1963.

Division of labor between the authors was as follows: one of us (A. W.) was involved in all the field work. The other was involved in the field work of 1963 and is responsible for the taxonomic section and the preparation of the manuscript.

NESTS AND LIFE CYCLE

SEASONAL CYCLE: All observations were made in the lowland parts of the province of Guanacaste, Costa Rica. This is a relatively arid savanna region with dry gallery forest along the streams. The dry season is from mid-December to May.

In February and March, 1954, *H. hesperus* was found to be extremely active provisioning cells. The nests contained young of all ages. Local inhabitants reported an extreme abundance of bees (probably males) flying over

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the sites in May. In August, 1962, we returned to the area and found no *Halictus*, either in nests or on flowers. In February, 1963, only a few nests were found, compared to the thousands that had been present in 1954, but in these the bees were active and provisioning cells. On June 25, 1963, we again returned to the same place. Although burrows were present, they were largely filled with soil and no *Halictus* were seen.

The nests of *H. lutescens* studied in June, 1963, contained many bees, some flying to flowers. All the bees were worn and all cells were empty or earth-filled.

These data suggest that both species are active during the dry season, probably terminating their activity with production of large numbers of sexual individuals in May. During the wet season, activity appears to be minimal, although in June some *lutescens* fly in and out, feed, and even carry pollen on the scopa.

The subgenus *Seladonia* is primarily an Old World group with a number of nearctic species. The neotropical species must be derived from nearctic ancestors. The adaptation of this temperate climate, sun loving insect to tropical conditions appears to have been by the limitation of reproductive activity to the dry season through ovarial diapause in the wet season.

NESTING SITES: *Halictus hesperus* nests were found in flat sandy ground along the west bank of the Río Tempisque, 7 miles southwest of Filadelfia, Guanacaste. The aggregation of nests extended along the river for several hundred meters, mostly in sunny areas of bare soil and grazed short grass. Since the nests were located only a few meters above the usual river level and just behind the steep river bank, they were covered by floods every year or so.

Another group of nests was found about one mile west of Filadelfia in bare soil along a little-used road somewhat farther from the river. Scattered nests were also common, and have been observed elsewhere, e.g., by Michener in a path near El Valle de Antón, Coclé Province, Panamá. FRIESE (2) recorded nests in a path at San José, Costa Rica (under the synonymous name *schmidti)* and COCKERELL (1) recorded nests in a road at Zamorano, Honduras (under the name *hondurasicus)*.

Nests of *H. lutescens* were scattered in the bare, flat, somewhat sandy soil of a little-used dirt road, about one half mile from the shore, at Playa del Coco, Guanacaste.

NESTS: Nests are of the same basic style as other *Seladonia* and most *Lasioglossum (Dialictus),* i.e., a branching burrow with sub-horizontal cells opening into the main burrow or its branches, type IIIb of SAKAGAMI and MICHENER (7). A few data on nests of *H. hesperus* were given by these authors, based on the unpublished notes made by one of us (A.W.) and H.V. Daly in 1954.

In *H. hesperus,* the nest entrance is constricted, about 2.5 mm in diameter at the soil surface, enlarging below to the burrow diameter of about 4 mm. The upper 15 mm or so of the burrow, that is, the entire part that is tapering from the usual burrow size to the narrowest part at the soil surface, is lined

with a thin, white, secreted material like that applied to nest entrances by *Lasioglossum versatum* (MICHENER, 4).

The branching pattern of the nests of *H. hesperus* and the positions of cells are shown in Figures 1 to 4. In March, 1954, in the midst of the dry season, there was usually a gradient from older cells above to younger ones below, as would be anticipated if the bees construct cells at progressively deeper levels as the surface soil dries. The deepest nest reached a depth of 81 cm (measured in a straight line). In all nests there were cells under construction or containing eggs and young larvae almost to the very bottom, an unusual feature unless the lowermost extremities of the burrows were missed. Cells are 9 to 10 mm long, abount 4 mm in diameter, shaped as is usual in related halictines, and closed with loose soil after egg laying. The food mass is the shape of a flattened sphere 3.5 mm in maximal diameter, topped by the usual curved egg, 2 mm long.

The nest entrances of *H. lutescens* were, at least in June, not constricted but enlarged to a diameter of about 6 mm toward the surface. Elsewhere burrow diameters were 4.5 to 5.0 mm.

The pattern of nests of *H. lutescens* is shown in Figures 5 and 6. No cells were in use in June (early wet season) but old cells were found at depths ranging from 10 to 140 cm. One nest showed much recent excavation in the intricate and often anastomosing branches 15 to 25 cm deep, as shown by the soil of the large tumulus (5 cm in diameter, 2 cm high) which came from that level. Although bees were found in the main burrow, many were also found in the branches, which are probably equivalent to the hibernaculae of temperate climate species. It seeems likely that new cells would have been constructed at that level at the beginning of the dry season or before, and that the level of cell construction would descend during the dry season. Dimensions of the old cells were 9 to 11 mm long, 4.5 to 5.0 mm in diameter.

NEST POPULATIONS: Although within the subgenus there are both solitary and social species (SAKAGAMI and FUKUSHIMA, 6), the Costa Rican species of *Seladonia* live in colonies. The scanty information available indicates that these colonies are primitively social.

Four nests of *H. hesperus* were opened on March 14 and 20. They had been active since before February 25, and contained young of all ages, from eggs to pupae. The scarcity of egg-layers and of young unworn bees in the nests is remarkable, but may be due to the difficulty experienced in following the nests. Because of lack of plaster of Paris, the extremities of the nests might have been missed. The numbers of adult females (no males) recovered from a nest varied from 13 to 60 with a total of 151 for four nests. The amount of activity per nest was enormous. Bees passing an entrance (in plus out) per hour ranged as high as 165 and the hourly average in 15 morning hours of observation was 54. Most of the individuals had mandibles much to very much worn (terminology of MICHENER and WILLE, 5), 3% had them well worn, 18% slightly worn, and 1% unworn. Thus most of the bees taken from the nests had been active in nest excavation. Of 146 bees from the four

nests, 73% had slender or very slender ovaries, 25% had slight enlargements posteriorly or one or two large oöcytes (as in group C of MICHENER and WILLE, 5), and two individuals (1.4%) had greatly enlarged ovaries with several almost full-sized eggs. Only the last two had sperm cells in the spermathecae. Thus of the 146 bees, only two were queens. Wing length varied from 4.9 to 6.3 mm; the most frequent size class was 5.2. The largest worker had a wing length of 5.6 mm; one queen was 6.3 but the other was, like most workers, only 5.2 mm in wing length. Even the large queen (unfortunately not preserved) showed no extraordinary cephalic development, nor do any of the field-collected specimens from Central America (SAKAGAMI and MOURE, 8).

These data for *hesperus* in the dry season show the large size of the colony and an abundant and probably physiologically distinct worker caste. Unless the deepest parts of the nests were missed and queens thereby lost, many queens must have died by mid-March, and most of the egg-laying must have been by unfertilized workers, of which about 13% had one or two well shaped and normal looking developing eggs.

The nests of *H. lutescens* opened on June 23 also contained large populations of adult female bees, and few males. The number of females from the only two nests fully opened for study were 33 and 342. Of these, 108 were dissected. Most (89%) had mandibles much to very much worn but 11% had them well worn. Thus all had worked at excavation. Most had wings not or little worn but 19% had eight or more nicks on the distal margins of the two fore wings. No meaningful relation could be discerned between wear and internal organs. Of the 108 dissected bees, 73% had slender ovaries (none very slender, like freshly emerged adults) and 26% had somewhat enlarged ovaries with one to several rather large oöcytes, almost always somewhat irregular in shape or with dark areas (when fixed in Kahle's solution) as though resorption were in progress. One individual (1%) had several oöcytes developing in each ovary. This bee had an oöcyte 1.79 mm long (approaching the size of an egg). A few others had one oöcyte each nearly that long, but in most the oöcytes were much smaller.

Of the 108 bees, 68% were unfertilized, 31% fertilized with sperm cells in the spermatheca. Ovarian size varied within both fertilized and unfertilized bees but slender ovaries were commoner among the unfertilized than among the fertilized indivuals, being found in 60% of all unfertilized bees and 41% of fertilized ones.

These data on *H. lutescens* in the wet season show large colony size and an abundance of workers, just as for *hesperus* in the dry season. Assuming that the life cycles of the two species are similar, one could easily imagine the wet season condition arising from that of the dry season through cessation of reproductive activity and fertilization of more females, a likely occurrence if many of the young produced in March were progeny of the unfertilized egg layers and therefore males.

TAXONOMIC NOTES

This section is provided to clarify the status of the four known Neotropical species of the genus *Halictus.* One, with no greenish coloration, is *H. (Halictus) ligatus* Say, a primarily North American species which ranges through Central America to Colombia (SANDHOUSE, 9). The other three species are all greenish forms of the subgenus *Seladonia,* a group which was included in *Halictus s. str.* by Sandhouse.

Names here applied to the three neotropical *Seladonia* are as follows: *hesperus* Smith, 1862, ranging from Mexico to Colombia; *lanei* (Moure, 1940) from Pará and Maranhão to Mato Grosso and Goiás, Brazil; and *lutescens* Friese, 1921, from México to Costa Rica. The first species is the one listed under the synonymous name *agilis* Smith by SANDHOUSE (9); the synonymy was indicated by MICHENER (3). The other two species, *lanei* and *lutescens,* were incorrectly placed in the synonymy of *hesperus* by SAKAGAMI and MOURE (8), although MICHENER (3) excluded both from the synonymy of *hesperus.*

H. lanei differs from the other species by its smooth and shining mesoscutum, the punctures being separated by more than a puncture width. The propodeal enclosure is transversely striate, more finely so than in *hesperus.* The male is not known to us.

The sympatric species *H. hesperus* and *lutescens* agree in the more densely punctate mesoscutum with punctures separated by less than a puncture width. They also agree with one another, and differ from nearctic species, in having an apical filament on the male gonostylus. The metasomal terga of the male are not constricted basally nor are the tergal margins depressed. The sixth metasomal sternum of the male has a weak longitudinal depression and the posterior margins of the fourth and fifth are slightly concave in both species. The two species differ from one another as indicated in Table 1 and Figs. 7 to 10. The known localities for each are shown in Figs. 11 to 12. Both occur from sea level to at least 1260 m, occurring together at that altitude 8 miles southeast of Tehuitzingo, Puebla, Mexico. The two species also occur together at various other localities.

Dr. E. Königsmann (personal communication, March 17, 1969) wrote that he could not find the type of *lutescens* in the Zoologisches Museum, Humboldt-Universität, Berlin. However, a specimen from San Mateo, Costa Rica, in the American Museum of Natural History, is labelled "Typus" with Friese's identification label, "*Halictus schmidti* v. *lutescens* Fr." There is no reason to question the identification.

TABLE 1

Differentiating characters of H. hesperus *and* H. lutescens

	hesperus	*lutescens*
Propodeal enclosure	transversely striate medially	irregularly roughened
Hypostomal carina	elevated posteriorly, in some ♀♀ forming triangular tooth	uniform, low
Metasomal color (margins of sclerites translucent in both)	black, rarely partly or largely reddish-yellow	reddish-yellow with blackish spots at sides of terga, or black with rear halves of terga reddish-yellow, rarely all black
Antenna ♂	segment 4 = 5	segment 4 shorter than 5
Sternum 4 of ♂	posterior margin bare medially	posterior part hairy throughout
Sternum 7 ♂, apex	bare, produced and narrowly rounded	hairy, more attenuate
Ventroapical lobe of gonocoxite, ♂	attenuate, with 1-2 hairs at tip	nearly absent
Gonostylus, ♂	Figs. 7-8	Figs. 9-10

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SUMMARY

This paper consists of descriptions of the life cycle and nest structure of the two known species of Costa Rican bees of the genus *Halictus* (subgenus *Seladonia), H. hesperus* and *H. lutescens*. All observations were made in the

lowland parts of the province of Guanacaste, Costa Rica, which has a dry season from mid-December to May. Although our observations on *H. hesperus* were largely carried out in the dry season and on *H. lutescens* entirely in the wet season, the life histories of the two species are presumably similar. Activity is largely in the dry season, with large colonies containing many workers and probably with extensive male and gyne production late in the dry season. The wet season is seemingly passed in a state of ovarian diapause in the nests, the bees making occassional feeding trips and excavating lateral burrows, however, at least in the case of *H. lutescens*.

The four known neotropical species of *Halictus* are distinguished in a taxonomic section and the distributions of the two Middle American species of the subgenus *Seladonia* are mapped.

RESUMEN

De las cuatro especies conocidas de abejas neotropicales del género *Halictus*, una de ellas, *H. (Halictus) ligatus*, de color oscuro, se extiende de Norte América a Colombia. Las otras tres especies son de color verdusco y pertenecen al subgénero *Seladonia: H. lanei* se encuentra en Brasil, *H. hesperus* de México a Colombia y *H. lutescens* de México a Costa Rica. El presente trabajo es un estudio de los nidos y ciclo de vida de estas dos últimas especies de *Seladonia*. Las observaciones se efectuaron en Guanacaste, Costa Rica. Se encontró que el ciclo de vida de ambas especies es muy parecido; la actividad de las colonias se lleva a cabo principalmente durante la estación seca (diciembre a mayo) y las formas sexuales se producen, al parecer, al final de dicha estación. Durante la estación lluviosa las abejas se encuentran en un estado aparente de diapausa ovárica; sin embargo, al menos en *H. lutescens*, las abejas salen a veces a alimentarse y excavan ramas laterales en sus nidos.

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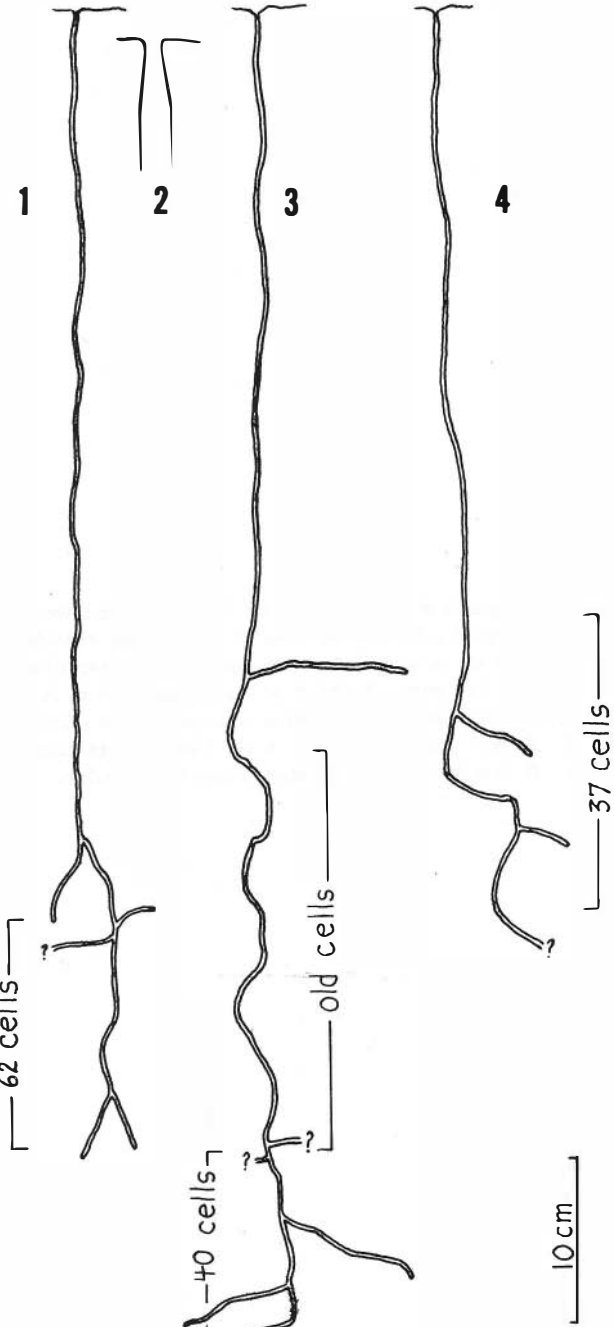
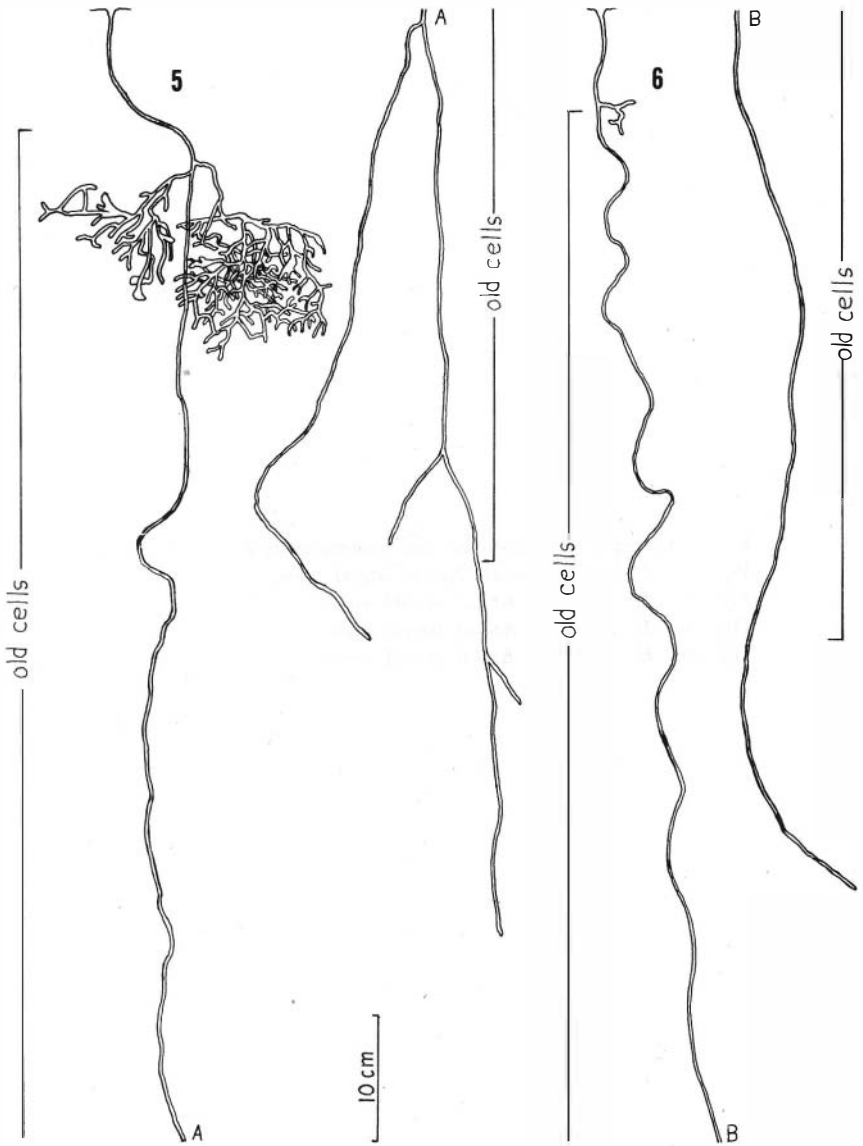
Figs. 1-4. Diagrams of nests of *Halictus hesperus.*
Fig. 1. A nest from which 13 adult females were taken.
Fig. 2. Nest entrance.
Fig. 3. A nest from which 54 adult females were taken, showing old, earth-filled cells.
Fig. 4. A nest from which 25 adult females were taken.


1
2
3
4
62 cells
40 cells
old cells
37 cells
10 cm

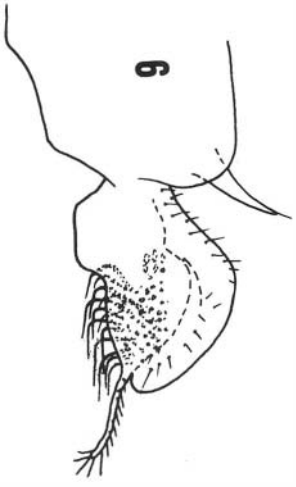
Figs. 5-6. Diagrams of nests of *Halictus lutescens*. There were no occupied cells, but locations of old, mostly earth-filled cells are shown. Each of the two nests is shown divided into two parts: A and B at the top match with A and B at the bottom of the figure to connect the sketches.

Fig. 5. A nest from which 342 adult females were taken.

Fig. 6. A nest from which 33 adult females were taken.


5
old cells
A
A
old cells
10 cm
6
old cells
B
B
old cells

Figs. 7-10. Apex of gonocoxite and gonostylus of male.
Fig. 7. *Halictus hesperus*. Apical lateral view.
Fig. 8. *H. hesperus*. Apical dorsal view.
Fig. 9. *H. lutescens*. Apical lateral view.
Fig. 10. *H. lutescens*. Apical dorsal view.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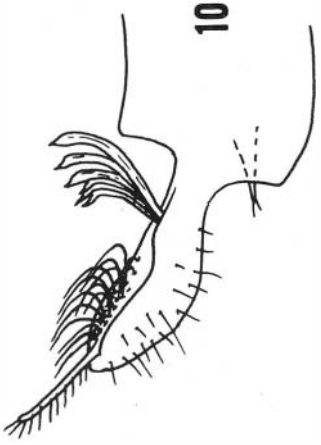
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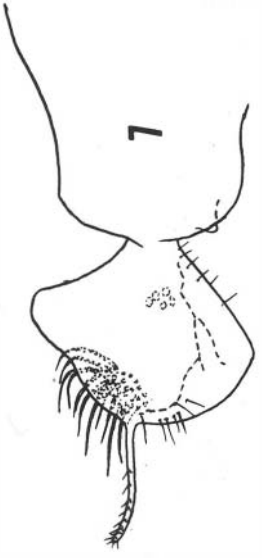
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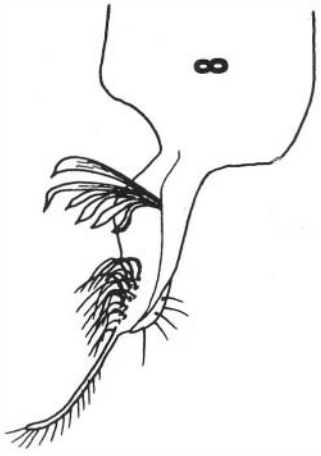
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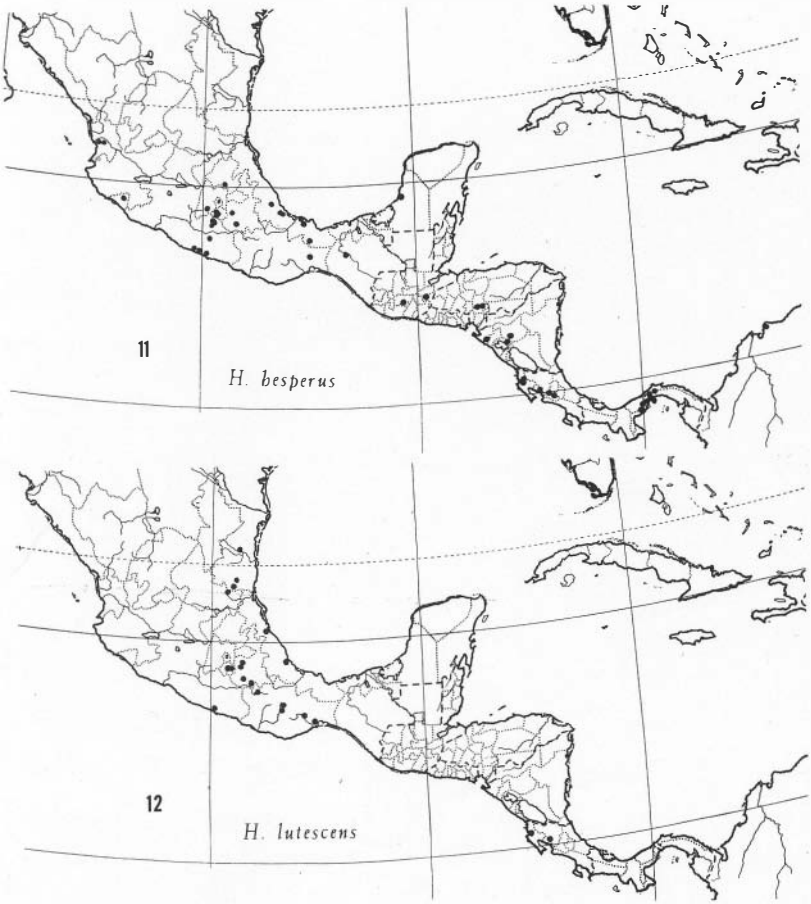
Figs. 11-12. Distribution of *Halictus hesperus* and *H. lutescens* based on specimens examined.


11
H. besperus
12
H. lutescens