

Apiolela Halictidae

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**NESTING HABITS AND OTHER NOTES ON AN INDO-
MALAYAN HALICTINE BEE, *LASIOGLOSSUM ALBESCENS*
WITH DESCRIPTION OF *L. A. IWATAI* SSP. NOV.
(HYMENOPTERA, HALICTIDAE)**

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NESTING HABITS AND OTHER NOTES ON AN INDO-MALAYAN HALICTINE BEE, *LASIOGLOSSUM ALBESCENS*,
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The sweat bees or Halictinae are one of the most dominant bee groups throughout the world, in numbers of both species and individuals. The recent advance on the comparative study of this group has revealed their unusually rich biological diversity (Sakagami and Michener, 1962). In this group, both solitary and social species are found side by side within the same genus or even subgenus. Their nest patterns are quite variable, showing successive steps of ethological evolution. However, the number of species, the biology of which was more or less studied, is still insufficient in comparison with the enormous number of species involved. Moreover, biological studies of this group have been published with a marked geographical imbalance. While there are a number of detailed studies upon the Holarctic and Neotropical species, only a few items of information have so far been reported from the vast extent of the Palaeotropical Regions. When I published, with Prof. C. D. Michener, a review on the nest architecture of this group, we could cite only a brief sentence by Maxwell-Lefroy and Howlett (1909): "*Halictus* is a small bee with many hill species, and a few plains ones which nest in wet soil". Recently, Batra (1966) published her observations made in Punjab and Mysore, India, on the nesting habits and social structure of 12 species. In the same year, Sakagami and Wain (1966) reported the queen-worker differentiation in an Indian species, *Halictus (H.) latisignatus* Cameron. This is virtually all the information so far published as to the biology of the Indo-Malayan species. Nevertheless this region has a number of species, many of which represent endemic groups and a comparative study of these is indispensable to obtaining a broader perspective of the biology of halictine bees.

In September, 1966, I stayed at Fraser's Hill Gap at the boundary of the States of Selangor and Pahang, Malaya to study wasp biology. During this stay, I discovered a nest aggregation of *Lasioglossum (Ctenonomia) albescens sepulchralis* Cameron and made some obser-

* Zoological Institute, Hokkaido University, Sapporo, Japan. Contributions from OCUSEA, 1966, No. 1, Entomological Group, No. 1, and Contributions No. 795 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

vations. The result is incomplete because of the limited time but is recorded in the present paper, first of all, in order to call to attention of resident entomologists to this interesting bee group. Some notes on the morphology and variation of the *L. albescens* complex are also given.

Nesting habits

NEST SITE: The nest aggregation was found on a well isolated steep slope (ca. 70°) along the road ascending from Kuala Kubu Bharu, Selangor, to Fraser's Hill, only a few hundred metres distant from the state boundary. The road side slopes were densely covered with thick herb carpets, but the cover was relatively sparse at the nesting site, about 3 x 2.5 m.sq. Within this area, about 30 nests were counted. Females was seen foraging in both morning and afternoon although activity was less intense in the latter. In many instances, several females, up to five, each carrying pollen loads on legs, were seen to enter a single nest, indicating the occupation of one nest by more than one female. At the same time, many males were flying to and fro over the nesting site and seeking the females. Actual copulation was observed only once. A male landed on and grasped a female resting on a leaf. The duration of copulation was brief, only a few seconds as in many other halictine species. Such synchronous occurrence of foraging and mating activities is not common in the temperate species.

NEST STRUCTURE: For lack of sufficient time, only four nests were excavated. The soil was brittle with an abundant admixture of pebbles, so that the nest pattern was traced completely only in one nest (Figs. 1, 2). But, combining all the data, the nest structure can be described accurately.

As in most other halictine species, the entrance is constricted to 3–3.3 mm in diameter, with no turret or special vestibule chamber. Soil excavated by bees forms, because of the sloping site, an excentric and elliptical tumulus around the entrance (Fig. 2). The main burrow descends obliquely, or at first obliquely then vertically, with irregular bends. The burrow was 4.5–4.8 mm in diameter, with smoothed but not particularly elaborated walls. The end of the lower blind burrow was 25 cm in vertical depth in one nest (Figs. 1, 2), and deeper in two other nests. In another nest, the main burrow showed a bifurcation at about 20 cm in depth and the ends of the two branches were respectively 25 and 30 cm in depth.

The cell arrangement is parodalous (Malyshev, 1935, or type II, 0(LChⁿ)^m (m>1), in Michener and Sakagami, 1962), (i.e., several

laterals are excavated in the walls of the main burrow), and a linear series of cells are constructed, starting from the end of the lateral. The order of construction is known from the immature individual in each cell; these are always older in the terminal cells. Only one uncompleted lateral was observed among four nests examined (Figs. 1, 2, uppermost lateral). In all nests examined, the upper one third or half of the main burrow was free from laterals and the lowest part formed a blind burrow, which is characteristic in halictine architecture. Laterals are more or less perpendicular to the axis of the main burrow, issuing radially. The length of each lateral is determined by the cells it contains, reaching 4.5–5 cm when three cells are made. The number of cells per lateral was: 2 cells (9 cases), 3(8), 5(1). The arrangement of cells is mostly linear (Fig. 3), occasionally winding (Fig. 4), or bent at right-angles (Fig. 5). Ramification was observed only in one instance (Fig. 6).

Each cell is 8.5–9 mm in length, 4.9–5.4 mm in maximum diameter and *ca.* 3 mm in neck diameter, with the shape as in other halictine species, the upper side being convex and the bottom flatter, but the latter feature is not so conspicuous as in other species, rather giving an impression of radial symmetry. The inner walls are smooth with a thin waxy lining. Pollen balls (Figs. 6, 7) are 4–5 mm in diameter and about 4 mm in height, spherical, with a rather flat top and the lower half mildly convergent; the texture is softer than in any other species so far observed by me. Eggs are about 2.4–2.5 mm long, the egg index is 0.92, (i.e., medium sized (*cf.* Iwata and Sakagami, 1966)). In cells with post-defaecation larvae or pupae, the faecal mass is deposited thickly at the end of the upper wall (Fig. 7). The distance between two successive cells within a lateral is 2–3 mm; this gap is filled with soil. The distance between the wall of the main burrow and the first, that is, the youngest cell, of the series, is 4–10 mm, mostly filled with soil. But in two cases, in which the laterals were open to the main burrow, the diameter was about 4.2 mm, slightly narrower than that of the main burrow but wider than the neck diameter of cells (Fig. 8).

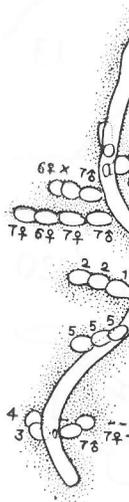
SOCIAL PATTERN: As already mentioned, the occupation of the same nest by several females was confirmed. In the four nests excavated, I found only 3, 2, 3 and 1 females respectively. The figures obtained are smaller than the actual number per nest indicated by the entry of foraging females, because only one nest was completely examined. Moreover, the excavation was made in daytime, so that some bees were certainly out of the nests. Among these females one individual possessed intact mandibles and wings, still rudimentary

ovaries and an empty spermatheca, indicating her recent emergence. Another female had intact mandibles and wings but was already inseminated and had slightly developed ovaries. All other females had more or less worn mandibles and wings, fully developed ovaries (in all individuals more than one ovariole contained a well to fully developed oocyte), the spermatheca full of sperms, and was carrying a trace of pollen particles on the hind legs. These features indicate that they were performing both reproductive and foraging activities and were equivalent in social status, without showing any sign of caste differentiations.

As the excavation of further nests was impossible, the females carrying pollen loads and returning to the nest site were swept by net. The result of the examination of these 23 individuals was the same as that described above. In all individuals, both mandibles and wings were more or less worn, more than one ovariole of each ovary with mature or submature oocyte, and all were inseminated. The variation in size among females was measured. As given below, the distribution of head width shows no positive evidence for the occurrence of even incipient caste differentiation: 2.15–2.20 mm (2 ♀ ♀), 2.21–2.25 (2), 2.26–2.30 (0), 2.31–2.35 (2), 2.36–2.40 (6), 2.41–2.45 (11), 2.46–2.50 (3), 2.51–2.55 (1), 2.56–2.60 (1). The evidence suggests that each nest was occupied by several equivalent females, each of which performed both oviposition and foraging, a relatively incipient stage in the social evolution in halictine bees.

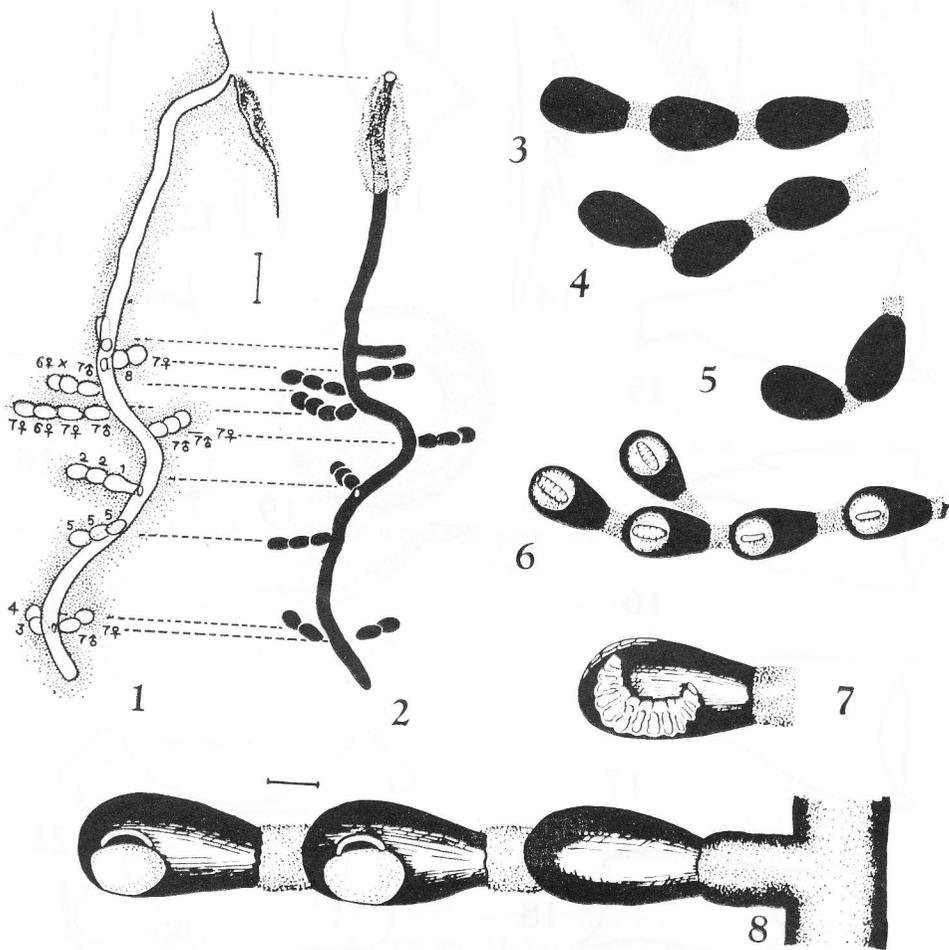
It is unknown how the laterals within the same nests are divided among nest mates. As noted above, the number of cells per lateral is generally two to three. As most halictine bees make more than three cells, and oviposit in each of them, within one brood rearing period, the completion of more than one lateral by each female is plausible.

The immature individuals found in the same lateral were, as shown in Fig. 1, mostly of the same stages or nearly so. This suggests that, if a single female makes more than one lateral, she makes them successively, not synchronously. In Fig. 1, five laterals are of earlier completion, and contained mostly young adults. It is possible that these laterals were constructed by five females of which two or three of them made a second lateral. Of course this assumption becomes invalid if more than one female shares the same lateral. There is no direct evidence to reject this possibility but it may be less plausible, judging from the bionomics of some other species (Michener and Lange, 1958; Sakagami, Hirashima and Ohé, 1966).



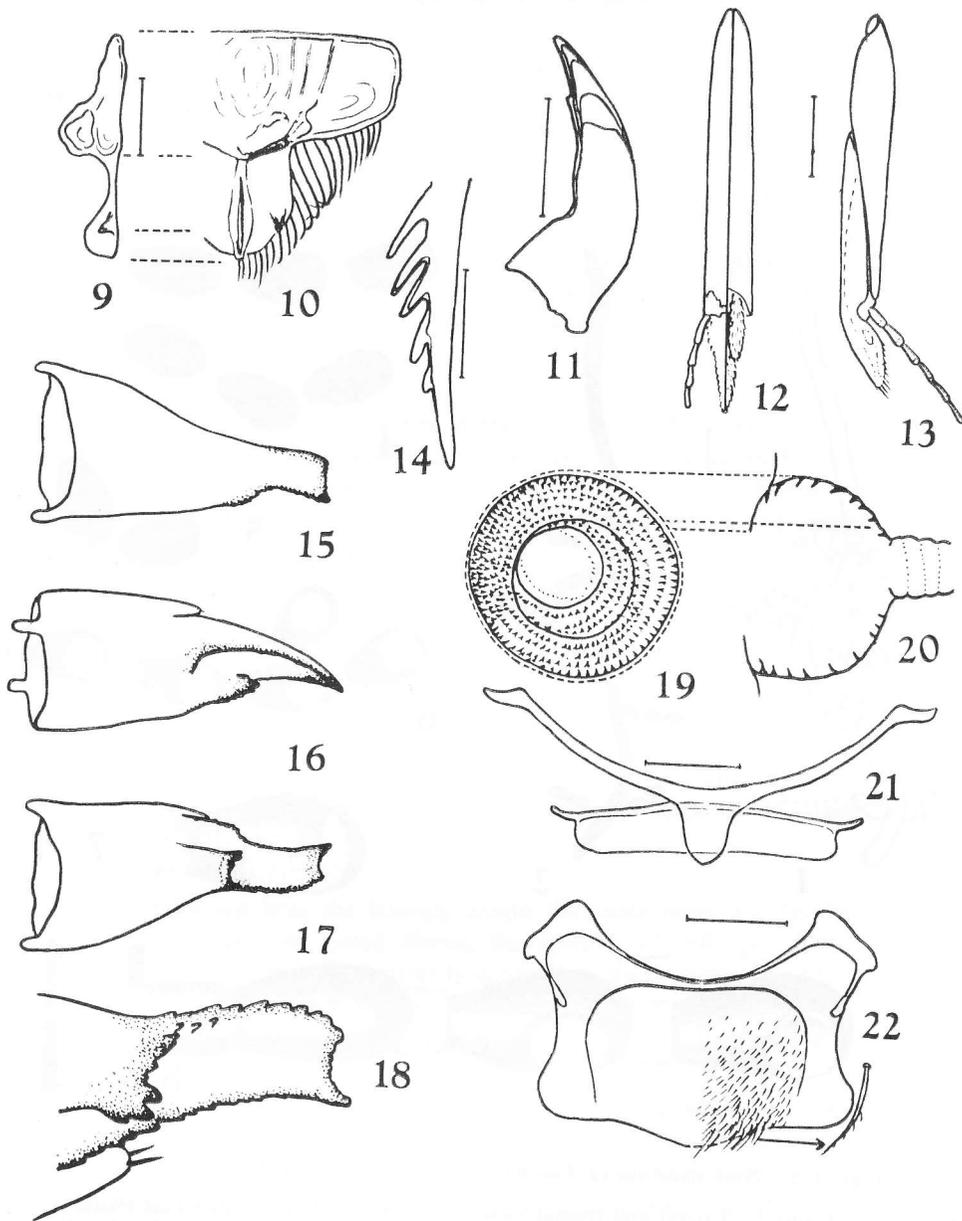
Figs. 1-8

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Figs. 1-8. Nest structure of *Lasioglossum albescens sepulchralis*.

1 and 2. Lateral and frontal views of a completely excavated nest (Scale = 2 cm). Numerals indicate immature stages contained: 1. Empty, lined cell, 2. Egg, 3. Small larva, 4. Large feeding larva, 5. Post-defaecation larva, 6. Pupa, 7. Pre-emergence adult, 8. Cell after emergence (X. De-composed). 3-6. Various types of cell arrangement in a lateral (Eggs and small larvae on pollen balls are shown in Fig. 6). 7. Cell with post-defaecation larva. 8. Lateral burrow with three cells, two with eggs on pollen balls, one still before oviposition (Scale = 0.25 cm).



Figs. 9-22. Some morphological features of *Lasioglossum albescens sepulchralis*.

9-10. Lateral and frontal views of female labrum (Scale = 0.2 mm). 11. Female mandible (Scale = 0.5 mm). Thin inside contours indicate various degrees of wear. 12. Female labium (Scale = 0.5 mm), seen from below (left) and above (right). 13. Female left maxilla. 14. Female inner hind tibial spur (Scale = 0.25 mm). Outer and inner contours show the variation range. 15-17. Dorsal, lateral and ventral views of larval mandible. 18. Apex of larval mandible. 19-20. Larval spiracle seen from above and profile. 21. Male metasomal sterna VII and VIII (Scale = 0.25 mm). 22. Male metasomal sternum VI (Scale = 0.5 mm).

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REMARKS ON BIOLOGY: Recently Batra (1966) described a single nest of *L. albescens* (Smith), probably the typical form, from Ludhiana, Punjab. Her findings differ from mine in the following two points: 1) The nest was occupied by a single female. 2) The nest pattern was heterodalous (= branched) and of the subtype IIIa, 0(LCh)ⁿB of Sakagami and Michener (1962) i.e., each cell is independently made, not forming a linear series, and each is connected to the main burrow by a narrower lateral).

The first discrepancy is easily understood. The nests of even socially more advanced species are usually founded by a solitary female. The second difference is more important, because the nest patterns of halictine bees are usually more or less similar among related species. The description and figure by Batra clearly show the heterodalous nest as in some species of *Lasioglossum* s. str. Leaving the solution for the future, I shall here enumerate some possible interpretations: (1) The nest pattern of *L. albescens* group is, like its morphological plasticity (see below), variable among even closely allied forms. Such an instance is seen in *Halictus* s. str., but the difference is greater in the present case. (2) Heterodalous and parodalous nests are, though quite different in the architectural plan, not so remote concerning the behaviour mechanism which is responsible for the realization of various nest patterns. In such case, closely allied species could make rather different nests. (3) The halictine nest patterns can sometimes transform rapidly, unaccompanied by any corresponding morphological change.

Further comparative data are clearly required. On this occasion, one important but often overlooked characteristic must be mentioned. The diameter of the lateral is decisively narrower than that of the main burrow in the heterodalous nests (for instance, each 2.7–3.0 mm and 4.5–5.5 mm in *L. albescens*, Batra, and in many other species, cf. Sakagami and Michener), while not so in parodalous nest (for instance, 3.5–4.5 mm and 4.5–5.5 mm in *Pseudagapostemon divaricatus* (Vachal), a parodalous nest-making species, Michener and Lange, 1958).

Up to the present, parodalous halictine nests are known only in the species belonging to *Agapostemon* and allied groups, all inhabiting the Western Hemisphere: *Agapostemon nasutus* Smith, Costa Rica; *Pseudagapostemon divaricatus* (Vachal), *P. perzonatus* (Cockerell), both South Brazil and *Ruizantheda mutabilis* (Spinola), Chile. Therefore, the discovery of this nest pattern in an Indo-Malayan species is interesting as an instance of parallel evolution. There is one slight difference between the nests of *L. albescens sepulchralis* and the New World species mentioned. In the latter, especially in *Pseudagapostemon*,

the distance between the final cell of each series and the main burrow is quite long, while in *L. a. sepulchralis*, the final cell is separated from the main burrow by a distance shorter than the length of each cell. It is open to further studies whether this difference is essential or not.

In the last mentioned three New World species, the occupation of one nest by more than one female is recorded, each inseminated and with developed ovaries. Their social pattern is therefore similar to that in *L. a. sepulchralis*, that is, the common use of one nest by several equivalent females. The same social pattern is also known in *Lasioglossum (Evylaeus) ohei* Hirashima & Sakagami, a Japanese species making heterodalous nests (Sakagami, Hirashima and Ohé, 1966).

Additional notes on morphology

L. albescens and allied forms are one of the most dominant and wide-spread groups in the Oriental Region. Their diagnostic characteristics have so far repeatedly been described. In reply to the recent opinion by Michener (1965), who put these forms into the subgenus *Ctenonomia*, here are given additional notes on some morphological features so far not or little mentioned (based upon both *sepulchralis* and typical *albescens*).

FEMALE LABRUM (Fig. 9, 10): Basal part transverse, medio-basally dully depressed, medioapically tuberculate, with a few fine submedian longitudinal carinas; Lateral areas disc-like, depressed and smooth, with thick margin; Apical process about as long as basal part and slightly wider than one third of basal part, lateral margins parallel or slightly divergent; Median keel lamellate, subapical lateral process with pointed apex; Marginal bristles long, partly curled at apex.

FEMALE MANDIBLE (Fig. 11): Bidentate but inner tooth weak.*

MOUTH PARTS (Figs. 12, 13): Both maxillae and labium of common halictine type without particular specialization. Maxillary palpi with joint I shortest, remaining joints more or less equal in length, joints I and II wider than others and VI narrowest. Glossa relatively slender, paraglossa about two thirds of glossa in length, labial palpi about as long as glossa, joint I longest and widest.

* This important characteristic is often worn away in aged females as shown in Fig. 11 with thin contours. Among 28 females from Fraser's Hill, the distribution of wear conditions was as follows: Intact (2), worn but tooth confirmed (2), tooth represented by an inconspicuous angle (7), tooth entirely absent (17).

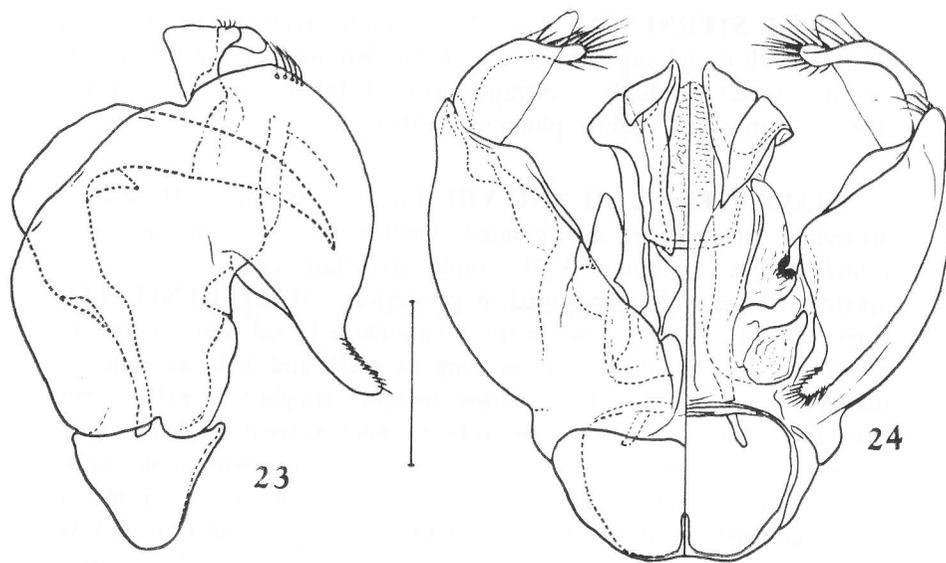
INNER SPUR OF FEMALE HIND TIBIA (Fig. 14): Provided with five inner teeth, apical one usually vestigial, but occasionally distinct (*cf.* Fig. 14). Or, often with only three distinct teeth and fourth one vestigial.

MALE STERNUM VI (Fig. 22): Gladulus rectangularly bending laterally with round angle, reaching submarginal area. Posterior margin slightly convex medially. Arrangement of bristles normal, longer, denser, stouter and slightly plumose postlaterally.

MALE STERNA VII AND VIII (Fig. 211) Sternum VII slender; apodemal lobe slender and pointed, median projection distinct with rounded apex. Sternum VIII simple and transverse, with pointed apodemal lobe, without postmedian projection. **MALE GENITALIA** (Figs. 23, 24): Robust and broad. Gonobase broad and continuing gonocoxal outline, about half as long as wide and half as wide as maximum capsular width; Anterior margin straight, lateral margin convergent basally. Gonocoxite robust, inner margin straight, outer margin convex; Ventroapical process enormous, semimembranous, seen ventrally, concealing majority of gonocoxal surface (more shrunk in dry specimens), basally with scattered bristles, apex roundly projecting with dense tuft of simple moderately long hairs. Gonostylus shorter than half of gonocoxite; Ventral part strongly chitinized, bending inwardly, apex bearing sparse long bristles; Dorsal part broad and membranous. Penis valve not exceeding beyond gonostylus, distinctly curved.

LARVAL STRUCTURE (Post-defaecation larva): Intersegmental line distinct, only weakened at thoracic segments. Dorsolateral tubercles of thoracic terga conspicuously pointed. Ventrolateral tubercles represented merely by broad elevations. Dorsolateral tubercles of abdominal segments distinct but flatter than in thorax. Head capsule with neither setae nor spicules; marginal sclerotization weak; Frons mildly raised, supraantennal convexity mild; Antenna as in other halictine species (*cf.* Michener, 1953). Mandible (Fig. 15-18) with conspicuous tubercle on outer surface bearing one or two setae; Apical part attenuate, margin microdenticulate, apex bidentate but seen as if truncate or slightly concave; Cusp multidentate and strongly chitinized. Spiracle of normal halictine type; Peritreme flat and thin; Primary tracheal opening without distinct collar; Spinous rows of atrium conspicuous.

PUPAL STRUCTURE: Similar to the description of *Lasioglossum* in Michener (1954), but basal protuberance of hind tibia not strong, while apical one of the same segment distinct. Rows of spiculus on I-V metasomal terga, stronger on II and III.



Figs. 23 and 24. Male genitalia of *L. albescens sepulchralis* (Scale=0.5 mm).

23. Lateral view. 24. Dorsal (left) and ventral (right) views.

Variation

The extreme variability exhibited by *L. albescens* group has repeatedly been mentioned (Blüthgen, 1926, '28, '31; Cockerell, 1930). Blüthgen classified this group as follows (synonyms in parentheses): *Halictus albescens albescens* Smith 1853 (*senescens* Smith 1879, *albozonatus* Smith 1879, *bengalensis* Cameron 1903, *manilae* Ashmead 1904, *javanensis* Strand 1909, *luzonicus* Strand 1909, *amblypygus* Strand 1914, *javanicus* Friese 1914, ? *speculithorax* Cockerell 1911), *H. a. sepulchralis* Cameron 1897 (*lahorensis* Cameron 1902, *salsettensis* Cockerell 1911, *reepeni* Friese 1918, *bryanti* Cockerell 1919, ? *postlucens* Cockerell 1919), *H. a. insularis* Blüthgen 1926, *H. a. gibber* Vachal 1892. Cockerell (1930) did not give a categorical classification, but his opinion seems to admit the following forms as distinct species (subspecies in parentheses): *luzonicus*, *albescens* (*albescens*, *senescens*), *sepulchralis* (*sepulchralis*=*lahorensis*, cf. Blüthgen, 1931, *salsettensis*, *convolvuli* Cockerell 1930).

A difficulty in classifying this group is its remarkable and often continuous variability. The extreme individuals could be regarded in safety as specifically distinct if collected in isolation. But intermediate specimens link the extremes. Blüthgen (1926) gave a synoptic table of the differences between typical *albescens* and *sepulchralis*. Comparing the specimens from Fraser's Hill with typical *albescens* from India (Lonavla, Eastern Ghat, collected by F. L. Wain), the former specimens satisfy all the items mentioned by Blüthgen as characteristic of *sepulchralis*, especially in: (1) Dark coloration of wings, hairs, tarsi and antennae, (2) Absence of white hair patches on metasomal tergum I (even in individuals soon after emergence), (3) Relatively sparse and minute punctures on mesoscutum with interspaces smooth and shiny (Figs. 26, 26). (4) Relatively sparse carinae on propodeal enclosure, with interspaces shiny (Figs. 29, 30). (5) Strong lateral carinae of propodeal declivity. After Blüthgen, *sepulchralis* is usually found from mountainous areas, while *albescens* more from plain and hilly areas. The occurrence of *sepulchralis* in Fraser's Hill coincides with this statement.

Examining further material from other areas, I found some specimens from Thailand and Cambodia, which can be ranked as a distinct subspecies as described below:

Lasioglossum (Ctenonomia) albescens iwatai subsp. nov.

More similar to *albescens* than *sepulchralis* in most features listed by Blüthgen, especially in clear coloration of wings, hairs, antennae and tarsi, relatively poor carinae on propodeal declivity, distinct white hair patches on metasomal tergum I, but differs from *albescens* and *sepulchralis* in the following characters: (1) Head relatively short. Ratio width/length is 1.08–1.14 (mean 1.11, n=12), as compared with 1.01–1.06 (mean 1.04, n=10) in *sepulchralis* and 1.03–1.08 (mean 1.06, n=8) in *albescens*. Correspondingly, outer orbital outline more rounded, not linearly convergent below. (2) Punctures on mesoscutum very dense and rather uniformly coarse, with slight admixture of minute ones. Interspaces extremely smooth and shining, with no microintrication on disc posteriorly even under high magnification (Figs. 25–27). (3) White, adpressed or tomentose hairs on lower paracular area, upper part of gena and mesopleura very dense and conspicuous.

In all specimens, wings without infuscation, veins and pterostigma brown to pale brown and tegulae dark brown with paler central spot.

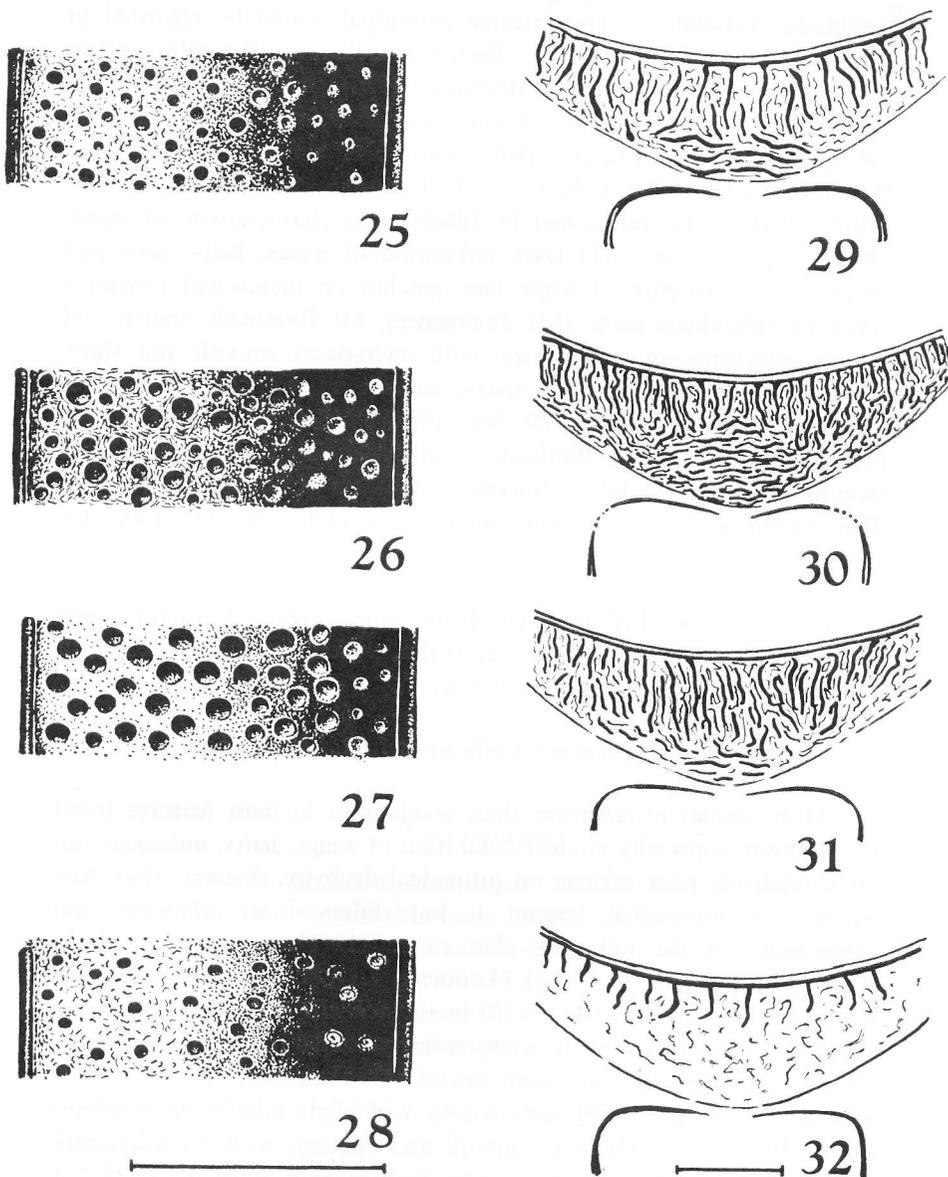
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Figs. 25-32. Sculpture of mesoscutum (left, scale=0.5 mm) and propodeal enclosure (right, scale=1/3 mm) in females of *Lasioglossum albescens* group.

25, 29. *Sepulchralis* (Fraser's Hill, Malaya). 26, 30. *Albescens* (Lonavla, India).
27, 31. *Iwatai* ssp. nov. (ChiengMai, N. Thailand). 28, 32. *Sepulchralis* (Fang, N. Thailand).

albescens
Malaya

Holotype 1 ♀, ChiangMai, N. Thailand, V 13 '61, Iwata leg.

Paratypes 3 ♀♀, ChiangMai V 15 '61, Yoshikawa leg.; 1 ♀, ChiangMai XII 31 '57, Umesao leg.; 4 ♀♀, Sanpatong near ChiangMai, VII 11 '62, Nakao & Nagatomi leg.; 1 ♀, Ubol, N.E. Thailand, XII 20 '62, Nakao leg.; 1 ♀, Puok, Cambodia, XII 8, '57, Yoshikawa leg.; 1 ♀, PhnomPenh, Cambodia, II 23 '57, Sato & Takayama leg.

The holotype is deposited in the Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo, and paratypes provisionally in my collection. The subspecies is dedicated to Prof. Kunio Iwata, Hyogo University.

The specimens from ChiangMai (including Sanpatong) are closely similar to those from the other localities. It is conceivable that this new subspecies inhabits the Thai and Cambodian lowlands throughout, as the plain vicariant of typical *albescens*. Cockerell (1937) recorded one specimen of "typical" *albescens* (in his interpretation) from Nan, North Thai town within the mountainous areas. It is very probable that this specimen is *iwatai*.

In this connection, it may be worth mentioning on the two specimens from North Thailand at my disposal, one from Doi Intanon, the other from Fang, both not too distant from ChengMai but in the montane areas bordering Thailand and Burma. These specimens coincide with *sepulchralis* in every feature cited by Blüthgen (except wing veins which are slightly paler). Moreover, they surpass typical *sepulchralis* by their mesoscutal and propodeal sculpture: Punctures on mesoscutal disc extremely minute and sparse, and the carinae on the propodeal enclosure very reduced, leaving the most part very shiny (Figs. 28, 32). These specimens may represent the montane *sepulchralis* populations in North Thailand. Cockerell (1930) described *H. convolvuli*, apparently belonging to the *sepulchralis* group, from Nan, where he recorded "*albescens*" (*cf.* above). This fact suggests the co-existence of both lowland and montane populations in boundary areas. But it is still premature to give any conclusion about the distribution of various "forms". Further variation-statistical studies are indispensable to solve the biosystematics of this common, widespread but difficult group.

Summary

The nesting habits of a halictine bee, *Lasioglossum (Ctenonomia) albescens sepulchralis* (Cameron), were observed at Fraser's Hill, Malaya. The nest pattern was parodalous, consisted of a main burrow

and several laterals, each of which serially contained two-five, mostly three, cells. Each nest contained several females, all inseminated and possessing well-developed ovaries, indicating the common use of one and the same nest by several equivalent females with no caste differentiation. Some additional notes on the morphology and variation of *L. albescens* group are given, together with the description of a new subspecies, *L. a. iwatai* ssp. nov.

Acknowledgement

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