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<https://doi.org/10.5109/22739>

出版情報：九州大学大学院農学研究院紀要. 13 (4), pp.673-703, 1966-02. Kyushu University
バージョン：
権利関係：



Bionomics of two new Japanese halictine bees*
(Hymenoptera, Apoidea)

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In the present paper, some biological observations of two new Japanese halictine bees are described. Both species have been observed at Misono, the suburb district of Kitami, Province Kitami, Hokkaido. The local climate is characterized by short summer and long, severe winter as indicated by the following meteorological data (taken from "Climate of Hokkaido", 1952):

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Mean
Air temperature (°C)													
Mean-Max.	-3.8	-3.4	1.7	9.8	16.9	21.3	25.0	26.3	21.3	15.5	7.3	-0.4	11.5
Mean	-10.7	-10.1	-4.8	3.8	10.0	15.0	19.4	20.6	15.5	9.0	1.9	-5.7	5.3
Mean-Min.	-17.6	-16.9	-11.3	-2.2	3.1	8.6	13.7	14.9	9.7	2.4	-3.5	-12.6	-1.0
Mean rainfall (mm)	49.5	37.6	41.8	42.9	51.8	60.9	91.5	114.0	115.3	69.0	58.3	38.1	Σ770.8

The nests of both species were discovered in a Ladino clover field. At the end of June, the clover grows to 20-25 cm and completely covers the soil surface. The soil is neither hard nor loose, but occupied by the dense root systems of the clover, and relatively humid by the dense foliage preventing the penetration of direct insolation.

Lasioglossum (*Lasioglossum*) *esoense* Hirashima et
Sakagami sp. n.

This species is a close relative of *Lasioglossum zonulum* (Smith), but is separated by the following combination of characters.

* Joint contribution from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan (No. 703, S.F.S.) and the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (Ser. 2, No. 229, Y. H.). In particular we thank the Publication Committee of the Faculty of Agriculture, Kyushu University for publishing this paper in the present journal.

Female: Head a little more round in front view; dorsal plates of pronotum more developed with sides more sharply truncated; dorsal face of propodeum with weaker wrinkles; metasoma, especially 2nd tergum, much more convex. Male: Vertex more round in front view; clypeus much more convex; metasoma, especially three basal terga, considerably more densely punctate; tuft of hairs on 6th sternum larger and more conspicuous.

This species is a relative of *L. mutilum* (Vachal) in the Japanese fauna, but is easily separated from the latter by the shape of the head and many other characters.

FEMALE. Length about 10 mm.

Black; mandibles reddened apically; flagellum beneath reddish brown; tegulae reddish brown, narrowly nearly transparent anteriorly; wings hyaline, veins and stigma yellowish; legs piceous, with tarsi reddish brown or more reddened; tibial spurs yellowish; posterior margins of metasomal terga hardly discolored, sometimes narrowly piceous.

Hairs on head and mesosoma, especially those on mesoscutum, sparser and finer than in *zonulum*, paler than in *L. occidentis* (Smith); hairs on legs similar to *occidentis* in color, or fuscous hairs on hind tibiae sometimes less pronounced; hair bands on bases of intermediate terga much more conspicuous than in *zonulum*, snow-white; hairs on apical portion of intermediate terga brown to fuscous, not conspicuous as in *occidentis*.

Head nearly round in front view with clypeus slightly producing below; clypeus well convex, subrugoso-punctate with interspaces smooth and shiny; frons with punctures less coarse and more close than in *zonulum*, slightly coarser than in *mutilum*; genae not distinctly receding, longitudinally striate behind; vertex well convex, rugulose. Pronotum with dorsal plates rather well developed, with sharp corners; mesoscutum shiny, densely punctate, rugose or nearly rugoso-punctate anteriorly; scutellum densely rugoso-punctate, flat; propodeum with dorsal face not well defined, primarily longitudinally wrinkled, with wrinkles weak to rather strong; posterior face of propodeum not distinctly keeled dorsally; lateral faces of propodeum rugulose, less pubescent than in *zonulum* or *mutilum*; mesopleura coarsely sculptured.

Legs with posterior spurs of hind tibiae serrate with about six small teeth. Metasoma elliptical, shiny; 1st tergum densely punctate basally and apically, median portion sparsely punctate with punctures a little stronger and irregular in distribution; 2nd tergum nearly uniformly densely punctate with punctures nearly as strong and dense as those on posterior portion of 1st tergum; 3rd and 4th terga with punctures weaker, apical depressions not well marked, impunctate.

MALE. Length about 9 mm.

Black; mandibles reddened apically; clypeus pale yellow apically; flagellum brown, slightly more paler beneath; tegulae brownish, paler posteriorly and narrowly transparent apically; wings hyaline, veins and stigma yellowish brown; legs black or nearly piceous, small segments of tarsi brownish; metasoma black or sometimes nearly piceous, posterior margins of terga hardly discolored.

Face including clypeus (primarily basal portion) densely covered with white, appressed, plumose hairs; hairs on vertex and genae rather sparse, whitish; hairs on mesosoma similar to those of female; basal hair bands on intermediate terga not conspicuous as in female although much conspicuous than in *zonulum*; hairs on 3rd and following terga primarily brown to fuscous; hairs on sterna pale.

Head round in front view, with clypeus slightly producing below; clypeus strongly convex, more convex than in *mutilum* and *zonulum*, coarsely punctured, shiny; punctures on clypeus stronger than in *mutilum* and *zonulum*; vertex well convex, round in front view, coarsely shagreened, shiny; genae well developed, shagreened, shiny; antennae slightly elongate, 1st flagellar segment broader than long, 2nd a little longer than each following segment, nearly one and one-half times as long as broad.

Pronotum with dorsal plates more developed than in *mutilum* and *zonulum*, with sides truncated; mesoscutum shiny, densely punctured; scutellum convex, shiny, densely punctured with punctures smaller than in mesoscutum; propodeum coarsely sculptured with punctures smaller than in mesoscutum; propodeum coarsely sculptured with strong wrinkles; crescent area hardly defined; posterior face of propodeum not carinate above; mesopleura sculptured nearly as in *mutilum*, less coarse than in *zonulum*.

Metasoma long oval, bases of intermediate terga strongly constricted; 1st tergum densely punctured nearly all over, with punctures on median portion almost as strong as or a little weaker than those on mesoscutum; 2nd and 3rd densely punctured with punctures weakened on posterior depressions which are well indicated and broad; 4th with punctures evanescent; hair patches on 6th sternum well developed.

Distribution: Japan (Hokkaido).

Type material: Holotype female, Botanical Garden, Sapporo, Hokkaido, 27. vi. 1958 (Y. Hirashima leg.); 4 paratype females, Higashikawa, Tokachi, Hokkaido, 22. vii. 1955 (Y. Hirashima leg.); 4 paratopotype males, on *Rudbeckia laciniata*, 17. vii. 1959 (S. F. Sakagami leg.); 1 paratype female, 28. vii. 1959, 1 paratype female, 14. viii. 1959, 1 paratype female, 9. ix. 1959, 1 paratype female, 15. ix. 1959, University campus, Sapporo, on *Rudbeckia laciniata*, (S. F. Sakagami leg.); 1 paratype female, Kitami,

Hokkaido, 29. viii. 1959 (Y. Ohé leg.).

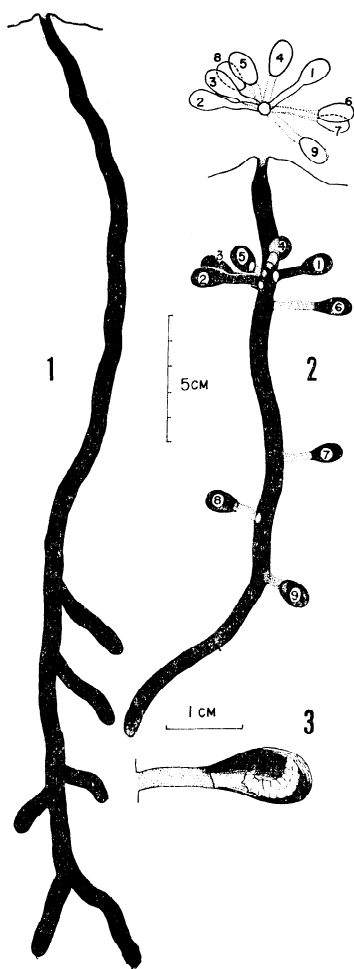
Type depositories: Holotype is deposited in the Entomological Laboratory, Kyushu University; paratypes will be found in the Entomological Laboratory, Kyushu University, Zoological Institute, Hokkaido University, British Museum (Nat. Hist.) and Snow Ent. Mus., University of Kansas.

The nests of this species were also discovered in Sapporo and Kushiro. Leaving the detailed accounts of the life-cycle elsewhere, here is given the biological observations made with the population in Kitami alone.

NEST STRUCTURE: The nests are of the typical branched halictine nest pattern, each cell connected with the main burrow by means of short lateral, the diameter of which is less than that of the main

burrow (type III a, Sakagami & Michener, 1962). The constriction of the entrance hole and presence of lower blind burrow agree with the majority of halictine nests so far described (Figs. 1-3).

Entrance occasionally with undifferentiated turret, constricted to 4-5 mm. Main burrow 5.5-7 mm wide, the inner wall more or less smooth but not polished, generally vertical, often with irregular bendings, occasionally ramifying below; bottom of lower blind burrow reaching 25 cm or more in late summer nests. Cells (Fig. 3), horizontal, mildly concentrated, mostly locating from 6 to 15 cm below earth surface, perpendicularly connected to main bur-



Figs. 1-3. Nest structure of *Lasioglossum esoense*. **1**, Old nest probably used for hibernation (No. 1, excav. on June 30, '60); **2**, Nest (No. 8, excav. on Aug. 21, '60) containing immature stages (Horizontal and vertical views). Numerals indicates the order of construction (1-3, empty after emergence; 4-5, black pupae; 6, black eyed pupa; 7, white pupa; 8-9, post-defecating larvae); **3**, Cell containing post-defecating larva.

row by means of short lateral, which is 8-15 mm long and 4-4.5 mm wide, filled with soil after oviposition. Each cell 12-14 mm in length, 7-8 mm in maximum diameter and 4 mm in neck diameter, shaped as in other halictine cells, elongate oval, bilaterally symmetric, bottom flatter, inner wall smooth and polished; larval defecation at end of upper wall. Developmental gradient more or less progressive and descending.

The entrance often forms a turret of about 2-3 cm in diameter, but this is obviously due to the accumulated soil mass not removed, does not mean the specialized architecture. The lower ramification of the main burrow was found only in one nest (No. 4 in Table 1). The developmental gradient is known in only two nests (Nos. 7 and 8), and distinct only in the latter. But there is no reason to deny the progressive and descending tendency, being general in halictine bees.

One nest (No 1, Fig. 1) was apparently the overwintering nest, being very deep, reaching 38 cm below the surface, and ramified in six branches at the bottom, probably each representing the hibernaculum of the overwintering female bees.

PHENOLOGY: Although so far known only from Hokkaido, this species is one of the latest species in the beginning of the spring activities, appearing only at the middle of June. The first records of nesting activities are those taken on June 16-18, 1960. The solitary foundation of three nests were observed on these days. In general, the activities at the nesting site continue to the end of August. No systematic collection on flowers was made in the locality concerned. Therefore, the phenological trend was estimated solely based upon the results of nest excavation as given below.

Nest No.	Date of discovery	Date of excavation	Depth of burrow bottom (in cm)	Number of adults and their conditions (*dead)	Number and contents of cells	Remarks
1	VI 17 '60	VI 30 '60	38	1 ♀ *	Without cell	Overwintering nest with lower ramification (Fig. 1)
2	" " " (just at digging)	" " "	14.5	1 ♀, wings intact, mandibles slightly worn, fertilized, ovaries fully developed, crop with abundant pollen	" "	
3	" 18 '60	VII 22 '60	18.5	1 ♀ *	" "	
4	" 16 '60 (just at digging)	" " "	10	"	" "	Burrow bifurcated at bottom
5	" " "	" " "	15.5	"	1, polished but still empty	

6	" 23 " " " "	14	"	6, all with pollen ball infested by fungi
7	" 16 '64 VIII 14 '64	33	1 ♀, wings mildly, and mandibles heavily worn, ovaries not examined	4 : 2 with postdefecating larvae, 2 with white pupae (1 ♀ 1 ♂)
8	— VIII 21 '60	22.5	1 old ♀, wings & mandibles heavily worn, fertilized, crop without pollen, ovaries degenerated. 3 ♀♀, soon after emergence, unfertilized, ovaries undeveloped. 2 ♂♂, newly emerged	9 : 3, empty with (Fig. 2) trace of defecation; 2 with black pupae, 1 with black eyed pupa; 1 with white pupa; 2 with postdefecating larvae
9	— IX 15 '60	26	No adults	6, all empty with trace of defecation

The data are still far from sufficient. In 1960, the population was apparently affected by adverse weather, especially by excessive soil moisture. Among 13 nests discovered until June 22, only two (Nos. 8 & 9) produced progeny. All others either disappeared during the season or were unsuccessful when excavated later (Nos. 3-6). In spite of such incomplete results, the data indicate only one generation per year, lasting about 2.5 months. After the hibernation, the females start the nest at the middle of June and produce the next generation, which emerges approximately at the end of August. The collection data in Sapporo also quantitatively confirm this annual cycle.

SOCIAL PATTERN: The nest No. 1 was discovered on June 17 by the appearance of the large entrance tumulus. On the same day, four new nests and on June 22 another one were found, all surrounding No. 1, within the radius of 30 cm, and one of them was just at the beginning of digging (No. 2). This fact strongly suggests that five bees overwintered in Nest 1, which possessed five branches at the bottom, presumably representing hibernacula, started their nests solitarily near the mother's nest. But it is premature to regard this as a rule. The absence of any females in No. 9 might suggest that all newly emerged females abandoned the nest. Further, the nests were found in other places either solitarily (2 cases) or forming groups of 2-3. Therefore, it is obvious that some females become pioneers, establishing the nests in the areas remote from the mother's nest.

As to the social pattern, the following items of evidence indicate that each female starts her nest and cares it solitarily: 1) The dura-

tion of active period, from middle June to late August, is too short to develop any complicated social systems between mother and daughters as in *L. (Evylaeus) duplex* Dalla Torre (Sakagami & Hayashida, 1958, '60, '61, cited as *Halictus duplex*). 2) There is also no marked change in body size and shape in the course of the active period. All females are approximately of the same size. All except newly emerged autumn females are fertilized. The ovaries develop first and later degenerate parallel to the season (Sakagami, unpub.). 3) All nests excavated by us, contained only one female. Nest No. 8 is exceptional, but it is doubtless that all females except the heavily worn one are newly emerged ones. 4) The number of cells in each nest (4-9) also suggests the solitary activity.

Therefore, the social pattern of this species is concluded as the simplest solitary type, that is, the type predominant in most other solitary bees. Only possible complication is the occasional presence of more than one female, all equivalent, in the same nest. Such facultative pleometrosis is often observed in some fundamentally solitary halictine species, or in the solitary phase of some social halictine bees (Cf. Sakagami & Hayashida, 1961). But such occurrence seems to be exceptional in *L. esoense*, even if possible.

In Nest 8, there is a discrepancy between the number of cells and that of brood including newly emerged adults, that is, five newly emerged adults were taken but only three empty cells were found. It is possible that some other cells were overlooked. But it is also plausible that some newly emerged ones, especially males, entered into the nest from the outside. Because one of two males was captured just at the moment of entering the nest. This is rather exceptional in halictine bees, the males of which usually do not return to the nests after departure.

Lasioglossum (Evylaeus) ohei Hirashima et Sakagami sp. n.

This species belongs to the group of *L. sexstrigatum* (Schenck) in a broad sense. This is separated from the allied species by the combination of characters such as the round head, convex and coarsely punctate clypeus, obliquely striated dorsal surface of the propodeum, elongated teeth on the posterior spur of the hind tibiae, and not conspicuously pubescent metasoma in the female, and the not elongated antennae in the male. The latter is especially characteristic for this species.

FEMALE (Figs. 5, 8, 9): Small and not robust species, length less than 6 mm.

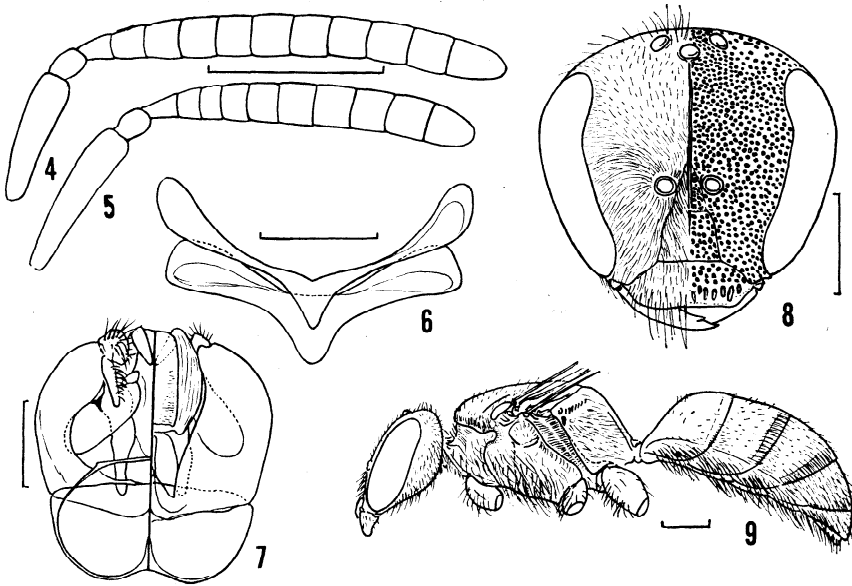
Black; mandibles reddened or piceous except bases; antennae broad-

ly brownish or more paler beneath; tegulae pale brownish transparent or nearly so; wings hyaline, veins pale brownish; legs piceous to brownish; tibial spurs yellowish; metasoma more or less piceous or brownish with posterior margins of terga pale yellowish brown transparent.

Hairs on body nearly uniform in color, whitish or pale golden, not conspicuous; cilia on metanotum dense in certain specimens; greyish hairs on 1st tergum microscopically fine, those on the following terga becoming longer and more conspicuous toward posterior terga; intermediate terga without hair bands but hairs becoming longer and denser toward posterior margin of each tergum; sterna with long hairs.

Head (Fig. 8) rather thin, nearly round in front view with clypeus slightly exceeding line running bases of orbits; clypeus convex transversely, strongly and coarsely punctate for the size of insect, with interspaces polished and shiny apically, microscopically tessellate above; supraclypeal area slightly convex, weakly tessellate-punctate with punctures as strong and large as or weaker than those on base of clypeus; frons convex, densely tessellate-punctate with punctures very small; genae receding. Mesoscutum shiny, very weakly or sometimes more or less distinctly tessellate, weakly and not so densely punctate; scutellum flat, sculptured nearly as in mesoscutum; propodeum shorter than scutellum, with dorsal face slanting and rounding into posterior face, wrinkled laterally; dorsal face of propodeum tessellate medially, triangular area not at all indicated. Legs with posterior spurs of hind tibiae with about four teeth, basal one or two of which are fairly long. Metasoma elongate oval; 1st tergum polished or microscopically finely punctate and transversely lineolate; 2nd and following terga hardly punctate, microscopically shagreened, shiny.

MALE (Figs. 4, 6-7, 10-14): Head extremely polymorphic as given later precisely. In small individuals, head (Fig. 12) round in front view; mandibles slender with sharp apices; vertex gently convex; genae narrower than orbit without projections; punctures on frons about as large as, on vertex smaller than smooth and shining interspaces. Face below fairly densely haired. Clypeus except base yellowish. Pronotal tubercles round, inconspicuous. In large individuals (Fig. 11), head monstrous, remarkably enlarged with huge, sharply pointed mandibles; head quadrate in front view with orbits hardly converging below; clypeus considerably transverse, scarcely convex; genae exceedingly well developed with a large, posteriorly projecting process; head strongly shiny, finely and sparsely punctate, or hardly punctate on vertex and genae, scanty of hairs; mandibles and clypeus except base nearly ferruginous; pronotum well developed, sharply



Figs. 4-9. *Lasioglossum ohei*. (Scale=0.25 mm in figs. 6-7, 0.5 mm in other figures).
 4 & 5, Left antennae of male and female (Frontal views); 6, Male 7th and 8th sterna; 7, Male genitalia; 8, Female head, viewed frontally; 9, Female in profile view.

truncate laterally.

Antennae brownish, more paler beneath, slightly elongate with three or four basal flagellar segments indistinctly broader than long, the following segments nearly as long as broad except for terminal segment, very weakly convex anteriorly. Mesosoma shiny; mesoscutum and scutellum smooth with very fine, rather sparse punctures; propodeum essentially as in female or more shiny with posterior and lateral faces finely shagreened or microscopically linedate; mesopleura nearly smooth, shiny, with punctures a little more irregular and a little coarser than those on mesoscutum. Legs brownish, tarsi and both extremities of tibiae yellowish. Metasoma brownish to blackish brown, shiny, nearly impunctate. Apical metasomal sterna and genitalia as illustrated (Figs. 6 & 7).

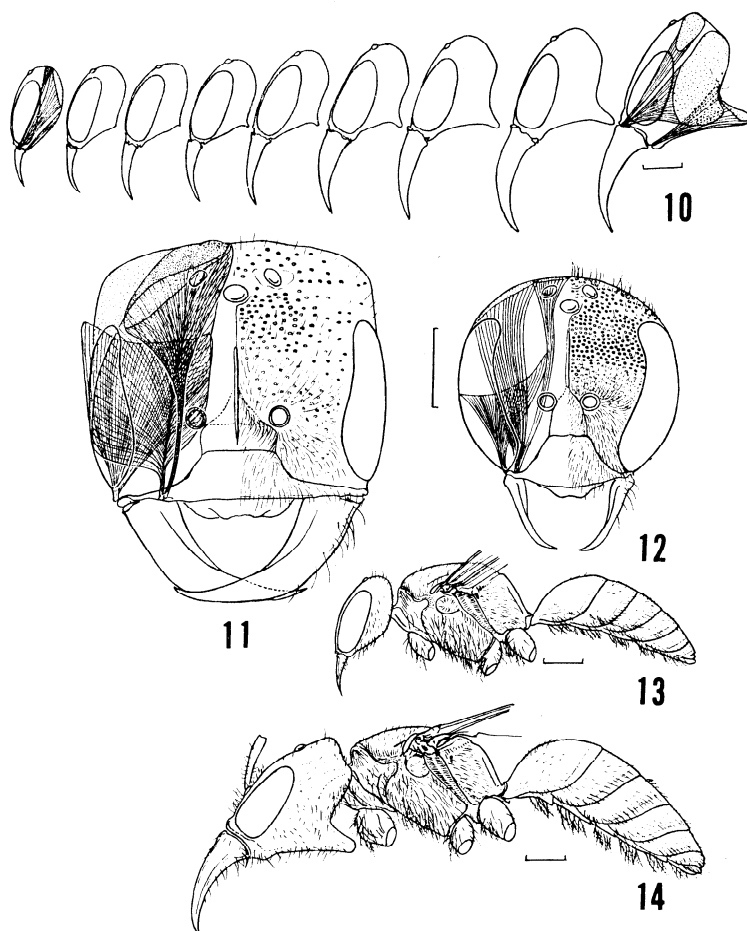
Distribution: Japan (Hokkaido).

Type material: Holotype female, 57 paratopotype females and 41 paratopotype males, all collected or reared from nests, Misono, Kitami City, Kitami Province, Hokkaido, during 1959-'64 (S. F. Sakagami and Y. Ohé).

Type depositories: Holotype is deposited in the Entomological Laboratory, Faculty of Agriculture, Kyushu University. Paratypes will

be preserved in the latter institution, Zoological Institute, Faculty of Science, Hokkaido University, Snow Entomological Museum, University of Kansas, British Museum (Nat. Hist.), and U. S. National Museum in Washington.

MALE POLYMORPHISM: The male polymorphism was given in the description. But this feature is so remarkable that is commented here in detail. As shown in Figs. 10-14, the polymorphism is principally caused by the allometric development of the head. To give



Figs. 10-14. Male polymorphism in *L. ohei*. (Scale=0.5 mm). **10**, Continuous series of males arranged according to head size. Mandibular muscles are shown in two extreme individuals; **11** & **12**, Head viewed frontally of two extreme individuals, showing sculpture, pilosity and mandibular muscles; **13** & **14**, Two extreme individuals viewed in profile.

some quantitative measures upon the relative proportion among various body parts, two extreme male individuals (in mesosomal width) were chosen. The measurements of various body parts of these specimens were converted to the ratios to the mesosomal width (= distance between outer margins of tegulae, respectively, 1.24 mm in the small male and 1.50 mm in the larger one). Then such relative values of the larger male were divided by the corresponding values of the small male and the results were arranged in the increasing order of the ratios (large male)/(small male) (s. the last column of the table). To facilitate a comparison, the same procedure was also taken with females, using two extreme individuals in mesosomal width, and the results were presented together with those in males.

Parts measured *Parts out of head; L, Length; W, Width; D, Distance	Ratio to mesosomal width				Ratio	
	Small ♀ a	Large ♀ b	Small ♂ A	Large ♂ B	b/a	B/A
1. *Mesosomal W	1.00	1.00	1.00	1.00	—	—
2. Ocellalveolar D	0.38	0.36	0.46	0.36	0.95	0.78
3. Clypeus L	0.23	0.24	0.24	0.20	1.04	0.83
4. Eye L	0.62	0.55	0.72	0.65	0.89	0.90
5. Flagella I-IV, comb. L	0.19	0.19	0.34	0.32	1.00	0.94
6. *Hind tibia L	0.68	0.68	0.74	0.73	1.00	0.99
7. Eye lateral W	0.24	0.23	0.29	0.30	0.96	1.03
8. *Metasomal W	1.02	1.05	0.93	0.97	1.01	1.04
9. *Mid tibia L	0.45	0.45	0.50	0.53	1.00	1.06
10. *Mesoscutal L	0.57	0.56	0.61	0.65	0.98	1.06
11. Scape L	0.37	0.35	0.37	0.40	0.95	1.08
12. Head L	0.92	0.88	1.00	1.11	0.96	1.10
13. *Pronotal W	0.59	0.59	0.53	0.61	1.00	1.15
14. Head W	0.96	0.95	1.05	1.22	0.99	1.16
15. *Fore tibia L	0.38	0.41	0.42	0.49	1.08	1.16
16. Orbitalveolar D	0.17	0.18	0.19	0.24	1.06	1.26
17. Upper interorbital D	0.59	0.56	0.71	0.90	0.94	1.27
18. Maximum interorbital D	0.68	0.64	0.71	0.91	0.92	1.28
19. *Fore coxa W	0.22	0.21	0.20	0.27	0.96	1.35
20. Interocellar D	0.18	0.19	0.19	0.26	1.06	1.37
21. Interlveolar D	0.10	0.10	0.13	0.19	1.00	1.46
22. Upper margin of clypeus L	0.21	0.19	0.20	0.30	0.90	1.50
23. Lower interorbital D	0.49	0.45	0.49	0.80	0.92	1.64
24. Ocellocular D	0.18	0.20	0.19	0.32	1.11	1.68
25. Mandible L	0.38	0.41	0.46	0.81	1.03	1.76
26. Genal W (excl. process)	0.20	0.18	0.21	0.67	0.90	2.15
27. Ocelloccipital D	0.10	0.10	0.10	0.22	1.00	2.20
28. Mandible basal W	0.13	0.13	0.11	0.26	1.00	2.36
29. Genal W (incl. process)	—	—	0.21	0.67	—	3.20

Obviously the ratios, consequently also the order among various

body parts may vary when a larger number of individuals are measured. But the results show clearly some definite trends as follows: a) Allometric trends result in the enlargement of the parts of the upper head both along (27) and across the body axis (20, 24), of genae downward (26, 29), and of the lower parts of the head across the body axis (21-23, 25) and of mandibles (25, 28), b) The middle parts of the head are relatively less affected including antennae (2-5) (The male antenna in Fig. 5 was drawn from a small, microcephalic specimen), c) The head enlarges itself laterally parallel to the increase of the body size (14), d) The parts other than the head were not extensively measured; but they are seemingly not much affected (8, 10) except for prothorax (13), in which the allometric trend reaches even to the legs (Compare 19, 6, 9, 15), e) No distinct allometric trend is detectable in females.

To know the relation between macrocephalic tendency and absolute body size closely, the following ratios were measured both in females (40 individuals) and males (43 indiv.): *Head width/Mesosomal width*, *Upper interorbital distance/Lower interorbital distance*, *Genal width/Eye width seen laterally*. In large males possessing genal processes, the genal width was measured in two ways, either including or excluding the process. These ratios were arranged in Fig. 15, according to the increase of the absolute head width. The figure shows distinctly the following facts: 1) The body size fluctuates itself more in males than in females as seen in the bottom graph. 2) All ratios concerned are nearly isometric in females, while distinctly increase in the males parallel to the increase of the absolute body size. Although the change is continuous (Fig. 10), the difference is enormous when both extreme are compared (Figs. 11-14). The larger males are gigantic by the enormously swollen occiput, conspicuously enlarged genae with remarkable processes, and extremely widened mouth, carrying formidable mandibles. Correspondingly, the pronotum is distinctly tuberculated and the fore coxae are remarkably thickened. Not only such metric characters, the surface structure, too, varies considerably (Figs. 11-14). The dense punctuation and pilosity on the face in smaller males gradually reduce the density parallel to the enlargement of the head, ultimately becoming very sparse, showing conspicuously shining interspaces. In the larger males, the mandibular muscles develop enormously. The inner walls of the enlarged head capsule offer wider surface for the attachment of these muscles. Moreover, the abductor muscles invade into the genal processes (Fig. 10).

Up to the present, several instances of such male cephalic gigantism have been known. *L. sexstrigatum* (Schenck), for example, offers itself such an instance. This species widely distributes in the Palaearctic region, and has been named several times by the different authors.

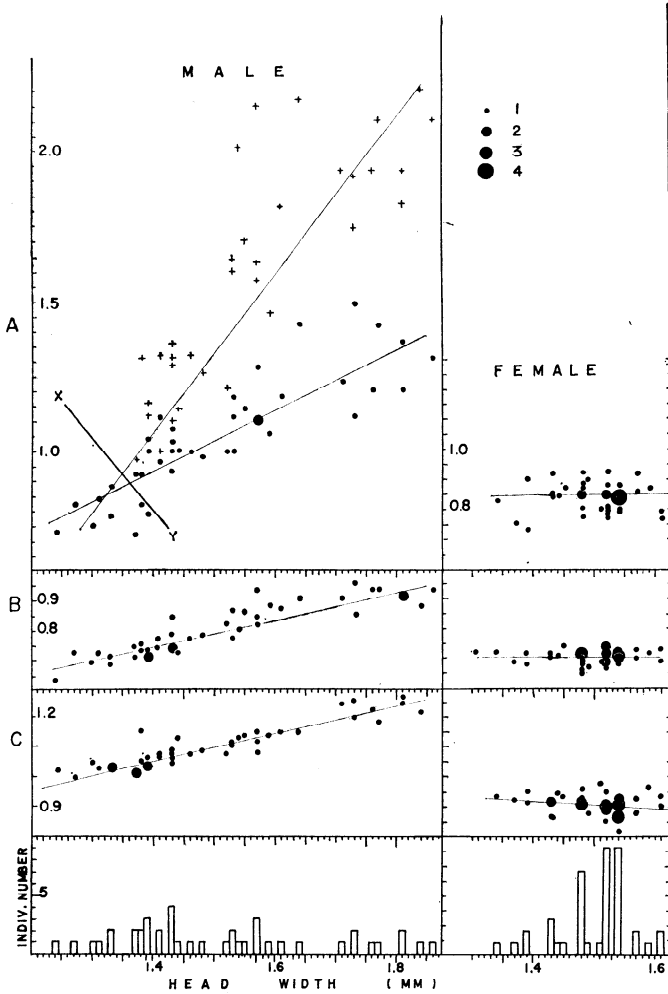


Fig. 15. Relation between body size and ratios of some body parts in *L. ohiei*. Abscissa, Head width (in mm). Ordinate, ratios and (at bottom) individual number. A, *Genal width/Eye width seen laterally*; B, *Lower interorbital distance/Upper interorbital distance*; C, *Head width/Mesosomal width*. Bottom graphs show the frequency distribution of mesosomal width in both sexes. In ratio *Genal width/Eye width* in males, the crosses represent the distribution of the ratio, in which genal width was measured including genal process and the dots represent the results measured excluding genal process. In small males distributing below line X-Y, this difference does not exist because genal processes are practically absent. The size of circles indicates the individual number as given right-hand top.

Alfken (1905) stated that *Halictus monstificus* Morawitz, described from Siberia by the male, is identical with *Halictus sexstrigatus*, and his statement was cited again by Blüthgen (1922) (Cf. Hirashima, 1957). Thus, *Halictus monstificus* is a gigantic male of *H. sexstrigatus*. Rayment also reported two similar instances from Australia. In *Halictus emeraldensis* Rayment, he discovered (1936-37) a large macrocephalic male together with normal small males. His figures show the allometric development of the head similar to that in our case, although the formation of the genal processes is not mentioned. This case is noteworthy because, after his comment, not only head but also genitalia change the structure as cited below: Whilst checking the virgin females of the February generation of *H. emeraldensis* as they emerge from their natal shaft, the author was astonished to see a bee, returning from the flowers, suddenly fall dead on to the colony site.....Microscopic examination proved it to be a mutation, with a huge quadrate-head capsule more than twice the size of that of the (typical) male, its apex of the abdomen has a large broad red plate, which is absent in the much smaller typical male; the genitalia has two more appendage as shown in Fig. III, 4, ...Another instance of cephalic polymorphism was found by Rayment (1955) in *Halictus* ("*Chloralictus*") *dimorphus* Rayment. In this species, the structure of the genitalia does not remarkably vary between micro- and macrocephalic males. On the other hand, the macrocephalism is linked with the formation of the genal processes as in *L. ohei*. As both to *H. emeraldensis* and *H. dimorphus*, Rayment explains the phenomenon by the appearance of the mutations. We have naturally no reason to reject such possibility. Unless confirmed by the crucial evidence, however, it seems to be more reasonable to regard such instances as already established polymorphisms than sudden appearance of mutations.

A third instance of the male macrocephalism or gigantism is the genus *Sudila*. Cameron (1897) erected this genus for the reception of two Ceylonese halictine bees, principally based upon such male gigantism. Later, Friese (1918) also erected the genus *Ceylonicola* for three species possessing similar feature, all from Ceylon. The latter genus was later regarded by Blüthgen (1930, cf. also 1931) as synonymous with *Sudila*. It might be quite excusable that Cameron erected the new group because the macrocephalic trend in halictine bees was not well known in his epoch and the morphological deformity of this feature was, if seen statically, indubitably remarkable. But after the discovery of the allometric trends linked with the head gigantism as given in the present work, it must be cautious to erect new supra-specific categories or even new species based upon such feature alone, however extremely aberrant in the appearance. Cameron writes that *Sudila* is characterized, besides the gigantic head in the male, also by

the possession of the longitudinal furrows on the mesonotum in the female. Therefore, it is conceivable that the erection of this genus is valid. But the description by Cameron (and also of *Ceylonicola* by Friese) is not so distinct that further critical studies are required.

Recently several instances of the cephalic polymorphism has been discovered in the females of certain halictine bees (Blüthgen, 1930; Quénu, 1959; Sakagami & Fukushima, 1961; Sakagami, 1964; Sakagami & Moure, in press; Wain & Sakagami, in press). The mode of deformation is, though not so exaggerated, approximately identical with that in the male polymorphism, showing the enlargement of occiput, genae and clypeus. The appearance of genal processes is also seen in *Halictus latissignatus* Cameron (Wain & Sakagami), *Megalopta genalis* Meado-Waldo (Michener, 1954; Moure & Sakagami). The decreased punctuation in the macrocephalic individuals is, though less remarkable, seen in *H. latissignatus*, too. In the case of female cephalic polymorphism, such allometric trends can appear in connection with the caste differentiation. There are at least three such instances, *H. (Halictus) scabiosae* (Rossi) (Quénu, 1959), *H. (H.) latissignatus* Cameron (Wain & Sakagami) and *H. (Seladonia) aerarius* Smith (Sakagami & Fukushima, 1961), in which the macro- and microcephalic females serve, respectively, as queen- and worker-like.

On the other hand, such functional significance is dubious in the male cephalic polymorphism linked with gigantism. So far is little known any fact that the male bees play any important role in the tribe maintenance except mating. Certainly the formidable mandibles of the gigantic males of *L. ohei* are operated by the enormous muscle masses. But it is very doubtful that such saber-shaped mandibles contribute to any works such as digging, building, etc. Further, it is difficult to assume that such mandibles are necessary in the mating response, because the males of many halictine bees, including the microcephalic males of the present species, possess the normal, slender mandibles. The cephalic polymorphism is not rare in aculeate Hymenoptera. But the exaggerated gigantism seems to be prevailing in males. The male of *Andrena halictoides* Smith shows cephalic polymorphism (Hirashima, 1965), and further the males of many species of *Andrena* (*Andrena* and *Hoplodrena*) have such sickled mandibles and genal processes (Hirashima, 1962, 1964). A similar instance is known in a crabronid wasp, *Ectemnius martjanowii* F. Morawitz (Tsuneki, 1956). Probably the aculeate Hymenoptera has a genetic tendency to develop such polymorphism. But such tendency may be exaggerated and retained much easily in males than in females by their haploid genetic make-up and their relative freedom from the selection pressure.

NEST STRUCTURE: The nests (Figs. 16-27) are essentially of the type similar to that of *L. esoense*: Each cell is connected to the main

burrow by means of short lateral. But most nests are inhabited by more than one female, and each of them usually has her own burrow. Therefore, the whole nest in general consists of several branch burrows, each issuing from the main burrow and having a number of cells each with narrow lateral.

Entrance mostly provided with conical tumulus, constricted to 1.5–3 mm, mostly 2–2.5 mm in inner diameter. Main burrow 4–5 mm, mostly 4.5 mm wide, with inner walls more or less smooth but not polished, descending approximately vertically, radiating branch burrows at 3–11 cm, mostly 5–7 cm below soil surface, often though not always at same level (Cf. Figs. 16–23). Sometimes but not always, one of branch burrow descending as continuation of main burrow. Each branch burrow as wide as and smoothed as main burrow, not specially constricted at entrance as in *Pseudagapostemon divaricatus* (Vachal) showing similar ramification (Michener & Lange, 1958a). Course of branch burrow variable, usually more or less vertical, but often gently sloping or horizontal or even slightly ascending at initial section (Fig. 16, Burrow A, D; 19, H; 23, C), ending in blind burrow, bottom of which 8–28 cm, mostly 12–16 cm deep. Sometimes, each burrow further ramifying (Fig. 24, A, B), each of such subbranches either carying cells or not.

Cells exceptionally opening to main burrow (Fig. 24), but mostly to branch burrow at 3–18 cm, mostly 6–12 cm below surface, mildly to often quite concentrated, minimum distance between two cells (=distance of inner walls of two cells) reaching less than 2 mm. Each cell perpendicularly connected to main burrow (though occasionally not as seen in Fig. 16, black silhouette figure) by means of short lateral of 1.5–2 mm wide and variably long, though mostly shorter than length of cell. After oviposition, lateral filled with loose soil. Each cell horizontal or slightly sloping downward, 7.5–8.5 mm, mostly 8 mm in length, 2.8–3.5 mm, mostly 3 mm in maximum diameter and 1.3–1.8 mm, mostly 1.5 mm in neck diameter, shaped and lined as in *L. esoense*. Larval defecation as in *L. esoense*. Developmental gradient fundamentally progressive and descending, although often quite irregular (Figs. 16–24).

After the diagnosis of the architectural pattern, some aspects, which are variable from nest to nest, are briefly referred to. The size of the entrance tumulus varies according to the season and the number of inhabitants. Among the nests studied at the same time, the tumulus is naturally larger in larger nests as seen from the comparison between Figs. 18–19 or 22–23. The size of the tumulus can therefore serve as an indicator to estimate the number of adult females and cells in the nests. At the maximum development, it attains 10–15 mm in height and 25–35 mm in basal diameter. The outer surface is not

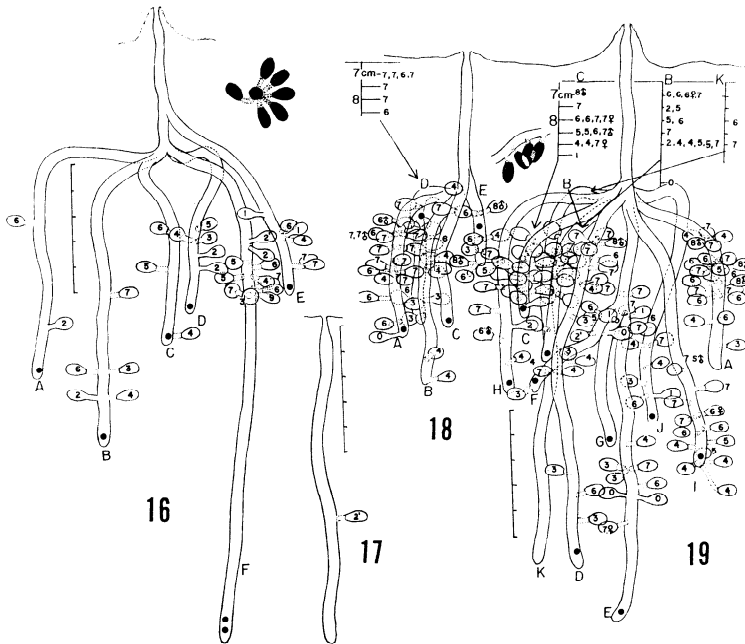


Fig. 16-19. Longitudinal view of four nests of *L. ohei*. **16**, No. 4, excav. on July 20, '64. One burrow very deep, with two females; **17**, No. 13', excav. on Aug. 13, '64. Abandoned nest with only one burrow and one cell; **18-19**, Nos. 9 & 8, excav. on July 22, '64. Two closely made nests, one of which very complicate.

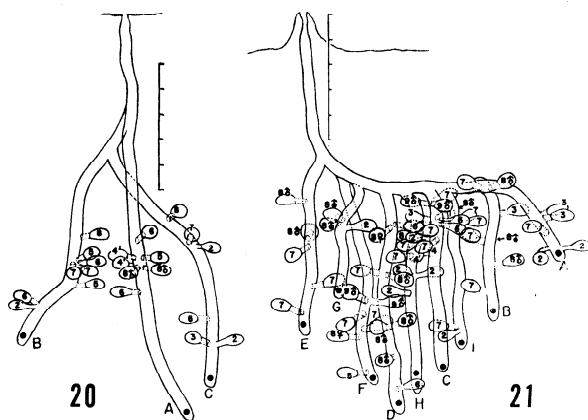
Some explanations common to Figs. 16-27 are given herewith:

1. The scale given in each figure=5 cm. Figures reproduce the depths of burrows and ramifications (and in Figs. 18-19 and 22-23, distance between nests) exactly. Depth of cells is mostly rounded to 0.5 cm unit. Width of burrows, length and width of laterals as well as those of cells are a little magnified. Black silhouette figures in Figs. 16 and 19 show the arrangement of some cells viewed from above.

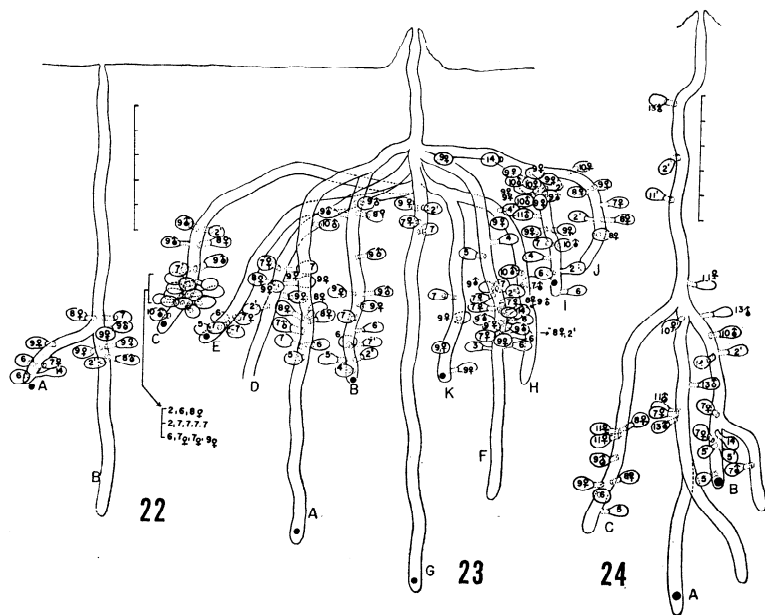
2. Contents of cells are numbered as follows: 0, empty, still not polished; 1, empty, already polished; 2, pollen ball alone; 3, pollen ball with egg; 4, young larva; 5, old larva still with food; 6, predefecating larva already without food; 7, defecating or post-defecating larva; 8, white pupa; 9, white pupa with coloured eyes; 10, white pupa with black eyes; 11, pigmented pupa; 12, pupa, immediately before emergence; 13, adult within cell; 14, empty cell after emergence.

3. Symbols 2', 7' etc. indicate the decomposition or death at respective stages. Symbols ♂ ♀ after stage number show the sex of immature stages (determined by rearing in pre-pupal stages). Black, half-black and white circles of each male symbol mean large, medium and small specimens. In Figs. 18, 19 and 23, the contents of cells at some concentrated parts are given separately, together with depths below surface.

4. Large black circles given in burrows indicate the occurrence of adult female. Lined and dotted laterals indicate respectively open and closed conditions,



Figs. 20-21. Longitudinal view of two nests of *L. ohei*.
20, No. 5; **21**, No. 6; both excav. on July 20, '64.



Figs. 22-24. Longitudinal view of three nests of *L. ohei*. **22** & **23**, Nos. 14 & 16. Two closely made nests, one of which very complicate. Both excavated on Aug 14, '64; **24**, No. 13. Three cells around main burrow, excav. on Aug 13, '64.

specially elaborated. The permanence of the tumulus is mostly due to the particular nest site preference. In the species preferring exposed surface such as *L. duplex* Dalla Torre (Sakagami & Hayashida, 1960) the tumulus gradually loses the incipient conical shape by the dessication of soil particles and ultimately disappears. In *L. ohei*, the nest entrance is often protected from dessication by the dense clover foliage, so that the tumulus maintains its conical shape, nevertheless it is not so particularly elaborated as to be called a turret.

The depth at which cells are found is quite variable as follows:

	Depth in cm (n cm means \leq n cm)																	
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
Total number of cells	4	12	21	29	66	80	67	62	35	28	11	7	4	11	7	4		
July	1	6	7	17	56	58	41	32	20	16	9	5	3	7	3	2		
August	3	6	14	12	10	22	26	30	15	12	2	2	1	4	4	2		
Examples																		
No. 6 (Fig. 21) standard				1	9	16	8	6	5	7	1	2						
No. 8 (Fig. 19) relatively deep						16	27	16	12	5	7	4	4	3	7	4	2	
No. 13 (Fig. 24) relatively deep	1				1	1				1	2	2	1	1	4	4	2	
No. 11 relatively shallow	1	6	5	3	2	1	1											
No. 16 (Fig. 23) relatively shallow	2	6	14	11	8	21	18	23	8	2								

As already referred, to, the progressive and descending gradient of cell construction is more or less seen in each branch burrow. But this order is often disturbed by the frequent construction of later cells at the upper section (For instance, Fig. 16, E; Fig. 23, F). Consequently, the vertical distribution of cells as a whole does not markedly vary between July and August (*Cf.* Table). This is also partly due to the marked intranidal difference. As shown in the table by several particular examples, the mean depth of cell is variable among nests. Seemingly, this partly relates to the soil humidity. The cells made at shallower level were mostly found in the nests at relatively humid places.

The depth of burrows and its relation to that of cells are also variable. The distribution of the depths of the bottoms of the burrows in July and August is as follows:

Depth (cm)	-8	-10	-12	-14	-16	-18	-20	-22	-24	-28
July	5	2	10	6	5		2	1	1	1
August	1	2	4	2	1	4	2	2	2	

The distributions in July and August suggest that the burrows are

generally, but not strictly, deepened parallel to the brood rearing activities. It is possible that some deep burrows found at the earlier phase of the brood rearing activities are the old burrows used for hibernation (Cf. Fig. 16, F). Even if such would be the case, it is obvious that no strict correspondence between progress of brood rearing and deepening of burrows exists. There is also no definite relation between the depth of the deepest cell and the length of the lower blind burrow (=length between the deepest cell and the bottom of the burrow) as follows:

Depth of deepest cell (cm)	≤6	≤8	≤10	≤12	≤14	14<	Total
Length of blind burrow (cm)							
0>			1			1	2
0		1	2	2			5
≤0.5		1	1	5	3		10
≤1.0			3	5			8
≤1.5		1	2	2	1	2	8
≤2.0	1			1	2		4
≤2.5			1		1		2
≤3.0							
≤4.0		1				1	2
≤5.0		1		1			2
5.0<		1	2	3			6
Total	1	6	12	19	7	4	49

In some burrows, the deepest cell often lies at the level near or even below the bottom of the burrow. The extreme instance is seen in Fig. 19, I.

The length of lateral, which can be traced not only in the cells before but also in those after oviposition when the soil filled in it is relatively loose, is reproduced in Figs. 19-24 not always exactly. Virtually it varies considerably as follows:

Length in mm	4	6	8	10	12	14	16
Number measured	8	5	8	6	0	1	4

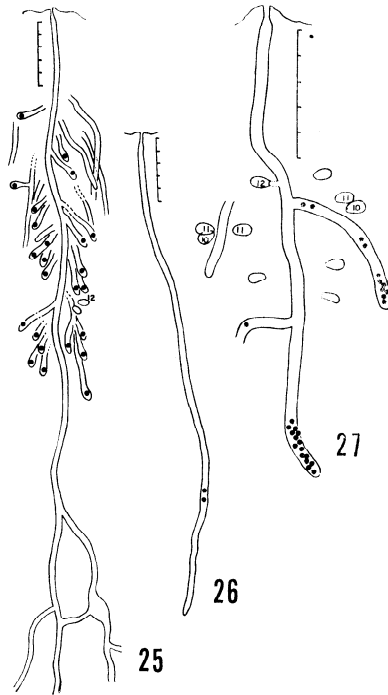
It is mostly shorter than the cell and often very short, though not completely omitted. In certain instance, however, it is longer than the cell and reaches 1.6 cm in the maximum (Cf. Fig. 19, I). The course of the lateral is, when possible to trace it, mostly straight and horizontal, but it occasionally curves (Fig. 16, Silhouette figure) or inclines (Fig. 19, I). In contrast to the length of the lateral, the size of the cell is relatively constant, showing no marked deviation from the usual variation range. There is no difference in the size of cell according to the immature stages involved, either male or female, and either small male or large one.

The newly emerging females are seen at first in the main burrow (Fig. 27). Later they excavate their own hibernating burrows around the summer burrows. Only a few nests of this phase were examined

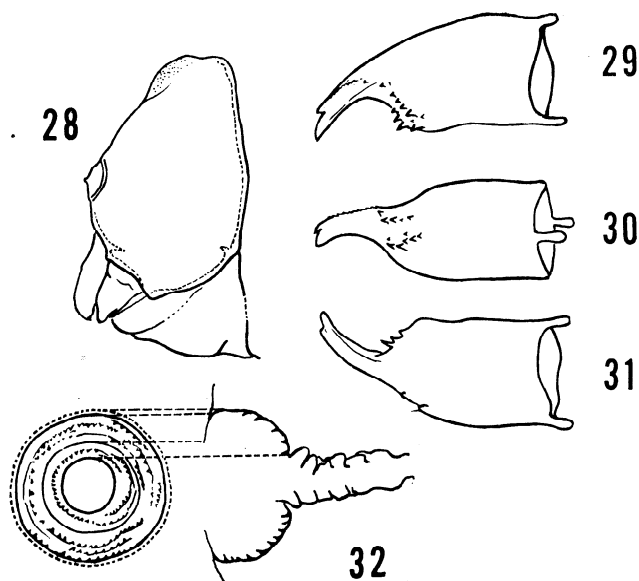
and none of them were carefully traced as to the course of the burrows. One relatively well studied case is shown in Fig. 25. In this nest, many short burrows are found around the main burrow. Each short burrow contains one female (with one exception which contains two) and the upper part is mostly closed from the inside so that does not communicate with the main burrow. This trait, the formation of the isolated particular hibernaculum by each female, is also observed in *L. duplex* (Sakagami & Hayashida, unpub., Cf. Sakagami & Michener, 1962, Fig. 13). In this nest, like that in Fig. 27, only the main burrow was traced. There were several other branch burrows, which were not accurately studied. Some of hibernacula in Fig. 25 drawn as if linked with the main burrow might belong to such other branch burrows. The main burrow was so deep that could be traced only down to 54 cm. At the level of about 40 cm below surface, the burrow shows a peculiar ramification involving loop and enlargement, the functions of which are uncertain. It is also unknown whether some hibernating females occurred or not at the deeper, unexamined parts.

LARVA: The structure of the larva does not much differ from that in other halictine bees (Cf. Michener, 1953) as given below based upon the final instar individuals (Figs. 28-32).

Intersegmental lines distinct except at cephalothoracic and caudal parts. Dorsolateral tubercles of thoracic terga distinct, similar to that in *L. kincaidii* (Cockerell). Ventrolateral tubercles less distinct. Head capsule (Fig. 28) carrying no setae, spicules nor any other peculiar



Figs. 25-27. Longitudinal section of three nests of *L. ohei* after brood rearing activities. **25**, Large hibernating nest with many hibernacula and lower ramification; **26**, Small hibernating nest with only two females, still not making hibernacula. Both excavated on September 9, '61. **27**, Nest after brood rearing activities, still containing a few immature stages. Females are still not making hibernacula. Excav. on Aug. 23, '59.



Figs. 28-32. Structure of larva of *L. ohiei*. 28, Head seen in profile; 29-31, Dorsal, inner and ventral views of right mandible; 32, Spiracle and its cross section.

structure; marginal sclerotization weak. Frons raised than in *L. duplex* but not so conspicuously as in *L. kincaidii*. Supra-antennal convexities moderate, approximately as in *L. duplex*.

Apical portion of mandibles attenuate (Figs. 29-31), lateral margins without conspicuous dents, though dorsally minutely denticulate; apical teeth, especially ventral one, less sharp than in *L. kincaidii*. Mandibular cusp with both dorsal and ventral rows of denticles distinctly separated from each other; dorsal row indistinctly continuous to denticular row of apical attenuate portion; no conspicuous dent between dorsal and ventral rows. Outside of mandibles with two very dull tubercles.

Spiracles (Fig. 32) similar to that of *L. sparsum* (Robertson). Primary tracheal opening slightly projecting but not forming collar. Denticles very minute. Peritreme flat and complete.

PHENOLOGY: The first spring nests of this species were discovered at the middle of June (VI 16-22, 1958-'64). Therefore the nesting activities begin nearly synchronously to those in *L. esoense*. In this species, too, no systematic sampling of adult bees on flower was undertaken. The information given below was obtained from the results of nest excavation. In some nests, several cells contained pollen balls or immature stages infested by molds. Excluding such cells, the contents of the cells of all accurately examined nests are chronological-

ly arranged as follows:

Year (0=1960, 2=1962 9=1959, others 1964)	0 0 2 0											9						0 0				
	July											August						Sept.				
	Date											Date						Date				
	5	17	20		21	22		24	30		13	14		23		9	15		17			
Nest No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Cell in construction								3														
Empty cell	1							8	1	4	5				2							
Pollen ball alone		4		6	3	8		3			3				1							
Egg	2	1	1	2	1	4		10	4						3							
Young larva	8	3	1	4		2		23	7	2	4				5							
Old larva with food	7	4		5	3	1		7		4	1	2			10							
Pre-defecating larva				7	5	6		29	12	6	1	1	2		24	↑		↑				
Post-defecating larva				5	3	17		32	17	4	1	5	2	1	12	↑		↑				
White pupa				3	4	15		5	2	↑	2	1	2	2	6	34	5	4				
Coloured eyed pupa						4							2	2	2	9	↓		2	2	2	
Black eyed pupa										8			2	3	2	1	↓	↓				
Pigmented pupa										↓			4		2				2		↓	
Adult within cell													4		2		?					
Cell after emergence													2	1	5		?	?	?	?	?	?
Fresh adult female															6	19		23	9	2	2	
Fresh adult male															1	4			1			
Old female	3	4	1	7	3		9	1	9	3	2	1	0	2	1	1 ₈₊₁	4	?				

These nests were excavated in different years without regular interval. The total number of nests examined is also still insufficient to give a quantitative estimation of brood development. Nevertheless the data clearly show the occurrence of only one generation per year and the absence of discrete production of broods as in *L. duplex* (Sakagami & Hayashida, 1958, '60) or *L. malachurum* (Kirby) (Noll, 1931; Bonelli, 1948). The oviposition ceases about at the end of July and the emergence of new adults begins at the middle of August. It is also seen in the table that the brood rearing activities vary from nest to nest. For instance, compared to the other nests of the same period, No. 16 is remarkable by its delayed development.

To know the difference of development between both sexes, the sex-known immature stages of July and August nests were separately

Immature stage	Number of individuals examined									
	July		August		July			August		
	♀	♂	♀	♂	large ♂	medium ♂	small ♂	large ♂	medium ♂	small ♂
Predefecating larva	2	2	2	2			2			
Postdefecat. larva	5	6	15	3	1	4	1	3	1	1
White pupa	7	33	12	16	8	4	21	6	8	2
Coloured eyed pupa		4	26	8			4	4		4
Black eyed pupa			4	2				1		1
Pigmented pupa			2	3				2		1
Adult in cell			1							
Total	14	45	62	34	9	8	28	16	9	9

summed up. The same procedure was taken as to the polymorphic series of males, dividing them arbitrarily in large, medium and small individuals. The sexes of some old larvae were determined by rearing them at least to the pupation.

The results mentioned in the table shown in the former page suggests the occurrence of a mild proterandry. The tendency is not so distinct as seen in many other halictine bees. But this was partly be affected by the intranidal fluctuation. The tendency is seen, though not distinctly, from Figs. 19-24, too. It is interesting that such difference is traced, though much obscurely, among differently sized males: The large males tend to appear later than the smaller ones.

SOCIAL PATTERN: From the phenology clarified in the preceding section, the possibility of the caste differentiation between mother and her earlier daughters as in *L. duplex* and *L. malachurum* is excluded. On the other hand, the occurrence of more than one female in one and the same nest requires further analysis. The results of the examination of ovarian state and related features in these females are as follows:

Nest No.	Date	Number of females	Mandibles	Wings	Ovaries	Crop content
1	VII 5 '60	3(3)	A(2),B	A(3)	A(3)	+b(2), +a
2	VII 17 '60	4(2)	A,B	A,B	A,x	+a, x
4	VII 20 '64	7(7)	B(7)	A(3),B(4)	A(7)	++a(2), ++b, ±a(3), ±b
5	"	3(3)	B(3)	A,B(2)	A(3)	Oo(2), +o
7	VII 21 '64	1(1)	B	B	A	+a
8	VII 22 '64	9(9)	B(9)	A(8),B	A(9)	Oo, ±a(5), +o, ++a, +a
10	VII 24 '62	2(2)	?	?	A	?
11	VII 30 '64	1(1)	B	A	A	++o
13	VIII 13 '64	4(2)	C,D	B,C	B,C	+o(2)
14	VIII 14 '64	2(1)	D	C	C	Oo
15	"	1(L)	D	C	C	++o
16	"	8+1(7)	C(5), D(2)	B(2), C(5)	C(7)	++a, ++o(5), Oo
17	VIII 23 '59	4(4)	D(4)	C(2), D(2)	C(4)	?

Explanation:

Number of females: The number of females in nest and, in parentheses, that examined with respect to the features concerned.

Mandibles: A, virtually intact; B, slightly worn; C, distinctly worn; D, heavily worn.

Wings: A, intact; B, very slightly worn; C, slightly worn; D, distinctly worn

Ovaries: A, fully developed, B, slightly degenerated, C, distinctly degenerated

Crop content: Nectar: ++abundant; + moderate, ± scarce; O, empty.

Pollen: o, absent; a, scarce; b, abundant.

Number of cases is given in parentheses. If unmentioned, represented by a single specimen, x means lack of observation.

As seen in the table, the ovaries are fully developed during July, while gradually degenerate in August. Correspondingly, the mandibles

and wings also gradually worn. The nectar content in the crop is variable but the pollen is usually taken at the initial part of the active season as in *L. duplex*. There is no marked difference in these features among the females in the same nests. Moreover, the spermathecae of all these females, except two (one in No. 4, the other in No. 16), which were not examined on this feature, are filled with sperms. Finally, there is no marked size difference among the females examined. Summarizing, all these females are equivalent with respect to the reproductive and other features examined.

Next the contents of cells in each accurately studied nest, each burrow separately, were examined as shown in the next page.

The table suggests that each female in general possess her particular burrow within the common nest, probably working there independently from other females. This assumption is supported by the following facts:

1) In earlier nests, Nos. 1-9, the number of females in each nest (F) approximately equal to that of branch burrow (B), especially in Nos. 1, 2, 5, 6.

2) When there is no strict correspondence between B and F , the difference is $B > F$ in three nests (Nos. 3, 8, 9) while $B < F$ only in one nest (No. 4). The latter case is interesting and will be referred to later. In three $B > F$ cases, it is always possible that some females died at earlier time. This is especially plausible in No. 3. In this nest only one burrow had the cell before oviposition and the number of cell per burrow was very low. On the other hand, the other two cases *could* be interpreted otherwise as given later.

3) The difference between F and B becomes greater in later nests. This would easily be explained by the gradual deaths of females. In these nests, too, the difference is always $B > F$ and not significantly high except for Nos. 11 and 15. In these two nests, the earlier deaths of some females are suggested from the relatively low number of cells per burrow inspite of such later period.

Therefore, it is assumed that the fundamental social pattern of this species is the independent activities of several females, each of them possessing her particular burrow and only sharing the entrance burrow one another. The equivalent conditions in ovaries and other features mentioned above are compatible to this interpretation. Such communal use of the entrance burrow by several independently working females are often known in some solitary bee. In Halictinae, *Pseudagapostemon* and allied genera (Michener & Lange, 1958 b; Claude-Joseph, 1926) show such social pattern.

Obviously it is possible that one and the same female successively makes two burrows. This cannot directly be confirmed in the present

Nest No.	Date	Total Number of			Number of cells and, in parentheses, youngest and oldest immature stages in each burrow ¹⁾ (*: with old adult female											Remarks
		old females	burrows	cells	A	B	C	D	E	F	G	H	I	J	K	
1	VII 5 '60	3	3	19	8* (1-5)	5* (4-6)	6* (4-5)									Still incipient nest
2	VII 17 '60	4	4	17+	5* (2-4)	9* (2-5)	3* (2-5)	7* (2-5)								Burrow D failed to examine
3	VII 20 '64	1	3	6	3 (2'-8)	2 (8)	1 (4)									Female in main burrow
4	"	7	6	32	2* (2-6)	5* (2-7)	3* (4-6)	5* (2-5)	7* (2-7)	11* (3-7)						Fig. 16. Two females in F
5	"	3	3	21	7* (5-6)	8* (2-8)	6* (2-8)									Fig. 20
6	"	9	9	56	5* (2-7)	6* (3-8)	9* (4-9)	9* (6-8)	5* (7-8)	6* (5-9)	3* (2-8)	8* (2-8)	5 (2-7)			Fig. 21. With marked variation in stages
8	VIII 22 '64	9	11	116	21 (3-8)	15* (2-7)	14* (1-8)	13* (3-8)	14 (0-7)	5* (7-8)	2* (0-1)	6* (2-7)	13* (4-7)	7 (1-7)	2 (6-2)	Fig. 19
9	"	4	5	43	17* (0-7)	4 (4)	2* (5-7)	12* (3-7)	8* (3-8)							Fig. 18
11	VII 30 '60	1	5	19	7 (1-8)	2 (2-4)	3 (4-8)	5 (1-2)	1 (5)							Female in Main burrow. E with trace of old cells
12	VIII 13 '64	0	1	1	1 (8)											Inactive since discovery
13	"	2	3	28	5* (7-13)	11* (5-14)	8 (5-11)									Fig. 24. Four cells in main burrow
13'	"	0	1	1	1 (2')											Fig. 17
14	VIII 14 '64	1	2	13	5* (6-14)	8 (7-9)										Fig. 22
15	"	1	4	25	10* (8-14)	8 (7-14)	1 (7)	6 (7-13)								
16	"	7+1	11	113	7* (5-8)	14* (5-9)	20* (2-10)	9 (7-10)	5* (5-7)	22* (6-14)	4* (7-9)	5 (7-10)	21 (2-14)	7 (7-10)	4* (7-9)	Fig. 23

1) Immature stages are numbered as in Figs. 16-24 (Cf. Legend in Figs. 16-17). Decomposed contents were given as the extremes when such cells alone exist.

species. But the following instance is suggestive to such possibility: No. 8, burrow K has only two cells of old stages and no adult female. On the other hand, burrow H has only two just constructed cells and one female.

Moreover, there are at least two items of evidence, which indicate the occasional deviation from the possession of the particular burrow by each female, that is, the use of the same burrow by two females:

1) In Nos. 8 and 16, some burrows carry very many cells, reaching 20-22 (Cf. Table), which is a little higher than the average number of cells produced by a single halictine female.

2) In No. 4, burrow F contains two females (Fig. 16). In the very burrow the number of cells is distinctly higher than in the other burrows. Moreover, there is no other burrow without adult female.

These items of evidence, especially the second one, suggest that the change to the common use of the same burrow. As to the appearance of such instance, the following phases are theoretically conceivable in halictine bees (Phase N+1 could facultatively appear in Phase N):

- I. *Solitary phase*: Each female has her own nest.
- II. *Apartment phase*: Several females are in the same nest, each of them having her particular burrow, sharing the entrance burrow alone.
- III. *Tolerance phase*: Several females work in the same burrow, each caring her own cells independently. (I→III without II is possible)
- IV. *Cooperative phase*: Several females share the same cells in building and/or provisioning, but still without division of labour among them.
- V. *Division of labour phase*: The oviposition and other activities are divided among the members of the same nest.

In *L. ohei* the final phase is apparently excluded because this postulates the caste differentiation, however incipiently. The phase I could frequently appear because the nests with only one burrow and only a few cells are occasionally discovered (Nos. 12, 13', Cf. Fig. 17). Phase II is obviously the pattern fundamental to this species with occasional appearance of II or IV. The occurrence of Phase IV is less probable but not always impossible judging from the occurrence of diverse social patterns in Halictinae (Michener, 1958; Sakagami & Michener, 1962). Deleurance (1949) observes the cooperative work of three females of *Osmia emarginata* Lepeletier, a normally strictly solitary bee, in the same nest, participating in the construction of one and the same cell.

Next the origin of composite nests must be considered. The nests containing more than one female may appear through two different ways; either by the adoption of maternal nests by several daughter

bees or by the invasion of some females to the nests solitarily started by other females, in other words, either by the *reuse of scattering* or by the *occurrence of gathering together*. The facts so far clarified in *L. ohei* upon this problem are as follows: 1) At least some nests develop by the reuse: In some earlier nests, one burrow are deeper than the other (Cf. Fig. 16, No. 4), and there are some other indication of older construction. In some other nests, old burrows are often discovered along new ones, usually without direct connection, indicating the later closing bees. 2) At least some females leave the maternal nests and start their new nests solitarily. This is confirmed by the occurrence of some small nests with only one or two burrows, or those with only a few cells headed by a single female. Furthermore, especially at the initial part of the active period, often more than one nest entrance are discovered closely together. In such instance, often one of them is provided with a large tumulus, while the other with relatively small tumulus (Figs. 22-23, but not always Figs. 18-19 indicate such instance). It is presumable that the nest with large tumulus is the old nest whereas the others are those newly made.

On the other hand, it is open to the question whether or not a composite nests are made by the later invasion of the females other than foundatrices as observed in *Pseudagapostemon divaricatus* (Michener & Lange, 1958a) and *Augochloropsis sparsilis* (Vachal) (Michener & Lange, 1958b). Many composite nests have no indication of old burrows but this might be explained by the repairing activities by the inhabitants. In No. 13, the main burrow carries four cells, containing older immature stages (Fig. 24). This might indicate the occurrence of the later union: The first female constructed her cells around the burrow made by herself, while the later invaded female made her own branch burrow.—But there is no crucial evidence to support this assumption.

It is not easy to prove the occurrence of such invasion. If a nest, the solitary foundation of which was confirmed, contained more than one female at later examination, this can be regarded as the direct evidence to support the invasion. Unfortunately we have no such observation. Another way to prove the invasion is to measure the number of old females per nest during the active period. If this value increases gradually in the course of the active period (of course before the production of new females), this may indicate the occurrence of invasion. But this method is ineffective in our instance because composite nests are common even at the earlier period.

The newly emerging bees appear from the middle of August as given in the section of phenology. These females stay at first in the main burrow (Fig. 27), but later make the hibernating burrows as mentioned in the section of nest structure. On the other hand, it is possible that some females leave the maternal nests and excavate their

own hibernating burrow. The nest shown in Fig. 26 consists of only one burrow, containing two females. There was found no branch around this burrow, either communicating with it or not. This might be the hibernating burrow excavated by the females found in it, or might represent the later phase of a small inactive nest as shown in Fig. 17. All these hibernating females are fertilized; their ovaries are rudimentary and the crop is filled with a large quantity of nectar but pollen.

In Nos. 14 (Aug. 14), 17 (Aug. 23) and 20 (Sept. 15), respectively, 1, 4 and 1 males were found in the main burrow. The males in Nos. 14 and 17 could be those soon after emergence and before departure. But it is hardly conceivable that the male taken from the last nest was in the same condition. Interestingly enough, all these males were gigantic in head form. Moreover, one of them in No. 17 was captured when entering the nest entrance after returning (or drifting from another nest ?) from the outside. Therefore, this species offers, together with *L. esoense*, a further exception concerning the habit of the halictine males, which are (in most other species so far observed) do not return to the nests after departure.

Summary

Two new Japanese halictine bees, *Lasioglossum* (*Lasioglossum*) *esoense* Hirashima et Sakagami sp. n. and *L. (Evyllaesus) ohei* Hirashima et Sakagami sp. n. were described, together with some biological notes. In both species the brood cells are connected to the main nest burrow by means of short and narrow laterals. Both species have one generation and one brood per year. *L. esoense* is strictly solitary. In *L. ohei*, many nests contain more than one burrow. Each burrow is usually occupied by one female, which seem to work in her own burrow independently from other individuals. But the occasional deviation from such social pattern, the common use of the same burrow by more than one female is suggested in some instances. *L. ohei* is remarkable by the cephalic polymorphism in males. The small males have normal head, while the larger ones monstrously developed quadruple head with enormous mandibles and genal processes. These extremes are linked with the intermediate type, forming a continuous allometric series.

References

- Alfken, J. D. 1905. Zweiter Beitrag zur Synonymie der Apiden (Hym.). Zs. Hym. Dipt., 5: 145-146.
 Blüthgen, P. 1930. Beiträge zur Synonymie der Bienengattung *Halictus* Latr. VI. Mitt. Deutsch. Entom. Ges., 70-78.

- 1931. Beiträge zur Kenntnis der indo-malayischen *Halictus*- und *Thrinchostoma*-Arten (Hym. Apidae, Halictini). Zool. Jb., Syst., 61: 285-346.
- Bonelli, B. 1948. Osservazioni biologiche sull' "*Halictus malachurus*" Kirby. Boll. Ist. Entom., Univ. Bologna, 17: 22-42.
- Cameron, P. 1897. Hymenoptera Orientalia, or contribution to a knowledge of the Hymenoptera of the Oriental zoological region V. Mem. Manchester Soc., 41: 1-144.
- Claude-Joseph, F. 1926. Recherches biologiques sur les Hyménoptères du Chili (Mélifères). Ann. Sci. Nat., Zool., (10) 9: 113-268.
- Deleurance, E. Ph. 1949. Phénomène social chez *Osmia emarginata* Lep. Bull. Soc. entom. France, 54: 9-10.
- Fries, H. 1918. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgeführt im Auftrage der Kgl. Preuss. Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. VII. Bienen aus Sumatra, Java, Malakka und Ceylon, gesammelt von Herrn prof. Dr. v. Buttel-Reepen in den Jahren 1911-1912. Zool. Jb., Syst. 41: 489-520.
- Hirashima, Y. 1957. A tentative catalogue of the genus *Halictus* Latreille of Japan, and her adjacent territories (Hymenoptera, Halictidae). Sci. Bull. Fac. Agr., Kyushu Univ., 16(1): 1-30.
- 1962. Systematic and biological studies of the family Andrenidae of Japan (Hymenoptera, Apoidea). Part 2. Systematics, 1. Journ. Fac. Agr., Kyushu Univ., 12 (2): 117-154.
- 1964. Systematic and Part 2. Systematics, 4. Journ. Fac. Agr., Kyushu Univ., 13(1): 71-97.
- (1965.) Systematic and Part 2. Systematics, 6. Journ. Fac. Agr., Kyushu Univ., 13 (3): 493-517.
- Michener, Ch. D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. Univ. Kansas Sci. Bull., 35: 987-1102.
- 1954. Bees of Panamá. Bull. Amer. Mus. Nat. Hist., 104: 1-176.
- 1958. The evolution of social behavior in bees. Proc. 10th Internat. Congr. Ent. (Montreal), 2: 441-448.
- & R. B. Lange 1958a. Observations on the behavior of Brazilian halictid bees (Hym., Apoidea). I. *Pseudagapostemon*. Ann. Ent. Soc. Amer. 51: 154-164.
- & — 1958 b. Observations on the behavior of Brazilian halictid bees (Hym., Apoidea). IV. *Augochloropsis*. Amer. Mus. Novit., 1924: 1-41.
- Noll, J. 1931. Untersuchungen über die Zeugnung und Staatenbildung des *Halictus malachurus*. Zs. Morph. Oekol. Tiere, 23: 285-368.
- Quénu, C. 1957. Sur les femelles d'été de *Halictus scabiosae* (Rossi) (Insecta, Hym.). CR. Acad. Sci. Paris, 244: 1073-1076.
- Rayment, T. 1936-37. Biology of a new halictine bee and specific description of its parasites. Arb. physiol. angew. Ent. Berlin-Dahlem 3: 289-294, 4: 30-60.
- Sakagami, Sh. F. 1964. Wiederentdeckung des Nestes einer Nachtfurchenbiene, *Megalopta* sp. am Amazonas (Hymenoptera, Halictidae). Kontyû, 32: 457-463.
- & K. Fukushima 1961. Female dimorphism in a social halictine bee, *Halictus* (*Seladonia*) *aerarius* (Smith) (Hymenoptera, Apoidea). Jap. J. Ecol., 11: 118-124.
- & K. Hayashida 1958. Biology of the primitive social bee, *Halictus duplex* Dalla Torre. I. Preliminary report on the general life history. Ann. Zool. Jap., 31: 151-155.

- & — 1960. Biology of II. Nest structure and immature stages. *Insectes Sociaux*, 7: 57-98.
- & — 1961. Biology of III. Activities in spring solitary phase. *J. Fac. Sci., Hokkaido Univ., Ser. VI, Zool.*, 14: 634-682.
- & Ch. D. Michener 1962. The nest architecture of the sweat bees. A comparative study of behavior. 135 pp. Univ. Kansas Press, Lawrence.
- & J. S. Moure (in press) Cephalic polymorphism in some Neotropical halictine bees (Hymenoptera, Apoidea). *Anais Acad. Brasil. Ciênc.*
- Tsuneki, K. 1956. On the taxonomical position, curious distribution and male polymorphism of *Ectemnius* (*Yanonius* nov.) *martjanowii* F. Morawitz 1892 (Hym. Sphec. Crabroninae). *Kontyû*, 24: 128-132.
- Wain, F. L. & Sh. F. Sakagami (in press) *Halictus latisignatus* Cameron, a polymorphic Indian halictine bee with caste differentiation (Hymenoptera, Halictidae). *Bombay J. Nat. Hist.*