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Bionomics of the Halictine Bees in Northern Japan III.
Lasioglossum (Evylaeus) allodatum, with Remarks on the Serially
Arranged Cells in the Halictine Nests¹⁾

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Abstract *Lasioglossum (Evylaeus) allodatum* EBMER et SAKAGAMI is solitary, vernal, univoltine and polylectic in northern Japan. The brood cells are arranged end-to-end serially. The presence of this nest type in the Halictinae is reviewed in connection with architectural and social evolution in the subfamily.

The present paper deals with the life cycle and nesting habits of the halictine bee *Lasioglossum (Evylaeus) allodatum* described recently as a member of the *L. nitidiusculum* group (EBMER & SAKAGAMI, 1985). *L. allodatum* arranges brood cells end-to-end serially. This arrangement is not widespread in the Halictinae. The presence of this nest type in other halictine bees is reviewed.

The field studies were mainly executed in Morioka, northern Honshu. Results of periodical samplings on flowers made in Sapporo, Hokkaido, are also incorporated.

Life Cycle

Nests of this species were discovered in 1977 on an artificial heap of humus sparsely covered with weeds in the Farm of Tohoku National Agricultural Experiment Station, together with nests of *L. sakagamii* reported previously (Fig. 1 in SAKAGAMI *et al.*, 1982). Nests of *L. sakagamii* were abundant on the E to SE slope while those of *L. allodatum* more on the N-slope. Nest contents examined by periodical excavations revealed a univoltine life cycle (Table 1).

Seasonal change of extranidal activities was observed in 1979 at irregular intervals. The first female was found on April 19. Flights of females searching for nesting places continued till late May and foraging flights from early May to early June, most actively in mid May. From Table 1 the duration from oviposition to pupation is roughly estimated at one month as in *L. sakagamii*. The dura-

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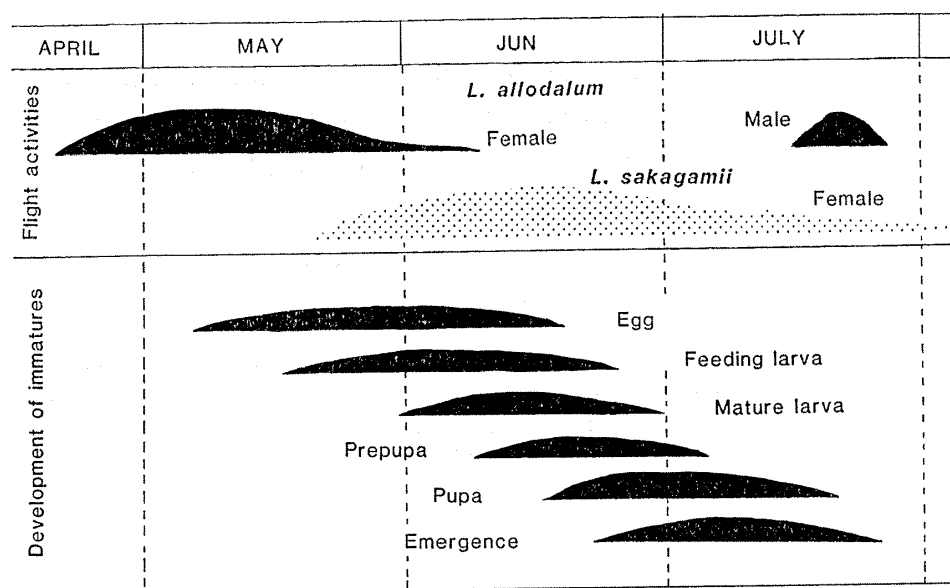


Fig. 1. Annual cycle of *L. allodalum* in Morioka. Flight activity of *L. sakagami* presented synoptically. On the local climate see Fig. 15 in SAKAGAMI *et al.*, 1982.

Table 1. Seasonal change of nest contents in *L. allodalum* given by the number of immatures or cells of successive stages (Morioka, results of 1977 and 1979 combined).

Successive Stage	Date									Total
	V	VI					VII	VIII		
	24	1	7	10	17	30	9	21	1	
Empty cells	1	1	1							3
Pollen balls		3	2							5
Eggs	1	8	8		2					19
Feeding larvae	5	11	4	2	2					24
Mature larvae*			9	3	1	1				14
Prepupae			1		4	2				7
Pupae					4	1	1	4		10
Total	7	23	25	5	13	4	1	4	0	82
No. of nests examined	2	18	13	2	10	3	2	1-3?	0	

* Post-feeding, pre-defecating larvae.

tion of prepupal stage was 5–6 days ($n=3$) and of pupal stage 14–16 days ($n=4$), both seemingly shorter in males. Most individuals reared in the laboratory emerged in early July but some ones in mid July. Males patrolled over the nesting area around July 20 but no flights of newly emerged females were seen there. Possibly they overwinter elsewhere. Fig. 1 summarizes the phenology of *L. allodalum* shown synoptically with that of *L. sakagami* nesting at the same place. Although the nesting activities of both species overlap considerably, the peak period is clearly

Table 2. Seasonal changes of mandibular wear and head width of females periodically sampled in Sapporo (1959) and Nokanan and Yukomanbetsu (1967 & 1968).

Sapporo		Date						
		IV 21	V 6	V 23-27	VI 4-6	VI 10	VI 18	VI 22
Degrees of* mandibular wear	I	1	1	3		1		
	II			5	3	1		
	III			1	1	4		1
	IV+V			1	1	4	2	
Total		1	1	10	5	10	2	1
Head width (mm)	1.55-			1				1
	1.60-			2		1		3
	1.65-			1	1	3	1	6
	1.70-			4	1	2		8
	1.75-	1	1	1	3	4	1	11
	1.80-			1				1

Nokanan (in parentheses) & Yukomanbetsu		Date							
		V 16	VI 8	VI 22	VII 6	VII 22	VIII 8	IX 6	IX 21
Degrees of mandibular wear	I	1 (3)						(1)	(1)
	II	1	28 (1)						
	III		58 (1)	4 (2)	1	(1)	(1)		
	IV+V		3	4 (2)	1	(5)			
Total		2(3)	89 (2)	8 (4)	2	(6)	(1)	(1)	(1)

* I=intact, II=slightly worn, III=distinctly worn, IV+V heavily worn (SAKAGAMI, 1974).

segregated from each other.

Table 2 (top) depicts the phenology of adult females in Sapporo, Hokkaido (43°03'N) captured on flowers by periodical bee samplings in 1959 on the campus of Hokkaido University including the Botanical Garden (SAKAGAMI & FUKUDA, 1973, this species is coded as *carinaless-Evylaeus* sp. 9). A total of 30 females and two males (July 8 and 27 respectively) collected occupied only 0.46% of all wild bees (6,843 individuals) or 0.83% of all halictine bees (3,838) sampled. The gradual increase of mandibular wear revealed again a univoltine life cycle, with a delay of about half a month from the sequence in Morioka (39°45'N), reflecting the latitudinal difference of the two localities. The absence of seasonal difference in head width of females also confirms a univoltine life cycle not accompanied with size-linked caste differentiation. The mean head width of females is 1.70 ± 0.06 mm and the coefficient of variation is 3.5%, which is within the range of those in some solitary bees given by LIN and MICHENER (1972). In 1964 ten females were collected during May 14 and June 18. All of them were inseminated with ovaries fully

developed, except for three females captured on June 16–18, which showed the beginning of degeneration with relaxed ovarioles or distinct corpora lutea. Table 2 (bottom) also shows phenology studied similarly at Nokanan (400 m alt.) and Yukomambetsu (1000 m) near Asahigawa (43°46'), central Hokkaido. The univoltine life cycle is obvious at these higher localities, too.

Thus, this species is univoltine, vernal and solitary in both Morioka and Hokkaido. Moreover, the paucity of males, which are collected much later not always accompanied by new females is also common in both areas. This tendency is also found in some other *Evylla* species and probably reflects differential responses of newly emerged females and males as for flower visits. How the populations south of Morioka behave seasonally is unknown. All females so far sporadically known from central Japan have been collected in April and May and one male (Gifu) in August and another (Fukui) in July. These poor records suggest the life cycle of southern populations similar to that in northern Japan, but further critical studies are requested.

A similar phenology, abundant females in spring and rare males in summer, is also recognized in the closest species *L. parvulum* in and near Linz, Austria (EBMER, 1971 cited as *L. minutum*, p. 145, fig. 123). BONELLI (1954, cited as *Halictus minutus* SCH.) published brief notes on diurnal activity and nests of this species studied in Sunninghill, England and assumed the univoltine cycle there. Little is known on the life cycle of other allied species. KNERER (1968) cited *L. rufitarse* as a solitary species without detailed documents.

Associated Animals and Flower Visits

The following two parasite species were reared from nests.

The parasitic halictine bee *Sphecodes etizenensis* TSUNEKI (♀, = *Sph. okuyetsu* TSUNEKI, ♂): One mature larva (June 17), one feeding larva, two prepupae and one pupa (June 30), two pupae (July 9), four pupae, two male adults and three female adults (July 16). The durations of both prepupal and pupal stages (respectively, 3–4 days, $n=5$; 12–13 days, $n=5$) are slightly shorter than those of the host but the emergence took place later (July 10–20, $n=7$). Flights of females were seen from mid May to late June at the nesting area.

The anthomyiid fly *Leucophora sponso* (MEIGEN). Two larvae from one brood cell on June 1 (Fig. 12) and also two from one cell on June 7, and five puparia each from one cell on July 21. Adults of this fly were seen at the nesting area since May. This species also infests the immatures of *L. sakagami* (SAKAGAMI *et al.*, 1982). BONELLI (1954) reported *Sphecodes* sp. and a fly *Haemmonyia griesea* as parasitic on the closely allied species, *L. parvulum*, in England.

The following records of flower visits taken at five localities indicate that *L. allodahum* is polytrophic as are most halictine bees (Number of records in parentheses, a single record if unmentioned. Plants marked with p and e are respec-

tively pollen sources, and either exotic or cultivated plants).

Yukomanbetsu: Females. *Aruncus sylvestris* (2)^p, *Lactua raddeana* (3), *Anaphalis margaritacea* var. *angustior* (2), *Aster glehni*, Male. *A. m.* var. *angustior*.

Nokanan: All females. *Prunus* sp., *Taraxacum officinale* (17)^{pe}, *Brassica campestris* (140)^{pe}, *Chelidonium majus* var. *asiaticum*, *Iris pseudacorus* (2)^{pe}, *Erigeron annuus* (2)^c.

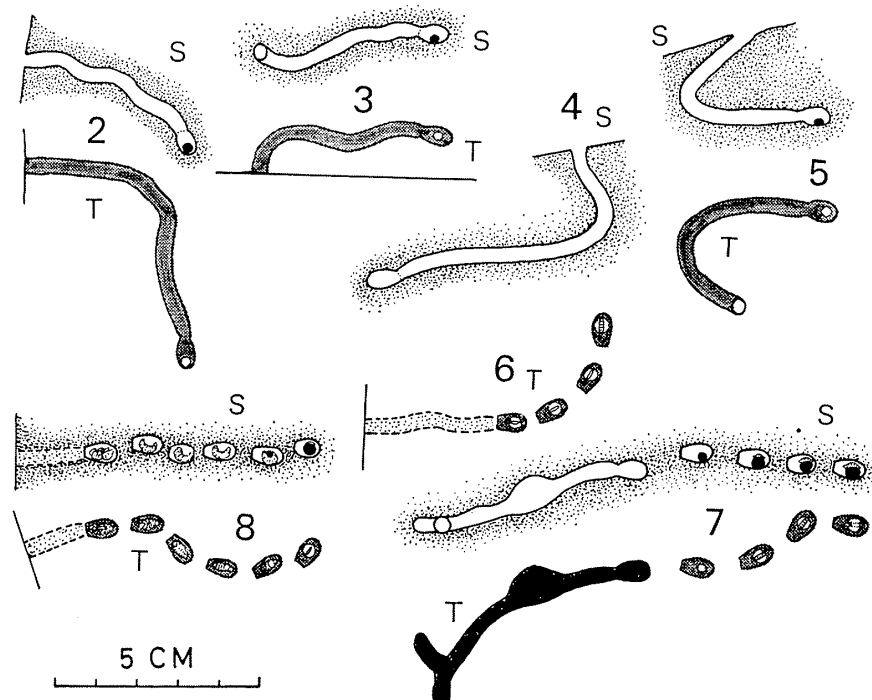
Sapporo: Females. *Gagea lutea*, *Taraxacum officinale*^{pe}, *Malus asiatica* (5)^p, *Spiraea betulifolia* var. *grandifolia* (8)^p, *Geranium erianthus* (2)^p, *Dentaria leucana*^p, *Brassica campestris* (3)^{pe}, *Spiraea cantoniensis* (20)^e, *Weigelia hortensis*^p, *Allium festulosum*^e, *Crataegus cuneata* (3)^{pe}, *Rosa rugosa*^p, *Salvia officinalis*^e, Males. *Deutzia crenata*, *Rudbeckia laciniata*^e.

Morioka: All females. *Petasites japonicus* var. *giganteus* (2)^p, *Salix* spp. (17)^p, *Prunus* spp. (5)^p.

Rifucho near Sendai: All females. *Copsella bursa-pastor*, *Ranunculus japonicus*, *Salix* sp. *Erigeron annuus*^e, *E. philadelphicus*^e, *Wisteria floribunda*.

Nest Architecture

Nest pattern II in SAKAGAMI and MICHENER (1962) and SAKAGAMI (1974), i.e.

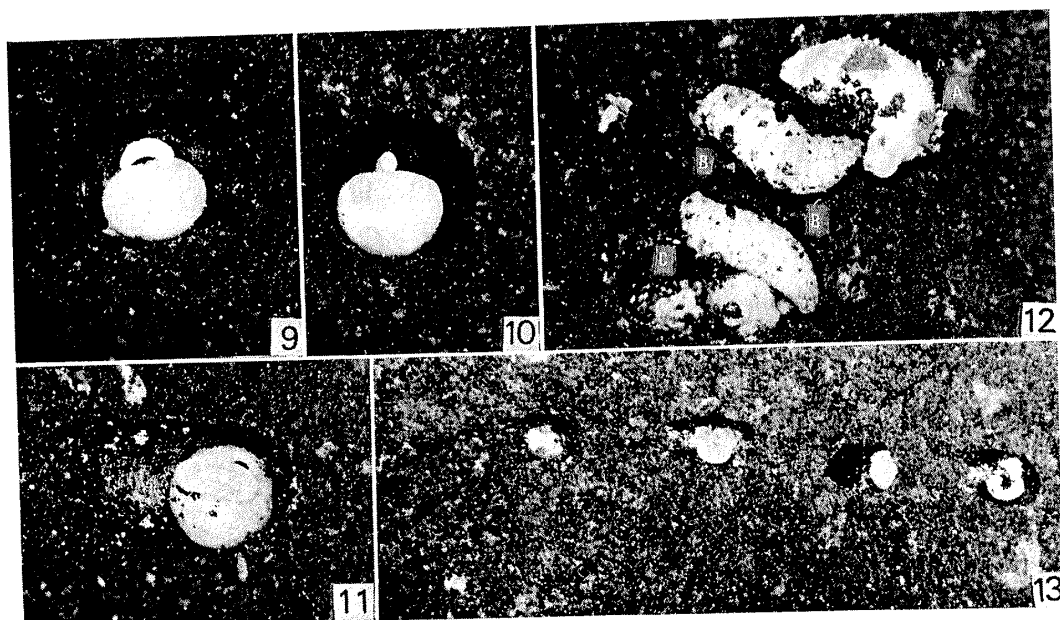


Figs. 2-8. Nests of *L. allodalum* S=side view, T=top view. — 4-5, In horizontal ground, all others in vertical wall; 2-5, young nests with only one cell; empty in 4, with pollen ball in others (2, 3, VI 1, '77; 4, 5, VI 7, '79); 6, nest with four cells, from the bottom, one feeding larva and three eggs on pollen balls, (VI 7, '79); 7, nest with five cells, three feeding larvae, one pollen ball and one empty cell (7 VI '77); 8, nest with six cells, from the bottom, one dead egg, one feeding larva, two mature larvae and one black pupa.

cells arranged end-to-end serially, the pattern relatively rare in Halictinae.

Entrance 3–4 mm in diameter, slightly to seldom constricted, provided with neither conspicuous tumulus nor turret. No special enlargement immediately below entrance. Main burrow 3.5–4 mm wide, wall more or less smooth but not polished, the main direction horizontal (Figs. 3, 7, 8) or slightly slanting (Fig. 2), sharply bending below the entrance when excavated in horizontal ground (Figs. 4, 5), without ramification (except a nest shown in Fig. 7 with a short branch and an enlargement amid the burrow), length of burrow 10–13 cm. Cells arranged serially, starting from the bottom of the burrow, *i.e.* terminal blind burrow characterizing most halictine nests absent (Figs. 6–8, 13). Cells (Figs. 9–11, 13) oval, bilaterally symmetric with bottom slightly but not conspicuously flatter, 8 cm long, 4 mm in diameter, with the neck 2.5 mm wide, the inner wall smooth and polished, without copious waxy coating, built horizontally or the rear end slightly slanting. Successive cells lying along the mid-line of the burrow but with occasional deviations (two bottom cells in Figs. 7, 8). Space of burrow between two successive cells filled with soil for 4–7 mm (Figs. 6–8, 13). Number of cells per nest 4–6. After completion of the last cell, remaining section of main burrow filled with soil to entrance (Figs. 6–8). Pollen ball 2.6–3.2 mm in diameter and 2.1–2.4 mm high, upper surface flatter; egg 1.6–1.7 mm long and 0.4–0.5 mm wide (Figs. 9, 10).

The nest architecture of this species is peculiar by the poor development of entrance constriction, serially arranged cells, cells not conspicuously flatter below, the absence of blind burrow, the main burrow filled with soil after brood rearing,



Figs. 9–13. Brood cells of *L. allodalum*. — 9–10, Cell with an egg on pollen ball (longitudinal and cross sections); 11, cell with medium feeding larva on pollen ball (top view); 12, cell infested by *Leucophora* (A: host larva; B: parasite larvae; C: pollen residue); 13, serially arranged cells (=nest in Fig. 7, side view).

all uncommon in the halictine nests, rather resembling nests of some *Andrena* species. Serially arranged cells are also recorded in an allied species, *L. n. nitidiusculum* (KNERER, 1969, cited as *Evyllaesus minutus*. The material was later re-studied by EBMER), although the nest has the ramification and lower blind burrow (see Section III). On the other hand, cells connected to the main burrow by short and narrow laterals, the pattern widespread in the carinaless *Evyllaesus* groups (Type IIIa in SAKAGAMI, and MICHENER, 1974; Ia in SAKAGAMI, 1974 and Fig. 14) were reported in *L. parvulum* (BONELLI, 1954; cited as *Halictus minutus* SCH., det. O. W. RICHARDS), the species closest to *L. allodatum* (EMBER & SAKAGAMI, 1985). No nests of the other species of the *L. nitidiusculum* group are known. HAESELER (1978) reported nesting of *L. rufitarse* in peat, a nest substrate unusual for halictines, but did not describe the nest pattern.

Notes on Serial Nests in the Halictine Bees

The simplest type of aculeate nests excavated in substrates is the unicellular nest, consisting of a single burrow leading to a brood cell. Nests of this type are frequently found in wasps and some of them may represent the most primitive step of aculeate nests. In bees, however, the unicellular nests are less common and appear in several different phyletic lines (STEPHEN *et al.*, 1969). In halictine bees the unicellular nest is known only in *Lasioglossum* (*Chilalictus*) *victoriellum* and possibly of the secondary origin as an adaptation to loose sandy substrate (SAKAGAMI & MICHENER, 1964). The prevailing nest type which is regarded as most primitive in soil nesting bees is that containing several brood cells which are connected with the main burrow by means of laterals, the latter being filled with soil after oviposition. In Halictinae, too, this type is widespread and characterized by the laterals which are narrower than the main burrow. Two features, constriction of the entrance and excavation of the terminal blind burrow, are also predominant in the subfamily. Fig. 14 shows the possible evolution of various halictine nest patterns starting from the above type (Ia) (revised from SAKAGAMI & MICHENER, 1962; SAKAGAMI 1974; EICKWORT & SAKAGAMI, 1979).

There are two principal ways of evolution. One way starts from type Ia and, through shortening of laterals (IIIa) and preparation of lateral burrows or cavities around the cell cluster (IIIc, III'c), attains the preparation of the cell cluster usually built within the cavity (IV and IV'). The other way is the preparation of end-to-end arranged serial cells as found in *L. allodatum* (Ia-Ic-II). The three tribes of Halictinae behave differently as to the nest types they developed. In the tribe Nomioidini, inhabitants of arid and warm Old World regions, only type Ia has been so far recorded (MARIKOVSKAYA, 1972), although an interesting advance (Ic) is mentioned by BATRA (1966) and RADCHENKO (1979). The tribe Augochlorini, confined to Western Hemisphere, behaves oppositely (EICKWORT & SAKAGAMI, 1979). Its most genera exhibit well evolved types (III'c, IC or IV') and the only known

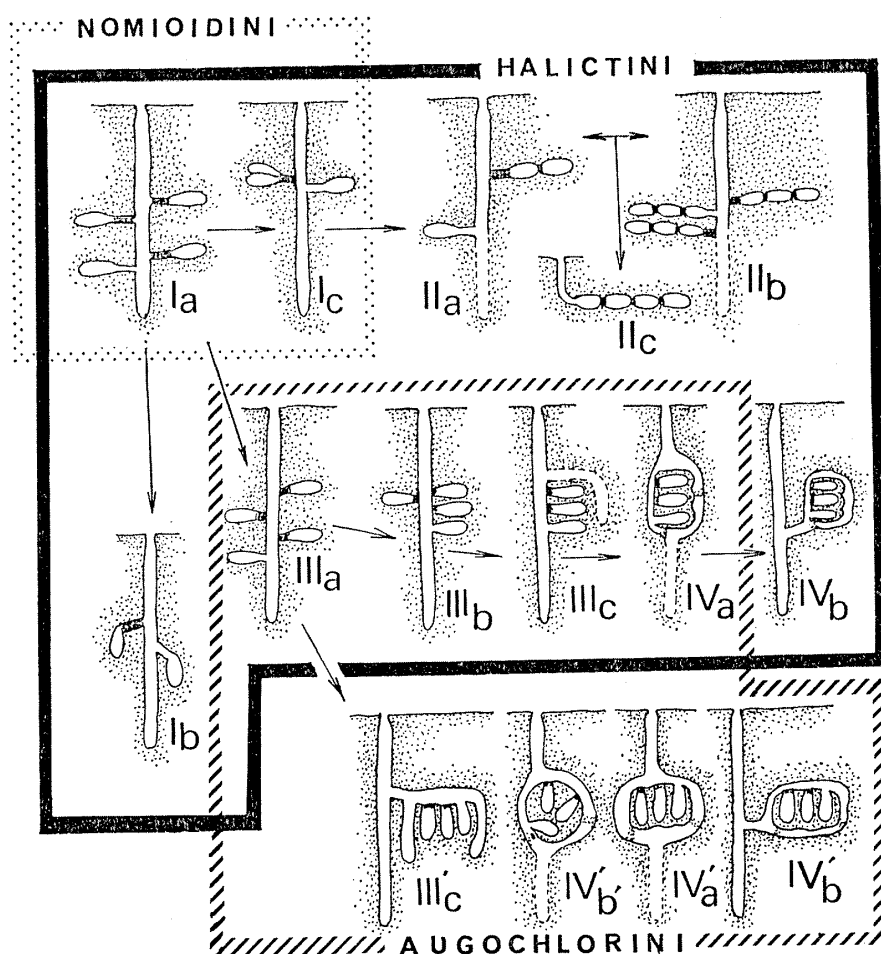


Fig. 14. Various nest types in three tribes of the Halictinae and their possible evolutionary courses. As for details on Augochlorini see EICKWORT and SAKAGAMI (1969).

case of type III (*Augochlora semiramis*) is possibly of secondary acquisition. Serially arranged cells have not been recorded in the both tribes.

The cosmopolitan tribe Halictini developed the both ways mentioned above. Serial cells are sporadically found in diverse genera, with variations concerning three aspects. (I) The lower blind burrow is present (B_1) or absent (B_2). The latter state is known obligatorily only in *L. allodalum*. (2) Cells are arranged in a single series, (O_1), or in multiple series, (O_2), which correspond to allodalous and parodalous nests by MALYSHEV (1935). (3) Number of cells per series is small 1–2 at most 3 (N_1) or often more (N_2). These items are affected by sociality. In communal nests the number of cell-series per nest and that of cells per series can increase, although the number of cells per series seems to remain small in some communal *Agapostemon* species. Previous records of serial cells are summarized as follows (known communal cases shown with asterisks): *Ruizantheda mutabilis* (CLAUDE-JOSEPH, 1926, Chile, $B_1O_2N_2$, cf. EICKWORT, 1969); *Pseudagapostemon*

*divaricatus** and *P. perzonatus** (MICHENER & LANGE, 1958, Brazil, B₁O₂N₂); *Agapostemon nasutus*, (DALY & WILLE, unpub.; cf. SAKAGAMI & MICHENER, 1962, Costa Rica, B₂O₂N₁; serial cells were not found by EICKWORT & EICKWORT, 1969, though the communal life was confirmed); *A. sericeus*, *A. cockerelli**, *A. texanus**, *A. angelicus* and *A. splendens* (EICKWORT, 1981, U.S.A., B₁O₂N₁); *A. virescens**, (ABRAMS & EICKWORT, 1980, New York, B₁O₂N₁), *Lasioglossum* (*Lasioglossum*) *bimaculatum* (recorded as *Evyllaesus*), *L. (Evyllaesus) nitidiusculum* (recorded as *E. minutus*), (KNERER, 1969, C. Europe, B₁O₂N₁₍₂₎); *L. (E.) allodolum* (B₂O₁N₂); *L. (Chilalictus) inclinans**, *L. (C.) lanarium** and *Homalictus demissus** (SCHWARZ & KNERER, 1976, 1978, Australia, B₁O₂N₂ or in *H. demissus* B_{1.2}O₂N₂); *Lasioglossum* (*Ctenonomia*) *albescens**, (SAKAGAMI, 1968, Malaya, B₁O₂N₂; MATSUMURA & SAKAGAMI, 1971, Nepal, B₂O₂N₁; serial cells not found by BATRA, 1977).

Probably the first step to serial cells was Ic in Fig. 14, where two cells are prepared at the end of a lateral. This state is known in *Nomioides variatgatus* (BATRA, 1966) and *N. minutissimus* (RADCHENKO, 1975) and suggested in some nests of *Agapostemon* (e.g. *A. cockerelli* and possibly *A. texanus*, EICKWORT, 1981). In this genus, formation of serial cells is facultative (cf. also ROBERTS, 1969) and the number of cells per series is mostly 1–2, even though the total number of cells per nest is sometimes very high in communal species. Moreover, in some carefully studied species (ABRAMS & EICKWORT, 1980; EICKWORT, 1981), laterals are always narrower than the main burrow. These features indicate the evolution of serial cells from Ia (not from IIIa), via Ic to IIa (B₁O₂N₁) and further IIB (B₁O₂N₂), that is, parodalous nests seem to be ancestral to allodalous nests which are known so far only in *L. allodolum*. Nest of this species has lost the laterals as like in type IIIa (Fig. 14). The diameter of the main burrow is about equal to that of cells.

Increase of cells per series (N₁→N₂) assumed above may represent a specialized condition implying an advanced labor economy. But the small number of cells per series may not necessarily be primitive. Many cells per series evoke two demerits: (1) emerged adults in the older cells must postpone their departure until emergence of the younger sibs, that is, labor economy is counteracted by time loss. (2) Work in a narrow lateral in which cells are serially prepared may be ineffective when two or more females stay there. The first demerit may be overridden if the older sibs can pass through the younger sibs without injuring them. Such trait is known in *Ceratina* bees (SAKAGAMI & MAETA, 1977) but so far in no halictine bees. A relatively small number of cells per series might be retained or regained as a compromise.

The second demerit, combined with the first one, may partly explain why no social levels higher than communal life (MICHENER, 1974) have evolved in the halictine species which adopted the serial arrangement of cells. In most communal species with serial cells, each lateral may not be shared by multiple females. It is interesting that the entrance of laterals to the main burrow is constricted in two *Pseudagapostemon* species (MICHENER & LANGE, 1958) as in the entrance of most

halictine nests.

The absence of the lower blind burrow may be facultative in some species but is obligatory in *L. allodatum*. Another frequently observed feature is branching of the main burrow. This appears to be commoner in communal species. However, KNERER (1969) illustrated a ramified nest of *L. nitidiusculum*, the solitary species close to *L. allodatum*. Although the both species prepare serially arranged cells, the nest patterns seem to be fairly different. Further, nests of *L. parvulum*, the species closest to *L. allodatum*, were the branched type (Ia in Fig. 14; BONELLI, 1954). Discovery of nests of other species in the *L. nitidiusculum* group is requested to clarify the evolution of serial cells in the halictine nests.

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References

- ABRAMS, J. & G. C. EICKWORT, 1980. Biology of the communal sweat bee *Agapostemon virescens* (Hymenoptera: Halictidae) in New York State. *Search Agriculture*, **1**: 1-19.
- BATRA, S. W. T., 1966. Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). *Ind. J. Ent.*, **28**: 375-393.
- BONELLI, B., 1954. Osservazioni biologiche sull' *Halictus minutus* SCH. *Boll. Soc. ent. Ital.* **84**: 18-21.
- CLAUDE-JOSEPH, F., 1926. Recherches biologiques sur les Hyménoptères du Chili (Mellifères). *Ann. Sci. Natur. Zool.*, (10)**9**: 113-268.
- EBMER, A. W., 1971. Die Bienen des Genus *Halictus* LATR. s.l. im Grossraum von Linz (Hymenoptera, Apidae). III. Nat. Jb. Linz, **1971**: 63-156.
- & Sh. F. SAKAGAMI, 1985. Taxonomic notes on the Palaearctic species of the *Lasio-glossum nitidiusculum* group, with description of *L. allodatum* sp. nov. (Hymenoptera, Halictidae). *Kontyû, Tokyo*, **53**: 297-310.
- EICKWORT, G. C., 1969. Tribal positions of Western Hemisphere green sweat bees, with comments on their nest architecture (Hymenoptera: Halictidae). *Ann. Ent. Soc. Amer.*, **62**: 652-660.
- 1981. Aspects of the nesting biology of five Nearctic species of *Agapostemon* (Hymenoptera: Halictidae). *J. Kansas Ent. Soc.*, **54**: 337-351.
- & K. P. EICKWORT, 1969. Aspects of the biology of Costa Rican halictine bees, I. *Agapostemon nasutus* (Hymenoptera: Halictidae). *J. Kansas Ent. Soc.*, **42**: 421-452.
- & Sh. S. SAKAGAMI, 1979. A classification of nest architecture of bees in the Tribe Augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian nest of *Rhinocorynura inflaticeps*. *Biotropica*, **11**: 28-37.
- HAESLER, V., 1978. Zum Auftreten aculeater Hymenopteren in gestörten Hochmoorresten des Fintlandsmoores bei Oldenburg. *Drosera* **78**: 57-67.
- KNERER, G., 1968. Zur Bienenfauna Niederösterreich. Die Unterfamilie Halictinae. *Zool.*

- Anzeiger*, **181**: 82-117.
- 1969. Synergistic evolution of halictine nest architecture and social behavior. *Canad. J. Zool.*, **47**: 925-930.
- & M. SCHWARZ, 1976. Halictine social evolution: The Australian enigma. *Science*, **194**: 445-448.
- & ——— 1978. Beobachtungen an australischen Furchenbienen (Hymenopteren; Halictinae). *Zool. Ang.*, **200**: 321-333.
- LIN, N. & C. D. MICHENER, 1972. Evolution of sociality in insects. *Quart. Rev. Biol.*, **47**: 131-159.
- MALYSHEV, S., 1935. The nesting habits of solitary bees. A comparative study. *Eos*, **11**: 201-309.
- MARIKOVSKAYA, T. P., 1972. Biologii pchelinikh (Apoidea) Yugo-vostoka Kazakhstana. *Trud. Vsesoyuzn. Entom. Obschtsch.*, **55**: 187-216.
- MATSUMURA, T. & Sh. F. SAKAGAMI, 1971. Bees from Nepal II. *Lasioglossum albescens*, with some bionomic notes. *Annot. Zool. Jap.*, **44**: 47-55.
- MICHENER, C. D., 1974. *The social behavior of the bees. A comparative study.* xi+404 pp. Harvard Univ. Press, Cambridge.
- & R. B. LANGE, 1958. Observations on the behavior of Brazilian Halictid bees (Hymenoptera, Apoidea) I. *Pseudagapostemon*. *Ann. Ent. Soc. Amer.*, **51**: 155-164.
- RADCHENKO, V. G., 1979. Gnezdozovanie pcheli *Nomioides minutissimus* (Rossi). (Hymenoptera, Halictidae). *Ent. Obozr.*, **58**: 762-765.
- ROBERTS, R. B., 1969. Biology of the bee genus *Agapostemon* (Hymenoptera: Halictidae). *Univ. Kansas Sci. Bull.* **48**: 689-719.
- SAKAGAMI, Sh. F., 1968. Nesting habits and other notes on an Indomalayan halictine bee, *Lasioglossum albescens*, with description of *L. a. iwatai* ssp. nov. *Malay. Natr. J.*, **21**: 85-99.
- 1974. Sozialstruktur und Polymorphismus bei Furchen- und Schmalbeinen (Halictinae). In SCHMIDT (ed.), *Sozialpolymorphismus bei Insekten. Probleme der Kastenbildung im Tierreich*, pp. 257-293. Wiss. Verlagsgesellschaft, Stuttgart.
- , A. W. EBMER, T. MATSUMURA & Y. MAETA, 1982. Bionomics of the halictine bees in northern Japan II. *Lasioglossum (Evylaeus) sakagamii* (Hymenoptera, Apoidea, Halictinae), with taxonomic notes of allied species. *Kontyû, Tokyo*, **50**: 198-211.
- & H. FUKUDA, 1973. Wild bee survey at the campus of Hokkaido University. *J. Fac. Sci. Hokkaido Univ., Zool.*, **19**: 190-250.
- & Y. MAETA, 1977. Some presumably presocial habits of Japanese *Ceratina* bees, with notes on various social types in Hymenoptera. *Insects Sociaux*, **24**: 319-343.
- & C. D. MICHENER, 1962. The nest architecture of the sweat bees. A comparative study of behavior. 135 pp., Univ. Kansas Press, Lawrence.
- STEPHEN, W. P., G. E. BOHART, & P. F. TORCHIO, 1969. The biology and external morphology of bees, with a synopsis of the genera of northwestern America. 140 pp., Dept. Printing, Oregon State Univ., Corvallis.