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**Nest Architecture and Related Notes of Stenogastrine Wasps
in the Province of Sumatera Barat, Indonesia
(Hymenoptera, Vespidae)¹⁾²⁾**

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Abstract Seventeen types of stenogastrine nests are described from the Province of Sumatera Barat. Of these, four belong to the genus *Liostenogaster*, four to *Eustenogaster* and nine to *Parischnogaster* (6 types belonging to the *striatula*-group, one to the *mellyi*-group and two to the *jacobsoni*-group). The material and architecture of nests vary considerably by species, though the basic features are to some degree taxon-specific at generic or specific level. All the nests examined are devoid of petiole. Typical comb is rather rare, mostly irregular and more or less disintegrated. In some nests of *Liostenogaster* and *Parischnogaster*, cells are arranged even separately on the flat substrate surfaces. Outer envelope is lacking in most types. In *Eustenogaster*, an envelope is built as an extension of walls of peripheral cells (=pseudenvelope), and in the *striatula*-group, a passage-way (a communal space surrounded by a modified pseudenvelope and walls of neighboring cells), to which cells open, is prepared.

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Introduction

The stenogastrine wasps are small, inconspicuous and secretive insects, but they are remarkable by an extreme diversity of nest architecture, as well as very primitively social organization (WEST-EBERHARD 1978). Such a diversity is fascinating from the point of comparative ethology and ultimately of evolutionary considerations, since the nest architecture represents the frozen behavior of wasps. Nevertheless, our knowledge of this aspect has remained fragmentary. Up to now, a total of about 25 types of nests belonging to five genera by a recent taxonomic system (*Liostenogaster*, *Eustenogaster*, *Parischnogaster*, *Metischnogaster*, and *Stenogaster*; VAN DER VECHT 1977) have been recorded (WILLIAMS 1919, PAGDEN 1958, IWATA 1967, 1976, SAKAGAMI and YOSHIKAWA 1968, YOSHIKAWA *et al.* 1969, SPRADBERRY 1975, VAN DER VECHT 1977).

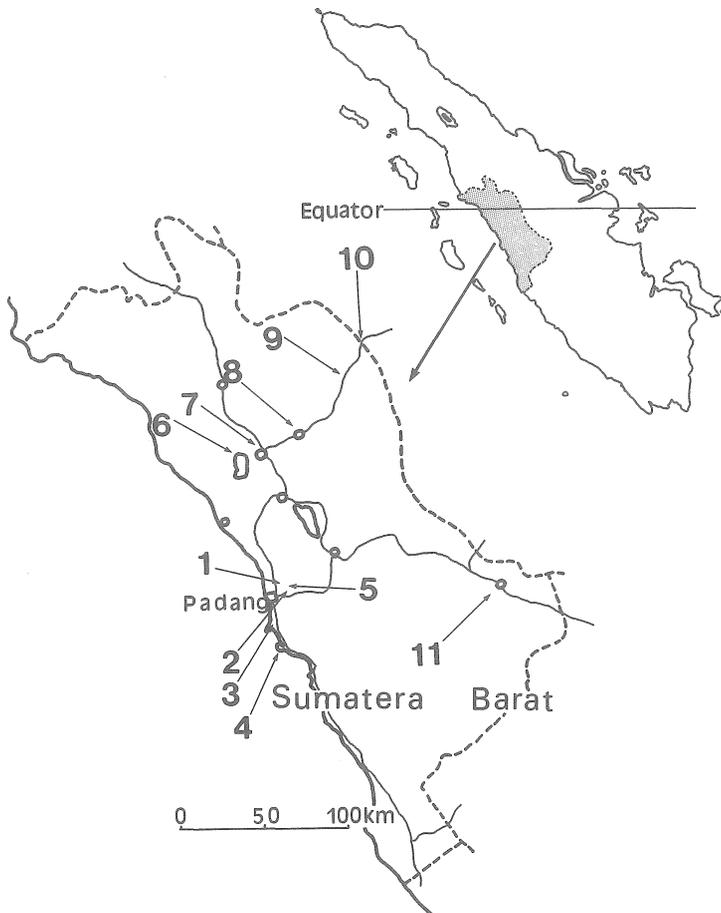


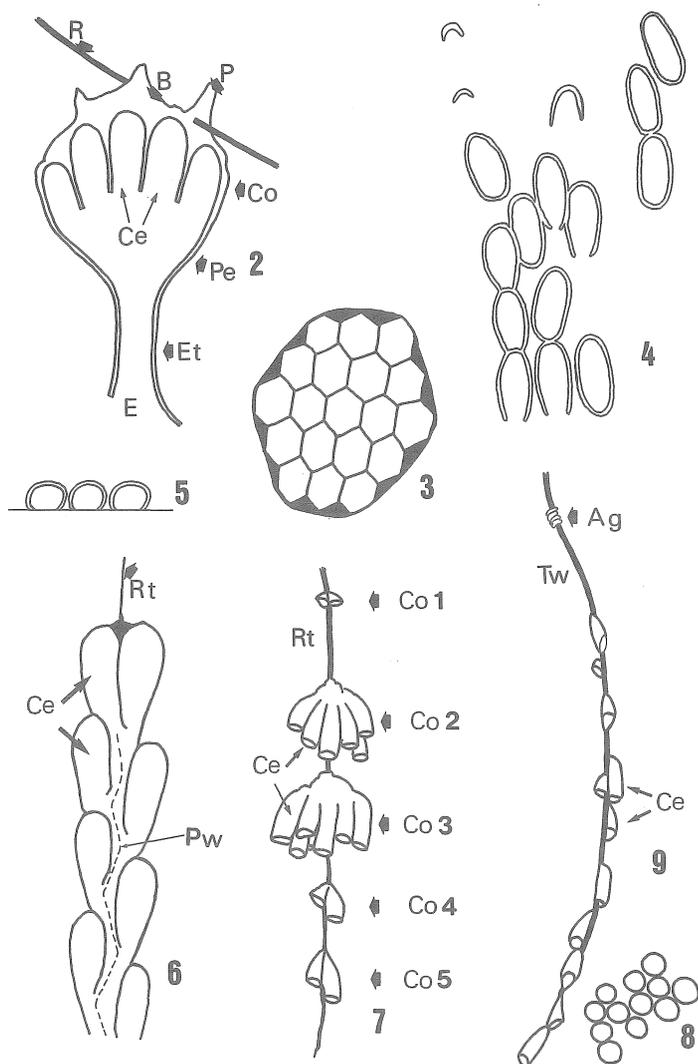
Fig. 1. Map showing localities of discovery and/or collection of stenogastrine nests in Sumatera Barat. 1. Lubuk Mintrun, 2. Ulu Gadut, 3. Teluk Kabung, 4. Siguntur Tua, 5. Limau Manis, 6. Muko Muko (Maninjau), 7. Bukittinggi, 8. Payakumbuh, 9. Lubuk Bangku, 10. Kota Alam, 11. Sungai Dareh

As the first report of a serial study on the architecture and related problems of stenogastrine nests, the present paper describes 17 types of nests, belonging to three genera (*Liostenogaster* : 4 types ; *Eustenogaster* : 4 types ; and *Parischnogaster* : 9 types), and gives a preliminary discussion on the stenogastrine nest architecture. The descriptions are based on surveys made in the Province of Sumatera Barat, Indonesia during 1980 and 1981, as a part of the Sumatra Nature Study (SNS) Project attended by Japanese and Indonesian scientists. Main collection localities are : in and near Padang (coastal zone), Bukittinggi and Payakumbuh (highlands at 500-1000m alt.), and Sungai Dareh (lowland area of the interior) (Fig. 1). The majority of the specimens are deposited in the Department of Biology, Kanazawa University and partly at SNS Laboratory, Andalas University, Padang. Because of an extreme taxonomic difficulty of Stenogastrinae, only three types were identified to the species, i.e., *Parischnogaster striatula*, *P. alternata* and *P. mellyi*, while the others only to generic or species group level. The material will be compared later with the taxonomic results now in progress by Dr. J. VAN DER VECHT, Leiden.

In addition to above, we have some other types of nests collected by two of us (RO and SFS) and Dr. K. YOSHIKAWA, during the Osaka City University 4th and 5th Scientific Expeditions to Southeast Asia (Malaya, Sabah, Sarawak, Thailand, Cambodia, etc.) sent in 1964-1966. The results were partly published (SAKAGAMI and YOSHIKAWA 1968, YOSHIKAWA *et al.* 1969), but main the bulk has remained untouched. These materials will be described subsequently, followed by an evolutionary consideration.

Terminology

The stenogastrine nests are characterized by the absence of the *petiole*, which is common to most vespine and polistine nests. Nests consist of several to some ten cells, rarely reaching a hundred, at least some of which are directly attached to the substrate. Cells are either arranged so as to form a single flat *comb* (Figs. 2, 3) or irregular comb(s) (Figs. 7, 8), or placed even separately or contiguously on a flat substrate (Figs. 4, 5). Nests of *Eustenogaster* (Fig. 2) have a single-layered envelope. Its lower, or apical, part is gradually or abruptly narrowed to form an *entrance tube*, at the apex of which an *entrance* opens. But except for one type (E_4), the envelope is structurally different from those made by vespine and polistine species in the point that it is never independent from the comb but merely an extension of outer walls of peripheral cells (= *pseudenvelope*, Fig. 2). Nests of the *striatula*-group have a peculiar structure called *passage-way*, a kind of modified pseudenvelope to which cells open (Fig. 6). Some species of the *jacobsoni*-group prepare *ant guard*, snail shell-like structure made from a material secreted from the abdominal tip of females, on the moderately but not much thin supporting substrate of the nests at a point close to or slightly distant from the basalmost cell (Fig. 9). Sizes of cells were measured as follows : Diameter (D, length between hexagonal sides in case of hexagons), length (L, measured for completed cell), and thickness of wall (T). Comb and other parts were also measured if necessary.



Figs. 2-9. Schematic representation of the architecture of representative stenogastrine nests. 2: Enveloped nest of *Eustenogaster*; 3: Ditto, comb seen from bottom; 4: Scattered arrangement of cells in *Liostenogaster*; 5: Ditto, cells seen from orifices; 6: Nest of *Parischnogaster striatula* showing the communal passage way; 7: Multiple-combed nest of *P. mellyi*; 8: Ditto, a comb with cells arranged irregularly, seen from bottom; 9: Linear nest of the *P. jacobsoni*-group, showing an ant guard.

Ag. ant guard, Ce. cell, Co. comb, E. entrance, Et. entrance tube, Pe. pseudenvelope, Pw. passage way.

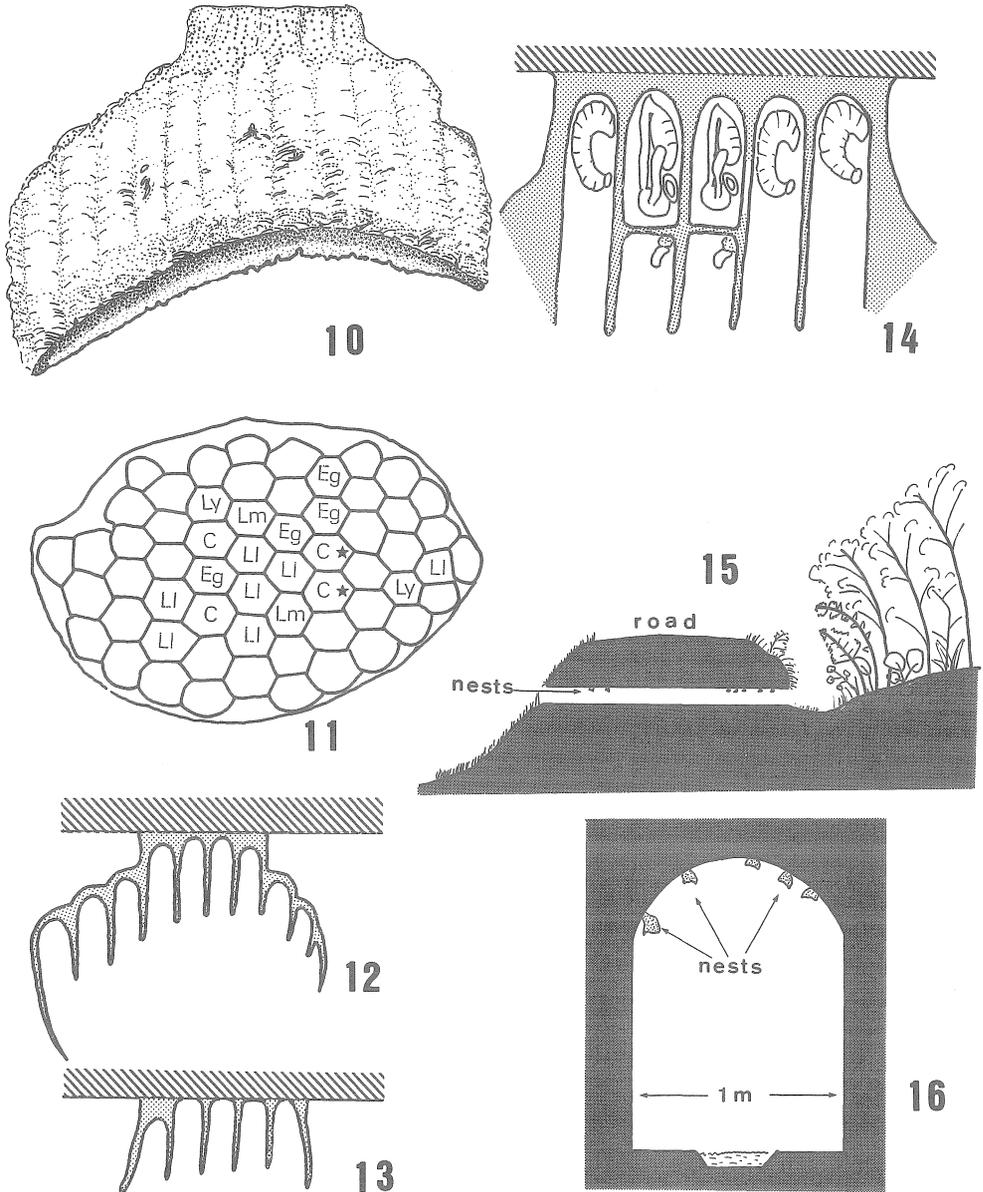
1. Genus *Liostenogaster*

Wasps of this genus are medium-sized, 14-17mm in total body length. Body color is usually brownish with yellow markings. The genus is distributed from Burma and Thailand to Celebes (VAN DER VECHT 1977). Their nests have been reported from the Philippines (WILLIAMS 1919), Thailand (IWATA 1967), Malaya (PAGDEN 1958, YOSHIKAWA *et al.* 1969), etc. Some species prepare nests solitarily but some others gregariously or clumpedly in a narrow space. Usually nests are built on flat undersurfaces of rocks, leaves, timbers, etc. Material and architecture of nests vary so remarkably that it is difficult to specify the generic pattern. Material is usually pure mud or mud admixed with sand, but in some types it is carton (triturated vegetable matter). The petiole and outer envelope are always absent. Some species make bell-shaped muddy combs which quite resemble the polistine combs (Type L₁), and others place carton cells in an array of horseshoe shape on the underside of rocks (Type L₂) or even scatteredly on leaves (Type L₃). Cells are circular or somewhat hexagonal in combed types or irregularly circular in non-combed types. Cell walls are shared by neighboring cells, except in a combed type (L₄) and a scattered-cell type (L₃). After cocoon spinning, cell orifices are mostly closed with the material same as for cells. Number of cells constructed rarely exceeds 100. Cells are reused for rearing brood twice or more. Empty nests are relatively rare, probably caused by frequent reuse of abandoned nests. Nests are initiated by single or multiple foundresses. Four types were found in Sumatera Barat.

Type L₁ (Figs. 10-16; Pl. I, A, B)

Liostenogaster sp. 1 = *L. flavolineata* (CAMERON) ? A nest aggregation was found at Teluk Kabung. Nest is bell shaped and a well known type of the genus. Similar nests were also reported from Thailand (cited as *Stenogaster* sp. in IWATA 1967, Fig. 1, B) and Malaya (cited as *Stenogaster flavolineata*-like species in PAGDEN 1958, Fig. 10 ; *Liostenogaster* sp. in YOSHIKAWA *et al.* 1969, Pls. 2, 5, 6), but some of them were hung from thin supports.

Substrate : Mostly ceiling of concrete cement pipes used for irrigation or watercourses (Fig. 15, 16; Pl. I, A, B). *Material* : Mud admixed with sand particles. *Color* : Greyish yellow and monochromatic. *Architecture* : Always single-combed ; in some nests central cells often initiated on a disc-like solid base of varying thickness (5-10mm) built on substrate (Fig. 12), but in others such base lacking and cells directly initiated on substrate (Fig. 13) ; later cells initiated laterally and concentrically to form a discoid comb, of which bottoms are not in contact with substrate (Figs. 10, 12 ; Pl. I, A) ; lower surface of comb concentrically concave (Fig. 12) ; cells cylindrical or hexagonal with walls shared one another ; outermost walls of comb often elongated downward in varying lengths (8-20mm) to form a rudimentary unilateral pseudenvelope on the shady side (Fig. 12). *Surface* : Not smooth, weakly granulated all over the outer surface. *Size* : Comb, 40-60mm D and 40-55mm L including the base ; cell, 4.7-4.9mm D and 10-14mm L ; cell wall, 1.1-1.3mm T. *No. of cells* : 60 and 74 (mean=67, n=2).



Figs. 10-16. Nests site of Type L₁ (*Liostenogaster* sp. 1=*L. flavolineata*?) observed at Teluk Kabung. 10: Mature nest in lateral view; 11: Cell map showing brood composition; 12: Vertical section of mature nest showing the base and cell walls extended at one side; 13: Ditto, without base and extended walls; 14: Ditto, double-tiered use of the same cells for brood rearing; 15: Nest site inside a concrete tunnel for a watercourse; 16: Ditto, cross section of the tunnel. In this and subsequent figures, developmental stages are coded as follows: Eg. egg, Ly. young larva, Lm. midium larva, L1. large larva, C. cocoon or closed cell, Ep. empty cell. Pw. young pupa, Pb. mature pupa. Cell with asterisk, double-storied cell.

Biological notes : Nests are constructed gregariously or clumpedly (Fig. 16 ; Pl. I, A,B). The aggregation at Teluk Kabung contained about 20 nests in an area of 5m². Some cells were occupied concurrently by two immatures of different stages in the upper and lower halves (Fig. 14). Such two-storied use of a single cell in the vespid combs is so far reported only for two polistine subgenera, *Nygmopolistes* and *Megapolistes* (YAMANE and OKAZAWA 1977).

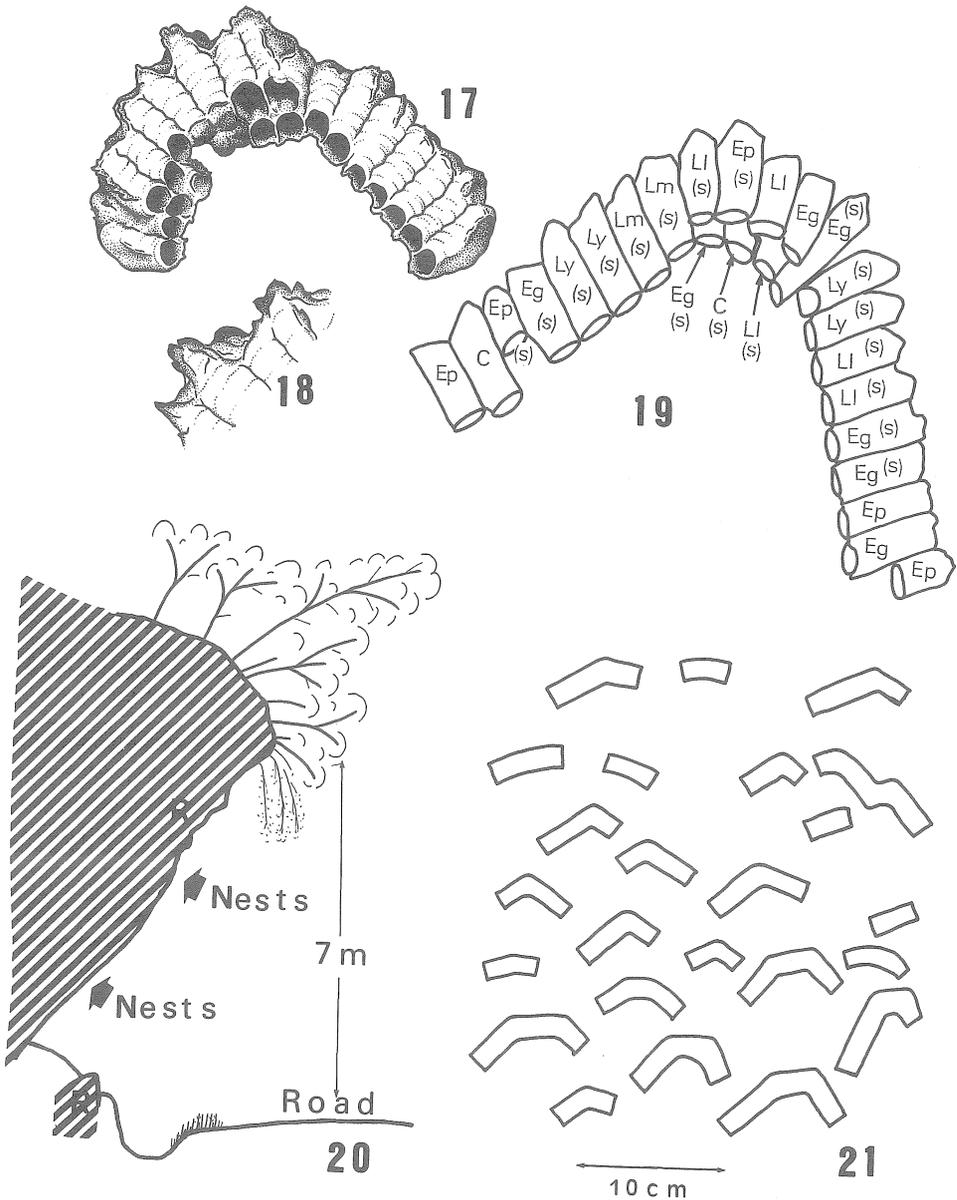
Type L₂ (Figs. 17-21 ; Pl. II, A-C)

Liostenogaster sp. 2. Some nest aggregations each containing several ten nests were discovered at a roadside in Lubuk Bangku (700m alt.) located near a road connecting Provinces of Sumatera Barat and Riau. This is one of the most peculiar types in the stenogastrines, consisting of a single or double tiers of cells arranged in a \wedge -or \cap -shape. Similar nests were reported from Malaya (cited as *Stenogaster* sp. in PAGDEN 1958, Fig. 12 ; *Liostenogaster* sp. in YOSHIKAWA *et al.* 1969, Pls. 7, 19).

Substrate : Underside of big rock overhangs (Fig. 20 ; Pl. II, A). *Material* : Brittle carton not admixed with mud or sand, more paper-like than that for cells of *Eustenogaster* nests (Types E₁ and E₂) ; surface coated with unidentified but probably inorganic matter consisting of fine, pulverized granules. *Color* : Reddish brown on cell proper, but greyish on elaborated surface, especially bottom surfaces and boundaries between cells. *Architecture* : Cells with a round bottom built directly on substrate with their axes in parallel with substrate surface, successive cells added bilaterally to form a \wedge -or \cap -shaped comb, with orifices facing inward (Fig. 17 ; Pl. II, C) ; a second layer often constructed before completion of first layer (Figs. 17, 19) ; no nest with more than two tiers discovered ; neighboring substrate surface also coated with carton as thick as other parts ; cell walls mostly shared by neighboring cells ; after cocoon formation orifices sealed with carton as for other parts (Fig. 17). *Surface* : After construction of first several cells, covered with pulverized matter, sometimes admixed with carton, thinly on side walls and thickly on bottoms and boundaries between cells, occasionally forming irregular, even horn-like ridges on bottom surface (Fig. 18 ; cf. also Pl. II, B, C) ; untreated surface slightly coarser and treated surface sandy. *Size* : Comb, 20-30mm x 40-55mm D, 4-10mm T ; cell, 5-6mm D, 12-14mm L ; cell wall, 0.3-0.4mm T. *No. of cells* : 8-27 (mean=20, n=12).

This type is closely similar to that of Malayan populations, but the Malayan type is more typically horseshoe-like by their rounded, not angulate curvature, occasionally even forming a complete ring, possibly in part caused by the less steep inclination of substrate there. The adults from the Sumatran and Malayan nests are very similar, at the present hardly distinguishable from each other. This type also resembles that of *Parischnogaster varipictus* (ROHWER) reported from Luzon (cited as *Stenogaster varipictus* in WILLIAMS 1919). But judging from WILLIAMS'S description (cf. Figs. 101, 102), the *varipictus* nest differs by the material being sandy mud admixed with decayed wood and the substrate surface not coated with the material and serving as wall of the cell.

Biological notes : All discovered nests were constructed gregariously in shady, but less



Figs. 17-21. Mature nest and nest site of Type L_2 (*Liostenogaster* sp. 2) observed at Lubuk Bangku. 17: General view of a double tiered nest; 18: Horn-like processes on the bottom surface; 19: Cell map of another nest ((s) : reused); 20: Rock overhang as nest site; 21: A nest aggregation on the vertical surface of a rock.

moist places (Pl. II, A) than in Malaya where nests were found on the ceiling of concrete pipes used for watercourses. In a sample, 25 nests were counted within a 30 x 35cm area (ca. 240 nests/m²) (Fig. 21). Most nests contained several females and varying number of males, only rarely attended by single females. This suggests the occurrence of the

polygynous colony founding. A cell map (Fig. 19) shows that the same cells are used at least twice for brood rearing. Few vacated nests were found in an aggregation closely studied, probably due to frequent reuse of abandoned nests by other females and/or rapid exploitation of material from such nests by conspecific females.

Type L₃ (Figs. 22-24 ; Pl. I , C)

Liostenogaster sp. 3. A newly recorded type, probably rarer than L₁ and L₂. Only one young nest and one mature nest were collected at Limau Manis near Ulu Gadut on 23 August 1982 and Teluk Kabung on 16 October 1980, respectively. This is rather similar to Type Pj₂ of the *jacobsoni*-group than to the other *Liostenogaster* nest types so far reported, since cells are placed contiguously, someones even separately on the flat substrate without forming a comb.

Substrate : Underside of living leaves of ferns (Fig. 22). *Material* : Rough and brittle carton made of coarse wooden particles. *Color* : Brownish with yellowish, greyish and dark brownish transverse stripes. *Architecture* : Cells initiated in parallel with substrate surface as in L₂ (Fig. 22 ; Pl. I , C) and elongated as in Fig. 24 (A-E), with round bottom and completely margined orifice, but differing from L₂ in two points : (1) Cells arranged irregularly though all with the same direction, and sometimes even separately on leaf, not forming a compact cluster. (2) Surface of leaf untreated with carton, serving as walls of cells, i.e., cells without proper wall on leaf. Cell walls shared when overlapping. *Surface* : Slightly coarse without particular elaboration. *Size* : Cell, 5.5mm D, 12-13mm L ; cell wall, 0.2mm T. *No. of cells* : 27 in the mature nest.

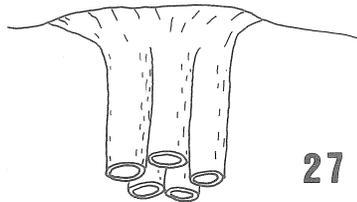
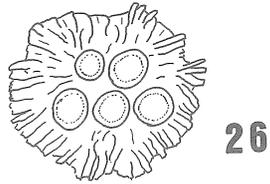
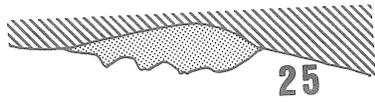
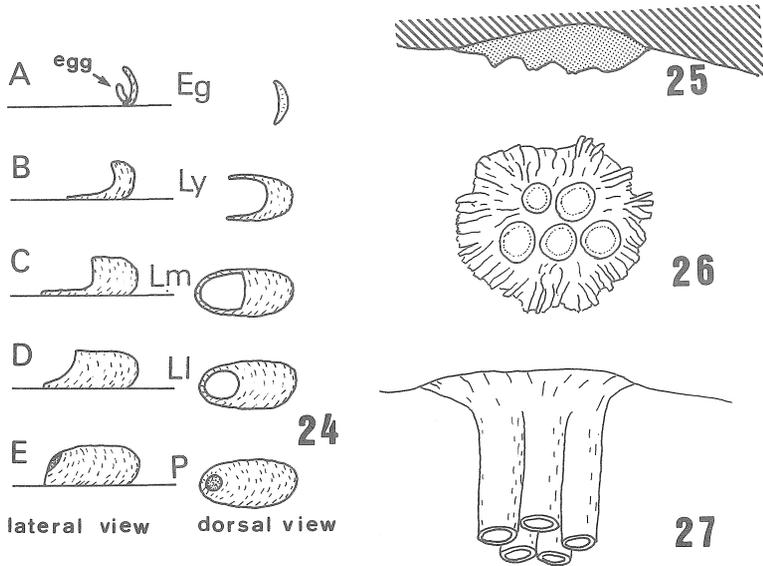
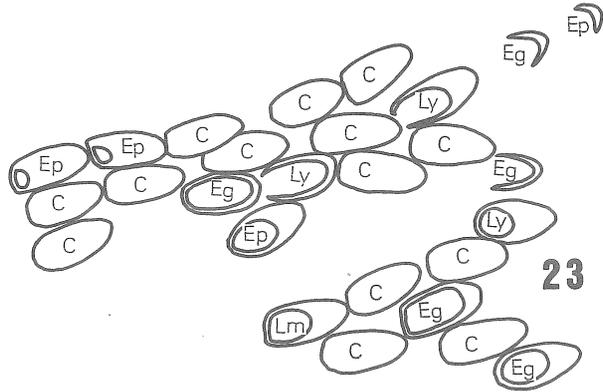
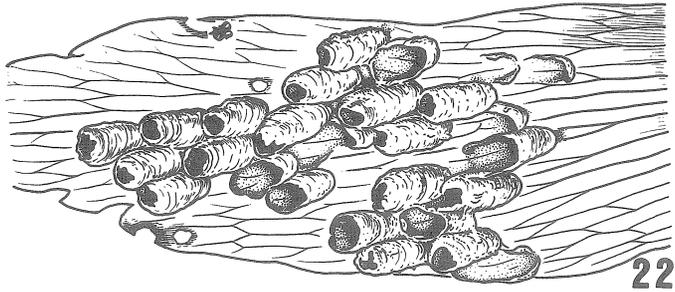
Biological notes : Nests probably do not form aggregations. The young nest was attended by a single female, suggesting the monogynous colony founding. The mature one had 2 females and 7 males (2 or 3 more adults escaped) and 23 immature stages, more than half of which were cocoons (Fig. 23). The large number of cocoons suggests that more than one female contributed in egg laying in this nest.

Type L₄ (Figs. 25-27)

Liostenogaster sp. 4. Probably a newly recorded type, though not discovered in the completed form. Only a rudiment of a nest was found on the same rock overhang used by L₂ at Lubuk Bangku. The nest was broken during the examination on the substrate and not preserved.

Substrate : Same as for L₂ (Pl. II, A). *Material* : Mud admixed with sand for both nest base and cells. *Color* : Reddish yellow and monochromatic. *Architecture* : Cells built vertically on thin base (Fig. 25) ; all cylindrical and walls not shared by one another at least in early stage (Fig. 26). *Surface* : Finely granulate, though less than L₁. *Size* : Cell, ca. 4mm D. *No. of cells* : 5.

A completed form is probably like the combs prepared by *Trypoxylon fabricator* SMITH (SAKAGAMI and ZUCCHI 1978) as imagined in Fig. 27. This type may represent the most primitive state in the genus, or in the entire subfamily.



Figs. 22-27. Mature nest of Type L₃ (*Liostenogaster* sp. 3; 22-24) and rudimentary nest of Type L₄ (*Liostenogaster* sp. 4; 25-27). 22. General view of L₃ nest, built on leaf at Teluk Kabung; 23: Ditto, cell map; 24, A-E: Development of cell; 25: Nest of L₄ built on the undersurface of rock overhang at Lubuk Bangku, vertical section; 26: Ditto, seen from bottom, showing cell walls which are not shared; 27: Imaginary sketch of a completed nest.

Biological notes : This species may be a forest dweller, but may prefer the places less moist than streamsides. The nest was attended by a single female.

2. Genus *Eustenogaster*

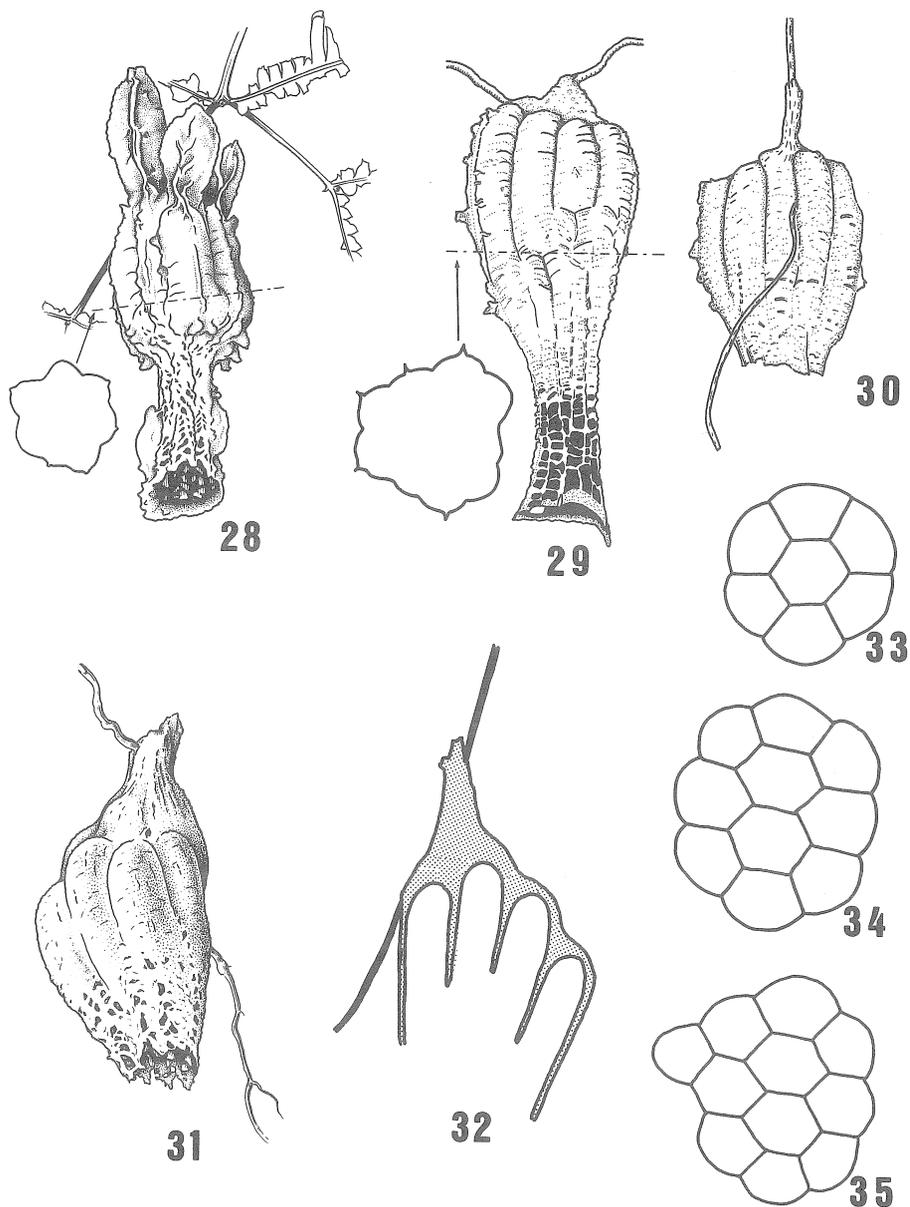
This genus, consisting of species with the largest size (ca. 20mm) and the yellow marked black body, is distributed from southern India to Celebes and the Philippines (VAN DER VECHT 1977). Species of the genus seem to be forest dwellers and relatively rare. Nests have been reported from LUZON (WILLIAMS 1919), Thailand (IWATA 1967, SAKAGAMI and YOSHIKAWA 1968), Malaya (PAGDEN 1958, YOSHIKAWA *et al.* 1969), etc. Nests are initiated on thin but rigid supports, e.g., horizontal or slanting aerial rootlets and fern stems, or flat surfaces, e.g., undersides of floor timbers, palm leaves used for roofs and rock overhangs. When suspended from rootlets, nests are attached to the midway, not to the tips, and in contact with them for some lengths. Nests are made from brittle carton, stiff in some species, sometimes containing a fraction of mud. They consist of single flat combs containing some ten cells and, except for *E. calyptodoma* SAKAGAMI *et* YOSHIKAWA, outer walls of peripheral cells extend to form a pseudenvelope and narrowed downward as an entrance tube, the architecture of which is often extremely elaborated and probably species-specific. Expansion of comb by additional cells is impossible after its completion by the pattern mentioned. Outer surfaces of the comb and pseudenvelope are elaborated in various ways. Central cells are almost hexagonal while peripheral ones rounded. Walls are always shared by neighboring cells. Cell orifices are never closed with cartonous matter after the cocoon spinning. Colonies are usually small, often containing only one female, suggesting the prevalence of monogynous colony founding. Four types were found in Sumatera Barat.

Type E₁ (Fig. 28, 33)

Eustenogaster sp. 1. A newly recorded type. Only one completed nest was collected under an overhanging rock at Teluk Kabung on 25 October 1980. This type is characterized by an elongated entrance tube with beautiful lacework and four big upward processes on the top.

Substrate : Thin stem of a fern. *Material* : Coarse and brittle carton not admixed with mud. *Color* : Pale chocolate brown and monochromatic. *Architecture* : Flask-shaped; pseudenvelope abruptly constricted below comb; with four big upward processes like donkey's ears on top; entrance tube long and at opening a little expanded; opening facing downward and radially asymmetrical with one side well lipped and slightly longer than the other. *Surface* : Rather coarse with several discontinuous ridges developed as series of dentate or spinous processes; zone boundary between comb and entrance tube with rather irregular processes; tube symmetrically ornamented with fine lacework and some vertical plate-like processes. *Size* : 19mm D, 61mm L (including entrance tube); thickness of envelope, 0.8mm; cell, ca. 10.5mm D, 20mm L. *No. of cells* : 7.

Similar type of nests are reported from Malaya (cited as *Stenogaster* sp. in PAGDEN



Figs. 28-35. Three types of *Eustenogaster* nests. 28: Mature nest of Type E_1 (*E. sp. 1*) built on a fern stem at Teluk Kabung, with a cross section; 29: Mature nest of Type E_2 (*E. sp. 2*) built on an aerial rootlet at Muko Muko, with a cross section; 30: Ditto, with the entrance tube broken; 31: Mature nest of Type E_3 (*E. sp. 3 = E. hauxwelli?*) with the entrance slightly broken, Teluk Kabung; 32: Ditto, vertical section; 33, 34, 35: Combs of E_1 , E_2 , E_3 , seen from bottom, respectively.

1958, Fig. 7, a, b), but they lack the ear-like processes on the top and the taxonomic relations are open to further studies. Nests of *E. fraterna* (BINGHAM) discovered in Malaya and Cambodia (erroneously cited as *Stenogaster micans* (SAUSSURE) in YOSHIKAWA *et al.* 1969, Pls. 4, 25) superficially resembles E_1 by frequent possession of upper processes and asymmetrically elaborated entrance tube. But the surface of *fraterna* nests are characteristically smooth (this may be a group-specific character) and females distinctly differ from those of the present nest.

Biological notes : This nest was found in a humid forest zone. It had 2 females whose social relation was unknown.

Type E_2 (Figs. 29, 30, 34)

Eustenogaster sp. 2. Two complete nests were collected at Muko Muko near Lake Maninjau on 22 October 1980 and at Siguntur Tua on 29 September 1981, respectively. They were found in small earthen hollows of which openings were fairly closed by plants and the interior was quite dark. One broken nest was taken at Siguntur Tua on 16 October 1980. In basic and surface structure, this is closely similar to E_1 , but differs by the absence of ear-like processes and the form of entrance. A similar abandoned nest was taken at Fraser's Hill, Malaya (cited erroneously as *Stenogaster calyptodoma* in YOSHIKAWA *et al.* 1969, Pl. 30).

Substrate : Exposed rootlets of trees. *Material* : Coarse and brittle carton as in E_1 , but containing a little mud. *Color* : Greyish yellow brown or chocolate brown and monochromatic. *Architecture* : Basically as E_1 , but top rounded, without upward processes ; entrance tube long, gradually narrowed downward, making boundary between comb and tube obscure, slightly expanded at apex ; entrance radially symmetrical (Figs. 29). *Surface* : Rather coarse as in E_1 , without distinct and pronounced vertical ridges on swellings of peripheral cell walls, whereas with scattered dentate, more or less serial processes on them ; entrance tube with about ten vertical ridges being continuous but not much pronounced, running from comb below to the lowest end of tube ; between these ridges with lacework prepared more uniformly than in E_1 . *Size* : 25-30mm D, 50-60mm L (including entrance tube, 25mm L) ; thickness of envelope, 0.7-1mm ; cell, ca. 11mm D, 21mm L. *No. of cells* : 10-16.

Biological notes : The living nest taken at Muko Muko had two females, one of which probably had just emerged.

Type E_3 (Figs. 31, 32, 35)

Eustenogaster hauxwelli (BINGHAM) ? Only one vacated nest was found at Teluk Kabung on 29 September 1981. This type differs from the other types by a peculiar form like some mantid oothecae, crepe-like surface and simple entrance tube. Similar nests have been reported from Thailand and Cambodia (cited as *Stenogaster micans* in SAKAGAMI and YOSHIKAWA 1968, Figs. 5, 6, C, D, E, G) and Malaya (cited as *Stenogaster* sp. in PAGDEN 1958, Fig. 8 ; *S. micans* in YOSHIKAWA *et al.* 1969, Pl. 27).

Substrate : Thin slanting rootlet. *Material* : Carton not containing mud, strongest and lightest of all *Eustenogaster* nests ever examined by us. *Color* : Pale grey and monochromatic. *Architecture* : Looking like some mantid oothecae (Fig. 31); top of nest projecting beyond substrate twig; without elongate entrance tube (entrance seems to be partially broken); successive cells added to position slightly lower of preceding ones (Fig. 32); swellings of peripheral cells obvious. *Surface* : Not rugged, but with dense, very fine and rather inconspicuous vertical ridges like crepe above, with lacework below being less finely elaborated as in E_1 and E_2 . *Size* : 22mm D, 35mm L; thickness of envelope, 0.4-0.5 mm; cell, 7mm D, 13-14mm L. *No. of cells* : 11.

The specimens collected in Thailand, Cambodia and Malaya cited as *S. micans* by SAKAGAMI and YOSHIKAWA (1968) and YOSHIKAWA *et al.* (1969) were later identified to *E. hauxwelli* by Dr. J. VAN DER VECHT. Nest described by PAGDEN (1958) seems to differ in the minute architecture of the surface. Nest of Cambodia illustrated by SAKAGAMI and YOSHIKAWA (1968) differs from the described nest by the presence of several vertical rows of denticles down to the lower half.

Type E_4 (Pl. III, A)

Eustenogaster calyptodoma (SAKAGAMI et YOSHIKAWA)? Only a fragment of the base of vacated nest was collected at Teluk Kabung on 4 November 1980. By the preparation of independent envelope, the unique exception in the stenogastrine wasps, the species may be identical with *E. calyptodoma* described from Sarawak (SAKAGAMI and YOSHIKAWA 1968, Figs. 4, 6, A, B, F; YOSHIKAWA *et al.* 1969, Pls. 26, 29).

Substrate : Undersurface of a big rock. *Material* : Coarse and brittle carton as in E_1 and E_2 , containing a little mud. *Color* : Greyish white and monochromatic. *Architecture* : About seven to 12 cells directly built on the rock surface and envelope made independently from comb; diameter 34mm at the base.

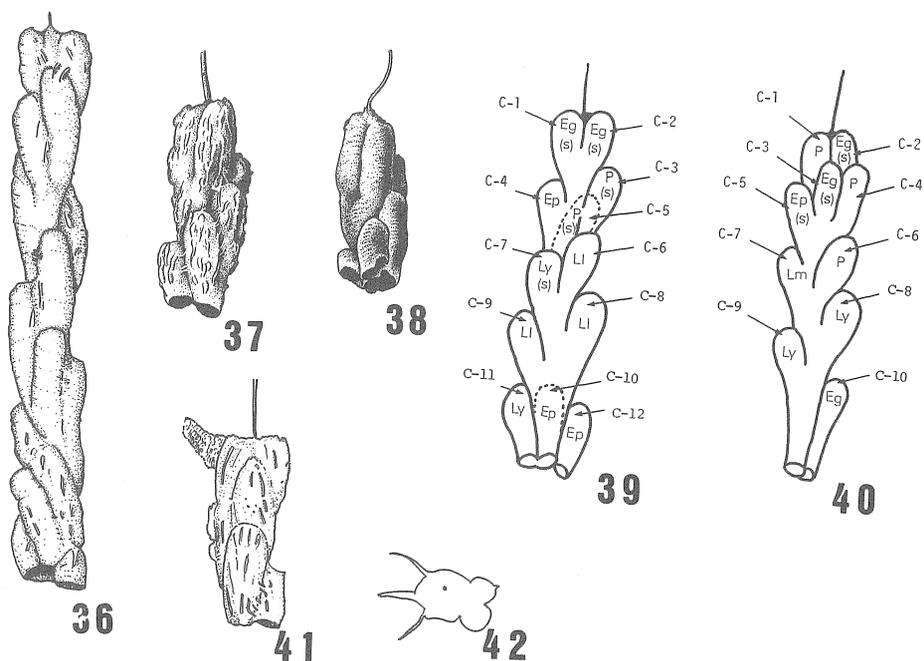
3. Genus *Parischnogaster*

This is the largest genus in the Stenogastrinae with wasps of rather small size, 14-15mm in total body length and yellow marked black bodies. Its distribution ranges from India to Celebes (VAN DER VECHT 1977), and nests have been reported from the Philippines (WILLIAMS 1919), Thailand (IWATA 1967, YOSHIKAWA *et al.* 1969, HANSELL 1981), Cambodia (YOSHIKAWA *et al.* 1969), Malaya (PAGDEN 1958, YOSHIKAWA *et al.* 1969), Java (TURILLAZZI and PARDI 1981), etc. Wasps of this genus are common in disturbed areas and build nests even in human habitations. Nests are built either on flat substrates or on thin supports. Material is, as a rule, carton with brittle or paper-like nature, sometimes admixed with various amounts of mud, or rarely built by pure mud. Nests can be classified into three major types in a good correspondence with the taxonomic groups (the *striatula*-group, the *mellyi*-group, and the *jacobsoni*-group, VAN DER VECHT, pers. comm.) of adults. Basic structure is group-specific. The petiole is absent in all the groups, while a peculiar

envelope-like structure (passage-way) is prepared in the *striatula*-group. Nine types were found in Sumatera Barat.

The *striatula*-group (Type Ps)

This includes nests of *P. striatula* (DU BUYSSON), *P. depressigaster* (ROHWER), *P. alternata* SAKAGAMI, and some unidentified species. Nests are usually built in shady places such as depression of cliffs, shades of rocks, etc. Most species hang nests from thin rootlets or from flat substrates. Nest material is brittle carton, with or without containing mud. This type is distinguishable from all the other types of *Parischnogaster* by the presence of the passage-way (=communal entrance tube surrounded by pseudoenvelope or walls of neighboring cells, to which cells open, Figs 39, 40, 44, 46, 50). Nests have some ten cells which form an atypical comb with a species-specific form. No species makes the polistine type flat comb. Cell walls are shared by neighboring cells. Cells are basically circular in cross section. As in *Eustenogaster*, this group does not close orifices of cells after cocoon formation. Six types have been found in Sumatera Barat.



Figs. 36-42. Nests of the *Parischnogaster striatula*-group, I. 36: Mature nest of Type Ps₁ (*P. striatula*) built on a thin aerial rootlet at Batang Palupuh (near Bukittinggi), with a few vertical ridges on the surface; 37: Ditto, immature nest found at Teluk Kabung with dense, pronounced ridges; 38: Ditto, with smooth surface, at the same site; 39, 40: Schematic arrangement of cells, construction order and brood compositions; 41: Immature nest of Type Ps₂ (*P. sp. 1*), built on a thin aerial rootlet at Bt. Hulusungaisalik (near Sungai Dareh); 42: Ditto, cross section, showing spiral arrangement of cells and lateral projections on the surface.

Type Ps₁ (Figs. 36-40, Pl. III, C)

Parischnogaster striatula (DU BUYSSON). Many nests were discovered and collected at Lubuk Bangku (700m alt.), Payakumbuh, Bukittinggi, Teluk Kabung, and Sungai Dareh. This type is characterized by a spiral arrangement of cells downward, resulting in a spirally cylindrical form. Similar nests are known from the Philippines (cited as *Stenogaster depressigaster* in WILLIAMS 1919, Figs. 96, 97), Thailand (*P. striatula*: YOSHIKAWA *et al.* 1969, Pls. 31-33), Malaya (cited as *Stenogaster* sp. in PAGDEN 1958, Fig. 15; *P. striatula*: YOSHIKAWA *et al.* 1969, Pl. 10).

Substrate: Fine rootlets; nests usually initiated at their lowermost tips. *Material*: Mostly brittle carton, but sometimes admixed with a fraction of mud. *Color*: Chocorate brown, often with indistinct light transverse stripes. *Architecture*: Cells constructed through the following process (Figs. 39, 40): First two cells C₁ and C₂ made on tip of a rootlet followed by their joining together to form a common orifice; C₃ initiated at a slightly lower position between C₁ and C₂, and joining the communal tube (passage-way, Pw); C₄ and subsequent cells built in the same way, finally resulting in a cylindrical, slender and twisted comb (Figs. 36-38; Pl. III, C). *Surface*: Slightly rugged, with scattered narrow but distinct keels which often branch reticulately (Figs. 36, 37), or without such sculpture (Fig. 38). Both types are syntopic. It is uncertain whether the presence or absence of keels depends merely on the age of nest (prepared only in aged ones) or on the behavioral plasticity of wasps. *Size*: Comb, 9-12mm D, 30-100mm L; cell, 4.5mm D, 12mm L; cell wall, 0.5-0.6mm T. *No. of cells*: Mean 9.1 ($n=9$) with a maximum of 16.

Biological notes: Nests are built solitarily or forming a small, loose aggregation, and usually attended by 1-3 females and 1-9 males. Cell maps of two nests are shown in Figs. 39 and 40.

Type Ps₂ (Figs. 41, 42)

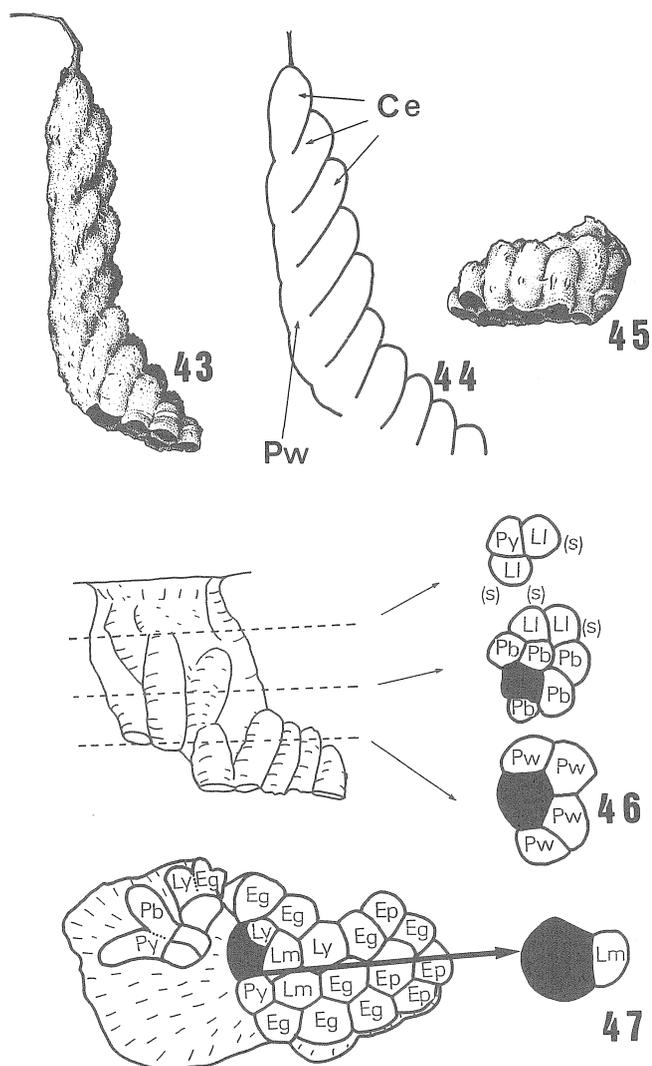
Parischnogaster sp. 1. Only one nest was collected at Bt. Hulusungaisalik near Sungai Dareh on 3 January 1980. Architecture is closely similar to Ps₁, except for the presence of plate-like projections on the top. Similar nest has been reported from Malaya (cited as unidentified species of *Stenogaster* in PAGDEN 1958, Fig. 13).

Substrate: Fine aerial rootlet. *Material*: Brittle carton without mud. *Color*: Dark chocorate brown and monochromatic. *Architecture*: Basically similar to that of *P. striatula*; three uppermost cells with big wing-like processes with fine openwork (Figs. 41, 42); outer surfaces of all cells with distinct but discontinuous keels as in Ps₁, someones more pronounced like plates (Fig. 41); comb size, 11mm D (excluding winglike processes), 26mm L; cell size, 12-13mm D, 6-7mm L; no. of cells, 5.

Biological note: This nest was attended by 2 females.

Type Ps₃ (Figs. 43, 44)

Parischnogaster alternata SAKAGAMI. Only one completed nest was found in a concavity of a cliff along sunny roadside at Kota Alam (600m alt.). This is characterized by the cells



Figs. 43-47. Nests of the *Parischnogaster striatula*-group, II. 43: Mature nest of Type Ps_3 (*P. alternata*) collected at Lubuk Bangku, lateral view; 44: Ditto, vertical section, showing cell arrangement and a communal passage-way; 45: Young nest of Type Ps_4 (Ps_4 -A) (*P. sp.* 2) built on a rock surface at Siguntur Tua, lateral view; 46: Ditto, mature nest (Ps_4 -B) with cross sections at three heights (black parts showing passage-way); 47: Ditto, seen from bottom, entrance enlarged.

arranged in a regular fashion and the presence of a single passage-way at the side. Similar nests were reported from Malaya (*P. alternata*: YOSHIKAWA *et al.* 1969, Fig. 1, I, Pl. 36).

Substrate: Fine aerial rootlet. *Material*: Brittle carton as in Ps_1 , without mud. *Color*: Greyish brown, with some creamy obscure stripes. *Architecture*: Cells slanting, orifices of completed cells soon covered with a round extension of their side walls (a kind of pseudenvelope), providing a linear passage-way, running from top cells down to near the

apex (Fig. 44); cells regularly added to two vertical rows and forming a slender and slightly curved comb; cells not sealed at pupation. *Surface*: Rugged, but not much as in E_1 ; mature nest with scattered, short inconspicuous keels (Fig. 43). *Size*: Comb, 21 x 8.5mm D (cross section compressed), 49mm L; cell, 5.5mm D, 12mm L; cell wall, 0.4mm T. *No. of cells*: 19.

Basic structure is the same as in Malayan nests, but they were directly initiated on the flat substrate (YOSHIKAWA *et al.* 1969).

Biological note: The nest was found solitarily and attended by 2 females and 2 males.

Type Ps_4 (Figs. 45-47)

Parischnogaster sp. 2. A newly recorded type. Two nests were collected at Siguntur Tua on 16 October 1980 (Ps_4 -A) and 29 September 1981 (Ps_4 -B). This type resembles Ps_3 , but differs from it by gross and short comb with cells arranged irregularly.

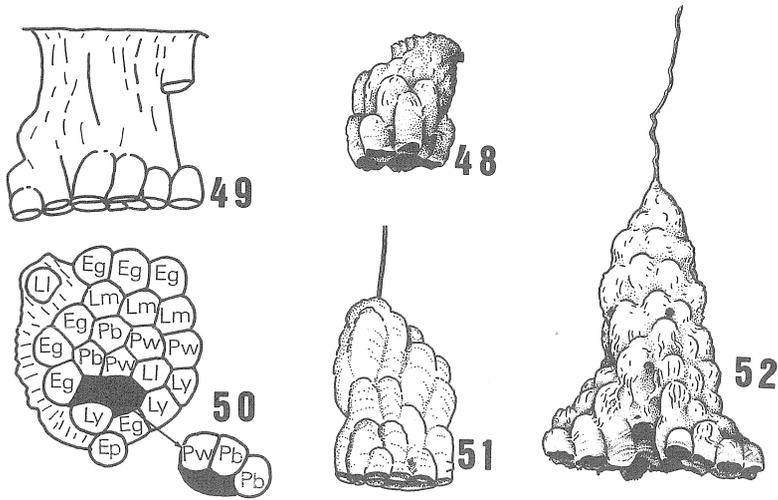
Substrate: Ceiling of a concrete tunnel. *Material*: Brittle carton more fragile than in Ps_3 . *Color*: Dark brown. *Architecture*: Several vertical cells initiated directly on the substrate; basal cells without proper bottom; additional cells also vertical, built downward and rather unilaterally in three or four vertical rows which are irregular (Figs. 46, 47) to form a curved comb (Fig. 46), probably with a single, more or less non-linear passage-way to which cells open at one side of comb. *Surface*: Slightly rugged, especially at base where cell boundaries are obscured by copious application of carton. *Size*: Comb, 22mm D, 28mm L for Ps_4 -A, and 27mm D, 28mm L for Ps_4 -B; cell, 4-6mm D, 11-15mm L; cell wall, 0.6mm T. *No. of cells*: 19 and 36 for Ps_4 -A and Ps_4 -B, respectively.

Biological notes: Most of nests observed were gregarious in concrete tunnel, and sometimes coexisted with nests of L_1 . Ps_4 -A had 7 females and 3 males, and Ps_4 -B 3 females and 4 males.

Type Ps_5 (Figs. 48-50; Pl. IV, C)

Parischnogaster sp. 3. A newly recorded type. Young and mature nests (Ps_5 -A and Ps_5 -B, respectively) were collected in the same concrete tunnel as for nests of *Liostenogaster* sp. 1 (L_1) at Siguntur Tua on 29 September 1981. This type closely resembles Ps_4 and differs only by the concentric downward growth of the comb without unilaterality, with more rows arranged irregularly.

Substrate: Ceiling of a dark concrete tunnel. *Material*: Brittle carton as fragile as in Ps_4 . *Color*: Brown, darker than in Ps_3 , and much as in Ps_4 . *Architecture*: Nest Ps_5 -B (Figs. 49, 50). Cells added downward concentrically, not unilaterally, so as to form a thick cylindrical comb; probably with a single nonlinear passage-way inside comb. Vertical cells built directly on substrate, forming irregular tiers; inside of comb (near the periphery) with a passage-way (Fig. 50). Some cells built sporadically on the outer surface and opening freely; cell walls shared by neighboring cells in both nests. *Surface*: Rugged as in Ps_4 , basal part thickly covered with carton making the cell boundaries obscure particularly in Ps_4 -A. *Size*: Comb, 22mm D, 18mm L for Ps_5 -A; cell, 4mm D, 9-10mm L; cell wall, 0.6mm T. *No. of cells*: 24 for Ps_5 -A.



Figs. 48-52. Nests of the *Parischnogaster striatula*-group, III. 48: Young nest of Type Ps₅ (Ps₅-A) (*P.* sp. 3), Built on a rock surface at Teluk Kabung, lateral view; 49: Ditto, mature nest (Ps₅-B) at the same place, lateral view; 50: Ditto, seen from bottom; 51: Mature nest of Type Ps₆ (Ps₆-A) (*P.* sp. 4) built on a thin aerial rootlet in a hollow of wooden stump at Siguntur Tua, lateral view; 52: Ditto, the biggest one (Ps₆-B), at the same place, lateral view.

Adults obtained from Ps₄ and Ps₅ resemble so closely that these types might manifest only intraspecific variations of one and the same species.

Biological notes: Nests of this type form a big aggregation. Ps₅-A was attended by 4 females and 4 males.

Type Ps₆ (Figs. 51, 52; Pl. III, D)

Parischnogaster sp. 4. A newly recorded type. More than ten nests were collected in dark cavities of wooden stumps at Siguntur Tua, Bukittinggi and Muko Muko during 3 January and 5 November 1980. This type is similar to Ps₄ and Ps₅, more closer to the latter, by the cylindrical form of the comb.

Substrate: Fine rootlets. *Material*: Brittle carton as fragile as in Ps₅. *Color*: Brown with yellowish stripes. *Architecture*: Vertical cells constructed so as to form a cylindrical and irregularly tiered, round-topped comb (Ps₆-A, Fig. 51), or bell-shaped, pointed-topped comb (Ps₆-B, Fig. 52); all cells opening at a communal passage-way; walls mostly shared by neighboring cells. *Surface*: Similar to Ps₄ and Ps₅, lacking any processes; with carton coating over cells at the basal half and swellings of cells becoming obscure. *Size*: Comb, 23mm D, 23mm L for Ps₆-A, and 33mm D, measured at apex, 41mm L for Ps₆-B; cell, 4mm D, 11-13mm L; cell wall, 0.6-0.7mm T. *No. of cells*: 20-more than 30.

It is not precluded that this is a mere variation (rootlet hanging type) of Ps₅. Different shapes of the comb between two nests (Fig. 51 vs. 52) may have resulted from differences in the colony size (2 females were captured on smaller one whereas 12 ones on bigger one)

and/or the age of nests.

Biological notes : Nests of this type were distributed clumpedly owing to the distribution pattern of suitable sites.

The *mellyi*-group (Type Pm)

Species of this group are slightly smaller than those of the *striatula*-group. They are commonly found in Southeast Asia, inhabiting not only humid area but also open disturbed areas and even in human constructs. Nests are hung from the tip of fine rootlets in depressions along roadcuts, fibers of palm leaves covering roofs, etc. Nests of this group consist of several irregular combs, which are often continuous or compose irregular tiers. They lack the passage-way, all cells opening freely outside. Orifices of cells are closed after cocoon spinning. Some types with different architecture described from other areas of Southeast Asia might represent several distinct species. Because of the presence of a cline in the architectural pattern, all the nests found in Sumatera Barat were regarded as those of the same species.

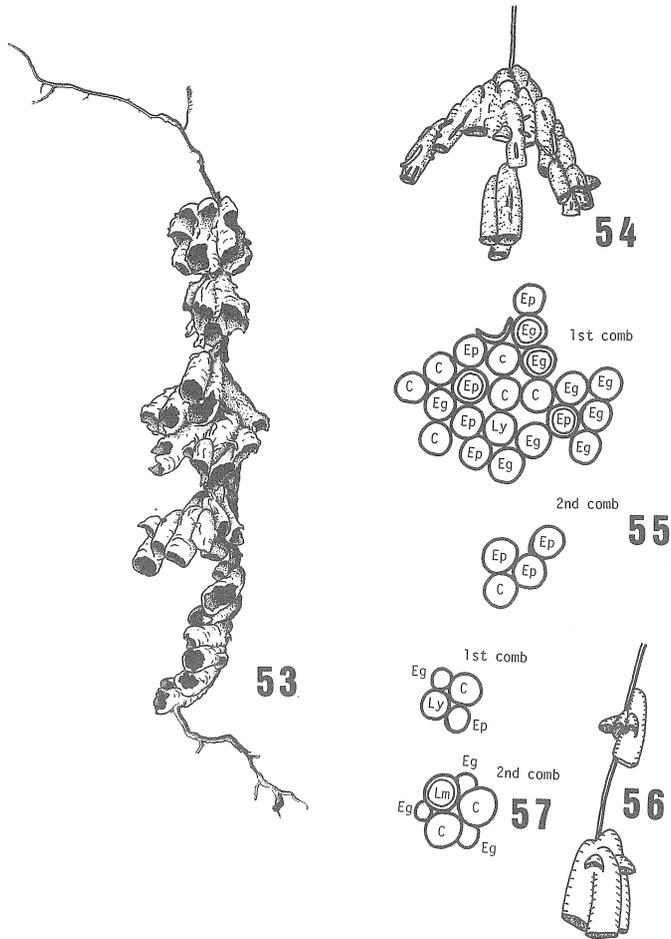
Type Pm₁ (Figs. 53-57 ; Pls. III, B, IV, A, B)

Parischnogaster mellyi (SAUSSURE). This is the commonest species and its nests were found everywhere in Sumatera Barat. This type is easily distinguishable from the others by the presence of unclearly tiered multiple combs. Similar nests are reported from Thailand (*P. mellyi*: IWATA 1967, Fig. 5, D, Pl. III, 10, 11 ; YOSHIKAWA *et al.* 1969, Pls. 9, 11, 37, 38 ; HANSELL 1981, Fig. 2), Malaya (cited as *Stenogaster mellyi* in PAGDEN 1958, Fig. 16), etc.

Substrate : Fine rootlets and plant fibers. *Material* : Brittle carton admixed with varying amounts of mud, sometimes built by pure mud. *Color* : Greyish to chocolate brown, sometimes with transverse stripes. *Architecture* : Consisting of several combs initiated separately or contiguously above and/or below the first comb before its completion (Fig. 54 *vs.* 56) ; cells irregularly circular, never typically hexagonal ; cell walls usually but not always shared ; some nests with a small, shallow cup-like appendix on support above top comb, in shape somewhat similar to ant guards of the *jacobsoni*-group, though prepared with carton instead of viscous secretion. *Surface* : Either smooth or irregularly sculptured by addition of carton streaks, often strikingly resembling lumps of mud hanging from rootlets. *Size* : Comb, varying by nests, e.g., 9mm D, measured for a comb with ten cells, 69mm L, measured between top and lowest combs, containing 4 combs ; cell, 3.5-4mm D, 10.5mm L ; cell wall, 0.3-0.4mm T. *No. of cells* : 7-35 (mean=14, *n*=22).

Material and architectural patterns vary considerably by nests. Wasps building various forms of nests are regarded as belonging to the same species, because of the morphological similarity of adults and occurrence of these nests at the same site.

Biological notes : This species is similar to *P. striatula* in habitat selection, but less stenotopic, occasionally found in more sunny places. Nests are founded by single females, and often abandoned but soon reoccupied by other females. At least some daughters (or

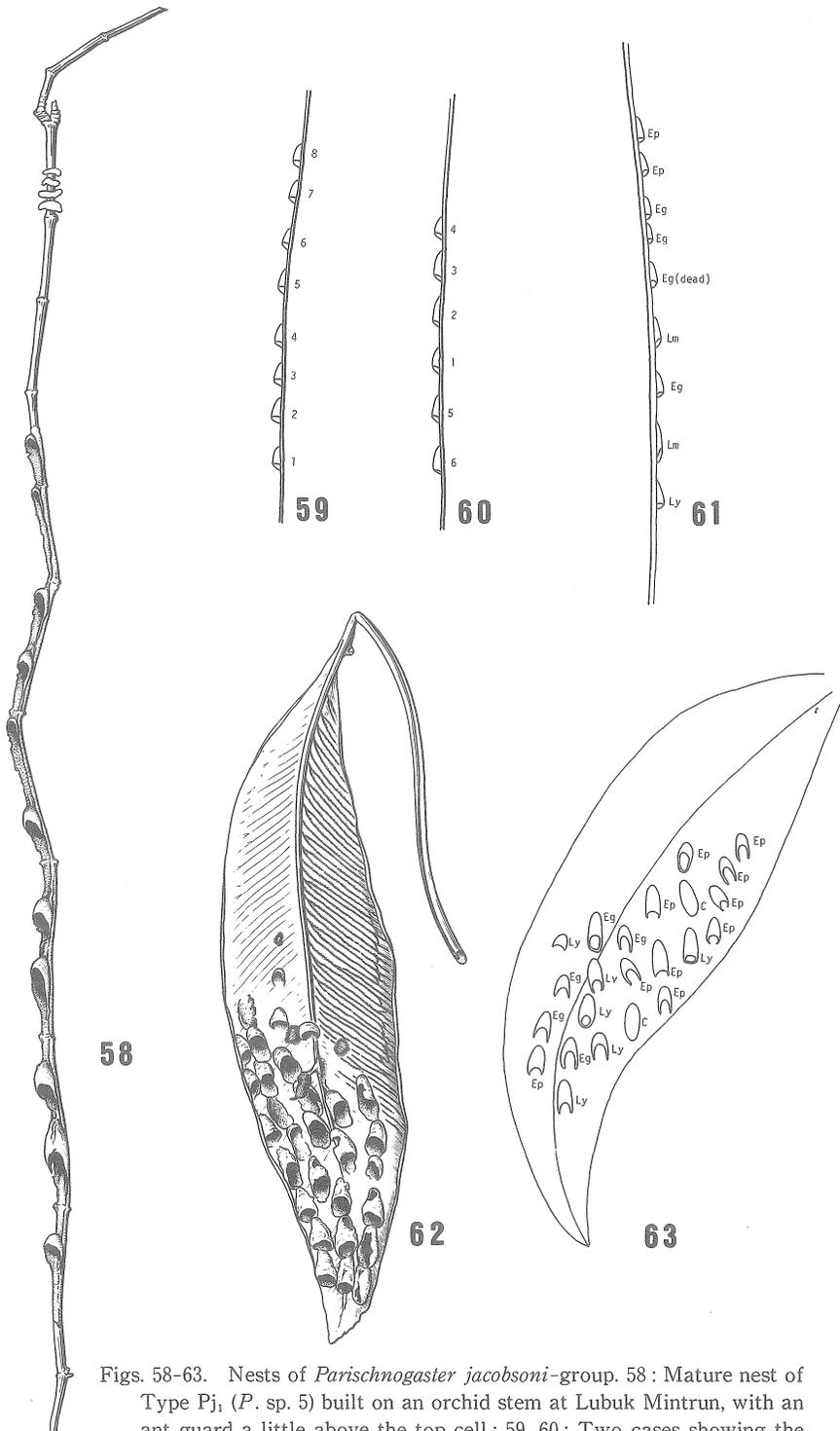


Figs. 53-57. Nests of Type Pm₁ (*Parischnogaster mellyi*) collected at Lubuk Mintrun. 53: Mature nest with four combs separated incompletely, built on a thin aerial rootlet, lateral view; 54: Nest with two combs; 55: Ditto, cell maps; 56: Young pre-emergence nest; 57: Ditto, cell maps. Double circles in 55 and 57 mean the orifice of the cell were narrowed by the adult wasps.

stepdaughters) serve as workers in natal nests for about 20 days after their emergences, and then leave it and start their own nests (YAMANE *et al.* in press).

The *jacobsoni*-group (Type Pj)

This group consists of the smallest species in *Parischnogaster*. They can inhabit open disturbed areas and are common even in human habitations (PAGDEN 1958, TURILLAZZI and PARDI 1981). Some species build nests on thin but relatively rigid supports such as orchid stems, twigs of trees, steel wires, etc., and rarely on undersurfaces of leaves, but they never nest on fine thread-like supports as in Ps and Pm. Nest material is tough and rather paper-like carton. Cell walls are thinner than in the other types and shared by neighboring cells



Figs. 58-63. Nests of *Parischnogaster jacobsoni*-group. 58 : Mature nest of Type Pj₁ (*P.* sp. 5) built on an orchid stem at Lubuk Mintrun, with an ant guard a little above the top cell ; 59, 60 : Two cases showing the construction order of cells by numerals ; 61 : Cell map ; 62 : Mature nest of Type Pj₂ (*P.* sp. 6) built on a fern leaf at Teluk Kabung ; 63 : Ditto, cell map showing brood composition.

when overlapping. Cells are placed in a single or double rows on the thin support, or scatteredly, but more or less serially, on the flat surface, arcuate in cross section. Orifices of cells are closed after cocoon spinning. At least species which build nests on thin supports prepare ant guards with abdominal secretions by females on the support at a little distance from the basalmost cell (TURILLAZZI and PARDI 1981). Their social organization has well been studied thanks to unidimensional nest plan (YOSHIKAWA *et al.* 1969, TURILLAZZI and PARDI 1981, YAMANE *et al.* unpublished). Two types were found in Sumatera Barat.

Type Pj₁ (Fig. 58-61 ; Pl. V, A, C)

Parischnogaster sp. 5. This type is common in Sumatera Barat, but rarer than those Ps₁ and Pm₁. It is easily distinguishable from the others by the serial arrangement of cells on thin supports, forming a narrow linear nest. Similar nests have been reported from Cambodia (*P. serrei* : IWATA 1967, Fig. 5, A, Pl. II, 6), Thailand (cited as *P. spp.* allied to *P. serrei* in IWATA 1967, Fig. 5, B, C, Pls. II, 8, 9 ; YOSHIKAWA *et al.* 1969, Pls. 39, 40 ; *P. sp.* : IWATA 1967, Pl. II, 7), Malaya (cited as *Stenogaster spp.* in PAGDEN 1958, Figs. 17-20 ; cited as *P. sp.* in YOSHIKAWA *et al.* 1969, Pls. 12, 13, 41-44), Java (*P. nigricans serrei* (DU BUYSSON) : TURILLAZZI and PARDI 1981, Figs. 1, 2), etc. Wasps building this type may involve several distinct species. Nests are found on both horizontal and vertical supports.

Substrate : Aerial rootlets (2-3mm T) of trees or stems of herbaceous plants (Fig. 58 ; Pl. V, A), fine but rigid plant fibers, etc. *Material* : Tough carton not containing mud, somewhat resembling that in *Ropalidia* nests. *Color* : Greyish brown, without remarkable stripes. *Architecture* : Cells built serially in a single, or rarely double rows on one side along support (Fig. 58) ; construction order of cells not fixed (Figs. 59, 60) ; cell axes in parallel with that of support ; front and bottom ends of cells often overlapping, sharing cell walls ; proper walls absent on support ; ant guard, small shell-like structure, prepared at distance a little above top cell with abdominal secretions by females (Fig. 58, Pl. V, C). *Surface* : Almost smooth, with up to 6-8 vertical, short and narrow keels on completed cells, but not on incipient cells. *Size* : 180mm L (including ant guard and 10 cells) ; cell, 2.7mm D, 5.3mm L ; cell wall, 0.2mm T. *No. of cells* : Up to 10.

Biological notes : This species inhabits syntopic with *P. mellyi*. Nests are initiated by single females. The ant guard is treated and refreshed every evening to keep defending effects against ants. A clear dominance order was confirmed among females in post-emergence nests (YAMANE *et al.* unpublished) as in *P. sp. aff. jacobsoni* in Malaya (YOSHIKAWA *et al.* 1969). A cell map is shown in Fig. 61.

Type Pj₂ (Figs. 62, 63 ; Pl. V, B)

Parischnogaster sp. 6. Very rare and only one nest was found at Teluk Kabung on 5 September 1980. This nest appears very similar at first sight to L₃, but differs by smaller size of cells and possession of proper cell walls on the substrate. A similar nest was reported from Malaya (erroneously cited as *Liostenogaster nitidipennis* (SAUSSURE) in YOSHIKAWA *et al.* 1969, Pl. 20.)

Substrate : Undersurface of a fern leaf. *Material* : Thin but tough carton not admixed with mud. *Color* : Mud yellow without stripes. *Architecture* : Cells rather rectangular or shot-shaped than oblong, with narrowed bottom and proper wall on substrate ; cells built serially on substrate and with the same direction in four rows, with some cells scattered ; front and bottom ends overlapping in some cells, and sharing walls as in Pj₁. *Surface* : Almost smooth, but with slight coating of carton, with short, vertical and inconspicuous keels on completed cells. *Size* : Cell, 4mm D, 9mm L, 0.2mm T. *No. of cells* : 33.

Biological notes : This species may be a forest dweller as most species of *Liostenogaster* and *Eustenogaster*. The nest was attended by two females.

Concluding Remarks

Types of nests and related aspects

Table 1 summarizes the architecture and composition of nests in the stenogastrine wasps found in Sumatera Barat together with some related biological aspects. The mentioned characters show a great diversity among groups or even species.

The nesting substrates are classified into two major categories, thin supports and flat substrates, each can be subdivided in two kinds : The thin supports involve thread-like supports (t₁), e.g., aerial rootlets and plant fibers, and moderately thin but rigid supports (t₂), e.g., twigs of trees and orchid stems. Flat substrates involve undersurfaces of rocks or timber (r) and leaves (l). About a half of *Parischnogaster* species utilize type t₁, and three *Eustenogaster* and a *Parischnogaster* species adopt type t₂ substrates. Three *Liostenogaster* and two *striatula*-group species adopt type r, and a *Liostenogaster* and a *jacobsoni*-group

Table 1. Nesting habits and colony composition of stenogastrine wasps in Sumatera Barat.

| | Substrate | Nest materials | Type of nest | No. of cells (maximum) | No. of larvae reared (maximum) | No. of female wasps (maximum) | Reuse of the same cells (maximum) | Vacated nests |
|------------------------|------------------|----------------|--------------|------------------------|--------------------------------|-------------------------------|-----------------------------------|---------------|
| <i>Liostenogaster</i> | | | | | | | | |
| L ₁ | r | M | F | 74 | 12 | 1 | | + |
| L ₂ | r | Cm | U | 40 | 20 | 4 | + | |
| L ₃ | l | Cw | C | 27 | 5 | 2 | + | |
| L ₄ | r | M | (F) | 5 | | 1 | | + |
| <i>Eustenogaster</i> | | | | | | | | |
| E ₁ | t ₁ l | Cw | E | 7 | | 1 | - | + |
| E ₂ | t ₂ | Cw | E | 16 | | 2 | - | + |
| E ₃ | t ₂ | Cp | E | 12 | | | - | + |
| E ₄ | r | Cw | E | 7 | | | - | + |
| <i>Parischnogaster</i> | | | | | | | | |
| Ps ₁ | t ₁ | Cw | P | 12 | 5 | 3 | + | |
| Ps ₂ | t ₁ | Cw | P | 7 | | 1 | | |
| Ps ₃ | t ₁ | Cw | P | 19 | | 2 | + | |
| Ps ₄ | r | Cm | P | 36 | 10 | 7 | | |
| Ps ₅ | r | Cw | P | 14 | 2 | 3 | + | |
| Ps ₆ | t ₁ | Cm | P | 30 | 11 | 12 | | |
| Pm ₁ | t ₁ | M-Cw | M | 35 | 8 | 3 | + | - |
| Pj ₁ | t ₂ | Cp | S | 10 | 4 | 3 | | |
| Pj ₂ | l | Cp | C | 33 | 6 | 2 | + | - |

Abbreviations, see in the text (p. 50-51).

species type 1. As a rule, one species seems to nest on one type of substrate. But use of both thin and flat substrates by one species is not precluded for some species, e.g., *P. sp.* 3 and *P. sp.* 4, which nest on t_1 and r substrates, respectively, but are very similar in adult morphology and likely to be the same species.

Nest materials are classified into four kinds: Brittle and fragile carton made from triturated wooden particles (Cw), which is often admixed with varying amounts of mud (Cm), the latter is most frequently used in all the genera; though paper-like carton (Cp) processed from fibrous plant matter is adopted by some *Eustenogaster* and *Parischnogaster* species (E_3 , E_4 , P_{j1} , P_{j2}), and pure mud, often incorporating sand (M), is adopted only by two *Liostenogaster* species (L_1 , L_4) and *P. mellyi* (P_{m1}), though the latter more often uses the carton of type Cm. All species except for *P. mellyi* seem to adopt single type of material.

Basic structure of nests is classified into seven major types: Flat comb like *Polistes* nests (F) (L_1 , L_4); flat comb with an envelope (E_4) or pseudoenvelope (E_1 - E_3) (E); multiple-combed nest (M), combs with cells arranged more or less irregularly (P_{m1}); \wedge or \cap -shaped comb (U), with cells in a single or double tiers and with cell axis in parallel with the substrate (L_2); regular or irregular and rather cylindrical comb possessing communal inside passage-way (P) (the *striatula*-group, P_{s1} - P_{s6}); serial arrangement of cells in a single or double rows (S) (P_{j1}); and flat cluster of cells which are scattered on leaf surfaces (C) (L_3 , P_{j2}).

The number of brood cells constructed varies by species but more or less constant within the genus. It ranged 7-16 cells in *Eustenogaster*, 7-36 in *Parischnogaster* and 27-74 in *Liostenogaster*. Reuse of the same cells for brood rearing was seen in all so far closely observed species of *Liostenogaster* and *Parischnogaster*, but it was not confirmed in *Eustenogaster*. Vacated or abandoned nests of *Eustenogaster* were relatively common, whereas those of the other two genera were rarely found. This rarity in the two genera is probably due to frequent reoccupation by other females, which was typically seen in *P. mellyi* (YAMANE *et al.* in press), and/or scraping materials from those nests by other wasps for construction of their own nests.

Notes on the stenogastrine nest architecture

JEANNE (1975) discussed the nest architecture of social wasps from the evolutionary aspects. He stressed that the nest architecture, especially that of tropical zones, has probably evolved against severe predation pressure of enemies. He suggested an asterocytarous nest consisting of a horizontal (rectinidal) comb devoid of envelope (gymnodomous), as representing the ancestral type of the vespid nests, and pointed out a nest pattern shown by YOSHIKAWA *et al.* (1969, Pls. 5, 6), i.e., Type L_1 in the present paper, probably as most ancestral. He also thought that the petiole has evolved as a countermeasure against ant attacks. Our observations, though made for a limited number of species, support in principle his idea. For the stenogastrine colonies, ants and *Vespa* are regarded as most serious enemies.

Type L_4 of *Liostenogaster* is probably asterocytarous and gymnodomous judging from

an incipient comb, and cells do not share the walls each other. Certainly this type is more primitive than L_1 mentioned by JEANNE and possibly the ancestral type as a direct descendant of the pre-comb stage. These types, L_4 and L_1 are not highly resistant against cursorial hunters such as ants, especially during the pre-emergence period. Nests of many *Liostenogaster* species are built on rock surfaces in relatively humid habitats where, by our experiences, foraging activities of ants seem to be lower than in open areas.

In the course of invasion into open habitats from shaded forest zones, two adaptive strategies may have been employed, i.e., preference of thin supports and adoption of vegetable matter for nest construction. Both are prevailing in *Eustenogaster* and *Parischnogaster*, although already appearing in some *Liostenogaster* (L_2 , L_3). The *Eustenogaster*, however, is still the forest dwellers.

Nests of *Parischnogaster* are mostly built on thin rootlets and orchid stems, which are apparently effective in defending the nests against ants. They (including at least some *Metischnogaster* spp. in VAN DER VECHT 1977 and *Stenogaster concina* VAN DER VECHT in SPRADBERY 1975) adopted fine supports instead of developing the petiole. Marked diversity of their forms is probably explained as a result of escape from strong predations by large visual predators. Among them *Vespa tropica* LINNÉ is the most serious because it exclusively feeds on immature stages of Polistinae (SAKAGAMI and FUKUSHIMA 1957) and Stenogastrinae. Some nest types are apparently cryptic within the surrounding background. Nests of *P. mellyi* (Pm_1) are very mimic to lumps of mud hanging from thin rootlets. *P. sp. 5* often builds nests on orchid stems, of which cells quite resemble nodes of the plants. These mimic nests may have more chances to survive by merging themselves into the surroundings.

Parischnogaster live in opener and drier habitats where the predation pressure seems to be higher than for *Eustenogaster* and *Liostenogaster*. They can live even in human habitations, disturbed areas, and insolated sites along roadsides. Nevertheless, they are more successful than the other two genera measured by the relative abundance. These facts, combined with the morphological specialization in male adults, suggest that this genus is the most advanced group among the Stenogastrinae. By occupying the new habitats, they have confronted with severer predation pressure. To solve this problem, they chose thinner substrates for nesting and developed various types of mimicry. The ant guard of the *jacobsoni*-group by self-secretion was probably devised to compensate the relative easiness of ant invasions due to substrates thicker than those used by other groups.

Previously various nest types of stenogastrines were regarded as the stages not yet reaching comb formation (YOSHIKAWA *et al.* 1969). The above consideration on nest patterns favors the assumption that non-combed or not typically combed nests, particularly of *Parischnogaster* represent rather a secondary adaptative disintegration of the comb system, i.e., post-comb than pre-comb stages.

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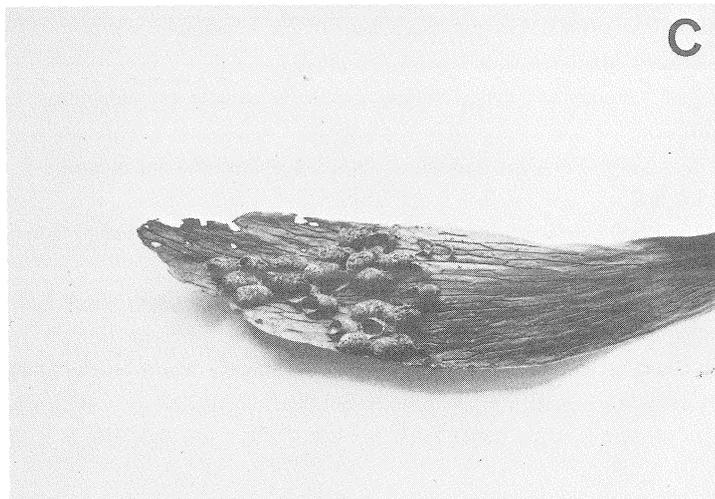
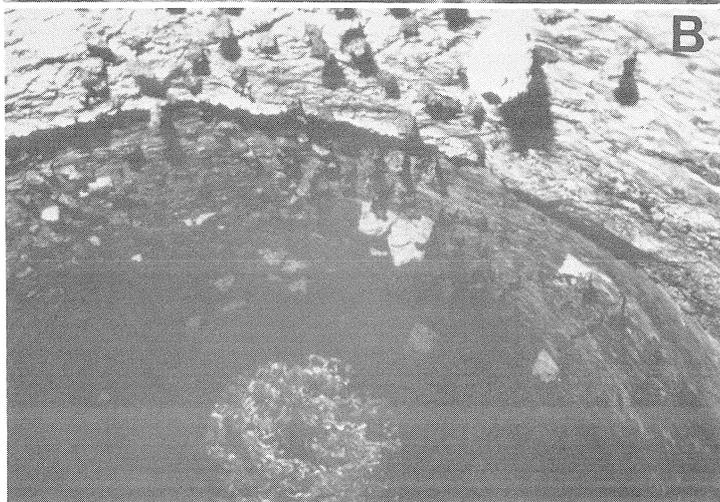
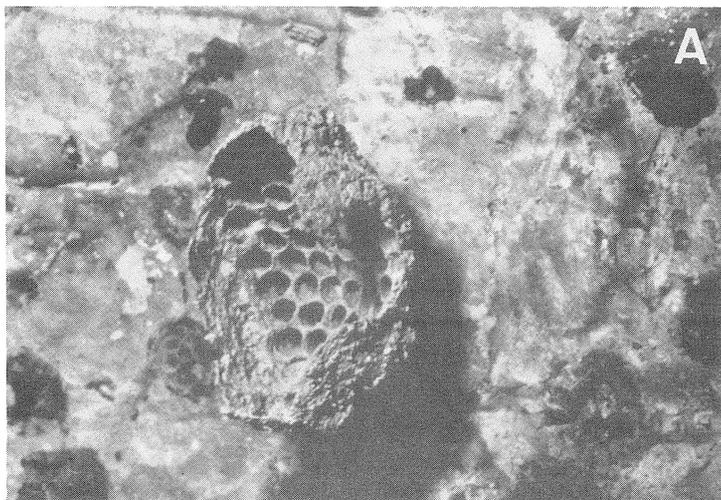


Plate I

- A. Nest of Type L₁ (*Liostenogaster* sp. 1=*L. flavolineata*?) inside a concrete tunnel for watercourse at Teluk Kabung.
- B. Aggregation of nest L₁ and Ps₄ (*Parischnogaster* sp. 2) inside the same tunnel as A.
- C. Nest of Type L₃ (*Liostenogaster* sp. 3) on a fern leaf at Teluk Kabung.

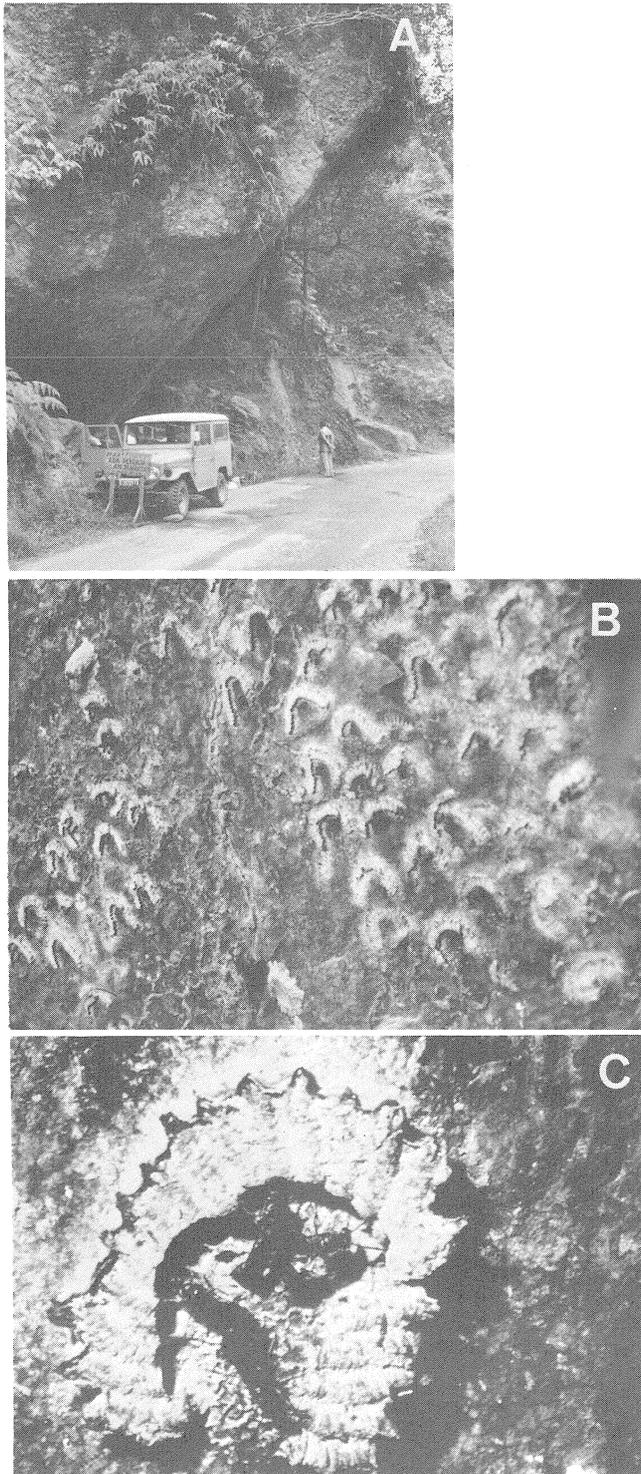


Plate II

- A. Nest site for Type L₂ (*Liostenogaster* sp. 2) at Lubuk Bangku.
- B. Aggregation of Type L₂ nest at the same place as in A.
- C. Mature nest of L₂, attended by four wasps.

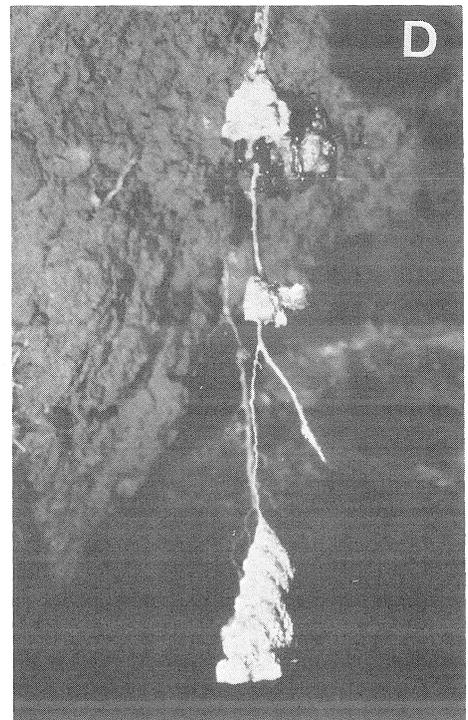
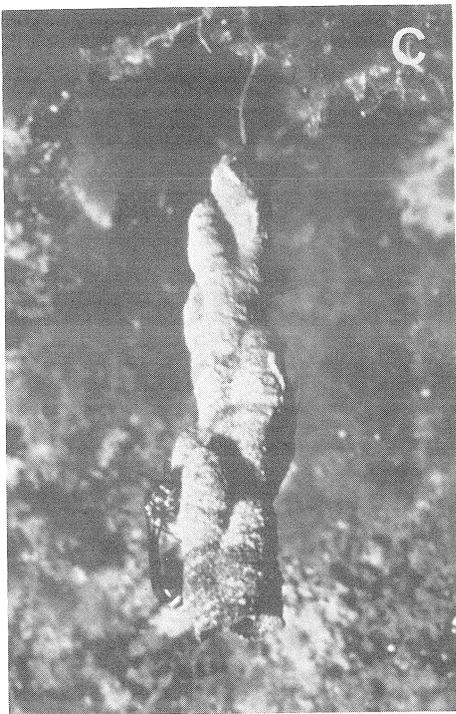
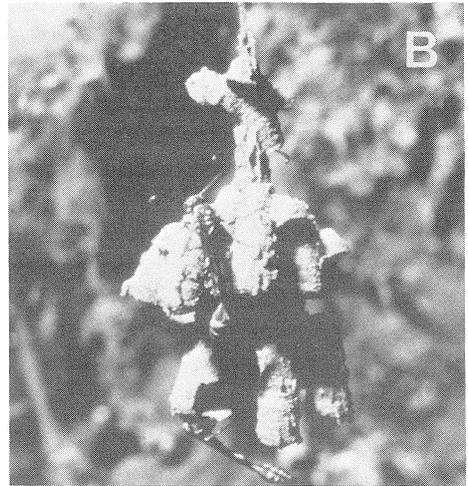
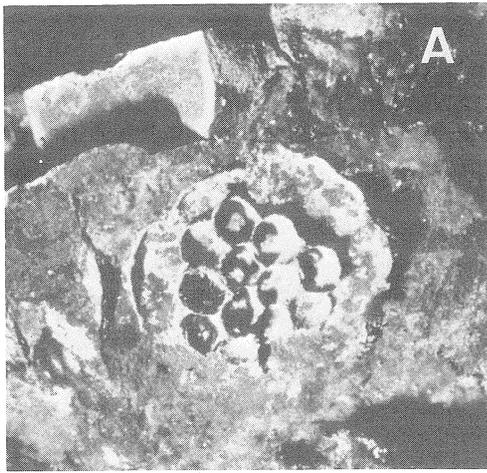


Plate III

- A. Basal fragment of Type E₄ (*E. sp. 4*=*E. calyptodoma*?) at Teluk Kabung.
- B. Mature nest of Type Pm₁ (*P. mellyi*) at Lubuk Mintrun.
- C. Nest of Type Ps₁ (*P. striatula*) at Lubuk Bangku.
- D. Mature nest of Type Ps₆ (Ps₆-B) (*P. sp. 4*) at Siguntur Tua.

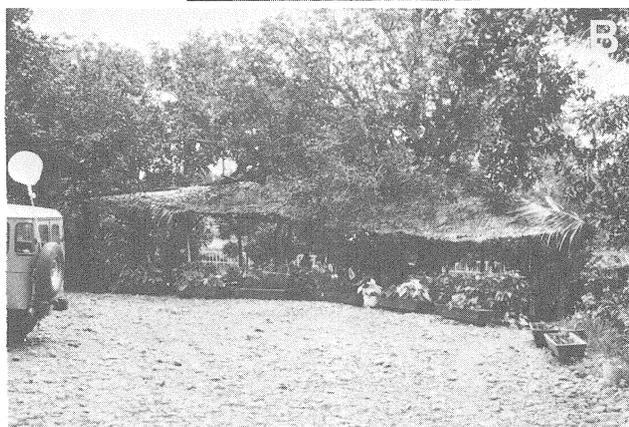


Plate IV

- A. Roadcut, nest site for Type Pm₁ (*P. mellyi*) at Teluk Kabung.
- B. Bamboo hut as nest site for Type Pm₁ and Pj₁, in the Horticultural Station, at Lubuk Mintrun.
- C. Nest of Type Ps₄ (*P. sp. 3*) inside a concrete tunnel at Sigtur Tua.

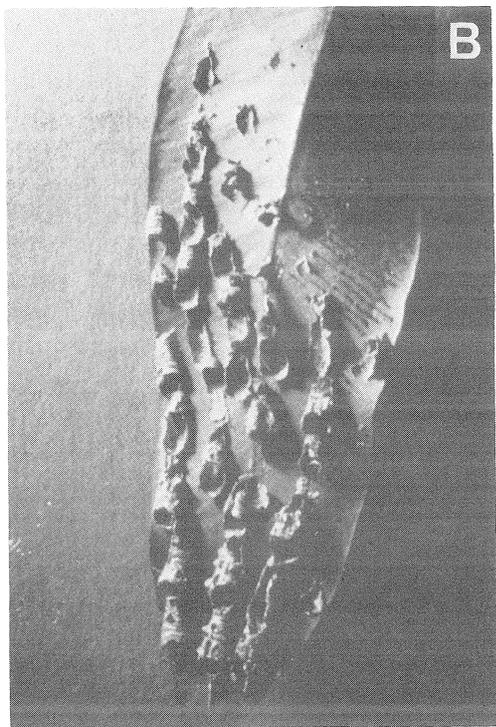
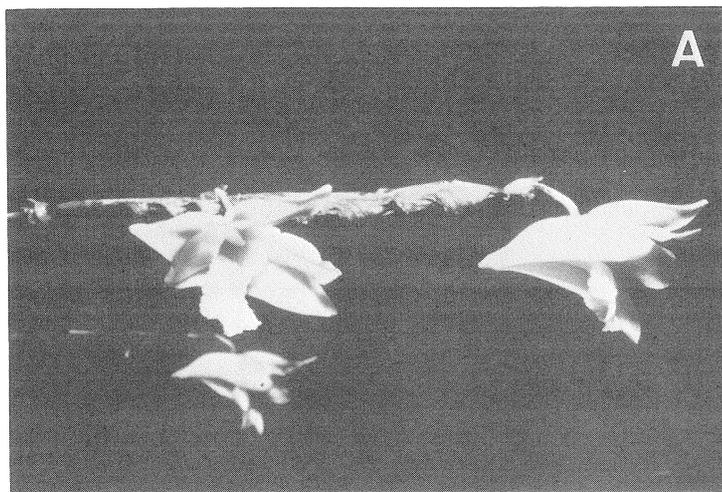


Plate V

- A. Mature nest of Type P_{j_1} (*P.* sp. 5) built on a living orchid stem at Lubuk Mintrun.
- B. Mature nest of Type P_{j_2} (*P.* sp. 6) on a fern leaf at Teluk Kabung.
- C. Ant guard of P_{j_1} .