The Halictine Bees of Sri Lanka and the Vicinity. III. Sudila (Hymenoptera: Halictidae) Part 2

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The Halictine Bees of Sri Lanka and the Vicinity.
III. *Sudila* (Hymenoptera: Halictidae) Part 2[1,2]

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Abstract. Phylogeny of 6 *Sudila* species was discussed. Four groups were recognized as follows: *(aulacophorum + jacobsoni) + kandiense +* *((alphenum + paralphenum) + bidentatum)*. *The Lasioglossum* (*Evylaeus*) *Zeiosoma* group was regarded as closest to *Sudila* tentatively. Cladistic analysis was used and the 2 species pairs, *jacobsoni-aulacophorum* and *alphenum-paralphenum are very* probably monophyletic and some dendrograms were presented. Cephalic polymorphism exhibited in *Sudila* species was noted and that recorded in some other Aculeata were reviewed. A role on the functional significance in male cephalic polymorphism was discussed.

Key words: Hymenoptera, Halictidae, *Sudila*, phylogeny, cephalic polymorphism.

Phylogenetic notes

In many halictine groups, distinction of species is not always easy, often being obliged to use subtle features like as integumental sculpture. Such difficulty does not exist in *Sudila*. We can soon recognize 4 taxonomic groups: (*aulacophorum* +

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jacobsoni) + kandiense + ((alphenum + paralphenum) + bidentatum).   Even in 2 pairs of subgroups, (au + *ja*) and (al + *pa),* sister species are easily distinguished by the features given in the preceding sections (Esakia, no. 36, p. 155, 166 and 174).   In a sense this state resembles a relictual xylocopine genus *Manuelia* distributed in the southernmost South America, involving 3 very different species.   There is another species-poor genus, *i.e.,* the best known and ecologically very successful *Apis,* with 3 subgenera, *Apis*, *Megapis* and *Micrapis.*   Each contains 3, 4 and 2 species, respectively, in a recent interpretation (Otis, 1991) which is approximately same to that suggested by Sakagami *et al.* (1977). In this case, however, it is still uncertain whether such species poverty reflects "a" relictual state or caused by the extreme ecological success of each species which might have disturbed active speciation.   It is noteworthy that all other 3 apid groups, bumblebees, orchid bees and stingless bees, produced each 150 to over 200 "good" morphospecies.

In *Sudila* the relictual state is well exhibited by the geographic distribution of each species (Fig. 36) and their confinement to high altitudes, as shown below by the number of specimens carrying altitudinal records (The records shown with 'feet' was converted to the metric system and those given with the range was replaced by the median, e.g., 1500-2000 m←1575 m).

Number of specimens arranged with altitudinal records

altitude (m)	100-200	200-500	. . .	1500-2000	over 2000	not mentioned
species						
kandiense	3 (1)*					
aulacophorum		81		10		
alphenum				10	9	6
parulphenum		13	1	0		
bidentatum		16	12	3		

* Kandy (type locality), altitude is not mentioned.   Estimate f250 m, but might have been lower.

The result shows the altitudinal range clearly confined to over 1500 m except *L. kandiense.*   The altitude of the collected locality of the only specimen of *L. jacobsoni* in Java is unknown, but may be as high as in other species.   The top of Gunung (= Mt.) Gedah (= Gede) is 2958 m alt.   However, our taxonomic knowledge on S. E. Asian halictines, particularly on small *Evylaeus* species is still poor.   Moreover, the 2 diagnostic features of *Sudila,* mesepisternal tubercle and dentate male inner hind tibial spur were first confirmed in this study.   We need to check these 2 features for any collected *Evylaeus* specimens in S. E. Asia, particularly those from high altitudes.   The results might change of the following interpretation, either partially or considerably. Anyhow, it is interesting that the sister species in 2 subgroups are both allopatric from each other, *alphenum,* Sri Lanka - *paralphenum*, *S.* India, and *aulacophorum*, Sri Lanka - *jucobsoni,* Java.
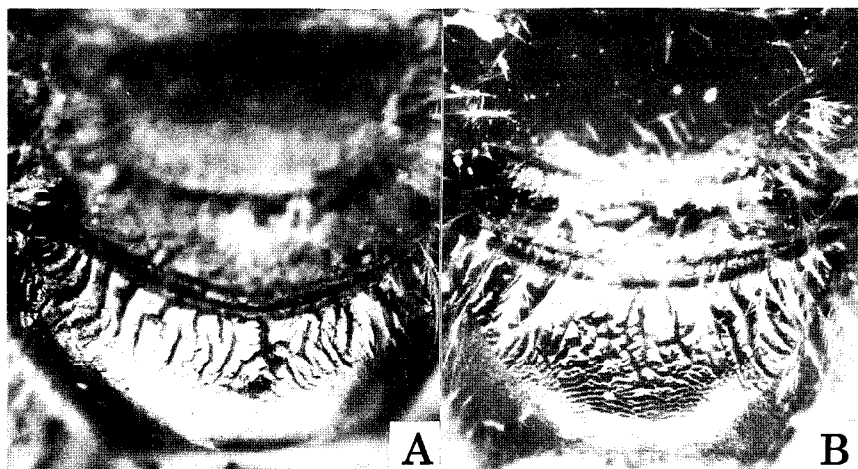
Fig. 37. Propodeal dorsum of *Lasioglossum (Evylaeus) kiosoma* A (♀), B (♂, holotype).   (Compare with Figs. 10 B, E; 14 C; 20 C, D).

The subgenus *Evylaeus can* be subdivided in 2 major groups (the carinate and carinaless groups).   The former has the propodeal dorsum separated from the vertical shield with distinct transverse carina, while the latter has not such carina.   The distinction is not categorical by the occurrence of subtle intermediate states and some species which have no such carina, nevertheless certainly belong to the carinate group by the general habitus (e.g., *L. (E.) subtropicum*, Sakagami *et d.,* 1994).   The carinate group is a rather compact group whereas the carinaless group is more heterogeneous. Generally the carinate species are larger, approximately as large as *Sudila* species except *L. (S.) kandiense* and most bionomically known species are eusocial and brood cells are combed within a pre-excavated cavity.   In the carinaless group most species are small, most bionomically known species are solitary with cells excavated in soil.   The distinction of these 2 groups is further complicated by the occurrence of both black and metallic species in each group at least in Palaearctics.

As all known *Sudila* have carinaless problem (Figs. 10, 11, 14, 20), this subgenus should have arisen from the carinaless *Evylaeus*.   Tentatively we regard the *L. (E.) leiosoma* group (Ebmer & Sakagami, 1985b) as closest to *Sudila*. This group involves some relatively large carinaless species (approximately as large as *L. (S.) kandiense)* predominantly distributed in S. E. Asia.   Moreover, they share with *Sudila* the absence of coarse punctation or reticulation and particularly the relatively long propodeal dorsum (about as long as mesoscutellum, Fig. 37) tapering postward and above slightly concave (compare with Figs. 10, 11, 14, 20).   Many species are long-headed and not always high-altitude inhabitants like as *L. kandiense*.   However, *L. kandiense* is a peculiar species with rather granular than punctate sculpture, fat-like propodeal ridges and whitish postmarginal tergal fimbriae.   Even if the *L. leiosoma* group is the real ancestor of *Sudila*,

L. kundiense may not be the direct link between the 2 groups but only relatively closer to the point of *Evylaeus* - *Sudila* departure than the other larger, high-altitude *Sudila* species. Among 6 *Sudila* species, *L. paralphenum* is devoid of the mesepisternal tubercle (Fig. 3). This peculiarity could be interpreted as either already lost (Posibility(P) I) or not yet acquired (P II).   P I suggests that *L. paralphenum* is a real member of *Sudila,* whereas P II regards it as an outgroup species.   We think P I is more likely than P II.   Let us choose 3 important characters and codify the character states (= features) as follows: 1- T, (T), t = metepisternal tubercle distinct, weak, absent; 2- M, m = metallic tint present, absent; 3- G, g = male cephalic gigantism present, absent.

As shown in Fig. 38, P I can explain the interspecific derivation only by single appearances of t→T, m→M, and g→G, but P II requires twice independent appearances of m→M and g→G.   The reduction of mesepisternal tubercle is also suggested in *L. bidentatum* (Fig. 3).   Moreover, P II ignores the remarkable similarity of *L. alphenum* and *paralphenum* in general habitus.   We adapt P I as more reliable until better interpretations would be obtained later.

As already mentioned, the distinction of consubgeners is easy by the occurrence of some very reliable specific features.   On the other hand, this ease itself makes the phylogenetic interpretation of consubgeners difficult, because these features seem often autapomorphic from the outgroup comparison as enumerated below, such features usually do not much help the cladistic analysis, however interesting for the evolutionary consideration.

L. aulacophorum:1- Extremely small male ventral lobe (Fig. 13) possibly plesiomorphic if it is homologous with that of some species of *L. leiosoma* group.   2- Wide, densely haired penis valve (Fig. 13).

L. kundiense: 1- Elongate head (Fig. 14, might be plesiomorphic if homologous with that of *L. leiosoma* group).   2- Postmarginal fimbriae of female metasomal terga.   3- Fan-like propodeal ridges (Fig. 14).

L. alphenum: 1- Basally widened male mandible (Fig. 21, 22 C, D).   2- Angulate male mid trochanter and femur (Fig. 22 E).

L. paralphenum: 1- Sexual dimorphism in mesoscutellar sculpture (Fig. 26). 2- Bifid male gonostylus (Fig. 28).   3- Absence of metepisternal tubercle (Fig. 3). As mentioned above, this feature was used for phylogenetic analysis, combined with other features (Fig. 38).

L. bidentatum:1- Unusually sparse hairs (Figs. 20 B, 31 C).   2- Partly or entirely reddish metasomal terga. 3- Subapically widened male mandible. 4- dentate male clypeus.   5- Developed male genal process (Male ventral retrose lobe is longer than in the other consubgeners, Figs. 35 vs. Figs. 13, 17, 23, 28).   The relative polarity of these 2 states is still unsettled, as both states are seen in the *L. leiosoma* group (Sakagami, unpubl.).
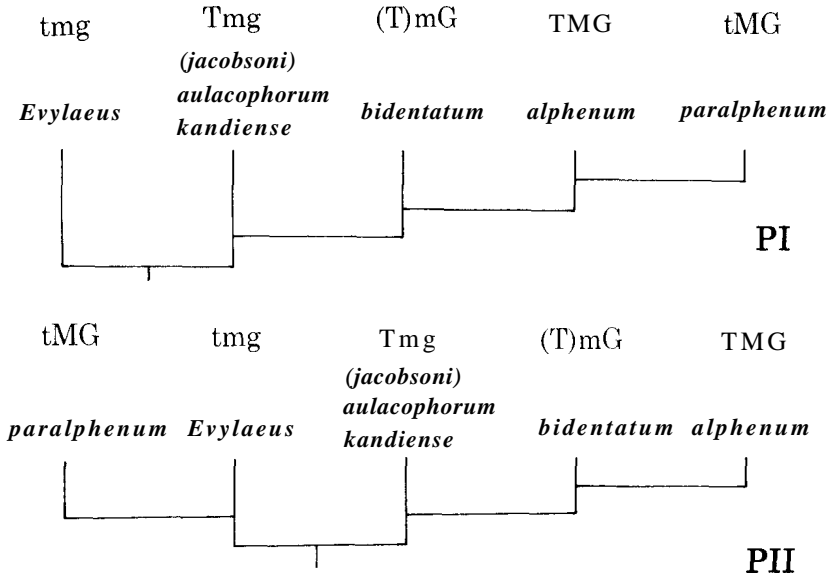
Fig. *38.* Two alternative cladograms of *Sudila.* T (T), t = mesepisternal tubercle distinct, weak or absent; M, m = body metallic or not; G, g = male giagantism present or not.
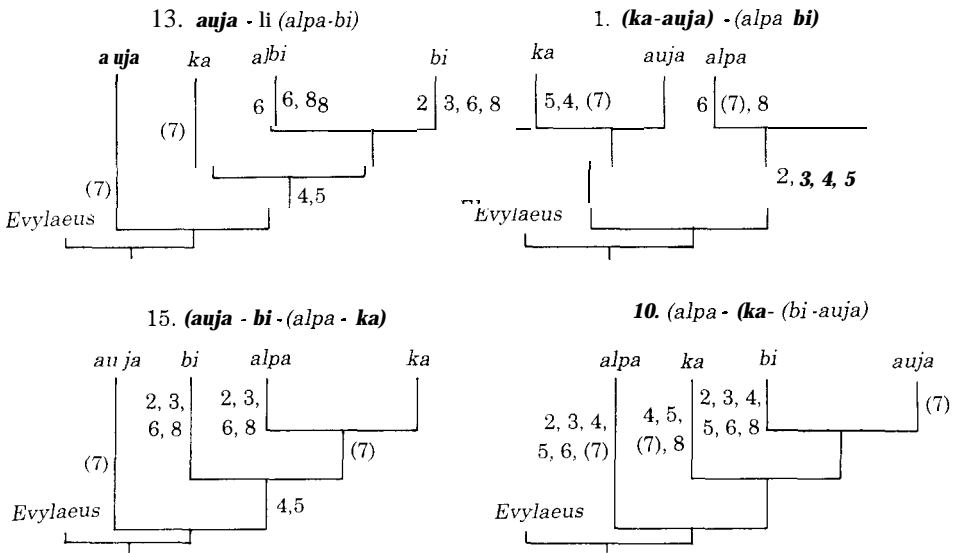

Fig. 39.   Three most parsimonious (codes 13, 1, 15, Table 6) and 1 least parsimonious (code 10, Table 6).   Cladograms in terms of the number of independent appearances of 7 synapomorphic character states (character 7 is parenthisized for the presence of *2* alternative hypotheses).

Table 5. Synapomorphic features (= character states) in *Sudila* species (P = plesiomorphic, A,= apomorphic, A_2 = more apomorphic than A,).

Apomorphies	Species					
	jacobsoni	**aulacophorum*	*kandiense*	*paralphenum*	*alphenum*	*bidentatum*
1 Metallic color	P	P	P	A,	A,	P
2 Male gigantism	?	P	P	A,	A,	A,
3 Black hairs on fore-body	P	P	P	A,	A,	A_2
4 Hairs sparser	P	P	A,	A,	A,	A_2
5 Sculpture weaker	P	P	A,	A,	A,	A,
6 Male F, below outcurved	?	P	P	P	A	A
7 Male retrose lobe reduced	?	A, (P)	A, (P)	A, (P)	A, (P)	P (A)
8 Metepisternal tubercle reduced	P	P	P	A_2	P	A,

* Male unknown

underlines indicate codes.

Synapomorphies to be used for further cladistic analysis are not many but available as listed in Table 5. Male cephalic gigantism involves several subcharacters but these are treated as if a single character, because these obviously had to differentiated conjointly. The 2 species pairs, *jacobsoni-aulacophorum* and *alphenum-paralphenum* (clustered as *ja-au, al-pa*) *are* very probably monophyletic, and each is intuitively regarded as a cladistic unit. These notes on Table 5 are added to: 1- Differences A_1-A_2 were not used for the analysis. 2- The elongate male retrose lobe in *bidentatum* might be apomorphic. Then this feature becomes autapomorphic and should be excluded from the analysis (see below). 4- Metallic color was not used because it becomes autapomorphic for the subgroup *al+pa*.

Table 6 shows the number of probable independent appearences of seven synapomorphic character states in 15 possible cladograms. Total number of independent appearances is given by the 2 ways, according to the interpretation of synapomorphy 7. If the state expressed by *L. bidentatum* is considered apomorphic, then it becomes autapomorphic and the character 7 should be excluded from the summation as parenthetically given in the column "total". Figure 39 presents the 3 most parsimonious cladograms (codes 13, 1, 15 in Table 6) and the least parsimonious case (code 10 in Table 6), showing the probable loci of the appearances of synapomorphic character states (character 7 given parenthetically). Table 6 and Fig. 39 suggest the 2 trends. 1- Three

Table 6.   The number of probable independent appearances of 7 synapomorphies in 15 possible cladograms.

Cladograms		Synapomorphies (cf. Table 5)							
Code	Structure	2	3	4	5	6	7	8	Total
1	*(ka -auja) - (alpa - bi)*	1	1	2	2	2	2	2	12(10)
2	*(ka -bi) - (auja - alpa)*	2	2	2	2	2	2	2	14 (12)
3	*(ka - alpa) - (bi -auja)*	2	2	2	2	2	2	2	14 (12)
4	*ka (bi (alpa- auja))*	2	2	3	3	2	2	2	16 (14)
5	*ka (auja (alpa -bi))*	1	1	2	2	2	3	2	13 (IO)
6	*ka (alpa (auja - bi))*	2	2	3	3	2	3	2	17 (14)
7	*bi (alpa (ka -auja))*	2	2	3	3	2	1	2	15 (14)
8	*bi (ka (auja -alpa))*	2	2	3	3	2	1	2	15 (14)
9	*bi (auja (alpa - ka))*	2	2	2	2	2	1	2	13 (14)
10	*alpa (ka (bi -auja))*	2	2	3	3	2	3	2	17 (14)
11	*alpa (bi (ka -auja))*	2	2	3	3	2	2	2	16 (14)
12	*alpa (auja (bi - ka))*	2	2	2	2	2	3	2	15 (12)
13	*auja (ka (alpa-bi))*	1	1	1	1	2	3	2	11 (8)
14	*auja (alpa (ka - bi))*	2	2	1	1	2	3	2	13 (10)
15	*auja (bi (alpa - ka))*	2	2	1	1	2	2	2	12 (10)

male-gigantic species, **L. alphenum,** *paralphenum* and **bidentatum are** rather specialized, occupying the loci distant from the probable origin of **Sudila.**   2- **The** species group *aulacophorum-jacobsoni* seems to occupy as if the locus near to the origin.   The first trend is reasonable, suggesting further differentiation of these gigantic species from the proto-*Sudila.*   On the other hand, the second trend seems as if opposing to the suggestion given at the top of this section, the possible affinity between the L. **(Evylaeus) leiosoma** group and **L. kandiense.**   However, the cladograms 13.1.15 merely suggest the isolation of the **au-ja** group from the other **Sudila** species. Further analysis is necessary to specify the real origin of **Sudila** by establishing a reliable set of useful characters from the comparison of relevant S. Asian **Evylaeus** groups including the **L. leiosoma** group.

    Finally some other characters of possible cladistic values are mentioned, although these were not used in the above analysis because their polarities are still unsettled.

    1- Male labrum: Probably a gradual differentiation goes from **L.** *aulacophorum* (Fig. 12 D) via **L.** *alphenum* (Fig. 22G) to **L. bidentatum** (Fig. 22 H), but the character state is still unknown in **L, kandiense, L. paralphenum** and in **L. leiosoma** group and other S. E. Asian carinaless **Evylaeus** for the lack of sufficient material.

± **0.25** mm in *aulacophorum*

ja   au   al   bi   le   ka
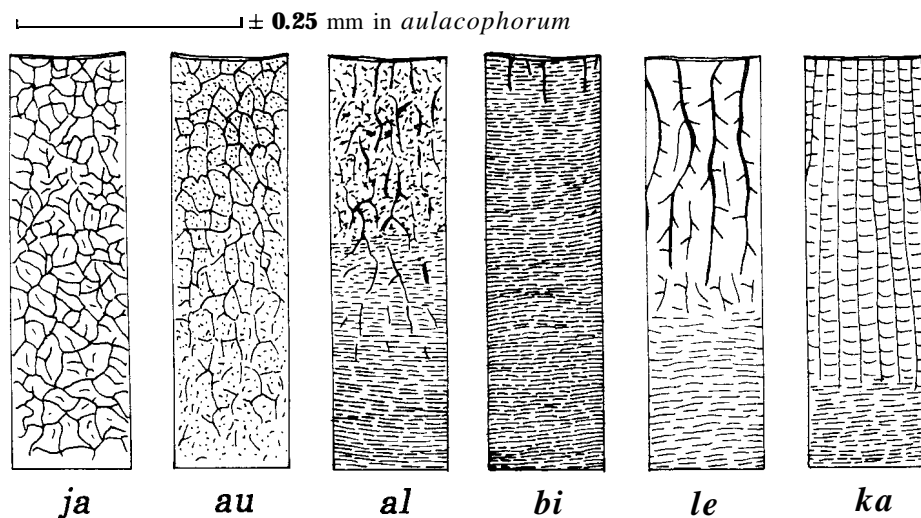
Fig. 40.   Propodeal sculpture of *Sudila* species and *Las.* (Ev.) *leiosoma,* all in females.
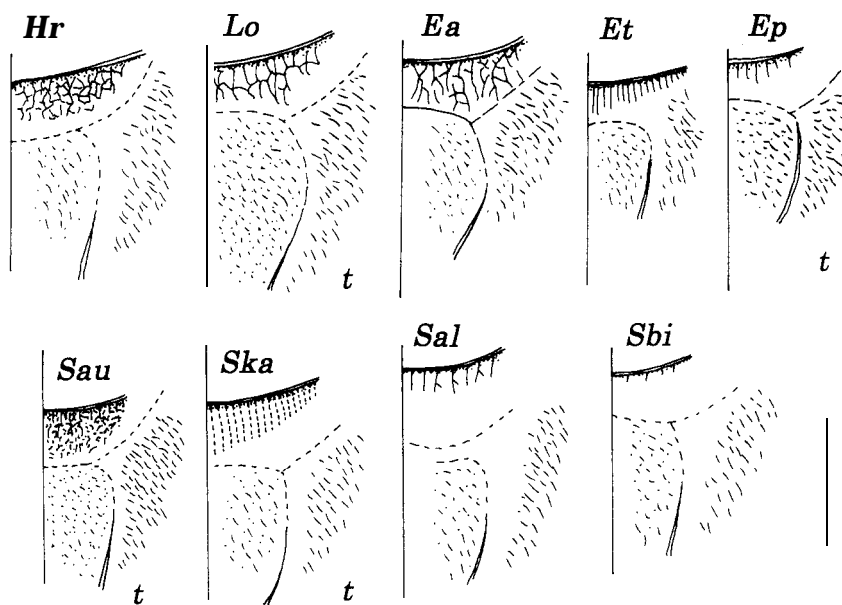

Fig. 41.   Pilosity on propodeal side and shield (schematically with sculpture of propodeal dorsum) of *Sudila* and some other halictines (all females).   *Hr = Halictus (Hdictus) rubicundus, Lo = Lasioglossum (L.) occidens, Ea = L. (Evylaeus) affine, Et = L. (E.) transpositum, Ep = L. (E.) problematicum, Sau = L. (Sudila) aulacophorum, Ska = L. (S.) kandiense, Sal = L. (S.) alphenum, Sbi = L. (S.) bidentatum,* t = propodeal shield tomented.   Scale = 0.5 mm in *Et, Ep, Ska,* and 1 mm in others.
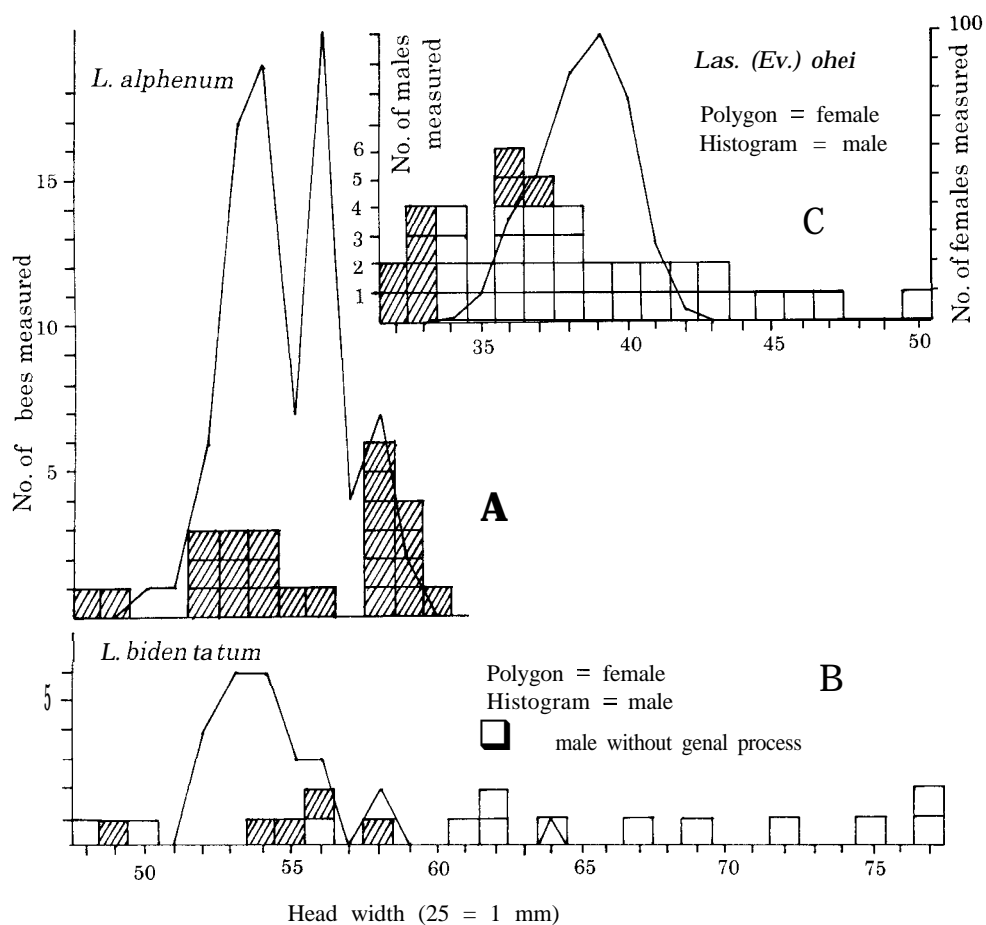
Fig. 42. Frequency distribution of head widths of both sexes in *L. (S.) alphenum* (A), *bidentatum* (B) and *L. (Evylaeus) ohei (C).*

2- Sculpture of propodeal dorsum: Fig. 40 (cf. also Fig. 41) suggests some directions such as *ja→au→al→bi* or *ja→au→le→al→bi*. The most likely sequence will be obtained through further comparative studies of S. E. Asian carinaless *Evylaeus*. *L. kandiense* deviates from the other cited taxa by its marked differentiation (see also Figs. 10 B, E, 14 C, 20 C, D).

3- Pilosity on the propodeal side and shield: On this character the *au-ja* group differs from other *Sudilu* species (Fig. 19). The bottom row of Fig. 41 shows the order *au→ka* → *(al + bi)* in *Sudila*, corresponding to the gradual poverty of hairs shown as synapomorphy 4 in Table 6. However, this character seems to vary rather sporadically
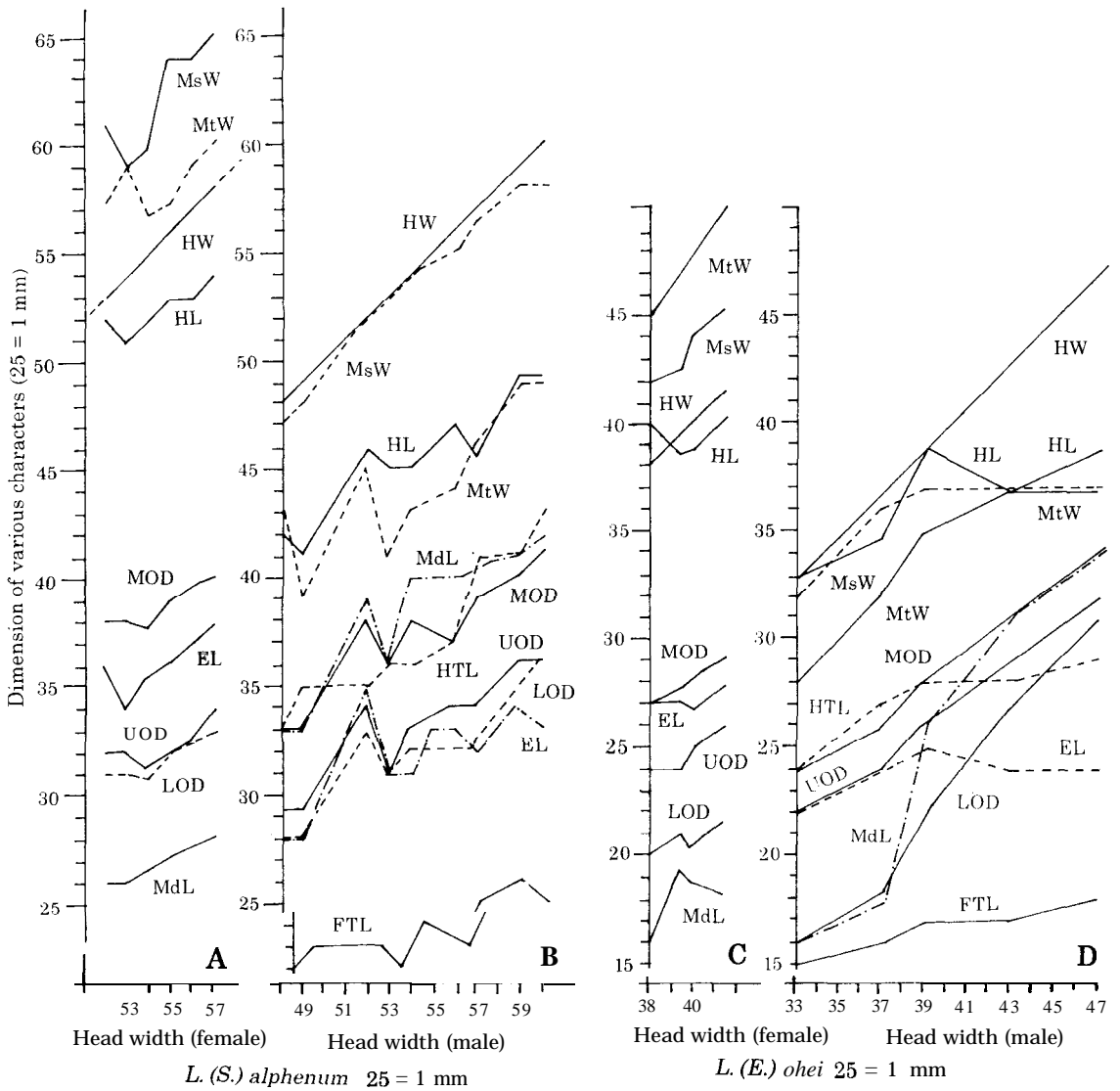
Fig. 43. Comparison of some large-scale characters in *L. (S.) alphenum* (A, B) and *L. ohei (C,* D) in both ♀(A, C) and ♂(**B,** D).

among other halictines as shown in the top row of Fig. 43.   The relation between its stability and diversity (including the presence or absence of tomentum on shield) in various halictine groups is not yet well known, to be studied in various groups including its possible cladistic value.

4- Shape and pilosity of penis valve: The penis valve of *L.* (S.) *aulacophorum* (Fig. 14) differs remarkably from those of other consubgeners by the tall dorsoventral shape and dense surface hairs.   In the latter species some marked differences are recognized (Figs. 17, 23, 28, 35). The discovery of the male of *L.* (S.) *jacobsoni*, the sister species, may help further elucidation.   These aspects were not used in the cladistic analysis because the inpolarities were still unknown.   Further comparison with other *Evylaeus* groups is requested.

Notes on cephalic polymorphism

The 2 *Sudila* species *L. alphenum* and *L. bidentatum* exhibit the conspicuous cephalic polymorphism in males.   Further morphometric detail of this peculiarity is described below.   Such polymorphism is also expected in the 3rd species with male gigantism, *L. paralphenum*, although still uncertain because at the present only 3 males are available. The cephalic polymorphism is sporadically known in males and females of some other Aculeata.   Using this occasion, a perspective of this phenomenon is given subsequently.

Male polymorphism in Sudila: Some morphometric results of 2 *Sudila* species are given below, compared with that of *L.*(*Evylaeus*) *ohei* Hirashima et Sakagami (Sakagami *et al.,* 1966) of the *L. (Evylaeus) sexstrigatum* group of which well known species exhibit similar cephalic polymorphism.   Figure 42 shows the frequency distribution of head widths in both sexes of the 3 mentioned species based on all available and measurable specimens.   In *L. alphenum* distributions look like bimodal in both sexes. This might be real to a degree but probably in part caused by the limited numbers of available specimens judging from the narrow valleys separating 2 peaks.   The variation range is similar in both sexes and all males have no genal process.   In *L. bidentatum* the variation range is distinctly wider in ♂♂ > ♀♀, and only small ♂♂ lack the genal process.   The difference between 2 species reflects the male cephalic polymorphism more exaggerated in *L. bidentatum.*   The pattern in *L. (E.) ohei* is very similar to that in *L. bidentatum,* suggesting a parallel evolution between the two remote taxa.

To know the nature of polymorphism more closely, some morphometric characters of the 3 species were compared in Figs. 43-46.   The adopted characters are abbreviated as given parenthetically (cf. also Part I, Tables 1-4, W, L, D = width, length, distance. Characters asterisked are only for ♂, and those with § newly used).

A (25 units = 1 mm): HW, HL (head W, L), MsW, MtW (mesosomal, metasomal W), EL (eye L), UOD, MOD, LOD (upper maximum, lower interorbital D), MdL [§] (mandible
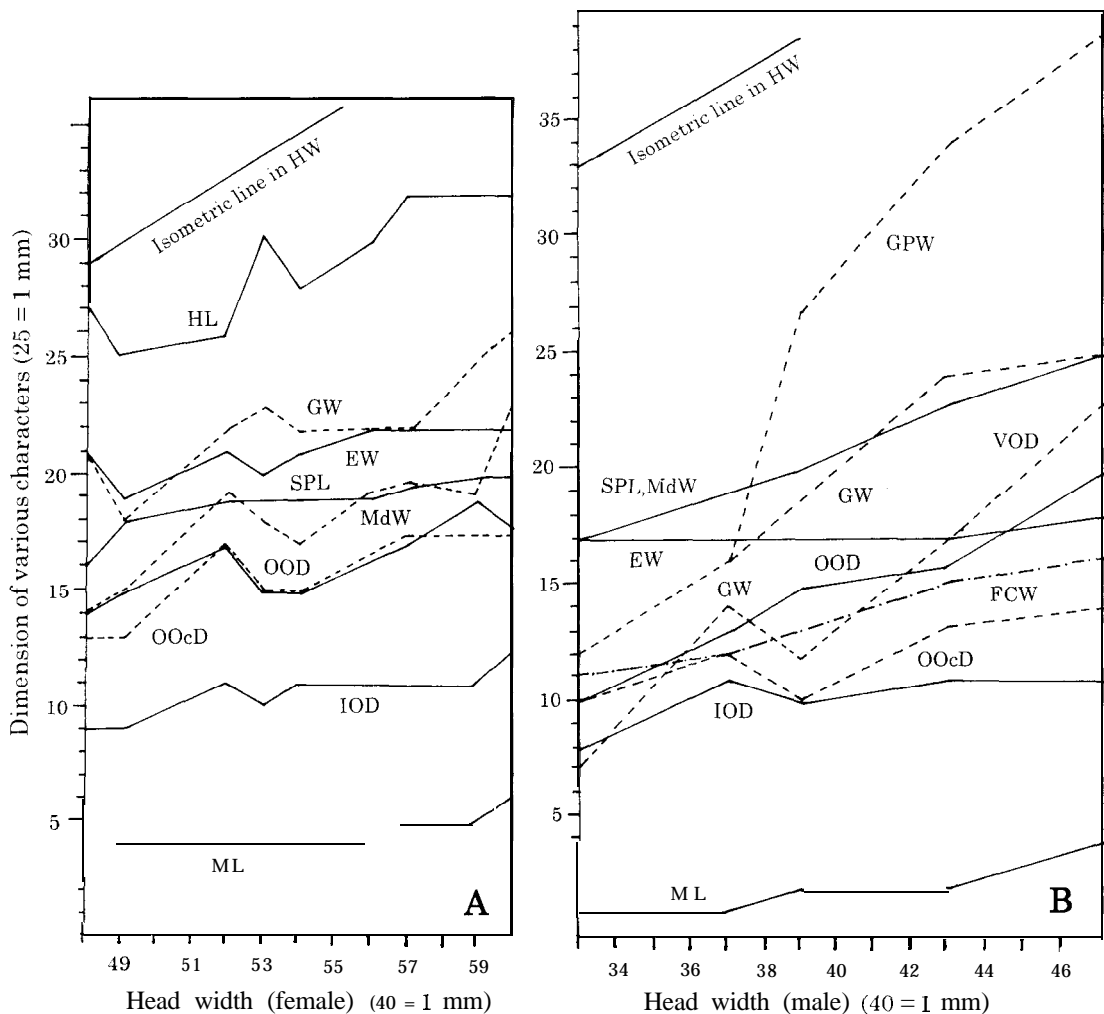
Fig. 44.   Comparison of some small scale characters (all cephalic except FCW) in ♂♂
of *L. alphenum* (A) and *L. ohei* (B).

L), FTL, HTL[§] (fore, hind tibia L).

    B (40 units = I mm): HW, SPL (scape L), EW, EG* (eye, gena W seen laterally),
MdW[§]* (mandible W), OOD, IOD (ocellocular, interocellar D), ML (malar L), GPW[§]*
(gena W incl. process, only in *L. bidentatum* and *ohei),* FCW[§]* (fore coxa frontal W),
CTV (clypeal tooth L, only in *L. bidentatum),* VOD (verticorbital D, tangential D between
summit of vertex and supraorbital line, only in *L. bidentatum* and *ohei),* OOcD
(ocelloccipital D,   D between postocellar line and occipital end seen dorsally, only in *L.
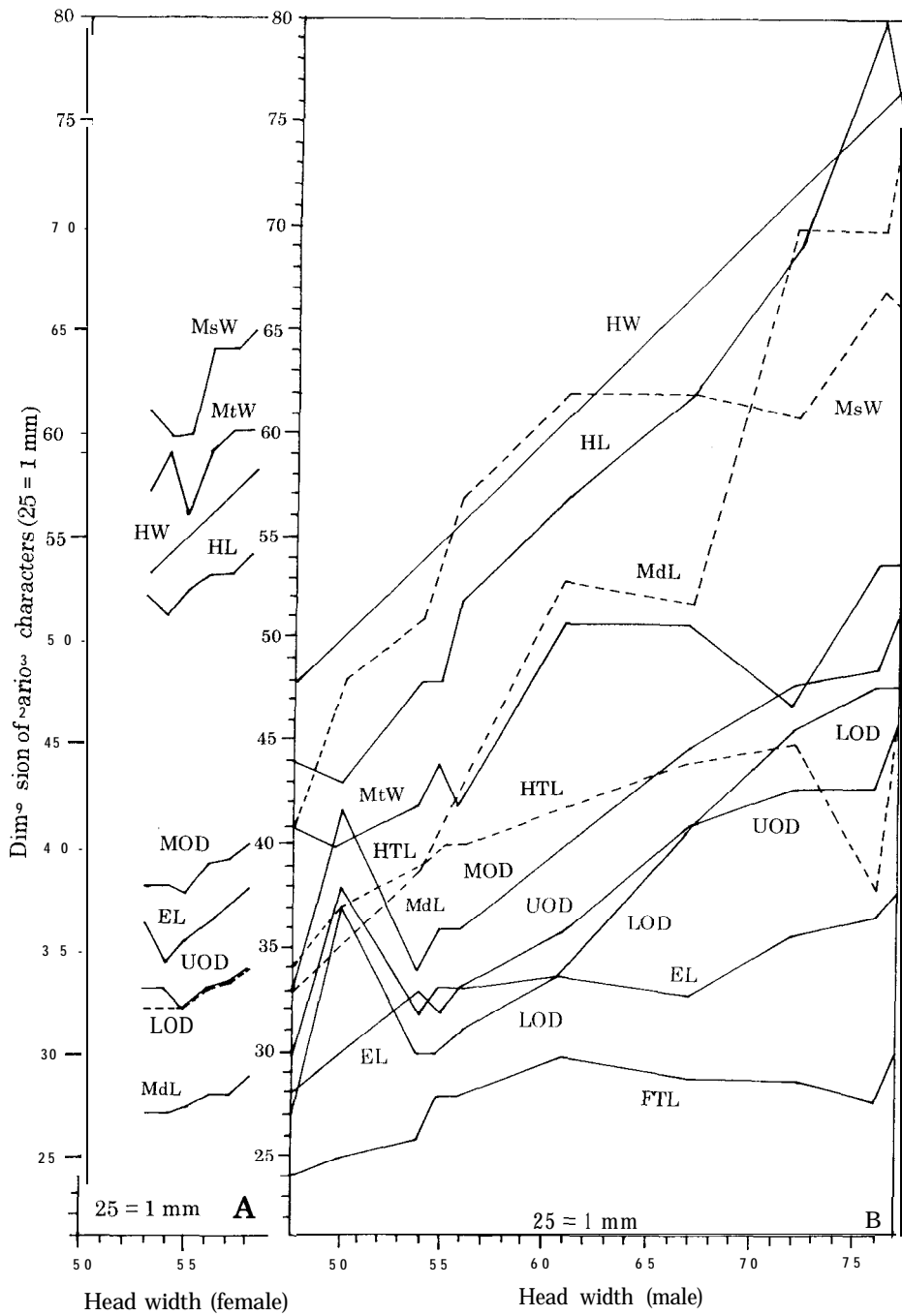bidentatum* and *L. ohei) .*

Fig. 45. Comparison of some large scale characters in ♀ (A) and ♂ (B) of *L. bia'entatum.*

Although morphometric data were used, the purpose of this comparison is primarily qualitative than quantitative to know some morphological trends in cephalic polymorphism.   From the specimens of which various characters were measured, 10 (*Sudila*) or 5 (*L.ohei*) individuals were chosen, of which measure values of many characters did not much overlap within the variation range.   The measured values of each character were plotted against that of head width and arranged in the ascending order of head width in Figs. 42-46.   When there were more than one specimen showing the same value in respective character for a given value in head width, the mean value was adapted.

Two remarks must be mentioned: 1- As many adopted characters are smaller- Scaled than head width, increase of their values in larger specimens is milder than the isometric HW/HW line given at the top of each graph (e.g., MdL in ♀ or FTL in ♂).   The comparison is meaningful only made between conspecific or among characters of similar dimension, e.g., IOD vs. OOD, or EW vs. GW, etc.   2- Expected monotonous increase in the graphs from the left to the right side is often disturbed by the individual differences. For example in Fig. 43 A (*alphenum* ♀) the 3rd ♂ had MOD, UOD, LOD higher than the 2nd and 4th males.   The variation trend can become irregular by such individual fluctuation.

The variation trends in females of all 3 species are similar in both the level of absolute sizes and the degree of variation, which are far less conspicuous than in males, particularly in *L. bidentatum.*

Comparing variations of the large scale characters the variation ranges are distinctly wider in *L. bidentatum.*   In *L. alphenum* the variation trends of most characters coincide with the isometric HW/HW line except for EL and FTL which increase mildly in all 3 species.   In *L. bidentatum,* MdL and LOD (relative to UOD) increase more steeply, the latter indicating increase of the width of the lower part of the head more conspicuously than the upper interorbital part.   This tendency is also suggested in *L. ohei.* In small-scale body parts, OOD and OOcD relative to IOD and GW relative to EW increase in all 3 species but more in *L. bidentatum,* especially accelerated in GW by the development of genal process.

Summarizing, main trends seen in males of 3 spp, in parallel to the increased body size are: 1- Upward and sideward enlargement of the head as shown by OOcD, OOD, VOD > IOD. 2- Enlargement of gena, and in *L. bidentatum* and *L. ohei,* development of genal process (GPW ≫ EW).   3- Enlargement of the lower head sideward (LOD ≧ VOD) combined with elongation and widening of mandibles. All these trends are exaggerated in *L. bidentatum* (and also to lesser degrees in *L. ohei).*   Further, 4- Sparser hairs. 5- Reduced punctures and genal striation. 6- Appearance of clypeal teeth. 7,8- Mandibles widened at base *(L. alphenum)* or subapically *(L. bidentatum).* And 9- Pronotal modification (Figs. 29-34).   These bizzare features, being traceable in lesser degrees also in *L. alphenum, paralphenum* and *L. ohei,* seemingly relate either directly or indirectly to the development of mandibles and accompanied mandible muscles which re-
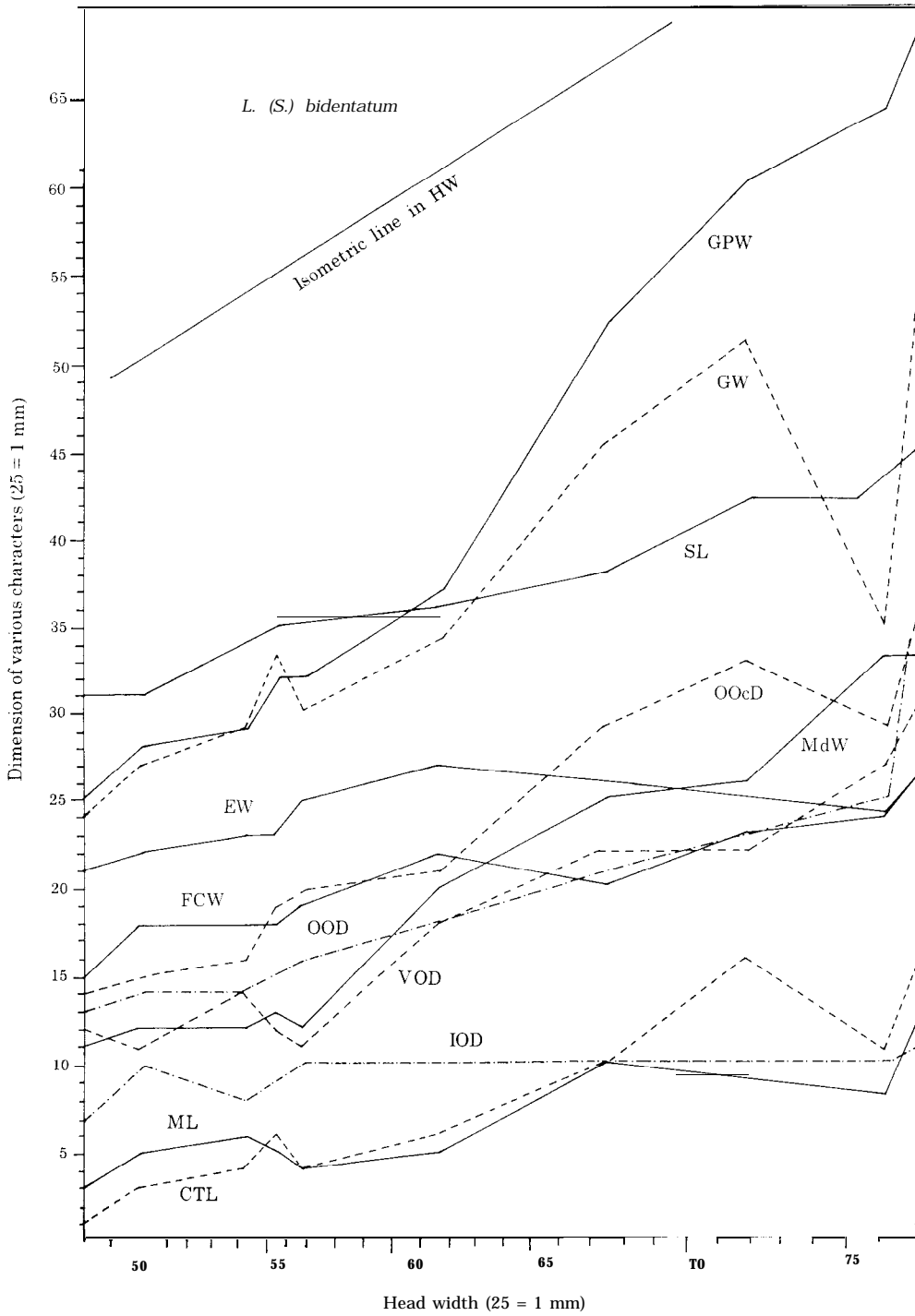
Fig. 46. Comparison of some small-scale characters in ♂ of *L. bidentatum*.

quire ampler surface within the head.   Such polymorphism expressed by gigantism is
also recorded in some other Aculeata as reviewed below, though not exhaustively.

Male cephalic polymorphism in some Aculeata

First the halictine species of the *Lasioglossum* (carinaless *Evylaeus*) *sexstrigatum*
group is dealt with.   This Palaearctic / Oriental groups is represented in Europe only by
the unique transpalaearctic species, *L. sexstrigatum* (Schenck), but by many not yet well
studied species in eastern to S. E. Asia.   Beside *L. ohei* in Japan, *L. sexstrigatum*, *L.
taniollelum* (Vachal), *L. pallilomum* (Strand), *L. simplicior* (Cockerell), *L. speculinum*
(Cockerell) (Sakagami, unpubl.), *L. smilodon* Ebmer & Sakagami (Ebmer *et al.*,1995),
L. sphecodicolor   Sakagami et Tadauchi (Sakagami & Tadauchi, 1995), and some other
undescribed species exhibit gigantic male polymorphism, and a mild polymorphism
comparable to *L. alphenum* in *L. japonicum* (Dalla Torre) (Sakagami, unpubl.).

Fig. 47.   A, B: Large gigantic and small normal males of *L. sexstrigatum, C:* gigantic
    male of *L. asteria* Ebmer (Holotype).

Moreover, there are several species with male gigantism are known scatteredly among the following halictine groups.   Probably these species may also exhibit the cephalic polymorphism as in *L. sexstrigatum* group, when the whole variation range would be clarified: *L. (Lasioglossum) eickworti* McGinley, Central America (McGinley, 1986), *L. (Ev.) asteria* Ebmer, Iran, of the *L. (Ev.) nitidulum* group, *L. (Ev.) vulcanium* (Blüthgen, 1928) (given as *L. vulcanicum* in the index by Blüthgen), Java, of the *L. (Ev.) Zeiosoma* groups., *L. (Ev.) ariadne* Ebmer, Crete, of the *L. (Ev.) alpigenum* group (Ebmer, 1981) and *L. (S.) paralphenum* described in this work.

Another case, *L. (Chilalictus) erythrurum* (Cockerell) and some allied species, is noteworthy (Houston, 1970; Knerer & Schwarz, 1976; Kukuk & Schwarz, 1988) by the polymorphism which could be called "duplicate" or "overlapped" type.   In a species well described by Houston (= *Las.* sp. 2 in Knerer & Schwarz, op. *cit**), the macrocephalic and more normal males (abbreviated as A and B males) form a discontinuous dimorphism. A- males share with the macrocephalic males of *L. bidentatum* all l-9 items enumerated above.   The differences are: 1'- Clypeal teeth issuing from the sides, not from the submedian part and of a different type.   2'- Mandibles with inner tooth. 3'- Eyes greatly reduced.   4'- Antennae flatter with shorter flagella.   5'- Wings shorter, incapable to fly.   6'- Fore femora (not mid femora as in *L. alphenum*) expanded below. 7'- Metasoma relatively wide.   While these A-males, evidently more specialized than the large macrocephalic males of *L. bidentatum, are* uniform, the more normal B-males form by themselves a continuous "subpolymorphism",   with their larger males with heads enlarged and quadrate, genae produced, mandibles longer, and fore femora below slightly expanded.   In other words, the subpolymorphism in B-males approximately corresponds to the male polymorphism in *L. bidentatum,* although possibly less exaggerated.   The A-males may be a disrupted and more specialized extremity of the ancestrally continuous polymorphism characterized by 3',4',5',7', which are absent in *L. bidentatum* and evidently suggest a modified mode of life of the bearers.   Knerer and Schwarz (op. *cit.) also* illustrated a head of *Homalictus* sp. which is very similar to those of *L. erythrurum* and allied species without any explanation.

Above cases of the continuous gigantic polymorphism are reminescent of horns in *Titanotheres*, a tertiary *Perissodactyla,* in which the horns appear corresponding to the allometric increase of body size (Hersch, 1934).   Such gigantic macrocephalism is also known in other Aculeata.   In some *Andrena* bees, e.g., subgenera *Andrena, Holandrena* and *Stenomelissa* (Hirashima, 1962, 1964, 1965, Tadauchi and Hirashima, 1988), the males often exhibit a cephalic polymorphism similar to that in halictines, but with the appearance of mandibular, instead of genal process (Fig. 48).

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* *Lm.* sp. 2 in Knerer & Schwarz = *L. (Chilalictus) hemichalceum* (Cockerell, 1923) by 1 female, 1 male normal, 1 male gigantism, gifts from Knerer to Ebmer collection.
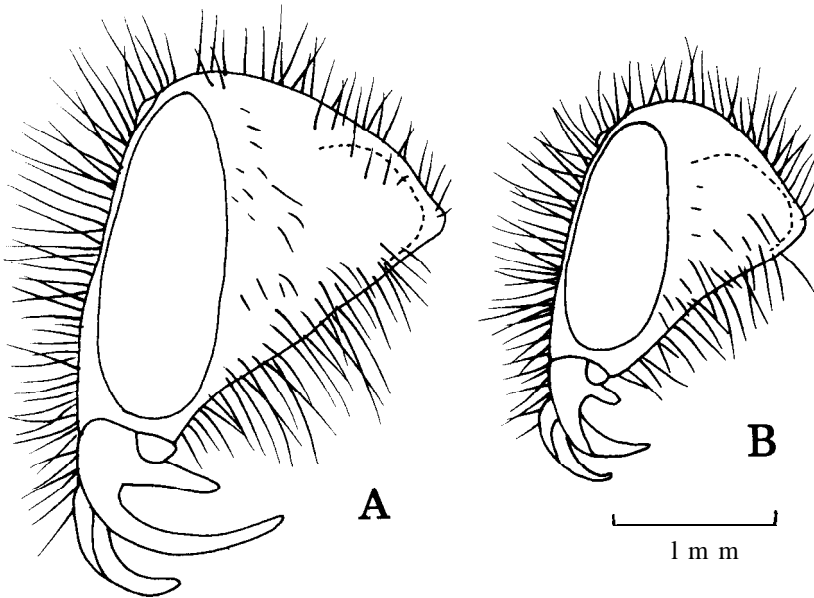
Fig. 48. Head of large (A) and small (B) males of *A ndrena (A ndrena)* **naw** *ai* Cockerell seen laterally.

In crabronid wasp, *Ectemnius martjanowii* Morawitz, small males are normal but in larger ones gradually show mandibles larger, genae wider with conspicuous process (Fig. 49). The males of *Synagris comuta* have enlarged heads, which are larger in some individuals with remarkably horned mandibles (Poulton, 19 13, cited by Hamilton, 1979). The bizzare male of *Polistes gigas* Kirby and Sponcer, the world largest vespid species for this male, could also be placed here (Fig. 50).

However, the most interesting and well studied case is of *Perdita portalis* Timberlake (Danforth, 1991). Summarizing, this is an andrenine counterpart of *Las. erythrurum* by the occurrence of discrete dimorphism in males, one is generally normal in head, etc. and flight-capable but with allometric size difference, whereas the other is uniform, flightless, with eyes reduced, mandibles enlarged, and genal process present. The males of 2 types emerge with about the similar ratio. The presence of clear dimorphism in wings and eyes together with macrocephalic polymorphism in normal males is just comparable to the male polymorphism in *L. erythrurum.* Before dealing with the functional significance of such male polymorphism, the cephalic polymorphism of females seen in some bees are reviewed below.

Female cephalic polymorphism in certain bees

Females of the halictine bees of the genus *Halictus* often exhibit a conspicuous cephalic polymorphism, characterized by the enlargement of the upper head and gena, and
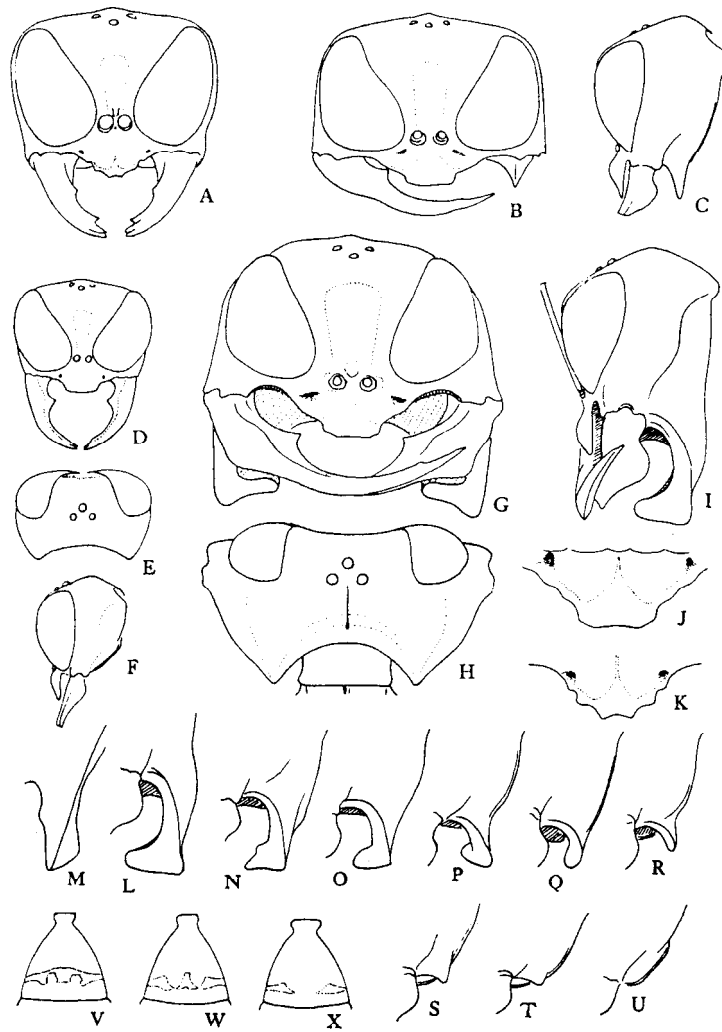
Fig. 49. Male gigantism in a crabronid wasp, *Ectemnius martjanowii* (cited from Tsuneki, 1956).

widening of clypeus accompanied with stouter mandibles, *i.e.,* a polymorphism quite similar to the type found in males as above enumerated, though less bizzare.

In social species the 2 types become more or less discrete and the queens are macrocephalic whereas the workers are normal. There are some species of which queens develop genal process as in *Halictus (Halictus) latisignatus* Cameron (Fig. 51, cited from Sakagami & Wain, 1966) and *H. (Seladonia) hesperus* Smith (Brooks & Roubik, 1983), suggesting a genetic mechanism at least partly common to the both sexes to induce such features.

On the other hand, the conspicuous cephalic gigantism is so far unknown in the social halictines of the genus *Lasioglossum*, despite the functional caste differentiation is more

advanced in well studied species of the latter genus (nearly all belonging to the carinate *Evylaeus*) (Sakagami, 1974; Sakagami et *al.*, 1994).   In some social *Halictus* species it is known that the mother queens function as guards at the nest entrance.   This has not been confirmed in some well observed social *Lasioglossum* species (reviewed by Maeta & Sakagami, 1995).   It is possible but uncertain whether this difference relates to the discrepancy between morphological and sociological differentiations between the 2 important halictine genera.

The cephalic polymorphism is also known in some neotropical halictines with enlarged upper head and gena, and occasionally accompanied with the appearance of genal process (*Megalopta genalis* Meado-Waldo, Fig. 52, cited from Sakagami & Moure, 1965) or clypeal process (*Rhynocorynura inflaticeps* (Ducke)).   It is easily understood that the gigantism in females does not attain so bizzare forms as known in males of some species.   Such structures might be effective at mating combats, either real or deceptive, between males, but should be troublesome to engage in various tasks practiced by females.

Another type of the cephalic polymorphism in the family Apidae is briefly mentioned here, because this aspect has been rather ignored despite the accumulation of various studies on these socially most advanced bees.   In the bumblebees queens have longer upper heads and malar spaces whereas there are shorter in workers, especially in dwarf ones (Fig. 53).   The same tendency is also recognized in honeybees and stingless bees, but as a neat dimorphism between the castes as follows (Sakagami, unpubl.): The ratio VOD / IOD (cf.- Explanations of Table 1) is much higher in queens.   The Q / **W** ratio of
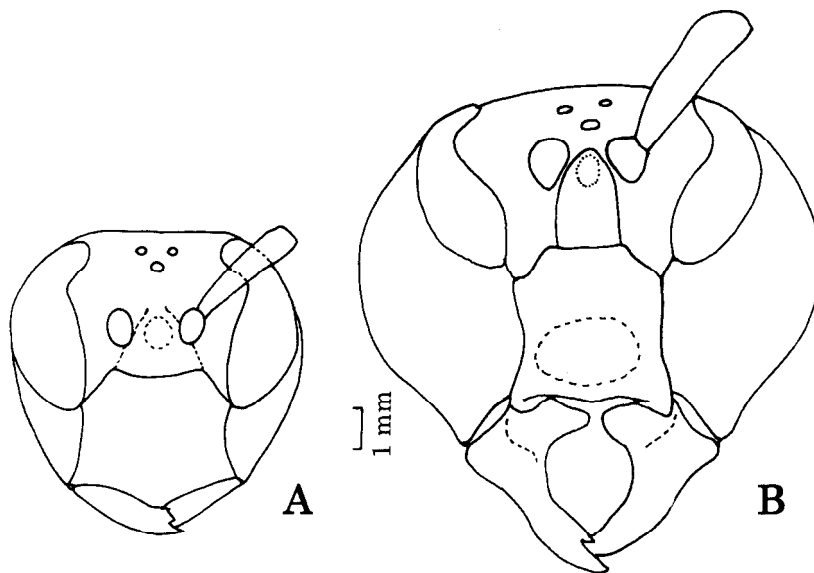

Fig. 50.   Worker (A) and male (B) of *Polistes (Gyrostoma) gigas* Kirby and Sponcer (specimens from Taiwan).
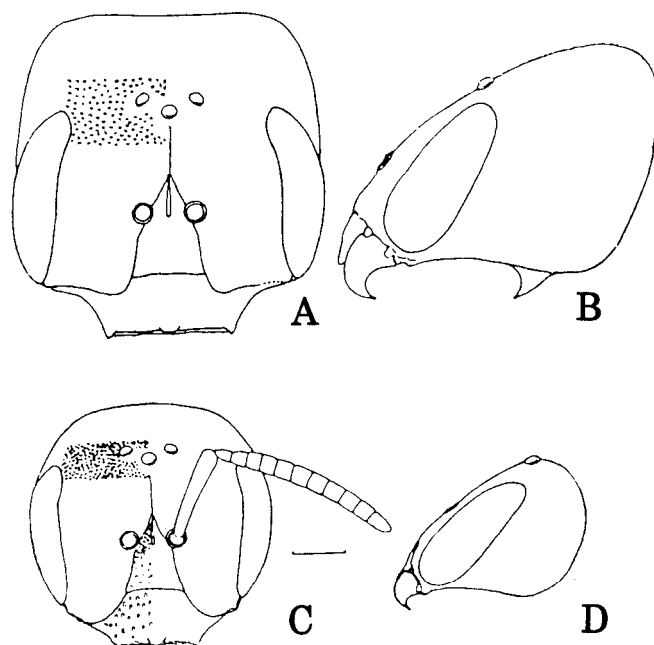
Fig. 51.   Cephalic polymorphism in females of *Halictus* (*Halictus*) *latisignatus* in India.   Large females (A, B), small females (C, D), both seen from front and in profile (cited from Sakagami & Wain, 1966).

VOD /IOD should be 1.0 if isometric, but 2.3-2.4 in *Apis mellifera* Linnaeus and *A. cerana* Fabricius, and ranges 1.3-1.8 (x = 1.54) in 14 stingless bee species covering 10 genera and subgenera, except for a cleptobiotic species *Lestrimelitta limao* (F. Smith) (0.93).   The Q / W ratio of ML / IOD is less than 0.8 in 2 *Apis* species, 1.1 in *L. limao* and 1.9-5.2 (x = 3.1) in 14 other stingless bee species covering various genera / subgenera.

    There are also some structural differences between bumblebees and the other 2 highly eusocial bees.   In bumblebees, whose queens should found the nests solitarily, the diagnostic sculpture, particularly those on ocellocular area, labrum and last visible tergum, are most developed in queens, but less in workers, especially in smaller ones, often making accurate identification of species difficult.   In stingless bees and honeybees, the queens, who are virtually parasitic on workers, the diagnostic features are very degenerated (possibly much more than in the queens of many ant species, who found at least solitarily the nests.   No caste-linked enlargement of gena is found in apid females. In halictine bees, macrocephaly in both sexes should be apomorphic from out- and intergroup comparisons, but in honeybees and stingless bees this could not always be true. Probably cephalic polymorphism in the Halictinae and the Apidae are not or only partially homologous in the origin.
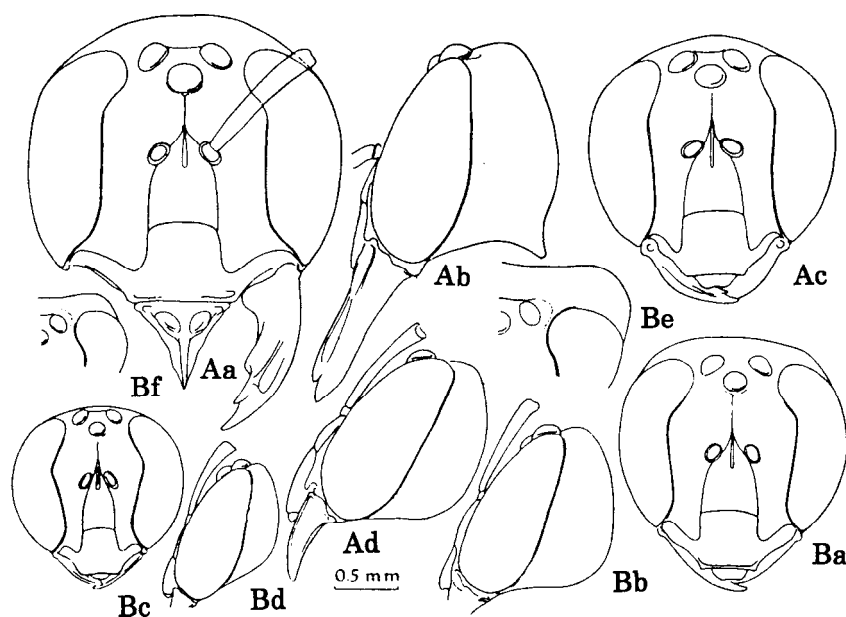
Fig. 52.   Cephalic polymorphism in females of *Megalopta genalis* (A) and *M. amoena* (B), a, c and b, d = frontal and lateral views in large and small females, and f, e = upper part of head seen obliquely of large and small females (cited from Sakagami & Moure, 1965).
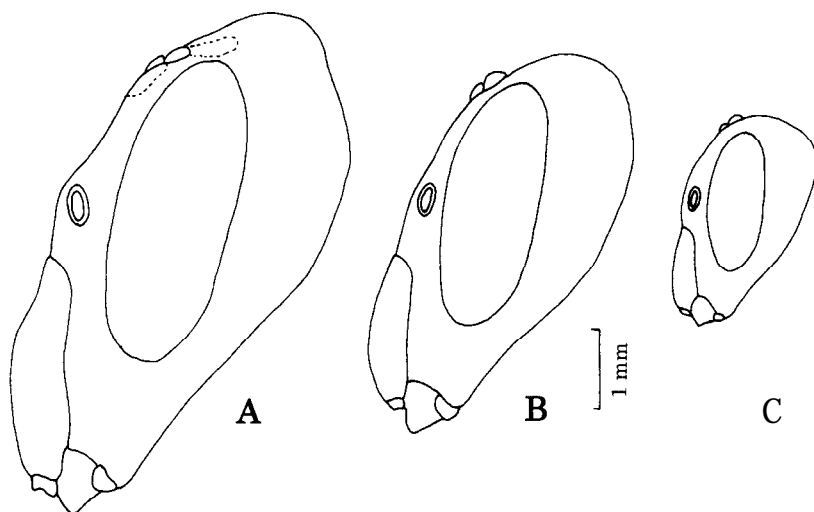

Fig. 5 3.   Head seen in profile of females of *Bombus (Diversobombus) diversus* Smith, A = queen, B and C = large and small workers (cited from Sakagani & Katayama, 1977).

A role on the functional significance of male cephalic polymorphism

The halictine macrocephaly may have been appeared in various taxa independently by the allometric pattern which can appear in both sexes, although we do not know well "why the allometric pattern exists" (Otte & Stayman, 1979). What common to the macrocephaly of both sexes, particularly in the halictines, is its linkage with the formation of stouter mandibles. To realize this trait, the lower part of head should have been widened for longer mandibles and the upper part of head and gena should have been elongated and widened, respectively, to have ampler space for the attachment of stronger mandibular muscles. Initially the both sexes "could" have been proceeded along the same way as seen in the coefficient of variation, which is higher in the females of *L. bidentatum* and *L. alphenum* with male macrocephaly than in those of *L. aulacophorum* (Table 3). However, this amphisexual differentiation could not continue further for the different roles of both sexes. The males could achieve the more extraordinary development of mandibles because they were taskless except mating. One of us (S. F. S.) previously doubted the functional role of the halictine macrocephaly (Sakagami *et al.,* 1966), and still think that not all diagnostic features which compose such adaptive syndrome are directly adaptive. But in view of the recent advances on the role of various "horns in beetles and other insects (Hamilton, 1979; Eberhard, 1979; Otte & Stayman,1979), and excellent observations on *Perdita portalis* (Danforth, 1991), it seems certain that "the mandibles as horns" of macrocephalic males so far reviewed are used for fighting around the mating chance. Houston (1970) and Kukuk & Schwarz (1988) suggested the role of the macrocephalic flightless male of *L. erythrurum as* guards. Their occasional guarding at the nest entrance may be likely, but if their stay at the nest entrance is as rare as in *P. portalis*, whose male polymorphism is astonishingly similar to that of *L. erythrurum,* the bizzare mandibles of the macrocephalic flightless males of the latter species may also function mainly for combat with other males within the nest.

Danforth *(op. cit.)* confirmed that small-headed males (with allometric size difference) were found, except those recently emerged, all or flowers, where they attacked various other insects, but more aggressively the conspecific microcephalic males and mated with the conspecific females. Macrocephalic flightless males remained in nests. They mate with females only soon before an oviposition, when they are preparing pollen ball as larval food, which lasts about 20 min., often repeated up to twice or thrice. In fighting the males are frequently killed by the wounded given to the neck region or membraneous roof of the proboscidal fossa by the mandibles of the opponent.

The differential behavior in *P. portalis* could be regarded as an extreme case of alternate mating methods proposed by Alcock (1979) based on the behavior of small and large males in *Centris pallida* Fox with continuous size polymorphism, and may also fit to the males of *L. erythrurum* in the presence of similar 2 types of males, mating on flowers by normal males and intranidal mating by macrocephalic males (Houston, 1970; Kukuk &

Schwarz, 1988).

Then how would behave the polymorphic males of *Sudila* and the *L. sexstrigatum* group? The available information are scarce: 1- Most known specimens, both larger and smaller, were captured on flowers and nests were precisely studied, although some of *L. ohei* and *L. pallilomum* were reared from the pupae.   2- Intranidal behavior was not observed in any species.   3- In *L. ohei* larger males tend to emerge later, and likely to stay in the nests longer.   In 3 nests, 1, 4, 1, distinctly macrocephalic males were collected from the main burrows and one just "entering" to the nest from the outside, whereas no normal or weakly macrocephalic males from the nest interior.   4- In *L. pallilomum* the extranidal male behavior was casually observed within a cage 3 x 1.5 x 2 (h) m with flower pots.   Each male seemed to have a home range with a considerable overlap. Extranidal mating was observed in both smaller and larger males. Neither intense interference nor fighting was seen among these males, although observations were casual, not well programmed.

It is difficult to assume the mating strategy adopted by these species, but the way between *Perdita portalis* and *Centris pallida* might be a possible compromise: Smaller males leave nests earlier and mate on flowers, while larger males stay in the nest longer and may mate there, although they eventually leave nests and mate also on flowers. Reflecting the continuous polymorphism in these bees, the 2 strategies would shift gradually, rather as tendencies than types: Larger males are likely to be more skillful to attack rivals within nests whereas smaller males more in dispersal and extranidal mating.

Finally some relevant accounts on the male cephalic polymorphism are enumerated.

1- Hamilton (1979) and Danforth (199 1) thought that intranidal mating should be selected more in the communal species with many acceptable females in the same nest, as this situation would increase the chance of intranidal mating.   This inference should be kept in mind in the to-be-coming studies of *Sudila* and other male-polymorphic bees.   In the *L. sexstrigatum* group, *L. ohei* (Sakagami *et al.)* and *L. speculinum* (Sakagami, unpubl.) are communal but *L. pallilomum* is solitary.   The last species is, however, seems to be communally disposed, as one 2-female nest was discovered (Sakagarni, unpubl.).

2- The assumption that the genal process of gigantic males may serve to defend the vulnerable neck region from the attack by conspecific males (Hamilton, 1972) became more likely by the fact that intranidal attacks by the males of *P. portalis* seem to be focussed to the neck (Danforth, 1991).   The genal process is particularly developed in the macrocephalic males of the *L. sexstrigatum* group, where a correlation between the shape of mandible and genal process seems to occur: Both are relatively short but robust in *L. ohei,* while long and slender in *L. pallilomum* and *L. simplicior* (Sakagami, unpubl.).

3- How the male polymorphism is ontogenetically produced is an interesting problem. Certainly it should in part be controlled by the amount of food provisions.   But how the

flightless and flight-capable males, which differ just as in queens and workers of eusocial insects, differentiate is not yet solved.

4- In some cases the male polymorphism seems to be influenced by voltinism.   In *L. sexstrigatum*, the population in Sapporo, Hokkaido is univoltine, and the males exhibit polymorphism, but the population in Morioka, N. Honshu is bivoltine.   The late spring males are monomorphic, but autumn males are polymorphic with smaller, normal to weakly gigantic individuals and larger conspicuously gigantic ones (Sakagami & Maeta, unpubl.).   A similar difference is also found between the spring and summer males of all 6 male-known Japanese species of *Andrena (Hoplandrena)* (Tadauchi & Hirashima, 1984).

5- As in many similar cases, on problem remains unsolved: How the incipient, still little functional state of head gigantism would be retained within the population until it becomes adaptive and positively selected.

Acknowledgments

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