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Sensilla on the Aedeagi of the Genus *Damaster* (Insecta, Coleoptera, Carabidae)

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Sensilla on the aedeagi of 4 species under the genus *Damaster* were studied using scanning electron microscopy. A total of 37 types of sensilla were distinguished from the aedeagi of the species examined. The number of sensilla types was the largest in *D.* (*Coptolabrus*) *smaragdinus branickii*, 25, and 23 in *D.* (*C.*) *jankowskii jankowskii*. In *D.* (*Acoptolabrus*) *gehinii gehinii* and *D.* (*Damaster*) *blaptoides blaptoides*, 22 and 21 types of sensilla were found, respectively. External morphology and distribution patterns of sensilla were also described. The phylogenetic relationships among the species were discussed based on their distribution patterns.

Studies of the insect sensilla have been focused mainly on the antenna and mouthparts, but little is known about the sensilla of the male external genitalia involved in the perception of stimuli during copulation in insects.

Kim and Yamasaki (1996) have recently examined external morphology of the sensilla on the aedeagus of a carabid beetle, *Carabus* (*Isiocarabus*) *fiduciarius saishutoicus*. Investigations for the sensilla of the genus *Damaster* also have been conducted for mouthparts (Kim and Yamasaki, 1998a) and the antenna (Kim and Yamasaki, 1998b). The genus *Damaster* consists of approximately 20 species under 3 subgenera and is distributed in eastern Asia including Japan, Sakhalin, and Taiwan (Ishikawa, 1986). This study describes the external morphology and distribution patterns of sensilla on the aedeagi of the genus *Damaster*. The results are expected to aid in the understanding of insect copulation and provide a morphological basis for insect phylogenetic research.

Materials and Methods

Four carabid species distributed among 3 subgenera of the genus *Damaster* were examined: *D.* (*Acoptolabrus*) *gehinii gehinii* and *D.* (*Damaster*) *blaptoides blaptoides* from Japan and *D.* (*Coptolabrus*) *jankowskii jankowskii* and *D.* (*C.*) *smaragdinus branickii* from Korea. For studying by scanning electron microscopy (SEM) the isolated aedeagi were cleaned by sonification for 3 min, dehydrated in a graded series of ethanol, and air-dried. The specimens were mounted on the specimen stubs by silver-conductive paint, and coated with approximately 30 nm of gold in a JEOL (JFC-1100E) ion sputter. Examinations were made in a JEOL (JSM-5300) scanning electron microscope. Types of sensilla were determined based at least on 3 different aedeagal specimens of each species. Dimensions were obtained by measuring 6 or more sensilla of each type.

The abbreviations used in this study are as follows: DA, type of the aedeagal sensilla in the genus *Damaster*; G, *D.* (*A.*) *gehinii gehinii*; J, *D.* (*C.*) *jankowskii jankowskii*; S, *D.* (*C.*) *smaragdinus branickii*; B, *D.* (*D.*) *blaptoides blaptoides*.

Results

The highly sclerotized aedeagi of the genus *Damaster* are cylindrical, arcuated, and weakly swollen medially with a narrowed end piece. The ostium lobe is present at the base of the ostium on the membranous part (preostium) of the aedeagus (Ishikawa, 1978, 1986).

From the aedeagi of 4 species under the genus *Damaster*, a total of 37 types of sensilla could be determined. Most of the sensillar shafts project from round floors of the depressions and some are situated in pits. Though accurate counting of the numbers were not carried out, more variable and abundant sensilla are recognized on the distal half of the aedeagus. The sensilla types and mean dimensions are shown in Table 1. The number of sensilla types was the largest in *D.* (*C.*) *smaragdinus branickii*, 25 and 23 types for *D.* (*C.*) *jankowskii jankowskii*. In 2 species, *D.* (*A.*) *gehinii gehinii* and *D.* (*D.*) *blaptoides blaptoides*, 22 and 21 types of sensilla were detected, respectively. The types of sensilla are described as follow:

DA 1. The shaft of these sensilla is tapered to the somewhat blunt apex and gently curved near the apex

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Table 1. Mean dimensions (μm, length×basal width) of sensilla on the aedeagus of the genus *Damaster*

Sensilla type	*D.* (*A.*) *gehinii gehinii*	*D.* (*C.*) *jankowskii jankowskii*	*D.* (*C.*) *smaragdinus branickii*	*D.* (*D.*) *blaptoides blaptoides*
DA 1	19.3 × 7.4	30.3 × 12.1	20.9 × 8.0	18.7 × 7.7
DA 2	11.0 × 7.7	11.6 × 8.3	11.0 × 7.7	11.0 × 7.4
DA 3	24.8 × 6.6	26.4 × 6.6	26.1 × 6.6	25.9 × 6.6
DA 4	20.4 × 4.8	21.3 × 5.3	20.8 × 5.0	-
DA 5	20.9 × 8.8	-	-	-
DA 6	-	21.7 × 5.4	-	-
DA 7	14.5 × 4.8	14.9 × 5.2	15.4 × 5.5	15.1 × 5.5
DA 8	-	17.6 × 7.2	14.9 × 5.5	17.1 × 5.5
DA 9	12.2 × 4.8	13.3 × 5.5	12.7 × 5.0	12.7 × 5.8
DA 10	-	9.4 × 4.1	10.5 × 4.8	10.0 × 4.5
DA 11	11.5 × 6.1	12.2 × 6.4	11.0 × 6.1	11.0 × 6.1
DA 12	-	9.0 × 5.5	8.3 × 5.0	8.8 × 5.2
DA 13	-	-	10.5 × 5.2	9.4 × 5.0
DA 14	-	-	13.8 × 5.2	13.0 × 4.8
DA 15	-	-	14.3 × 6.3	13.8 × 5.8
DA 16	12.1 × 5.5	13.2 × 5.5	-	-
DA 17	7.2 × 5.2	-	-	-
DA 18	7.7 × 6.5	9.0 × 7.6	8.3 × 7.2	7.5 × 6.2
DA 19	7.7 × 7.2	8.3 × 7.5	7.7 × 7.2	-
DA 20	-	5.5 × 5.0	5.5 × 5.0	5.5 × 4.8
DA 21	4.4 × 6.6	5.8 × 6.4	5.5 × 6.0	5.0 × 5.8
DA 22	-	5.8 × 6.6	5.5 × 6.6	-
DA 23	3.6 × 4.8	3.9 × 5.0	-	-
DA 24	-	-	-	? × 3.7
DA 25	? × 4.1	-	? × 4.4	? × 4.4
DA 26	-	? × 4.5	? × 4.4	? × 4.2
DA 27	5.5 × 3.9	-	-	-
DA 28	4.4 × 4.4	4.5 × 5.5	5.0 × 5.2	-
DA 29	7.2 × 5.0	-	-	-
DA 30	15.0 × 6.4	16.0 × 7.1	15.4 × 6.6	15.0 × 6.1
DA 31	-	-	29.2 × 9.1	27.5 × 8.3
DA 32	-	17.1 × 5.8	16.5 × 5.5	-
DA 33	11.0 × 9.9	-	-	-
DA 34	12.7 × 8.8	-	-	-
DA 35	18.2 ×12.1	-	-	-
DA 36	-	27.5 × 11.6	25.8 × 11.6	-
DA 37	-	-	-	24.8 × 7.2
Total no	22	23	25	21

- = absence of appropriate type of sensilla.
? = accurate measurement was not possible because of sensillar position in the depression.

(Fig. 1A). They occur chiefly on the ostium lobe and preostium or occasionally at the median part of the aedeagus in all the species examined.

DA 2. These sensilla are smoothly tapered to the blunt apex and have a pore near the base (Fig. 1B). They occur also on the ostium lobe and preostium, and occasionally at the median part in *D.* (*A.*) *gehinii gehinii* and *D.* (*C.*) *jankowskii jankowskii*. In *D.* (*C.*) *smaragdinus branickii* and *D.* (*D.*) *blaptoides blaptoides*, these sensilla are found only at the median part.

DA 3. An apical pore is found on these long, apically tapered sensilla (Fig. 1C). They are distributed at the distal part in all the species examined. In *D.* (*C.*) *smaragdinus branickii*, these sensilla are dominantly present at the end piece of the aedeagus.

DA 4. A pore is present at the subapical part of these long, slender sensilla (Fig. 1D). They occur mainly at the distal part of the aedeagus. In *D.* (*D.*) *blaptoides blaptoides*, this type is not confirmed.

DA 5. These elongate sensilla have a thick basal part (Fig. 1E). They occur rarely at the distal part only in *D.* (*A.*) *gehinii gehinii*.

DA 6. These sensilla are similar to type DA 4, but are characterized by their evidently thicker shaft and have more or less a blunt apex (Fig. 1F). They are found at the distal part in *D.* (*C.*) *jankowskii jankowskii*.

DA 7. The shaft of these sensilla is tapered almost linearly to the uniporous apex (Fig. 1G). In all the species examined, they occur at the subdistal part of the aedeagus.

DA 8. These somewhat cylindrical sensilla (Fig. 1H) are narrowed weakly to the uniporous apex. They occur rarely at the subdistal part in *D.* (*C.*) *jankowskii jankowskii*, *D.* (*C.*) *smaragdinus branickii*, and *D.* (*D.*) *blaptoides blaptoides*.

DA 9. The distal part of these smoothly curved sensilla is abruptly tapered near the subapical part (Fig. 1I). They are found from the subdistal to the median part in all the species examined.

DA 10. These sensilla are similar in shape to type DA 7, but are apparently smaller in size and have a more pointed apex (Fig. 1J). Except *D.* (*A.*) *gehinii gehinii*, this type is found at the median part in the other three species.

DA 11. A pore or slit is situated at the apex of these sensilla (Fig. 1K). The shaft is gently narrowed to the blunt apex. They are observed at the median part in all the species examined.

DA 12. These apically uniporous sensilla are smoothly narrowed and are more or less constricted near the blunt apex (Fig. 1L). They are found at the median part, except for *D.* (*A.*) *gehinii gehinii*.

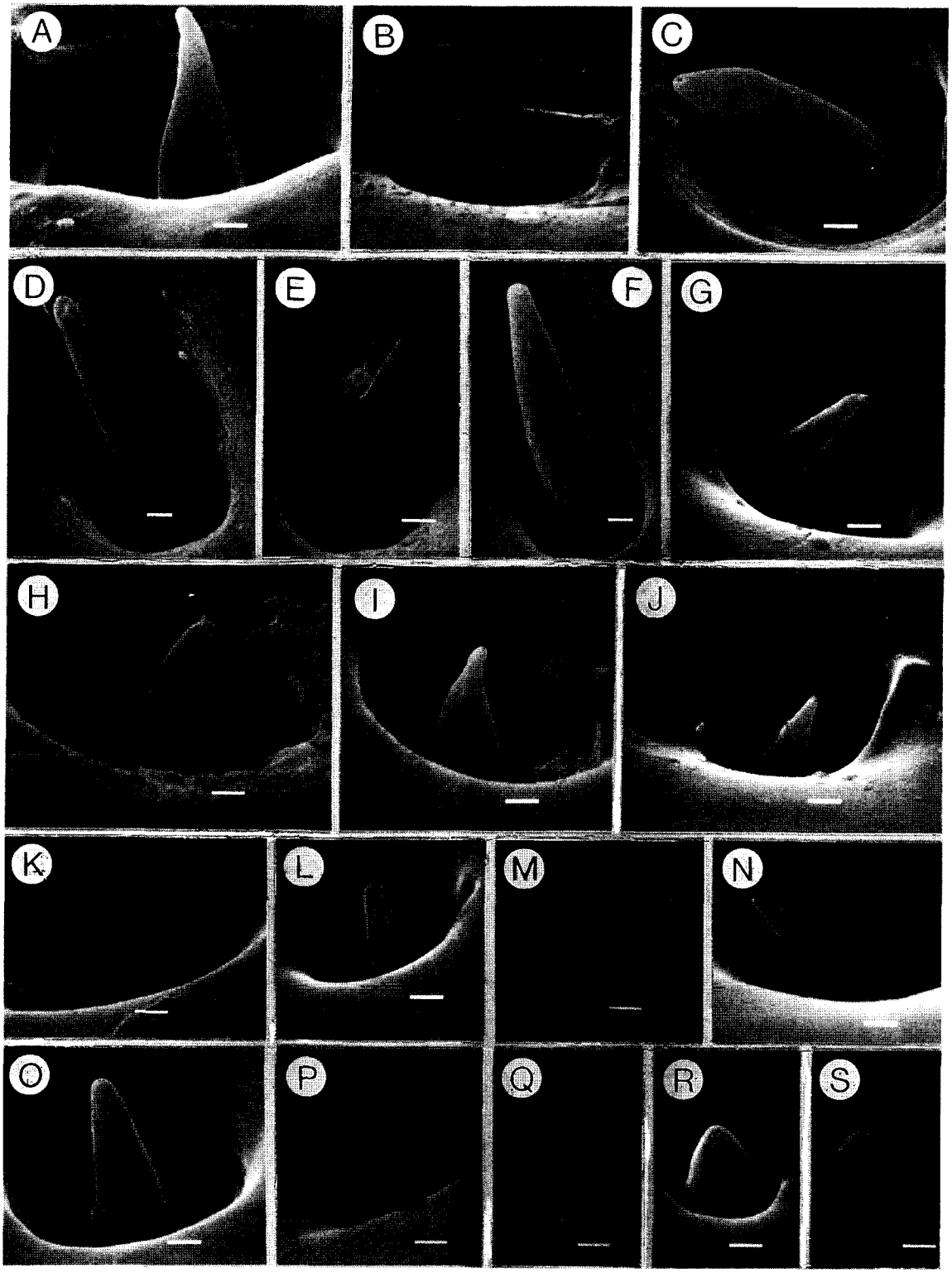

Fig. 1. Sensilla on the aedeagus of the genus *Damaster*. *D.* (*Coptolabrus*) *smaragdinus branickii* A, D, I, L, N, O, R, and S. B, C, E, F, G, and J, D. (*Coptolabrus*) *jankowskii jankowskii*, *D.* (*Damaster*) *blaptoides blaptoides* H, K, and M. (*Acoptolabrus*) *gehinii gehinii* Pand Q. Scale bars=1 μm.

DA 13. The shaft of these peg-like sensilla (Fig. 1M) is straight and observed at the median part in *D.* (*C.*) *smaragdinus branickii* and *D.* (*D.*) *blaptoides blaptoides*.

DA 14. These apically acute and smoothly curved

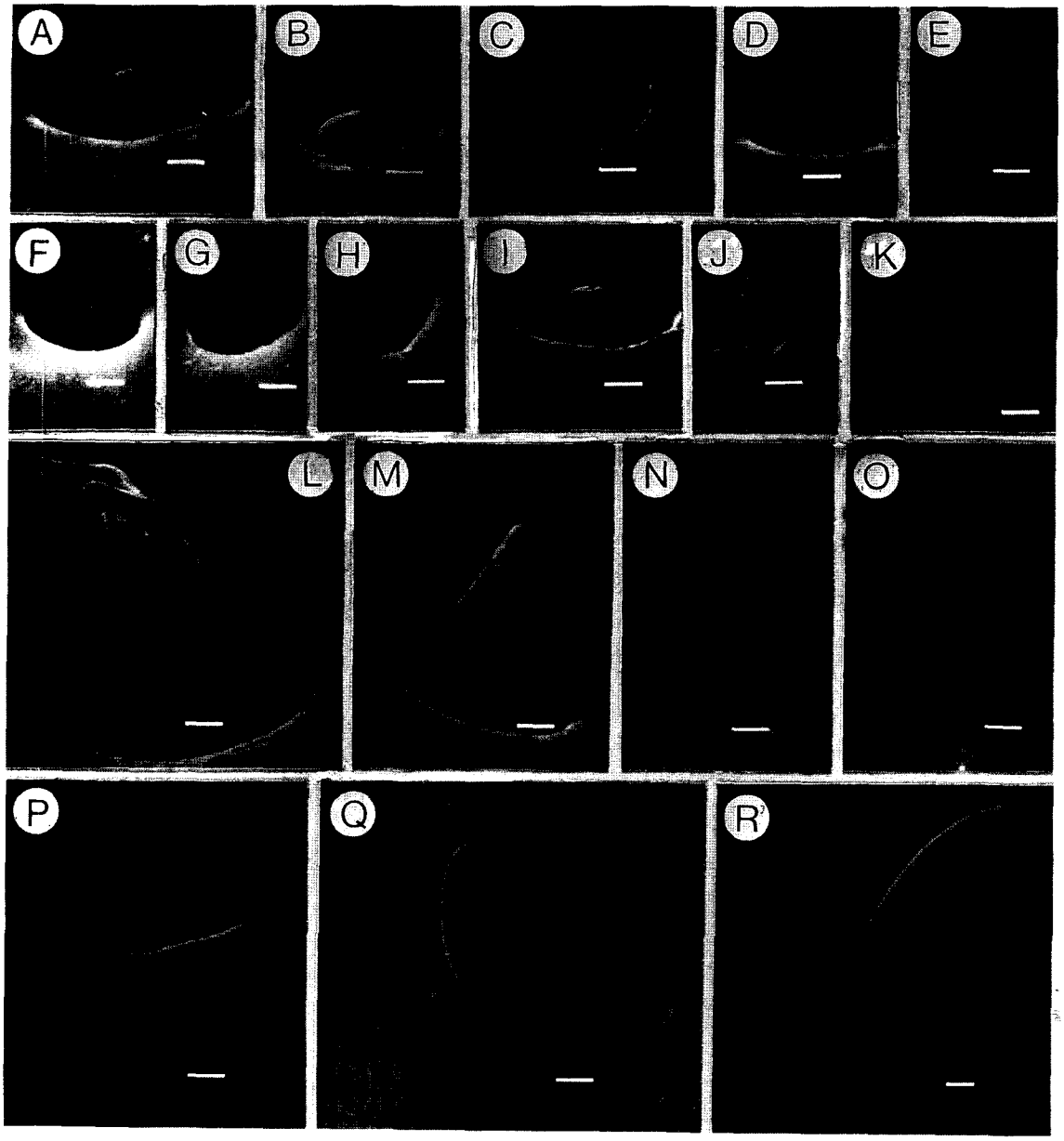

Fig. 2. Sensilla on the aedeagus of the genus *Damaster*. *D.* (*Coptolabrus*) *smaragdinus branickii* (A, C, F, G, K, L, and M). *D.* (*Acoptolabrus*) *gehinii gehinii* (B, H, J, N, O, and P), *D.* (*Coptolabrus*) *jankowskii jankowskii* (D, I, and Q), *D.* (*Damaster*) *blaptoides blaptoides* (E and R). Scale bars=1 μm.

sensilla (Fig. 1N) occur at the median part in *D.* (*C.*) *smaragdinus branickii* and *D.* (*D.*) *blaptoides blaptoides.*

DA 15. These straight, distally narrowed peg-like sensilla have a pore at the median part of the shaft (Fig. 1O). They are distributed at the medio-distal part in *D.* (*C.*) *smaragdinus branickii* and *D.* (*D.*) *blaptoides blaptoides.*

DA 16. A protuberance near the subapical part characterize these apically uniporous sensilla (Fig. 1P). In *D.* (*A.*) *gehinii gehinii* and *D.* (*C.*) *jankowskii jankowskii*, these sensilla are observed at the median part.

DA 17. These sensilla are narrowly protruded from the median part to the blunt apex and have a pore at the distal one-third (Fig. 1Q). They occur at the median part only in *D.* (*A.*) *gehinii gehinii.*

DA 18. A pore is present at the distal one-third of these cone-shaped sensilla (Fig. 1R). In all the species examined, they occur at the median part.

DA 19. These small, blunt sensilla with an apical pore (Fig. 1S) are found at the median part, except *D.* (*D.*) *blaptoides balptoides.*

DA 20. Except *D.* (*A.*) *gehinii gehinii*, these dome-shaped sensilla with an apical pore (Fig. 2A) are distributed at the median part in the other 3 species examined.

DA 21. These relatively flattened small sensilla have

Table 2. Comparisons of common and specific distribution patterns of sensilla on the aedeagus of the genus *Damaster*

Estimation unit	Types of sensilla (DA)																																								No. types
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37					
GJSB	o	o	o	×	×	×	o	×	o	×	o	×	×	×	×	×	×	o	×	×	o	×	×	×	×	×	×	×	×	o	×	×	×	×	×	×	×					9
GJS	o	o	o	o	×	×	o	×	o	×	o	×	×	×	×	×	×	o	o	×	o	×	×	×	×	×	×	o	×	o	×	×	×	×	×	×	×					12
GJB	o	o	o	×	×	×	o	×	o	×	o	×	×	×	×	×	×	o	×	×	o	×	×	×	×	×	×	×	×	o	×	×	×	×	×	×	×					9
GSB	o	o	o	×	×	×	o	×	o	×	o	×	×	×	×	×	×	o	×	×	o	×	×	×	o	×	×	×	×	o	×	×	×	×	×	×	×					10
JSB	o	o	o	×	×	×	o	o	o	o	o	o	×	×	×	×	×	o	×	o	o	×	×	×	×	o	×	×	×	o	×	×	×	×	×	×	×					14
GJ	o	o	o	o	×	×	o	×	o	×	o	×	×	×	×	o	×	o	o	×	o	×	o	×	×	×	×	o	×	o	×	×	×	×	×	×	×					14
GS	o	o	o	o	×	×	o	×	o	×	o	×	×	×	×	×	×	o	o	×	o	×	×	×	o	×	×	o	×	o	×	×	×	×	×	×	×					13
GB	o	o	o	×	×	×	o	×	o	×	o	×	×	×	×	×	×	o	×	×	o	×	×	×	o	×	×	×	×	o	×	×	×	×	×	×	×					10
JS	o	o	o	o	×	×	o	o	o	o	o	o	×	×	×	×	×	o	o	o	o	o	×	×	×	o	×	o	×	o	×	o	×	×	×	o	×					20
JB	o	o	o	×	×	×	o	o	o	o	o	o	×	×	×	×	×	o	×	o	o	×	×	×	×	o	×	×	×	o	×	×	×	×	×	×	×					14
SB	o	o	o	×	×	×	o	o	o	o	o	o	o	o	×	×	o	×	o	o	×	×	×	o	o	×	×	×	×	o	o	×	×	×	×	×	×					19
G	×	×	×	×	o	×	×	×	×	×	×	×	×	×	×	×	o	×	×	×	×	×	×	×	×	×	×	o	×	o	×	×	×	o	o	o	×	×				7
J	×	×	×	×	×	o	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					1
S	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					0
B	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	o	×	×	×	×	×	×	×	×	×	×	×	×	o					2

o = presence of appropriate type of sensilla.
× = absence of appropriate type of sensilla.

a nipple-like protuberance at the apex (Fig. 2B). They are found at the median part in all the species examined.

DA 22. These small sensilla are characterized by their slightly depressed apical structure (Fig. 2C). They occur at the median part in the species examined of the subgenus *Coptolabrus*.

DA 23. These stout sensilla resemble type DA 22 sensilla, but have a smooth apical structure (Fig. 2D). They are found at the median part in *D.* (*A.*) *gehinii gehinii* and *D.* (*C.*) *jankowskii jankowskii*.

DA 24. These small, cone-like sensilla are situated in the simple pit which are larger than the glandular pore (Fig. 2E). They are found chiefly at the median part only in *D. (D.) blaptoides blaptoides*.

DA 25. These small, pit-peg sensilla are similar in shape to type DA 24 sensilla, but have a more narrowly protruded apex (Fig. 2F). They are observed mainly at the distal part, except for *D.* (*C.*) *jankowskii jankowskii*.

DA 26. These sensilla are also situated in the small pit, but distinguished from the other small sensilla by the bulbous appearance (Fig. 2G). They are not found in *D.* (*A.*) *gehinii gehinii*. In *D.* (*C.*) *smaragdinus branickii*, this type and type DA 25 sensilla are abundantly distributed at the distal part.

DA 27. These spiculate sensilla are situated in the simple pit as in types DA 24 to 26 sensilla (Fig. 2H). They are observed at the median part in only *D.* (*A.*) *gehinii gehinii*.

DA 28. These small sensilla have a pore at the somewhat oblique apex and are situated in the wide pit (Fig. 2I). They are found at the median part in *D.* (*A.*) *gehinii gehinii*, *D.* (*C.*) *jankowskii jankowskii*, and *D.* (*C.*) *smaragdinus branickii*.

DA 29. These small, uniporous sensilla are similar in shape to type DA 28 sensilla, but distinguished by a somewhat slender appearance and evidently narrower surrounding pit (Fig. 2J). They are present at the median part only in *D.* (*A.*) *gehinii gehinii*.

DA 30. A pore is evident at the median part of these two-humped sensilla (Fig. 2K). They are found at the basal part in all the species examined.

DA 31. These sensilla are bifurcated from the distal 3/4 and tapered distally (Fig. 2L). The prongs are slightly or abruptly curved, or occasionally straight. A pore is located at the median part of the shaft. They occur at the basal part in *D.* (*C.*) *smaragdinus branickii* and *D.* (*D.*) *blaptoides blaptoides*.

DA 32. These straight sensilla are swollen medially where a pore is situated (Fig. 2M). They have a blunt apex and are found at the basal part in *D.* (*C.*) *jankowskii jankowskii* and *D.* (*C.*) *smaragdinus branickii*.

DA 33. These cone-shaped sensilla have a constricted apex with a subapical pore (Fig. 2N). This type is found at the basal part in *D.* (*A.*) *gehinii gehinii*.

DA 34. These somewhat urceolated sensilla are abruptly narrowed apically from near the median part (Fig. 2O). They occur at the basal part in *D.* (*A.*) *gehinii gehinii*.

DA 35. These long, cone-shaped sensilla have a pore at the mid-portion (Fig. 2P). They are found at the basal part in *D.* (*A.*) *gehinii gehinii*.

DA 36. These uniporous sensilla are smoothly tapered to a blunt apex and somewhat abruptly curved near the tip (Fig. 2Q). They are distributed at the basal part in *D.* (*C.*) *jankowskii jankowskii* and *D.* (*C.*) *smaragdinus branickii*.

DA 37. These sensilla are similar in shape to type DA 36 sensilla, but are more sharply pointed and gently curved (Fig. 2R). A pore is situated at the median part of the sensilla. They are found at the basal part in *D.* (*D.*) *blaptoides blaptoides*.

Common and specific distribution patterns of the sensilla are presented in Table 2. Nine types occur commonly in all the species examined (GJSB). From the comparisons of the three by three species, the number of common types of JSB and GJS are 14 and 12, respectively. Ten common types are found in GSB and 9 common types are in GJB. In the comparisons of the two by two species, the largest number of common types (20 types) occurs in JS. 19 common

types were noted in SB. Fourteen common types are noticed in GJ and JB, respectively. Thirteen common types are found in GS. In GB, 10 common types are observed. In *D.* (*A.*) *gehinii gehinii*, an outstandingly larger number of specific types (7 types) are observed. In *D.* (*C.*) *smaragdinus branickii*, however, no specific type is found. Two types of specific sensilla are found in *D.* (*D.*) *blaptoides blaptoides* and one type in *D.* (*C.*) *jankowskii jankowskii*.

Discussion

The external morphology and distribution patterns of sensilla on the aedeagus of the genus *Damaster* were investigated. Although the presence or absence of pore(s) in some types was not confirmed, many sensilla have a pore on their shaft. Kim and Yamasaki (1996) distinguished 8 types of sensilla on the aedeagus of *Carabus* (*Isiocarabus*) *fiduciarius saishutoicus*. Among them, the aporous peg sensilla type was distributed at the basal part, and the other 7 types of uniporous pit-peg sensilla occurred at the distal part. In the present study, however, we found that all the basal sensilla had a pore on the shaft. This indicates that they might be chemoreceptors (Zacharuk, 1980, 1985). However, the function of these sensilla on the aedeagus is not known.

The general distribution patterns of sensilla on the structure are also similar to patterns from the previous study (Kim and Yamasaki, 1996). That is, more variable and abundant sensilla are recognized on the distal half of the aedeagus. This may be related to the copulation behavior of beetles as suggested by Ishikawa (1987) and Kim and Yamasaki (1996). During copulation, the distal part of the aedeagus is inserted into the female vagina, and these sensilla may receive stimulation from the female. However, the relationship between the distribution pattern and the practical function of the sensilla are not known.

In the phylogenetic revision study, Ishikawa (1986) proposed that among 3 subgenera under the genus *Damaster*, if sister groups are given the same rank, *Acoptolabrus* and *Damaster* s. *str.* are ranked as subgenera, and *Coptolabrus* is treated as one of the two sections in the subgenus *Damaster*. The fact that the number of common types of JSB (i.e. of subgenera *Coptolabrus* and *Damaster*) was the largest and an outstandingly larger number of specific types in *D.* (*A.*) *gehinii gehinii* supporting Ishikawa's suggestion that *Acoptolabrus* is the remotest among the subgenera. Ishikawa (1986) also suggested that *D.* (*C.*) *jankowskii* and the very close kin species, *D.* (*C.*) *fruhstorferi*, are closely related to the subgenus *Damaster*. Through two by two comparisons in this study, two species (JS) under the subgenus *Coptolabrus* have naturally shown the largest number of common types, the following was, however, SB instead of JB. It will be ascertained by further data whether this result is due to the limitation of character selection in this study. Nevertheless, for determining a more realistic insect phylogeny study, the sensillar characters are expected to provide additional morphological criteria as suggested by Barlin and Vinson (1981) and Hashimoto (1991).

References

Barlin MR and Vinson SB (1981) Multiporous plate sensillum in antennae of the Chalcidoidea (Hymenoptera). *Int J Insect Morphol Embryol* 10: 29-42.

Hashimoto Y (1991) Phylogenetic study of the family Formicidae based on the sensillum structures on the antennae and labial palpi (Hymenoptera, Aculeata). *Jpn J Entomol* 59: 125-140.

Ishikawa R (1978) A revision of the higher taxa of the subtribe Carabina (Coleoptera, Carabidae). *Bull Natn Sci Mus Ser A Zool* 4: 45-68.

Ishikawa R (1986) Phylogeny and Subgeneric Classification of the Genus *Damaster* Kollar (Coleoptera, Carabidae). *Entomol Pappres Kurosawa*, Tokyo, pp 115-130.

Ishikawa R (1987) On the function of the copulatory organs of *Ohomopterus* (Coleoptera, Carabidae, Genus *Carabus*). *Kontyû Tokyo*, 53: 202-206.

Kim JL and Yamasaki T (1996) Sensilla of *Carabus* (*Isiocarabus*) *fiduciarius saishutoicus* Csiki (Coleoptera: Carabidae). *Int J Insect Morphol Embryol* 25: 153-172.

Kim JL and Yamasaki T (1998a) Sensilla and comparative morphology of the apical segments of the female maxillary and labial palpi in the genus *Damaster* (Colpeotera, Carabidae). *Entomol Sci* 1: 365-369.

Kim JL and Yamasaki T (1998b) Sensilla on the female antenna of five carabid species of the genus *Damaster* (Coleoptera, Carabidae). *Entomol Sci* 1: 371-375.

Zacharuk RY (1980) Ultrastructure and function of insect chemosensilla. *Annu Rev Entomol* 25: 27-47.

Zacharuk RY (1985) Antennae and sensilla. In: Kerkut GA and Gilbert LI (eds), Comprehensive Insect Physiology, Biochemistry and Pharmacology, Pergamon Press, Oxford, Vol 6, pp 1-69.

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