

Methodological Research in the Taxonomy of Aleocharinae*

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The taxonomic research of Aleocharinae has a long history. In the work of LINNÉ (1758) all the species of Staphylinidae were described under the generic name *Staphylinus* without regard to the characters to divide Aleocharinae from the other groups of this large family. GRAVENHORST (1802) was the first who erected the aleocharine genera *Aleochara* and *Callicerus*, and separated them as a distinct subfamily. His work was followed by MANNERHEIM (1831) and others, who described many species which are different in length, colouration, surface reflection and punctuation of head, pronotum, abdomen and elytra. In the succeeding period of research ERICHSON (1837) and FAUVEL (1873) endeavoured to increase the knowledge of each species of Aleocharinae, paying attention to the details of the body structure in addition to the characters mentioned above; the number and ratio of the tarsal segments of each leg, the form of the glossa, the shape of the labial palpus etc. were reasonably adopted as diagnostic characters of each species and genus. As a result many European species were reexamined and newly added. The revisional work of the European Aleocharinae by GANGLBAUER (1895) is a masterpiece of the efforts in this direction. Side by side with the achievements made by these authors by which our knowledge of the European Aleocharinae has been greatly intensified, the research of the species outside Europe made a great advance, too. Many elaborate works such as those by SHARP (1874, 1878) on the species in Japan and Amazon Valley, CASEY (1893) in North America, CAMERON (1930) in India, and BERNHAUER (1907) in the whole world were published, and all these works were crowned by FENYES (1918-21) who, in his voluminous monographic work, enumerated all the known genera and species of the world including about 650 genera and 5000 species ever described, although the majority of them were poorly described and are incompletely known to us.

In Japan ADACHI (1957) listed up 203 species of Aleocharinae known there at that time. Yet our knowledge of the Japanese Aleocharinae is so meager that it is very difficult to determine the scientific name of even the commonest species being found around Kyoto unless it is compared with the type-specimen, since most species of Aleocharinae belonging to the same genus resemble each other in appearance. The difference is sometimes so delicate that it is almost impossible to express in words.

Such a chaotic state is due mainly to the fact that the studies of Aleocharinae have been made, exclusively using easily observed characters without dissecting

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specimens. Recently the necessity of the more effective method in the research of Aleocharinae has been tentatively discussed in Europe. The first effort was made by HOEG (1945) introducing the pattern of the distribution of setulae on pronotum and elytra. Then follows a series of large, elaborate works of BRUNDIN (1944, 1948, 1953, etc.), who has paid special attention to the structure of male genital organ. In his studies, however, observations were made mainly on the shape of the aedeagus and the examination of the inner structure, copulatory piece, suspensoria, etc. was neglected. As in other groups of Coleoptera it is not difficult in many cases to identify each species only by the shape of the aedeagus. But this procedure has a great drawback, because only the male specimens are determinable. Unless they are collected in copula the female can not be identified especially in such a large genus as *Atheta*, many species of which are coexisting in a habitat and all of them resemble each other in appearance. In the course of the present study, therefore, it was aimed to find some new specific characters common to both sexes besides the routine of aedeagal research.

In my previous works of Aleocharinae I have faithfully followed the nomenclature system of BLACKWELDER 1952. But since his conception of some generic names were suppressed and rejected by the International Nomenclature Committee, the classic use of the European authors have to be adopted in my present and subsequent works.

METHOD

To facilitate the anatomical studies all materials are conveniently fixed and preserved in 70% alcohol. The alcoholic specimens are softened before dissection by warming each specimen on a piece of hollow glass adding a small quantity of lactic acid, which makes the body rather transparent. Then the specimen is mounted with glycerine and dissected under the high magnification of binocular microscope. A sharp needle is thrust into the gular plate posterior to the mentum to destroy the muscular attachment of the mouth parts and to isolate the labium, mentum and maxilla from the cephalic armature. The antennae, labrum and mandible are also detached one by one. With the similar process the abdominal segment VIII is isolated and its tergite and sternite are removed together with the genitalia. The leg is cut off at the basis of the tibia.

For the examination of the genital organ of the male, a pair of lateral lobes are first detached. The main body of the aedeagus must be observed of its dorsal, ventral and lateral view and then dissected to bring the inner chitinous apparatus out of the capsule. Conveniently it is made by picking the dorsal side of the capsule with fine needles and digging out the whole content on a separate slide. Usually the copulatory piece, suspensoria and trabeculae may be brought out in a mass and best observed from the ventral side of it.

The parts of the body thus separated are put on a slide glass, mounted with glycerine and observed. The structure of the labrum prementum and mentum are

examined under the magnification of $\times 400-850$, but to investigate the detailed structure of the labral margin and labial palpus, the large magnification of $\times 1500-2000$ by an oil-immersed lens system is necessary.

SELECTION OF EFFECTIVE CHARACTERS

By handling the specimen with the above mentioned procedure many new characters of Aleocharinae have proved to be available for the research. From the taxonomic point of view it is necessary to evaluate the characters to find out those which really represent the characteristics of each species. The characters adopted must be those: 1) exhibiting the specificity and phylogenetic relation of each species, 2) having the least individual variability, and 3) being scarcely deformed by the treatment of the specimen.

Among 35-40 characters found by the above procedure, the following were selected out as important ones in view of the standard mentioned above.

1. Location of the primary setae of the labrum
2. Arrangement and form of the sensory elements along the anterior margin of the labrum
3. Form of the prostheca of the mandible
4. Shape of the distal lobe of the galea
5. Structure of the distal comb of the lacinia
6. Filamentous sensillae on the distal segment of the maxillary palpus
7. Arrangement of the setae and sensory pores of the prementum
8. Presence and form of the sensory element on the inner side of the glossa
9. Arrangement of the setae and sensory pores of the labial palpus
10. Arrangement of the setae on the antero-lateral corner of the mentum
11. Pattern of the setulae on the head, pronotum and elytron
12. Form of the tarsal empodium
13. Microsculpture of the integument on terg.VIII
14. Chaetal arrangement on terg.VIII and on stern.VIII in male and female
15. Structure of the paramere of the aedeagus
16. Outer form and inner structure of the median lobe of aedeagus
17. Form and structure of spermatheca

SPECIES SPECIFICITY OF THE NEWLY ADOPTED CHARACTERS

To clarify how these newly adopted characters vary from one species to another, some 50 species of Aleocharinae from various habitats and localities have been investigated. The results are as follows and are summerized in the Table attached:

1. **Labrum:** (Fig. 1 A) (1970a, p. 22-23, Fig. 1): Labral setae are classified into large primary setae and small secondary setae. The large primary setae are arranged in three transverse rows, each consisting of two setae. Their loci are quite constant

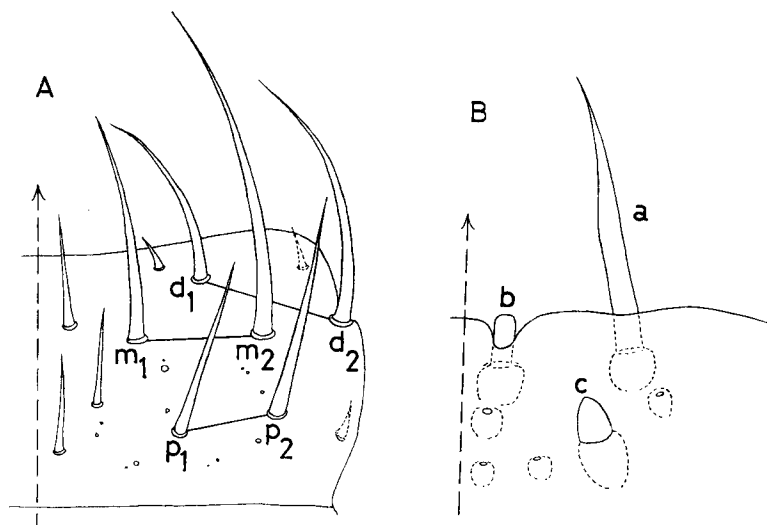


Fig. 1. A, Labral chaetotaxy of Aleocharinae; B, Labral margin, (diagrammatic).

within a given species. The anterior margin of the labrum (Fig. 1 B) is provide with minute sensillae. Among these a pair of setaceous sensillae (*a*-sensilla) are completely reduced in *Tomoglossa* (1970b, p. 44–46, Fig. 8C and 1971a, p. 44–45, Fig. 11A), while they are long and inwardly derected in *Atheta garuda* (1971b, p. 70–72, Fig. 5C).

2. **Mandible** (Fig. 2): Mandible is strongly sclerotized, protruded and situated immediately in front of the eyes. It is not symmetrical, the right and the left mandi-

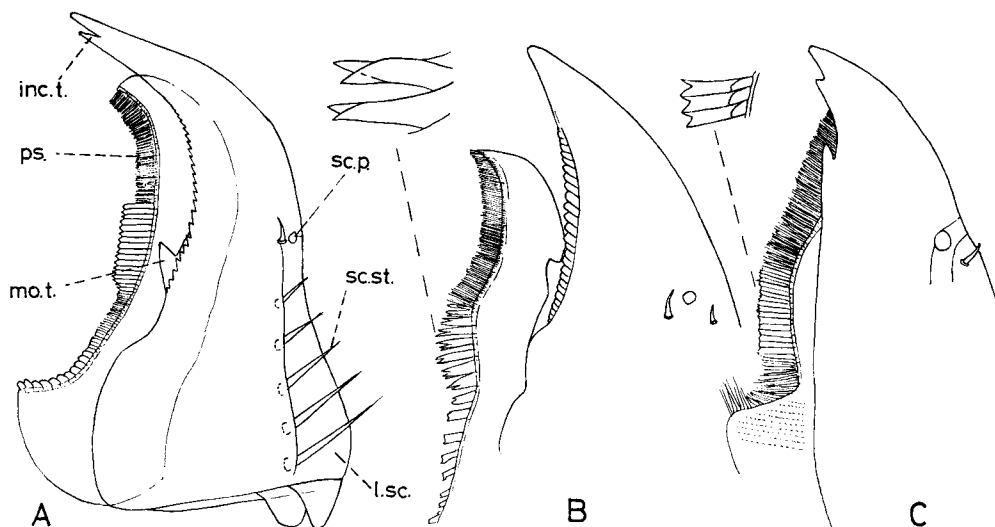


Fig. 2. A, Mandible of Aleocharinae (diagrammatic); B, Do. of *Atheta sordida* (MARSHAM); C, Do. of *Brachida brevipennis* BERNHAUER from Seto, Wakayama.

bles being different in structure. It may have the incisor tooth (*inc. t.*) subapically and a molar tooth (*mo. t.*) below the middle, the latter is well developed in the right mandible and usually absent in the left mandible. Laterally the mandible bears a lateral scrobe (*l. sc.*) as a longitudinally carinate thickening and along its outer side there is a row of setae to be named as scrobal setae (*sc. st.*). Distally it is terminating by a small pore with a few setulae which may be named as scrobal pore (*sc. p.*). Along the inner margin of the mandible a narrow membranous lobe is extending from the base to the apex to form a prostheca (*ps.*), whose margin is very finely ciliated or serrated. It is assured that the shape of the whole body and the condition of its ciliation is fairly constant within a given species. In *Atheta sordida* it is coarsely serrated at the middle (Fig. 2 B), while it is rather uniform throughout the whole length in *Brachida brevipennis* (Fig. 2 C). In *Diaulota densissima* (1971, p. 83, Fig. 7E) the prostheca is reduced to a short lobe.

3. **Maxilla** (Fig. 3 A): In Aleocharinae the maxilla is composed of five parts: cardo (*c.*), stipes (*st.*), maxillary palpus (*mx.p.*), galea (*gal.*) and lacinia (*lac.*). The cardo is obovate in shape and heavily sclerotized. The stipes is divided into 3 parts by distinct sutures to form inner (*i.sc.*), medial (*m.sc.*) and outer (*o.sc.*) sclerites. The maxillary palpus (*mx.p.*) is composed of four segments in most cases; the first segment is very small, with a few pores and setulae, the second segment is elongate, more or less dilated anteriorly, the third segment is the largest and strongly dilated in the middle, the fourth segment is attenuate, subulate and with a fine setiform apical process (*a.pr.*). In *Aleochara* and its allies the fourth segment of maxillary palpus bears a small subsegment (Fig. 3 B) so that the palpus is apparently of five-segmented. The same segment has a bundle of filamentous sensillae (*f.s.*) on its basal part, and their characters are fairly constant within a given species; in *Atheta sordida* (Fig. 3 F) some 8 elements are almost fused and converging distally, while in *A. prolata* they are separated diverging (Fig. 3 G). In *Bryothinusa nakanei* (1971, p. 88, Fig. 3 D) it is developed to a distinct bundle of filaments, while it is much reduced in *B. minuta* (1971, p. 83, Fig. E). Galea (*gal.* in Fig. 3 C) is an outer lobe of the maxillary endites. It is composed of proximal sclerite (*p.sc.*) and distal lobe (*d.l.*). The former is the elongate sclerite bearing some sensory pores and the latter is a membranous lobe with some basal sensillae (*b.s.*). In *Atheta sordida* (Fig. 3C) the basal sensillae are composed of two setulae, while in *Schistoglossa yosii* (1970, p. 32, fig. 11 C) it is developed to a large setiform sensilla, whereas, in *Bryothinusa algarum* (Fig. 3 F) it is quite reduced leaving a minute pore at the place. The general shape of the distal lobe of the galea is also variable according to the species; in *A. sordida* it is broad, more or less pointed and with uniformly short cilia in the outer margin, while in *Zyras comes* (Fig. 3 E) it is an obtuse short lobe densely ciliate throughout as not to discern the outer margin of the galea. In *Bryothinusa algarum* (Fig. 3 D) it is reduced to narrow furcating processes. The lacinia (*lac.* in Fig. 3 C), the inner lobe of the maxillary endites, is different according to the species. In *Atheta sordida* (Fig. 3 C) it has a distal comb (*d.c.*) composed of 6 spines standing side by side and a large marginal dilation (*m.d.*) on which some five isolated spines (*i.sp.*) are

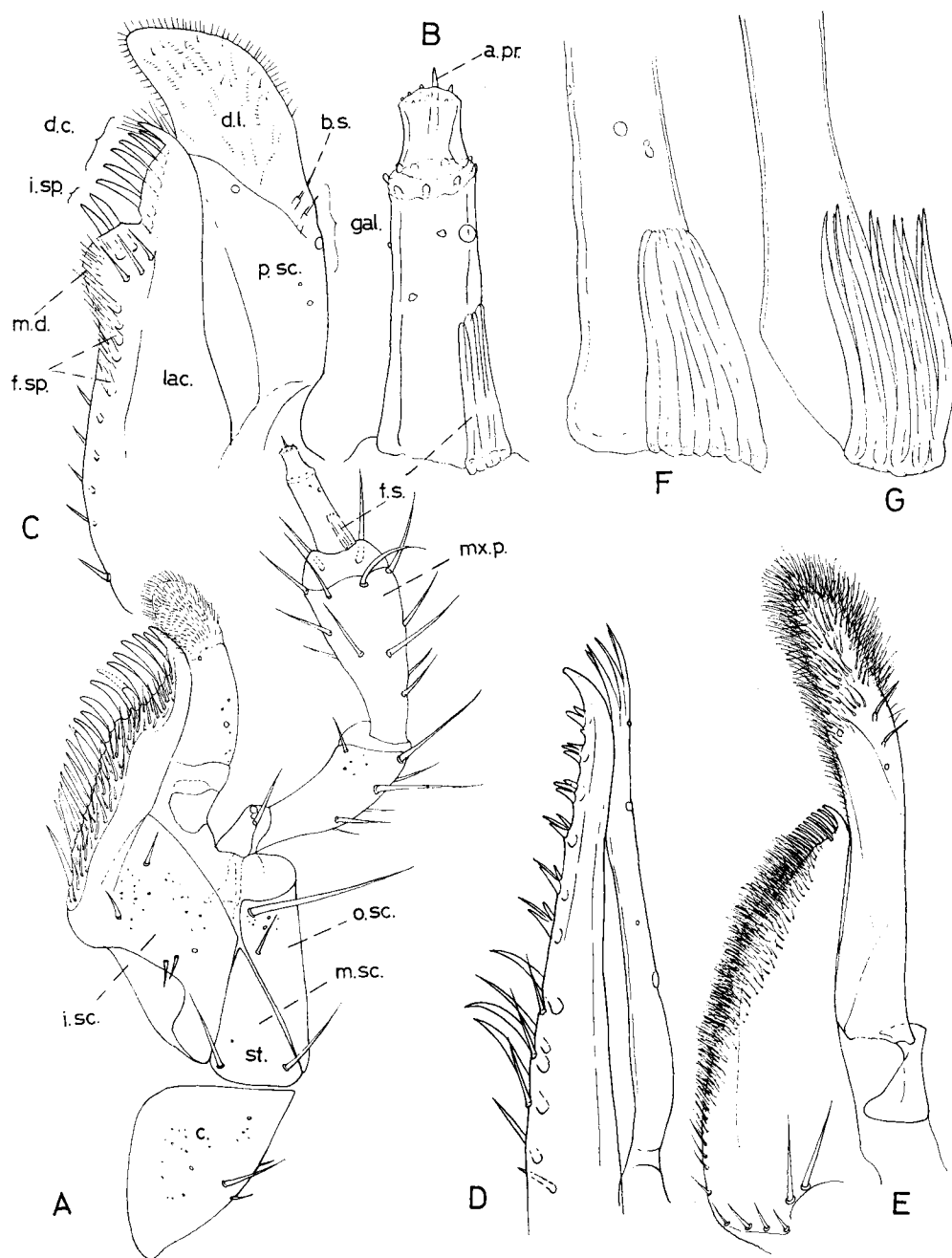


Fig. 3. A, B, Maxilla and last palpal segment of *Aleochara fucicola* SHARP from Seto, Wakayama; C, Lacinia and glossa of *Atheta sordida* (MARSHAM); D, E, Do. of *Bryothinusa algarum* K. SAWADA and *Zyras comes* (SHARP) from Ohara, Kyoto; F, G, Filamentous sensillae of *A. sordida* (MARSHAM) and *A. prolata* (K. SAWADA).

present in the heavily ciliation of the portion. In *Aleochara fucicola* the lacinia has no marginal dilation and there is a series of up to 15 spines in a row without forming an apical comb (Fig. 3 A), while in *Zyras comes* (Fig. 3 E) the inner margin is densely ciliated on its whole length and spines are restricted to the compact apical comb. In *Bryothinusa algarum* (Fig. 3 F) the lacinia is styloform, the distal comb is transformed into a row of trifurcate spines and the basal isolated spines are represented by a few long, curved spinules.

4. **Labium** (Fig. 4 A): Labium of the Aleocharinae is composed of four parts: prementum (*p.m.*), mentum (*mt.*), glossa (*gl.*) and a pair of labial palpi (*l.p.*).

Premantum (1970a, p. 28, Fig. 4): The principal portion of the prementum is divided into a median area (*m.a.*) and a pair of lateral ones (*l.a.*), and provided with a pair of distal setae (*d.s.*), basal pores (*b.p.*), setal (*s.p.*), real (*r.p.*) and pseudopores (*p.s.*). All their arrangements serve well to distinguish each species. The setal and real pores are arranged longitudinally in *Tomoglossa punctifoveata* (1970b, p. 44–46, Fig. 8 F). The distal setae are situated longitudinally in *Leptusa deplanata* (1970a, p. 40–41, Fig. 8 B) and *L. kitazawai* (1970a, p. 41–42, Fig. 9B). They are represented by a single seta in *Gyroghaena hanedai* (1970b, p. 39–41, Fig. 6 D) and *Brachida brevipennis* (1971a, p. 292–294, Fig. 1 E), while they are completely reduced in *Diaulota aokii* (1971a, p. 104, Fig. 9E), *D. pacifica* (l.c. p. 101, Fig. 8 E), *D. densissima* (l.c. p. 98, Fig. 7 F) and *Genoplectes uenoi* (1971d, p. 106, Fig. 10 E).

Mentum (1970a, p. 29, Fig. 4; 1970b, p. 33): The location of three main setae (*u. v. w*) on the anterior corner of the mentum is characteristic of each species as shown in 1970a, Fig. 5–6.

Glossa (1970a, p. 24–27, Fig. 4): The presence or absence of the bifurcated glossa has been already used for taxonomy by previous authors, but the degree of bifurcation is not constant in each species. By the present research it has been affirmed that the loci, number and size of minute sensillae and setae of its inner side are constant in a given species. The inner surface of the glossa is provided with some sensillate elements (*s.g.*) and their arrangement, approximate loci and shape are constant to a given species. The cases of *Atheta sordida* (Fig. 4 B) and *A. ushio* (Fig. 4 C) are illustrated.

Labial palpus (1970a, p. 28–29, Fig. 4; 1970b, p. 33, Fig. 1): In the course of the present study the chaetotaxy of the labial palpus has proved to be the most significant character in the taxonomy of Aleocharinae. Previously the number of segments in the labial palpus (usually two- or three-segmented, rarely one or four) is regarded as one of the most fundamental characters in many cases, but the condition of the segmental articulation of the labial palpus seems to be very ambiguous and obscure when closely observed. In *Leptusa* spp. (1970b, p. 35, Fig. 2 D, B) the first segment of the labial palpus is much reduced, while in *Brachida* spp. (1971a, p. 293, Fig. 1 D) it is not reduced but perfectly fused with the second segment, although in both cases the palpus is really “two segmented”. In *Diaulota* spp. the first segment of the palpus is half-confluent with the second segment leaving a slight sign of the fusion. Therefore, it is naturally unreasonable to include all of them in the same category. Besides, the

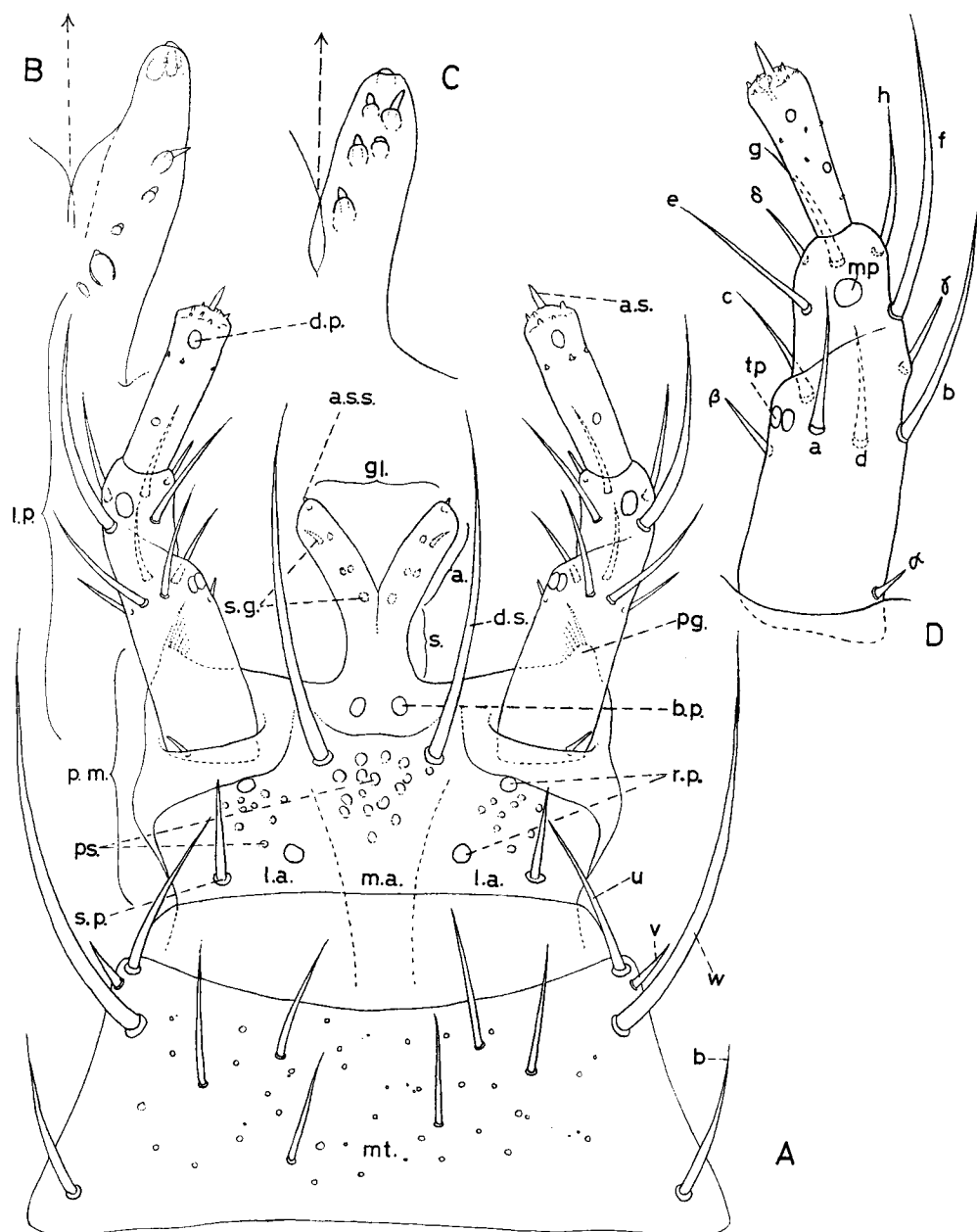


Fig. 4. A, Labium of Aleocharinae (diagrammatic); B, C, Glossa of *Atheta sordida* (MARSHAM) and *A. ushio* (K. SAWADA); D, Labial palpus (diagrammatic).

chaetotaxy of the labial palpus is very significant in the taxonomy of Aleocharinae. The labial palpus bears eight setae (*a-h*), four setulae (α - δ) and two foveae (*tp*, *mp*) (1970b, p. 34, Fig. 1). Their arrangement in each species is quite specific and furnishes the most effective character for the identification of species.

Seta a, is in most cases, placed lateral to *tp*, but in *Brachida brevipennis* (1971a, p. 292-294, Fig. 1 D) it is reduced to a short setula, and in *Aleochara fucicola* (1971a, p. 309-312, Fig. 8 D), and *A. trisulcata* (ditto, p. 312-314, Fig. 9 D) it is remote from *tp*.

Seta b is usually on the same level with *tp* and posterior to *f*, but in *Diestota luzonica* (1971b, p. 63-65, Fig. 2 D) it is characteristically moved to the base of the first segment.

Setae c and *d* are located near the level of *tp* opposite to *a*, but in *Brachida brevipennis* (1971a, p. 292-294, Fig. 1 D) *d* is much shorter than *c*, while in *Gyrophaena hanedai* (1970b, p. 39-41, Fig. 6 E) *c* is completely reduced.

Seta e is located lateral to *mp* at the middle of the inner margin of the second segment, but it is placed close to *tp* in *Gyrophaena hanedai* (l.c.), on the apex of the segment in *Amaurodera philippinensis* (1971 b, p. 65-68, Fig. 3 D) and close to *mp* in *Atheta yosii* (1970b, p. 39, Fig. 3 K).

Seta f is the largest of all the setae of the labial palpus. It is very remote from *mp* in *Diestota luzonica* (1971b, p. 63-65, Fig. 2 D) and close to *mp* in *Schistoglossa yosii*ana (1970b, p. 34, Fig. 2 D).

Setae g, h are placed near the apex of the second segment. Characteristically seta *g* is larger than *h* in *Tomoglossa punctifoveata* (1970b, p. 44-46, Fig. 8 G) and *T. cuspidata* (1971a, p. 294-296, Fig. 2 D), while *g* and *h* are proximal to *mp* in *Leptusa deplanata* and *L. kitazawai* (1970b, p. 34, Figs. 2A, B). In *Brachida brevipennis* (1971a, p. 292-294, Fig. 1 D) and *Diestota luzonica* (1971b, p. 63-65, Fig. 2 D) *h* is missing.

Setula α : It is basal in position, but in *Homoeusa prolongata* (1970b, p. 57-60, Fig. 14 E) it is more distally placed, while it is much reduced in *Myrmecopora algarum* (1971a, p. 296-299, Fig. 3E).

Setula β : Its relative locus to *tp* must be noted. It is well developed and close to *tp* in *Atheta uncinata* (1971c, p. 80-82, Fig. 1 D), but completely reduced in *Amaurodera philippinensis* (1971b, p. 65-68, Fig. 3 D).

Setula γ : Its length and locus in relation to *b* and *f* are to be noted. It is well developed and close to *b* in *Atheta yosii* (1970b, p. 39, Fig. 3 K), close to *f* in *Brachida brevipennis* (1971a, p. 292-294, Fig. 1 D) and posterior to *b* in *Atheta bogorensis* (1971b, p. 72-75, Fig. 6E).

Setula δ : It is well developed into a long seta in *Oxyptoda imadatei* (1970b, p. 56-57, Fig. 13 E), *O. producta* (1970b, p. 51-53, Fig. 11 E) and *Homoeusa prolongata* (1970b, p. 57-60, Fig. 14 E), but reduced to a minute element in *Atheta ushio* (1971a, p.

304–306, Fig. 6 D), and in *Eccoptygenia rufa* (1971b, p. 61–63, Fig. 1 D) anterior to *e. Twin pores (tp)*: They are paired, contiguous pores located near the apex of the first segment. They are much reduced in *Gnybeta aokii* (1970b, p. 34, Fig. 2C), *Aleochara fucicola* and *A. trisulcata* (1971a, p. 309–314, Figs. 8 D, 9 D), while they are located separately from each other in *Zyras iridescens* (1970b, p. 49–51, Fig. 10 F).

Median pore (mp): It is usually larger than *tp* and located at about the middle of the second segment. It is laterally dislocated to the outer margin in *Gyrophaena henadai* (1970b, p. 139–141, Fig. 6 E) and is characteristically reduced in *Aleochara fucicola* (1971a, p. 309–312, Fig. 8 D).

5. **Chaetal Pattern**: Chaetal pattern of the head, pronotum and elytra has been already studied in detail and its availability in the taxonomy of Aleocharinae has been witnessed by BRUNDIN (1942, etc.), HOEG (1945) and others. At present I have no further results to add to these authors.

6. **Tarsal Empodium** (Fig. 5A): An empodial seta (*emp.*) is present between the paired claws (*cl.*) of each leg. It is shorter than the claw in *Atheta sordida* (Fig. 5 B), longer than the claw in *A. ushio* (Fig. 5 C) and completely absent in *A. uncinata*.

7. **Microsculpture**: Tergites of Aleocharinae are usually covered with minute structures and these microsculptures may be observed most conveniently at the median part of the abdominal tergite VIII. They are either imbricate (Fig. 5 D), reticulate (Fig. 5 E) or transversely striate (Fig. 5 F) according to the species.

8. **Abdominal Tergite VIII** (Fig. 5 G): In Aleocharinae the posterior margin of terg. VIII often reveals the sexual dimorphism as already known in various species. Besides the arrangement of large principal setae is peculiar to each species. They are to be named as *a-1*, *a-2*, *a-3*, *p-1*, *p-2*, *p-3*.

9. **Abdominal Sternite VIII** (Fig. 5 H): The arrangement of the principal setae and the outline of the sternite serve well to distinguish the species. The principal setae are often reduced in number in female examples compared to males (*Atheta tokiokai*, 1971a, p. 306, Fig. 7J). On the contrary the sternite is often provided with a row of fringed modified setae along the posterior margin in females as already referred in BRUNDIN (1942) etc.

10. **Lateral Lobe** (Fig. 6 A, B): Median lobe of the male genitalia is embraced by a pair of lateral lobes. It is composed of three segments, the proximal (*px.s.*), medial (*md.s.*) and distal (*dt.s.*), and is articulated to the ventral side of the median lobe. The first segment is an elongate sclerite, the second segment is large, triangular and jointed to the first segment at about the middle of its inner margin. The third or the distal segment is small and attached to the apical portion of the second segment. In Aleocharinae the distal segment always possesses four setulae and their loci and relative lengths are quite constant in each species or species-group as already cited K. SAWADA 1970b, p. 33, Fig. 5. The outline of the distal segment is also fixed; in *Oxyptoda producta* it is narrowly elongate, (1970b, p. 52, Fig. 11 L), while in *Aleochara fucicola* it is oblong (1971a, p. 310, Fig. 8 N) in form. Besides the lateral lobes is provided with

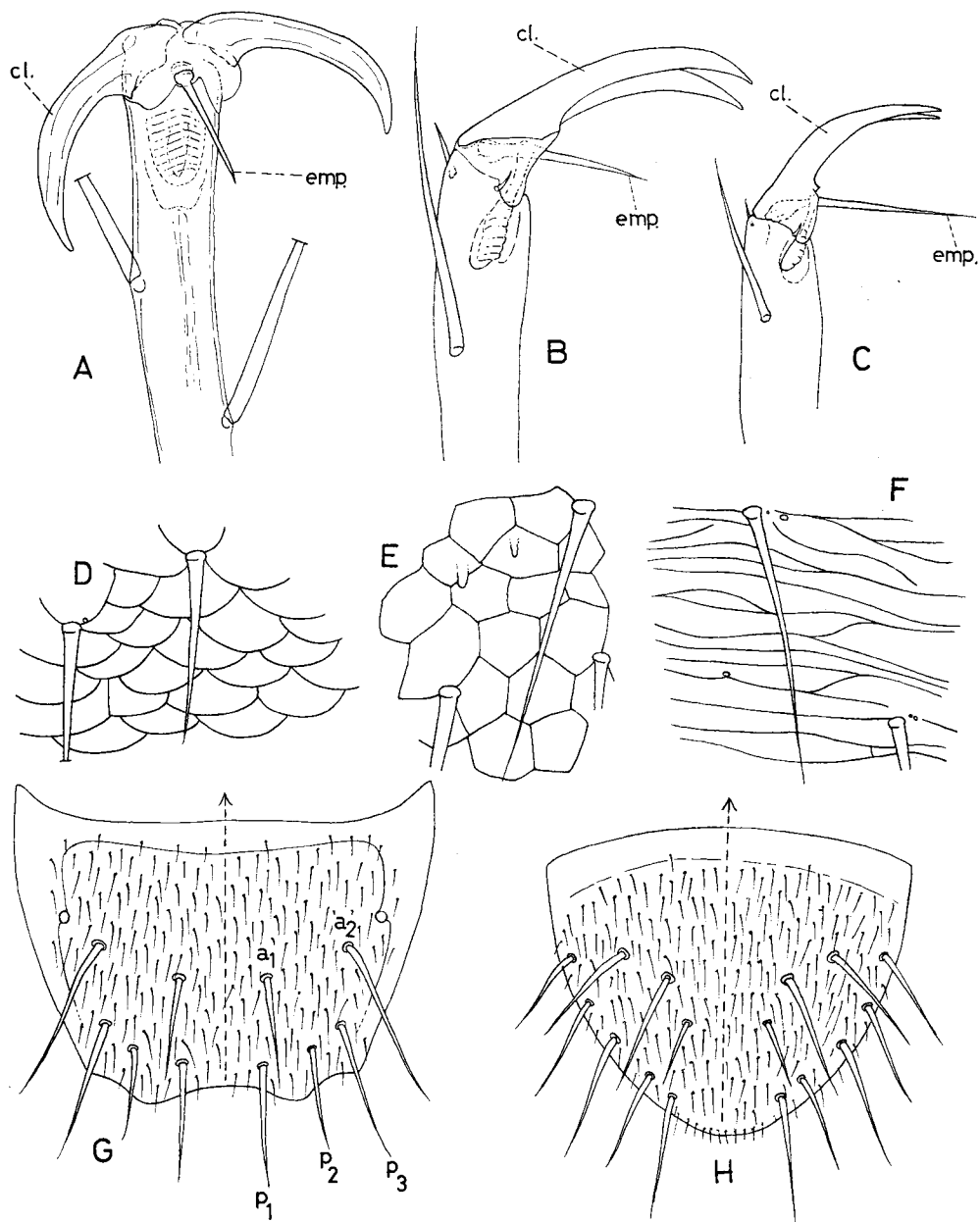


Fig. 5. A, B, Empodium of *Atheta sordida* (MARSHAM); C, Do. of *A. usio* (K. SAWADA); D, E, F, Microsculpture of tergite VIII; G, Tergite VIII; H, Sternite VIII (diagrammatic).

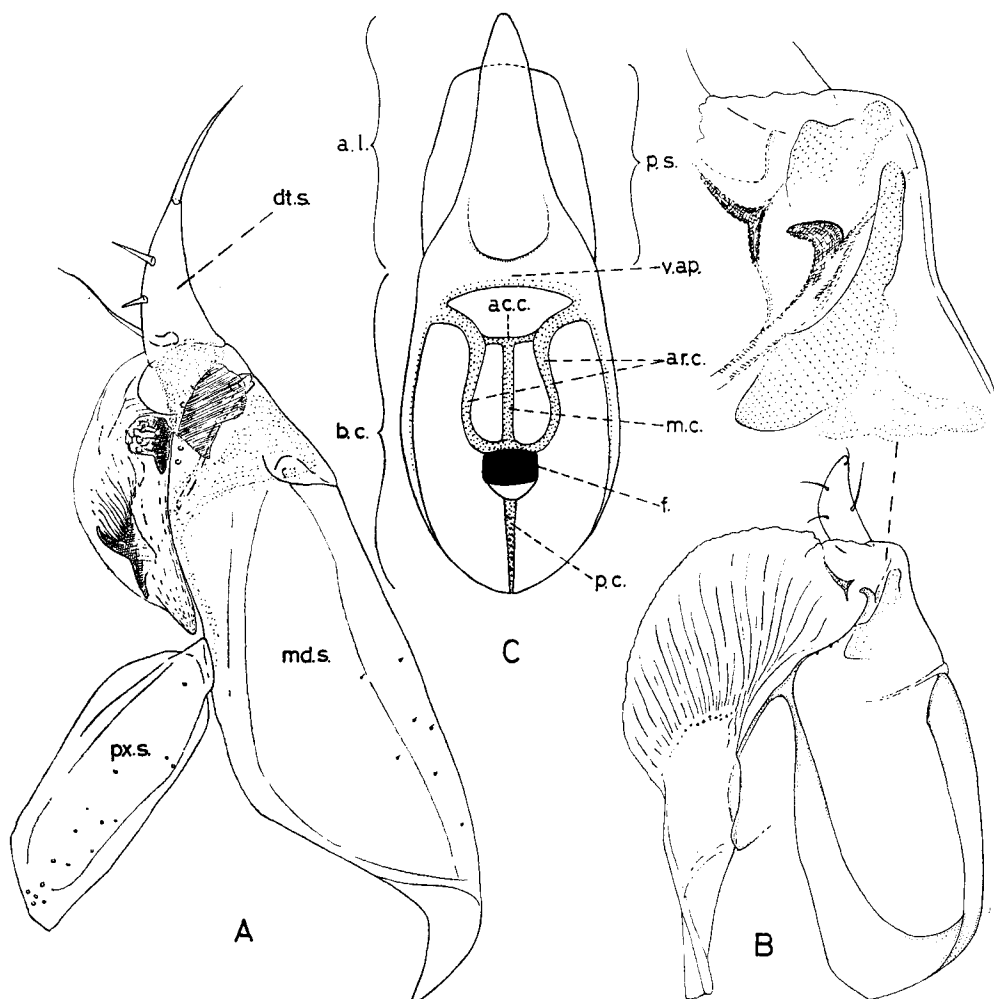


Fig. 6. A, Lateral lobe of *Atheta sordida* (MARSHAM); B, Do. of *A. ursi* sp. n.; C, Median lobe of aedeagus showing costation (diagrammatic).

prominent broad lamellae on its inner side. When closely observed, they are not simple lamellae but a kind of flat sacculus somewhat eversible when fully extended. The lamellae may be separately present or, as may be seen in the majority of cases, confluent to form a complicated mass. Their inner and outer surfaces may have minute radiating structures and with some thick apodemes which, sometimes, may become prominent processes or condyli. As their structures are so variegated but constant to each species that their evaluation in the taxonomic studies of Aleocharinae must be discussed in each case. Lateral lobes of two representative species, *Atheta sordida* and *ursi* have been illustrated in Fig. 6 A, B.

11. **Median Lobe** (Fig. 6 C): The median lobe of Aleocharinae is relatively poorly

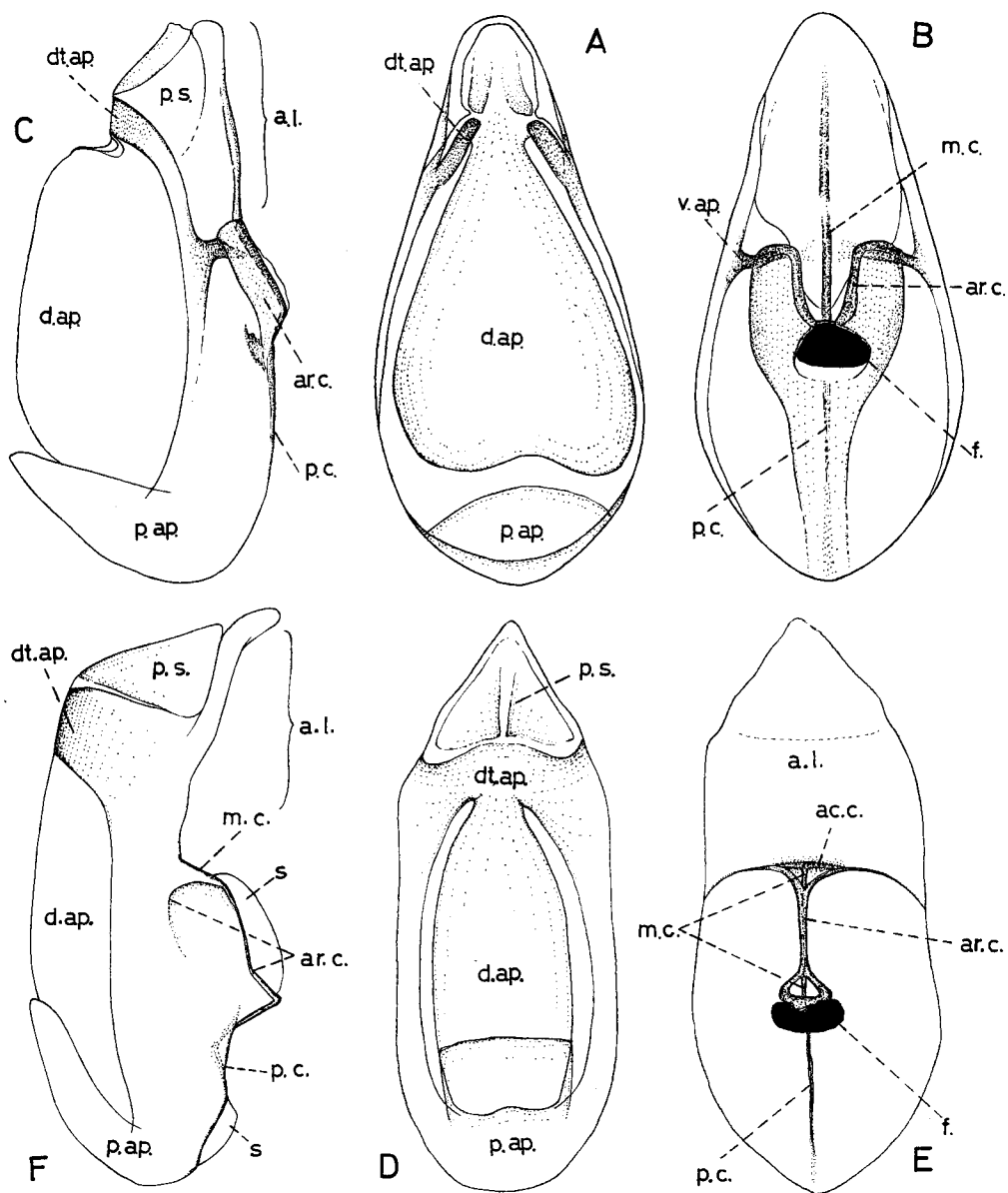


Fig. 7. A, B, C, Median lobe of *Atheta sordida* (MARSHAM): D, E, F, Do. of *A. atramentaria* (GYLLENHAL) from Seto, Wakayama (dors. ventr. and lat. view).

sclerotized compared to other Coleoptera. Its general shape is already treated by many previous authors, but it must be investigated more in detail.

It is composed of three parts; the basal capsule (*b.c.*), praeputial sac (*p.s.*) and apical lobe (*a.l.*). Ventrally there is a median foramen (*f.*), through which the genital duct is reaching to the copulatory apparatus. The wall of the basal capsule is strengthened by many costae, whose arrangement reveals to be of taxonomic importance. In Fig. 6 C, its main component is diagrammatically shown. Proximal costa (*p.c.*), accessory costa (*ac.c.*), and ventral apodeme (*v.ap.*) may be present or absent. Distal to the foramen there is a peculiar framework of costae composed by a median costa (*m.c.*) and a pair of lateral or arcuate costae (*ar.c.*). The latter is paramedian and often fused distally. In *Atheta sordida* (fig. 7 B) it may be recurved. Dorsally there may be seen three pairs of apodemes: the dorsal (*d.ap.*), proximal (*p.ap.*) and distal (*dt.ap.*) apodemes. Dorsal apodeme is usually a large lobe covering the main part of the median lobe (fig. 7 A). Distal apodeme is sometimes contiguous (fig. 7 D) and sometimes separate (fig. 7 A) at the middle. Usually it is extended laterally and united with the paramedian costa of the ventral side. For the praeputial sac and apical lobe, especially of the latter, we have nice works of Brundin (1952) for which no additional note is to be necessary. Interior of the basal capsule is very difficult to observe, it may be investigated, as stated before, only when it is extirpated from the basal capsule. In reality, as the interior mass is very musculous, the process may be better expressed as "peeling" of the basal capsule, which is effectively to be made from the dorsal side of the organ. The inner mass may be observed from dorsal and the ventral side in case when it is very complicated in structure.

Fig. 8 A is the diagram of the content of the inner sac. There is a copulatory piece (*c.p.*) with a round annellus (*an.*), an apical process (*a.pr.*) and a pair of basal processes (*b.pr.*). To each side of the copulatory piece there is a suspensorium (*su.*) which is usually elongate and articulated with the basal process of the copulatory piece. In some rare cases such as *Atheta atramentaria* (Fig. 8 C) two pairs of suspensoria were detected and although their homological identification is still uncertain, the presence of the inner suspensoria may be admitted. In *A. uncinata* (Fig. 8 D) the suspensoria are long, with a pair of distinct distal hooks, while in *A. tokiokai* (Fig. 8 E) the suspensoria is more reduced. Besides the suspensoria-complex there are some more sclerites distal to it, they are apparently the derivatives from the inner wall of the praeputial sac. These sclerites are greatly diversified according to the species, but in principle there seems to exist an unpaired median apophysis (*m.ap.*) and a paired paramedian apophysis (*pm.ap.*). The structure of the male genital organ is highly specific to be a firm basis for identifying each species and their general trends, especially the costation of the basal capsule and the development and form of the suspensoria would furnish the characters of determining the subgenus of the group within the large genera such as *Atheta* or *Oxyptoda*.

12. **Spermatheca** (1070a, p. 38): The outline of the whole spermatheca is characteristic of each species as well as the shape of the umbilicus and the surface corrugation.

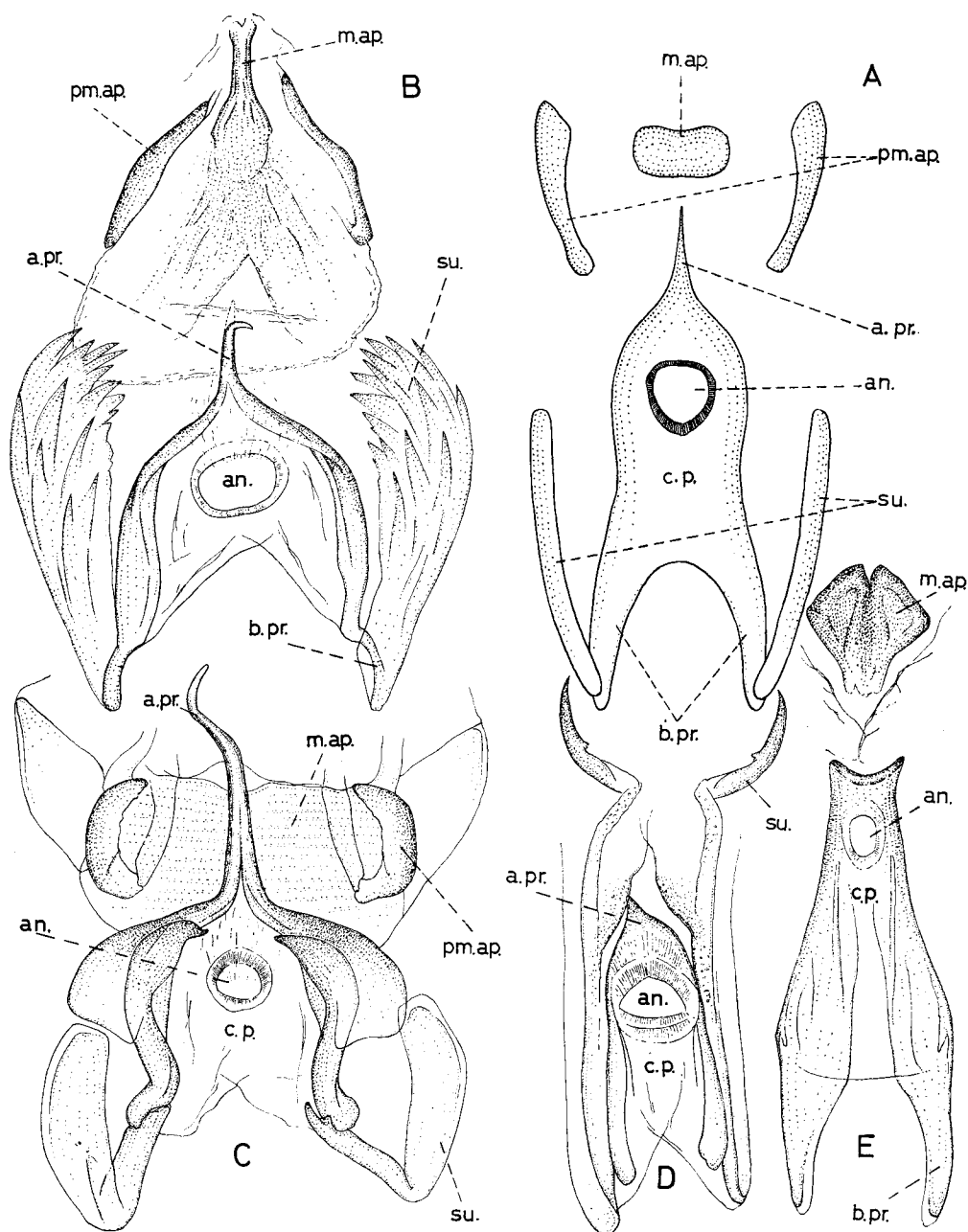


Fig. 8. A, Copulatory piece and suspensoria of Aleocharinae (diagrammatic); B, Do. of *Atheta sordida* (MARSHAM); C, Do. of *A. atramentaria* (GYLLENHAL) from Seto, Wakayama; D, Do. of *A. uncinata* (K. SAWADA) from Midorogaike, Kyoto; E, Do. of *A. tokiokai* (K. SAWADA) from Seto, Wakayama.

VARIABILITY OF THE NEWLY ADOPTED CHARACTERS

The next problem is to what extent these newly adopted characters vary in one to the localities. As an example *Atheta sordida* (MARSHAM 1802), a cosmopolitan species, from various parts of Japan (Mizorogaike, Kyoto; Iwaizumi, Iwate Pref.; Sapporo,

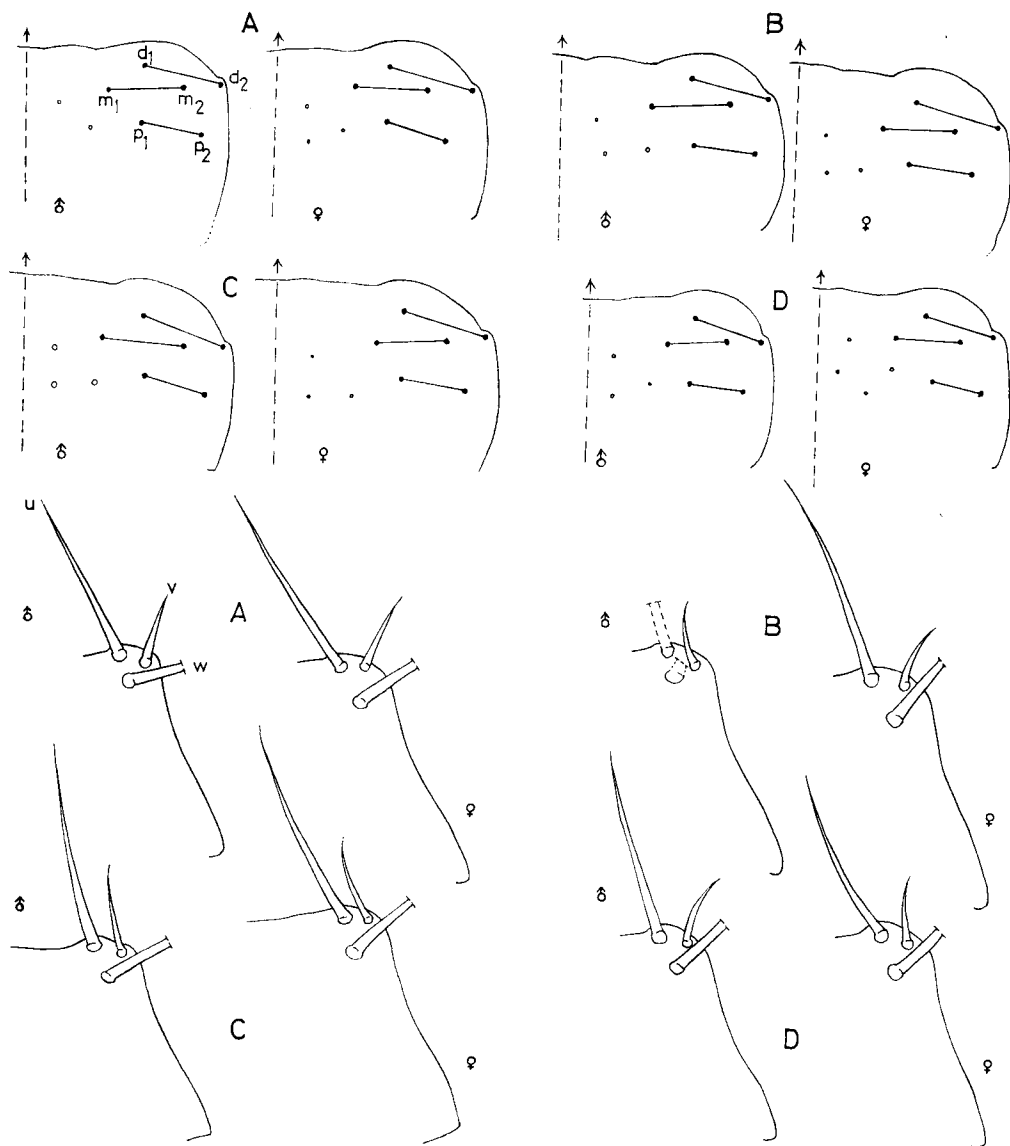


Fig. 9. Labral chaetotaxy (above) and setal arrangement of mentum (below) of *Atheta sordida* (MARSHAM) from Midorogaike, Kyoto (A); Iwaizumi, Pref. Iwate (B); Sapporo (C); Burgenland, Germany (D).

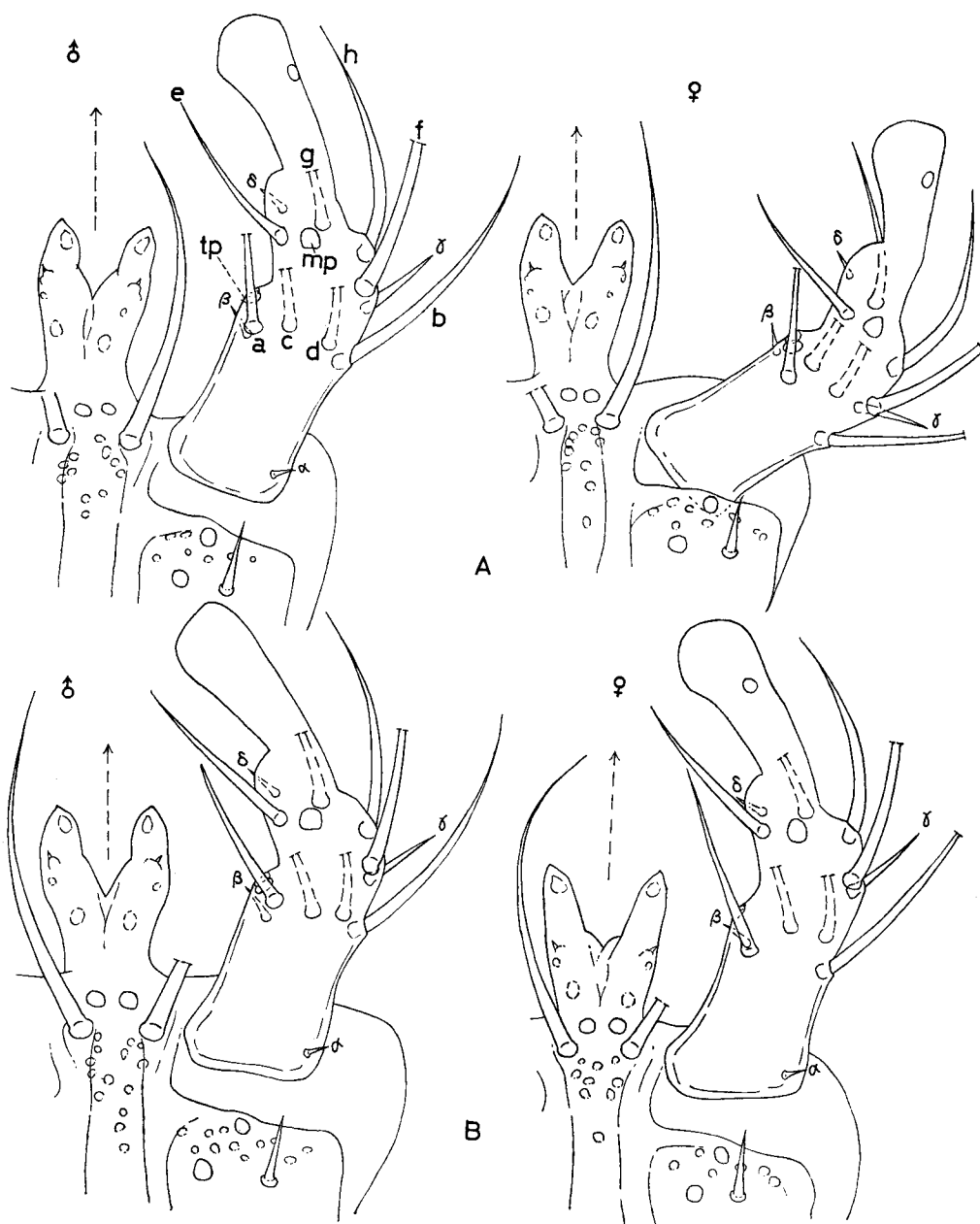


Fig. 10. Labial palpus, glossa and prementum of *Atheta sordida* (MARSHAM) from Midorogaike, Kyoto (A); Iwaizumi, Pref. Iwate (B).

Hokkaido) are compared with that from Germany (Burgenland). As may be seen in the figures 9–13, these newly adopted characters show a nice concordance notwithstanding the difference in sexes and localities; labrum (Fig. 9 C, D) is quite the same in the arrangement of the primary setae; labial palpus (Figs. 10, 11) bears well developed

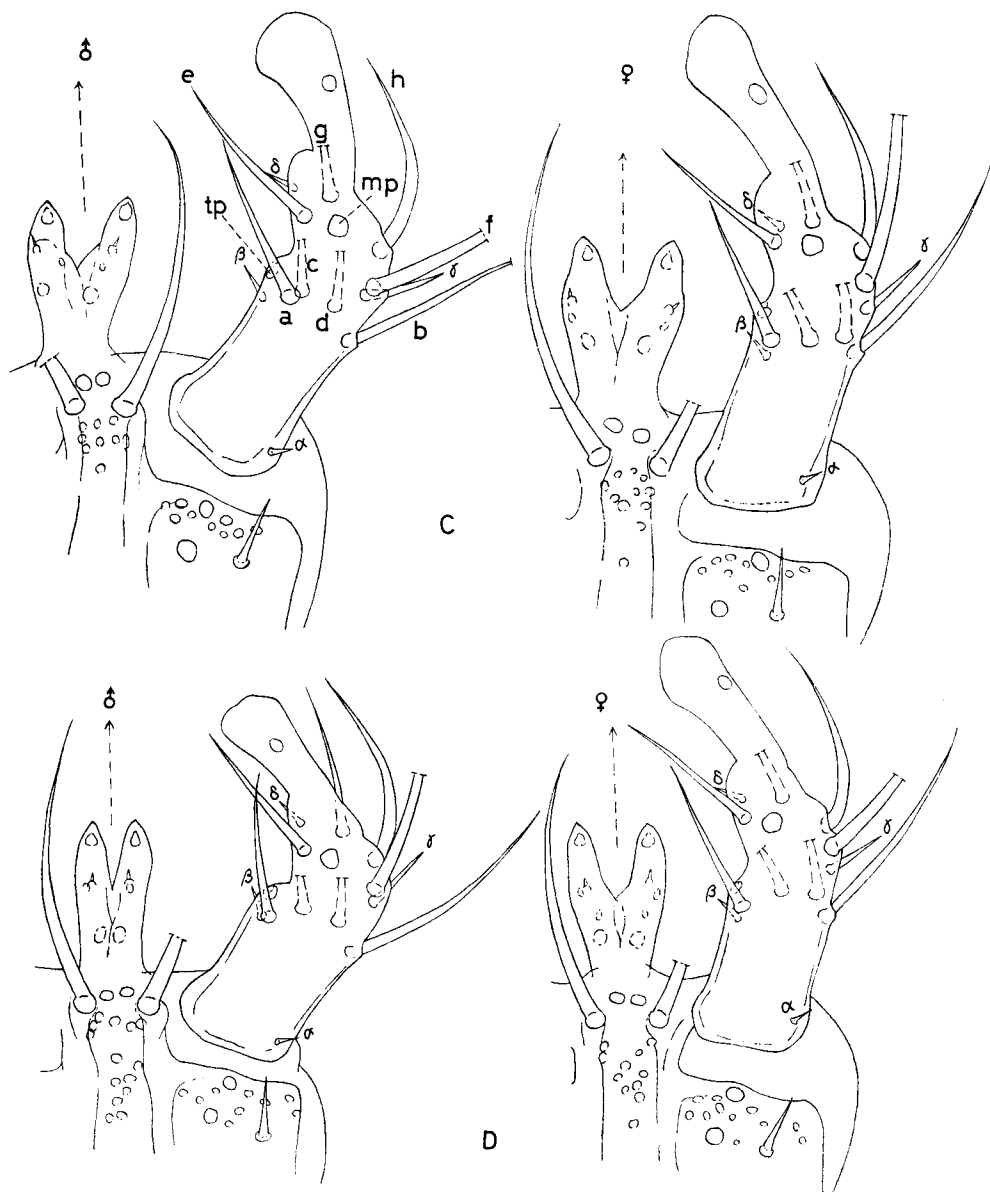


Fig. 11. Labial palpus, glossa and prementum of *Atheta sordida* (MARSHAM) from Sapporo (C); Burgenland, Germany (D).

β and δ ; glossa has only one pair of minute sensory elements; premental distal setae are remote to each other on their basis and the median area has pseudopores; three setae on the antero-lateral corner of the mentum (Fig. 9 A, B) and four setae of terg. VIII (Fig. 12 A, B) are all the same in arrangement; microsculpture on terg. VIII (Fig. 12 A, B) is always transverse in pattern. In the male genitalia, however, the copulatory piece (Fig. 13 A-D) is slightly broader, and the setae of the distal sclerite

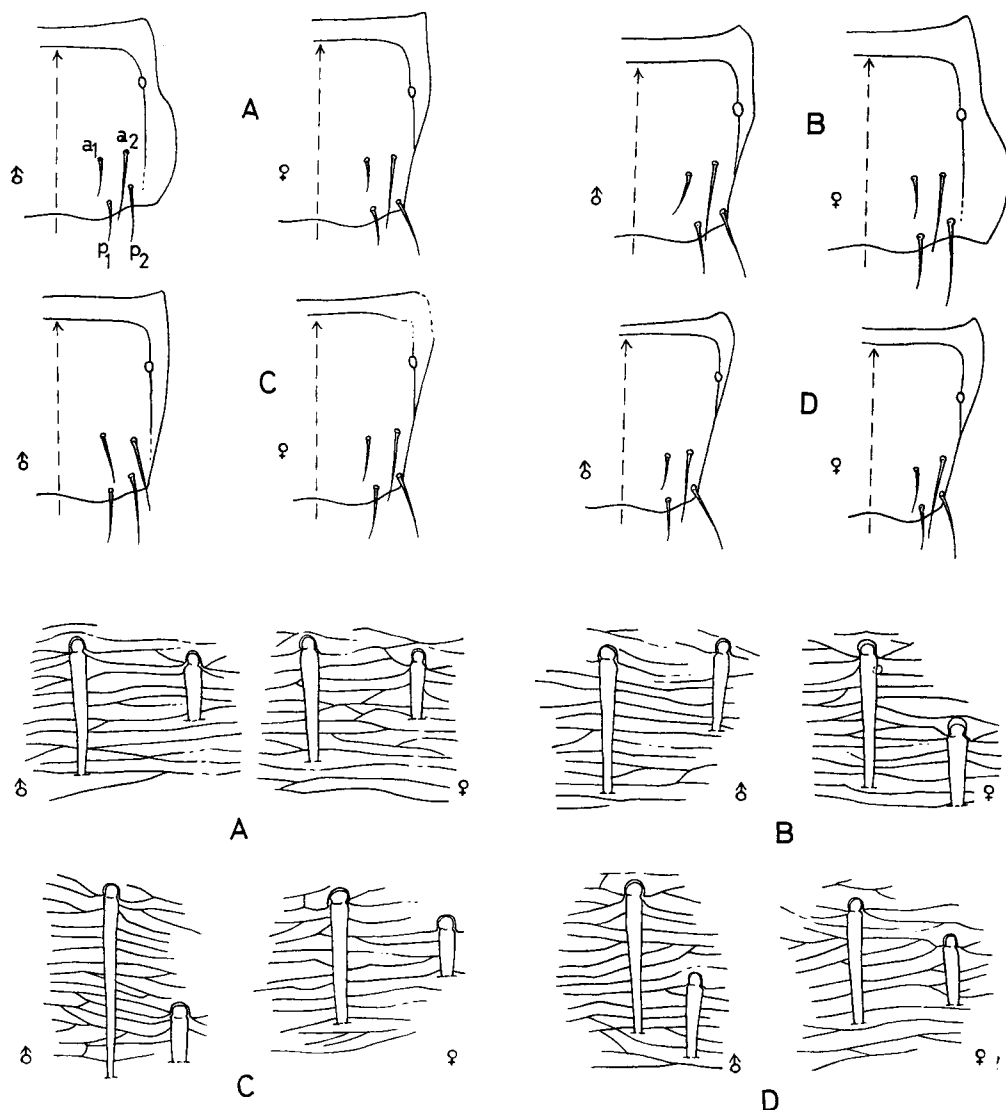


Fig. 12. Setal arrangement and microsculpture of tergite VIII of *Atheta sordida* (MARSHAM) from Midorogaike, Kyoto (A); Iwaizumi, Pref. Iwate (B); Sapporo (C); Burgenland, Germany (D).

(Fig. 13 A–D) are more distally located in German specimens when compared with Japanese ones, but the difference is too trivial to divide them into different species or subspecies. The figures clearly show that most of these characters, especially those of

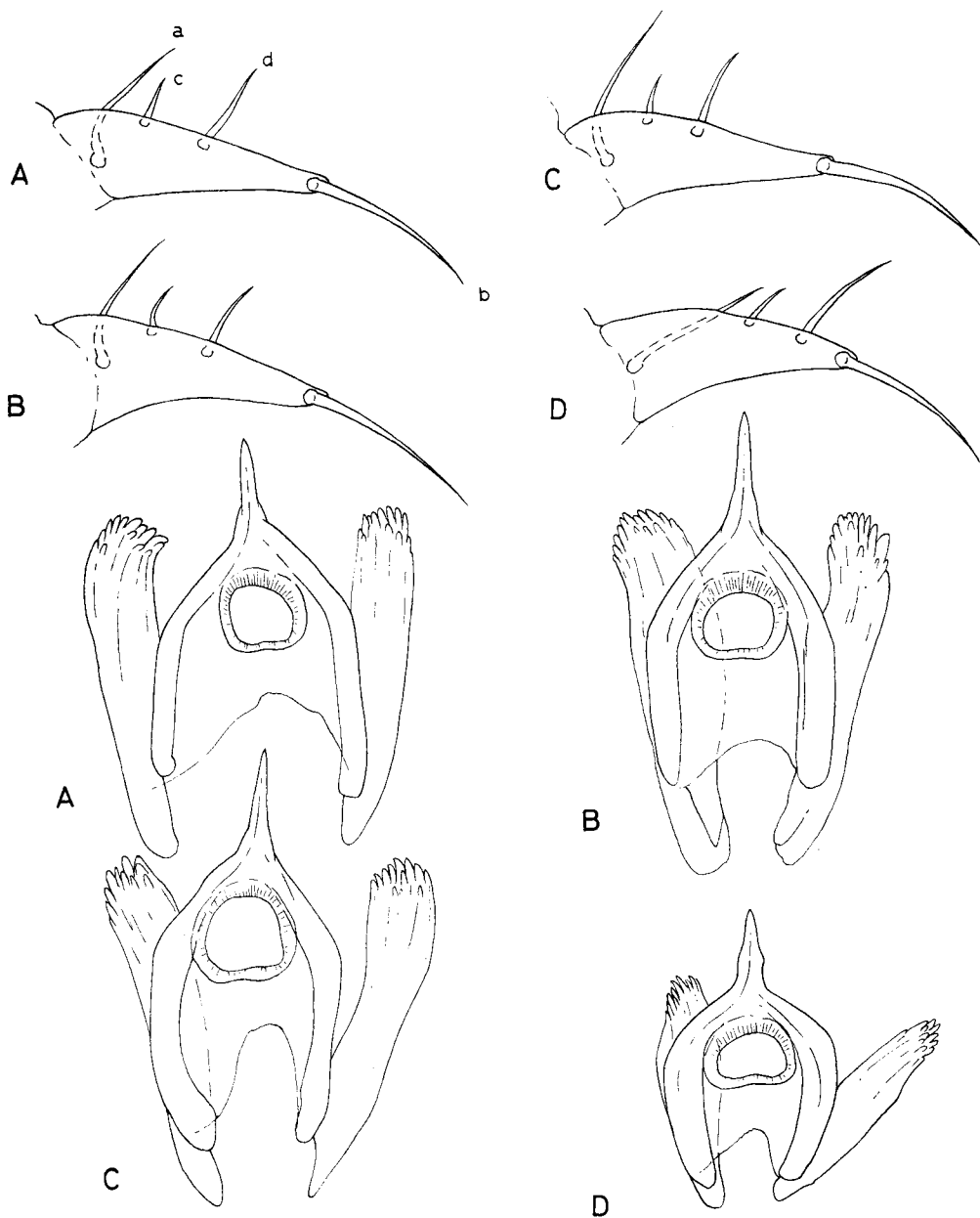


Fig. 13. Copulatory piece and distal segment of lateral lobe of *Atheta sordida* (MARSHAM) from Midorogaike, Kyoto (A); Iwaizumi, Pref. Iwate (B); Sapporo (C); Burgenland, Germany (D).

the head and mouth parts reveal no sexual difference, so that it is possible to identify the species by the examination of the female example alone. In other species of Aleocharinae already examined by the author, the degree of the variability is about the same as in case of *A. sordida* with respect to these adopted characters.

EXAMPLES OF THE REDESCRIPTION OF THE SPECIES IN VIEW OF THE NEWLY ADOPTED CHARACTERS

Atheta sordida (MARSHAM 1802) is a cosmopolitan species that has been described many times by various authors. Among them the most reliable diagnosis of the species is that of BRUNDIN (1952), p. 100–101.

When the author redescribes this species applying the newly proposed procedure, based on the materials collected from the Garden of the Kyoto Imperial Palace, the diagnosis can be revised in the following way:

***Atheta sordida* (MARSHAM 1802)**

Fig. 14

♂: Dark brown in ground colour, subopaque anteriorly by extremely fine granules densely covering the whole surface. Head, pronotum are similarly dark brown, while elytra are rufescent more or less; abdomen is paler toward the end; antennae are uniformly brown and legs are paler in colour. Head is not modified; pubescence is longer than on pronotum, but decreasing in number; its bases are finely produced giving a granulose appearance to the surface. Eyes are large, much larger than the post-ocular region in lateral view, with many setulae which are about as long as the diameter of each facet. Antenna slender, weakly dilated distally, their segmental ratio as: I 23×11 : II 18×10 : III 25×15 : IV 12×17 : X 15×17 : XI 18.5×43 . Labrum (Fig. 14 B) bears three rows of setae which are subequally short; $p-1$ is anterior to $p-2$. b -sensilla of the labral margin (Fig. 14 C) is reniform. The right mandible has a very small molar tooth together with a fine inner marginal serrulation as in Fig. 7F. Setulae on the lateral scrobe are 6 in number. Prostheca is much serrated behind the middle. Segment II of maxillary palpus is weakly dilated distally; basal filamentous sensillae of IV do not reach the middle of the segment. Distal comb of lacinia is large, composed of 6 slender spines sparsely arranged. Distal lobe of galea is densely ciliate along its outer margin. Glossa (Fig. 14 D) is elongate, forked from the middle and lightly pointed at the apex; inner surface bears three pairs of secondary pores, and a pair of minute spiniform sensillae are placed at about the middle. The third segment of labial palpus (Fig. 14 D) is fairly dilated; β is large, normal in position; r is well developed; δ is large, on the same level of g ; a is on the same level of b ; c and d are on the same level; f is situated proximal to mp and widely separated from it. The median area of prementum (Fig. 14 D) has some pseudopores scattered anteriorly. Two real pores and one setal pore of the lateral area are well defined. Pronotum is evenly convex above, not modified, with extremely short, dense pubescence and minute laterally erecting setae. Prosternum is convex along the middle, forming an obsolete carina.

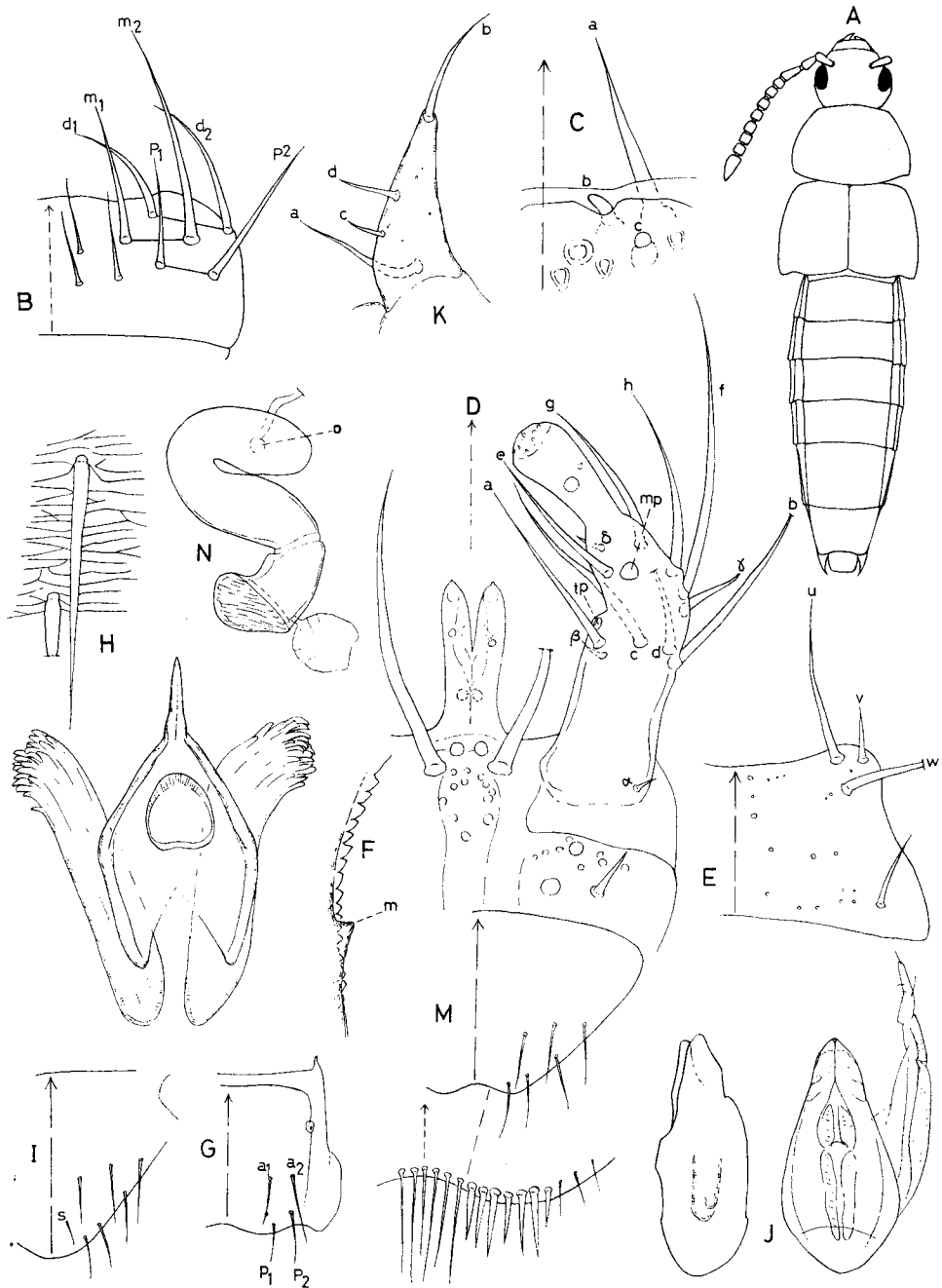


Fig. 14. *Atheta sordida* (MARSHAM, 1802) from Imperial Palace Garden, Kyoto. A, Habitus; B, Labrum; C, Labral margin; D, Labium; E, Mentum; F, Inner margin of mandible; G, Terg. VIII; H, Microsculpture of terg. VIII; I, Stern. VIII; J, Median lobe of aedeagus (dors. and lat. view); K, Distal segment of lateral lobe; L, Copulatory piece; M, Stern. VIII in female; N, Spermatheca.

Mesosternum bears a fine but distinct median carian on its basal half, as a distinct character of this species. Elytron is deeply emarginate postero-externally. Abdomen is more sparsely pubescent than elytron. Tarsal segments as: 9 : 11 : 12 : 24 in fore-; 12 : 15 : 15 : 14 : 21 in mid-; 20 : 20 : 19 : 17 : 28 in hind-legs. Empodium of each tarsus reaches the middle of the claw. Tergite VIII (Fig. 14 G) is shallowly emarginate at the middle of the posterior margin; *a*-2 is far remote from the stigma and close to *a*-1; the microsculpture on the middle area is very fine transverse reticulation as in Fig. 7 H. Sternite VIII (Fig. 14 I) is triangularly produced behind, with 7+7 principal setae.

Aedeagus is 0.60 mm long. In dorsal view (Fig. 7 A) the median lobe is ovate basally and gradually narrowed anteriorly; the dorsal apodeme (*d.ap.*) is dilated behind and broadly emarginate at the middle of the basal margin; the distal apodeme (*dt.ap.*) is widely separating, leaving a short process on each side. In ventral view (Fig. 7 B) the apical lobe is moderately produced distally, with an obtuse apex; the arcuate costa (*ar.c.*) is not converging distally, but rather parallel to each other and suddenly recurved behind surrounding a slightly sclerotized area. Ventral apodeme (*v.ap.*) is almost evanescent at the middle; the median costa (*m.c.*) is well developed. In profile (Fig. 7 C) the area distal to the foramen is little produced and the margin behind the foramen is quite even, and almost straight to the proximal end of the basal capsule. Copulatory piece (Fig. 8 B) is 0.24 mm, broad at the base and suddenly acuminate distally, with a narrowly elongate, pointed apical process; annellus (*an.*) is large for the corpus. Suspensorium (*su.*) is developed to a large plate, with heavily fringed distal end; median apophysis (*m.ap.*) is narrow, dilated proximally; paramedian apophysis (*pm.ap.*) is narrowly elongate. Lateral lobe is shown as in Fig. 6 A; distal segment (Fig. 14 K) is elongate triangularly; setae *a* and *b* are long, infusate, *a* is locse to the basis, and *b* is placed just on the apex, *c* is smaller than *d*, and both of them are at about the middle of the inner margin.

In Japan there is another species of Aleocharinae, very closely allied to *A. sordida* in appearance. By the classic method this species is to be distinguished from *A. sordida* on the basis of narrower body, broader 10th and shorter 11th segment of antennae, a little longer pronotum, and coarser punctures of the abdomen. These distinctive characters are, however, rather subjective ones and not exactly decisive. The description may become objective and accurate when it is described as follows:

***Atheta ursi* sp. n.**

Fig. 15

♂: Brown in ground colour, subopaque by the presence of microsculpture. Head and pronotum are uniformly dark brown, but the former is more infusate than the latter; elytra are clearly paler than the pronotum; abdomen is infusate toward the extremity; antennae are dark in colour; all legs are pale brown. Head is gently deplanate above, with a shallow depression on the vertex; the post-ocular region is rounded and a little dilated behind; the integument bears minute granules and with

alutaceous microsculpture throughout. Eyes are moderate in size, with minute setulae longer than the diameter of each facet. Antenna is rather short, weakly dilated distally, their segmental ratio as: I 27×14 : II 20×11 : III 20×13 : IV 14×14 : X 12×19 : XI 31×20 . Labrum (Fig. 15 B) is shallowly emarginate; seta $p-1$ is posteriorly placed to $p-2$. a -sensilla of labral margin (Fig. 10 C) is short, convergent; b is broad; c is large. Right mandible (Fig. 15 D) has a well developed molar tooth and is clearly serrulate along the inner margin. Segment II of maxillary palpus is distinctly dilated toward the extremity, with an imbricate reticulation on the exterior surface; III is much longer, but not broader than II, and its margins are almost parallel on anterior half; IV is less than a half of III in length, with broad filamentous sensillae not reaching the middle of the segment. Distal comb of lacinia is relatively small; two isolated spines are rather reduced. Galea has no sensory pores on the middle; the distal lobe bears very dense, subequally short cilia throughout, whose apices are minutely hooked. Glossa (Fig. 15 E) is forked from the basal one-fourth into two parallel arms each having 4 minute sensillae in a row. On labial palpus (Fig. 15 F) setula β is fairly remote from tp ; γ is proximal to b ; δ is on the same level of e ; a is much shorter than b , and is close to tp ; b is on the same level of a ; c and d are on the same level; e is near mp and apart from the margin; f is at about the middle of b and h ; the distal segment is not dilated apically and devoid of apical spinula. Median area of the prementum (Fig. 15 F) is broad, clearly incised in front, with a paired basal pores and some smaller pseudopores. On the lateral area 2 real and 1 setal pores are present. Mentum (Fig. 15 G) is strongly transverse and protruding laterally; v -seta is moderately long and on the same level with u ; proximal seta (p) is medially located. Pronotum is evenly convex above, uniformly rounded laterally and with reduced lateral setulae; the surface is covered with short pubescence and roughly sculptured. Elytra are faintly sinuate postero-laterally and a little rougher sculptured than the pronotum. Abdomen has fine punctures, those on the last segment are coarser than on other segments. Pronotal epipleuron is visible in lateral view. Prosternum is convex above and entirely carinate in its full length. Mesosternum is simple, with a short posterior process. Terg. VIII (Fig. 15 H) is broadly truncate posteriorly, with $5+5$ principal setae and $a-2$ is remote from the stigma; microsculpture on the middle (Fig. 15 I) is dense transverse reticulation. Sternite VIII (Fig. 15 J) is broadly rounded posteriorly and with $7+7$ principal setae. Tarsal segments as: 10: 12: 12: 27 in fore-; 12: 15: 15: 15: 27 in mid-; 20: 22: 16: 17: 32 in hind-legs. Empodium is shorter than the half of the claw in fore- and hind legs and subequal to it in mid-legs. Aedeagus is 0.48 mm. In dorsal view (Fig. 15 L) the median lobe is broadly ovate basally, and distinctly narrowed distally; dorsal apodeme ($d.ap.$) is constricted distally and strongly dilated proximally, with emarginate basal margin; distal apodeme ($dt.ap.$) is separating, interrupted at the median part. Ventrally (Fig. 15 M) the apical lobe is with parallel margins; arcuate costae ($ar.c.$) are confluent directly distal to the foramen, and suddenly recurved behind not reaching the proximal end; ventral apodeme ($v.ap.$) is obsoletely present laterally and with some three rounded markings of the wall; median costa ($m.c.$) is also obsolete.

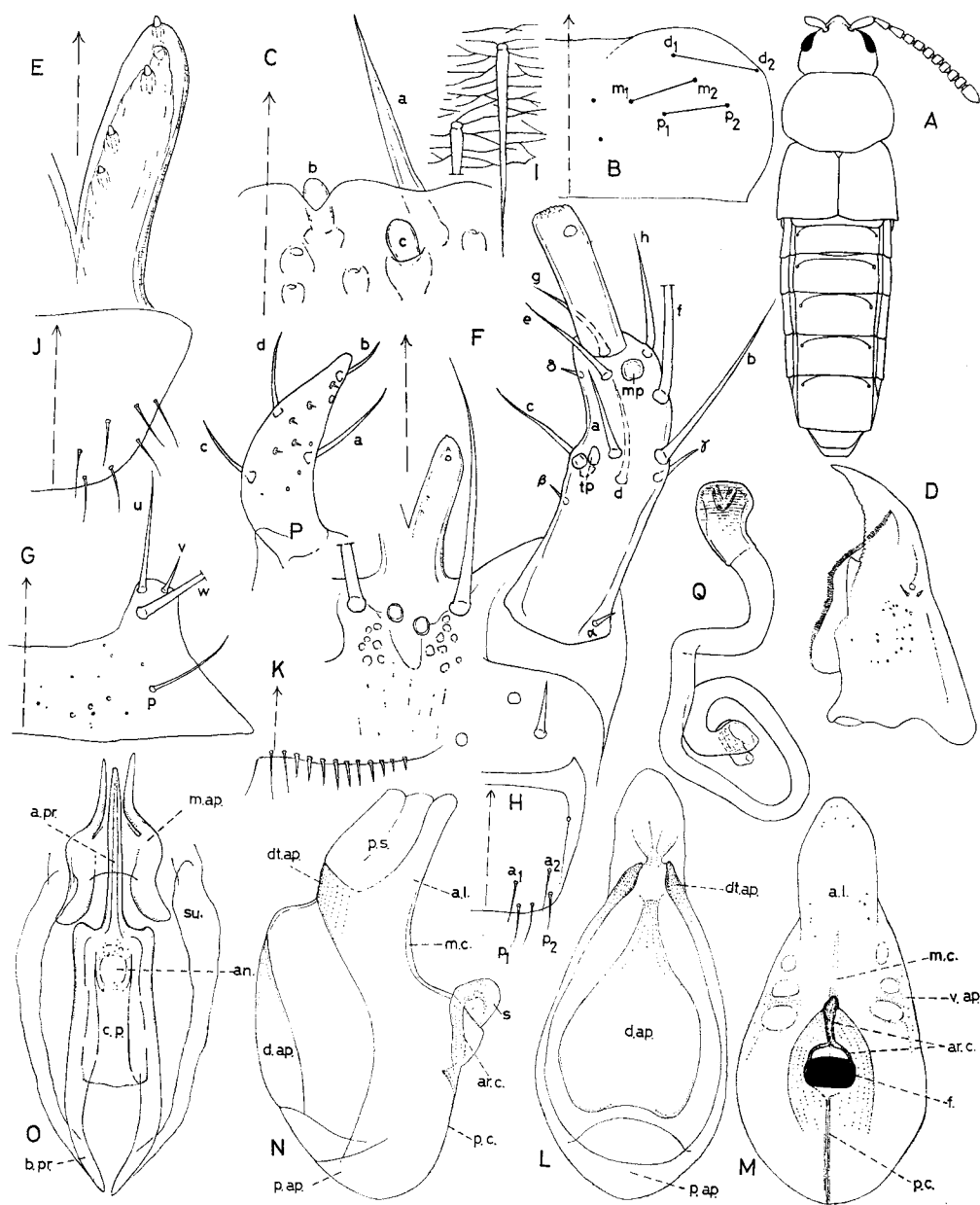


Fig. 15. *Atheta ursi* sp. n. A, Habitus; B, Labral chaetotaxy; C, Labral margin; D, Mandible; E, Sensillae of glossa; F, Labium; G, Mentum; H, Terg. VIII; I, Microsculpture of terg. VIII; J, Stern. VIII; K, Margin of stern. VIII in female; L, L, M, N, Median lobe of aedeagus (dors. ventr. and lat. view); O, Copulatory piece and suspensoria; P, Distal segment of lateral lobe; Q, Spermatheca.

In profile (Fig. 15 N) there may be seen a well chitinized apodeme of the arcuate costa; proximal costa is normally present. Copulatory piece (Fig. 15 O) is 0.27 mm long, narrowly elongate and slightly constricted distally; apical process (*a.pr.*) is long and straight, so that the humeral region is well defined; annellus (*an.*) is rather small. Suspensorium (*su.*) is narrowly elongate, and finely wrinkled in most part; median apophysis (*m.ap.*) is composed of a pair of thin sclerites, each with a pointed, narrow process distally and lobate proximally; paramedian apophysis absent. Lateral lobe (Fig. 6 B) is quite different from that of *A. sordida*; the basal segment is elongate, contiguous with the succeeding second segment and with large, broad marginal flap, the latter is again contiguous with the marginal flap of the second segment. In *A. sordida*, however, the basal segment is distinctly articulated with the second and bears no marginal flap. Distal segment (Fig. 15 P) is short and triangular; *a* is at the middle of the outer margin; *b* is near the apex; *c* is behind the middle, while *d* is before the middle of the inner margin; all of them are subequally short.

Length, 3.70 mm (Head 0.47 mm $\times$ wide 0.60 mm; pronotum 0.63 mm $\times$ 0.80 mm; elytra 0.62 mm $\times$ 0.93 mm).

♀: Head is without vertical deression. Stern. VIII possesses some 6+6 principal setae; the posterior margin is broadly truncate, feebly emarginate at the middle, and provided with up to 10+10 spiniform setae as in fig. 10 K. Spermatheca (Fig. 15 Q) is 0.37 mm; the duct is long, irregularly coiled and shortly contorted at the end; the bursa is short, weakly corrugated and with a stout umbilicus.

Holo-(♂), all-(♀) and paratypes (1♂, 7♀): Nukabira Valley, (2200 m alt.), Hidaka Mts., Hokkaido (20. VII. 1968, anonymous).

The comparison of these two ways of descriptions is very impressive. The ambiguous characters hitherto adopted to discriminate these species are replaced by the distinct qualitative discrepancies in 1) sensory elements of the glossa (Figs. 4A, 15E) whether they are in four uniform pairs (*A. ursi*) or not (*A. sordida*), 2) in the chaetal arrangement of the labial palpus (Figs. 14D, 15F) whether *r* is situated distally (*A. sordida*) or not (*A. ursi*), 3) in the lateral area of the prementum (Figs. 14D, 15F) it has many pseudopores (*A. sordida*) or not (*A. ursi*), and in 4) lateral corner of mentum (Figs. 14E, 15G) whether it is highly protruded (*A. ursi*) or not (*A. sordida*), together with other differences in the structure of the lateral and median lobes as well as in the form of the copulatory piece and suspensoria (Figs. 6 A,B, 7A,B,C, 15 L,M,N,O). Thus it may be taken as granted that the new procedure has its effectiveness in recognizing these two species more objectively.

DISCUSSION AND CONCLUSION

In the foregoing chapter the author has compared two representative species of Aleocharinae, *A. sordida* and *A. ursi*, on the basis of the newly adopted characters, and paid attention to their differences, and in the Table below he has shown how these new

characters vary from one species to another. The distinction of the species by the characters newly adopted may indicate the following:

In case of *A. sordida* and *ursi* the difference is represented by the form and structure of the glossa, labial palpus, prementum and mentum as well as by the genital organ of the male, and the specific solidarity of the two species concerned is quite obvious. In general the validity of the conception of species of the previous authors was assured in many cases, even when they used such a renewed taxonomic standard as shown in Table and it seems that the new procedure probably brings no great confusion by its application to Aleocharinae. In some other cases examined, however, the old species must be split into some independent species. Thus a Japanese specimen which was discriminated as European *A. fungi* was separated as *A. yosii*, and that which was regarded as European *A. aterrima* was distinguished as *A. uncinata*. In either case the differences between the two similar forms appear in many of the newly adopted characters synchronously, not in one of them. This is true of all the other cases of Aleocharinae examined.

Naturally the author has no intention to deny the presence of the "key" character with which to separate each species. Therefore, the discrimination between *A. fungi* and *yosii* is possible by the difference in the setal number of terg. VIII: *A. fungi* has 6+6 principal setae, while *A. yosii* has 4+4 (1970b, p. 37, Fig. 4 K). In case of *A. aterrima* and *A. uncinata* the difference in the shape of the copulatory piece (Fig. 8D) (1971c, p. 81, Fig. 1J) which may be a "key" character with which to separate these similar species. But these "key" must be regarded as the most convenient, but not as only ones for separating these species.

The fact that the specific differences are seen in many characters synchronously facilitates the taxonomic studies of Aleocharinae. In experience the author has not yet encountered any contrary to the principle. When one character of a species significantly differs from those of other species, the other characters are also different, showing in altogether the specificity of the given species.

Sometimes a certain genus or a higher taxon is represented by a single species which has specific characters never seen in the members of other genus or taxon. Such characters may probably be regarded as indicating the specificity of the genus, subtribe, tribe etc., but the author's experience is not yet enough to use them for the rearrangement of the whole Aleocharinae. At present it would be reasonable to summarise them as follows:

- A. Labral margin: concentration of sensory elements in *Brachida*, *Gyrophana* and *Diestota*. Reduction of *a*-sensilla in *Tomoglossa*.
- B. Labial palpus: reduction of the basal segment in *Leptusa*, similarity of the chaetotaxy in Zyrasini (*Santhota*, *Zyras* and *Amaurodera*), reduced size of the twin pores in *Gnypeta*, *Aleochara*, elongate shape of the labial palpus in Myllaenini (*Bryothinusa*, *Halorhadinus*).
- C. Prementum: longitudinal arrangement of the distal setae in *Bolitochara*, *Leptusa*, their unpaired occurrence in *Brachida* and absence in *Diaulota*, *Genoplectes*.

Certain species of Aleocharinae have the secondary sexual characters on terg. VIII, stern. VIII and rarely on elytra, and other parts of the body. In the newly adopted characters treated in this paper, however, when the genital organ is excluded, the sexual difference is not observed at all except on the cited terg. VIII and stern. VIII, so far as the species examined by the author are concerned. The individual variability of the newly adopted characters is also narrow in range as revealed in case of *A. sordida* and other species examined by the author. Local variation is little known in Aleocharinae, as each species has no distinct features and is rather obscure in appearance. A unique but impressive case is found in the halobious examples of Aleocharinae taken from the shore of Seto (Hatakejima), Wakayama Pref., these examples should be identified as *Genoplectes uenoi* K. SAWADA, 1955, although they are larger in size, with larger heads, and more infuscate in colour as compared with the type-specimen from the Tokara Islands with regard to the newly adopted characters. At the same time it has been indicated that this species is considered as the near relative of another halobious genus *Diaulota*; almost all the characters are common to the two genera.

The new taxonomic method in the study of Aleocharinae proposed in this paper has brought some interesting results. The genus *Atheta* includes more than 1,000 species described from the whole world, and these species are so much alike to each other, that their identification has been a matter of great difficulty for all taxonomists. Now that the new procedure proposed in the present study is very useful and effective to classify the genus *Atheta*, we have a firm ground to make a revisional research of this large genus. Moreover, the result is not confined to the distinction of species. Previously the number of the tarsal segments in fore-, mid- and hind-legs (tarsal number) has been regarded as separating the tribe of Aleocharinae, but it has been proved by the new method of investigation that it is a species-specific character as far as the halobious genus *Diaulota* is concerned (1971d, p. 97); the tarsal number is 4,4,5 in *D. densissima*, 4,4,4 in *D. aokii*, and 3,3,4 in *D. pacifica*. According to the former method of taxonomy *D. densissima* must be placed in Myllaenini, *D. aokii* in Oligotini and *D. pacifica* in a group hitherto unknown, but as they are similar to each other in other main characters, they have to be placed in one genus *Diaulota* which is belonging to the tribe Hygronomini.

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Table. Diversity of newly adopted characters in each species of Aleocharinae

Genera and species		Labrum		Cilia of distal lobe of galea	*Distal comb of lacinia	Filament. sens. of maxillary palpus	Prementum		Labial palpus			v-setula of mentum	Microsculpture of terg. VIII	Setae of terg. VIII
		Principal setae	Margin				Distal setae	Median area	tp	Sensillae	Setae			
<i>Myllaena</i>	sp.**	distal row short, oblique, proximal setae indistinct	a-sens. scaly, b-, broad	galea styliform, branched at apex	c	reduced	reduced, close together	smooth	longitudinal	γ -sens. scaly β -, absent	e-seta absent, b, f, g, h, scaly	normally long	imbricate	4+4
<i>Bryothinusa</i>	<i>minuta</i>	each row subequally short	a-sens. fusiform	galea styliform, branched at apex	c	normally long	contiguous	smooth	longitudinal	normally arranged	a-seta absent	reduced	reticular	4+4
	<i>tsutsuii</i>	each row subequally short	a-sens. spiniform	galea styliform, branched at apex	c	normally long	contiguous	smooth	longitudinal	normally arranged	b-, f-setae placed basally	reduced	reticular	4+4
	<i>nakanei</i>	medial row shortest	a-sens. spiniform	galea styliform, branched at apex	c	normally long	contiguous, longitudinal	smooth	longitudinal	normally arranged	b-, f-setae placed basally	reduced	reticular	4+4
	<i>algarum</i>	proximal row shortest	a-sens. dilated	galea styliform, branched at apex	c	reduced	close together	smooth	longitudinal	normally arranged	b-, f-setae placed basally	reduced	reticular	4+4
<i>Halorhadinus</i>	<i>aequalis</i>	medial row placed apically	a-sens. setiform, long	galea spiniform, densely ciliate	c	developed	contiguous	smooth	contiguous	normally arranged	b-, f-setae placed	reduced	reticular	5+5
	<i>inaequalis</i>	medial row placed apically	a-sens. setiform, long	galea spiniform, densely ciliate apically	c	developed	contiguous	smooth	contiguous	normally arranged	basally b-, f-setae placed basally	absent	imbricate	4+4
<i>Brachida</i>	<i>brevipennis</i>	m-2 placed proximally	all sens. concentrated	uniformly fringed	many spines	reduced	unpaired	smooth	contiguous, developed	β -sens. absent	a-seta reduced, h, absent	normally long	obliterate	5+5
	<i>clara***</i>	m-2 anterior, remote from distal row	all sens. concentrated	densely ciliate	many spines	normally long	unpaired	smooth	contiguous, developed	β -sens. absent	h-seta absent	long	obliterate	5+5
<i>Gyrophæna</i>	<i>nana**</i>	three rows separating, proximal row longest	all sens. concentrated	densely ciliate	many spines	normally long	unpaired	smooth	contiguous, developed	β -sens. absent, γ , distal to f	c-, h-setae absent	long	imbricate	4+4
	<i>hanedai</i>	proximal row longest	all sens. concentrated	uniformly fringed	many spines	normally long	unpaired	smooth	contiguous	β -sens. absent	a-seta reduced, c, h, absent	long	imbricate	4+4
<i>Diestota</i>	<i>luzonica</i>	distal row oblique	all sens. concentrated	uniformly fringed	a	reduced	contiguous	smooth	separating	γ -sens. absent	a-seta reduced, c-, absent	reduced	obliterate	4+4
<i>Eccoptygenia</i>	<i>rufa</i>	p-2 close to distal row	a-sens. falciform	uniformly fringed	b	normally long	close together	porous	contiguous, developed	β -sens. absent	a-seta absent	reduced	absent	4+4
<i>Diaplotsa</i>	<i>pacifica</i>	m-2 close to proximal row, lateral sens. normally long	a-sens. short, b-, c-, separating	uniformly fringed	b	normally long	absent	porous	contiguous	β -sens. absent δ -, developed	b-seta absent, g-, reduced	absent	reticular	2+2
	<i>densissima</i>	m-2 close to proximal row, lateral sens. normally long	a-sens. short, b-, c-, close together	uniformly fringed	b	reduced	absent	porous	contiguous	β -sens. absent, δ -, developed	a-seta absent, g-, reduced	absent	imbricate	4+4
	<i>aokii</i>	m-2 close to proximal row, lateral sens. developed	a-sens. long, b-, c-, separating	uniformly fringed	b	normally long	absent	porous	contiguous	β -sens. absent, δ -, developed	a-seta absent, g-, reduced	absent	reticular	3+3
<i>Genoplectes</i>	<i>uenoi</i>	m-2 remote from distal row, lateral sens. normally long	a-sens. short, b-, c-, separating	uniformly fringed	b	normally long	absent	smooth	reduced	β -sens. absent, δ -, developed	b-, c-, d-setae absent	absent	obliterate	4+4
<i>Leptusa</i>	<i>kitazawai</i>	proximal row long	a-sens. straight	uniformly fringed	b	reduced	longitudinal	smooth	contiguous, developed	developed	normally arranged	reduced	obliterate	3+3
	<i>deplanata</i>	proximal row short	a-sens. bent	uniformly fringed	b	reduced	longitudinal	porous	contiguous, developed	developed	normally arranged	reduced	reticular	4+4
<i>Bolitochara</i>	<i>lobata</i>	proximal, medial rows subequally short	a-sens. setiform, b-, obtuse	uniformly fringed	b	reduced	longitudinal	porous	contiguous, developed	normally arranged	h-seta reduced	normally long	imbricate	4+4
	<i>varipes***</i>	proximal row much longer than medial row, m-2 on distal row	a-sens. broad basally, b-, c-, conical	uniformly fringed	b	normally long	contiguous, longitudinal	smooth	contiguous	δ -sens. reduced	normally arranged	reduced	reticular	5+5

(Continued)

Genera and species		Labrum		Cilia of distal lobe of galea	*Distal comb of lacinia	Filament. sens. of maxillary palpus	Prementum		Labial palpus			v-setula of mentum	Microsculpture of terg. VIII	Setae of terg. VIII
		Principal setae	Margin				Distal setae	Median area	tp	Sensillae	Setae			
<i>Myrmecopora</i> (s. str.)	<i>algarum</i>	m-2 is out of distal row	c-sens. pointed	uniformly fringed	a	reduced	close together	porous	contiguous	normally arranged	normally arranged	normally long	reticular	4+4
<i>Gnypeta</i>	<i>aokii</i>	proximal row not parallel to medial row, m-2 remote from distal row	b-sens. reduced	uniformly fringed	a	normally long	normally separating	smooth	contiguous, reduced	δ -, γ -sens. reduced	d-seta reduced	reduced	reticular	4+4
	sp.**	proximal row sub-parallel to medial row, m-2 on distal row	b-sens. reduced	uniformly fringed	a	reduced	close together	smooth	contiguous, reduced	γ -sens. posterior to b	a-seta placed posteriorly	reduced	reticular	4+4
<i>Schistoglossa</i>	<i>yosii</i> ana	three rows separating together	a-sens. reduced	uniformly fringed	a	developed	widely separating	porous	contiguous	normally arranged	all setae thick	reduced	reticular	4+4
<i>Tomoglossa</i>	<i>punctifoveata</i>	distal row shortest	a-sens. absent	uniformly fringed	b	developed	widely separating	porous	contiguous	β -, δ -sens. reduced	d-, h-setae reduced	reduced	imbricate	5+5
	<i>cuspidata</i>	distal row shortest	a-sens. absent	uniformly fringed	b	normally long	widely separating	porous	contiguous	normally arranged	d-, h-setae reduced	reduced	reticular	5+5
<i>Atheta</i>	<i>uncinata</i>	distal row long, oblique	b-sens. conical	uniformly fringed	a	reduced	normally separating	porous	contiguous	all sens. developed	normally arranged	normally long	imbricate	4+4
	<i>yosii</i>	distal row short, less oblique	a-sens. short, b-, reduced	mingled	b	normally long	normally separating	porous	contiguous	β -, δ -sens. developed	normally arranged	normally long	transverse	4+4
	<i>annuliventris</i>	m-2 on distal row, proximal row short	b-sens. long	uniformly fringed	a	reduced	close together	smooth	contiguous	normally arranged	normally arranged	normally long	absent	4+4
	<i>sordida</i>	distal and medial rows subequally short, m-2 remote from distal row	a-sens. short, c-, strongly reduced	uniformly fringed	a	normally long	normally separating	porous	contiguous	β -, δ -sens. developed	normally arranged	developed	transverse	4+4
	<i>vivida</i>	m-2 close to distal row	b-sens. long	mingled	a	normally long	close together	smooth	contiguous, reduced	β -, δ -sens. reduced	normally arranged	developed	obliterate	4+4
	<i>fungi***</i>	three rows subequally short, m-2 on distal row	b-, c-sens. reduced	uniformly fringed	a	normally long	close together	smooth	contiguous	δ -sens. developed	normally arranged	normally long	imbricate	6+6
	<i>aterrima***</i>	three rows subequally short, m-2 remote from distal row	b-sens. conical	mingled	a	developed	normally separating	porous	contiguous	δ -sens. developed	a-seta reduced	normally long	imbricate	4+4
<i>(Oreostiba)</i>	<i>garuda</i>	m-2 on distal row, proximal row long	c-sens. developed	uniformly fringed	a	reduced	normally separating	porous	contiguous	normally arranged	normally arranged	developed	reticular	4+4
<i>(Plataraea)</i>	<i>punctifrons</i>	three rows equal in length	b-sens. fairly slender	uniformly fringed	a	normally long	normally separating	porous	contiguous	β -sens. developed	normally arranged	developed	reticular	6+6
<i>(Chaetida)</i>	<i>multipunctata</i>	m-2 on distal row, proximal row short	c-sens. reduced	uniformly fringed	a	reduced	normally separating	porous	contiguous	δ -sens. reduced	a-seta reduced	normally long	imbricate	5+5
<i>(Hygroecia)</i>	<i>spinula</i>	distal row longer than others	a-sens. converging	mingled	a	normally long	close together	smooth	contiguous	normally arranged	normally arranged	normally long	reticular	4+4
<i>(Philhygra)</i>	<i>ushio</i>	m-2 out of distal row	b-sens. reniform,	uniformly fringed	a	developed	normally separating	porous	contiguous	β -, δ -sens. reduced	normally arranged	normally long	reticular	5+5
	<i>debilis</i>	medial row much longer than distal row, m-2 on distal row	b-sens. reniform, c-, reduced	uniformly fringed	a	developed	close together	porous	contiguous	β -sens. reduced	normally arranged	reduced	imbricate	4+4
<i>(Metaxya)</i>	<i>prolata</i>	medial row long, m-2 remote from distal row	a-sens. short, stout	uniformly fringed	a	normally long	close together	smooth	contiguous, reduced	normally arranged	normally arranged	normally long	imbricate	4+4
<i>(Dinaraea)</i>	<i>tokiokai</i>	medial row long, m-2 on distal row	a-sens. peg-like	uniformly fringed	a	normally long	normally separating	porous	contiguous	δ -sens. reduced	normally arranged	normally long	imbricate	4+4
<i>(Anopleta)</i>	<i>tortuosa</i>	medial row long, close to distal row	a-sens. straight, diverging	uniformly fringed	b	normally long	contiguous	porous	contiguous, developed	δ -sens. developed	b-seta absent	normally long	imbricate	4+4

(Continued)

Genera and species		Labrum		Cilia of distal lobe of galea	*Distal comb of lacinia	Filament. sens. of maxillary palpus	Prementum		Labial palpus			v-setula of mentum	Microsculpture of terg. VIII	Setae of terg. VIII
		Principal setae	Margin				Distal setae	Median area	tp	Sensillae	Setae			
(<i>Ousipalia</i>)	<i>nakanei</i>	three rows subequally short	c-sens. spatulate	mingled	a	reduced	close together	smooth	contiguous	β -sens. developed	normally arranged	developed	reticular	4+4
(Microdota)	<i>bogorensis</i>	three rows long, m-2 close to distal row	a-sens. reduced	mingled	a	developed	close together	smooth	contiguous	normally arranged	normally arranged	developed	imbricate	4+4
	<i>unidentata</i>	three rows subequally short	b-sens. narrow	mingled	a	normally long	close together	smooth	contiguous	δ -sens. developed	normally arranged	normally long	imbricate	4+4
	<i>oviformis</i>	distal row much longer than medial row	b-, c-sens. reduced	mingled	a	normally long	close together	smooth	contiguous	β -, δ -sens. reduced	normally arranged	normally long	imbricate	4+4
	<i>multispina</i>	medial row short, many second. setae	b-sens. peg-like	uniformly fringed	a	normally long	normally separating	porous	contiguous	normally arranged	normally arranged	developed	reticular	4+4
	<i>constricta</i>	three rows subequally long	b-sens. elongate	uniformly fringed	b	normally long	widely separating	porous	contiguous	β -, δ -sens. reduced	normally arranged	reduced	imbricate	4+4
(Dimetrota)	<i>atramentaria</i>	medial, distal rows long, m-2 remote from distal row	c-sens. reduced	uniformly fringed	a	developed	normally separating	porous	contiguous	normally arranged	normally arranged	normally long	transverse	4+4
	<i>tenuiducta</i>	m-2 anterior in position	a-sens. converging	uniformly fringed	a	normally long	normally separating	porous	contiguous	δ -sens. reduced	normally arranged	developed	transverse	4+4
	<i>separata</i>	three rows long, sub-parallel to each other	b-sens. obtuse	uniformly fringed	a	reduced	normally separating	porous	contiguous	β -sens. reduced	d-seta reduced	developed	transverse	4+4
	<i>longisetosa</i>	distal row long, with long secondary setae	a-sens. converging, b-, reduced	mingled	b	normally long	normally separating	porous	contiguous	normally arranged	normally arranged	developed	transverse	4+4
<i>Santhota</i>	<i>sparsa</i>	medial row reduced, m-2 close to d-1	margin fairly emarginate	uniformly fringed	b	normally long	widely separating	porous	separating	normally arranged	c-, d-, e-, h-setae reduced	reduced	absent	6+6
<i>Zyras</i>	<i>iridescens</i>	proximal row oblique to medial row, as long as distal row	b-sens. subdivided	densely ciliate	b	normally long	widely separating	porous	separating	δ -sens. reduced	d-, e-setae reduced	doubled	obliterate	many
	<i>haworthi</i> ***	proximal row subparallel to medial row, much longer than distal row	b-sens. reduced, pointed	densely ciliate	b	reduced	widely separating	porous	separating	δ -sens. lateral to e	b-seta much shorter than a	reduced	absent	many
<i>Amaurodera</i>	<i>philippinensis</i>	medial row short, m-2 close to d-2	a-sens. reduced	uniformly fringed	b	reduced	widely separating	porous	separating	β -, δ -sens. absent	c-, d-, e-, g-setae reduced	many	obliterate	7+7
<i>Homoeusa</i>	<i>prolongata</i>	medial, proximal rows close to each other	b-sens. long, spiniform	uniformly fringed	b	normally long	widely separating	porous	contiguous	β -, δ -sens. absent	a-, d-, e-, g-setae reduced	reduced	reticular	many
(s. str.)	<i>obtusa</i>	m-2 on distal row	a-sens. broad, b-, elongate	uniformly fringed	b	reduced	normally separating	porous	contiguous	β -sens. developed	all setae reduced	normally long	imbricate	many
(Podoxya)	<i>kuramotoi</i>	m-2 on distal row	a-sens. acicular, b-, short	uniformly fringed	b	reduced	normally separating	porous	contiguous	β -, δ -sens. developed	all setae reduced	normally long	obliterate	8+8
<i>Oxyptoda</i> (Demosoma)	<i>imadatei</i>	distal row missing	abnormal	uniformly fringed	b	normally long	contiguous	porous	contiguous	β -, δ -sens. developed	c-, d-setae reduced	normally long	imbricate	6+6
(Baeoglana)	<i>producta</i>	m-2 remote from distal row	a-sens. setiform	uniformly fringed	b	normally long	contiguous	porous	contiguous, reduced	β -, δ -sens. developed	all setae reduced	reduced	imbricate	6+6
(Emplenota)	<i>fucicola</i>	distal row reduced, m-2 close to it	margin emarginate, b-sens. developed	uniformly fringed	b	developed	widely separating	porous	contiguous, reduced	δ -sens. developed	all setae reduced	reduced	obliterate	many
<i>Aleochara</i> (Triochara)	<i>trisulcata</i>	proximal row short, m-2 close to d-1	margin faintly emarginate	uniformly fringed	b	developed	normally separating	porous	contiguous, reduced	β -, δ -sens. developed	all setae reduced	normally long	imbricate	many
<i>Ocyota</i>	sp.**	three rows sub-equal in length, m-2 on distal row	a-sens. not diverging, b-, c-, reduced	uniformly fringed	b	developed	close together	porous	separating	γ -sens. largest, β -, far remote from tp	e-seta reduced, a-, b-, anterior in position	developed	transverse	6+6

* Type of the distal comb of lacinia: **a**; distal comb composed of some 6 contiguous spines and 2 isolated spines. **b**; distal comb with a row of contiguous spines only. **c**; distal comb is substituted by irregular or obliterate dentition without forming the isolated spines.

** Species not cited in the present study.

*** Species cited in the present study.