

Female Reproductive Organs of Cerambycid Beetles from Japan and the Neighbouring Areas

V. General Consideration¹⁾

Akiko SAITO

Natural History Museum and Institute, Chiba,
955-2 Aoba-chô, Chûô-ku, Chiba-shi, 260 Japan

Abstract Phylogenetic aspect of the cerambycoid groups excluding Lamiinae is discussed on the basis of their female genitalia. Out-group comparison method is applied for determining relative polarities of character states. It is suggested that the Lepturinae plus Cerambycinae can be discriminated into four groups, one of which comprising the O브리ini and Stenopterini is considered most derivative of the whole Cerambycidae. Some comments are made on the Lamiinae, whose female genitalia are rather uniform in spite of remarkable diversity of external features.

In the last chapter of this series of papers, I am going to take up the phylogenetic aspect of the cerambycoid groups excluding Lamiinae as viewed from the results of my studies on their female genitalia. These groups are herewith regarded as being monophyletic in accordance with current taxonomic treatment based primarily upon external morphology. My study has clarified that with the exception of the vesperids, they have in common an apomorphic character state of the proctiger, which is either short or obliterated. I have excluded the Lamiinae from this study, because the subfamily is, though containing a large number of diverse species, a well defined group, in which basic plan of female genitalia does not show much variation. This does not mean that they are monotonous and useless for classification; the spermathecae and their glands, in particular, exhibit a great diversity, which is unrivaled by those of any other groups of the family. I will show it briefly in a later part of this chapter.

It must be noted here that I have no intention to set up a new phylogeny of the Cerambycidae. To do it is beyond the scope of this paper, since for doing it, all the other features, both imaginal and larval, than the female genitalia should be carefully scrutinized and taken into account, and since many foreign, especially tropical, species should be examined for comparative study. The Japanese Islands lie at the northern periphery of distribution of many groups of the Cerambycidae, and lack many critical tribes and genera that may be important for constructing phylogeny. In this paper, I am going to show what can be said or suggested from the comparative morphology of female genitalia, which has not been carefully studied before from taxonomic view-

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point. Needless to say, I have taken external characteristics into account here and there, but they are auxiliary, and my discussion is primarily based on the female genitalia alone.

It is necessary to note that ovaries, oviduct and accessory glands are not examined in this study. They form important parts of female reproductive organs and may give some reliable information. This fault mainly arose from technical reasons. For examining these organs, it is necessary to secure fresh materials or alcoholic specimens, which are not easily available except for commoner species. Accomplishing the object of the present study requires examination of many rare species, at least a representative species from each genus currently recognized, which can be obtained or borrowed only as dried specimens generally useless for a detailed study of the organs in question.

It is also necessary to make some comments on possible relation between the structure of the 9th abdominal segment and ovipositing behaviour. It has been known that most lamiine species make preparation for oviposition by chewing into barks of trees or grasses. Such a behaviour may affect modification of abdominal segments, though nothing has been known about relationship between the ovipositing behaviour and the morphology of the 9th abdominal segment.

Such an ovipositing preparation has not been known in all the cerambycoid groups other than the Lamiinae. Though chewing before oviposition was reported on *Megasemum quadricostulatum* (Spondylinae) and *Massicus raddei* (Cerambycinae), KOJIMA (1960) threw strong doubt on these observations and no similar report has been made since then. Apart from preparation for oviposition, CHEREPANOV (1979, p. 24) recorded a peculiar behaviour observed in the Oabriini and Purpuricenini that the haired emargination of the 4th abdominal sternite (in the former) or the long hairs on the 8th sternite (in the latter) were used for concealing laid eggs with fine detritus of tree barks. In these tribes, the ovipositor has undergone considerable modification as described before, but it is difficult to determine whether this modification is a result of behavioral adaptation or the strange behaviour is achieved as a result of shortening of the ovipositor. At present, I am inclined to consider that the shortening of the ovipositor took place in the first place, since modification of hairs necessary for egg-concealing habit seems to be completed much easier than the remarkable modification of ovipositor.

Ovipositing behaviour of cerambycoid beetles other than lamiines is fundamentally similar to one another in that the eggs are laid in fissures of tree barks or narrow spaces beneath loose barks or in the soil by inserting the ovipositor. This similarity seems to deny the possibility that modification of the 9th abdominal segment as seen in cerambycids has always proceeded in accordance with behavioral changes. For instance, two species of *Purpuricen*, *P. temmincki* and *P. spectabilis*, have very similar 9th abdominal segment in the female, and yet, the former lays its eggs on thick stout bamboos, whereas the latter does so on aceraceous or lauraceous trees. These plants are utterly different from each other in the texture, hardness and other details.

In view of these evidences, I evaluated various characters of the female genitalia

on the premise that they have little modified as a result of adaptation to ovipositing behaviour, at least in most groups taken up in the present study.

Terminology

The terminology adopted in this paper was explained in the Material and Method section of my 1989 paper (SAITO, 1989 a, pp. 68–69, figs. 1–2). I have mainly followed HUTCHESON (1980) in naming various parts of female genitalia, since his naming seems concise and clear-cut, and is convenient for description. It is, however, necessary to correlate his terms with those of fundamental morphology, as will be given below.

This paper	Fundamental morphology
Paraproct	Ninth sternite
Paraproct baculum	Baculum of 9th sternite
Valvifer	Basal part of the appendage of 9th sternite
Coxite	Main part of the appendage of 9th sternite
Coxite lobe	Divided apical part of the appendage of 9th sternite
Stylus	Articulated apical appendage of 9th sternite
Dorsum of paraproct to coxite	Ninth tergite
Dorsal baculum	Baculum of 9th tergite
Proctiger	Tenth tergite
Proctiger baculum	Baculum of 10th tergite

Analysis of Characters

To determine relative polarities of the character states, out-group comparison method introduced by WATROUS and WHEELER (1981) was adopted. This was, however, not very successful, since no coleopteran group directly related to the Chrysomeloidea has been found. I therefore sought the outgroup in the Clavicornia and Heteromera, randomly picking up 10 species (2 Cucujidae, 1 Erotylidae, 4 Tenebrionidae, 1 Oedemeridae and 2 Pyrochroidae) and examining their female genitalia. They are much diversified, but invariably have very long proctiger. It is therefore probable that the shortened proctiger in the Cerambycidae and its allies except Vesperidae represents an autapomorphy.

Since the Chrysomelidae is an undubitable sister-group of the Cerambycidae, representative species of its subfamilies were examined for their female genitalia. They were roughly discriminated into two groups. One of them, consisting of Orsodacninae, Zeugophorinae and Megalopodinae, has a long paraproct which is tubular and wholly membraneous, and much reduced styli. Besides, the proctiger is long in *Orsodacne*, occupying more than half the length of ovipositor. In all the other subfamilies including Donaciinae and Synetinae, the paraproct is either much reduced or obliterated, and the coxite is heavily sclerotized and usually devoid of styli. This must be an

Table 1. Summary of polarities of the characters adopted. The letter P means plesiomorphic, and A apomorphic; transformation series of apomorphic states are indicated by numerals.

1. Eighth segment (Fig. 225)	1, sclerotized and separated into tergite and sternite(P); 2, rather membranous, tergite fused with sternite(A)
2. Paraproct (Fig. 226)	1, long(P); 2, moderate(A1); 3, short(A2); 4, very short(A3); 5, extremely short without baculum(A4)
3. Components of paraproct	1, distinct(P); 2, indistinct(A)
4. Paraproct baculum (Fig. 226)	1, one pair (P); 2, two pairs(A)
5. Stylus (Fig. 227)	1, articulated to the apex of each coxite lobe (P); 2, translocated to the lateral or dorsal face of coxite lobe, or reduced (A)
6. Ninth tergite (Fig. 228)	1, sclerotized (P); 2, membranous with baculi (dorsal baculi present)(A1); 3, membranous, short and without baculum(A2)
7. Proctiger (Fig. 229)	1, long(P); 2, moderate(A1); 3, short (A2); 4, absent(A3)
8. Proctiger baculum (Fig. 230)	1, one pair(P); 2, two pairs(A)
9. Vagina (Fig. 231)	1, membranous(P); 2, partially sclerotized(A)
10. Vaginal plates (Fig. 232)	1, absent(P); 2, membranous(A1); 3, partially sclerotized(A2); 4, almost wholly sclerotized(A3)
11. Bursa copulatrix (Fig. 233)	1, membranous (P); 2, partially sclerotized, or 2', with an impression at the basal part(A)
12. Spermatheca (Fig. 234)	1, saccate(P); 2, sclerotized and straight capsular(A1); 3, sclerotized and weakly bent capsular(A2); 4, sclerotized and strongly bent capsular(A3)
13. Spermathecal duct (Fig. 235)	1, short (P); 2, long and straight(A1); 3, long and sinuate(A2); 4, long, thin and coiled(A3)
14. Sclerotization of spermathecal duct (Fig. 235)	1, not sclerotized (P); 2, heavily sclerotized and forming a part of the spermatheca (A)

apomorphic state as is seen in certain cerambycine groups. At any rate, the two major groups of the Chrysomelidae do not seem to be closely related, and may represent two different branches in the phylogeny.

The Bruchidae, sometimes included in the Chrysomelidae, has peculiar female genitalia, so far as concerned with the species examined, *Bruchidius dorsalis*. The proctiger is long and bears a pair of very long baculi extending anteriad and arcuately diverging; the stylus is extremely small and articulated to the lateral face of the coxite lobe. If these peculiarities are characteristic of the family, the Bruchidae cannot be regarded as a sister-group of the Chrysomelidae or Cerambycidae.

Thus, we have to determine polarities of the character states mostly in the Cerambycidae itself. In the following lines, the characters adopted in the descriptions will be scrutinized one by one (Table 1). A character state matrix based on the characters whose polarities were determined by these scrutinies is as shown in Table 2.

1) Eighth abdominal segment (Fig. 225). In most species of the Cerambycidae, the 8th abdominal segment is only lightly sclerotized and becomes membranous, and the tergite is fused with the sternite. This is considered apomorphic. Plesiomorphic character state is the heavy sclerotization of the segment, which remains distinctly separated into the tergite and sternite. This condition is sporadically found in *Pa-*

Table 2. Character state matrix. Question marks indicate unconfirmed data.
Scientific names with asterisks were recently changed, and are different
from those given in the descriptive parts of this paper. Arrangement
of tribes follows that adopted in the Conclusive Remarks.

Species / No. of character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Vesperidae														
Philini														
<i>Philus pallelescens</i>	2	1	2	1	1	2	1	2	1	1	1	1	1	1
<i>Mantitheus pekinensis</i>	2	1	2	1	1	2	1	2	1	1	1	1	1	1
Vesperini														
<i>Vesperus strepens</i>	2	1	2	1	1	2	1	2	1	1	1	1	1	1
Disteniidae														
Disteniini														
<i>Distenia gracilis</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	2
<i>Tengius ohkuboi</i>	2	3	2	1	1	2	2	1	1	2	1	4	1	2
Cerambycidae														
Parandrinae														
<i>Parandra formosana</i>	1	1	1	1	2	2	4	1	1	2	1	4	1	1
Prioninae														
Prionini														
<i>Prionus insularis</i>	2	2	2	1	2	1	2	1	1	2	1	4	2	1
<i>Megopsis formosana</i>	2	2	2	1	2	2	2	1	1	2	1	3	1	1
<i>Aegosoma sinicum</i>	1	1	2	1	2	3	2	1	1	2	1	3	1	1
Apatophysinae														
<i>Apatophysis barbara</i>	2	1	2	1	2	2	2	1	1	2	1	3	1	1
Spondyliinae														
Spondyliini														
<i>Spondylis buprestoides</i>	2	2	2	1	2	2	2	1	1	2	1	4	3	1
Asemmini														
<i>Tetropium castaneum</i>	2	2	2	1	2	2	2	1	1	2	1	4	1	1
<i>Nothorhina punctata</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	1
<i>Asemum amurense</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Arhopalus coreanus</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Megasemum quadricostulatum</i>	2	1	2	1	1	2	2	1	1	2	1	4	3	1
<i>Cephalallus unicolor</i>	2	1	2	1	1	2	2	1	1	2	1	4	3	1
Atimiini														
<i>Atimia okayamensis</i>	2	3	2	1	1	2	2	1	1	2	1	4	3	1
Lepturinae														
Rhagiini														
<i>Encyclops olivacea</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>Rhagium japonicum</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Enoploides bicolor</i>	2	3	2	1	1	2	2	1	1	2	1	4	1	1
<i>Sachalinobia koltzei*</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Stenocorus coeruleipennis</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	1
<i>Toxotinus reini</i>	2	5	2	1	2	3	2	1	1	2	1	3	2	1
<i>Pachyta lamed</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Brachyta punctata</i>	2	3	2	1	2	2	2	1	1	2	1	3	1	1
<i>Evodinus borealis</i>	2	3	2	1	2	2	2	1	1	2	1	4	1	1
<i>Gaurotes (Paragaurotes) doris</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>G. (Carillia) atripennis</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>Lemura nishimurai</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>Dinoptera minuta</i>	2	3	2	1	1	2	2	1	1	3	1	4	2	1
<i>Acmaeops septentrionis</i>	2	3	2	1	1	2	2	1	1	3	1	4	1	1
<i>Macropidonia ruficollis</i>	2	3	2	1	1	2	2	1	1	2	1	4	1	1
<i>Pseudosieversia japonica*</i>	2	3	2	1	1	2	2	1	1	2	1	3	1	1
<i>Pidonia (Pidonia) obscurior</i>	2	3	2	1	2	2	2	1	1	2	1	4	2	1
<i>P. (Cryptopidonia) insuturata</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>P. (C.) oyamae</i>	2	3	2	1	1	2	2	1	1	2	1	4	1	1
<i>P. (Mumon) aegrota</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>P. (Omphalodera) testacea</i>	2	3	2	1	1	2	2	1	1	2	1	4	3	1
Lepturini														
<i>Caraphia lepturoides</i>	2	3	2	1	1	2	2	1	1	2	1	4	2	1
<i>Alosterna chalybeella*</i>	2	2	2	1	2	2	2	1	1	4	1	4	1	1
<i>A. tabacicolor</i>	2	2	2	1	2	2	2	1	1	4	1	4	1	1

Table 2 (Continued).

Species / No. of character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Pseudalosterna misella</i>	2	2	2	1	2	2	2	1	1	4	1	4	1	1
<i>Ohbayashia nigromarginata</i>	2	2	2	1	1	2	2	1	1	2	1	3	1	1
<i>Pyrrhona laeticolor</i>	2	2	2	1	1	2	2	1	1	2	1	3	2	1
<i>Formosopyrrhona satoi</i>	2	1	2	1	1	2	2	1	1	2	1	2	3	1
<i>Corennys sericata</i>	2	2	2	1	2	2	2	1	1	2	1	4	3	1
<i>Pachypidonia bodemeyeri</i>	2	2	2	1	2	2	2	1	1	2	1	4	1	1
<i>Nivellia sanguinosa</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	1
<i>Judolia japonica</i>	2	2	2	1	1	2	2	1	1	3	1	4	1	1
<i>Pachytodes cometes*</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Judolidia bungi</i>	2	2	2	1	1	2	2	1	2	2	1	4	1	1
<i>Kanekoa azumensis</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Anoploderomorpha monticola</i>	2	2	2	1	1	2	2	1	2	2	1	4	1	1
<i>Brachyleptura pyrrha</i>	2	1	2	1	1	2	2	1	1	2	1	4	2	1
<i>Anastrangalia scotodes</i>	2	1	2	1	1	2	2	1	2	2	1	4	1	1
<i>Corymbia succedanea</i>	2	1	2	1	1	2	2	1	2	2	1	3	1	1
<i>Konoa granulata</i>	2	1	2	1	2	2	2	1	1	2	1	4	3	1
<i>Leptura mimica</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	1
<i>L. ochraceofasciata</i>	2	2	2	1	1	2	2	1	2	2	1	4	4	1
<i>Nakanea vicaria*</i>	2	1	2	1	1	2	2	1	1	2	1	4	3	1
<i>Stictoleptura variicornis*</i>	2	1	2	1	1	2	2	1	1	2	1	4	3	1
<i>Pedostrangalia femoralis*</i>	2	2	2	1	1	2	2	1	1	3	1	4	3	1
<i>Macroleptura regalis*</i>	2	1	2	1	1	2	2	1	1	2	1	4	2	1
<i>Oedechnema gebleri*</i>	2	1	2	1	1	2	2	1	1	2	1	4	3	1
<i>Eustrangalia distenioides*</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Japanostrangalia dentatipennis</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Strangalomorpha tenuis</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Parastrangalis lesnei</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>P. shikokensis*</i>	2	2	2	1	1	2	2	1	2	2	1	4	3	1
<i>P. nymphula*</i>	2	2	2	1	1	2	2	1	1	2	1	4	2	1
<i>Idiostrangalia contracta*</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Strangalia attenuata</i>	2	2	2	1	1	2	2	1	1	2	1	4	3	1
<i>Mimostrangalia kurosonensis</i>	2	1	2	1	1	2	2	1	1	3	1	4	3	1
Necydalini														1
<i>Necydalis harmandi</i>	2	1	2	1	1	2	2	1	1	2	1	3	1	1
Cerambycinae														
Methiini														
<i>Xystrocer a globosa</i>	2	2	2	1	1	2	2	1	1	2	1	2	1	1
<i>Leptoxenus ibidiiiformis</i>	2	2	2	1	1	2	2	1	1	2	1	3	3	1
Thraniini														
<i>Thranus multinodeatus</i>	2	2	2	1	2	2	2	1	1	2	1	4	1	1
Callichromini														
<i>Aromia moschata</i>	2	2	2	1	1	2	2	1	1	2	1	3	1	1
<i>Chloridolum (Chloridolum) lochooanum</i>	2	2	2	1	1	2	2	1	1	2	2'	4	3	1
<i>C. (C.) thaliodes</i>	2	2	2	1	1	2	2	1	1	2	2'	4	3	1
<i>C. (Leontium) viride</i>	2	2	2	1	1	2	2	1	1	2	2'	4	3	1
Callidiini														
<i>Ropalopus signaticollis</i>	2	2	2	1	1	2	4	-	1	4	1	3	2	1
<i>Callidium violaceum</i>	2	1	2	1	1	2	3	1	1	2	1	3	1	1
<i>Callidiellum rufipenne</i>	2	1	2	1	1	2	2	1	1	2	1	3	4	1
<i>Semanotus japonicus</i>	2	1	2	1	1	2	3	1	1	2	1	3	1	1
<i>Phymatodes (Phymatodes) testaceus</i>	2	2	2	1	1	2	2	1	1	2	1	3	1	1
<i>P. (Phymatodellus) vandykei</i>	2	2	2	1	1	2	4	-	1	3	1	3	1	1
<i>P. (Poecilium) maaki</i>	2	2	2	1	1	2	4	-	1	3	1	3	1	1
<i>P. (Paraphymatodes) albicinctus</i>	2	2	2	1	1	2	4	-	1	3	1	3	1	1
Cleomenini														
<i>Kurarua rhopalophoroides</i>	2	2	2	1	1	2	2	1	1	0	1	4	3	1
<i>Artimpaza setigera</i>	2	2	2	1	1	2	3	1	1	2	1	4	3	1
Hesperophanini														
<i>Gnatholea eburifera</i>	2	1	2	2	2	2	2	1	1	4	1	3	1	1
<i>Stromatium longicorne</i>	2	2	2	1	1	2	2	1	1	4	1	4	1	1
<i>Trichoferus campestris</i>	2	2	2	1	1	2	2	1	1	4	1	3	2	1

Table 2 (Continued).

Species / No. of character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cerambycini														
<i>Massicus raddei</i>	2	2	2	1	1	2	2	1	1	2	1	4	1	1
<i>Aeolesthes chrysothrix</i>	2	2	2	1	1	2	2	1	1	4	1	4	2	1
<i>Dymasius hirayamai</i>	2	2	2	1	1	2	2	1	1	4	1	4	3	1
Phoracanthini														
<i>Allotraeus (Allotraeus) sphaerioninus</i>	2	2	2	1	1	2	2	1	1	4	1	4	2	1
<i>A. (Nysina) insularis</i>	2	2	2	1	1	2	2	1	1	4	1	4	2	1
Callidiopini														
<i>Curtomerus flavus</i>	2	2	2	1	1	2	2	1	1	2	1	3	3	1
<i>Stenygrium quadrinotatum</i>	2	2	2	1	1	2	2	1	1	4	1	4	2	1
<i>Stenodryas clavigera</i>	2	3	2	1	1	2	4	1	1	4	1	4	3	1
<i>Ceresium sinicum</i>	2	3	2	1	1	2	2	1	1	4	1	4	2	1
<i>Parasalpinia kojimai</i>	2	2	2	1	1	2	3	1	1	4	1	3	3	1
Molorchini														
<i>Leptepania japonica</i>	2	2	2	1	1	2	4	-	1	4	1	2	3	1
<i>Epania shikokensis</i>	2	2	2	1	1	2	4	-	1	4	1	4	3	1
<i>Molorchopania mizoguchii</i>	2	2	2	1	1	2	4	-	1	4	1	4	1	1
<i>Molorchus pinivorus</i>	2	2	2	1	1	2	4	-	1	4	1	4	2	1
<i>Glaphyra nitida</i>	2	2	2	1	1	2	4	-	1	4	2	4	3	1
Rosalini														
<i>Rosalia batesi</i>	2	2	2	1	1	2	2	1	1	4	1	4	3	1
Clytini														
<i>Xylotrechus cuneipennis</i>	2	1	2	1	1	2	4	-	1	4	1	4	3	1
<i>X. rusticus</i>	2	1	2	1	1	2	4	-	1	4	1	4	3	1
<i>Perissus kiusiuensis</i>	2	2	2	1	1	2	4	-	1	4	1	4	4	1
<i>Cyrtoclytus caproides</i>	2	2	2	1	1	2	4	-	1	4	1	4	3	1
<i>Brachyclytus singularis</i>	2	2	2	1	1	2	4	-	1	4	1	4	3	1
<i>Clytus melaenus</i>	2	2	2	1	1	2	4	-	1	4	1	4	4	1
<i>Kazuoclytus lautoides</i>	2	2	2	1	1	2	4	-	1	4	1	4	4	1
<i>Plagionotus pulcher</i>	2	1	2	1	1	2	3	1	1	4	1	4	3	1
<i>Rhaphuma xenisca</i>	2	1	2	1	1	2	3	1	1	4	1	4	3	1
<i>R. diminuta</i>	2	1	2	1	1	2	3	1	1	4	1	4	3	1
<i>Chlorophorus japonicus</i>	2	1	2	1	1	2	3	1	1	4	1	4	3	1
<i>Grammoglyphus notabilis</i>	2	1	2	1	1	2	3	1	1	4	1	4	3	1
<i>Epiclytus yokoyamai</i>	2	3	2	1	1	2	4	-	1	4	1	4	1	1
<i>Amamicyltus subnitidus</i>	2	2	2	1	1	2	4	-	1	4	1	4	4	1
<i>Hayashicyltus acutivittis</i>	2	2	2	1	1	2	3	1	1	4	1	4	3	1
<i>Demonax transilis</i>	2	2	2	1	1	2	3	1	1	4	1	4	3	1
Anaglyptini														
<i>Paraclytus excultus</i>	2	2	2	1	1	2	3	1	1	4	1	4	2	1
<i>Anaglyptus (Anaglyptus) matsushitai</i>	2	2	2	1	1	2	2	1	1	4	2	4	1	1
<i>A. (Akajimatora) bellus</i>	2	2	2	1	1	2	3	1	1	4	1	4	1	1
<i>Oligoenoplus rosti</i>	2	2	2	1	1	2	3	1	1	4	1	4	1	1
<i>Hirticyltus comosus</i>	2	2	2	1	1	2	3	1	1	4	1	4	1	1
Pyrestini														
<i>Pyrestes nipponicus</i>	1	4	2	1	1	2	4	-	1	2	1	4	1	1
Purpuricenini														
<i>Purpuricenius spectabilis</i>	1	4	2	1	1	2	2	1	1	4	1	4	3	1
<i>P. lituratus</i>	1	4	2	1	1	2	2	1	1	4	1	4	3	1
<i>Amarysius sanguinipennis</i>	1	4	2	1	1	2	2	1	1	4	1	4	3	1
Obrini														
<i>Comusia testacea</i>	1	5	2	1	2	3	4	-	1	2	1	2	1	1
<i>Stenomalus cleroides</i>	1	5	2	-	1	3	4	-	1	2	1	4	3	1
<i>Longipalpus dilatipennis</i>	1	5	2	-	1	3	4	-	1	2	1	4	3	1
<i>Pseudiphra elegans</i>	1	5	2	-	1	3	4	-	2	2	1	4	3	1
<i>Obrium nakanei</i>	1	5	2	-	1	3	4	-	1	2	1	4	4	1
<i>O. brevicorne</i>	1	5	2	-	1	3	4	-	1	2	1	4	3	1
<i>O. japonicum</i>	1	5	2	-	1	3	4	-	1	2	1	4	4	1
Stenopterini														
<i>Stenopterus flavicornis</i>	1	5	2	-	1	3	4	-	1	2	1	4	4	1
<i>Callimellum abdominale</i>	1	5	2	-	1	3	4	-	1	?	1	4	4	1
<i>Merionoeda (Ocytasia) formosana</i>	1	5	2	-	1	3	4	-	1	2	1	4	4	1
<i>M. (Macromolorchus) hirsuta</i>	1	5	2	-	2	3	4	-	?	?	1	4	3	1

randra, *Aegosoma*, Obriini, Stenopterini, Purpuricerini and *Pyrestes*.

2) Ninth sternite (Fig. 226). The paraproct of the 9th sternite is usually long and bears a pair of baculi, but is extremely shortened and loses baculi in Obriini, some Stenopterini, Purpuricenini and *Pyrestes*, and bears two pairs of baculi only in *Gnatholea eburifera*. The latter two states are deemed apomorphic and seem to have developed independently.

3) Appendages of ninth sternite.

(a) Valvifer and coxite. The appendage of the 9th sternite excluding apical lobes is called coxite if the baculi are continuous, but if the baculi are divided into the basal and apical portions, the basal part of the appendage bearing the basal portions of baculi is called valvifer and is distinguished from the coxite. Both the states are found as a parallelism in all the subfamilies except Lamiinae, and their polarities cannot be determined.

(b) Coxite lobes. The bilobed apical part of the appendage of the 9th sternite is called coxite lobes. They are usually cylindrical, and are variable in the length, breadth and the degree of sclerotization. Such variants occur in all the cerambycid groups and is deemed to be a parallelism. Their polarities cannot be determined.

(c) Stylus (Fig. 227). The stylus is an elongate apical appendage usually articulated to the apex of each coxite lobe. It is translocated to the lateral face of the coxite lobe in the following groups: *Parandra*, Prioninae, *Apatophysis*, *Spondylis*, *Tetropium*, *Toxotinus*, *Brachyta*, *Evodinus*, *Pidonia* (*Pidonia*), *Alosterna*, *Pseudalosterna*, *Pachypidonia*, *Corennys*, *Konoa*, *Gnatholea*, *Comusia*, *Merionoeda* (*Macromolorchus*) and *Thranis*. It is particularly small in the three genera, *Aegosoma*, *Pachypidonia* and *Corennys*. The outward translocation and reduction of the stylus seem apomorphic, and in *Parandra*, *Apatophysis* and *Spondylis*, this state is no doubt brought about for protecting styli from the heavy sclerotization of the coxite.

4) Ninth tergite (Fig. 228). In the cerambycid groups, the 9th tergite becomes elongated by the shortening of the proctiger and bears a pair of baculi, called dorsal baculi. This apomorphic state is common to almost all the cerambycids, but in the Obriini and Stenopterini, the baculi become disappeared by exceptional shortening of the 9th segment. It is considered that the 9th tergite is plesiomorphic in a sclerotized state and apomorphic in a membranous state, and that the absence of baculi on the membranous 9th tergite is more apomorphic than their presence.

5) Tenth tergite (Figs. 229–230). The tenth tergite, or proctiger, is short in all the cerambycoids other than the Vesperidae, and is obliterated in some Callidiopini, Molorchini, some Clytini, Obriini and Stenopterini. It is usually very long in other coleopteran families, so that the vesperid state must be plesiomorphic and the character states in the other cerambycoids apomorphic.

Though plesiomorphic in the non-reduction of the proctiger, the Vesperidae is peculiar in bearing two pair of proctiger baculi, which is considered apomorphic.

6) Vagina (Figs. 231). The vagina is a tubular organ sometimes dilated at the basal part. In certain species of the Lepturinae, this dilatation takes place in com-

compensation of the reduction of bursa copulatrix and is considered to play its role. In some others, however, dilatation is developed without regard to the size of bursa copulatrix. It is, therefore, difficult to determine the polarity of this character state. On the other hand, partial sclerotization of the vagina found in some Lepturini is considered apomorphic.

7) Vaginal plates (Figs. 232). These seem to be the apparatuses to which attach the muscles connecting the vagina with the base of the 9th segment. So far as I am aware, the vaginal plates exist only in the cerambycoids exclusive of the Vesperidae, and its presence is an apomorphic character state. It varies in shape and sclerotization, from filamentous to broadly lamellar and from membranous to heavily sclerotized. Sometimes, the two sclerotized plates are fused at the bases and form the shape of V or U. This is considered apomorphic.

8) Bursa copulatrix (Fig. 233). The bursa copulatrix varies greatly in both size and shape. It is sometimes large or very large, widely ovoid or tubular, and sometimes small or even obliterated. Similar variations are observed in other families of the Coleoptera, and it is difficult to determine their polarities. However, partial sclerotization or the presence of an impression found in *Glaphyra*, *Chloridolum* and *Anaglyptus* may be apomorphic.

9) Spermatheca (Fig. 234). The saccate state of the spermatheca in the Vesperidae is considered plesiomorphic, the straight capsular state found in *Formosopyrrhona*, *Xystrocera*, *Leptepania* and *Comusia* seems to follow it, the bent capsular state is apomorphic. Heavy sclerotization of the capsule is also considered apomorphic.

10) Spermathecal gland. The spermathecal gland exists in almost all the cerambycoids, but varies in shape and position of attachment without rule.

11) Spermathecal duct (Fig. 235). The short and thick state of the spermathecal duct is the most plesiomorphic, followed by the slender straight state. It is particularly long in *Leptura ochraceofasciata*. The most apomorphic state is the multi-coiled state as seen in the Stenopterini and Clytini.

The spermathecal duct shows a unique modification in the Disteniidae. It coils in an intricate manner, becomes heavily sclerotized, and forms a part of the spermatheca. No membranous duct remains between the spermatheca and the bursa copulatrix. This is no doubt apomorphic.

Conclusive Remarks

As was demonstrated in the preceding section with the accompanying character state matrix, it is impossible to set up a convincing phylogeny of the Cerambycidae in a strict sense on the basis of female genitalia. It is true that the isolated status of the Vesperidae and Disteniidae is confirmed by my study of their female genitalia, and that phylogenetic relationships between the Parandrinae, Prioninae, Apatophysinae and Spondylinae are clarified to a considerable extent, but relationships between tribes and genera in the subfamilies Lepturinae and Cerambycinae and affinities of these sub-

families themselves cannot be determined, with some important exceptions of tribal affinities. The following is a summary of these results.

Vesperidae — This family is regarded as a monophyletic group because of the presence of such an apomorphic character as the existence of two pair of proctiger baculi (8-2). On the other hand, it retains the most primitive characters in the cerambycoid complex, since it shows such a plesiomorphy as very long proctiger (7-1) and saccate membraneous spermatheca (12-1).

Disteniidae — This family is also considered monophyletic, because of apomorphy of the spermathecal duct, which is heavily sclerotized, intricately coiled and not separable from the heavily sclerotized spermatheca (14-2). Its affinity to other groups is not clear, because of the absence of appreciable symplesiomorphy.

Parandrinae — The parandrines are apomorphic in the absence of proctiger (7-4) and reduction of styli which are situated on the dorsal side of coxite lobes (5-2), though they lack in autapomorphy. On the other hand, they are peculiar in possessing plesiomorphic character state of paraproct, which is clearly distinguished into tergite and sternite at its anterior part (3-1).

Prioninae and Apatophysinae — In *Aegosoma* of the Prioninae, the tergite of the 9th abdominal segment is in an apomorphic state by being membraneous and lacking baculi (6-3). This character state is, however, not autapomorphic, since it is found in certain groups of other subfamilies as parallelism. In this particular case, the modification seems to have taken place as a result of functional degradation of the 9th segment, since the 8th segment is prolonged and takes the role of ovipositor.

The Apatophysinae possesses the same apomorphic character as the Prioninae in the position of the styli, which move to the lateral faces of the coxite lobes (5-2). This character state is, however, not autapomorphic, so that it is difficult to say from the study of the female genitalia alone that these subfamilies are really monophyletic.

Spondyliinae — In this subfamily, only the genera *Spondylis* and *Tetropium* show an apomorphy same as the Prioninae in the lateral position of the styli (5-2). In all the others, the female genitalia are basically similar to those of many genera belonging to the Lepturinae and Cerambycinae and are different from those of the Prioninae.

Lepturinae and Cerambycinae — The female genitalia are basically identical between these two subfamilies, hence they cannot be clearly distinguished from each other by these characteristics alone. Based on the character state matrix, however, four groups might be recognized in them as given below.

a) Group I (Rhagiini, Lepturini, Necydalini, Methiini, Thraniini, Callichromini, Callidiini and Cleomenini). All these tribes do not show any autapomorphy in their female genitalic characters, with the exception of the following features derived from parallelism: very short paraproct and 9th tergite lacking in their baculi (2-5, 6-3) of *Toxotinus*, and almost fully sclerotized vaginal plates (10-4) in *Alosterna*, *Pseudalosterna* and *Ropalopus*. This group is, therefore, not natural but a mere assemblage of the tribes which do not show any characteristics indicative of their relationships.

b) Group II (Hesperophanini, Cerambycini, Phoracanthini, Callidiopini, Mo-

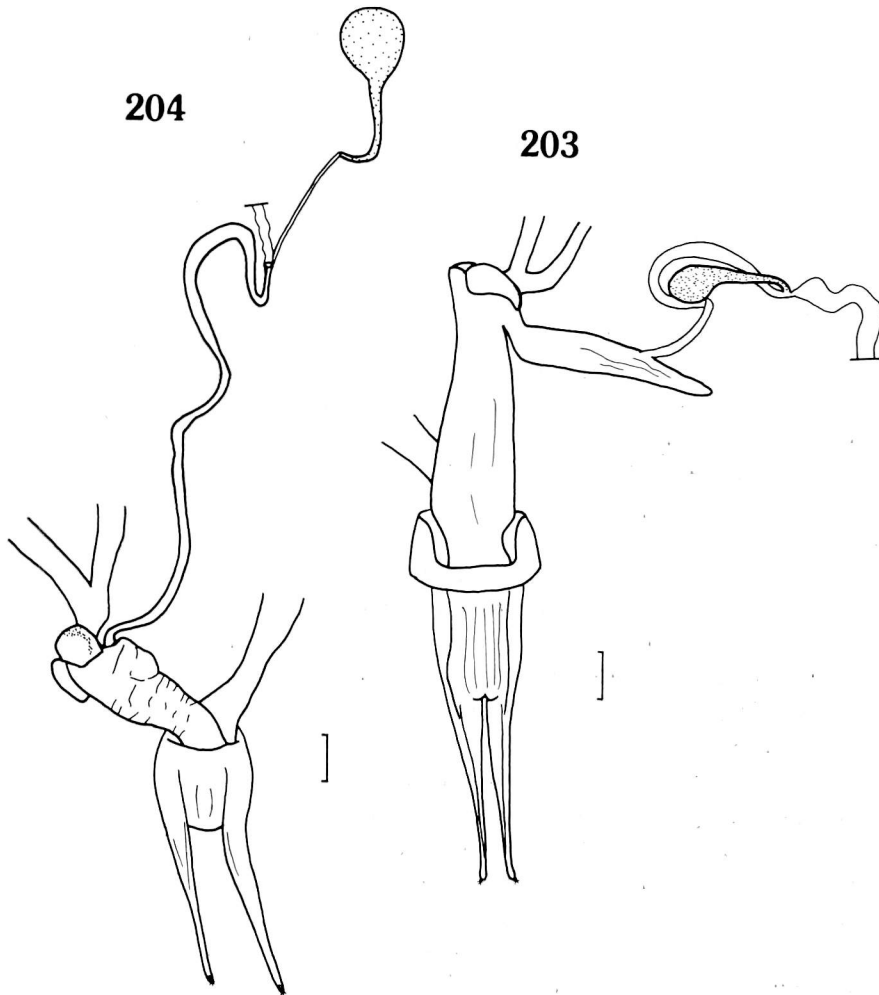
lorchini, Rosaliini, Clytini and Anaglyptini). These tribes show an apomorphic character state of almost wholly sclerotized vaginal plates (10–4), with the exception of *Massicus* and *Curtomerus*, in which the vaginal plates remain in a plesiomorphic state. All the species examined of the Molorchini and many of the Clytini possess an apomorphic character state of the proctiger (7–4), which becomes disappeared, but the same character state is also found in such various groups as *Parandra*, some Calidiini, Pyrestini, Obriini and Stenopterini, so that it cannot be regarded as a clear indication of monophyly of the two tribes in question.

c) Group III (Pyrestini and Purpuricenini). These tribes possess an apomorphic character state of the paraproct (2–4), that is, it is extremely short but bears a pair of baculi. This character state is less apomorphic than in the members of Group IV, but is autapomorphic among the cerambycoid groups. It is therefore considered that the two tribes have a monophyletic origin. Incidentally, heavily sclerotized vaginal plates (10–4) possessed by the Purpuricenini may have resulted from a parallelism.

d) Group IV (Obriini and Stenopterini). The Obriini and Stenopterini show an apomorphic character state of the paraproct and the 9th tergite, which are extremely short and devoid of baculi (2–5, 6–3), and must have been derived from a monophyletic origin. The same apomorphic character states are found in the lepturine genus *Toxotinus*, but the phenomenon must have resulted from a parallelism and cannot be regarded as an indication of its direct relationship with the obriines or stenopterines. Many of the members of these tribes also possess such apomorphic characters as the absence of proctiger (7–4) and coiled spermathecal duct (13–4). All of these suggest that they are the most derivative groups of the Cerambycidae. On the other hand, no reliable feature is detected in the female genitalia to discriminate one from the other.

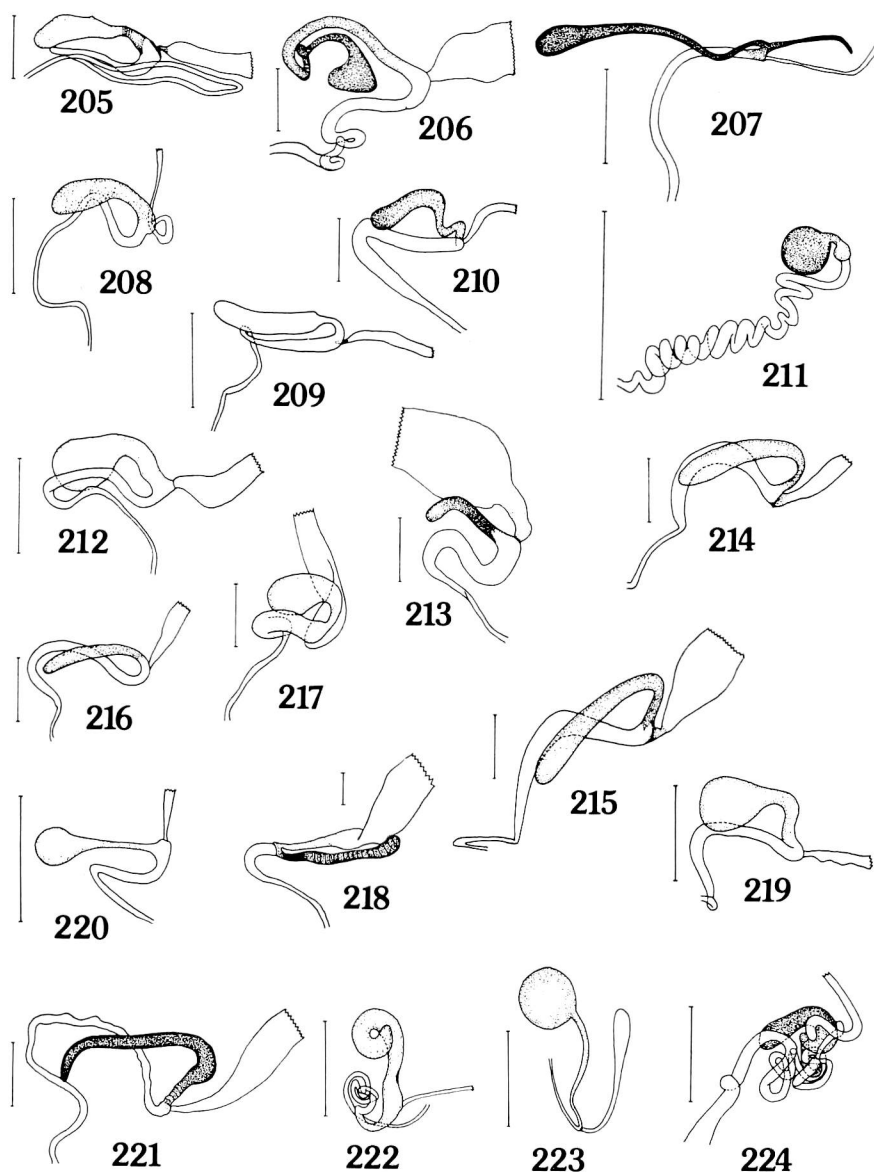
Incidentally, the genus *Comusia*, which was recently removed from the Methiini to the Obriini, is an indubitable member of one of these tribes judged from the conformation of the female genitalia. *Merionoeda* (*Macromolorchus*) *hirsuta* is rather isolated in showing an apomorphic state of the styli, which are articulated to the apico-lateral faces of the coxite lobes (5–2), but this seems to be a result of parallel specialization, not indicative of its phylogenetic independency.

Here, some words seem necessary for outlining the female genitalia of the cerambycid beetles belonging to the subfamily Lamiinae. As was already pointed out at the beginning of this chapter, they are rather uniform in spite of marked diversity of external features. The paraproct is very short and always devoid of baculi; the coxite lobes are very long and bear small styli; the dorsal baculi are absent; the proctiger is either absent or much reduced; and, the spermatheca is heavily sclerotized and bears a well developed gland (Figs. 203–204). I have examined the female genitalia of 44 species of 25 genera of Japanese lamiines, which represent 15 out of the 21 tribes known from Japan (Mesosini, Homonoieini, Apomecynini, Agapanthiini, Pteropliini, Phrissomini, Lamiini, Ancyronotini, Crossotini, Dorcaschematini, Xenoleini, Rhodopinini, Acanthocinini, Saperdini, and Astathini). They invariably possess a combination of the characters delineated above. On the other hand, the spermathecal

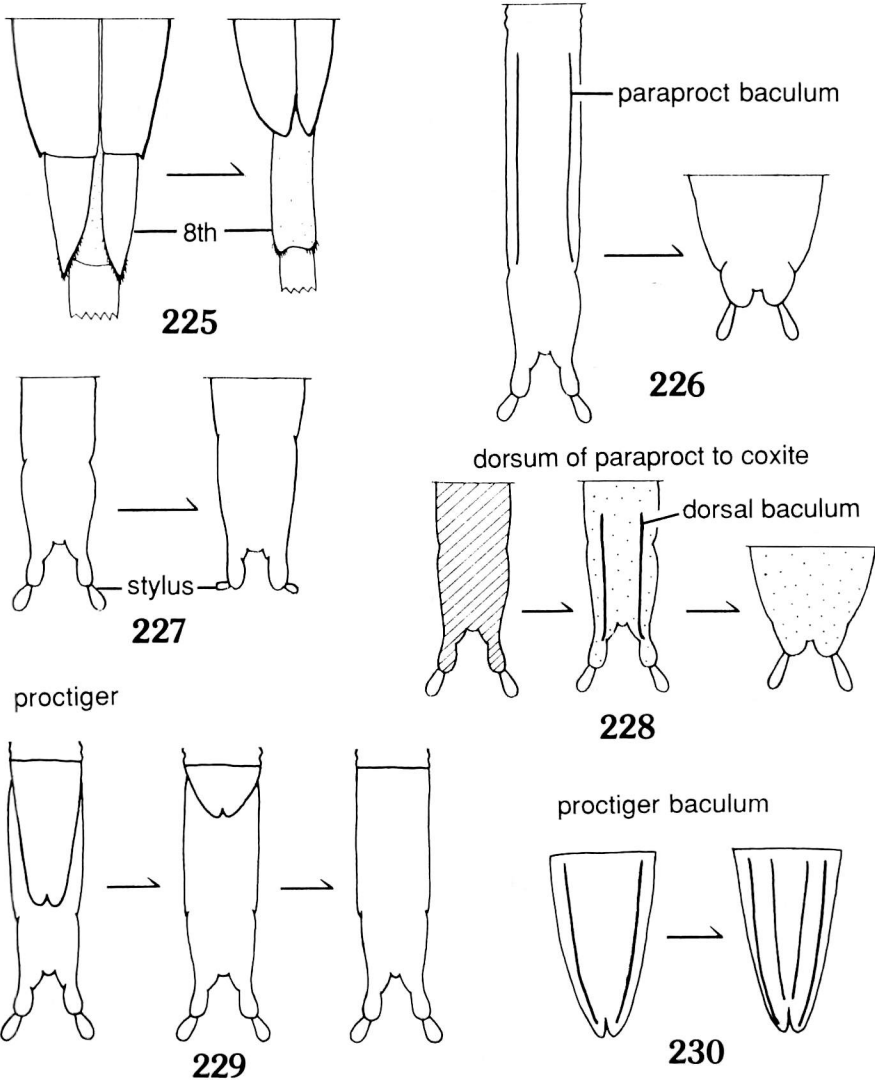


Figs. 203–204. Ovipositors and internal reproductive organs in the Lamiinae, ventral view. —
 203, *Psacotha hilaris hilaris* (PASCOE, 1857); 204, *Cagoshima sanguinolenta* THOMSON, 1864.
 (Scale: 0.5 mm.)

capsules are, though similar to one another in fundamental structure, strikingly variable in configuration (Figs. 205–224). They are species-specific and are useful for classifying lamiine species. Similar modification of the 9th abdominal segment is also found in the genus *Aegosoma* of the subfamily Prioninae and the tribes Obriini and Stenopterini of the Cerambycinae. In the former case, the segment is similar to that of the Lamiinae in the elongation of coxite lobes and the reduction of stylus. This is, however, apparently a modification in accordance with that of the 8th segment. In the latter case, on the contrary, modification of the 9th segment seems related to the

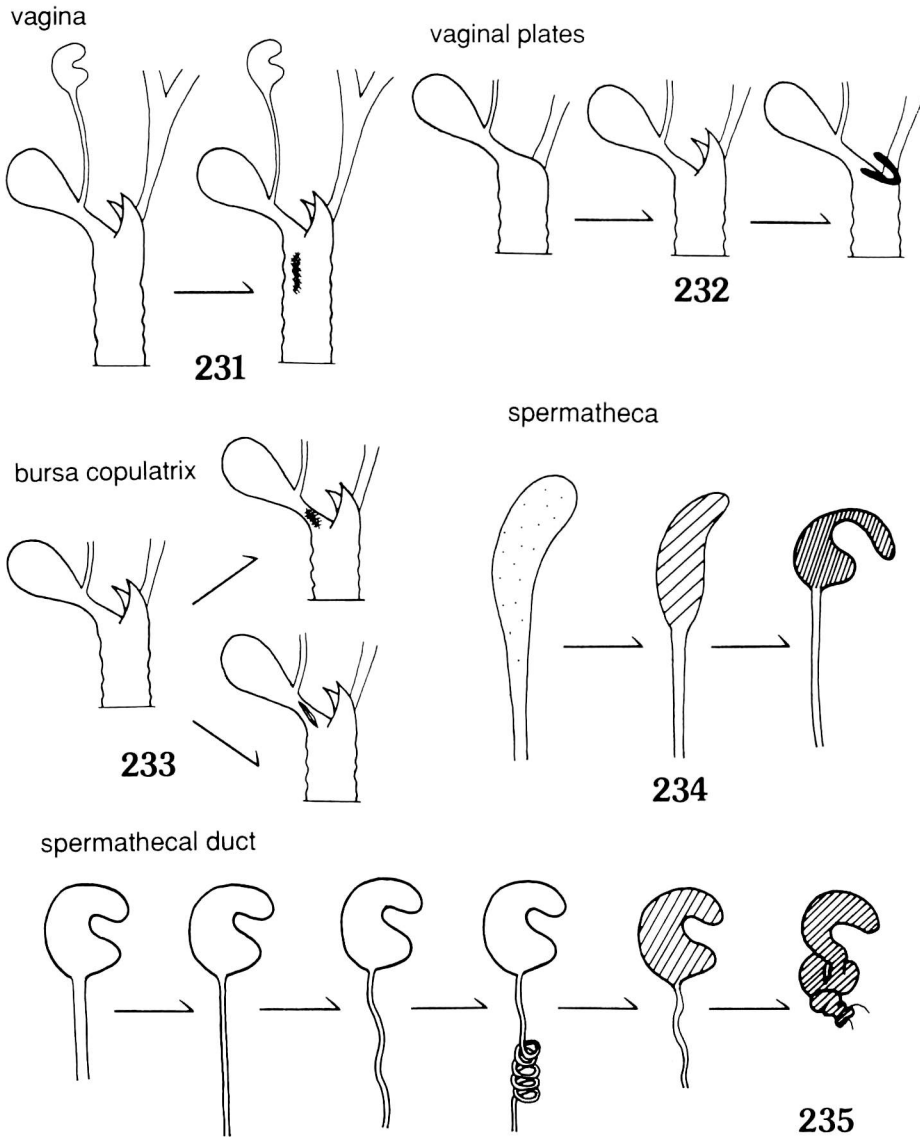


Figs. 205–224. Spermathecae in the Lamiinae. — 205, *Mesosa (Mesosa) japonica* BATES, 1873; 206, *Bumetopia oshimana heiana* HAYASHI, 1963; 207, *Asaperda agapanthina* BATES, 1873; 208, *Sybra (Sybrodiboma) subfasciata subfasciata* (BATES, 1884); 209, *Ropica tsushimensis* HAYASHI, 1972; 210, *Agapanthia daurica daurica* GANGLBAUER, 1884; 211, *Egesina (Nijimana) bifasciata bifasciata* MATSUSHITA, 1933; 212, *Pterolophia (Pterolophia) caudata caudata* (BATES, 1873); 213, *Abryna (Abryna) obscura* SCHWARZER, 1925; 214, *Parechthistatus gibber tsushimanus* OHBAYASHI, 1961; 215, *Mesechthistatus furciferus meridionalis* (HAYASHI, 1951); 216, *Xenicotela pardalina* (BATES, 1884); 217, *Palimna liturata* (BATES, 1884); 218, *Moechotypa diphyis* (PASCOE, 1871); 219, *Olenecamptus formosanus* PIC, 1914; 220, *Xenolea asiatica* (PIC, 1925); 221, *Rhodopina lewisii lewisii* (BATES, 1873); 222, *Acanthocinus griseus orientalis* OHBAYASHI, 1939; 223, *Glenea (Glenea) relicta relicta* PASCOE, 1868; 224, *Bacchisa (Bacchisa) fortunei japonica* (GAHAN, 1901). (Scale: 0.5 mm.)



change of ovipositing behaviour, resulting in the disappearance of both the proctiger and the paraproct baculi. This resemblance between the Obriini–Stenopterini and the Lamiinae must be a convergence, since the pattern of ovipositing behaviour is decisively different between them as was mentioned before.

Recently, WANG and CHIANG (1991) published a paper on the “evolution in the higher taxa of the Cerambycidae,” in which they recognized five subfamilies, Prioninae (including *Parandra*), Lamiinae, Cerambycinae, Lepturinae (including Necydalini and *Apatophysis*) and Aseminae (including *Spondylis*). The Disteniidae (including Phi-



Figs. 225–235 (on pp. 212–213). Schematic representation of female genitalia of cerambycoid beetles, showing their modification from primitive to derivative states. — 225, Eighth abdominal segment; 226, 9th sternite; 227, stylus; 228, 9th tergite; 229, 10th tergite (proctiger); 230, 10th tergite (proctiger baculum); 231, vagina; 232, vaginal plates; 233, bursa copulatrix; 234, spermatheca; 235, spermathecal duct.

linae and Vesperinae) was regarded as an independent family and was not dealt with in their paper. Their analysis is careful and fairly persuasive, but is largely based upon supposed past radiation and dispersal in relation to continental drift and

differentiation adaptive to diversification of host plants. They concluded that the ancestral cerambycid stock became first diverged into the prionine group and the remainings, then into the Lamiinae and the others, from which the Cerambycinae became diverged next, followed by the divergence of the Lepturinae, and the asemine group was left as the youngest subfamily.

Their opinion can be disputed in that the time scales given at the left-hand side of the diverging points in their phylogenetic diagrams seem too old to be convincing. No reliable fossil data were reported on existence of cerambycids in the Jurassic, and though some fossil beetles with long antennae and cerambycid-like features were recorded from the late Jurassic formation of Karatau in southern Kazakhstan, all of them were placed by MEDVEDEV (1968) in the chrysomelid subfamily Protoscelinae, and the total absence of Cerambycidae in this largest known bed of fossil beetles in the world was commented "noteworthy" (ARNOLDI *et al.*, 1977, p. 13). Based on MEDVEDEV's data, CROWSON (1981, p. 675) inferred that "the basic division of the Cerambycid and Chrysomelid lines may well date from the late Jurassic and be related to a division between Coniferae and Cycadeoids as basic food plants." According to ARNOLDI and others (*op. cit.*, p. 15), "beetles externally similar to the primitive Cerambycidae" were found only in the early Cretaceous, and KIREJTSHUK (1992) mentioned nothing about ancestral cerambycids in his recent paper on the evolution of the mode of life in fossil beetles, with the exception of some surmises.

My own impression is that the evolution of cerambycid beetles proceeded rather rapidly like that of birds, even though primitive ancestral groups may date back to the middle Mesozoic. There are ample evidences that fossil cerambycids similar to Cenozoic forms became commoner in the late Cretaceous when angiosperms became predominant among plants, and their number rapidly increased in the early Tertiary, when many present-day genera of the subfamilies Prioninae, Spondylinae, Lepturinae, Cerambycinae and Lamiinae were already in existence (HANDLIRSCH, 1907, pp. 785–791). Such a rapid diversification must have been achieved in accordance with the rapid multiplication of flowering trees, and this is probably why the Cerambycinae and Lepturinae became remarkably differentiated in rather a short geological time without changing the basic plan of their genitalia, in contrast to the marked genitalic divergence in other groups excluding Lamiinae, which must have required much longer time.

From the study of the female genitalia, it is difficult to decide at what stage of the cerambycid evolution the divergence of the Lamiinae took place. In this subfamily, every component of the 9th abdominal segment in the female shows an apomorphic state, and besides, general conformation of the ovipositor formed by this segment is uniform throughout the subfamily in spite of considerable diversification of external morphology. This may suggest that the origin of the subfamily is relatively late and that the radiation of its genera and species has taken place in rather a short time. But on the other hand, uniformity of ovipositor may only mean that ovipositing behaviour has not changed for a long time throughout this subfamily however great the modifi-

cation of external characters may have been. This subfamily seems to have originally developed by adaptation of specialized ovipositing behaviour, which could have taken place at any stage of the evolutionary history of cerambycid beetles.

In recent years, phylogenetic importance of female genitalia has received due attention from some coleopterologists, and attempts have been made to take their characteristics into consideration for phylogenetic analyses (cf. MANN & CROWSON, 1992; COCA-ABIA & MARTIN PIERA, 1992). When similar studies are made in various groups of the Coleoptera, particularly of the suborder Polyphaga, we shall be able to throw a new light on the systematics of this tremendous insect group, even if the results to be obtained may not drastically differ from current classifications.

要 約

斉藤明子：日本および近隣地域に産するカミキリムシ類の雌生殖器。V. 考察。——日本とその近隣地域に分布する，フトカミキリ亜科を除くカミキリムシ類の雌生殖器について精査した結果から，外群比較法により雌生殖器の各形質の極性を判定し，各種群についての系統解析を試み，得られた見解をまとめた。合わせて，フトカミキリ亜科について若干の考察を加えた。

ムカシカミキリ科とホソカミキリ科では，前者は担肛節に2対の棒状片をもつ，後者は受精囊と受精囊管が強く節片化してたがいに融合する，という新形質を示すことから，それぞれの単系統性が示唆された。ニセクワガタカミキリ亜科では，担肛節がなく尾状体が陰端節の側面に位置するという新形質と，肛側片が背板と腹板とに明らかに分かれるという旧形質を合わせもつ。Apatophysinae では，ノコギリカミキリ亜科とともに，尾状体が陰端節の側面に位置するという新形質を示すが，これらの亜科が真の単系統群かどうかはわからない。クロカミキリ亜科は，クロカミキリ属 *Spondylis* とトドマツカミキリ属 *Tetropium* で，尾状体の位置がノコギリカミキリ亜科の場合と同様の新形質を示すが，その他の種では，ハナカミキリ亜科やカミキリ亜科の雌生殖器と基本的に違いがない。ハナカミキリ亜科とカミキリ亜科とは，雌生殖器の形態から明確に区別することができなかったが，形質分布表からこれらを通じてよっつの族群が認められた。とくに，アメイロカミキリ族とモモトコバナカミキリ族は，肛側片が極端に短くて棒状片がないという新形質を示し，カミキリムシ科でもっとも派生的な族群だと考えられる。フトカミキリ亜科では，全般的に雌生殖器が新形質を示し，外部形態のいちじるしい多様化にもかかわらず，同質的であった。このことは，フトカミキリ亜科の起源が比較的遅く，種分化が急速に起きたことを暗示している。

Additional References

Those given at the ends of Parts I and IV are omitted.

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