

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

I. Philini through Atimiini

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Abstract Female reproductive organs are examined on 22 species of smaller groups of cerambycid beetles from Japan and the neighbouring areas. From the results obtained, in combination with other characteristics of adults and larvae, it is concluded that the following classification of families and subfamilies may be reasonable: Vesperidae (including Philini), Disteniidae, Cerambycidae — Parandrinae, Prioninae (including Anacolini), Apatophysinae, and Spondyliinae (including Asemimi and Atimiini).

Dealing with the female genitalia of lepturine cerambycid beetles mainly from Japan, I laid special emphasis on the taxonomic importance of these organs in determining their phylogenetic relationship (SAITO, 1989). Since then, I have followed up the same line of researches, and now I am going to present the results of my studies on the female reproductive organs of other groups of cerambycid beetles.

In the first part of this series of papers, I will take up the following smaller groups: Philini, Vesperini, Disteniini, Parandrini, Prionini, Anacolini, Apatophysini, Spondyliini, Asemimi and Atimiini. With the exception of the Prioninae in a strict sense, all these groups have been subject to argument as to their systematic status and phylogenetic relationship. Some of them have been regarded as independent families or subfamilies, while others were treated as tribes or even synonymized. Different opinions about their classification will be delineated in the discussion following descriptions of representative species, and I will put forth my own opinion on the subject based mainly upon the study of their female reproductive organs.

Needless to say, my opinion to be given in this paper is not conclusive; there still remain many problems that should be clarified or confirmed. For instance, larval characters are still unknown about philines including *Mantitheus*, which show a very close similarity to *Vesperus* so far as concerned with the female genitalia. Besides, my study is limited mainly to Japanese forms because of difficulty in obtaining adequate material of critical foreign species. However, I have taken into consideration as many available data on non-genitalic characters as possible, and am confident that my conclusion is not far afield.

The method and terminology adopted in this study are the same as those explained

in my previous paper (cf. SAITO, 1989, pp. 67–69).

This study could never have been completed were it not for kind support of many colleagues and friends of mine. First of all, I have to thank Dr. Shun-Ichi UÉNO, chief curator of entomology at the National Science Museum (Nat. Hist.), Tokyo, who not only supervised and encouraged my study but helped me in every possible way. But for his leading and support, my study might not have reached the present achievement. Heartly thanks should be expressed to the following persons, who helped me either in obtaining rare specimens of critical species or in consulting with rare literature: Professors Katsuo KANEHISA, Katsura MORIMOTO, Yoshiaki NISHIKAWA, Masataka SATÔ, Drs. Michitaka CHÛJÔ, Nobuo OHBAYASHI, Messrs. Hideo AKIYAMA, Sadanari HISAMATSU, Hiroshi MAKIHARA, Tatsuya NIISATO, Masahiro SAKAI, Tohru SHIMOMURA and Masatoshi TAKAKUWA.

Results

Family Vesperidae

Tribe Philini

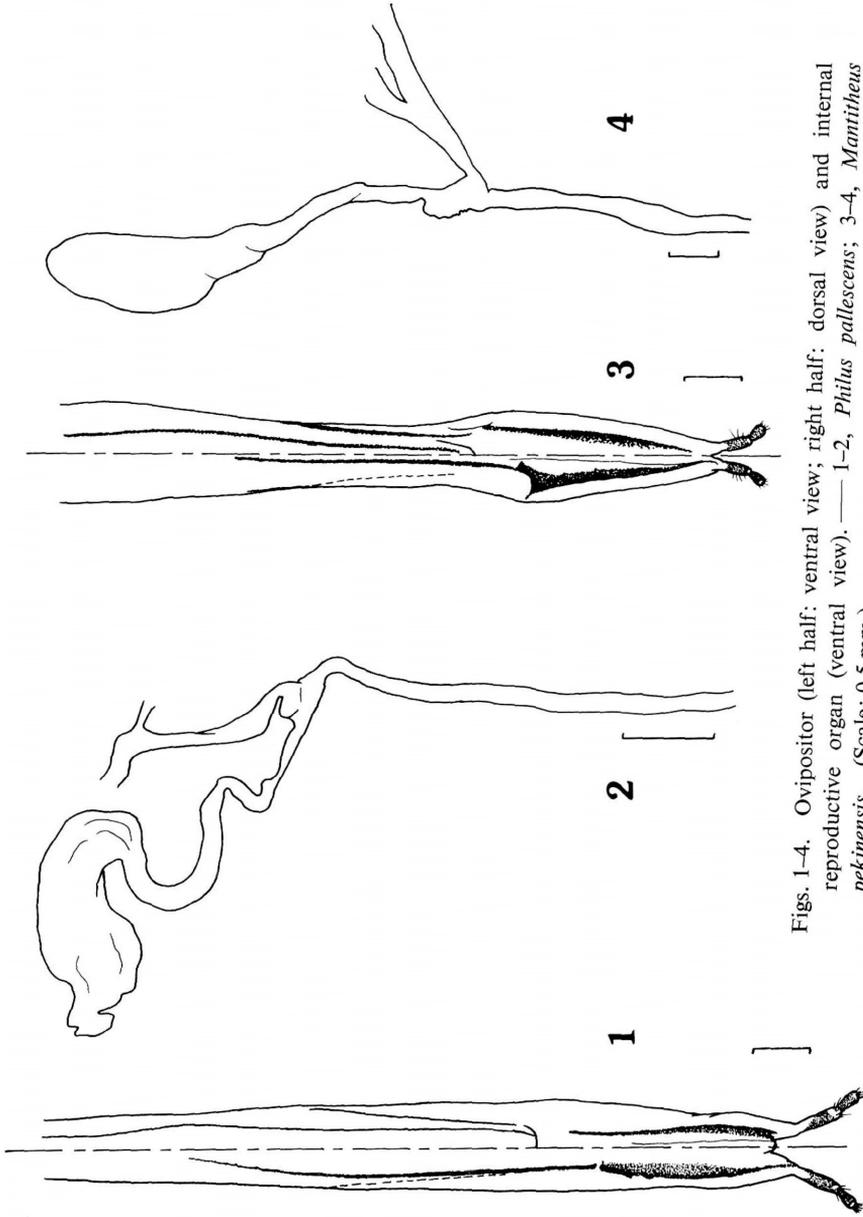
Philus pallelescens BATES, 1866

(Figs. 1–2)

Collecting data of the material used. Horisha (=Pu-li), Taiwan, V–1942, collector unknown; Chiayi, Taiwan, 27–V–1976, collector unknown.

Paraproct long, each baculum thick though thin at the anterior part; valvifer indistinct; coxite slightly narrowed at middle, its baculi very thick and slightly sinuate; coxite lobes long and very narrow, sclerotized except for basal and apical portions, with tactile hairs at the apices; stylus moderate in size, articulated to the tip of each coxite lobe, sclerotized except for apex, and with tactile hairs; dorsal baculi very short, very thick, and thickened posteriorly; proctiger extremely long, and a little shorter than paraproct, with two pair of thin baculi, the inner one of which are very long, a little longer than paraproct baculi, and slightly sinuate, and the outer one a half as long as the inner; vagina very long and narrow, bent near the base, which is somewhat swollen; vaginal plates absent; bursa copulatrix absent; spermatheca not forming a sclerotized capsule, but present as a large membraneous pouch; spermathecal duct not clearly distinguished from spermatheca, thick, widely curved three times, and entering into the swollen part of vagina.

Notes. As described above, the female reproductive organs of *Philus pallelescens* are very peculiar in that the proctiger is extremely long and bears two pair of baculi, that the vagina is swollen at the base and lacks the bursa copulatrix, and that the spermatheca does not become differentiated and remains membraneous, though it forms a large pouch with rather a stiff duct. Such a combination of diagnostic features has



Figs. 1-4. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 1-2, *Phylus pallescens*; 3-4, *Manitheus pekinensis*. (Scale: 0.5 mm.)

not been known in any other cerambycids so far as I am aware, and seems to suggest isolatedness as well as primitiveness of the species.

Mantitheus pekinensis FAIRMAIRE, 1889

(Figs. 3-4)

Collecting data of the material used. S. Shan-si, N. China, 1-VIII-1941, K. SHIRAHATA leg.

Paraproct long, its baculi thick, rather short, and almost straight; valvifer indistinct; coxite narrowed posteriorly, each baculum broadened both inwardly and laterally at the base, though tapered towards apex; coxite lobes very narrow, sclerotized except for basal and apical portions, with tactile hairs at the apices; stylus moderate in size, sclerotized except for apex, and with tactile hairs; dorsal baculi very short and thick, thickened in apical third; proctiger extremely long, with two pairs of thick baculi, the inner one a little shorter than paraproct, and slightly sinuate, and the outer one a half as long as the inner; vagina long and narrow, somewhat swollen at base; both vaginal plates and bursa copulatrix absent; spermatheca not forming a sclerotized capsule, but existing as a large membraneous pouch; spermathecal duct not clearly distinguished from membraneous spermatheca, thick, almost straight, and entering into the swollen part of vagina.

Tribe Vesperini

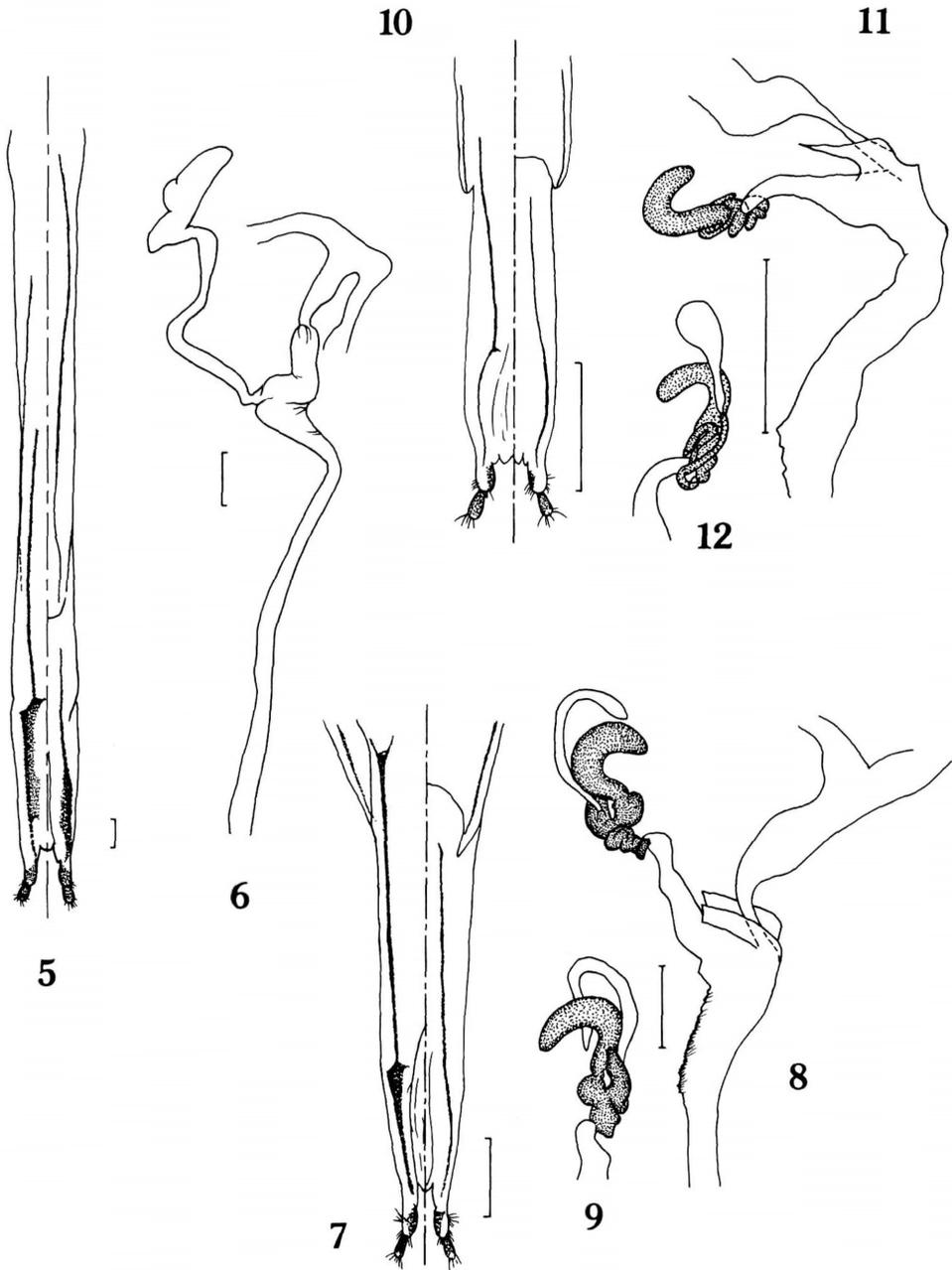
Vesperus strepens (FABRICIUS, 1792)

(Figs. 5-6)

Collecting data of the material used. San Rema, Italia, F. MULER leg.; Venelles, Bouches du Rhone, France, VIII-1982, J. DUTRU leg.

Paraproct rather long, its baculi thick and almost straight; valvifer indistinct; each coxite baculum very thick but thinned in apical fourth; coxite lobes sclerotized except for basal and apical parts, with tactile hairs; stylus moderate in size, articulated to the tip of each coxite lobe, and bearing tactile hairs; dorsal baculi very short, thickened towards posterior parts but thinned at apices; proctiger extremely long, with two pair of baculi, the inner one about one and half times as long as paraproct baculi, and slightly sinuate, the outer one three-fourths as long as the inner; vagina long and narrow, bent near base, its basal part obviously swollen and constricted at the part connected with common oviduct; vaginal plates absent; bursa copulatrix absent; spermatheca not forming a sclerotized capsule, but existing as a curved membraneous pouch; spermathecal duct not clearly distinguished from spermatheca, entering into the swollen part of vagina.

Notes. *Vesperus strepens* has the female reproductive organs basically very similar to those of *Philus*. In fact, it is almost impossible to find any important difference



Figs. 5-12. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 5-6, *Vesperus strepens*; 7-9, *Distenia gracilis* – separated spermatheca is shown in Fig. 9; 10-12, *Tengius ohkuboi* – separated spermatheca is shown in Fig. 12. (Scale: 0.5 mm.)

between the two, though the membranous spermatheca of the former is smaller than that of the latter and is of different configuration. This led me to conclude that the two genera belong to the same group, as will be discussed in the next chapter.

Family Disteniidae

Tribe Disteniini

Distenia gracilis (BLESSIG, 1872)

(Figs. 7-9)

Collecting data of the material used. Tobira Spa, Nagano Pref., 21 ~ 26-VII-1971, H. KOBAYASHI leg.

Paraproct moderate in size, its baculi very thick, straight and somewhat bifurcate at the base; valvifer indistinct; coxite with rough surface, each baculum very thick at base and narrowed towards apex; coxite lobes sclerotized at each inner part, with tactile hairs; stylus articulated to the tip of each coxite lobe, sclerotized except for apex and bearing tactile hairs; dorsal baculi slightly sinuate and longer than paraproct baculi; proctiger baculi long and almost straight; vagina rather broad at basal part, and with many fine wrinkles behind bursa copulatrix; vaginal plates oblong, truncated at each apex; vagina rather broad at basal part, and with many fine wrinkles behind bursa copulatrix; bursa copulatrix tubular; spermatheca large, heavily sclerotized and of very intricate structure, its main part narrow, strongly bent at middle and basally with a protrusion, basal part irregularly twisted and with rather broad protrusion to which attaches the gland at the middle part, and directly connected with the apex of bursa copulatrix; spermathecal duct absent.

Notes. This species is very peculiar in the intricate structure of the spermatheca, which directly joins the bursa copulatrix. Absence of the spermathecal duct has not been known in the other groups of cerambycid beetles, and as will be shown for the genus *Tengius*, may be regarded as being characteristic of the disteniines.

Tengius ohkuboi MATSUSHITA, 1938

(Figs. 10-12)

Collecting data of the material used. Komenono, Ehime Pref., 15-VI-1980, Y. KUSUNOKI leg.

Paraproct rather short with almost straight baculi; valvifer indistinct; coxite baculi thin and sinuate; coxite lobes rather broad, sclerotized at each inner part, with tactile hairs; stylus articulated to the tip of each coxite lobe, sclerotized except for apex and bearing tactile hairs; dorsal baculi slightly sinuate and longer than paraproct baculi; proctiger baculi very long and thin; vagina curved near base; vaginal plates wide at bases, and narrowed towards apices which are acute; bursa copulatrix tubular, somewhat broad at basal part but narrowed towards apex; spermatheca heavily scler-

rotized and of very intricate structure, its apical part narrow and C-shaped, basal part very narrow and strongly twirled several times, with two narrow protrusions, the gland being attached to the apex of one of the protrusions, and directly connected with the apex of bursa copulatrix; spermathecal duct absent.

Notes. Though considerably differing from *Distenia* in external morphology, *Tengius* has the female reproductive organs basically identical with those of the latter. This seems to serve as a sound proof for the isolated status of the group.

Family Cerambycidae

Subfamily Parandrinae

Parandra (Parandra) formosana MIWA et MITONO, 1939

(Figs. 13–14)

Collecting data of the material used. Bansho, Taiwan, VIII, T. KANO leg.

Paraproct rather long, gently narrowed towards apical portion, not perfectly tubular, and distinctly separated into sternite and tergite at its anterior part, the former well sclerotized and forming a plate which is warped dorsally at the lateral parts; paraproct buculi long, thick and straight, extending throughout; valvifer indistinct; coxite, without baculi, very short and heavily sclerotized at the ventral part; coxite lobes also heavily sclerotized, not clearly separated from coxite, rather rapidly narrowed towards apices, and with tactile hairs in a shallow lateral depression lying at about apical third of each lobe; stylus small, very short, transverse, heavily sclerotized, and articulated to the dorsal side of coxite lobe, with the tip divided into two convexities and devoid of tactile hairs; dorsal baculi clear in apical part, though disappearing in anterior part; neither proctiger nor intersegmental membrane, so that the vagina and vaginal plates are wholly embraced by paraproct; vagina very short; vaginal plates oval and stiff; bursa copulatrix ovoid, narrowed basally to form a short bursal duct; spermatheca with many fine wrinkles in narrow basal part, abruptly bent behind the narrow portion, with two small convexities lying transversely at the inner side of the middle part, and slightly curved at the apical part, with the gland opening near the base; spermathecal duct thin, short, slightly sinuate, and entering into the base of bursa copulatrix.

Notes. Judging from the female reproductive organs of this species, *Parandra* seems to be most primitive in all the cerambycids in a strict sense, because the paraproct, which is heavily sclerotized, is not perfectly tubular, being separated into clearly defined sternite and tergite in the anterior part, and completely embraces the vagina and its plates, and the styli are articulated to the dorsal side of the coxite lobes. These features are not found in any other cerambycids that I have examined.

Subfamily Prioninae

The female reproductive organs of the representative Japanese species of this sub-

family were studied by KUBOKI (1980), who described and illustrated those of six species. Though his terminology is to some extent different from mine, his accounts accord well with the results of my own study, and I do not think it necessary to repeat. Only the problem is in his observation of the female genitalia of *Megopis* (*Aegosoma*) *sinica*, which is not very accurate and needs a re-examination. In the following lines, I will give descriptions and illustrations of those of this species in comparison with those of *M. (Spinimegopis) formosana ishigakiana*.

Tribe Prionini

Megopis (Spinimegopis) formosana ishigakiana

YOSHINAGA et NAKAYAMA, 1972

(Figs. 15–16)

Collecting data of the material used. Bannadake, Ishigakijima Is., Okinawa Pref., 14–V–1973, T. NAKANE leg.

Paraproct moderate in size, and with rough surface, its baculi very thick, almost straight; valvifer indistinct; coxite with rough surface, each coxite baculum very wide at base, tapered towards apex, and briefly extending anteriorly as a narrow baculum; each coxite lobe short and very thick, sclerotized in apical half, with a bundle of fine tactile hairs on the ventral face, and with very short tactile hairs at the apex; stylus articulated to the lateral face of coxite lobe, sclerotized except for the apex which bears tactile hairs; dorsal baculi fairly short and almost straight; proctiger baculi very short, thick and abruptly bent at apices; vagina short and broad, bent just behind base; vaginal plates narrow and sinuate; bursa copulatrix forming a large pouch, with many wrinkles on the surface; spermatheca bent at apical third, somewhat broadened in basal half, with narrow gland on the lateral face; spermathecal duct rectangularly bent near base, and entering into bursa copulatrix near its base.

Notes. In the other species of this subgenus, *Megopis (Spinimegopis) malasiaca* HAYASHI, 1976, from Malaysia, the female reproductive organs are similar in general features to those of this species, with the exception of longer coxite lobes and smooth surface of bursa copulatrix without wrinkles.

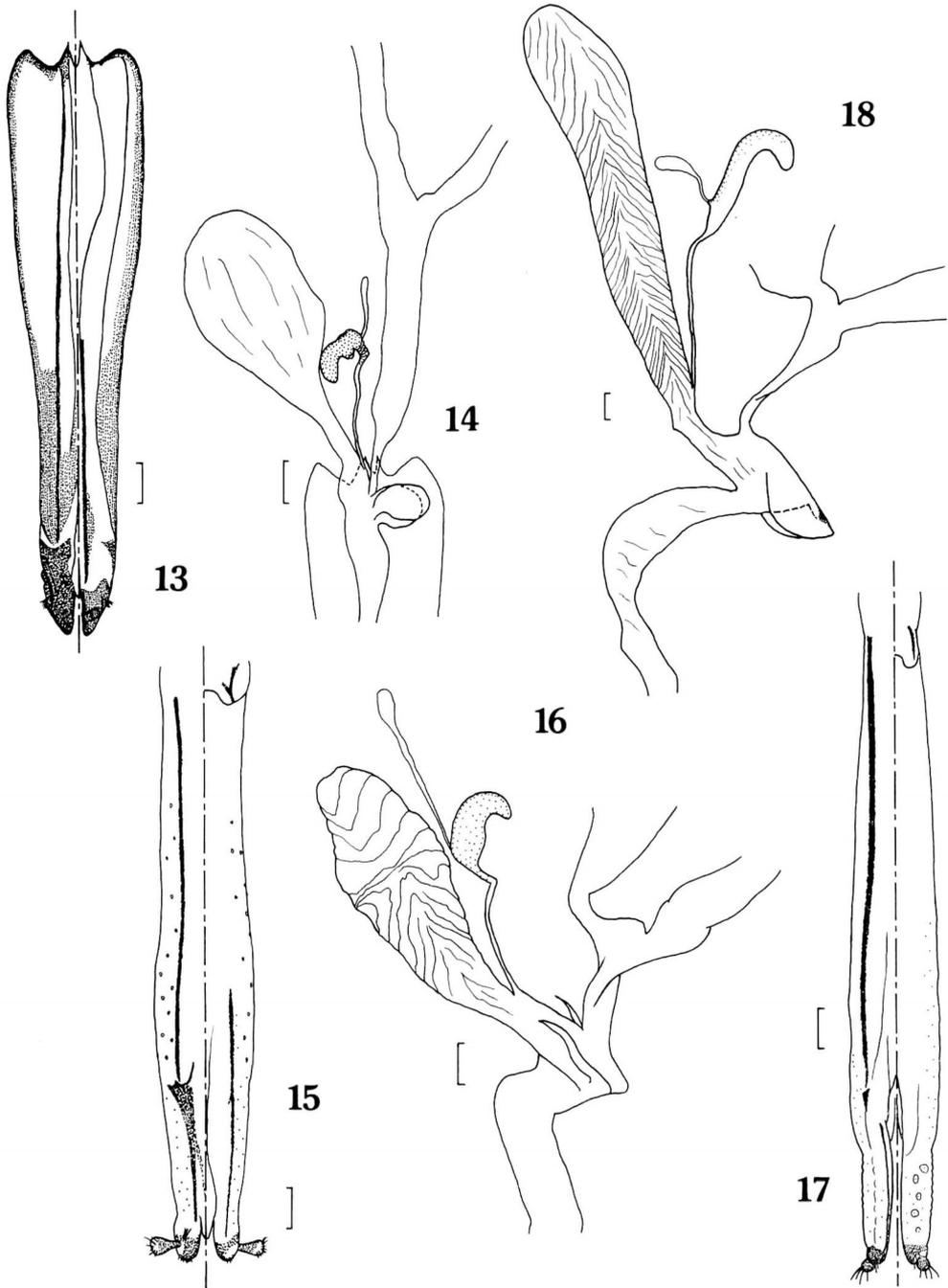
Aegosoma sinicum sinicum WHITE, 1853

(Figs. 17–18)

KUBOKI, 1980, *New Entomol.*, Ueda, **29**, p. 71, fig. 3.

Collecting data of the material used. Komoro-shi, Nagano Pref., VII–1968, Y. NAGASHIMA leg.

Paraproct rather long, its baculi very thick and almost straight; valvifer indistinct; coxite extremely short, with a pair of very short baculi; coxite lobes very long, broad, rough on the surface, and slightly constricted before sclerotized apices, with thin baculi



Figs. 13-18. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 13-14, *Parandra (Parandra) formosana*; 15-16, *Megopis (Spinimegopis) formosana ishigakiana*; 17-18, *Aegosoma sinicum sinicum*. (Scale: 0.5 mm.)

along the internal sides; stylus small and subglobular, articulated to the apico-lateral face of the dorsal side of each coxite lobe, sclerotized except for apex, and with long tactile hairs; dorsal baculi absent; proctiger baculi thin, very short and almost straight; vagina broad and curved; vaginal plates stiff, semicircular, fused to each other along the anterior margins, and with a pair of small sclerotized patches; bursa copulatrix very long and broad, with many fine wrinkles on the surface; spermatheca long and narrow, bent at apical third, poorly sclerotized except for the outer surface, and with the gland on the lateral face of basal part; spermathecal duct thin, curved near the capsule, and entering into the basal part of bursa copulatrix.

Notes. Though the peculiarity of the female genital organs of this species was already pointed out by KUBOKI (*loc. cit.*), his description and drawing are not sufficient for illustrating it. I therefore give here a more detailed description and drawings. They are peculiar because the paraproct lacks dorsal baculi, that the coxite is extremely short, and the coxite lobes are very long, bear baculi, and surmounted with small styli at the dorso-lateral faces just before the apices. These modifications seem to have been formed in relation to the extreme elongation of the 8th abdominal segment, which takes the role of ovipositing. As was already shown, *Megopis formosana ishigakiana* does not show any of these peculiarities of the female genitalia. The differences between them cannot be considered merely specific, and I herewith revive the generic status of *Aegosoma* though it has usually been regarded by recent specialists as a subgenus of *Megopis*.

Subfamily Apatophysinae

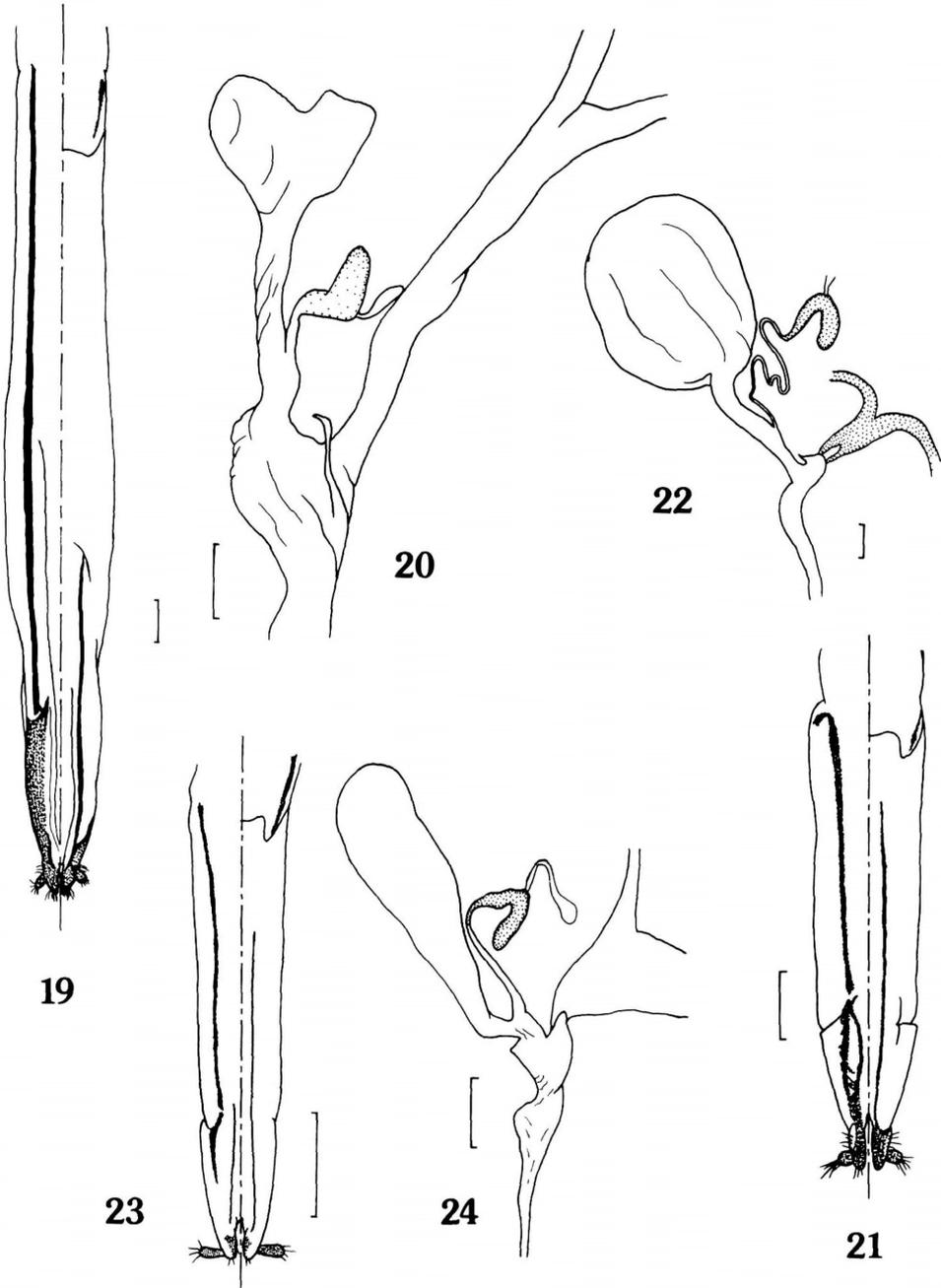
Apatophysis barbara LUCAS, 1858

(Figs. 19–20)

Collecting data of the material used. Mraier, MARTIN leg.

Paraproct very long, each baculum very thick and almost straight; valvifer indistinct; coxite somewhat narrowed towards the apical portion, its baculi very thick and extending almost all through the ventral side of coxite; each coxite lobe well sclerotized, with tactile hairs on the lateral face of basal and apical portions; stylus small, dorso-laterally articulated to the middle part of coxite lobe, and bearing tactile hairs at the apex; dorsal baculi thick, straight, and about a half as long as paraproct baculi; proctiger baculi very short, almost straight; vagina broad at base; vaginal plates very narrow and sinuate; bursa copulatrix broad in apical half and tubular in basal half; spermatheca broad, poorly sclerotized, lightly bent at middle, and with the gland at the lateral side of its middle part; spermathecal duct short, very thick, and entering into the basal part of bursa copulatrix.

Notes. This species closely resembles the prionines in the following features of the ovipositor: coxite and coxite lobes heavily sclerotized; styli articulated to coxite lobes dorso-laterally; both dorsal and proctiger baculi very short. It is most probable



Figs. 19-24. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 19-20, *Apatophysis barbara*; 21-22, *Spondylis buprestoides*; 23-24, *Tetropium castaneum*. (Scale: 0.5 mm.)

that the true affinity of *Apatophysis* is towards the Prioninae, rather than towards the Lepturinae or Cerambycinae.

Subfamily Spondylinae

Tribe Spondylini

Spondylis buprestoides (LINNÉ, 1758)

(Figs. 21–22)

Collecting data of the material used. Shimonome D.I., Ishioka-shi, Ibaraki Pref., 18–VII–1981, M. KUBOTA leg.

Paraproct moderate in size, each baculum very thick, almost straight but curved at base and extending laterad; valvifer indistinct; coxite clearly separated from paraproct, rapidly narrowed towards coxite lobes, its baculi being thick and longitudinally twofold in basal halves; coxite lobes rather heavily sclerotized except for latero-basal parts which bear tactile hairs, and narrowed towards apices which also bear tactile hairs; stylus very short and articulated to the lateral face of each coxite lobe, being almost globular in form, and bearing long tactile hairs; dorsal baculum thick, almost straight, and slightly longer than paraproct baculi; proctiger baculi very short; vagina simple, short and narrow; vaginal plates broad at bases, and narrowed towards acute apices; bursa copulatrix very large and widely swollen in apical half, the other half forming a narrow bursal duct; spermatheca narrow and strongly bent at middle; spermathecal duct very thin, curved many times, and entering into bursal duct; lateral and common oviducts unusually stiff.

Notes. *Spondylis buprestoides* is peculiar in having the coxite clearly separated from the paraproct, very small subglobular stylus articulated to the lateral face of each coxite lobe, and unusually stiff oviduct. So far as concerned with the female reproductive organs, it resembles members of the prionines rather than those of the asemines. This problem will be taken up again in the Discussion to be given on later pages.

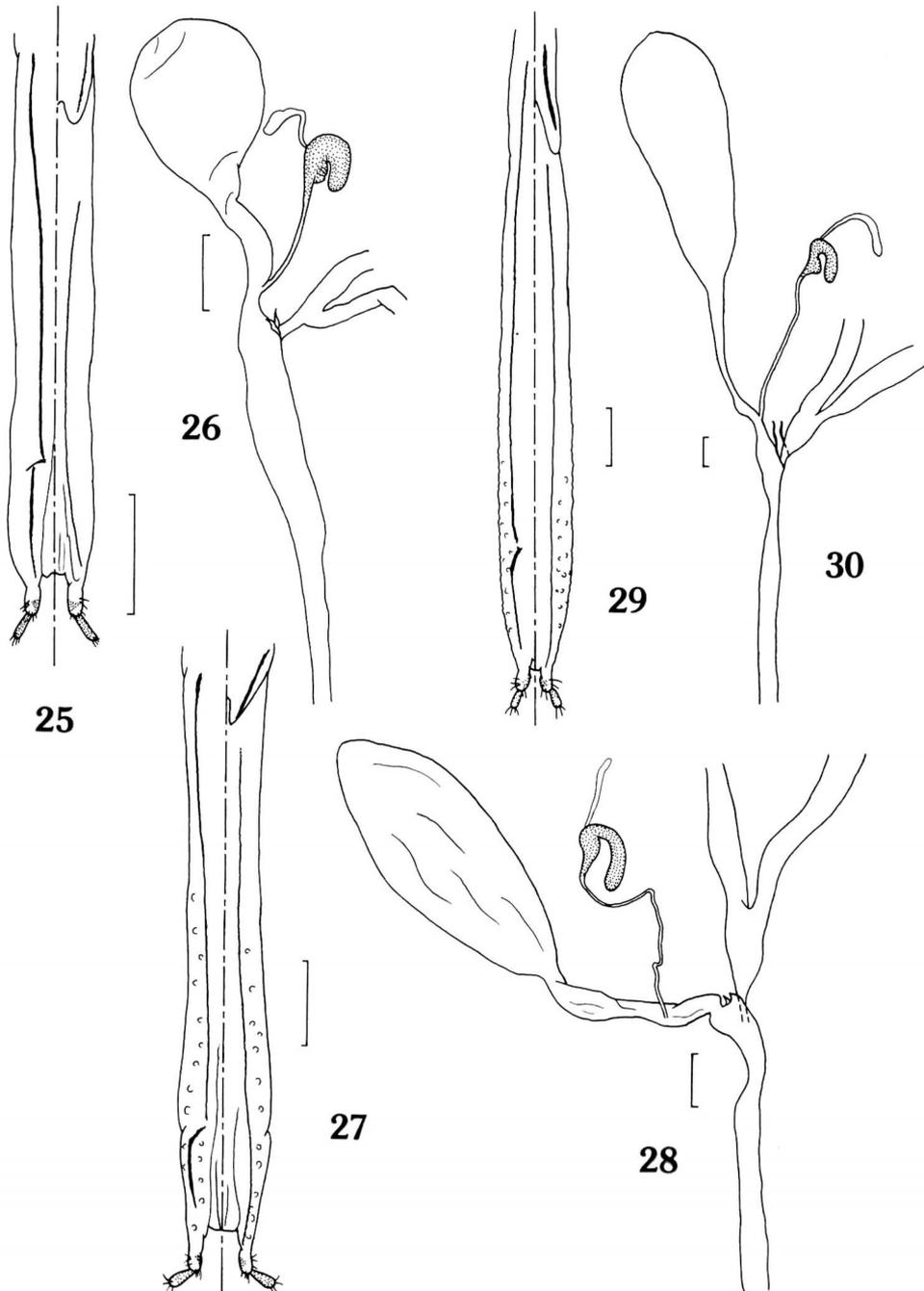
Tribe Asemini

Tetropium castaneum (LINNÉ, 1758)

(Figs. 23–24)

Collecting data of the material used. Tomuraushi, Hokkaido, 5–VII–1968, S. OKAJIMA leg.

Paraproct of moderate size, its baculi thick and almost straight; valvifer distinct, with thick baculi, which are bent inwards at basal third, and not continuous to coxite baculi, the latter being thin and almost straight; coxite lobes short, obtusely pointed at apices, sclerotized at each inner part, and with tactile hairs; stylus moderate in size, abaxially articulated to the lateral face of coxite lobe, and bearing tactile hairs at the



Figs. 25-30. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 25-26, *Nothorhina punctata*; 27-28, *Asemum amurense*; 29-30, *Arhopalus coreanus*. (Scale: 0.5 mm.)

apex; dorsal baculi almost the same in length as paraproct baculi; proctiger baculi thick and straight; vagina constricted near base; vaginal plates very broad at bases, narrowed towards rounded apices; bursa copulatrix long, tubular, dilated towards apex; spermatheca narrow, strongly bent at middle, lightly swollen near middle, and narrowed towards base, with the gland at about middle; spermathecal duct rather thick, straight, and entering into the base of bursa copulatrix.

Notes. This species is characterized by having distinct valvifer and the styli abaxially articulated to the lateral faces of the coxite lobes. It is, however, otherwise similar to other asemines.

Nothorhina punctata (FABRICIUS, 1798)

(Figs. 25–26)

Collecting data of the material used. Tama-bochi, Fuchû-shi, Tokyo Met., 6–IX–1979, T. NIISATO leg.

Paraproct rather long, with almost straight baculi; valvifer indistinct; coxite baculi almost straight, and weakly sclerotized; each coxite lobe rather narrow, weakly sclerotized at the inner part, and bearing tactile hairs; stylus long and very narrow, only slightly dilated apicad, weakly sclerotized except for apex, and with tactile hairs; dorsal baculi slightly shorter than paraproct baculi; proctiger baculi almost straight; vagina long, tapered posteriorly; vaginal plates short, very narrow and sinuate; bursa copulatrix tubular in basal half but forming a large pouch in apical half, and narrowed near the middle; spermatheca rather broad, strongly bent at middle, and inwardly constricted at base, with the gland before the middle; spermathecal duct narrow, straight, and entering into the base of bursa copulatrix.

Notes. Among the Japanese species of asemine cerambycids, this species is peculiar in that the styli are unusually narrow.

Asemum amurense KRAATZ, 1879

(Figs. 27–28)

Collecting data of the material used. Ochiai, Yamanashi Pref., 29–VI–1977, K. SASAKI leg.

Paraproct very long with rough surface, its baculi thin and very slightly sinuate; valvifer indistinct; coxite with rough surface, each baculum rather thick and moderately curved at the anterior part; coxite lobes lightly sclerotized at each inner part, with tactile hairs; stylus rather long, sclerotized except for the apex which bears tactile hairs; dorsal baculi thin, very long, obviously longer than paraproct baculi, and slightly sinuate; proctiger baculi almost straight; vagina lightly arcuate near the base; vaginal plates very broad at bases and abruptly narrowed towards acute apices; bursa copulatrix very large, ovoid in apical two-thirds, with rather long bursal duct; spermatheca narrow, rather rapidly dilated from near the base, and abruptly bent at middle; spermathe-

cal duct very thin, sinuate and then twisted, entering into the basal third of bursal duct.

Arhopalus coreanus (SHARP, 1905)

(Figs. 29–30)

Collecting data of the material used. Anegasaki, Miyako-shi, Iwate Pref., 1~2–VIII–1981, A. TAKASU leg.

Paraproct very long with rough surface at the posterior part, its baculi thin and almost straight; valvifer indistinct; coxite with rough surface, its baculi lightly curved; each coxite lobe moderate in size, slightly sclerotized at the inner part, and with tactile hairs; stylus slightly sclerotized only at base, and bearing tactile hairs; dorsal baculi thin, slightly longer than paraproct baculi, and almost straight; proctiger baculi straight; vagina straight though constricted behind base; vaginal plates very thin, filamentous, and sinuate; bursa copulatrix very large, elongated ovoid, with bursal duct which occupies basal third; spermatheca narrow, strongly bent at middle, with an inner protrusion before the base; spermathecal duct very thin, slightly sinuate, and entering into the basal part of bursa copulatrix.

Megasemum quadricostulatum KRAATZ, 1879

(Figs. 31–32)

Collecting data of the material used. Arashiyama, Asahikawa-shi, Hokkaido, 29–VII–1981, T. MATSUMOTO leg.; Pippu, Hokkaido, 29–VII–1978, T. MATSUMOTO leg.

Paraproct extremely long, with the surface rough at the posterior part; paraproct baculi almost straight, rather thick, and becoming thicker anteriorly; valvifer distinct, its baculi not continuous to coxite ones, extending obliquely to the external sides of the latter; coxite baculi also oblique, straight, and subparallel to valvifer baculi, each internally branching off a short spur behind middle; coxite lobes moderate in size, slightly sclerotized at each inner part, with tactile hairs; stylus slightly sclerotized except for apex, with tactile hairs; dorsal baculi extremely long, slightly longer than paraproct baculi, thin and slightly sinuate; proctiger baculi straight; vagina narrow and curved at the anterior part; vaginal plates narrow, externally convex behind middle, and blunt at the tips; bursa copulatrix very long, tubular in proximal two-thirds, and swollen in apical third, with two minute pouches at the apex; spermatheca narrow, strongly bent at middle, slightly broadened inwards at base; spermathecal duct narrow, coiled twice, and entering into the basal part of bursa copulatrix.

Notes. Among the Asemini, *Megasemum* and *Cephalallus* are peculiar in having distinctly formed valvifer, whose baculi are divergent posteriad and run obliquely to the external sides of the coxite baculi. The same peculiarity is also found in *Tetropium*, but in this genus, the styli are articulated to the external faces of the coxite lobes as was already described, a feature which does not exist in *Megasemum* nor in *Cephalallus*.

Cephalallus unicolor GAHAN, 1906

(Figs. 33–34)

Collecting data of the material used. Yuwan, Uken-son, Amami-Oshima Is., Kagoshima Pref., 12~14-X-1988, A. SAITO leg.; Taken, Uken-son, Amami-Oshima Is., Kagoshima Pref., 12-X-1988, Y. NISHIKAWA leg.

Paraproct long, with thin straight baculi; valvifer distinct, each baculum discontinuous to coxite one, running to the external side of the latter; coxite baculi subequal in length to valvifer baculi and feebly divergent posteriad; coxite lobes hardly sclerotized, and bearing tactile hairs; stylus also hardly sclerotized, with tactile hairs; dorsal baculi long and thin, longer than paraproct baculi; proctiger baculi straight; vagina gradually narrowed towards apex; vaginal plates filamentous and sinuate; bursa copulatrix very large and long, its basal half being narrow but the remaining part forming an elongated ovoid pouch; spermatheca narrow, strongly bent at middle, slightly constricted at the apical fourth, and slightly convex inwards in basal half; spermathecal duct narrow, coiled once just behind the base of spermatheca, and entering into the basal part of bursa copulatrix.

Tribe Atimiini

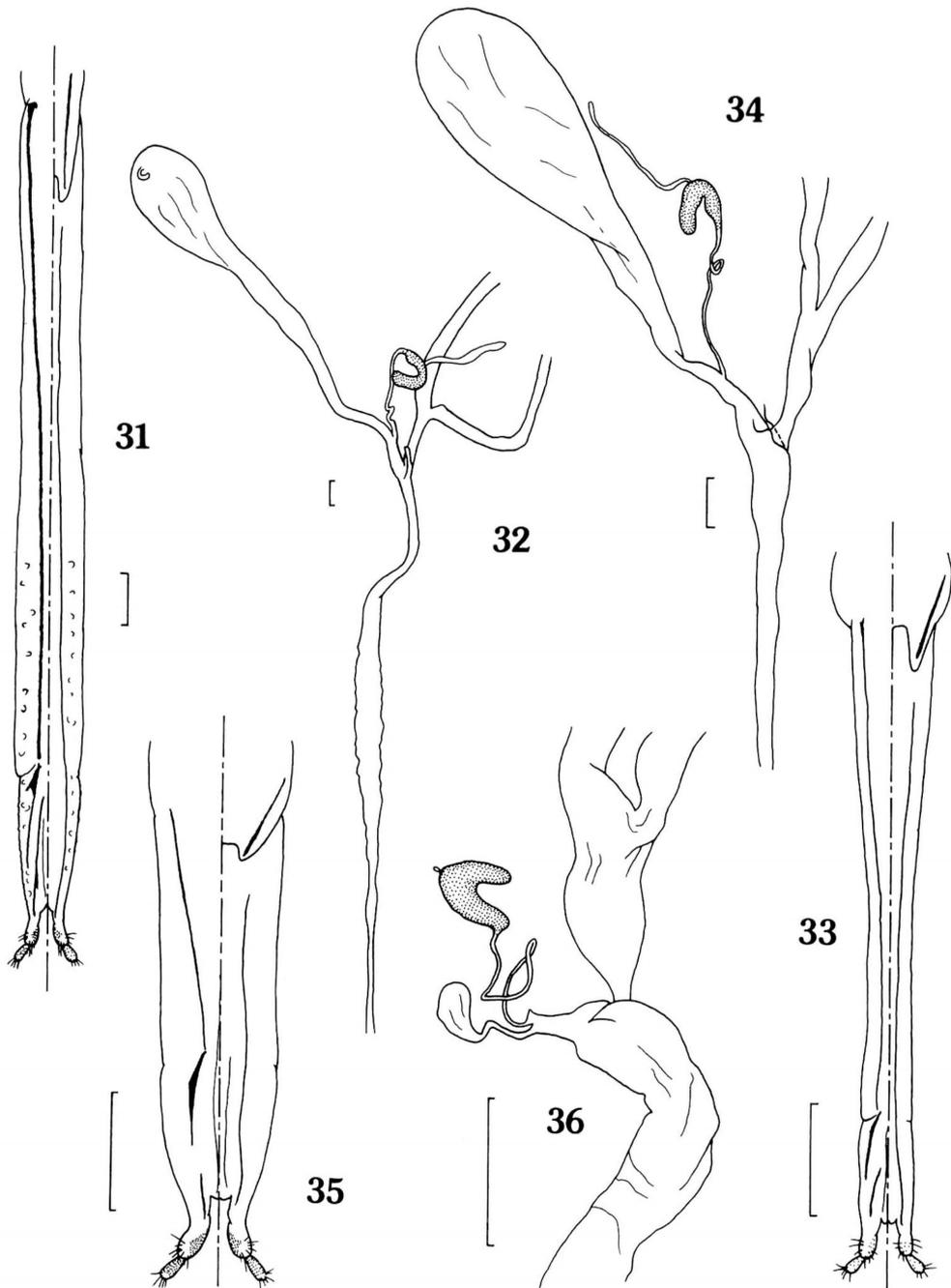
Atimia okayamensis HAYASHI, 1972

(Figs. 35–36)

Collecting data of the material used. Takamatsu, Okayama Pref., 24-IV-1976, T. WAKEJIMA leg.

Paraproct broad and very short, its baculi straight; valvifer distinct, with its baculi rather thick though weakly sclerotized, and distant from very short coxite baculi; coxite lobes moderate in size, sclerotized at each inner part, and with tactile hairs; stylus narrow and rather long, sclerotized except for the apex, and bearing tactile hairs; dorsal baculi thin and very slightly sinuate, much longer than paraproct baculi; proctiger baculi straight; vagina bent near the base; vaginal plates very broad at bases and rapidly narrowed towards acute apices; bursa copulatrix very small, fairly broad in basal third, very narrow at middle, and somewhat swollen in apical third; spermatheca clearly distinguished from the duct as a capsule, not gradually continuing to the latter, strongly bent and broadest at the middle part, and strongly constricted at the base; spermathecal duct very thin, curved and entering into the apical end of the broad basal third of bursa copulatrix.

Notes. This species is characterized by the very short paraproct, distinct valvifer whose baculi are evidently distant from very short coxite baculi, clearly defined spermatheca with complete basal part, and small bursa copulatrix. For these reasons, the tribe Atimiini can be separated from the Asemini, and may be regarded as a link between the Spondyliinae and Lepturinae.



Figs. 31–36. Ovipositor (left half: ventral view; right half: dorsal view) and internal reproductive organ (ventral view). — 31–32, *Megasemum quadricostulatum*; 33–34, *Cephalallus unicolor*; 35–36, *Atimia okayamensis*. (Scale: 0.5 mm.)

Discussion

As was mentioned in the introduction, systematic status and relationship of most groups dealt with in this paper have been repeatedly discussed from various angles, and yet, consensus of specialists' opinions has not been gained for many of them. It cannot be said that even nomenclatorial problems have been clarified satisfactorily. It is for this reason that rather lengthy explanations seem needed for illustrating an outline of historical taxonomic changes before giving the results of my own studies on respective groups.

Philines and Vesperines

The beetles belonging to the Philini and Vesperini are very peculiar in facies; many of them are fully winged and not unlike lepturines, but females of certain species are apterous and almost look like crickets at first sight. They are very similar to each other not only in general appearance but also in many basic features including absence of the labial peduncle and the mesonotal stridulatory file, poor development of the lacinia, and presence of plurisetose empodium on the claw segment. They are, however, different in several seemingly critical characters that include cephalic conformation, presence or absence of distinct lateral margins on prothorax, and wing venation. Very strange larvae with many peculiarities are known for several *Vesperus*, which led ŠVÁCHA to conclude that the vesperines do not belong even to the cerambycoid complex. Unfortunately, larvae have not been known for any philines, which may prove very important for determining the true relationship between the two tribes.

It was THOMSON (1860, pp. 284, 297) who first recognized the isolated status of *Philus*. He erected the Philitae as a division of the Groupe Prionitae Verae of the Tribu Prionitae. LACORDAIRE (1869 a, pp. 157, 159) also regarded *Philus* as a prionine, but instead of recognizing its own group in the subfamily, he placed it in his Groupe Monodesmides.

The arrangement proposed by THOMSON and LACORDAIRE was accepted by many later workers. For instance, GAHAN (1906, pp. 4, 54) regarded it as a group (=tribe) of the Prioninae, though he commented that the Philini "occupy a somewhat exceptional position among the Prioninae and appear to be primitive in relation to the other members of the subfamily." He also noted that the members of the Philini "are closely related to *Mantitheus*, FAIRM., a genus that inhabits Northern China, and are related also, but less closely, to the Mediterranean genus *Vesperus*, LATR., which some authors class with the Lepturinae." GRESSITT (1951, pp. 9, 29–31) followed GAHAN's classification and placed the tribe Philini at the end of the Prioninae, but in his later work collaborated with RONDON (1970, pp. 5, 12, 22), he treated it as an independent subfamily and placed it between the Prioninae and the Aseminae. LINSLEY (1962, p. 11) also was "inclined to consider the tribe as prionine, but as partly bridging the gap between the Prioninae and Lepturinae."

On the other hand, BOPPE (1921, pp. 13, 15, 25) regarded the Philini as a tribe of the Lepturinae and considered it to be an intermediary between the monodesmine

prionines and the lepturines. A similar view was adopted by TAMANUKI (1939, p. 54), who treated the Philini as an isolated tribe in the Lepturinae.

Finally, CROWSON (1955, pp. 141, 148) regarded the philines as belonging to an independent subfamily of the Cerambycidae. He noted that "there is some reason to regard them as on the whole the most primitive groups of the family." ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, p. 12) also considered the philines to be an independent subfamily, and emphasized probable importance of their larval characters, which he surmised "may well lead to great taxonomic changes." It can be said that most recent authors abandoned the idea to place the Philini in the Lepturinae and regarded it as one of the most primitive groups of the cerambycid complex.

Next to be considered is the problem concerning the Vesperini, which was first recognized by MULSANT (1839, p. 214) under the name of the Vespéaires as a Branche of his Famille Rhagiens of the Groupe Dérécéphalides (MULSANT's concept of Tribus and Familles is reverse to our present usage of families and tribes). He placed two Branches, Vespéaires and Rhagiaires, in the Rhagiens, and together with the Famille Lepturiens, put it in one of the three Groupes of the Tribu des Longicornes (=Family Cerambycidae). THOMSON (1860, p. 159) did not accept MULSANT's opinion, and placed *Vesperus* in his Division Stenocoritae in the Sous-groupe Pseudolepturitae of the Groupe Lepturitae Verae, whereas LACORDAIRE (1869 b, pp. 233, 236) placed *Vesperus* in the Tribu Vespérides, and put it, together with the Tribu Apatophysides, in the Cohorte II (Cérambycides Vrais Souterrains) of the subfamily Cérambycides.

Later authors almost invariably regarded *Vesperus* as an aberrant member of the Lepturinae, with the exception of GAHAN (1906, p. 55) who considered it to be related to the Philini. AURIVILLIUS (1912, pp. 157–159) placed it in the Lepturini together with *Mantitheus*, though he (pp. 156–157) regarded the Philini as an independent tribe of the Cerambycinae. BOPPE (1921, pp. 13, 15, 28) classified the Vesperini as a tribe of the Lepturinae, and put it next to the Philini. PLANET (1924, pp. 37, 38) also regarded the Vespéaires (=Vesperini) as a section of the Tribu Lepturiens (=Lepturinae) but considered it to be a much isolated group. CROWSON (1955, p. 148) provisionally included *Vesperus* in the Lepturinae, noting that the Lepturinae have "possible connections to the Philini (via forms like *Vesperus* and *Mantitheus*)." He also pointed out the peculiar aspects of *Vesperus*, which distinguish it from the typical lepturines.

In 1987, a drastic taxonomic change was proposed by ŠVÁCHA in ŠVÁCHA and DANILEVSKY (pp. 11, 17–24), who not only regarded the Vesperidae as an independent family but noted that it "lacks any Cerambycid specializations, differing in principal characters from all other present families, and should be no longer treated in the Cerambycoid complex."

ŠVÁCHA's opinion was based mainly upon larval peculiarities of *Vesperus*, but agrees well with the result of my examination of the female reproductive organs of *V. strepens*. As was described in the previous chapter, the female genitalia of this species lack the vaginal plates, the bursa copulatrix and the sclerotized spermatheca,

the last one of which remains membranous though fairly stiff. This must be a primitive condition not found in any other groups of cerambycid beetles. This alone can be regarded as a feature of familial importance, though I cannot dare to say that *Vesperus* does not belong to the cerambycid complex simply on the basis of this peculiarity.

So far as I am aware, the only other group that possesses the same type of female genitalia is the Philini, of which *Philus pallescens* and *Mantitheus pekinensis* were available for my study. Their reproductive organs are basically identical with those of *Vesperus*, and the very close similarity cannot be explained simply by convergence or other causes. They must be regarded as a positive proof that the Philini and Vesperini are sister groups derived from a common ancestry. I am therefore going to unite the two into a single family, the Vesperidae.

Here arises the problem of three major differences, which have usually been considered diagnostic for distinguishing the Vesperini from the Philini. One of them, the presence or absence of prothoracic lateral margins, which has been used in placing the Philini in the Prioninae and the Vesperini in the Lepturinae, does not seem so important to me, since the elevated margins are not perfect even in the former and probable vestiges of them, though extremely brief, can be observed in the latter. The difference in cephalic conformation, constricted at the neck in the latter but not so constructed in the former, does not seem decisive, either, since exceptions have been known among the true lepturines. Thus, only the clear difference now recognized between the Philini and the Vesperini is in the wing venation, which is of the lepturine type in the latter but characterized by the presence of a large anal cell in the former. Mainly for this reason, I provisionally retain the two tribes, Philini and Vesperini, in the family Vesperidae, though even the wing venation is otherwise similar to each other.

Disteniines

The disteniines form a small group of lepturine-like beetles mainly characterized by the following combination of imaginal and larval features: in the adult, scalpriform mandibles, clypeus oblique to frons, metendosternite not hylecoetoid, and wings lacking a spur in the radio-medial cross-vein; in the larva, complete absence of gular bridge, which makes the submentum directly articulating with prothoracic praesternum, and very broad metatentorial bridge forming a large part of cranial ventral wall.

THOMSON (1860, pp. 134, 181) is the first author who recognized a supra-generic taxon for *Distenia* and others. He erected the Distenitae as a Groupe of his Sous-tribu Cerambycites Verae, and noted that "ces insectes sont très-remarquables par leurs antennes insérées en avant des yeux, ce qui les distingue de tous les autres groupes de Cérambycites vrais, et offrent une certaine analogie avec les Lepturites." LACORDAIRE (1869 b, p. 225) followed THOMSON, but separated it, together with the Hystérarthrides, from all the other Cérambycides, considering that the division to which they belong was much isolated.

Most later authors regarded the disteniines as an independent subfamily, and sought its affinity to the Lepturinae. GAHAN (1906, pp. 2, 58) considered it to be

closely related to the Lepturinae, but noted that "the differences between them are at the same time strong." BOPPE (1921, p. 2) treated it as a subfamily related to the Prioninae, with the comment that the wing venation is of the lepturine type. It was regarded by TAMANUKI (1939, p. 1) as the closest relative of the Lepturinae, and was placed by GRESSITT (1951, pp. 8, 43) between the Aseminae and Lepturinae. PLAVILSTSHIKOV (1936, pp. 103, 104, 479, 492) classified the members of the Cerambycinae into three major groups, Disteniites, Lepturites and Cerambycites. On the other hand, CROWSON (1955, pp. 141, 148) noted that the Disteniinae is a "clearly defined and natural" subfamily, but that "its affinities are by no means evident."

At the beginning of his classic work on the Cerambycidae of North America, LINSLEY (1961, pp. 59–68; 1962, p. 1) excluded the disteniines from the Cerambycidae and regarded them as to form an independent family. This view was based upon the combination of characteristics summarized at the head of this section, and was supported by GRESSITT and RONDON (1970, pp. 5–11), who divided the family into two tribes Cyrtanopini and Disteniini, and by ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, pp. 11–12, 33–38), who laid much emphasis upon the larval peculiarities, especially upon the absence of gula. However, LINSLEY's opinion has not been approved by Japanese specialists, all of whom retained the Disteniinae in the Cerambycidae (e.g., KOJIMA & HAYASHI, 1969, pp. XIX–XX, 6; HAYASHI, 1979, p. 1, 1984, pp. 1–2; KUSAMA & TAKAKUWA, 1984, pp. 151–152), nor by CHEREPANOV (1979, p. 60).

My study of the female reproductive organs of the two Japanese species, *Distenia gracilis* and *Tengius ohkuboi*, has shown that they are unique in the conformation of the spermathecae. The spermatheca itself is highly differentiated and is of extremely complicated structure. Besides, it directly joins the apex of the bursa copulatrix, and the duct which usually connects the two organs disappears completely. Such a peculiarity as this has never been known in all the other groups of cerambycid beetles, and seems to bear importance of higher taxonomic category. Adding these genitalic features to the external characteristics, I have concluded that the Disteniidae should be regarded as an independent family, which does not bear any direct relationship to the Lepturinae or any other subfamilies of the Cerambycidae.

Parandrines

Parandra LATREILLE, 1804, was originally placed in the famille des Cucujides, but was later transferred to the Longicornes. Though it was still separated in an independent family by THOMSON (1860, p. VIII) and others, all the authors after LACORDAIRE (1869 a, pp. 20, 21) regarded it as a close relative of the prionines. LACORDAIRE (*loc. cit.*) placed it in the Tribu des Parandrines, which he classified in the Prionides Aberrants of the Sous-famille des Prionides. The same view was adopted by LAMEERE (1919, p. 13), PLAVILSTSHIKOV (1936, p. 51) and GRESSITT (1951, p. 9), all of whom regarded it as a tribe of the Prioninae.

On the other hand, GAHAN (1906, p. 13) noted that the Parandrines "will have to be excluded" from the Prioninae and "may be regarded as a distinct subfamily."

CROWSON (1955, pp. 139, 145–147) recognized the Parandrinae as a subfamily, but made the following comment: “It seems more probable to me that *Parandra* is a true Prionid which has been modified at a fairly early stage to spend most of its imaginal life under bark.” LINSLEY (1961, pp. 61–70; 1962, pp. 1–3) considered it to be a subfamily related to the Prioninae and the most primitive extant cerambycid, and his view was supported by GRESSITT and RONDON (1970, p. 11) and recent Japanese authors (e.g., KOJIMA & HAYASHI, 1969, pp. XIX, 2; HAYASHI, 1979, p. 2, 1984, pp. 1, 2; KUSAMA & TAKAKUWA, 1984, p. 131). ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, pp. 14, 72–82) also treated parandrines as a subfamily but pointed out that it is probably included in the Prioninae and that it is not the most primitive cerambycid.

In short, close relationship between the parandrines and prionines has been recognized by all the recent specialists of cerambycid beetles. What brought about the difference of opinion about the taxonomic rank of the former is the unique external morphology of adult *Parandra*, which is not only *Passandra*-like in general appearance but also characterized by the slender pentamerous tarsi without pubescent ventral pad and the absence of a closed cell in the anal sector of the wing.

Unfortunately, I have been unable to examine the female reproductive organs of any Japanese specimens of the two species of *Parandra*, which are exceedingly rare and difficult to obtain. However, I have dissected a Taiwanese specimen of *P. formosana*, one of the two species recorded from the Ryukyus, and found that its genitalia are similar to those of North American *P. brunnea* (FABRICIUS) described and illustrated by KUBOKI (1980, p. 17, fig. 1).¹⁾ Main differences in the descriptions between KUBOKI's and mine seem to be attributable to poor observation of the former author, and the female genitalia of *Parandra* may be uniform so far as concerned with their basic structure.

What is most surprising about the *Parandra* genitalia is the conformation of the ovipositor, which possesses clearly separated sternite and tergite of the paraproct, and though unusually stiff, embraces the vagina and its plates with their anterior parts. Also, the styli are very small and of unique conformation, and are articulated to the dorsal side of the coxite lobes. These unique features clearly distinguish *Parandra* from the Prioninae and other subfamilies, and I feel it better to recognize the subfamily Parandrinae than to include *Parandra* in the subfamily Prioninae. Contrary to ŠVÁCHA's opinion (1987, p. 14), *Parandra* seems to me to be the most primitive type of cerambycid beetles, though my view is mainly based upon the characteristics different from those used by LINSLEY (1961, pp. 61–70) in forming his opinion.

Prionines proper

Though very diverse in general appearance of the adults, the prionines proper have usually been regarded as a well-defined phyletic group. This was supported by the structure of the female reproductive organs, that is, the styli articulated to the lateral faces of heavily sclerotized coxite lobes, short dorsal baculi, weakly sclerotized

1) KUBOKI misspelled the name as *Parandra* “*brunnae*”.

spermathecae, and so on. They are basically similar to one another except for *Aegosoma* (cf. KUBOKI, 1980, pp. 70–74, figs. 2–7).

The female genitalia of *Aegosoma sinicum* are peculiar in that the paraproct lacks the dorsal baculi, that the coxite is very short and with very long lobes, each of which bears a baculum, and that the styli are very small and articulated to the dorso-lateral faces of the coxite lobes. However, all these striking modifications seem to have taken place in relation to the unusual modification of the 8th abdominal segment, which becomes exceedingly elongated and functions as an ovipositor. In *Megopis* (*Spinimegopis*) *formosana ishigakiana*, which is obviously related to *A. sinicum* even though generically separated, the female genitalia do not show any of such modifications and the 8th abdominal segment is not modified to form an elongate tube, which seems to me to be a positive proof that the striking modification of the female genitalia found in *Aegosoma* is merely apomorphic. Besides, other genitalic features are essentially common between *Megopis* (*Spinimegopis*) and *Aegosoma*, which indicates that the latter is an aberrant offshoot of the typical prionine stock.

The female reproductive organs of *Psephactus remiger* are characterized by the small bursa copulatrix without bursal duct and the small and relatively simple spermatheca. I cannot say that these features are truly characteristic of the tribe Anacolini to which belongs the species under consideration, since the tribe is represented in Japan by only two species of *Psephactus*, and since no other anacolines, mostly tropical, were available for this study. For the time being, therefore, I prefer to regard them as the peculiarities of the Anacolini, leaving the final conclusion for future investigations.

As was noted at the beginning of this section, adults of the prionines proper are diverse in general appearance. They are usually large, beautiful, and often ornamented with spines and other accessories. No doubt because of this reason, they have attracted attention of collectors since old times and have been classified into many tribes and subtribes. Already at about the middle of the 19th century, THOMSON (1861, pp. 284–328) classified his Prionitae Verae into 12 Divisions (including the Philitae, etc.), and LACORDAIRE (1869 a, pp. 35–192) split his Prionides Vrais into 39 Groupes of 3 Cohortes (including *Philus*, etc.). LAMEERE's (1919) classification of the Prioninae comprises 7 Groupes (including the Parandrini) which are split up into 29 Sous-groupes.

Unfortunately, I am not in a position to discuss about the tribal classification of the subfamily. East Asia lies at the northern periphery of the distributional range of the prionines, which are essentially tropical. Only 13 prionine species belonging to 8 genera occur in the Japanese Islands, and the number and diversity do not increase much if the neighbouring areas are taken into account. It seems to me, however, that many of the tribes currently adopted are over-splitting and not equivalent to the tribes in the other subfamilies. In fact, many of them have been recognized solely on apomorphic characters, which are not reliable in classifying higher taxa. In my opinion, the eight prionine genera occurring in Japan had better be classified into only two tribes, Prionini and Anacolini, so far as judged from the comparative study of the

female reproductive organs. This view is, however, provisional, since more extensive investigations are necessary for drawing a satisfactory conclusion as regards the systematic status of the other "tribes" recognized in current classification.

ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, pp. 12–13) considered that the Prioninae including the Parandrini is sharply different from all the other subfamilies of the Cerambycidae, mainly because of the characteristic ventral structure of the head capsule and the flat type of the main sensillum on the second antennal segment in the larvae. I agree with his opinion from the study of the female reproductive organs, though *Spondylis* and *Apatophysis* show certain affinity to the prionines in this respect. This problem will be taken up in the following sections.

Apatophysines

Like the vesperines, the apatophysines were usually regarded as an aberrant group of the Lepturinae. THOMSON (1860, p. 368) placed *Apatophysis* in his Division Stenocoritae of the Lepturitae Verae. LACORDAIRE (1869 b, pp. 233, 234) erected the Tribu Apatophysides for *Apatophysis* and two other genera, and placed it, together with the Vespérides, in the Cohorte II (Cerambycides Vrais Souterrains) of the subfamily Cérambycides. AURIVILLIUS (1912, p. 160) placed it at the side of *Vesperus* and *Mantitheus* in the Lepturini, and GAHAN (1906, pp. 68–71) regarded it as a lepturine. PLAVILSTSHIKOV (1936, pp. 108, 109) classed *Apatophysis* in the Xylosteini of the Gruppya Lepturites of the Cerambycinae, and the same view was held by GRESSITT (1951, pp. 48–50), though the latter author regarded it as a subgenus of *Centrodera* J. LECONTE. In his later work with RONDON (1970, p. 26), GRESSITT raised it to a full genus though still classifying it in the Xylosteini.

Recently, DANILEVSKY (1979, p. 827) gave a subfamilial status to the Apatophysini LACORDAIRE, 1869, and based upon his study on the female, pupa and larva, showed that it is not related to the Lepturinae but has an affinity to the Cerambycinae. This opinion was supported by ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, p. 14), also on the basis of larval morphology.

I have been unable to examine any species of *Apatophysis* occurring in East Asia, but have dissected a female of *A. barbara* from North Africa. The result obtained clearly shows that it is widely different from the lepturines, but contrary to DANILEVSKY's opinion, it bears a close affinity to the prionines. Though the paraproct is unusually long for a prionine, both the dorsal and proctiger baculi are very short, the coxite with its lobes is heavily sclerotized, and the styli are articulated to the dorso-lateral faces of the coxite lobes, all characteristic of the prionines. In view of the combination of non-genitalic features of adults and larvae pointed out by DANILEVSKY and ŠVÁCHA, I am convinced that the Apatophysinae can be accepted as a good subfamily, but my opinion based upon the female reproductive organs is that the subfamily is related to the Prioninae and remote from the Cerambycinae.

Spondylines

Because of the aberrant external morphology of the adults, the spondylines were always regarded, in old times, as an isolated group of the Cerambycidae. For instance, MULSANT (1839, pp. 16, 17) treated the Spondyliens as one of the three familles (=tribes) of his Groupe des Procéphalides. THOMSON (1860, pp. 131, 261) regarded his Spondylitae as one of the three major groups of the Tribu Cerambycites, and noted that "les Spondylites font manifestement le passage des Cérambycites vrais aux Prionites." The same view was adopted by LACORDAIRE (1869 a, pp. 194, 197) though under the tribal name Spondylides.

However, most authors in this century placed the spondylines at the side of the asemines, either as a tribe or as a subfamily. PLAVILSTSHIKOV (1940, pp. 2, 5, 614, 616) regarded them as a tribe in his Gruppa Cerambycites of the subfamily Cerambycinae. GRESSITT (1951, pp. 31–32) regarded them as a tribe of the Aseminae, and the same view was held by CROWSON (1955, p. 149) and CHEREPANOV (1979, pp. 410–411). LINSLEY (1961, pp. 61–70; 1962, pp. 1, 62–63) raised it to a subfamily related to the Aseminae and Lepturinae, but commented that it "agrees in its more primitive characters with the Parandrinae, and to a lesser extent with the Prioninae." GRESSITT and RONDON (1970, pp. 11, 24) followed LINSLEY's arrangement, placing the Spondylinae between the Philinae and Aseminae, and this classification has been adopted by most Japanese authors.

Recently, ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, pp. 15, 133) made a drastic change in the current classification, synonymizing the Spondylinae with the Asemini of the Aseminae mainly on the basis of larval morphology. Later, he (1988, p. 123) changed the subfamilial name to the Spondylinae, because the name Spondylinae SERVILLE, 1832, has priority over the Aseminae THOMSON, 1860. According to his opinion, therefore, the Asemini became a junior synonym of the Spondylini.

ŠVÁCHA's opinion seems very important for the study of cerambycid phylogeny. Very close larval similarity between the spondylines and asemines seems to be an infallible indication that the two groups have been derived from a common ancestry. However, the unique external morphology of adult *Spondylis* should not be underestimated in determining its systematic position. Above all, the slender pentamerous tarsi without pubescent ventral pads and the presence of a broad terminal lamella of the protibiae distinguish *Spondylis* from all the asemines.

My study of the female reproductive organs of *Spondylis buprestoides* also showed that they are considerably different from those of the other asemines. As was already pointed out, the coxite is clearly separated from the paraproct, the styli are very small and articulated to the lateral faces of the coxite lobes, and the oviduct is unusually stiff, all suggesting its affinity to the Prioninae rather than to the Aseminae in a strict sense. In my opinion, *Spondylis* should be placed in its own group, Spondylini, which had better be regarded as a tribe of the Spondylinae (=Aseminae) in view of the irrefutable evidence produced by the comparative study of larval morphology.

Asemines

The asemines were invariably placed in the subfamily Cerambycinae before the World War II, though usually separated from the others in their own group. MULSANT (1839, pp. 61–70) classified *Aseum*, *Criocephalus* and two others into the Branche Hespérophanaires of the Famille Cérambycins in his Groupe des Procéphalides. THOMSON (1860, pp. 139, 259) gave the name Asemitae to the group and put it in his Sous-tribu Cerambycitae Verae, and the same view was adopted by LACORDAIRE (1869 a, pp. 203, 205) though he used the name Asémides. GAHAN (1906, pp. 91, 94) regarded the Asemini as a group (=tribe) of the Cerambycinae. Even PLAVILSTSHIKOV (1940, pp. 3, 9, 614) regarded the Asemini as a tribe in his Gruppa Cerambycites of the subfamily Cerambycinae.

Most recent authors regarded the asemines as an independent subfamily closely related to the Lepturinae (e.g., LINSLEY, 1939, p. 64, 1962, p. 67). However, ŠVÁCHA in ŠVÁCHA and DANILEVSKY (1987, p. 15) pointed out that “some Aseminae might be closer to the Lamiinae, or the Cerambycine stock, than to any Lepturinae.” He then (p. 133) stated that “the genera *Nothorina*, *Tetropium*, *Spondylis*, *Aseum*, *Megasemum* and *Arhopalus* comprise a well-defined tribe Asemini” so far as concerned with the larval morphology. My examination of the female reproductive organs has also shown that these genera, with the obvious exception of *Spondylis*, form a homogeneous group, even though some aberrancies are found in *Tetropium*, *Megasemum* and *Cephalallus*, all of which have distinct valvifer. Besides, the styli are abaxially articulated to the lateral faces of the coxite lobes in *Tetropium*, and the valvifer baculi extend obliquely to the external sides of the coxite ones in the latter two. These modifications seem to be related to their ovipositing habits and to have been developed secondarily.

So far as concerned with the female reproductive organs, it is difficult to determine to which of the Lepturinae and Cerambycinae the asemines are more closely related. Relatively simple and similarly formed spermathecae in the Asemini seem to indicate primitiveness of the tribe, which may have given rise to other groups. This does not necessarily mean that the asemines are directly ancestral to the lepturines and are rather remote from the cerambycines.

Atimiines

The genus *Atimia* comprises a small number of small cerambycids with densely pubescent body. It was placed by THOMSON (1861, p. 373) between *Gracilia* and *Obrium* in the Division Ibidionitae of his Groupe des Cerambycitae Verae, and by LACORDAIRE (1869 b, p. 144) in the Groupe Smodicides of the Sous-famille Cérambycides. The Smodicides is the Groupe XL in LACORDAIRE's system, while the Asémides is the Groupe I, and they are placed in different sections of the Cohorte I (Cérambycides Vrais Sylvains).

Recent authors, however, invariably recognized the tribe Atimiini for *Atimia* and *Paratimia*, and placed it in the subfamily Aseminae. This arrangement was first proposed by LINSLEY (1939, pp. 63–65), who carefully examined the external char-

acters of both adults and larvae, and associated the tribe Atimiini with the Asemini. On the other hand, CROWSON (1955, p. 149) suggested that the existence of some indication of prothoracic side-borders in the Atimiini could be a possible indication of its affinities to the Philini.

My examination of the female reproductive organs of *Atimia okayamensis* proved that LINSLEY's opinion was perfectly correct. They are basically identical with those of the members of the Asemini, but are peculiar in the very short paraproct, the discontinuation of the valvifer and coxite baculi, the latter of which are very short, and so on. On the other hand, similarly formed female genitalia are found in certain lepturines (cf. SAITO, 1989), which may indicate that the atimiines have relationship with the lepturines. For the time being, the atimiines should be regarded as a tribe of the Spondyliinae related to the Asemini, and as a link between the Spondyliinae and Lepturinae. Their resemblance to the philines, if any, is superficial and does not show true relationship between the two.

Conclusion

From the discussions given in the foregoing chapter, it is concluded that the following families, subfamilies and tribes had better be recognized for the smaller groups of East Asian cerambycid beetles dealt with in this part of my studies. This conclusion was drawn mainly from the comparative study of the female reproductive organs, but non-genitalic diagnostic characters of adults and larvae were also scrutinized and taken into consideration.

1. Family Vesperidae
 Tribes Vesperini and Philini
2. Family Disteniidae
 Tribe Disteniini
3. Family Cerambycidae
 - a. Subfamily Parandrinae
 - b. Subfamily Prioninae
 Tribes Prionini (provisional) and Anacolini
 - c. Subfamily Apatophysinae
 - d. Subfamily Spondyliinae
 Tribes Spondyliini, Asemini and Atimiini

要 約

齊藤明子：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。I. カンショカミキリからケブカマルクビカミキリまで。——日本とその近隣地域に分布するカミキリムシ類のうち、ハナカミキリ亜科、カミキリムシ亜科およびフトカミキリ亜科以外の各群に含まれる属の代表的な種を選んで、雌生殖器を精査した。その結果を、成虫の外部形態や幼虫の研究に基づく従来の分類方式と比較検討して、それらの類縁関係や分類学的地位に関する見解をまとめた。

台湾などに分布するカンショカミキリ (*Philus*) と、中国北部産の *Mantitheus* とでは、産卵管の肛節 (proctiger) がひじょうに長くて2対の棒状片 (baculi) をそなえ、腔の基部が膨れているが交尾囊 (bursa copulatrix) はなく、また、受精囊 (spermatheca) が膜質のまま特定の分化を示さない。これらの顕著な特徴は、ヨーロッパ南部に分布するムカンカミキリ (*Vesperus*) と共通であって、外部形態にみられるいくつかの相違点を考慮にいれても、両者が同一の系列に属することはまず間違いない。それで、これらを独立のムカンカミキリ科 (*Vesperidae*) としてカミキリムシ科から分離し、そのなかにムカンカミキリ族とカンショカミキリ族とを認めた。

ホソカミキリ類は、成虫、幼虫ともに頭部の構造が特異であり、成虫の後胸部や翅脈にもほかのカミキリムシ類には見られない特性があるので、従来からしばしば独立の科と認められてきた。雌生殖器の構造からみても、受精囊がきわめて複雑に分化し、しかも受精囊管を介さずに直接、交尾囊に接続するという特異性が、ほかのカミキリムシ類の場合とまったく異なっているので、ホソカミキリ科として分離した。

成虫の特異な形態から、一般にカミキリムシ科のうちの独立の亜科と認められているニセクワガタカミキリ類は、雌生殖器の構造からみても、その原始性と独立性が支持される。肛側片 (paraproct) の背板と腹板とが明瞭に区別され、尾状体 (styli) が縮小して横位になり、陰端節 (coxite lobe) の背面に位置する。また、産卵管全体のいちじるしい硬化や、関節間膜がなく腔が産卵管のなかに包みこまれていることなど、特異性がいちじるしい。

狭義のノコギリカミキリ類は、従来から同質な亜科のひとつだと考えられてきたが、雌生殖器の形態からもこれが裏づけられた。多くの族や亜族に分割されているが、表面的な相違に基づいて細分されすぎた傾向があり、雌生殖器からみれば、ノコギリカミキリ族とコバネカミキリ族とのふたつぐらいにまとめたほうがよさそうに思われる。ただし、邦産種の数が少ないので、この問題の解決は将来の研究にゆだねた。なお、トゲウスバカミキリ類とウスバカミキリ類とは、第8腹節の構造や雌生殖器の形態からみて、明らかに別属であろうと考えられる。

Apatophysis は、外観がムカンカミキリ科の甲虫に似たカミキリムシで、中央アジアを中心にして中国東部まで分布している。以前はハナカミキリ亜科のムカンハナカミキリ族におかれていたが、最近、独立の亜科と認められ、カミキリムシ亜科に類縁の近いものと考えられるようになった。しかし、雌生殖器の構造はノコギリカミキリ亜科のものと基本的に同じであって、両者の類縁関係が近いことは確実である。

クロカミキリ類も独立の亜科におく意見が少なくないが、幼虫の形態からみると、疑いもなくマルクビカミキリ類と同じ群に含まれるべきものである。しかし、雌生殖器の構造は、陰基節 (coxite) が肛側片から明瞭に区分され、尾状体がひじょうに小さくて陰端節の外側面に関節し、輸卵管 (oviduct) が異例の硬化をするなど、ノコギリカミキリ亜科のものに似ている点が多い。いっぽう、狭義のマルクビカミキリ類はよくまとまった同質的な一群で、一部に産卵習性に応じた適応ではないかと思われる特殊化が認められるものの、全体としてひとつの族だと考えてよい。ケブカマルクビカミキリも同じ系列に属するが、肛側片がひじょうに短いうえ、担弁節 (valvifer) の棒状片が陰基節のものから広く離れている。以上の事実に基づいて、これらをクロカミキリ亜科にまとめ、そのなかに、クロカミキリ族、マルクビカミキリ族およびケブカマルクビカミキリ族の3族を認めた。なお、この亜科は、ハナカミキリ亜科に類縁の近いものだとする意見が多いが、雌生殖器の構造からみれば、比較的、祖先的な一群だろうとは考えられるものの、ハナカミキリ亜科とカミキリムシ亜科とのどちらにより近い類縁関係をもつかはわからない。

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