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Kojima, Hiroaki

Entomological Laboratory. Faculty of Agriculture, Kyushu University

Morimoto, Katsura

Entomological Laboratory. Faculty of Agriculture, Kyushu University

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Systematics of the Flea Weevils of the Tribe Ramphini
(Coleoptera, Curculionidae) from East Asia
II. Phylogenetic Analysis and Higher Classification¹⁾

Hiroaki KOJIMA and Katsura MORIMOTO

Entomological Laboratory, Faculty of Agriculture,
Kyushu University, Fukuoka, 812-81 Japan

Abstract. Phylogenetic analysis of East Asian Ramphini was performed to make a classification system based on the inferred phylogenetic relationships of the genera and subgenera. Phylogenetic reconstruction was carried out by the computer program PAUP Version 3.1.1 (Swofford, 1993) on 36 characters.

From the result obtained by this analysis, following genera and subgenera are recognized: *Sphaerorchestes*, *Imachra*, *Synorchestes*, *Ramphus*, *Isochnus*, *Tachyerges*, *Hyporhynchaenus*, *Indodinorrhopalus*, *Rhynchaenus*, *Orchestes* and *Pseudorchestes*. *Rhynchaenus* of traditional sense was regarded as paraphyletic and divided into two independent genera: *Rhynchaenus* and *Orchestes*, of which the latter includes three subgenera: *Orchestes s. str.*, *Alyctus* and *Nomizo*.

New system of higher classification of this tribe is proposed on the hypothesis about the phylogenetic relationship.

Introduction

Weevils of the tribe Ramphini are remarkable in having the swollen hind femora with metafemoral apodeme which enable them to jump on case of danger, and well known as "flea weevils". The adults of this weevils live on the leaves of broad leaved-trees excepting *Pseudorchestes* associated with herbaceous plants and feed on them externally, and the larvae are mostly leaf-miners of young leaves and often cause serious damage by defoliation. Up to the present 13 genera and about 200 species are known from the world, mainly in the Old World and none of them occur in Neotropical region. The faunas of European countries (Hoffmann, 1958; Smrezynski, 1976; Angelov, 1980; Lohse, 1983) and Japan (Morimoto, 1982) of the Old World and the New World (Anderson, 1989) have recently been revised. As all the genera and subgenera of this tribe excepting 2 genera occur in the East Asia, this tribe may possibly be diversified in this region.

¹⁾ Contribution from the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka (Ser. 4, No. 110).

Phylogenetic analysis of the tribe Ramphini was only attempted by the phenetic on the overall similarity for the subgenera of *Rhynchaenus* mainly on the Japanese and European species by Morimoto (1984) and a dendrogram of their relationship was depicted. The sister group relationship between *Isochnus* and *Ramphus* was only suggested by Anderson (1989). As these facts indicate, our knowledge of the phylogenetic relationship among genera and subgenera of the Ramphini are insufficient at present.

Present study is aimed to propose a classification system of the Ramphini based on the hypothesis about the phylogenetic relationships of the genera and subgenera, because subgenera of *Rhynchaenus* auct. are apt to be upgraded to full genera as done by Pajni & Sood (1981), Anderson (1989) and Korotyaev (1991) without giving the comprehensive discussion from the view point of phylogeny.

Methods

We examined the state distribution of 36 characters in 14 taxa including *Pseudorches* not occur in East Asia and hypothetical ancestor. Data matrix is presented in Table 1.

Polarity of character states was determined using ingroup and outgroup comparison criteria. Ingroup is defined all the genera and subgenera of East Asian Ramphini. Outgroup is defined as other weevils, with emphasis on the tribes Dinorhophalini and Ochyromerini as discuss below, because the sister group of Ramphini is uncertain.

Phylogenetic reconstruction was accomplished by the computer-aided reconstruction using PAUP version 3.1.1 (Swofford, 1993). A hypothetical ancestor with all characters coded plesiomorphic, was used for analysis. Branch and bound search algorithm was used to guarantee discovery of the shortest trees. Trees discovered were analyzed using the computer program, Mac Clade version 3.0 (Maddison & Maddison, 1992). Tree lengths and consistency and rescaled consistency indices are calculated by Mac Clade.

Of the 36 characters used in the analysis, 26 are binary and 11 are multistate. We treated 2 characters of the former as irreversible and 6 of the latter as ordered in computer analysis. Character types are indicated in the character analysis.

Monophyly of Ramphini

The Ramphini was recognized as a monophyletic group by the following combination of characters: The rostrum is perpendicular to the axis of body or received upon breast in repose. The maxillary palpi consist of two or one segments. The antennae are inserted usually in the basal half of the rostrum. The hind femora are more or less swollen and greater than the anteriors and each has a jumping apodeme, which is J-shaped in all taxa examined except for spiraled in *Ramphus*. The hind tibiae are always devoid of uncus or mucro at tip. The tarsal groove of hind tibiae lies on the outer edge. The claws diverge widely, each has a broad flat process and a fine seta at the base except for *Ramphus* (*Ramphus*). Posterior margin of the second to fourth ventrites curve posteriorly at each side except for *Ramphus* s. lat., which has straight ventrites. The pygidium is almost vertical and broadly exposed in male. The metendostemite with a pair of anterior tendons widely separated each other. The tegmen of the aedeagus opens dorsally. The eighth stemite (spiculum relictum) is paired as a narrow sclerites.

The larvae are conspicuous and characteristic by the head, which is retracted, deeply and broadly emarginates at posterior margin, the endocarina is prominent posteriorly, and the

hypopharyngeal bracon is absent (Morimoto, 1984), and the prosternum has three pigmented spots.

The biology of the larvae are mostly known as leaf-miners, but some feed on other tissues; namely, the larvae of *Rhyngaenus hustachei* live in the galls made by aphids on the leaves of *Alnus* (Marshall, 1951; Morimoto, 1984), the new adults of *R. lateritius* emerged from the seeds of *Ulmus* by rearing, and *R. flacourtiae* was bred from fruits of *Flacourtia* (Marshall, 1957). They pupate in mines or within the feeding cavity.

Most of characters listed above occur in the closely related taxa, but the character that the maxillary palp with two or one segments is considered to be autapomorphic to this tribe. Jumping apodeme of hind femora is known from some taxa of Coleoptera (Furth & Suzuki, 1992). This apodeme, however, regarded to be autapomorphic because it is not known among the other taxa related to the Ramphini and characteristic to them in shape and function.

Outgroup

Sister group of Ramphini has not been demonstrated. Marshall (1931, 57) and Voss (1957, 58, 59, 62) treated the subfamily Anthonominae in a broad sense including all or part of the Rhynchaenini (=Ramphini), Anthonomini, Endaeini (=Ochyromerini), Demimaeini, Ellescini and Acalyptini. Morimoto (1962) raised some of these tribes to subfamilial rank following principally after the treatments in *Coleopterorum Catalogus*, defined the Rhynchaeninae including Rhynchaenini and Dinorhopalini, and illustrated the relationship of these subfamilies by setting the Rhynchaeninae as sister group of the subfamilies Tychiinae, Acalyptinae, Anthonominae and Curculioninae. Though these facts indicate the close relationship of these taxa, their appropriate relationships have not yet been inferred from the view point of phylogeny. In the recent tendency, these subfamilies are apt to be treated in tribal rank and classified in the subfamily Curculioninae after Kuschel (1995), but these downgrade merely converts the problem of their phylogeny from the subfamily rank to that of tribes and the essential problem remains unchanged. Morimoto (1984) defined Rhynchaeninae including Dinorhopalini, however, most of characters given by him occur in other subfamilies of Curculionidae excepting the absence of hypopharyngeal bracon in larvae (Anderson, 1989). Absence of hypopharyngeal bracon is unique within Curculionoidae as far as we know and both tribes are considered to be closely related to each other, but the knowledge about larvae related to the Ramphini is very limited at present. If the character is excluded from the consideration, these are not any other autapomorphy supporting the monophyly of the Rhynchaeninae including Dinorhopalini, and consequently the Ramphini and Dinorhopalini are treated in this paper as independent tribes. These tribe are also considered to be close to Ochyromerini by the characters of venter, of which the second to fourth ventrites are broadly curved posteriorly at sides, widely diverged tarsal claw and similar genital segments. Therefore, these tribes are emphasized for determining the character polarity by outgroup comparison in this study.

Ingroup

The ingroup includes all the genera and subgenera known from Asia excepting *Exotorrhamphus* Voss (1957) from Indonesia (Java), which is established in the Rhynchaenini but is excluded in this paper from the Ramphini judging from the uncinat hind tibiae and scarcely swollen hind femora as seen in the original description and illustration.

Rhynchaenus auct. is the largest genus including subgenera *Alyctus*, *Anomorrhynchaenus*, *Euthoron*, *Hyporhynchaenus*, *Isochnus*, *Orchestes*, *Rhynchaenus* s. str., *Pseudorchestes*, *Pseudendaeus*, *Tachyerges* and *Threticus*. Morimoto (1984) described subgenus *Nomizo* from Japan, and he treated *Threticus* as a synonym of *Alyctus* and *Euthoron* as *Orchestes* and recognized 7 subgenera in this genus. Thereafter, Anderson (1989) raised *Tachyerges*, *Isochnus*, *Hyporhynchaenus* and *Pseudendaeus* to generic rank in his monograph of the Rhynchaeninae in the North America. Recently, Korotyaev (1991) raised *Pseudorchestes* to generic rank by giving the special weight to the diagnostic characters and biological specificity. Remaining subgenera of *Rhynchaenus* auct. recognized by Morimoto (1984) are divided into two genera, *Rhynchaenus* and *Orchestes*. The former is equivalent to the subgenus *Rhynchaenus*, and the latter comprises three subgenera *Nomizo*, *Alyctus* (include *Threticus*), and *Orchestes* s. str. (include *Euthoron*) according to the result of the present analysis. Other genera included in this analysis are *Ramphus*, *Zmachra*, *Sphaerorchestes*, *Synorchestes* and *Indodinorrhopalus*.

Characters used in the phylogenetic analysis

HEAD:

1. Relative width of forehead between eyes to rostrum at the base.

0. A little narrower than the base of rostrum.

1. Narrower than half the width of rostrum.

Forehead between eyes is usually a little narrower than the base of rostrum in outgroup and this state is regarded as plesiomorphic. Ramphini have eyes more or less closed to each other on frons in most species, but they are distant from each other in species of most *Pseudorchestes* and part of *Isochnus* and *Indodinorrhopalus*. Basis for polarity: outgroup comparison.

2. Conditions of forehead between eyes.

0. Distant from each other or as widely distant as the width of scape.

1. Narrower than the width of scape.

2. Linear or partly contiguous to each other.

As was noted in character 1, narrower forehead is considered to be apomorphic. Among Ramphini forehead between eyes is narrower than scape in *Synorchestes* and part of *Imachra*, *Alyctus*, *Orchestes* s. str. and *Isochnus*, and it is linear with a row of setae or partly contiguous to each other in *Imachra*, *Sphaerorchestes*, *Tachyerges*, *Hyporhynchaenus*, *Ramphus*, *Rhynchaenus*, *Indodinorrhopalus*, *Nomizo*, *Alyctus* and *Orchestes* s. str. Contrarily, forehead between eyes is as wide as scape in part of *Isochnus*, *Orchestes* s. str. and *Alyctus* and it is much wider than scape in some taxa listed in character 1. Basis for polarity: ingroup comparison.

3. Rostrum to the axis of body.

0. Frontoventral.

1. Perpendicular.

2. Received upon breast or between coxae.

Rostrum is usually directing frontoventral in outgroup and this state is regarded as plesiomorphic. In Ramphini, rostrum is perpendicular to the axis of body in most taxa and

it is evenly curved in dorsal contour and received upon breast in **Pseudorchestes**, **Orchestes s. str.**, *Nomizo* and *Alyctus*. Among the latter condition (3²), most apomorphic state occurs in **Ramphus**, which head is strongly bent and rostrum is somewhat flattened and always received between coxae. Basis for polarity: ingroup and outgroup comparison. [ordered]

4. Position and direction of antennal **scrobes** on rostrum.

0. Lateral in position, running to the lower part of eye.

1. Oblique, running to the lower part of eye.

2. Oblique, running straightly toward beneath the base of rostrum.

Among Ramphini most taxa are in the state 4⁰, but it is in 4² in *Imachra* and **Sphaerorchestes** and that of **Synorchestes** is in intermediate condition of them. Basis for polarity: ingroup comparison.

5. Antennal insertion into rostrum in male.

0. Inserted in or before the middle of rostrum.

1. Inserted behind the middle of rostrum.

In outgroup, antennae usually insert before the middle of rostrum in male and we consider this state plesiomorphic. Among Ramphini antennae are inserted behind the middle of rostrum in most of taxa, whereas antennae are inserted in or before the middle of rostrum in *Imachra*, **Sphaerorchestes** and **Synorchestes** and part of *Isochnus*, **Rhynchnenus**, **indodinorrhopalrrs** and **Orchestes s. str.** Basis for polarity: outgroup comparison.

6. Antennal insertion index in male. (The index is the distance between socket and the anterior margin of eye divided by that between the apex of clypeus and the anterior margin of eye seen laterally and measured in a straight line x 100)

0. More than 40.

1. 40-20.

2. Less than 20.

As was noted in character 5, antennal insertion near or a little beyond, the middle of rostrum is considered to be plesiomorphic. Among Ramphini antennal insertion index is more than 40 in *Imachra*, **Sphaerorchestes**, **Synorchestes**, **Isochnus**, *Indodinorrhopalus*, **Rhynchaenus** and part of **Orchestes s. str.**, and it is 40-20 in most of this tribe. Most apomorphic state occurs in **Pseudorchestes**, **Ramphus** and part of **Orchestes s. str.** the index is less than 20. Basis for polarity: ingroup and outgroup comparison.

7. Antennal insertion into rostrum in female.

0. Inserted in or before the middle of rostrum.

1. Inserted in basal half of rostrum.

Antennae are usually inserted in the middle or often before the middle of rostrum in female of outgroup. In Ramphini antennae are inserted in basal half of rostrum in female and considered to be synapomorphic for this tribe. Basis for polarity: outgroup comparison.

8. Antennal insertion index in female.

0. More than 40.

1. 40-20.

2. Less than 20.

Antenna1 insertion in female is a little more basal in rostrum rather than those of male. Basis for polarity: ingroup and outgroup comparison.

9. Scape of antenna.**0.** As long as or longer than funicle.

1. Shorter than funicle.

Weevils of outgroup have antenna1 scape as long as or longer than funicle in general and this state is considered to be plesiomorphic. Among Ramphini, antenna1 scape is as long as funicle in *Sphaerorchestes* and part of *Imachra*, and it is usually shorter than funicle in remaining taxa. Basis for polarity: outgroup comparison.

10. Relative length of scape to first segment of funicle.**0.** Much longer than the first segment of funicle combined.

1. About as long as the first segment of funicle.

As was noted in character 9, the more shorter scape is considered to be apomorphic. Among Ramphini, antenna1 scape is very short and nearly as long as first segment of funicle combined in *Ramphus*, *Pseudorchestes*, *Nomizo* and part of *Orchestes*. The scape has a tendency to becoming shorter in relation to the antenna1 insertion to rostrum more basal. Basis for polarity: ingroup and outgroup comparison.

11. Funicle of antenna.**0.** Seven-segmented.

1. Six-segmented.

Weevils in general have funicle of antennae seven-segmented and this state is considered to be plesiomorphic instead of that is six-segmented or less. Among Ramphini antenna1 funicle is seven-segmented in *Imachra*, *Synorchestes*, *Ramphus*, *Tachyerges* and *Hyporhynchaenus*. In *Isochnus*, funicle is visible six-segmented in most species, but in *I. saliceti* and *I. sequensi* it is seven-segmented. By the close examination of the club of antennae in *Isochnus sorbi* on preparation through microscope, first segment consists of two parts in the arrangement of setae and internal rim is also observed at basal third through the transparent light. As these facts suggest the fusion of seventh segment of funicle to club, the state of *Zsochnus* on this character is coded seven-segmented. In the remaining taxa of this tribe funicle consists of six segments. Basis for polarity: ingroup and outgroup comparison.

12. Maxillary palp. [Figs. 2-7]**0.** Three-segmented.

1. Two- or one-segmented.

Maxillary palp of weevils consists of three segments in most taxa, but this is two- or one-segments in Ramphini. This structure is unique and considered to be synapomorphic for this tribe and treats as irreversible character state in reconstruction using PAUP. In *Ramphus*, rostrum is always received between fore coxae and prementum is almost obsolete (Fig. 3). Basis for polarity: ingroup and outgroup comparison. [irreversible]

THORAX:

13. Prosternal sulcus. [Morimoto, 1984: Fig. 8; Morimoto & Miyakawa, 1996: Figs. 33, 443

0. Absent.

1. Present.

Prosternal sulcus before coxae occurs in parallel in many taxa of weevils and we consider the presence of this structure apomorphic. Among Ramphini, it is presented and synapomorphic for *Imachra* and *Sphaerorchestes*. Basis for polarity: ingroup and outgroup comparison.

14. Coxal cavity of prothorax. [Morimoto, 1984: Fig. 8; Morimoto & Miyakawa, 1996: Figs. 33, 38, 44, 50]

0. Continuous.

1. Narrowly separated.

2. Widely separated by developed prosternal process.

Fore coxae and coxal cavities are separated in various degrees and this occurs in parallel among weevils. Therefore, we consider the condition of separated coxal cavities as apomorphic. Among Ramphini, coxal cavities are usually continuous, but it is separated according to the position of rostrum when received. It is narrowly separated by the linear prosternal process but connate internally in a part of *Alyctus* and *Orchestes*, by a little wider than former in *Ramphus*, *Hyporhynchaenus* and *Nomito* (14¹) and distinctly separated by the prosternal process in *Imachra* and *Sphaerorchestes* (14²). Basis for polarity: ingroup and outgroup comparison.

15. Mesosternal process. [Morimoto, 1984: Fig. 8; Morimoto & Miyakawa, 1996: Figs. 33, 441

0. Narrower than a coxa.

1. As wide as a coxa.

Among Ramphini, mesosternal process is usually narrower than a coxa and we consider this state plesiomorphic, but it is as wide as a coxa in *Nomizo*, *Sphaerorchestes* and a part of *Imachra*. Basis for polarity: ingroup comparison.

LEGS:

16. Fore and middle femora. [See Morimoto, 1984; Anderson, 1989; and Morimoto & Miyakawa, 1996 for figures]

0. Without denticle.

1. Armed each with a denticle like spine.

2. Armed each with a denticle with spine.

Among Ramphini, fore and middle femora are armed with characteristic spine, which borne on a conical small projection in *Nomizo*, and part of *Orchestes* s. str., *Alyctus* and *Pseudorchestes*. We consider this structure apomorphic. Tooth of *Hyporhynchaenus* is a little different from that of the former and same as in most weevils like curved thorn and we code them in different state (Morimoto & Miyakawa, 1996: Fig. 53). Basis for polarity: ingroup and outgroup comparison.

17. Jumping apodeme of hind femora. [Morimoto, 1984: Fig. 7; Morimoto & Miyakawa, 1996: Figs. 42, 70]

0. Absent.

1. Present.

Ramphini is distinctive within related taxa by having metafemoral apodeme and we consider this structure synapomorphic for this tribe. Apodeme is J-shaped in most taxa and twisted in **Ramphus**. Basis for polarity: outgroup comparison. [irreversible]

18. Posterior margin of hind femur. [See Morimoto, 1984; Anderson, 1989; Dieckmann, 1963; Morimoto & Miyakawa, 1996 for figures]

0. Simple.

1. Often one or few denticles with spine.

2. With some denticles with spine.

The swelling of hind femur accompanies the development of characteristic denticles with spines along posterior margin in Ramphini. Hind femur arms often one or few denticles with spine in **Alyctus**, **Nomito** and part of **Pseudorchestes**, and the number of denticle is increased in **Orchestes s. str.** and **Pseudorchestes**. Basis for polarity: ingroup and outgroup comparison. [ordered]

19. Long setae on the posterior margin of hind femur. [Morimoto, 1984: Fig. 14E]

0. Absent.

1. Present.

Among Ramphini having characteristic denticle on the posterior margin of hind femur, the denticle provides with a long seta in **Orchestes s. str.** and a part of **Alyctus** and **Nomizo** and always absent in **Pseudorchestes**. Basis for polarity: ingroup comparison.

20. Long elongate-oval spines on the posterior margin of hind femur. [Morimoto, 1984: Fig. 14E].

0. Absent.

1. Present.

Among Ramphini having characteristic denticle on the posterior margin of hind femur, the denticle provides with a long elongate-oval spines in **Orchestes s. str.** and part of **Alyctus** and **Pseudorchestes**. Basis for polarity: ingroup comparison.

21. Uncus of fore tibia. [See Morimoto, 1984 and Morimoto & Miyakawa, 1996 for figures]

0. Developed.

1. Small, originated from the middle.

2. Absent.

Unci of fore and middle tibiae are usually developed in outgroup and this state is considered to be plesiomorphic. Among Ramphini, uncus of fore and middle tibiae are conspicuous, sickle-shaped and originated from the dorsal edge of the apical margin in most taxa, but it is reduced and small in **Rhynchaenus** (Morimoto, 1984: Fig. 14A; Morimoto & Miyakawa, 1996: Fig. 82) and absent in **Indodinorrhopalus** (Morimoto & Miyakawa, 1996: Fig. 70), **Imachra**, **Sphaerorchestes** and **Synorchestes**. Basis for polarity: ingroup and outgroup comparison. [ordered]

22. Hind tibia. [Morimoto, 1984: Figs. 13, 14]

- 0. Simple and almost straight.
- 1. More or less sinuate internally.

Hind tibia is usually straight and simple in outgroup and most genera of Ramphini. Among the latter, hind tibia becomes more or less sinuate internally according to the swelling of hind femur in *Orchestes* s. str. and a part of *Pseudorchestes* and carinate on the outer face of flat surface along the interior edge of tibiae in *Orchestes* s. str. Basis for polarity: ingroup and outgroup comparison.

23. Tarsal groove. [Morimoto, 1984: Fig. 11F; Morimoto & Miyakawa, 1996: Fig. 36]

- 0. Not extending to the base.
- 1. Extending to the base.

Tarsal groove is usually delimited at the apex of tibia. But it is ascended to the base and forming entirely bare exterior surface in *Imachra* and *Sphnerorchestes*, and this structure is considered to be synapomorphic for them. Basis for polarity: ingroup and outgroup comparison.

24. Tarsus.

- 0. Third segment not widely bilobed, fourth segment slender, usually more than twice as long as third.
- 1. Third segment widely bilobed, fourth segment a little longer or less than twice the length of third.

Tarsus with fourth segment (morphologically fifth) usually slender in outgroup and most of genera of Ramphini. Among the latter, third segment of tarsus is widely bilobed and fourth segment is a little exceeding it in *Synorchestes*, *Sphaerorchestes* and *Imachra* and we consider this structure synapomorphic for them. Basis for polarity: ingroup and outgroup comparison.

STRIDULATORY APPARATUS ON SEVENTH TERGITE OF ABDOMEN:

25. Scraper for stridulatory organ on seventh tergite. [Figs. 20-29, 106, 111]

- 0. Many, often arranged in a pair of rows.
- 1. A pair on anterior margin.
- 2. One or two pairs and arranged in a pair of rows or absent, if scraper presents arranged in a pair of rows, foremost pair is located on anterior corner of projection of seventh tergite.

Among weevils stridulatory organ is found in scattered taxa and the scraper is on seventh tergite, contacted with file on the underside of elytral near apex in general. In Ramphini and it related taxa, stridulatory organ is presented as far as we have examined. The scraper on the seventh tergite are one pair on the anterior margin in Ochyromerini (Kojima & Morimoto, 1995: Figs. 1G, H). In Dinorhopalini, it is many pairs on anterior part in *Dinorhopala* (Fig. 110), and arranged in a pair of rows in *Ixalma* (Fig. 111).

Among Ramphini, condition of scraper on seventh tergite is various and divided into following types.

Type I. Scrapers are a paired on the anterior margin, often on the weakly sclerotized projection: *Imachra*, *Sphaerorchestes* and *Synorchestes*.

Type II. Scrapers are two paired on the anterior margin: *Tachyerges* and *Hyporhynchaenus*.

Type III. Four to six scrapers are arranged in a pair of rows, foremost pair is on anterior corner of projection of seventh tergite: *Rhynchaenus* and *Indodinorhopalus*.

Type IV. Scrapers are a paired on anterior corner of more or less bilobed anterior projection: *Pseudorchestes*, *Orchestes* s. str., *Alyctus* and *Nomizo*.

Type V. Scraper is absent: *Ramphus* and *Isochnus*.

These are separately coded in characters 26 to 30 for analysis. Type I is almost the same to that of Ochyromerini, but this is slightly different from it by the position on weakly sclerotized projection of anterior margin and unique in Ramphini. Therefore, we consider this structure synapomorphic for *Zmachra*, *Sphaerorchestes* and *Synorchestes*. Type II is unique among Ramphini and outgroup, and considered to be synapomorphic for *Tachyerges* and *Hyporhynchaenus* (character 30). Type III is similar to that of Dinorhopalini, but different from it in number and arrangement of scrapers and the foremost pair on the projection of the anterior margin. We therefore consider this synapomorphic for *Rhynchaenus* and *Indodinorhopalus* (character 27). Type IV is similar to Type I, but each scraper is located on anterior corner of projection and different from the latter. This structure is regarded as characteristic among weevils and synapomorphic for *Pseudorchestes*, *Orchestes* s. str., *Alyctus* and *Nomizo*. Among them, bilobed anterior projection of *Psectorchestes* is a little weaker than those of remainings (character 28). Type V is considered to occur secondarily by disappearance of scrapers from Type II or III, and the absence of it is considered to be synapomorphic for *Ramphus* and *Isochnus* (character 29). Basis for polarity: ingroup and outgroup comparison. [ordered]

26. Anterior margin of seventh tergite. [Figs. 26-28, 106; Anderson, 1989: Figs: 36-39]

- 0. Without projection.
- 1. With projection in the middle.

Among Ramphini anterior margin of seventh tergite is projected in the middle and the foremost pair of scrapers is on anterior corner of it in *Rhynchaenus*, *Indodinorhopalus*, *Pseudorchestes*, *Orchestes* s. str., *Alyctus* and *Nomizo*. We consider this structure synapomorphic for these taxa. Basis for polarity: ingroup and outgroup comparison.

27. Arrangement of scrapers for stridulatory organ on seventh tergite. [Figs. 26-28]

- 0. One or two pairs, or absent.
 - 1. Arranged a pair of rows and the foremost pair is on projection of seventh tergite.
- See discussion of character 25. Basis for polarity: ingroup and outgroup comparison.

28. Scraper for stridulatory organ in relation to the projection of seventh tergite. [Figs. 24, 25; Anderson, 1989: Figs: 36-39]

- 0. Scraper various in number and arrangement, if a pair of scrapers present on anterior projection, each scraper is not located on anterior corner of it or without distinct bilobed projection.
 - 1. A pair on anterior corner of distinctly bilobed projection of anterior margin.
- See discussion of character 25. Basis for polarity: ingroup and outgroup comparison.

29. Distinctness of scraper for stridulatory organ on seventh tergite. [Fig. 29; Anderson, 1989: Figs. 128-132]

0. Present.

1. Indistinct.

See discussion of character 25. Basis for polarity: ingroup and outgroup comparison.

30. Number of scraper for stridulatory organ on seventh tergite. [Figs. 22-23]

0. One paired, more arranged in a pair of rows, or absent.

1. Two pairs.

See discussion of character 25. Basis for polarity: ingroup and outgroup comparison.

WING-HOLDING SPICULE PATCHES ON TERGUM OF ABDOMEN:

31. Wing-holding spicule patches on seventh tergite. [Figs. 8-19, 105, 110, 11 1]

0. Present.

1. Reduced.

2. Absent.

Weevils in general have wing-holding spicule patches on seventh tergite. Among Ramphini, these patches on seventh tergite are much smaller than those on fifth and sixth tergites and located on distinct paler patches in *Indodinorrhopalus*, *Ramphus*, *Tachyerges*, *Hyporhynchaenus* and part of *Rhynchaenus* and absent in remaining taxa. We consider the reduction of these patches on seventh tergite as apomorphic. Basis for polarity: ingroup and outgroup comparison. [ordered]

32. Wing-holding spicule patches on fourth tergite. [Figs. 8, 12, 17, 18]

0. Absent.

1. Present.

In outgroup, wing-holding spicule patches on fourth tergite are absent as far as we know. Among Ramphini, these spicule patches are present in *Indodinorrhopalus*, *Rhynchaenus*, a part of *Ramphus* and *Imachra*, but we are not certain whether the presence of these patches on 4th tergite is apomorphic or not. Basis for polarity: ingroup and outgroup comparison.

SPERMATHECA OF FEMALE GENITALIA

33. Spermatheca. [Figs. 38-68; Anderson, 1989: Figs. 31-35, 79-81, 123-127]

0. Capsule without swollen basal half, duct and gland close to each other.

1. Capsule with swollen basal half, more or less forming lateral lobe and gland located on it lobe.

2. Capsule with gland separated from duct and located near or beyond the middle of capsule.

Spermatheca varies in shape and structure within weevils and consists of three parts: capsule, gland and duct. Among Ramphini, gland varies in position on capsule. It is located near the middle or in lateral lobe, and more or less separated from duct in *Indodinorrhopalus*, *Rhynchaenus*, *Ramphus*, *Isochnus*, *Tachyerges*, *Hyporhynchaenrrs*, *Nomizo*, *Alyctus* and *Orchestes s. str.* Among these taxa, gland is located near or beyond the middle of capsule in *Ramphus*, *Isochnus*, *Tachyerges*, *Hyporhynchaenus* and *Indodinorrhopalus*. We consider this condition most apomorphic among this tribe and coded 33². On the contrary, duct and gland are close to each other in *Zmachra*, *Sphaerorchestes* and

Synorchestes and very close to the condition of Ochyromerini of outgroup and we consider this state plesiomorphic. Remaining taxa are coded 33¹. [ordered]

34. Lateral lobe of spermatheca. [Figs. 58, 62-68]

0. Capsule without or with indefinite lateral lobe.

1. Capsule with distinct lateral lobe.

Among Ramphini coded 33¹, capsule has distinct lateral lobe in part of *Alyctus* and *Orchestes* and we consider this state apomorphic. Basis for polarity: ingroup comparison.

35. Location of gland on spermathecal capsule. [Figs. 45-49]

0. Duct and gland close to each other or gland located on the lateral lobe, if gland located near the middle, capsule is thinner.

1. Capsule robust, gland located near the middle of it.

Among Ramphini coded 33² spermatheca with gland located near the middle in *Tachyerges* and *Hyporhynchaenus*. This is close to the state of *Indodinorrhopalus*, but distinguished from it by the robust capsule, and also separable from the remaining taxa of state 332. Therefore, we consider this structure synapomorphic for *Tachyerges* and *Hyporhynchaenus*. Basis for polarity: ingroup comparison.

36. Location of gland on spermatheca capsule. [Figs. 42-44]

0. Gland located before the middle.

1. Gland distant from duct, located beyond the middle or near apex of capsule.

Among Ramphini coded 33² spermatheca with gland distant from duct and it is located beyond the middle in *Ramphus* and on subapical in *Isochnus*. We consider this structure synapomorphic for *Ramphus* and *Isochnus*. Basis for polarity: ingroup comparison.

Phylogenetic analysis

Analysis of 13 taxa with unweighted 36 characters produces 3 trees of 67 steps in length with consistency and rescaled consistency indices 0.72 and 0.53, respectively. These trees are only different in the relationships among *Orchestes* s. str., *Alyctus* and *Nomizo*. One of the three parsimonious cladograms is presented in Fig. 1. The tribe Ramphini is divided into two principle lineages, one is compact group including (*Imachra* + *Sphaerorchestes*) + *Synorchestes*, and the other lineage is diverse comprising remaining taxa. Among the latter lineage, *Rhynchaenus* of traditional sense is displayed as paraphyletic group including two lineages, *Rhynchaenus* s. str. and others comprising *Orchestes* + *Alyctus* + *Nomizo* and *Pseudorchestes*. Judging from this analysis, these lineages are considered to be different from each other in generic level by the morphological characters and the taxa on them are better to be treated as independent genera: *Rhynchaenus* and *Orchestes*, and the latter includes three subgenera: *Orchestes* s. str., *Alyctus* and *Nomizo*. Among them, *Orchestes* s. str. and *Nomizo* is distinctive by several unique characters and *Alyctus* is considered to be paraphyletic group. *Orchestes* s. str. defined in this study is the largest subgenus including about more than half species in this tribe from the world, these species are known to be considerably heterogeneous (Morimoto, 1984), and many undescribed species from the Oriental and Ethiopian regions are remaining in the collections at present. Therefore, the relationship among the subgenera of the genus *Orchestes* is left unsolved in this study

because of insufficiency of our data. *Pseudorchestes* is considered to be an independent genus as was done by Korotyaev (1991).

Phylogenetic relationship

Monophyly of the Ramphini (clade A) is supported by the two unique synapomorphies: Maxillary palp two- or one-segmented (character 12) and hind femora with jumping apodeme (character 17).

The tribe Ramphini is divided into two principle lineages: clades B and D. Clade B shows sister group relationship between *Synorchestes* and *Imachra* + *Sphuerorchestes* (clade C) and is supported by four synapomorphies, of which two are unique: antenna1 scrobe oblique on rostrum (character 4) and tarsus with third segment widely bilobed and fourth segment a little longer than third (character 24). Other two are homoplastic: absence of uncus (character 21) and absence of wing holding spicule patch on tergite 7 (character 31).

Sister group relationship between *Imachra* and *Sphuerorchestes* (clade C) is convincingly supported by four unique synapomorphies: antenna1 scrobe running directly to beneath the base of rostrum (character 4), prosternal sulcus before coxa (character 13), coxal cavities widely separated by developed prosternal process (character 14) and tarsal groove of tibia extending to base (character 23).

Clade D is the other one of two principle lineages of Ramphini and the monophyly is supported by two unique synapomorphies: scraper for stridulatory organ (character 25) and spermatheca with gland and duct more or less separated each other (character 33). This glade is subdivided into two lineages: clades E and H.

Monophyly of clade E is based on the single synapomorphy: spermatheca with gland distinctly separated from duct and at least located about middle (character 33). Sister group relationship between *Ramphus* and *Isochnus* (clade F) is supported as was stated by Anderson (1989) by two unique synapomorphies: absence of scraper (character 29) and spermatheca with gland distant from duct (character 36). *Tachyerges* and *Hyporhynchaenus* is displayed as sister group (clade G) by two unique synapomorphies: seventh tergite with two pairs of scrapers (character 30) and spermatheca with gland located near middle (character 35).

Clade H is the other subdivision of clade D and the monophyly is based on two synapomorphies, of which one is unique: seventh tergite produced on anterior margin (character 26) and the other one is homoplastic: funicle of antenna six-segmented (character 11). This clade is further divided into two lineage's: clades I and J. Monophyly of clade I is supported by three unique synapomorphies: uncus of tibiae reduced (character 21), scrapers arranged in a pair of rows (character 27) and spicule patch of 4th tergite present (character 32). *Rhynchaenus* and *Indodinorhopalus* are appeared as sister group relationship. The other clade J displays sister group relationship between *Orchestes s. lat.* and *Pseudorchestes* and it is supported by four synapomorphies, of which two are unique: rostrum received upon breast (character 3), antennae inserted in basal half of rostrum in male (character 5) and scape of antennae about as long as first segment of funicle (character 10) and remaining one is homoplastic: spicule patch of tergite 7 absent (character 31).

Relationships of subgenera of *Orchestes* s. lat. (clade K) is remaining unsolved. The monophyly of this genus is supported by single unique synapomorphy: paired scraper located on distinctly bilobed projection of anterior margin of 7th tergite (character 28).

Key to genera of Ramphini from East Asia

- 1(6) Rostrum with antennal scrobe running obliquely toward beneath the base of rostrum. Antennae inserted in apical half at least in male, with scape tightly retracted in scrobe; club usually elongate, loosely segmented. Tibiae unarmed at tip. Tarsi with third segment broadly bilobed, fourth usually robust, not more than twice the length of third. Seventh tergite with a pair of scrapers for stridulatory organ at anterior margin, without wing-holding spicule patch. Spermathecal capsule not swollen at basal half, with gland and duct close to each other.
- 2(5) Antennal scrobe at the base distant from eye and invisible in profile. Antennal scape often as long as funicle. Tibiae with tarsal groove ascended upwards to the base and forming entirely bare exterior surface. Prosternum before coxae canaliculate, fore coxae separated by flat prosternum. Mesosternal process almost as wide as a coxa.
- 3(4) Antennae with funicle 7-segmented. Head more or less concave behind eyes. Rostrum short, robust and straight. *Imachra* Pascoe
- 4(3) Antennae with funicle 6-segmented. Rostrum weakly curved, slender and reaching 1st ventrite when rested. Body broadly ovate.
..... *Sphaerorchestes* Morimoto et Miyakawa
- 5(2) Body large; more than 4.5 mm in length. Antennal scrobe with its dorsal edge close to lower corner of eye and visible laterally. Antennae with scape shorter than funicle, funicle 7-segmented, club loosely segmented. Tibiae with tarsal groove not ascended. Prosternum not canaliculate before coxae, which are contiguous to each other. Mesosternal process narrower than a coxa. Pygidium broadly exposed in both sexes, propygidium exposed in male.
..... *Synorchestes* Voss
- 6(1) Rostrum with antennal scrobe lateral in position, with its dorsal edge directing basally to lower part of eye. Antennal insertion, scape and club various, but antennae inserted usually in basal half, with short scape and compact club. Tarsi with 4th segment slender, more than twice as long as 3rd. Spermathecal capsule comma-shaped, more or less swollen at basal half or with distinct lateral lobe. Seventh tergite with scraper various among genera or absent.
- 7(14) Antennae with funicle 7-segmented, if visible 6-segmented, club with 1st segment much longer than the others by the fusion of 7th of funicle with it. Pronotum and elytra without erect setae at sides. Fore and middle tibiae uncinatate at tip. Spermatheca with gland distant from duct.
- 8(11) Antennae inserted before the middle of rostrum in male, funicle with 7th segment longer than broad. Hind wing functional, normal in size. Tergum with spicule patches from 5th to 7th, of which 7th is reduced in size, with two pairs of scrapers on anterior margin of 7th tergite. Spermatheca with gland located near middle of capsule.

- 9(10) Antennae with club ovate, each segment transverse. Eyes contiguous to subcontiguous to each other. Scutellum densely covered with whitish hairy scales, contrasted to black derm. Elytra often maculated by hairy scales. Prosternum with fore coxae contiguous to each other.
 **Tachyerges** Schoenherr
- 1 0(9) Antennae slender, with club fragile, loosely segmented, each segment longer than wide. Forehead between eyes linear, with a row of setae. Derm evenly covered with hairs, scutellum not contrasted to the remaining by vesture. Elytra immaculate. Prosternum with coxae narrowly separated.
 **Hyporhynchaenus** Voss
- 11(8) Antennae inserted in the middle of rostrum or in forehead, funicle with 7th segment transverse or close to or fused with club. Elytra immaculate. Tergum with 7th tergite without scraper. Hind wing reduced in size. Spermatheca with gland inserted in apical half of capsule.
- 12(13) Head strongly bent between forehead, therefore rostrum always retracted between fore coxae. Eyes approximate dorsally. Antennae inserted in forehead, not geniculate, with oval scape as long as 1st segment of funicle. Scutellum bare or thinly clothed with hairs. Hind femora distinctly swollen, with spiraled apodeme. Pronotum with coxae separated to each other, but usually concealed by retracted rostrum. Venter with 2-4 ventrites straight in posterior margin. Adeagus not strongly bent ventrally. Spermatheca with gland located on the middle or beyond the middle of capsule. **Ramphus** Clairville
- 13(12) Head normal, rostrum perpendicular to the axis of body. Eyes more or less separated. Antennae inserted in rostrum, geniculate, scape much longer than first. Scutellum, lateral pieces of meso- and metathoraces densely covered with white plumose scales. Hind femora slightly swollen, with J-shaped apodeme. Prosternum with coxae contiguous to each other. Venter with posterior margins of 2-4 not straight at sides. Adeagus strongly bent ventrally. Spermatheca with capsule narrowed to the apex, gland located close to apex.
 **Isochnus** Thomson
- 14(7) Antennae with funicle 6-segmented. Pronotum and elytra often with erect setae at sides. Tergum with 7th segment more or less projected in the middle of anterior margin.
- 15(18) Fore and middle tibiae unarmed or minutely uncinat at tip, femora without denticle or spine. Tergum with spicule patches from 4th to 7th, of which on 4th and 7th reduced in size, 7th with scrapers in a pair of rows. Derm yellowish to reddish brown. Rostrum not received in breast in reposed.
- 16(17) Femora unarmed at tip. Spermatheca with capsule slender, gland located near middle of it. **Indodinorrhopalus** Pajni et Sood
- 17(16) Fore and middle femora minutely uncinat at the middle of apical margin. Spermatheca with weak lateral lobe near base, with gland located on it.
 **Rhynchaenus** Clairville et Schellenberg
- 18(15) Fore and middle femora each with a sickle-shaped large uncus from dorsal edge a little behind the apex, fore and middle femora often with denticle with spine, hind femora often with denticles with long setae or spine. Tergum with spicule patches on 5th and 6th tergites, 7th tergite bilobedly produced at the middle of

anterior margin and with a pair of scrapers on it. Derm various in color.
 Rostrum received on breast in reposed. **Orchestes** Illiger

Key to East Asian subgenera of *Ramphus* Clairville

- 1(2) Derm thinly clothed with hairs. Claws each with a broad flat basal process. Tergum with spicule patches from 5th to 7th tergites. Spermatheca with gland located beyond the middle of capsule. **Trichorhamphus** Korotyaev
 2(1) Derm bare. Claws each with basal tooth indefinite. Tergum with spicule patches from 4th to 7th tergites. Spermatheca with gland located in the middle of capsule.
 *Ramphus* s. str.

Key to East Asian subgenera of **Orchestes** Illiger

- 1(4) Hind tibiae simple, without flat surface internally, without erect long setae along internal margin.
 2(3) Prosternum with coxae narrowly separated by flat prosternal process. Mesosternal process as wide as a coxa. Fore and middle femora each with a denticle with spine, hind femora often with a denticle with spine and long setae. Body broadly ovate.
 **Nomizo** Morimoto
 3(2) Prosternum with coxae contiguous or narrowly separated by linear prosternal process. Mesosternal process narrower than a coxa. Fore and middle femora each often with a denticle with spine, hind femora often one or a few denticles with spine and long setae. Body various. *Alyctus* Thomson
 4(1) Hind tibiae curved, with carinae along the both edges of flat surface along inner margin, and with a row of long setae along inner face of flat surface. Fore and middle femora armed with a denticle with spine, often absent. Hind femora each with denticles, spines and setae. **Orchestes** s. str.

Summary of classification of East Asian Ramphini

Ramphini Schoenherr

- = Rhamphides Schoenherr, 1826: 49.
- = Rhynchaeninae Winkler, 1932: 1629.
- = Rhynchaenini Bedel, 1884: 122.
- = Orchestina Thomson, 1859: 141.

Autapomorphies: As shown in Fig. 1.

Included taxa: **Indodinorrhopalus** Pajni et Sood, **Rhynchaenrrs** Clairville & Schellenberg, **Tachyerges** Schoenherr, **Isochnus** Thomson, **Ramphus** Clairville, **Pserrdorchestes** Bedel [Europe (excepting northern part), North Africa, West and Central Asia], **Orchestes** (**Orchestes**) Illiger, **Orchestes** (**Nomizo** Morimoto), **Orchestes** (**Alyctus** Thomson), **Orchestes** (**Anomorrhynchaenus** Voss) [North Africa], **Hyporhynchaenus** Voss, **Pseudendaeus** Voss [West Asia], **Synorchestes** Voss, **Sphaerorchestes** Morimoto et Miyakawa, **Imachra** Pascoe.

Rhynchaenus Clairville & Schellenberg

Two species are contained and known from Europe and eastern Asia. Larva of ***R. lonicerae*** feeds on the leaves of *Lonicera xylosteum* of Caprifoliaceae.

Autapomorphies: None is shown in Fig. 1, but yellowish brown derm and minute unci of fore and middle tibiae are characteristic.

Included species: ***Rhynchaenus lonicerae*** (Herbst) [northern and central Europe]; ***R. pacificus*** Faust (= *Rhynchaenus terminassinnae* Egorov) [Russian Far East, Korea, Japan].

Examined: Two species listed above.

Indodinorrhopalus Pajni et Sood

Three species are known only from mountain areas of India, Nepal and Thailand. No information is available on biology.

Autapomorphies: As shown in Fig. 1. One is homoplastic.

Included species: *Indodinorrhopalus imphalensis* Pajni et Sood [India]; *I. okushimai* Morimoto et Miyakawa [Thailand]; *I. guttatus* Morimoto et Miyakawa [Thailand, Nepal].

Examined: Two species excepting type species.

Tachyerges Schoenherr

Nine species are known from Holarctic and feeding Salicaceae and following 7 species are known to occur in East Asia as listed below.

Autapomorphies: None is shown in Fig. 1, but black derm, with white scutellum densely covered with setae and usually maculate elytra are characteristic.

Included species: ***T. stigma*** (Germar) [Japan, Siberia, Europe]; ***T. pseudostigma*** (Tempere) [Europe to North China]; ***T. saficis*** (Linnaeus) [Japan, Siberia, Sakhalin, Kuril Isls., Europe, North America]; ***T. awomoriensis*** (Roelofs) [Japan]; ***T. dauricus*** (Faust) [Russian Far East, Japan]; ***T. empopulifolis*** (Chen) [China]; ***T. nakamurai*** Morimoto et Miyakawa [Japan]; ***T. pubescens*** (Motschulsky) [Kamchatka].

Examined: All species excepting ***T. pseudostigma***, ***T. empopulifolis***, ***T. pubescens*** and ***T. awomoriensis*** were examined. Some European and North American species were also examined: ***T. decoratus*** (Germar) [Europe]; ***T. niger*** (Horn) [North America]; ***T. ephippiatus*** (Say) [North. America]; ***T. rufitarsis*** (Germar) [Europe].

Hyporhynchaenus Voss

Two species are known from Oriental region. No information is recorded on biology.

Autapomorphies: As shown in Fig. 1. One is homoplastic.

Included species: ***Hyporhynchaenus lartracae*** (Voss) [Indonesia: Java]; ***H. sphinxoides*** Morimoto et Miyakawa [West Malaysia].

Examined: ***Hyporhynchaenus sphinxoides*** Morimoto et Miyakawa.

Isochnus Thomson

Nine species are known from boreal, temperate, subarctic and high arctic zones of Holarctic region and feeding Salicaceae, and probably Betulaceae and Rosaceae. Only one species, ***I. sorbi*** from Japan is known to occur in East Asia.

Autapomorphies: As shown in Fig. 1, one is homoplastic and the other is reversal. The others are pulmose scales on various parts of the thoracic sterna, pronotum and scutellum and markedly ventrally directed aedeagus.

Examined: *Isochnus sorbi* Morimoto, *I. angustifrons* (West).

Ramphus Clairville

No less than 20 species are known from Palaearctic, Ethiopian, Australian and Oriental regions and following 4 species are known to occur in East Asia. The adults feed leaves of various families in wide range. Larval hosts are recorded as follows: *Crataegus*, *Pyrus*, *Malus*, *Prunus* and so on of Rosaceae, *Betula* of Betulaceae, *Salix* and *Populus* of Salicaceae and *Acer* of Aceraceae. Korotyaev (1984) divided into three subgenera, *Rhamphus* s. str., *Nanorhamphus* and *Trichorhamphus*, of which the former 2 occur in East Asia.

Autapomorphies: As is shown in Fig. 1, all are homoplastic. The others are antennal insertion into forehead, straight posterior margins of 2-4 ventrites (reversal), maxillary palp with one segment and absence of prementum.

Included species: *Ramphus* (*Ramphus*) *choseniae* Korotyaev [Russian SFSR]; *R. (R.) pulicarius* [Japan, Korea, Taiwan, China, Kuril Isls., Sachalin, Siberia, Europe]; *R. (R.) tsaidamicus* Korotyaev [China]; *R. (Trichorhamphus) hisamatsui* Chûjô et Morimoto [Japan, Taiwan, Kuril Isls.].

Examined: *Ramphus pulicarius* (Herbst), *R. hisamatsui* Chûjô et Morimoto, *R. sp.* (East Malaysia).

Orchestes Illiger

Three subgenera and about 50 species are known from East Asia, feeding the leaves of broad leaves trees of various families, but not known from conifers. Recorded larval host plants are *Zelkova*, *Celtis*, *Ulmus* of Ulmaceae, *Quercus*, *Castanea*, *Castanopsis*, *Fagus*, *Lithocarpus* of Fagaceae, *Alnus*, *Betula*, *Carpinus* of Betulaceae, *Myrica* of Myricaceae, *Populus* of Salicaceae and *Mangifer* of Anacardiaceae. Some adults were captured from other plants listed above: *Heritiera* of Sterculiaceae, *Dipterocarpus* of Dipterocarpaceae, *Malus* of Rosaceae, *Salix* of Salicaceae, *Eugenia* of Myrtaceae, *Pterocarya* of Juglandaceae.

Autapomorphies: As shown in Fig. 1.

Included subgenera: *Orchestes* s. str., *Alyctus* Thomson and *Nomizo* Morimoto

Included species and examined: See the following review of each subgenus.

Orchestes (subgenus *Orchestes* s. str.)

= *Euthron* Thomson

Following 36 species are included from East Asia as listed below.

Autapomorphies: As shown in Fig. 1. The other is carinated hind tibiae along the both edges of flat surface internally with a row of long setae.

Included species: *Orchestes koltzei* Faust [Russian Far East]; *O. scitus* Faust [Russian Far East]; *O. similis* Faust [Russian Far East]; *O. fasciculatus* Faust [Russian Far East]; *O. miyatakei* (Morimoto), **comb. nov.** [Japan]; *O. sanguinipes* Roelofs [Japan]; *O. lateritius* (Morimoto), **comb. nov.** [Japan]; *O. horii* (Kôno), **comb. nov.** [Japan]; *O. harunire* (Morimoto), **comb. nov.** [Japan]; *O. nitens* (Morimoto), **comb. nov.** [Japan]; *O. yokoe* Morimoto et Miyakawa [Japan]; *O. mutabilis* Boheman [Japan, Sakhalin, Siberia]; *O. hustachei* (Klima), **comb. nov.** [Japan]; *O. truncatipennis* (Morimoto), **comb. nov.** [Japan]; *O. excellens* Roelofs [Japan]; *O. japonicus* Hustache [Japan]; *O. nomizo* Kôno [Japan,

Sachalin]; *O. villosus* (Morimoto), **comb. nov.** [Japan]; *O. amurensis* Faust [Japan, Korea, Russian Far East]; *O. jota* Fabricius [Japan, Russia, Europe]; *O. variegatus* Roelofs [Japan]; *O. hidakai* (Morimoto), **comb. nov.** [Japan]; *O. heritierae* (Morimoto), **comb. nov.** [Japan]; *O. dorsoplanatus* Roelofs [Japan, Taiwan, China]; *O. trifasciatus* (Morimoto), **comb. nov.** [Japan]; *O. nigrofasciculatus* (Voss), **comb. nov.** [China: Fukien]; *O. albosetosus* (Pajni et Sood), **comb. nov.** [India]; *O. manipurensis* (Pajni et Sood), **comb. nov.** [India]; *O. maculatus* (Pajni et Sood), **comb. nov.** [India]; *O. aureus* (Pajni et Sood), **comb. nov.** [India]; *O. mangiferue* (Marshall), **comb. nov.** [India]; *O. ffuvirostris* (Marshall), **comb. nov.** [Indonesia]; *O. rugosus* (Marshall), **comb. nov.** [Vietnam]; *O. maculosus* (Yang et Zhang), **comb. nov.** [North East China]; *O. praenotatus* (Voss), **comb. nov.** [China: Fukien]; *O. purvidens* (Voss), **comb. nov.** [China: Fukien]; *O. anoploideus* Hustache [Singapore].

Examined: Excepting *Orchestes koltrei*, *O. similis*, *O. fasciculatus*, *O. albosetosus*, *O. manipurensis*, *O. maculatus*, *O. aureus*, *O. rugosus*, *O. maculosus* and *O. anoploideus*, all the species distributing in East Asia are examined.

Orchestes (subgenus *Nomizo* Morimoto)

One species is known from Japan. Another one species of this subgenus described by Yang & Dai (1991) from China is doubtful its position from the original description. Pajni & Sood (1981) described *Pseudorchestes nigricans* from India, but it may probably a species of this subgenus. Some undescribed species have been collected from Southeast Asia.

Autapomorphies: As shown in Fig. 1.

Included species: *Orchestes kumiyui* (Morimoto) [Japan].

Examined: *Orchestes kumiyui* Morimoto, *O. sp.* [East Malaysia], *O. sp.* [Philippine].

Orchestes (subgenus *Alyctus* Thomson)

= *Threticus* Thomson

Following nine species are included in this subgenus from East Asia.

Included species: *Orchestes rusci* (Herbst) [Japan, Kuril Isls., Kamchatka, Europe]; *O. cylindricus* (Morimoto), **comb. nov.** [Japan]; *O. galloisi* Kôno [Japan, China]; *O. jozanus* Kôno [Japan]; *O. kimotoi* (Morimoto), **comb. nov.** [Japan]; *O. aterrimus* Roelofs [Japan, Kuril Isls., Sakhalin]; *O. subbifusciatus* Faust [Russian Far East]; *O. amplithorax* Faust [Russian Far East]; *O. basirostris* (Voss), **comb. nov.** [China: Fukien, Afghanistan]; *O. funicularis* (Voss), **comb. nov.** [China: Fukien]

Autapomorphies: None shown in Fig. 1. This is designated in this genus by the lack of synapomorphy.

Examined: All species were examined. Some European and North American species were also examined: *O. testaceus* (Müller), **comb. nov.** [Europe and North America]; *O. avellanae* (Donov.), **comb. nov.** [Europe, Siberia]; *O. griseus* (Sleeper), **comb. nov.** [North America]; *O. pallicornis* Say [North America]; *O. mixtus* Blatchley [North America].

Synorchestes Voss

One species is known from China (Fukien) and Taiwan. No information is recorded on biology.

Autapomorphies: One (reversal) is shown in Fig. 1. The others are loosely segmented club, broadly exposed propygidium in male and exposed pygidium in both sexes.

Included species: *Synorchestes grisescens* Voss [China: Fukien, Taiwan]

Examined: One species listed above.

Sphaerorchestes Morimoto et Miyakawa

Three species are known from Oriental region. No information is recorded on biology.

Autapomorphies: One homoplastic apomorphy is shown in Fig. 1.

Included species: ***Sphaerorchestes kuwasei*** Morimoto et Miyakawa [Japan], *S. nepalensis* Morimoto et Miyakawa [Nepal], *S. kojimai* Morimoto et Miyakawa [East Malaysia: Sabah].

Examined: All species listed above.

Zmachra Pascoe

No less than 14 species are known from Oriental region. *I. maetai* was captured on *Cinnamomum japonicum* of Lauraceae.

Autapomorphies: None is shown in Fig. 1, but short, robust and straight rostrum is unique in this genus.

Included species: ***Zmachra ruficollis*** Pascoe [East Maysia: Sabah, China]; *I. oculatus* (Morimoto) [Japan]; *I. albosuturalis* Morimoto et Miyakawa [East Malaysia: Sabah]; *I. maetai* (Morimoto) [Japan]; *I. inornatu* (Voss) [China: Fukien]; *I. bivittata* (Marshall) [Burma]; *I. decipiens* (Roelofs) [Japan, Taiwan, China: Fukien]; *I. nipponicu* (Morimoto) [Japan]; *I. mundus* (Voss) [China: Fukien]; *I. saigusai* Morimoto et Miyakawa [Taiwan]; *I. shirozui* (Morimoto) [Japan, Taiwan]; *I. bifasciata* Morimoto et Miyakawa [East Malaysia: Sabah]; *I. sabuhnu* Morimoto et Miyakawa [East Malaysia: Sabah]; *I. siamensis* Morimoto et Miyakawa [Thailand].

Examined: All species excepting *Imachra inornata*, *I. bivittata*, and *I. mundus*.

Incertae sedis

1. *Rhynchaenus flacourthiae* Marshall [Indonesia: Java]

This is characteristic by having 7 segments in the funicle and the biology, which is bred from the fruits of ***Flacourria*** (not leaf-miner!!) and the first appearance is similar to the species of ***Tachyerges*** or *Hyporhynchaenus* from the illustration of original description. However, occurrence of ***Tachyerges*** in the Oriental region is considered improbable

2. *Rhynchaenus (Tachyerges) freyi* Voss [Ceylon]

From the original description, fore and middle femora each arms with a denticle and hind femur also arms with denticles with spine. These features are unusual in ***Tachyerges*** and may not be the member of this subgenus, but a possibility of ***Orchestes*** by misobservation of the funicle.

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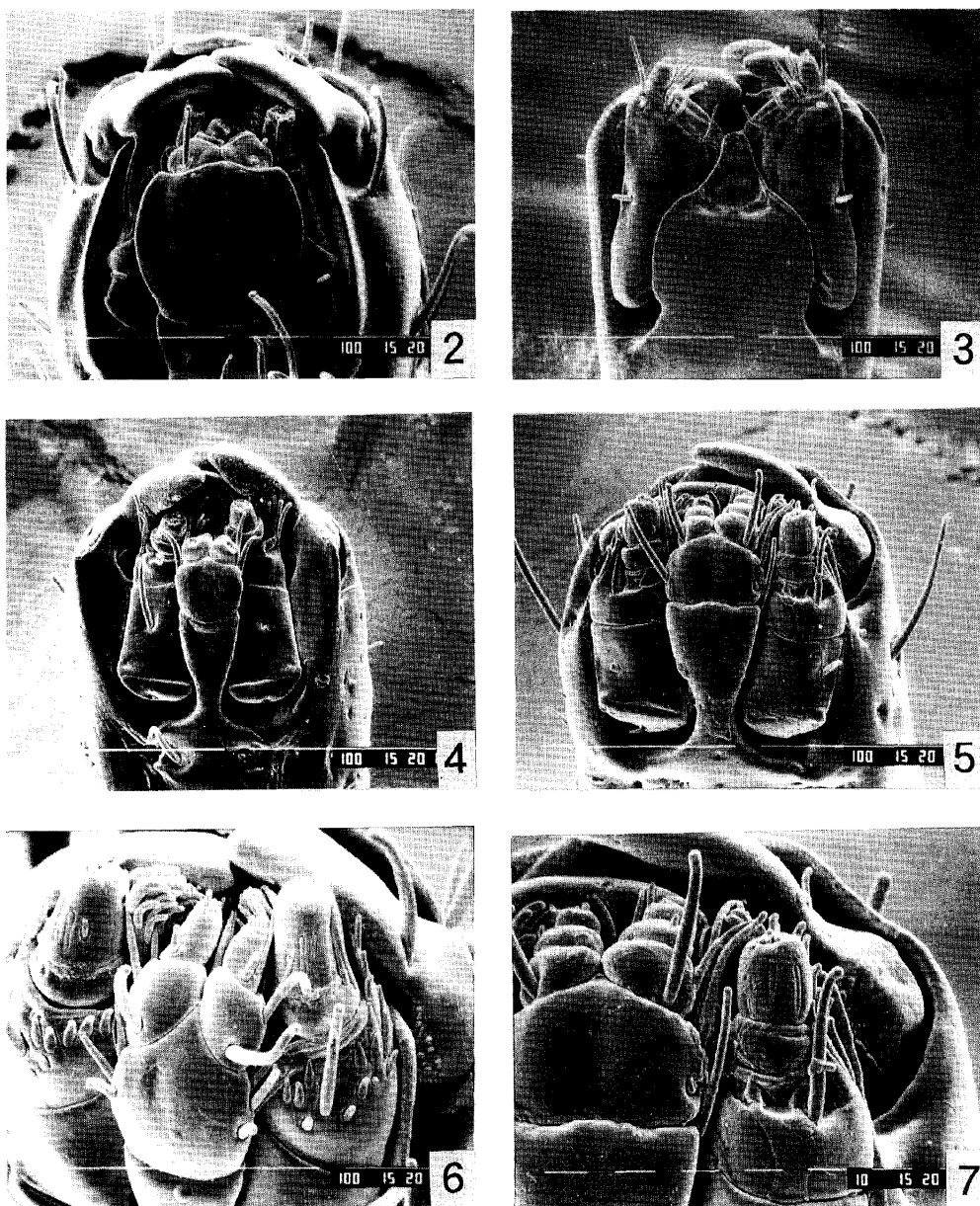
Research on the part of Kojima was supported by a Grant-in-Aid, Ministry of Education, Science and Culture, Japan. Kojima also thanks to Associate Prof. O. Tadauchi, Associate Prof. M. T. Chûjô and Assistant Prof. S. Kamitani of Kyushu University for their continuous guidance.

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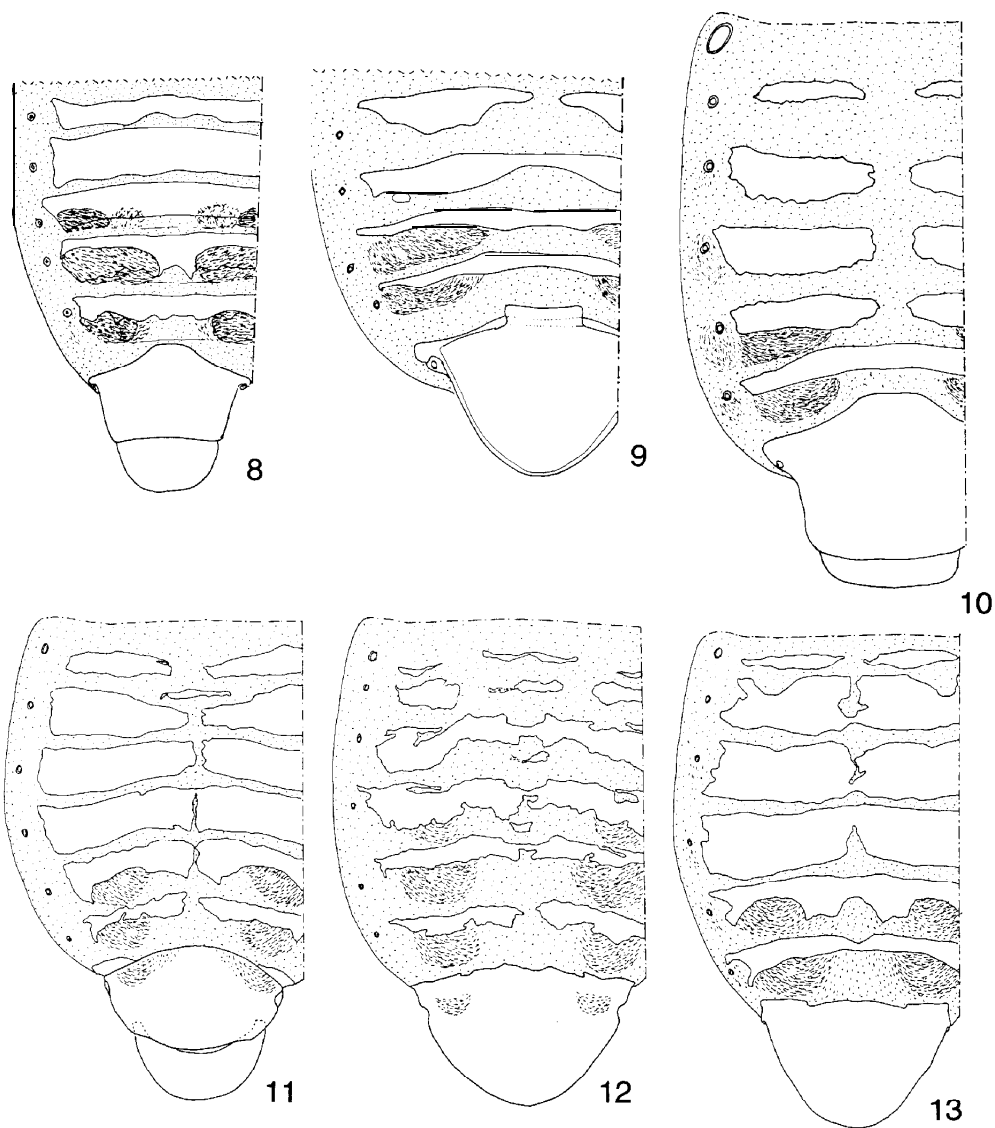
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Table 1. Data matrix. Taxon abbreviations: Aly = *Alyctus*, anc = hypothetical ancestor, Hyp = *Hyporhynchaenus*, Ima = *Imachra*, Ind = *Zndodinorrhopafus*, Iso = *Isochnus*, Nom = *Nomizo*, Orc = *Orchestes*, Pse = *Pseudorchestes*, Ram = *Ramphus*, Rhy = *Rhynchaenus*, Sph = *Sphaerorchestes*, Syn = *Synorchestes*, Tac = *Tachyerges*. Other symbols: "0,1" = taxon dimorphic, with both states 0 and 1; "O-2" = taxon polymorphic, with states 0 through 2; "?" = character state unknown.

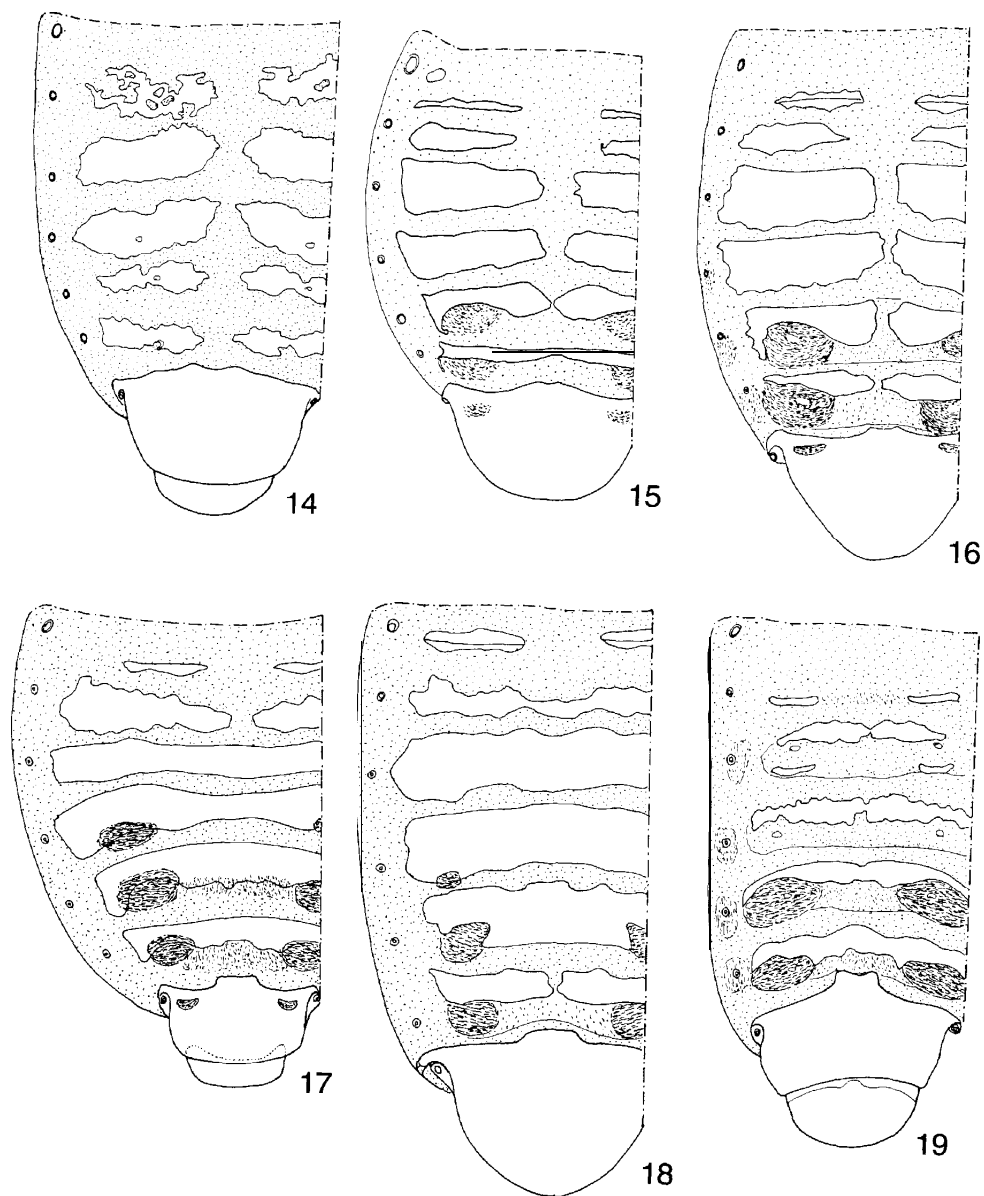


Figs. 2-7. Mouth parts by SEM, ventral aspects of:
2: *Imachra nipponicus*; 3: *Ramphrta hisamatsui*; 4: *Isochnus angrtstifrons*. 5, 7:
Tachyerges nakamurai; 6: *Rhynchaenus pacificus*.



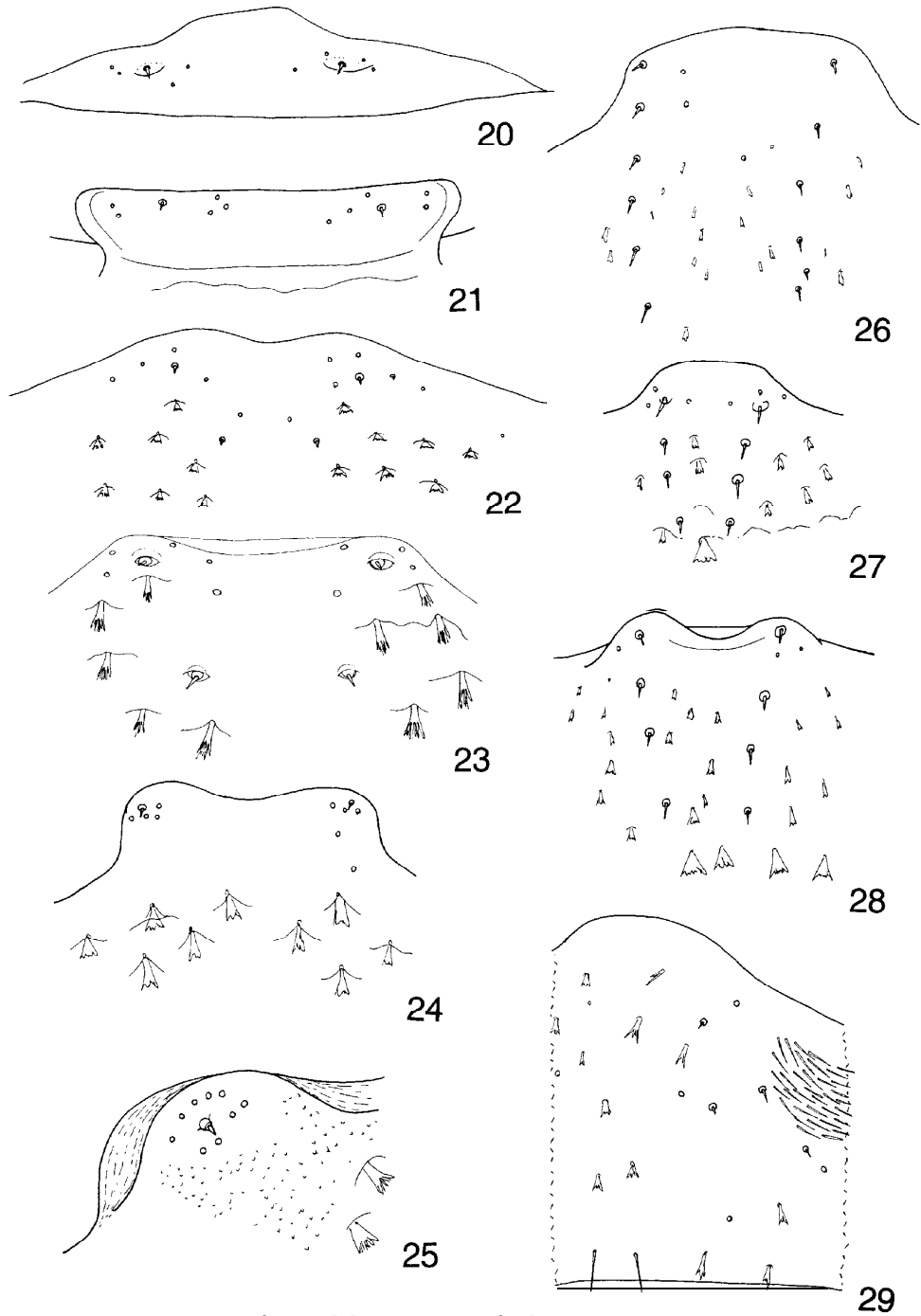
Figs. 8-13. Tergite of:

8: *Imachra decipiens*; 9: *Sphaerorchestes kawasei*; 10: *Synorchestes grisescens*; 11: *Ramphus (Trichorhamphus) hisamatsui*; 12: *R. (Ramphus) pulicarius*; 13: *Isochnus angustifrons*.



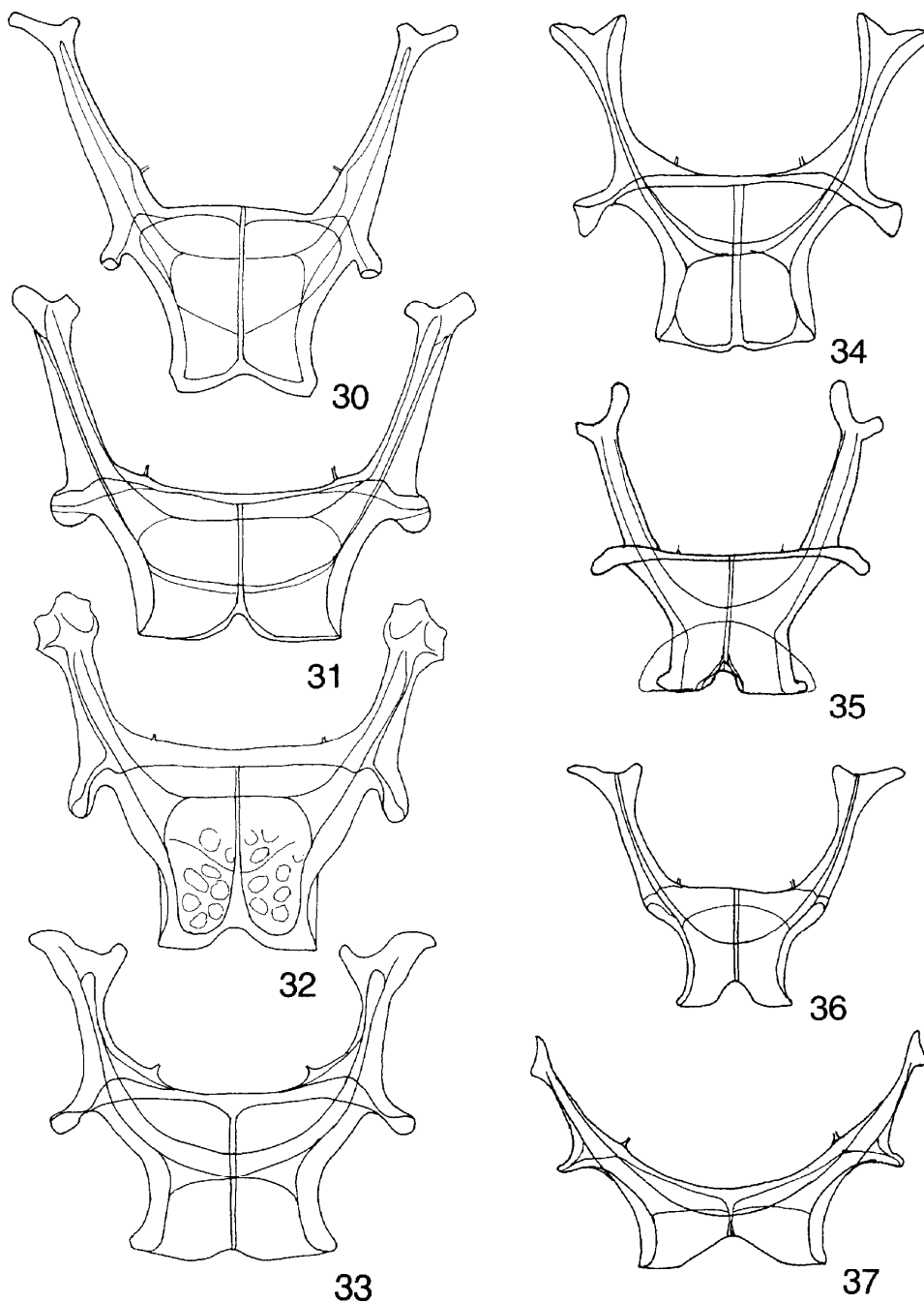
Figs. 14-19. Tergite of:

14: *Isochnus sorbi*; 15: *Hyporhynchaenus sphinxoides*; 16: *Tachyerges stigma*; 17: *Indodinorrhopalus guttatus*; 18: *Rhynchaenus lonicerae*; 19: *Orchestes horii*.



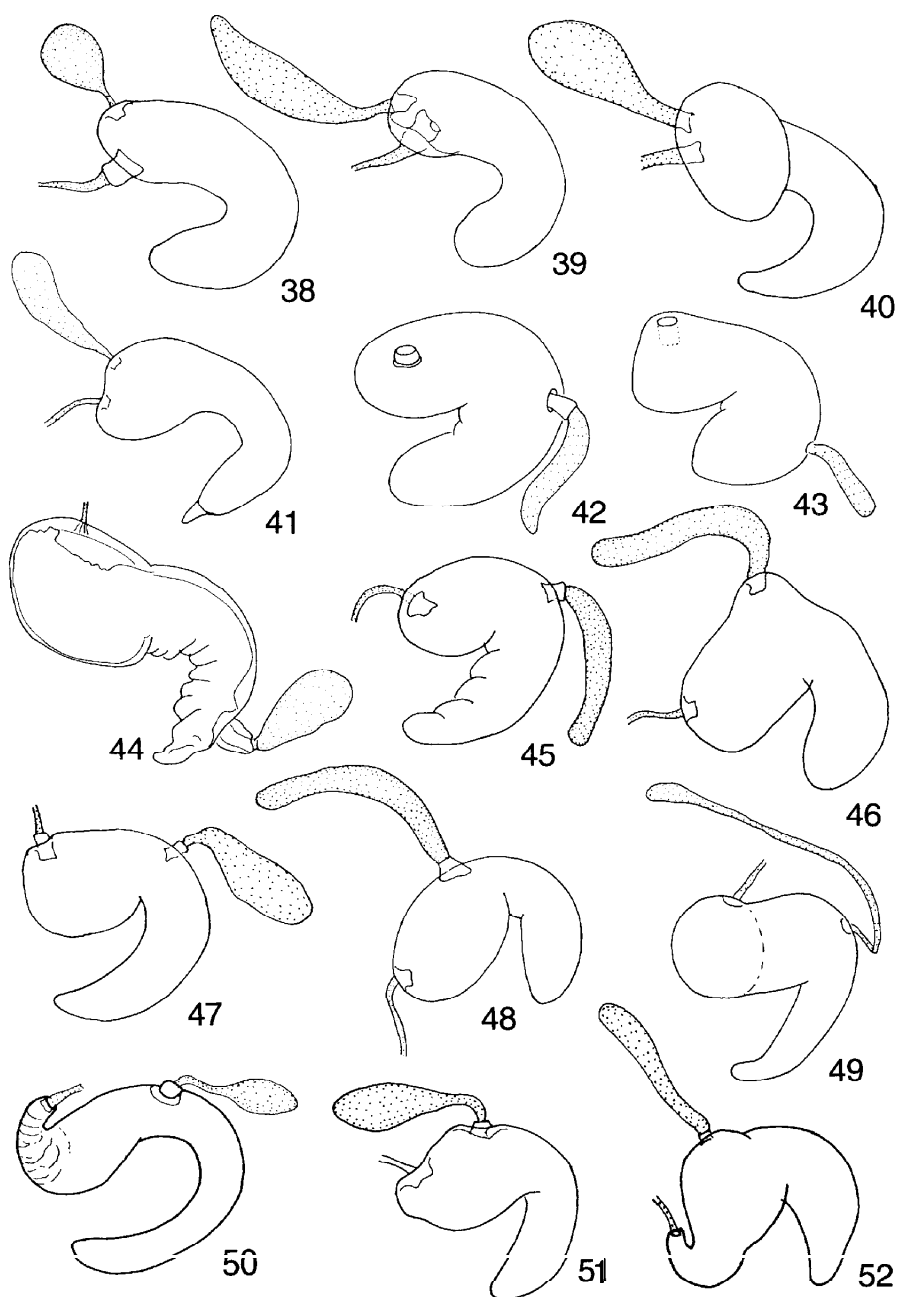
Figs. 20-29. Scrapers for stridulatory organ of 7th tergite:

20: *Imachra nipponicus*; 21: *Sphaerorchestes kawasei*; 22: *Hyporhynchaenus sphinxioides*; 23: *Tachyerges nakamurai*; 24: *Orchestes horii*; 25: *O. hustachei*; 26: *Rhynchaenus pacificus*; 27, 28: *Zndodinorrhopalus guttatus* (27: male; 28: female); 29: *Ramphus pulicarius*.



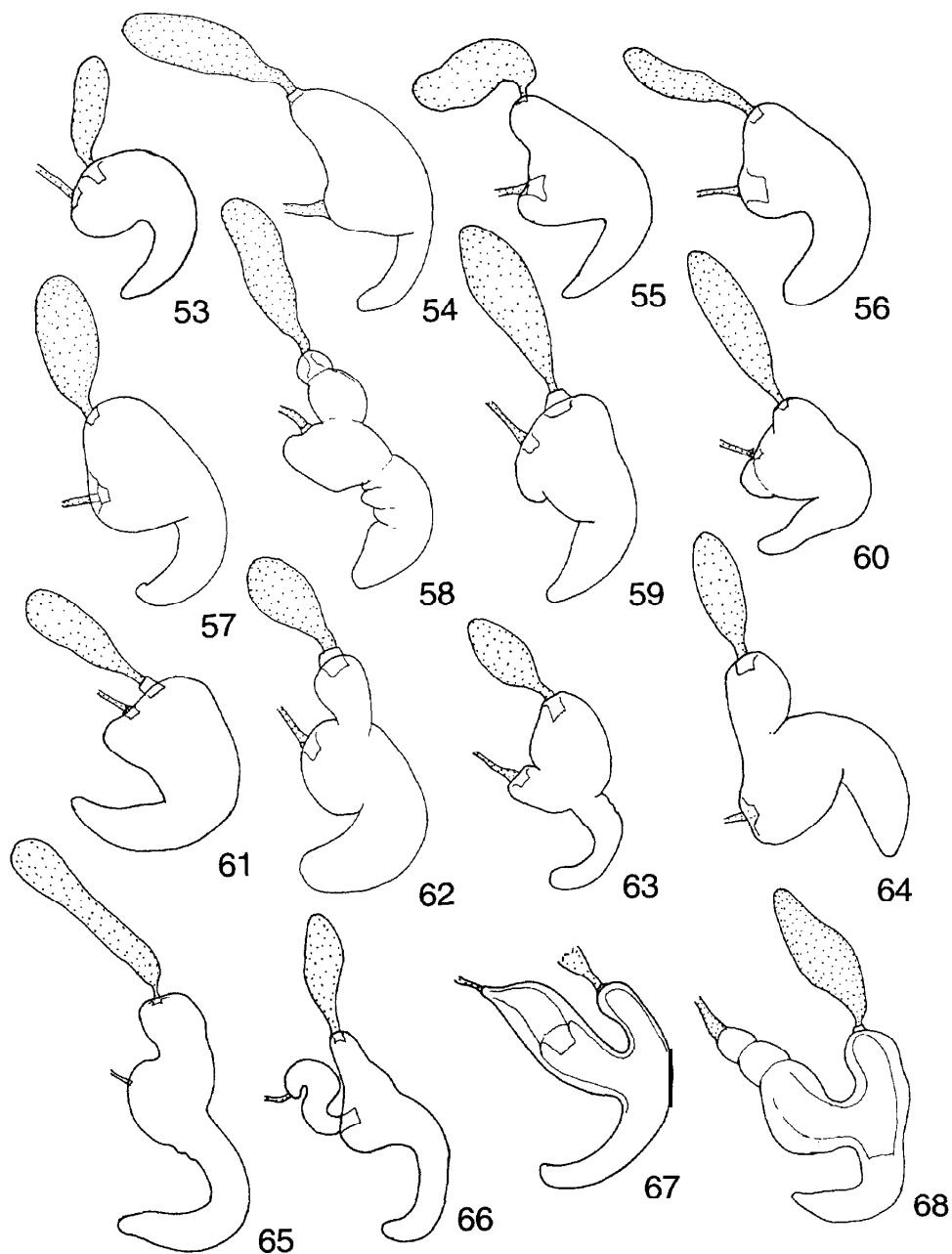
Figs. 30-37. Metendosternite of:

30: *Imachra decipiens*; 31: *Sphaerorchestes nepalensis*; 32: *Synorchestes grisescens*;
 33: *Orchestes (Orchestes) japonicus*; 34: *Orchestes (Alyctus) cylindricus*; 35:
Indodinorrhopalus guttatus; 36: *Ramphus pulicarius*; 37: *Isochnus sorbi*.



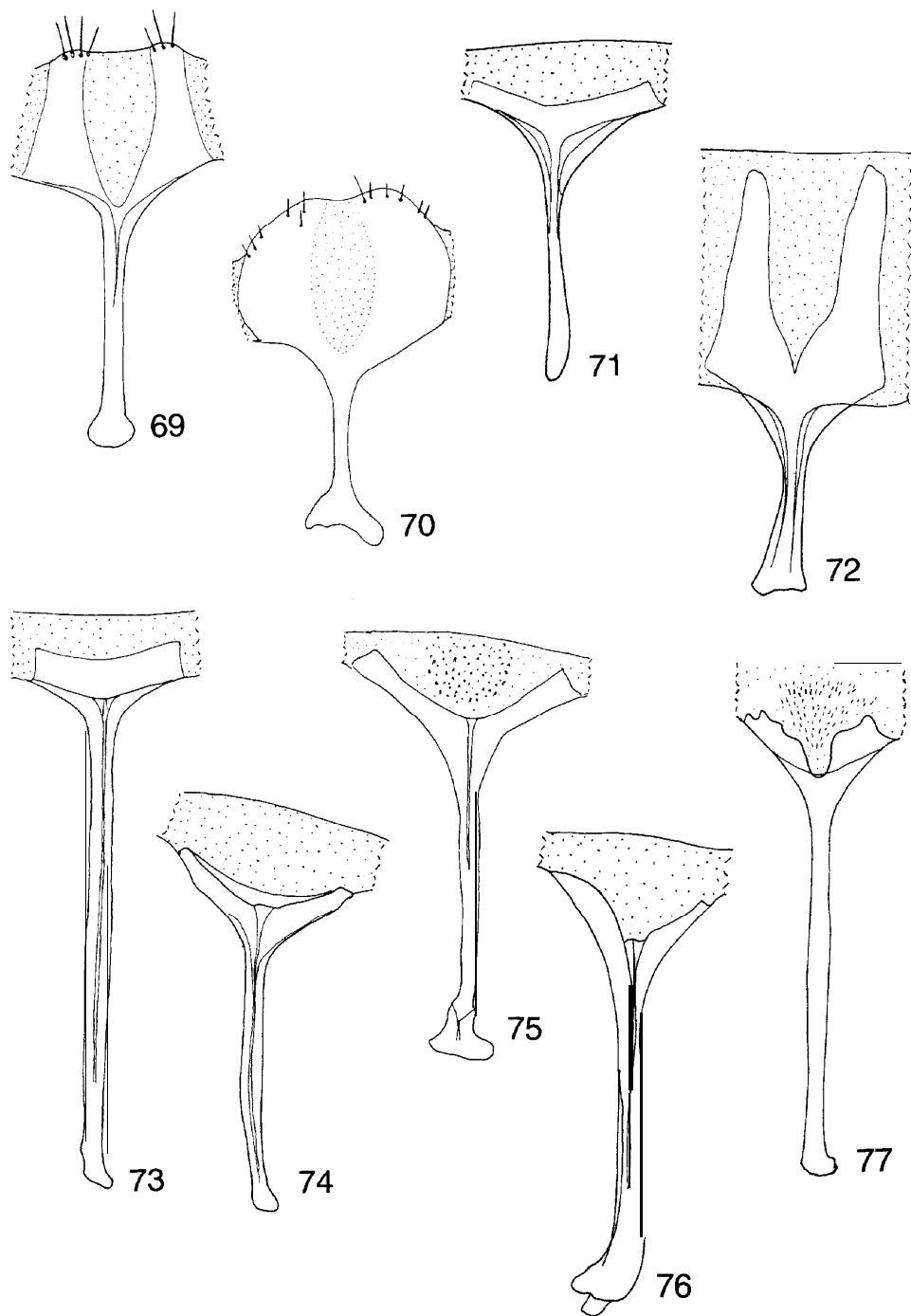
Figs. 38-68. Spermatheca of:

38: *Imachra maetai*; 39: *I. decipiens*; 40: *Sphaerorchestes nepalensis*; 41: *Synorchestes grisescens*; 42: *Ramphus* (*Ramphus*) *pulicarius*; 43: *R. (Trichorhamphus) hisamatsui*; 44: *Isochnus sorbi*; 45: *Tachyerges dauricus*; 46: *T. nakamurai*; 47: *T. salicis*; 48: *T. stigma*; 49: *Hyporhynchaenus sphinxioides*; 50: *Indodinorrhopalus guttatus*; 51: *Rhynchaenus lonicerae*; 52: *R. pacificus*.



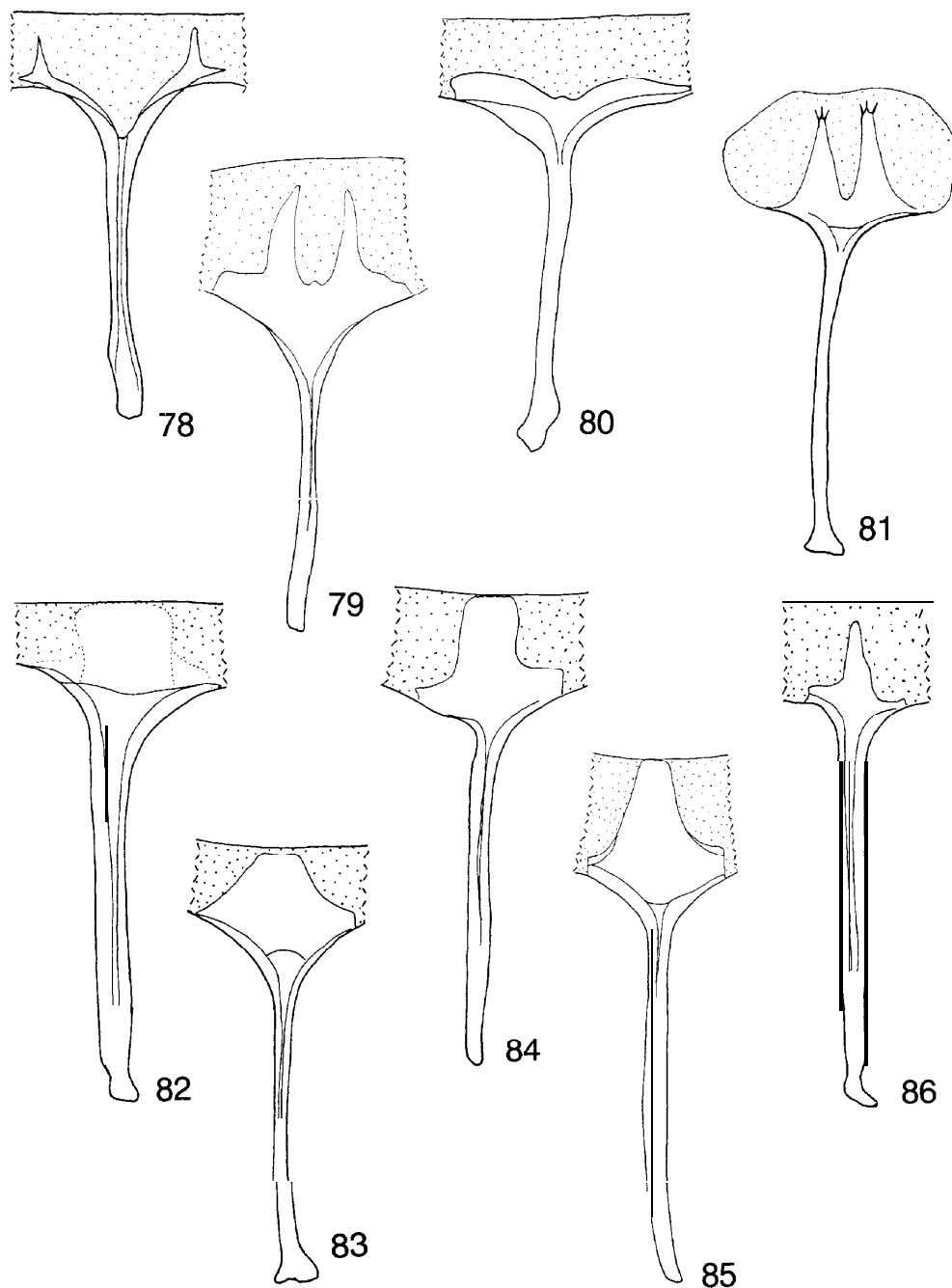
Figs. 53-68. Spermatheca of:

53: *Orchestes*(*Nomizo*)*kamiyai*; 54: *O. (Alyctus) rusci*; 55: *O. (A.) galloisi*; 56: *O. (A.) jozanus*; 57: *O. (A.) aterrimus*; 58: *O. (A.) testaceus*; 59: *O. (Orchestes) miyatakei*; 60: *O. (O.) nomizo*; 61: *O. (O.) villosus*; 62: *O. (O.) sanguinipes*; 63: *O. (O.) horii*; 64: *O. (O.) hustuchei*; 65: *O. (O.) juponicus*; 66: *O. (O.) fagi*; 67: *O. (O.) dorsoplunutus*; 68: *O. (O.) quercus*.



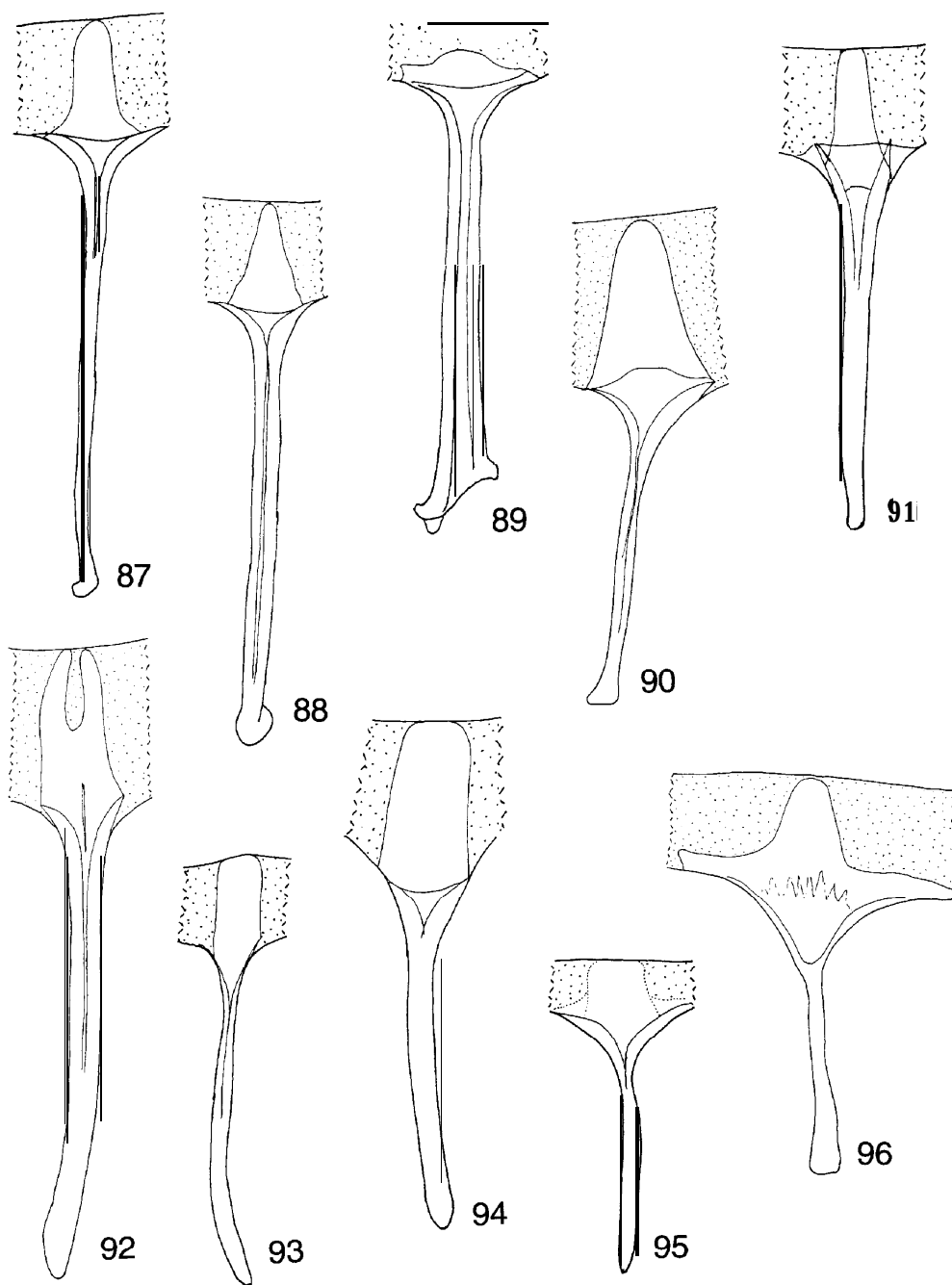
Figs. 69-77. Spiculum ventrale of:

69: *Sphaerorchestes nepalensis*; 70: *Imachra maetai*; 71: *I. dentipes*; 72: *Synorchestes grisescens*; 73: *Ramphus plicarius*; 74: *Isochnus sorbi*; 75: *Tachyerges dauricus*; 76: *T. salicis*; 77: *T. nakamurai*.



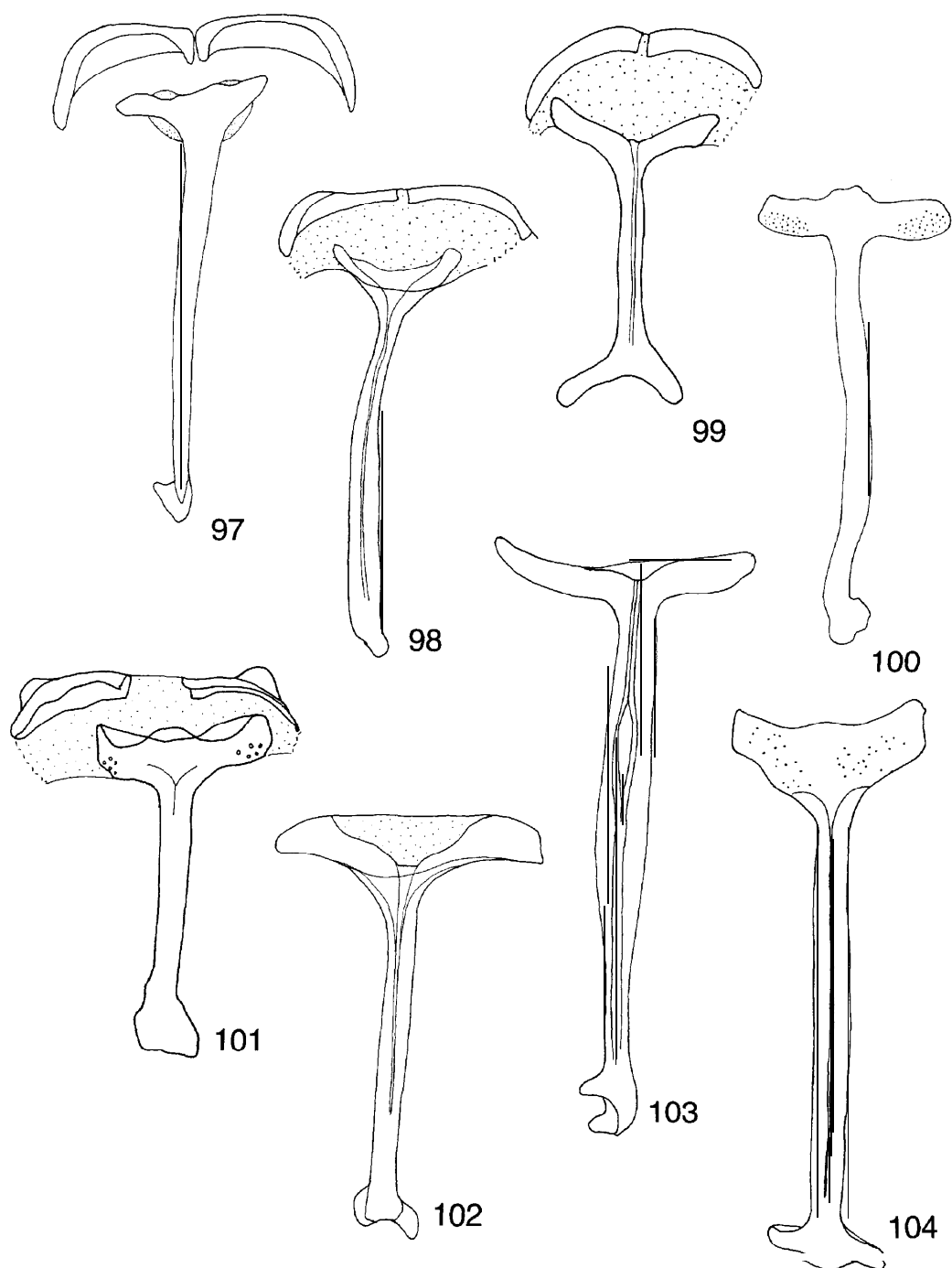
Figs: 78-86. Spiculum ventrale of:

78: *Hyporhynchaenus sphinxoides*; 79: *Rhynchaenus pacificus*; 80: *R. lonicerae*; 81: *Indodinorrhopalus guttatus*; 82: *Orchestes (Alyctus) rusci*; 83: *O. (A.) galloisi*; 84: *O. (A.) jozanus*; 85: *O. (A.) testaceus*; 86: *O. (Nomizo) kamiyai*.



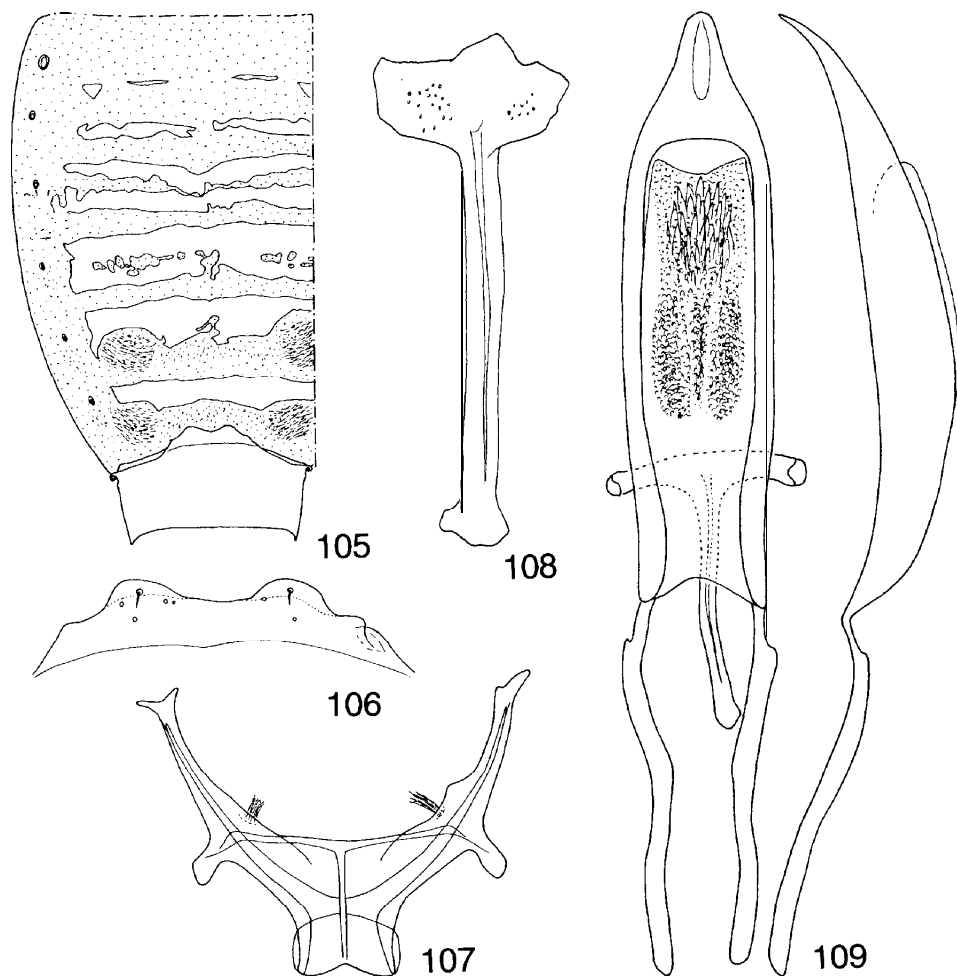
Figs: 87-96. Spiculum ventrale of:

87: *Orchestes (Orchestes) nomizo*; 88: *O. (O.) villosus*; 89: *O. (O.) miyatakei*; 90: *O. (O.) quercus*; 91: *O. (O.) fagi*; 92: *O. (O.) japonicus*; 93: *O. (O.) horii*; 94: *O. (O.) sanguinipes*; 95: *O. (O.) dorsoplanatus*; 96: *O. (O.) hustachei*.



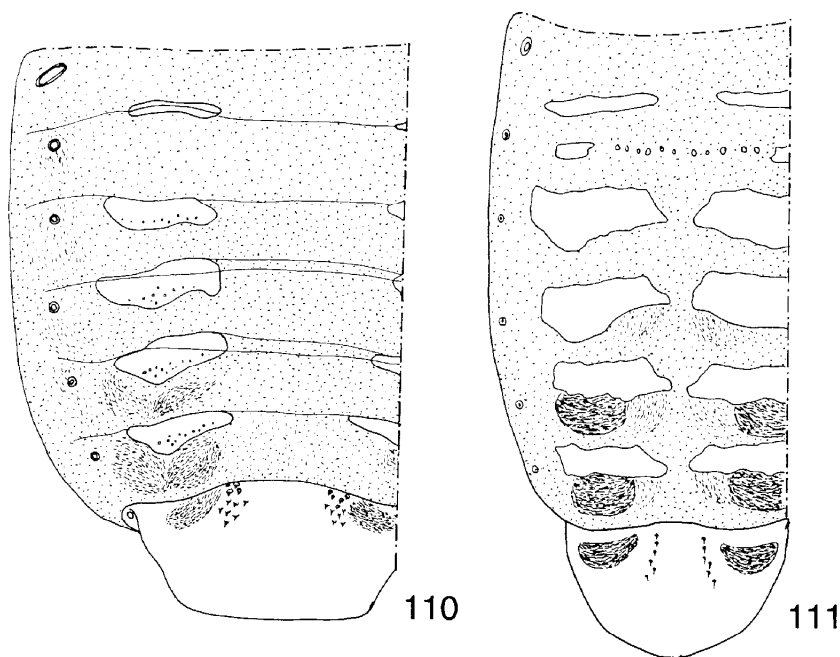
Figs. 97-104. Spiculum relictum and spiculum gastrale of:

97: *Zmachra maetai*; 98: *I. dentipes*; 99: *Rhynchaenus pacificus*; 100: *Tachyerges nakamurai*; 101: *Indodinorhupalus guttatus*; 102: *Tachyerges stigma*; 103: *T. dauricus*; 104: *Orchestes (Orchestes) kimotoi*.

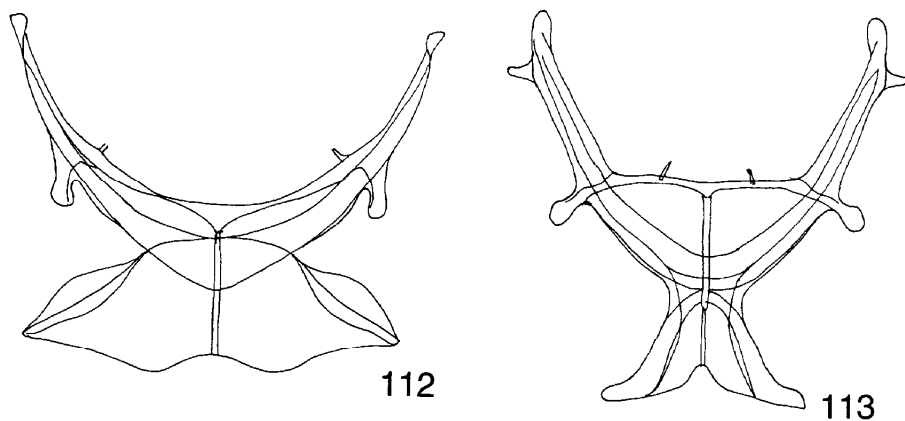


Figs. 105109. *Pseudorchestes ermischi* (Dieckmann).

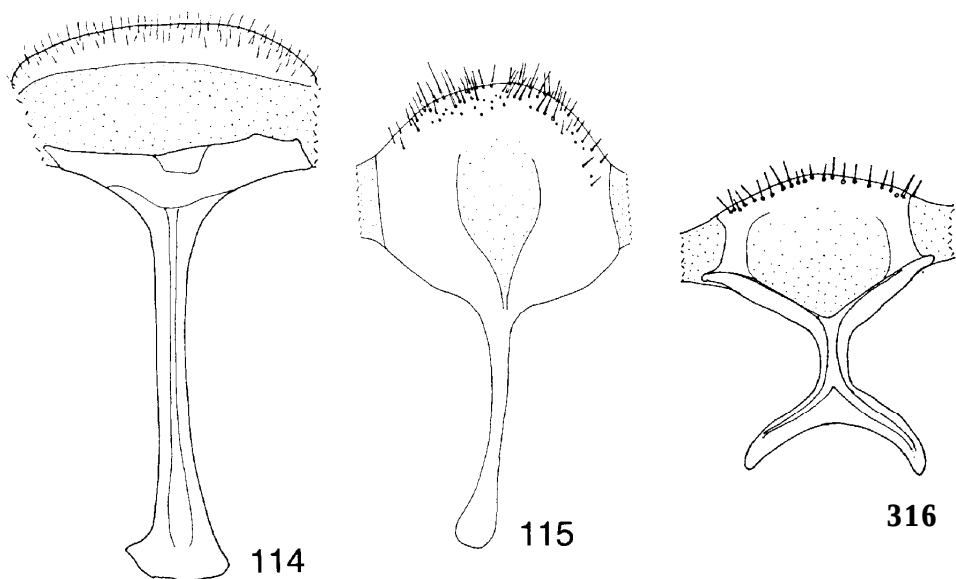
105: Tergite. 106: Scraper for stridulatory organ of 7th tergite. 107: Metendostemite. 108: Spiculum gastrale. 109: Penis.



Figs. 110-111. Tergite of Dinorhopalini:
110: *Dinorhopala takahashii*; 111: *Ixalma dentipes*.

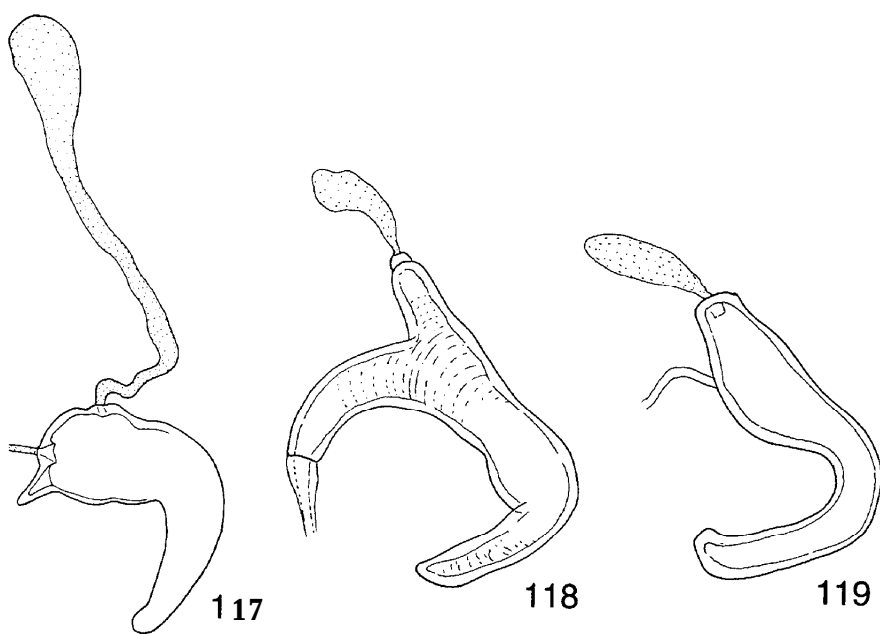


Figs. 112-113. Metendostemite of Dinorhopalini:
112: *Dinorhopala takahashii*; 113: *Ixalma dentipes*.



Figs. 114-116. Spiculem ventrale of Dinorhopalini:

114: *Dinorhopala takahashii*; 115: *Ixalma nigriventris*; 116: *I. hilleri*.



Figs. 117-119. Spermatheca of Dinorhopalini:

117: *Dinorhopala takahashii*; 118: *Ixalma okadui*; 119: *I. hilleri*.