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**A SYSTEMATIC STUDY OF THE GRASSHOPPER TRIBE PODISMINI
IN JAPAN (ORTHOPTERA: ACRIDIDAE)**

By GEN ITO

Abstract

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This research presents evaluation of morphology in systematics of the tribe Podismini through the following studies.

Morphology of the Podismini is studied and their transformation series are discussed by examination of the body parts including the male and female genitalia. Detailed descriptions of the female internal genitalia of the grasshoppers are given firstly. The terminology of the female internal genitalia is revised.

Phylogenetic relationships among 13 podismini genera in the Far East are inferred on the basis of morphology using cladistic methodology. The topology of the consensus tree is somewhat similar to that of the mtDNA and/or rDNA tree proposed previously. Based on the result, subtribes are revised: a new subtribe Tonkinacridina is proposed for the genera *Tonkinacris*, *Sinopodisma*, *Fruhstorferiola* and *Parapodisma*, excluding them from the subtribe Miramellina. The result suggests paraphyly of the genus *Parapodisma*, endemic to Japan and adjacent regions. Chromosome number possibly changed at least twice in Podismini.

Phylogenetic relationships among *Parapodisma* species are inferred on the basis of morphology using cladistic methodology. The result suggests that speciation in this genus occurred almost allopatrically in 3 lineages.

All the 22 species of 9 genera of Japanese Podismini are described based on the above discussion.

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INTRODUCTION

The Melanoplineae are the third largest acridid subfamily, represented by more than 120 genera and 890 species from Eurasia and Americas (Otte 1995, including “Podisminae”): 42 genera and 215–220 species are distributed in Eurasia, 47 genera and 399–410 species in North America, and 42 genera and 235–250 species in South America (Sergeev 1999). Previously, part of the species was often treated to form another subfamily, Podisminae. Although Otte (1995) also recognized the Podisminae as distinct from Melanoplineae in his catalog, these two taxa are regarded as synonymous with each other in the current classification (*e.g.*, Vickery 1997). Most genera comprise less than 10 species, sometimes one or only a few species, but *Melanoplus* is the largest grasshopper genus in the family Acrididae (Otte 1995). The classification and subdivision of this subfamily are still unclear, in spite of many recent studies (*e.g.*, Rehn & Randell 1963; Vickery 1977; Skareas & Hsiung 1998; Litzenberger & Chapco 2001, 2003; Chintauan-Marquier *et al.* 2011, 2014; Woller *et al.* 2014). This has been caused by several reasons. First, each tribe or subtribe is not well defined. For instance, even in the most recent arrangement of tribes and subtribes by Vickery (1997), each taxon is discussed only on the basis of its type genus and, moreover, no diagnoses are given to his new tribes. Second, some species often resemble with each other at a glance, while they seem to be quite distant phylogenetically. For example, *Pseudopodisma* looks like *Podisma* at a glance, and they have been included in “Podismae” since the establishment of this group by Rehn & Randell (1963), but they are quite different in their karyotypes and genitalia. The third is the occurrence of great geographic variation in morphology within one species, as a consequence of low dispersal ability. As mentioned later, some *Parapodisma* species are very variable geographically, causing much taxonomic confusion. The statement by Otte (2002) on *Melanoplus* is applicable to *Parapodisma*: “the treatment of species has been inconsistent and many of the original papers are not useful in distinguishing the species”.

According to the current classification by Vickery (1997), all species of the Japanese Melanoplineae except for those of *Prumna* belong to the tribe Podismini. However, Rehn & Randell (1963) treated *Prumna* as a member of Primnoae, one of the subgroups of Podismini. In Vickery’s (1997) classification, all subgroups in Rehn & Randell (1963) were treated as subtribes in Podismini except for Primnoae. However, he gave no explanation for this treatment.

Taxonomy on Podismini in Japan was studied actively in the 1980’s and 1990’s, mainly by Japanese entomologists (Inoue 1979a, 1979b, 1985; Ishikawa 1996, 1998; Ito 1999; Kobayashi 1983, 1986; Kanô 1985, 1986, 1990, 1996; Kanô *et al.* 1992; Storozhenko 1993a, 1993b; Storozhenko & Kanô 1992; Tominaga 1983, 1989, 1996; Tominaga & Ishikawa 2001; Tominaga & Kanô 1987; Tominaga, Storozhenko & Kanô 1996; Tominaga & Uchida 2001; Yamasaki 1980) with a long blank after Shiraki (1910, 1930) and Furukawa (1929, 1939), founders of Japanese Orthopterology. At that time, several new podismine species were described one after another. It may be difficult to expect any species of Podismini remaining to be described from Japan. Now the tribe should be reexamined and reviewed. Current information on Podismini is given mainly by scattered descriptive works. Moreover, in most descriptions of species, characters commonly observed in a genus, or sometimes even in the tribe or the family, are mixed together with those of species-specific and diagnostic ones. Even if diagnoses are

provided, these are often very ambiguous. Morphology of Podismini was investigated by several authors (e.g. Mistshenko 1951, 1952; Harz 1975), but most of them aimed only to distinguish taxa from related ones. Thus, it is needed to clarify diagnostic characters in each taxonomic rank by evaluating morphological characters and to know which characters are evolutionary significant.

This paper is composed of three parts: in Chapter 1, comparisons of morphological characters are presented. In Chapter 2, cladistic analyses are performed for the Far Eastern podismine genera and evolutionary changes of several characters are inferred. In Chapter 3, descriptions of Japanese Podismini are given on the basis of the results of the previous chapters. The characters examined involve those not used in the traditional grasshopper taxonomy. Some female characters are examined and evaluated for the first time. Throughout this paper, terminology follows Snodgrass (1928, 1929, 1935), Harz (1975) and Jones (1981) for general body parts, Eades (2000) for male genitalia, and Slifer (1939, 1940b) for female genitalia.

MATERIALS AND METHODS

The materials used in this study, dry or ethanol-preserved, are kept in the following institutions or private collections, though the greater part is deposited in SEHU. The specimens used in taxonomic study are listed in Online Appendix (Hokkaido University Collection of Scholarly and Academic Papers: <http://eprints.lib.hokudai.ac.jp/journals/index.php?jname=188>). These are dry specimens except for a few ones preserved in alcohol marked with “wet”.

Depository

ELEU: Entomological Laboratory, Ehime University, Matsuyama
ENTU: Department of Entomology, National Taiwan University, Taipei, Taiwan
FRU: Fûjikan, Ryûkyû University, Okinawa
MNCN: Museo Nacional de Ciencias Naturales, Madrid, Español
NIAES: The National Institute for Agro-Environmental Sciences, Tsukuba
NSMT: National Science Museum, Tôkyô
OMNH: Ôsaka Museum of Natural History, Ôsaka
SEHU: Systematic Entomology, School of Agriculture, Hokkaidô University.
Gc: Ito Gen's private collection (ITO Gen)
Ic: Ishikawa's private collection (ISHIKAWA Hitoshi, Shizuoka)
Kc: Kohama's private collection (KOHAMA Tsuguo, Naha)

Species examined

In addition to the species distributed in Japan, specimens of the following species have been examined: *Melanoplus frigidus*, *M. femurrubrum*, *Prumna litoralis*, *P. primnoa*, *P. ussuriensis*, *Podisma pedestris*, *Zubovskya mistshenkoi*, *Miramella solitaria*, *Kisella irena*, *Pseudopodisma fieberi*, *Peripodisma tymphii*, *Micropodisma salamandra*, *Pseudoprumna faldensis*, *Italopodisma acuminata*, *I. fiscellana*, *I. trapezoidalis*, *Odontopodisma albanica*, *Odontopodisma decipiens*, *Odontopodisma schmidtii*, *Oropodisma tymphrestosi*, *Oropodisma macedonica*, *Oropodisma parnassica*,

Epipodisma fedemontana, *Indopodisma kingdoni*, *Niitakacris rosacaenum*, *Sinopodisma emeiensis*, *S. formosana*, *S. houshana*, *S. kodamae*, *S. kawakamii*, *S. kelloggii*, *S. lofaoshana*, *S. kelloggii*, *S. rostellocera*, *S. shirakii*, *S. splendida*, *S. yingdensis*, *Tonkinacris sinensis*, *Fruhstorferiola omei*, *F. tonkinensis*, *F. viridifemorata*.

Dissection of male and female genitalia

For female, tip of the abdomen was taken off from the body and, for male, the phallic complex were removed from the body. The male genitalia or the tip of female abdomen were preserved in 5% solution of KOH for several hours at room temperature, then washed in water to remove softened muscles, trachea, etc. and dissected. The genitalia were preserved in glycerin using a small glass tube pinned with the body.

CHAPTER 1. COMPARATIVE MORPHOLOGY OF PODISMINI GRASSHOPPERS

In comparative biology, the first important stage is to find homologous characters, and careful examinations of structures across the taxa studied are necessary for that purpose. In Podismini, morphological characters have usually been restricted to diagnosing very limited taxa. Therefore, the first section presents comparative morphology of Podismini in the Far East and Europe, evaluating taxonomic significance of each morphological character. In the second section, female genitalia are compared. Although the anatomical structure of grasshoppers has been studied well (e.g., Snodgrass 1935, Jones 1981), female genitalia have not been studied well in any taxa. They should provide useful characters for a group in which the male genitalia are diversified as in Melanoplinae, particularly *Parapodisma*.

1.1. General morphology (Whole body is shown in Fig. 1.1)

Fastigium and frontal costa (Fig. 1.2–5)

The *fastigium* (Fm) is a preoccipital region above the compound eyes, which is usually inclined in melanopline grasshoppers. The *frontal costa* (fC) is a median frontal prominence situated below Fm, and the marginal ridges that set it off are termed the *frontal carinae* (fc). The shapes of Fm and fC are often used for diagnosing at the generic level in Catantopinae and Eyprepocnemidinae. In Podismini, fC shows only slight differences among genera occurring in Japan (Fig. 1.2), but distinct differences among European species (Fig. 1.3). In the Japanese species, a pair of fcs is distinct and parallel, fC is relatively narrow, depressed almost evenly throughout its length. In the European species, the following 3 types of fC have been recognized:

1. fC depressed throughout its length.
2. fC depressed only around median ocellus.
3. fC flat and relatively broad.

The 1st type is found in *Pseudopodisma*, *Kisella* and *Odontopodisma schmidtii*. Their fCs are quite similar to those in the Japanese species. The 2nd type is found in *Epipodisma*, *Micropodisma*, *Italopodisma*, *Peripodisma* and *Odontopodisma albanica*,

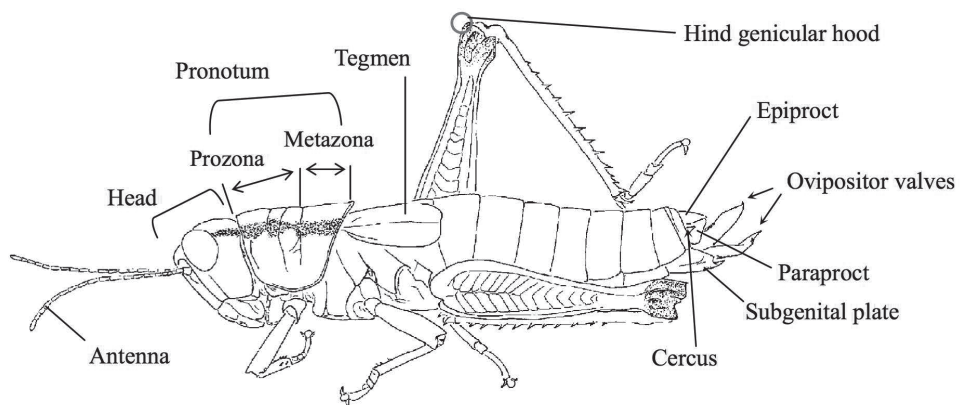


Fig. 1.1. Whole body of a podismini grasshopper, *Tonkinacris ruficerus* female.

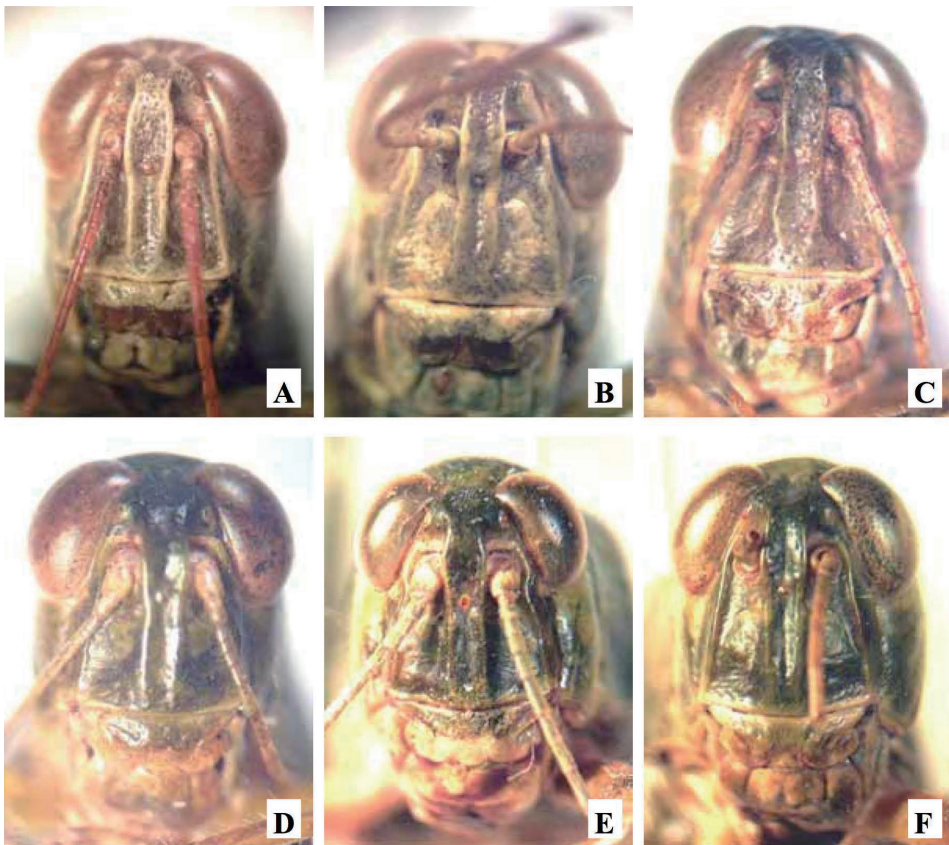


Fig. 1.2. Heads of six podismini females in Japan. A: *Fruhstorferiola okinawaensis*; B: *Sinopodisma aurata*; C: *Sinopodisma punctata*; D: *Parapodisma subaptera*; E: *Parapodisma mikado*; F: *Parapodisma setouchiensis*.

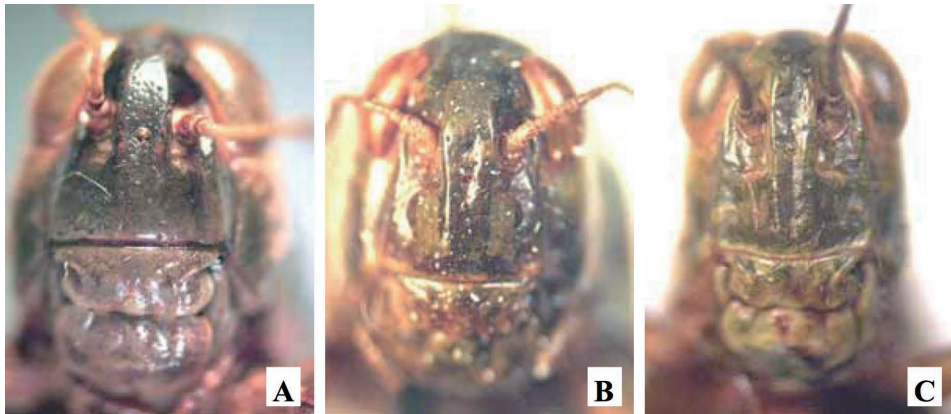


Fig. 1.3. Heads of three podismini females in Europe. A: *Oropodisma parnassica*; B: *Epipodisma pedemontana*; C: *Odontopodisma schmidtii*.

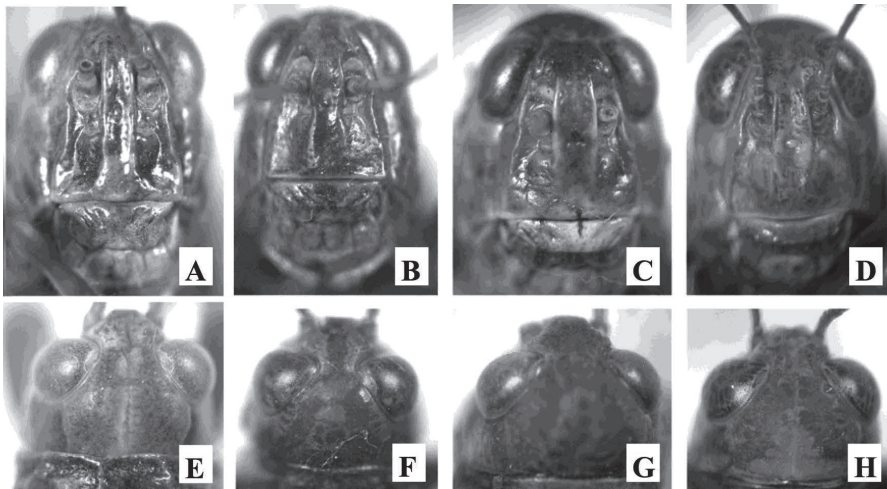


Fig. 1.4. Heads of four *Prumna* females. A, E: *P. hayachinensis*; B, F: *P. primnoa*; C, G: *P. ussuriensis*; D, H: *P. litralis*. Note that *P. hayachinensis* has the narrowest frontal costa among these four species, and that the shape and relative size of the compound eyes are slightly different among them.

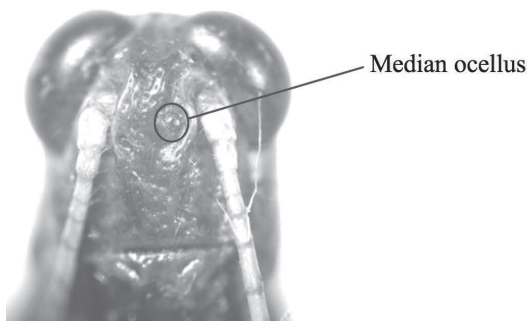


Fig. 1.5. Head of *Tonkinacris sinensis* male. Damaged possibly during molt. The frontal costa is twisted and the median ocellus is dislocated laterally.

and the 3rd in *Oropodisma parnassica*, *Pseudoprumna*. In *Oropodisma* fC is different among species or between the sexes. The male of *O. macedonica* has fC of the 2nd type and the female of the 3rd type. In *O. tymphrestosi*, the male belongs to the 1st type but the female to the 3rd. In the characters of fC the European Podismini have changed many times in evolution, while Japanese genera have remained almost the same.

In *Prumna* female, fC is variable in shape (Fig. 1.4). *Prumna hayachinensis* has the narrowest fC among the four species examined. The shape and relative size of the compound eyes are slightly different among them. Although intraspecific variation is also recognized, it might be due to some environmental factors during ontogenetic process. For example, the shaping of some body parts is liable to be disturbed during molt, because the cuticle is very soft and can be deformed during, just before, and just after molt. A male individual of *Tonkinacris sinensis* has a twisted fC (Fig. 1.5) probably due to disturbance during molt. Thus, it may not always easy to decide whether the variation of the fC shape is strictly genetic or not.

Compound eyes (Fig. 1.6–7, Table 1.4)

In Melanoplineae, the compound eyes are shaped almost the same, but their size is variable among genera and, thus, taxonomically informative. *Tonkinacris* have relatively large compound eyes (Fig. 1.6A, B), while *Zubovskya* relatively small ones (Fig. 1.6C, D). The compound eyes in the female are always smaller than in the male. The relative eye size can be shown by the ratio HW/IS (IS: width of inter-ocular space; HW: head width (= width of two eyes + IS, see Fig. 1.7)). The HW/IS values in the males of 13 podismini genera are shown in Table 1.4.

Chang (1940) used the ratio of IS to the width of the frontal costa in his key to divide *Podisma* (IS broader), *Melanoplus* (including *Miramella*, IS narrower) and *Caudellacris* (= *Fruhstorferiola*, IS slightly narrower in the female and distinctly narrower in the male). My observation agrees with his view. In this study, however, IS is used in calculating HW.

Antennae

No significant modification has been found in the antennal morphology of Podismini. The antennae are filiform, and usually composed of 22–25 segments (rarely with fewer segments: the antennae of *Zubovskya koeppeni parvula* in Hokkaidô have 18–20 segments). In most species, the antennae are colored yellowish brown or brown, but in some species bright red (*Kingdonella* spp., *Tonkinacris ruficerus* and *Fruhstorferiola okinawaensis*).

Prosternal process (Fig. 1.8)

The prosternal process originates from the basisternum. It is inferred by Uvarov (1966) as a structure controlling movements, particularly of the front legs. It occurs in some grasshopper subfamilies, and its shape is diversified among genera. For example, in Eyprepocnemidinae, the shape varies from conical to cylindrical or plate-like, with the

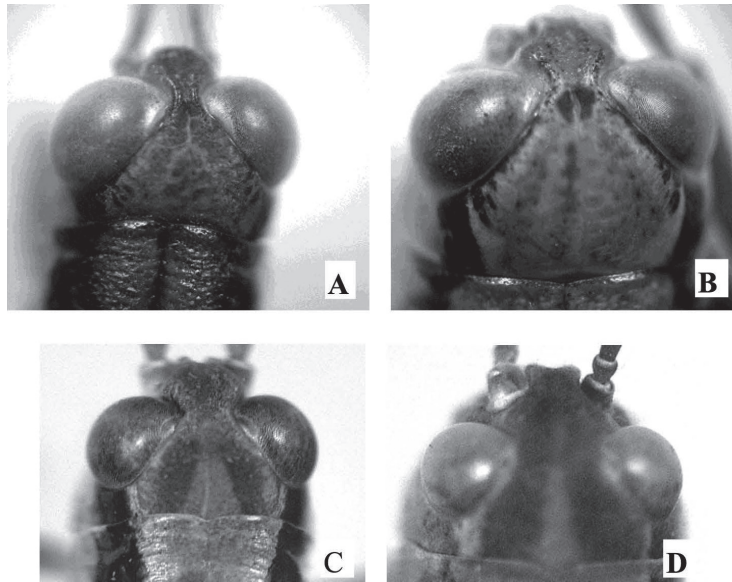


Fig. 1.6. Heads of *Tonkinacris ruficerus* (A, male; B, female) and *Zubovskya koeppeni parvula* (C, male; D, female). The compound eyes are relatively large in *Tonkinacris* (HW/IS: 7–10) and relatively small in *Zubovskya* (HW/IS: 4–5). Note that the relative size of the female eyes are always smaller than that of the male. For HW and IS, see Fig. 1.7.

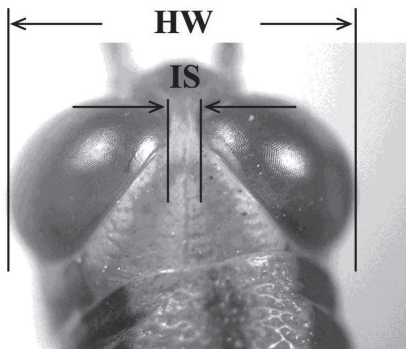


Fig. 1.7. Measurements of head width (HW) and distance of interocular space (IS). This exemplar is a male of *Sinopodisma aurata*. In this individual the index of relative compound eye size (HW/IS) is 8.2.



Fig. 1.8. Prosternal processes in males of Podismini, lateral view. A: *Zubovskya koeppeni parvula*; B: *Parapodisma mikado*; C: *Sinopodisma punctata*; D: *Ognevia longipennis*.

apex rounded, bilobate or trilobate. In podismini genera, however, the prosternal process is conical and not much variable, differing mainly in profile and in the apical structure. In the Japanese species, the process can be classified into the following 3 types:

1. Process very short and robust, with the apex subacute or obtuse.
2. Process moderate length in the tribe, with the apex acute or subacute.
3. Process moderate in length, with the apex obtuse.

The 1st type is found in *Zubovskya* and *Podisma*, the 2nd type in *Anapodisma*, *Sinopodisma*, *Tonkinacris*, *Fruhstorferiola* and *Parapodisma*, and the 3rd type in *Ognevia*. However, 2 types occur in *Prumna*: the 1st type (*P. primnoa* and *P. ussuriensis*) and the 2nd type (*P. hayachinensis* and *P. litoralis*). The 3 types, therefore, are not always applicable to phylogenetic analysis at the generic level.

Sternal plate

(Fig. 1.9)

The mesosternum, the metasternum and the 1st abdominal sternite are closely fused, forming a sclerotised plate called the sternal plate, which is divided into several parts by sutures (Fig. 1.9A, B). The mesosternal interspace is formed by the mesofurcal suture and a pair of mesosternal sutures. The metasternal interspace is formed by the metafurcal suture. Their shapes and widths are effected by the structure of the furcae and musculature, and often useful in subfamily-level classification, but not useful at the generic level in Podismini. However, the ratio between the width (SpW) and the length (SpL) of the sternal plate (SpW/SpL) can be an indicator for the relative width of the thorax or the 1st abdominal segment. Slight differences can be observed between relatively robust species (e.g., *Prumna hayachinensis*, SpW/SpL=1.1, A) and species with moderate width (*Parapodisma mikado*, SpW/SpL=1.0, B), while distinct differences can be usually observed between the male and female (*Parapodisma tenryuensis*, male, SpW/SpL=0.8, C; female, SpW/SpL=1.0, D). This index is useful for identifying the sexes within a species rather than identifying genera or species.

Pronotum

(Fig. 1.10)

The pronotum of acridoid grasshoppers has 3 transverse sulci, and from the 3rd one, a sheet of membrane originates and is connected to the mesonotum, the former pterothorax. The surface of the pronotum is usually punctate. Density and depth of the punctures are different among podismini species, and even in the same genus the difference is sometimes distinct. For example, the pronotum of *Fruhstorferiola tonkinensis* (Fig. 1.10A) is deeply and uniformly punctate and on the prozona slightly rugose, while that of *F. viridifemorata* (B) is punctate deeply and uniformly on the metazona but smooth and sparsely punctate on the prozona. In *Prumna hayachinensis* (J) the pronotum is wholly shining, with the transverse sulci deep, and punctate densely on the metazona but sparsely on the prozona, while in *P. litoralis* (K) and *P. ussuriensis* (L) it is shining only on the lateral sides, being frosted dorsally, the transverse sulci are shallow, and the integument is smooth. This pronotal integument pattern is also found in *Zubovskya koeppenii parvula* (N), *Z. mistshenkoi* and *Kingdonella* spp. On the contrary, several genera show another pattern. The pronota of *Ognevia* (C), *Podisma* (H) and

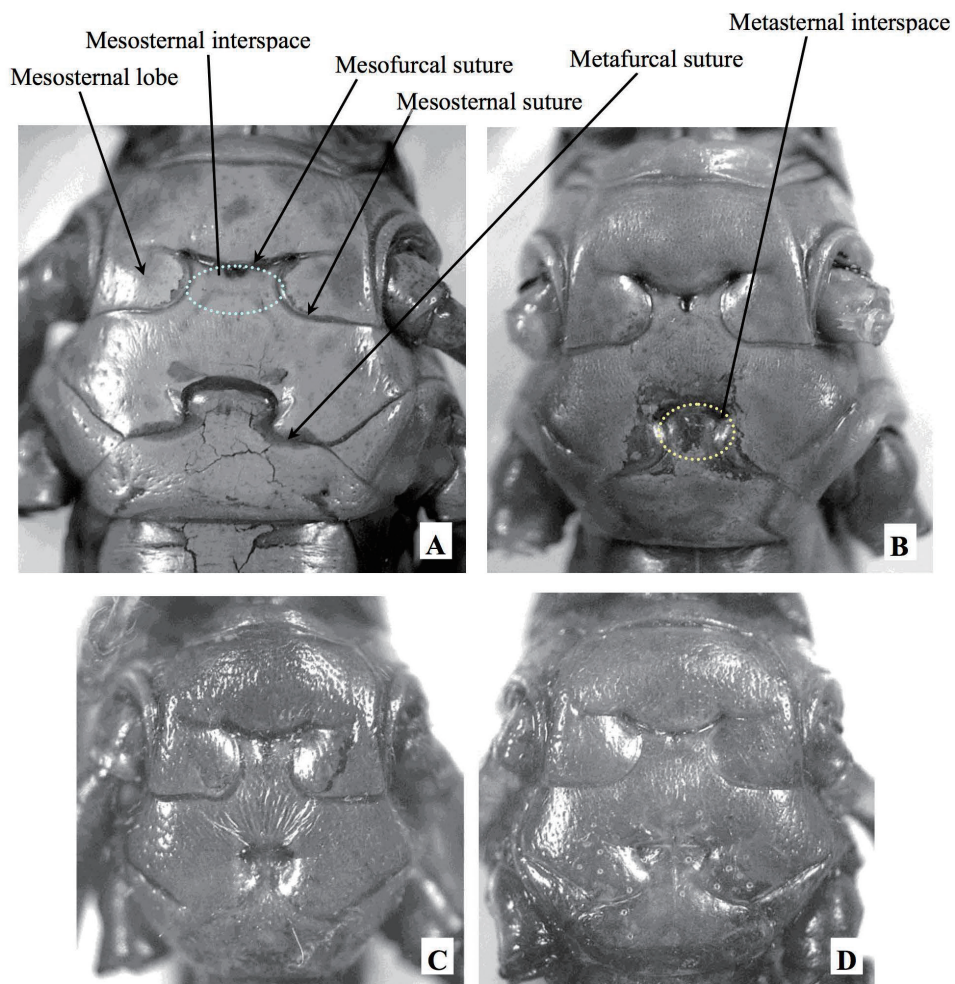


Fig. 1.9. Sternal plates of Podismini, ventral view. A: *Prumna hayachinensis*, female; B: *Parapodisma mikado*, female; C: *Parapodisma tenryuensis*, male; D: *Parapodisma tenryuensis*, female.

Anapodisma (I) are smooth, and punctate sparsely on the prozona, but uniformly and densely on the metazona. In *Anapodisma* the transverse sulci are very shallow, while in *Ognevia* and *Podisma* they are deep. The punctures on the metazona of them are shallower than those in *Fruhstorferiola*, etc. In *Tonkinacris* (D), *Parapodisma* (E, F, M) and *Oropodisma* (O) the punctures are sparse on the prozona, and dense and uniform on the metazona, while in *Sinopodisma* in Ryûkyû (G) and Taiwan the punctures are uniform and dense.

In Podismini, the differences in the pronotal shape seem to be correlated with the development of the tegmina and wings. The posterior margin of the pronotum is always distinctly produced in long-winged species, while it is emarginate in apterous or

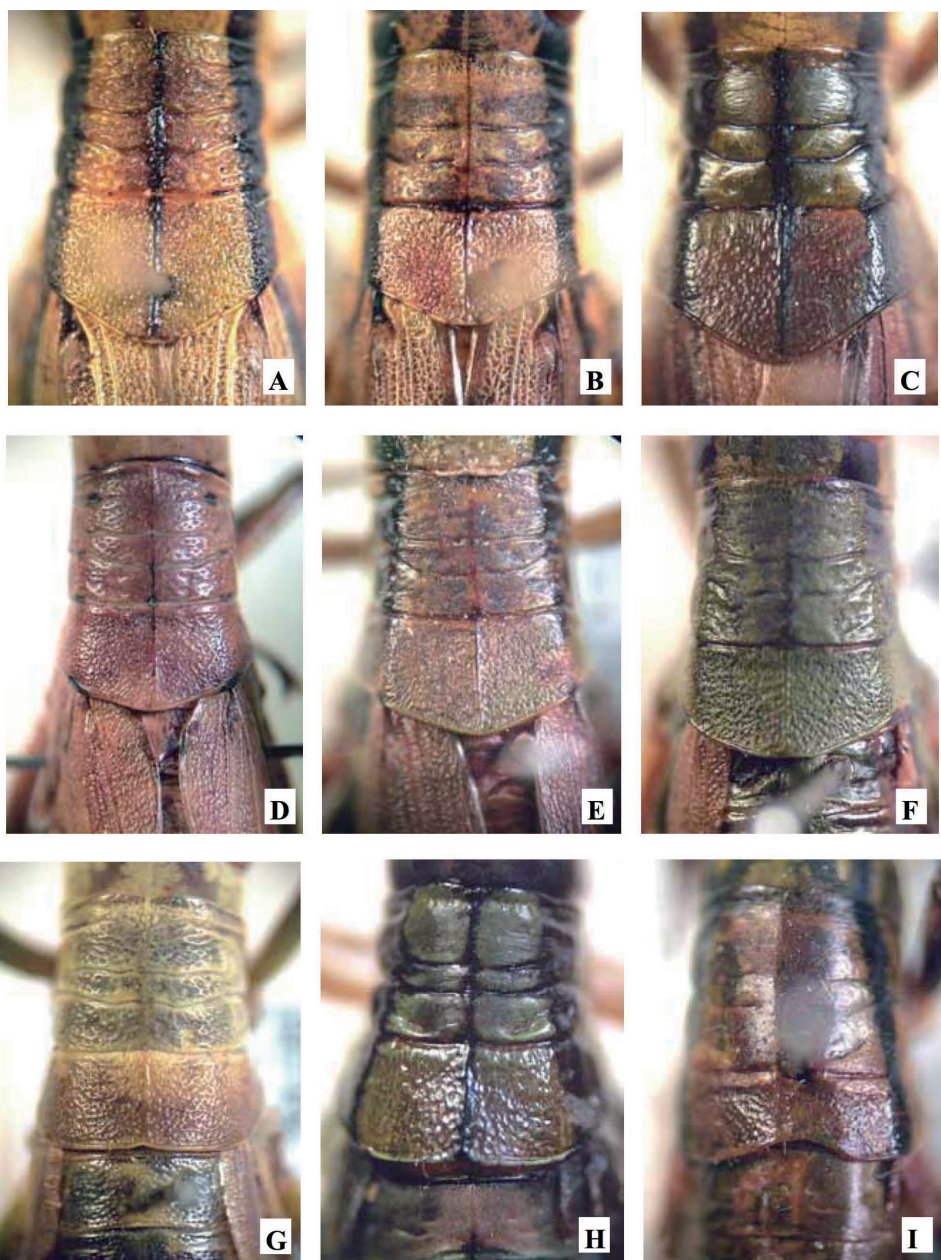


Fig. 1.10. Pronotum and metanotum of podismini females, dorsal view. A–C: long-winged species (A: *Fruhstorferiola tonkinensis*; B: *F. viridifemorata*; C: *Ognevia sergii*); D–F: brachypterous or micropterous species (D: *Tonkinacris yaeyamaensis*; E: *Parapodisma niihamensis*; F: *P. tenryuensis*); G–I: micropterous species (G: *Sinopodisma aurata*; H: *Podisma sapporensis*; I: *Anapodisma miramae*).

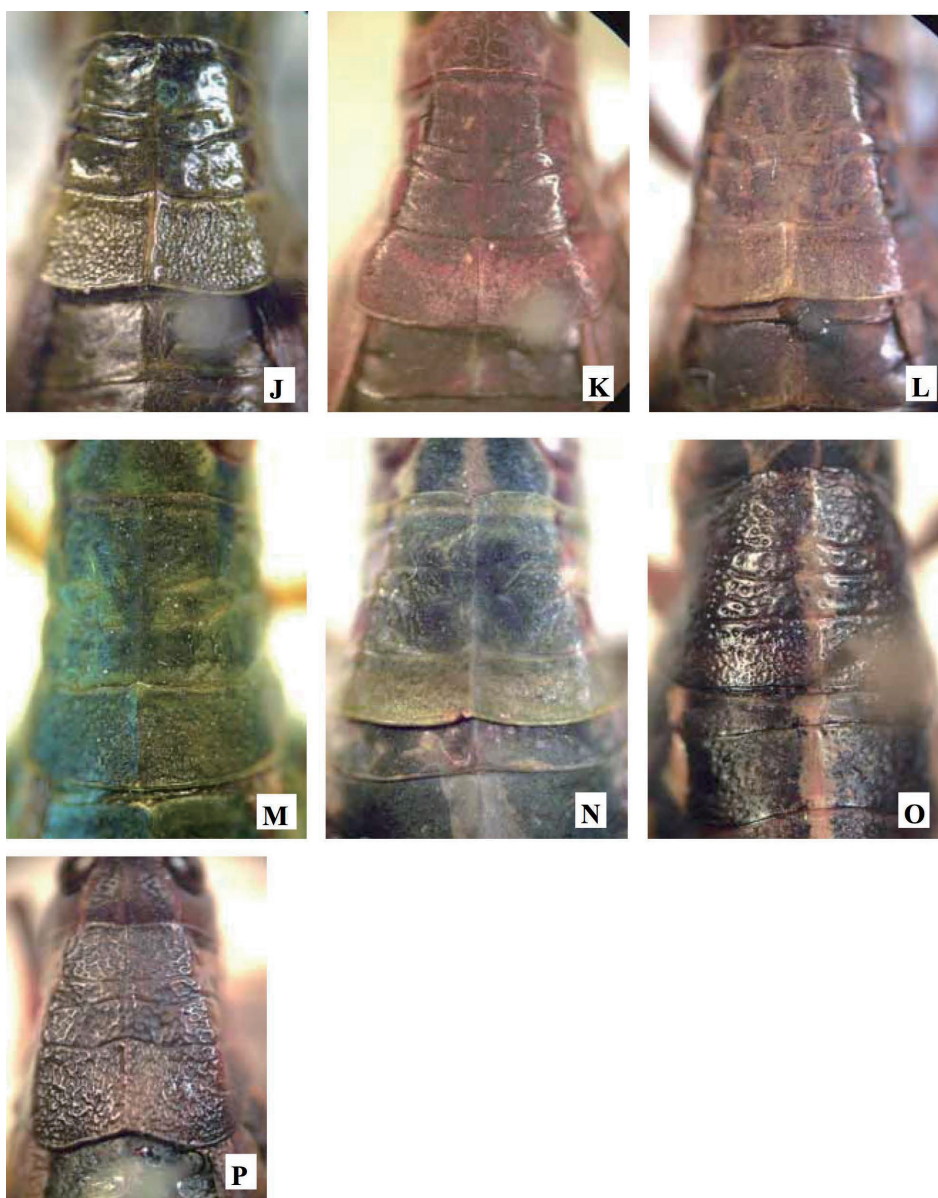


Fig. 1.10. Continued. J–L: micropterous *Prumna* species (J: *P. hayachinensis*; K: *P. litoralis*; L: *P. ussuriensis*). M: subapterous species, *Aopodisma subaptera*. N–O: apterous species (N: *Zubovskya koeppeni parvula*; O: *Oropodisma parnassica*). P: micropterous, having unique pronotum species, *Niitakacris rosacaenum*.

micropterous species (see Table 1.2, 3).

Development of the tegmina and wings: relationships with thorax and tympanal organs
(Fig. 1.11–16, Table 1.4)

The tegmina and wings of most podismini species are abbreviated and they are incapable of flight. In flightless podismini, the tegminal length and shape often show considerable variation between/within populations. In some species the tegminal length

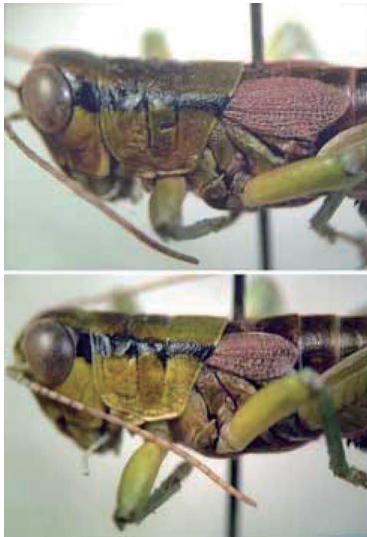


Fig. 1.11. Tegminal variation between sibling males of *Parapodisma tenryuensis* originally from Mt. Enkaizan, Yokohama-City, bred in laboratory.



Fig. 1.12. Scoring scheme for tegmen length (TL). Score increases by each half tergite length. This example is *Parapodisma mikado*, scoring 5.

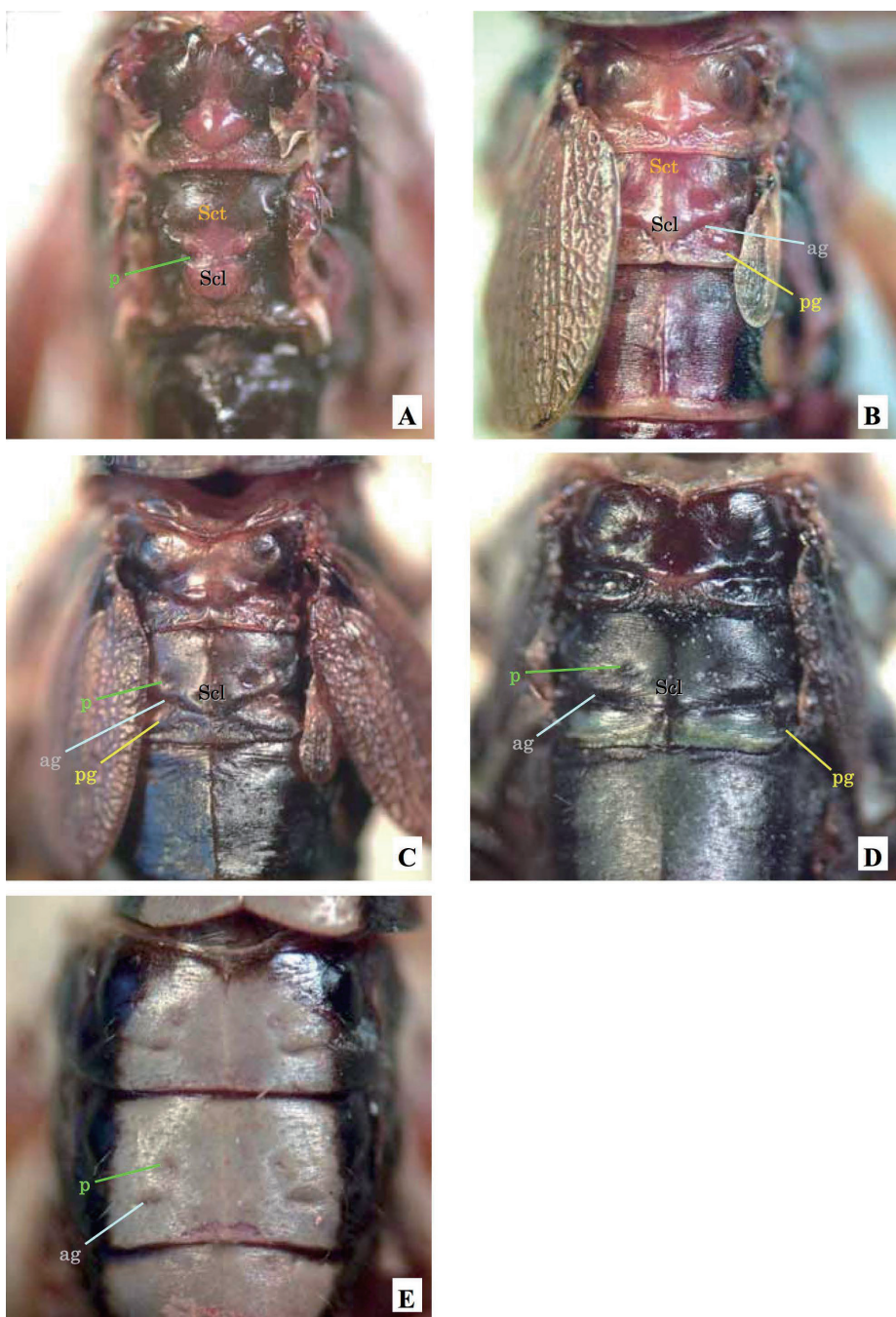


Fig. 1.13. Mesonota and metanota of podismini species (male), dorsal view. A: *Ognevia longipennis* (Fully winged); B: *Parapodisma mikado* (TL=5); C: *Parapodisma tenryuensis* (TL=4); D: *Podisma sapporensis* (TL=3); E: *Zubovskya koeppeni parvula* (Apterous). ag: anterior groove on metanotum; p: scutellar pit; pg: posterior groove on metanotum; Scl: scutellum; Sct: scutum.

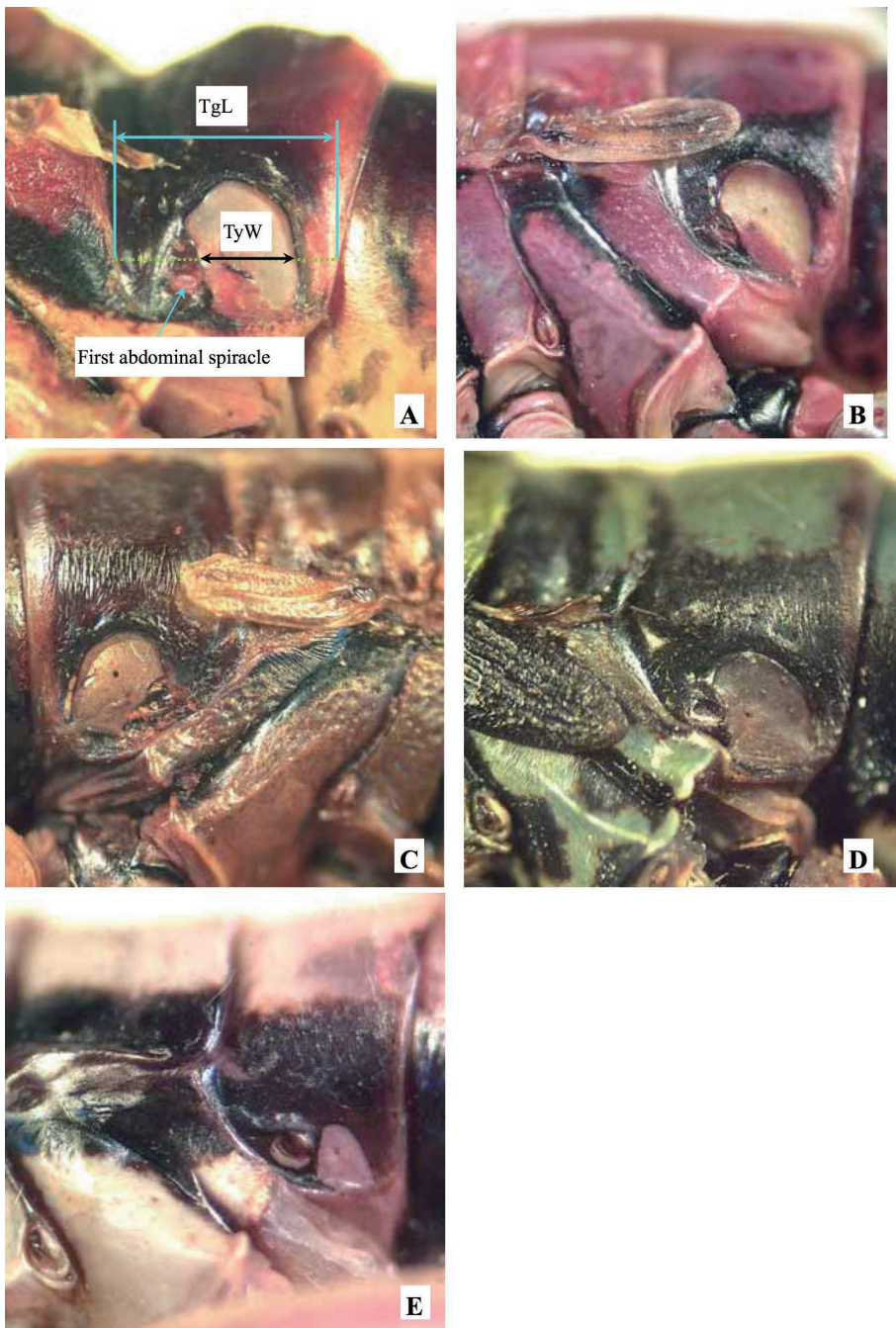


Fig. 1.14. Tympana in the same individuals as Fig. 1.13, lateral view. A: *Ognevia longipennis* (TyW/TgL=0.55); B: *Parapodisma mikado* (TyW/TgL=0.54); C: *Parapodisma tenryuensis* (TyW/TgL=0.42); D: *Podisma sapporensis* (TyW/TgL=0.54); E: *Zubovskya koeppeni parvula* (TyW/TgL=0.26).

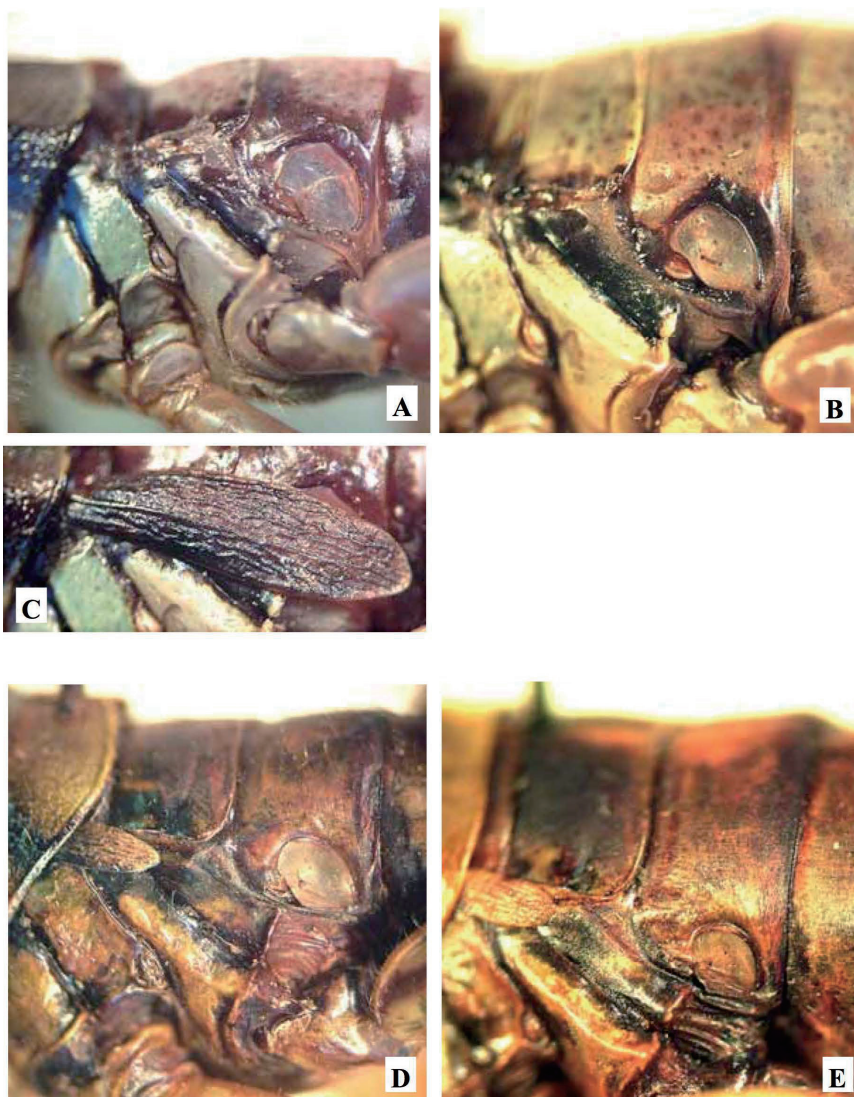


Fig. 1.15. Tympana in two *Prumna* species. A–C: *P. hayachinensis* (A: male; B: female; C: before tegmen removal of A); D, E: *P. ussuriensis*. (D: male; E: female). TyW / TgL = 0.71 (A), 0.58 (B), 0.52 (D), 0.42 (E).

is shortened and its width is not much reduced (brachypterous), while some other species have the tegmina reduced in both length and width, thus shaped like bamboo leaves (micropterous). Akimoto et al. (1993) ascertained that tegminal length is highly plastic in *Podisma sapporensis* within and among populations. This may be true also in many other species. For example, two sibling males of *Parapodisma tenryuensis* showed the tegmina clearly different in length and shapes (Fig. 1.11). The base is usually concealed with pronotum and invisible in usual dry specimens. In order to describe and evaluate the

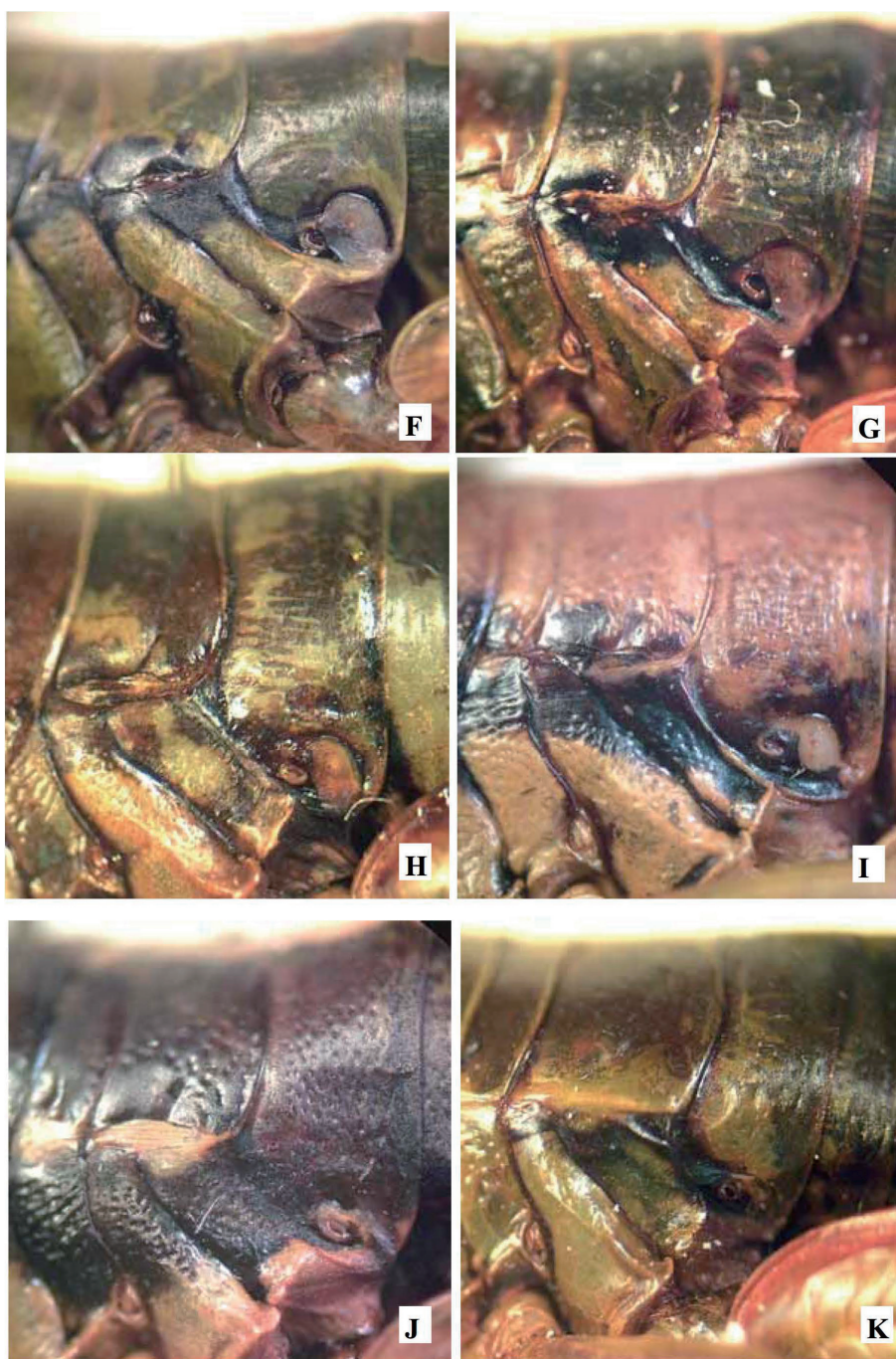


Fig. 1.16. Tympana of six apterous species (female). F: *Micropodisma salamandra*; G: *Pseudoprumna baldensis*; H: *Peripodisma tympii*; I: *Sinopodisma emeiensis*; J: *Oropodisma parnassica*; K: *Epipodisma fedemontana*. $TyW / TgL = 0.43$ (F), 0.44 (G), 0.35 (H), 0.23 (I), 0 (J, K).

Table 1.1. Classification of tympanal organs in Podismini based on the size.

	Vestigial		Small		Medium		Large	
♂ TyW/TgL	-----	0.3	-----	0.5	-----	0.7	-----	
♀ TyW/TgL	-----	0.2	-----	0.4	-----	0.6	-----	

tegmina length (TL) concisely, I adopted a scoring scheme as shown in Fig. 1.12. The score starts from 0 (tegmina ending within the posterior margin of the mesonotum) and increases by each half tergite length. TL was classified and scored for all species except two long-winged species, *Fruhstorferiola okinawaensis* and *Ognevia longipennis*.

The mesonotum and the metanotum are variable in shape in Podismini, as mentioned by La Greca (1987). This is directly related with the development of the flight muscles, and may also be related with some other flight organs such as the tegmina and wings. The metanota of five species with wings various in length are shown in Fig. 1.13. In a fully winged and flyable species, *Ognevia longipennis* (Fig. 1.13A), the scutum and scutellum are strongly raised, with a membranous area between them. In brachypterous species, *Parapodisma mikado* (B) and *P. tenryuensis* (C), the scutum and scutellum are not well developed and nearly fused (B) or completely fused (C), the groove between them are reduced and forming a pair of pits (p). In brachypterous species, the membranous area is also reduced, but the anterior and posterior scutal grooves (ag, pg) become evident (La Greca 1987). In a micropterous species, *Podisma sapporensis* (D), the reductive change is so conspicuous that the metanotum is flattened much more. In the apterous *Zubovskya koeppenii parvula* (E), the meso- and metanotum are smooth, having only a pair of scutal pits and a pair of vestigial scutal grooves.

The pronotum (Fig. 1.1) is separated into the prozona, the part anterior to the sulcus, and the metazona, the posterior part. The ratio prozonal length / metazonal length (P/M) is correlated with tegmina length (TL). La Greca (1987) stated that one of the functions of the pronotal prolongation is to hold the tegmina in place during flight. However, even in flightless species P/M and TL seem to be correlated with each other (Table 1.2). In Podismini, when the tegmina and wings are more developed, the meso- and metanotum are more complex in structure (Fig. 1.13). The complex structure includes the membranous areas on the scutum and scutellum. These areas are not covered by the tegmina and wings. It seems more likely that the prolongation protects these membranous areas from injury. In *Podisma*, even micropterous or apterous forms have the mesonotum more complex than some other micropterous genera (e.g., *Anapodisma*). P/M in *Podisma* are relatively low (e.g., ♀ 1.2–1.5; ♂ 1.5–1.8 in *P. sapporensis*), that is, the pronotal prolongation is stronger in *Podisma*.

It seems that the development of the tympanal organs is also related to the tegmina development (Fig. 1.14). In macropterous species the tympanal organs are always developed (Fig. 1.14A), and in wingless species the organs are often vestigial (Fig. 1.14E). In order to estimate relative tympanum size, I measured the tympanal width and the 1st tergite width above the 1st abdominal spiracle, and calculated the ratio of the tympanal width to 1st tergite width (TyW/TgL). As a consequence, the following results have been

Table 1.2. Tegminal states and their relationships with shapes of pronotal parts and tympanal organs in Podismini.

	Apterous	Micropterous	Brachypterous	Long winged and flyable
Exemplars	<i>Zubovskya, Oropodisma, Peripodisma, Pseudoprugna, Italopodisma</i>	<i>Prumna, Anapodisma, Podisma, Sinopodisma, Aopodisma, Odontopodisma</i>	<i>Tonkinacris, Parapodisma, Miramella, Kisella, Fruhstorferiola</i> (in part)	<i>Ognevia</i>
TL	Absent	1-6	3-16	Oblong
P / M (male)	2.0-2.3	1.2-2.5	1.2-1.6	0.8-1.1
Posterior margin of pronotum	Truncate or emarginate	Rounded, truncate or emarginate	Produced, rounded	Strongly produced
Metanotum	Smooth, only with small scutellar pits (grade 0)*	With scutellar pits and scutal grooves (grade 1)*		Scutum and scutellum well raised, with developed scutellar ribs (grade 2)*
Tympanum	Absent-vestigial-small-medium	Small-medium		Medium

* For concise description, roughly classified metanotal complexity.

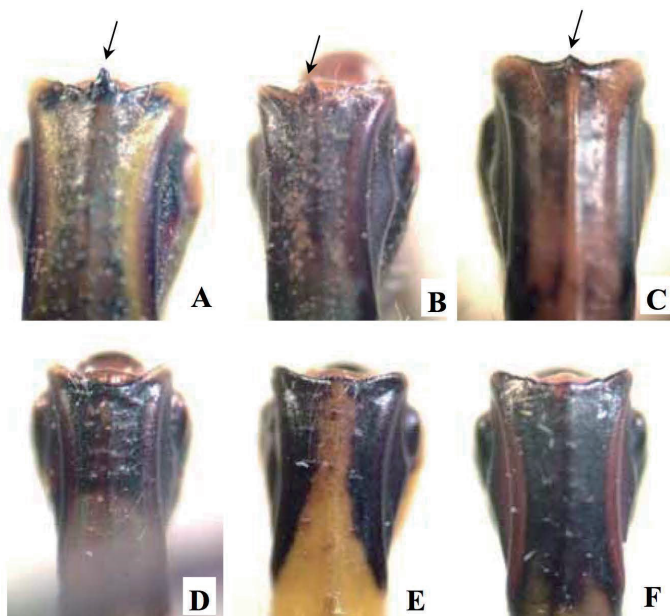


Fig. 1.17. Tip of hind femora with a spine at the apex of hind knee. A, B, C, spine is present, and D, E, F, spine is absent. A: *Parapodisma mikado*; B: *Sinopodisma kodamae*; C: *Tonkinacris yaeyamaensis*; D: *Miramella solitaria*; E: *Anapodisma miramae*; F: *Podisma kanoi*. Arrows indicate the spines.

obtained. 1: There are no macropterous species with vestigial tympanal organs. 2: Female TyW/TgL shows about 4/5 of male (Fig. 1.15). 3: Even in the wingless condition, some species have normal tympanal organs, which is highly variable in size (Fig. 1.16). In this study I divide the obtained relative tympanal sizes into 3 classes as shown in Table 1.1. The characters discussed above are compared in Table 1.2.

The spine of the hind genicular hood
(Fig. 1.17, Table 1.4)

The presence of a spine on the hind margin of the genicular hood on the hind femur is a generic character of *Parapodisma* adopted in distinguishing the genus from *Miramella* (Mistshenko 1947). This spine is occasionally abbreviated or almost absent in *Parapodisma*, but always absent in *Miramella*. It is useful in recognizing other genera (Fig. 1.17, Table 1.4), it occurs also in other subfamilies. This spine is so small that its function is still unknown.

1.2. Genital morphology

Male furculae of the 10th abdominal tergite, epiproct, subgenital plate
(Fig. 1.18–20, Table 1.5)

The tip of the male abdomen including the concealed genitalia provides important taxonomic characters of Acrididae. The 10th abdominal tergite is divided and sometimes forms a pair of projections named furculae. The presence or absence and the shape of them have been used in recognizing genera and species. The function of the furculae is still unknown. Podismini can be divided into two generic groups based on the presence or absence of furculae. One group is characterized by the presence of distinct furculae (*Prumna*, *Zubovskya*, *Anapodisma*, *Miramella*, *Ognevia*, *Podisma*, *Niitakacris* and *Melanoplus*), and the other by their absence or the presence of very weak furculae (*Sinopodisma*, *Parapodisma*, *Tonkinacris* and *Fruhstorferiola*).

The epiproct is shaped diversely in *Prumna* (Fig. 1.18). It is pentagonal and expanded laterally from the basal half to the basal 3/4 in *P. hayachinensis* (A), *P. primnoa* (C) and *P. ussuriensis* (D); on the other hand, it is triangular with lateral sides expanded in *P. litoralis* (B). The tubercles on the epiproct are also different in shape among species. In other genera (Fig. 1.19–20), no remarkable difference has been observed except in *Ognevia* (Fig. 1.19C) and *Parapodisma mikado* (Fig. 1.20B). In *Ognevia*, the epiproct is emarginate on the lateral margins in apical 1/4; in *P. mikado*, the epiproct is pentagonal. The other genera examined have a triangular epiproct with the margin slightly swelling and an apical protuberance. Usually it is as long as wide. The shape of the median furrow and the color of the epiproct are highly variable, but in the species studied of *Prumna* and *Sinopodisma* the epiproct, the cerci and the subgenital plate are uniformly colored.

The male subgenital plate can also be variable intraspecifically as in *Parapodisma setouchiensis* (*sensu* Kawakami, 1999, in this paper. Fig. 1.20L₁–L₃). However, the “strongly and acutely projecting” subgenital plate provides a good specific character for *P. yasumatsui*. The subgenital plate sometimes possesses an anterior projection on the hind margin. This projection when present is usually stable (Fig. 1.20D: *P. awagataensis*; E:

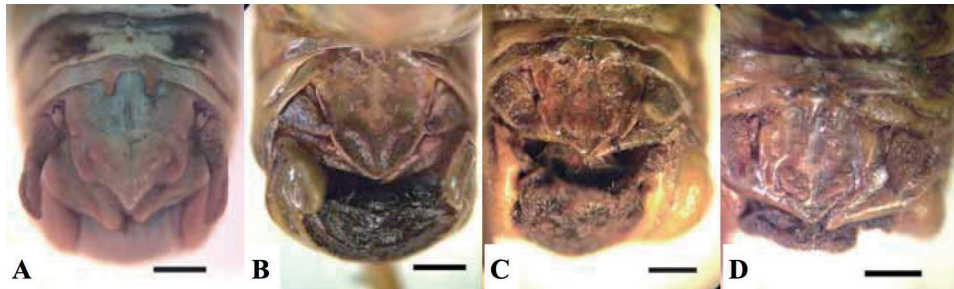


Fig. 1.18. Male epiprocts of *Prumna* species, dorsal view. A: *P. fauriei*; B: *P. liotralis*; C: *P. primnoa*; D: *P. ussuriensis*. Scale: 1mm.

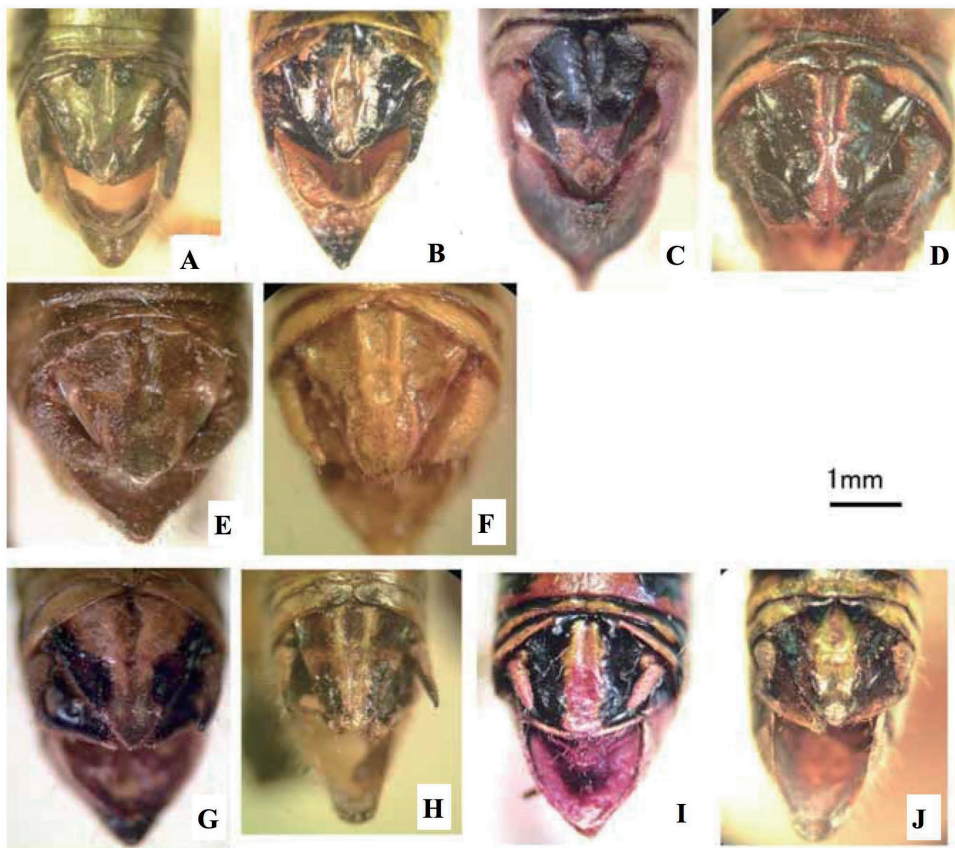


Fig. 1.19. Tip of male abdomen of podismini species, dorsal view. A: *Zubovskya koeppeni parvula*; B: *Anapodisma miramae*; C: *Ognevia longipennis*; D: *Fruhstorferiola okinawaensis*; E: *Sinopodisma punctata*; F: *Sinopodisma aurata*; G: *Tonkinacris yaeyamaensis*; H: *Tonkinacris ruficerus*; I: *Podisma sapporensis*; J: *Podisma kanoi*.

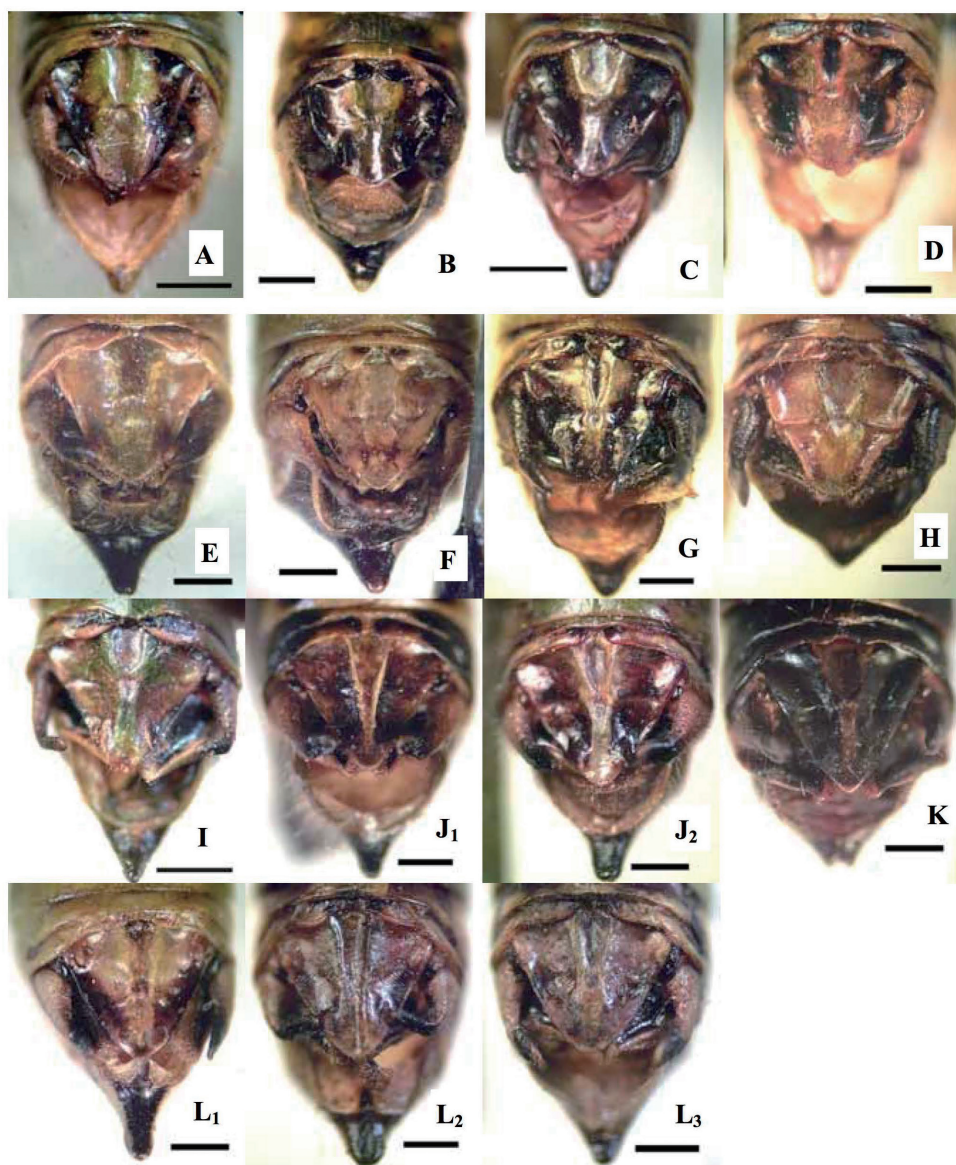


Fig. 1.20. Tip of male abdomen of *Aopodisma* and *Parapodisma* species, dorsal view. A: *A. subaptera*; B: *P. mikado*; C: *P. dairisama*; D: *P. awagatakensis*; E: *P. etsukoana*; F: *P. subastris*; G: *P. hiurai* (Ômiya-Town, Mie); H: *P. niihamensis* (Shionoe-Town, Kagawa); I: *P. yasumatsui*; J₁: *P. tenryuensis* (Shitara-Town, Aichi Pref.); J₂: *P. tanzawaensis* (Yokohama-City, Kanagawa Pref.); K: *P. caelestis*; L₁: *P. setouchiensis* (Yawata-City, Kyôto Pref.); L₂: *P. setouchiensis* (Mt. Hiei, Shiga Pref.); L₃: *P. setouchiensis* (Kôzuki-Town, Hyôgo Pref.). Scale: 1mm.

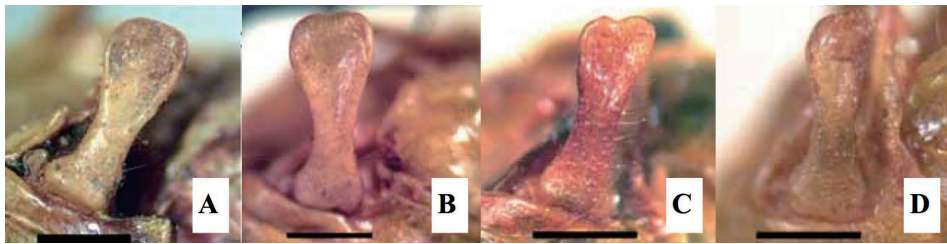


Fig. 1.21. Geographic variation of cerci in *Prumna hayachinensis*. A: Mt. Yûrappu, Hokkaidô; B: Mts. Minami-Hakkôda, Aomori Pref.; C: Mt. Iwaki, Aomori Pref.; D: Mt. Chôkai, Akita Pref. Scale 1mm.

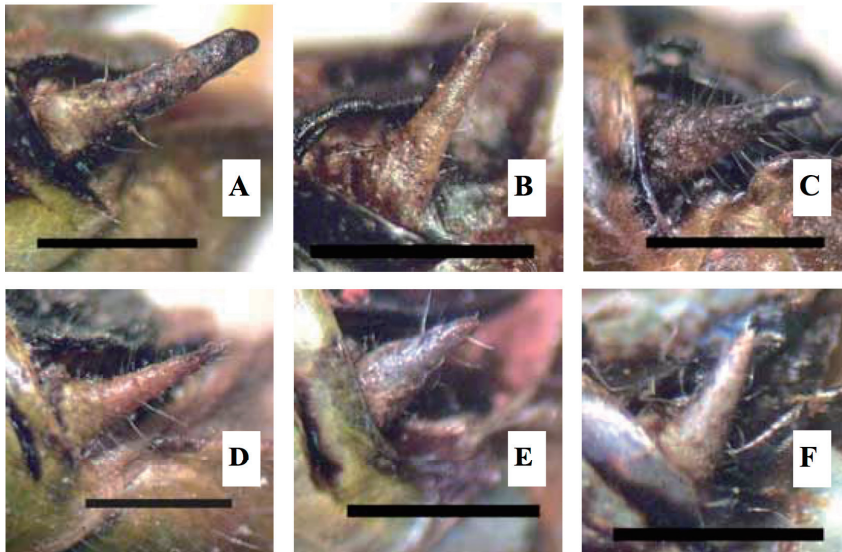


Fig. 1.22. Simple-shaped cerci. A: *Zubovskya koeppeni parvula*; B: *Miramella solitaria*; C: *Anapodisma miramae*; D: *Ognevia longipennis*; E: *Podisma kanoi*; F: *Podisma sapporensis*. Scale=1mm.

P. etsukoana), but in *P. setouchiensis* it is highly variable and occasionally absent (Fig. 1.20L₁–L₃).

Male cerci (Fig. 1.21–27, Table 1.5)

The male cerci are sometimes very variable in shape intraspecifically (Fig. 1.21: *Prumna hayachinensis*; Fig. 1.26: *Parapodisma setouchiensis*; Fig. 1.26: *Parapodisma tenryuensis*), or interspecifically (Fig. 1.23: *Fruhstorferiola* spp.; Fig. 1.25: *Parapodisma* spp.), while in other species the variation among different species is very small (Fig. 1.22). The male cerci seem to have a function in copulation. In Callimptaminae the cerci are very large and grasping the tip of the female abdomen (Uvarov 1977). Some podismini species have rather large and complex cerci (e.g., species of *Parapodisma* and

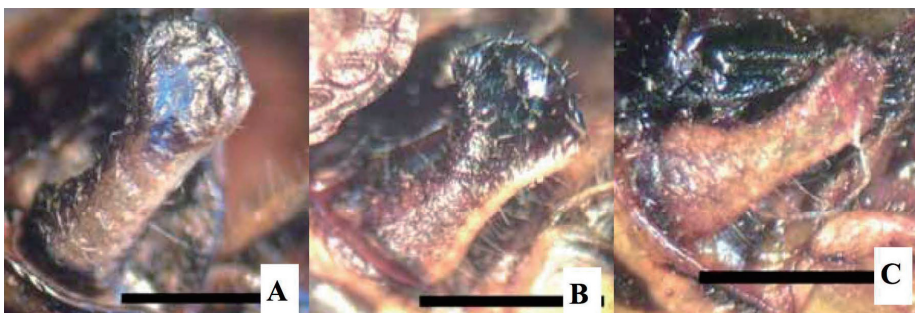


Fig. 1.23. Cerci of *Fruhstorferiola* species. A: *F. okinawaensis*; B: *F. viridifemorata*; C: *F. tonkinensis*.

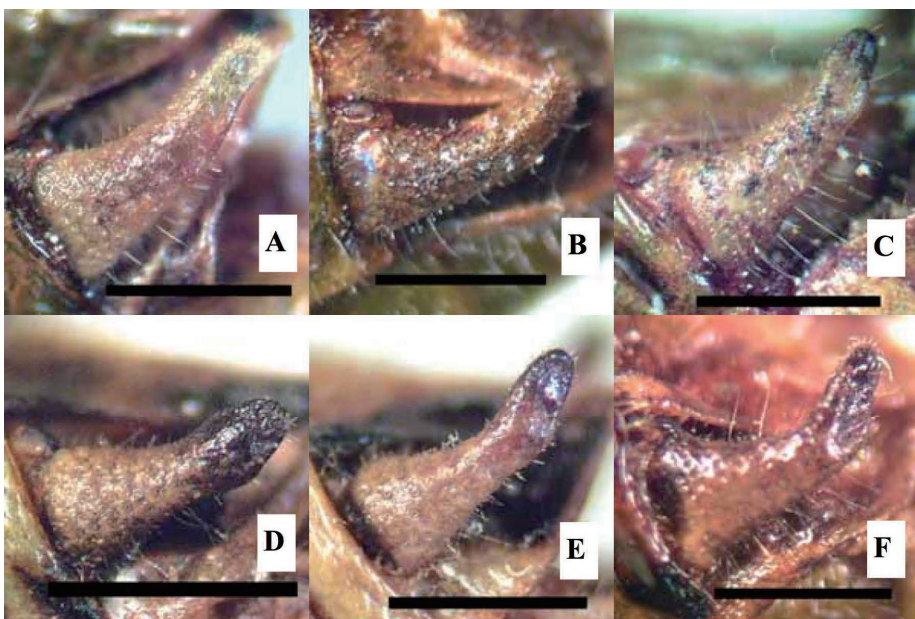


Fig. 1.24. Cerci of *Sinopodisma* and *Tonkinacris* species. A: *S. aurata*; B: *S. punctata*; C: *S. formosana*; D: *T. ruficrus*; E: *T. yaeyamaensis*; F: *T. sinensis*. Scale=1mm.

Fruhstorferiola), while some others have small and conical cerci (e.g., *Podisma*, *Ognevia* and *Anapodisma*). Functions in copulation seem different between the two types of cerci. Although this type of cerci may function in copulation, this function does not need an exact agreement in shape. This supposition could be supported by a relatively remarkable intraspecific variation in species with large cerci (Fig. 1.21: *Prumna hayachinensis*; Fig. 1.26: *Parapodisma setouchiensis*; Fig. 1.27: *P. tenryuensis*). In *Parapodisma tenryuensis* cercal shape shows a geographic cline as in Fig. 1.27: the apex is widened in central localities of the distribution area, and is narrowed in the eastern and western localities.

Male genitalia — Epiphallus and Aedeagal valves
(Fig. 1.28–31, Table 1.5)

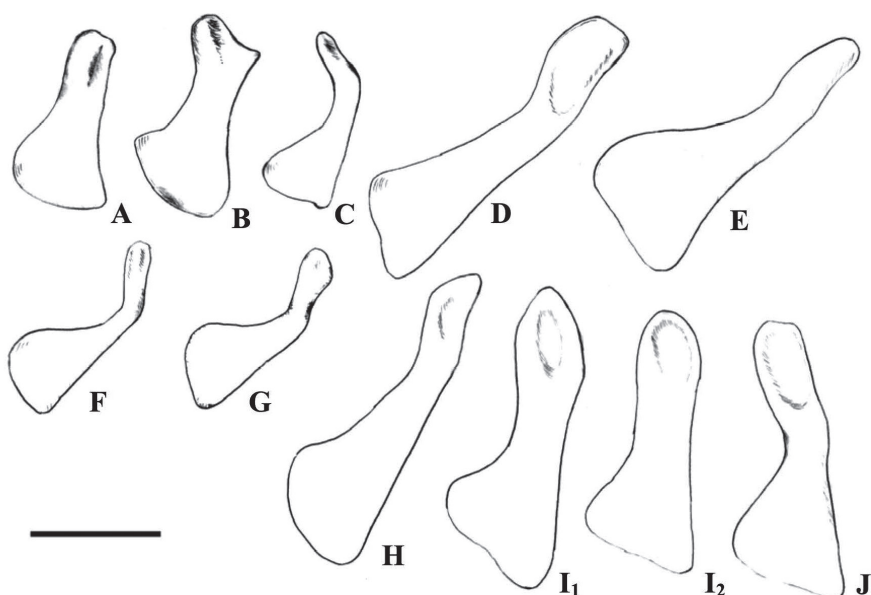


Fig. 1.25. Cerci of *Aopodisma* and *Parapodisma* species. A: *A. subaptera*; B: *P. mikado*; C: *P. dairisama*; D: *P. niihamensis* (Shionoe-Town, Kagawa); E: *P. hiurai* (Ômiya-Town, Mie); F: *P. yasumatsui*; G: *P. awagatakenis*; H: *P. subastris*; I₁: *P. caelestis*; I₂: *P. caelestis* (same population with I₁); J: *P. etsukoana*. Scale=1mm.

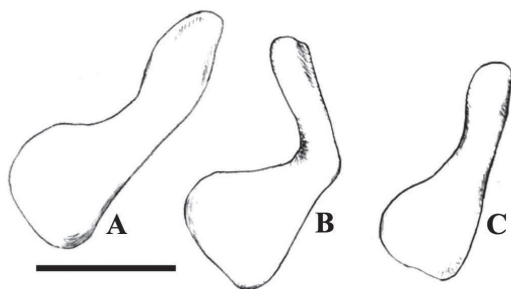


Fig. 1.26. Geographic variation in cercus of *Parapodisma setouchiensis*. A: Kôzuki-Town, Hyôgo Pref.; B: Ôtsu-City, Shiga Pref.; C: Ryûjin-Vil., Nara Pref. Scale=1mm.

The first comprehensive study on the male phallic complex of grasshoppers was made by Roberts (1941), and some useful taxonomic characters were found in the shapes of epiphallus, aedeagal valves, *etc.* Dirsh (1956) studied more species, discussed taxonomic value, and inferred evolutionary changes and functions of the parts of the phallic complex. The phallic complex has been studied so precisely that some new higher taxa have been established on the basis of its characters alone.

The subfamily Melanoplinae has been treated as a close relative of the highly heterogeneous subfamily Catantopinae (Dirsh 1975). In some Catantopinae (Fig. 1.28B, *Traulia ornata*) and Oxyinae, the bridge of epiphallus is divided, the ancorae are articulated and a distinct ectophallic plate is present. In some other Catantopinae

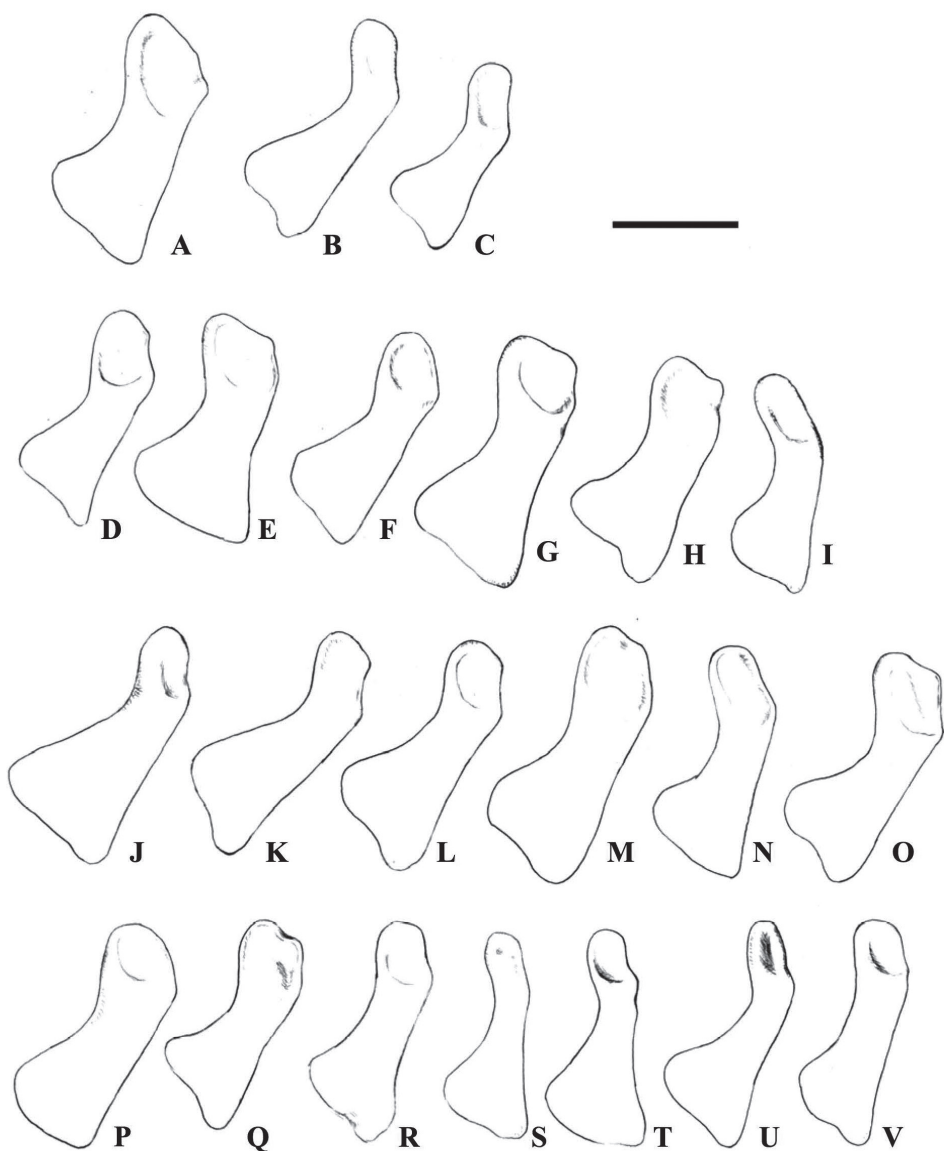


Fig. 1.27. Geographic variation in cercus of *Parapodisma tenryuensis*. A: Tochimoto, Chichibu-City; B: Mikabo-rindô, Onishi-Town; C: Narao, Yoshida-Town; D: Ôtaki-Vil.; E: Aoki-Vil.; F: Daimyôjin, Shikishima-Town; G: Lake Motosu, Shimobe-Town; H: Misaka-Tôge, Misaka-Town; I: Mt. Takao, Hachiôji-City; J: Kôrankei, Asuke-Town; K: Kawamuki, Shitara-Town; L: Tôei-Town; M: Funaba, Mori-Town; N: Sakuma-Town; O: Sudo River, Fuji-City; P: Kakesuhata, Fujinomiya-City; Q: Ôkoyama, Fujinomiya-City; R: Yamabushi-Tôge, Yamanakako-Vil.; S: Mt. Shiroyama, Yugawara-Town; T: Mt. Enkaizan, Yokohama-City; U: Mt. Tomisan, Tomiyama-Town. (A, C: Saitama; B: Gumma; D, E: Nagano; F-H, R: Yamanashi; I: Tôkyô; J-L: Aichi; M-Q: Shizuoka; S, T: Kanagawa; U: Chiba.) Scale=1mm.

(Fig. 1.28A, *Stenocatantops splendens*) the epiphallus is bridged, the ancorae are not articulated and the ectophallic plate is absent, while a pair of hardened areas are present on the ectophallic membrane. The phallic complex of Melanoplineae is more closely similar to the latter condition. However, examination on more subfamilies is needed to know relationships between these subfamilies.

Skareas & Hsiung (1998) studied the phallic complex in several melanopline genera mainly from the Nearctic Region and revealed their complexity in shape and structure. Although not mentioned by them, the pair of hardened areas on the ectophallic membrane could provide a good taxonomic character. Unfortunately, this part is easy to be broken and usually thrown away during dissection. This feature can be observed in other subfamilies, but is useful in distinguishing Melanoplineae from some genera of Catantopinae and Eyprepocnemidinae. Eyprepocnemidinae are characterized by the presence of the dorsal and ventral ectophallic plates. There is an additional sclerite between the pair of sclerites in a few species of *Parapodisma* (Fig. 1.28C, W), but most species have only the paired sclerites.

The epiphallus is usually species-specific in shape, but show similar transformation patterns in some phylogenetically different lineages. For example (Fig. 1.29), the apical emargination of the lophi is observed in *Zubovskya koeppenii parvula* (C), *Tonkinacris* spp. (K, L), *Parapodisma awagatakenis* (Q), and *P. etsukoana* (R), whereas these species have relatives with earlobe-like lophi such as *Z. morii*, *T. sinensis*, and *Parapodisma* spp. (N, O, P, T, U, V, W, X).

The aedeagal valves have provided useful characters for grasshopper classification. The dorsal and ventral aedeagal valves (*dav*, *vavs*) and the valves of the cingulum (*cv*) have been main taxonomic characters in Podismini. However, in many descriptions an important point was overlooked: the dorsal aedeagal valve (*dav*) is not always derived from the dorsal aedeagal sclerite (*das*), but sometimes the sheath of the cingulum is extended to form the valves (Eades 1961, 2000). The dorsal aedeagal sclerite is considered to be derived from the endophallus and the sheath from the ectophallus (Eades 1961). Therefore, the dorsal aedeagal valves are not always homologous. In Podismini, these different types are found.

In *Prumna* (Fig. 1.30A), the dorsal aedeagal sclerite is fused with the sheath forming the dorsal aedeagal valve. In this genus many species have strongly curved ventral aedeagal valves. In *Zubovskya*, *Miramella* and *Anapodisma* (Fig. 1.30B–D), the dorsal aedeagal sclerite and the sheath are merged together and sometimes the boundary between them is not clear (*Anapodisma*, Fig. 1.30D). The ventral aedeagal valves in these genera are nearly straightly elongate under the dorsal aedeagal valve. These valves are similar in structure to those of *Ognevia* and *Podisma*: they are relatively small, the dorsal aedeagal sclerite is fused with the sheath at its apical part, and the ventral aedeagal valves are simple, slender, and rectangular. *Ognevia* has a pair of articulated membranous lamellae at the apical part of the dorsal aedeagal sclerite (but its origin is unknown), while *Podisma* does not have such a feature.

Sinopodisma (Fig. 1.30H, I) has an elongate dorsal aedeagal valve, which is simply formed by the dorsal aedeagal sclerite. A pair of membranous apical exposed parts is the ventral aedeagal valves and is attached to the ventral aedeagal sclerites. *Tonkinacris* (Fig. 1.30J, K) has a well developed sheath, which form the cingulum surrounding the dorsal aedeagal sclerite wholly.

In *Parapodisma setouchiensis* (Fig. 1.31F, G), the dorsal aedeagal sclerite is

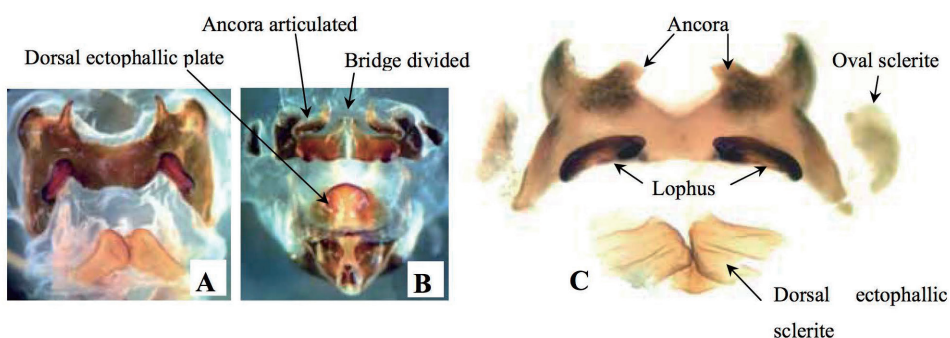


Fig. 1.28. Male ephiphallus. A: *Stenocatantops splendens* (Catantopinae); B: *Traulia ornata* (Catantopinae, the whole phallic complex); C: *Parapodisma tenryuensis* (from Shitara-Town, Aichi Prefecture).

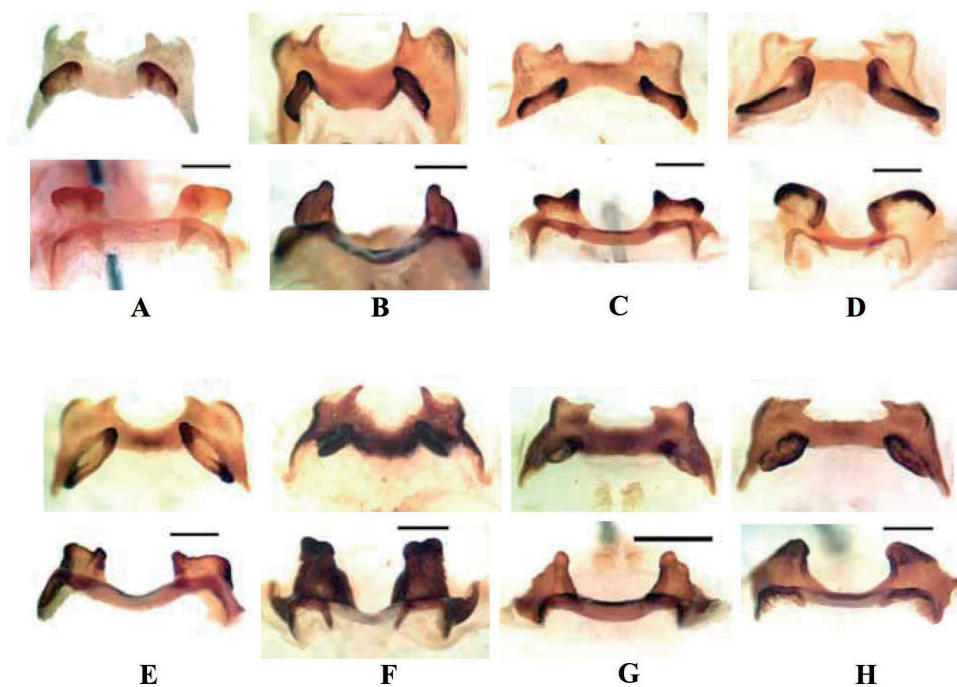


Fig. 1.29. Male ephiphallus. Dorsal view shown in the upper part and anterior view in the down part. A: *Melanoplus frigidus*; B: *Prumna hayachinensis*; C: *Zubovskya koeppeni parvula*; D: *Anapodisma miramae*; E: *Miramella solitaria*; F: *Ognevia longipennis*; G: *Podisma kanoi*; H: *Podisma sapporensis*. Scale=1mm.

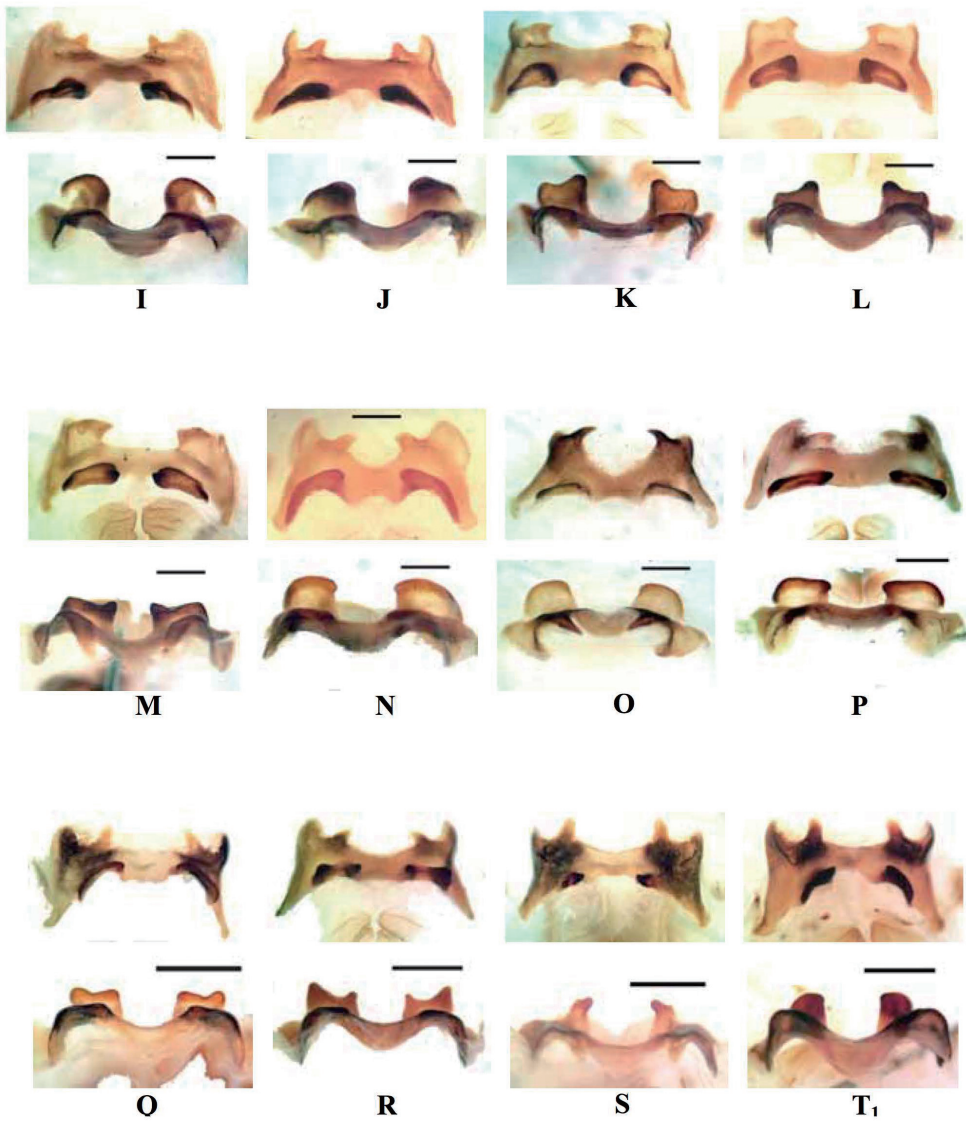


Fig. 1.29. Male epiphallus (continued). Dorsal view shown in the upper part and anterior view in the down part. I: *Sinopodisma punctata*; J: *Sinopodisma aurata*; K: *Tonkinacris ruficerus*; L: *Tonkinacris yaeyamaensis*; M: *Fruhstorferiola okinawaensis*; N: *Aopodisma subaptera*; O: *Parapodisma mikado*; P: *Parapodisma dairisama*; Q: *Parapodisma awagataensis*; R: *Parapodisma etsukoana*; S: *Parapodisma subastris*; T₁: *Parapodisma hiurai* (Ômiya-Town, Mie). Scale=1mm.

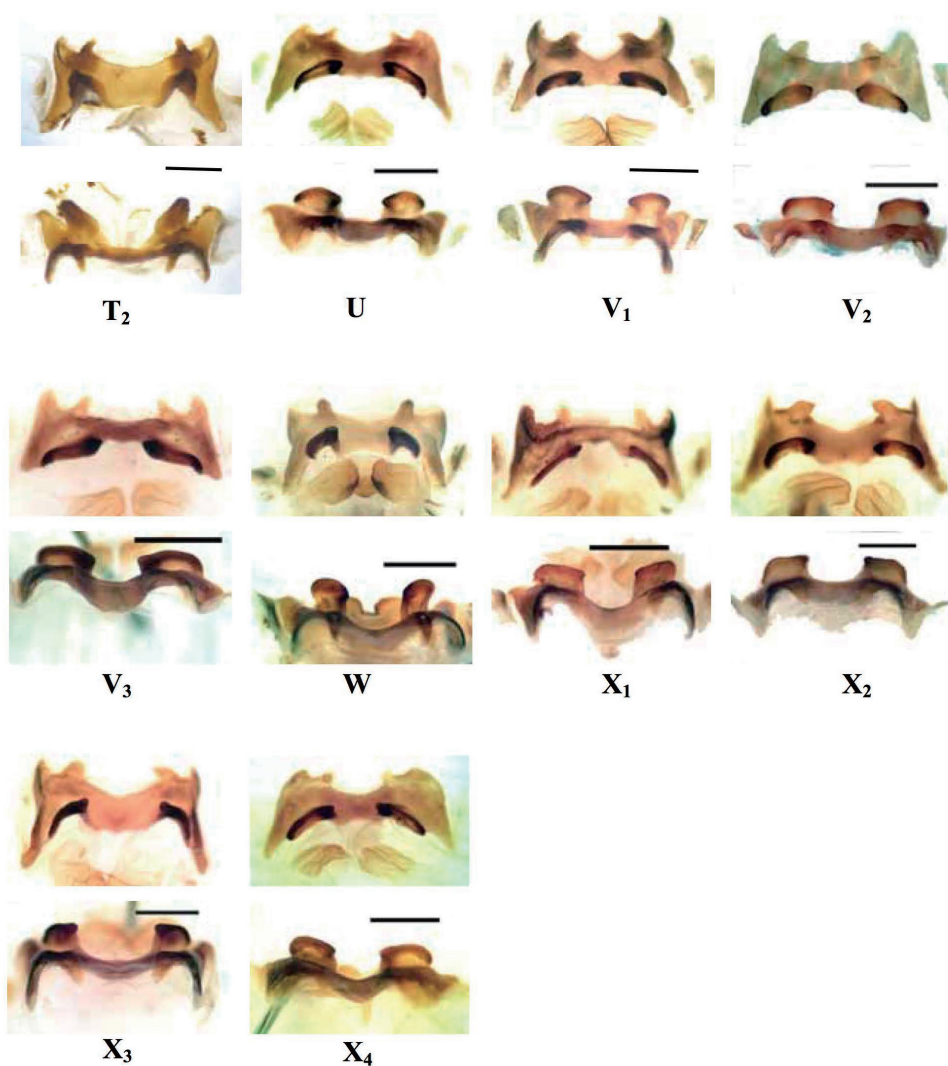


Fig. 1.29. Male epiphallus (continued). Dorsal view shown in the upper part and anterior view in the down part. T₂: *Parapodisma niihamensis* (Kamiyama-Town, Tokushima); U: *Parapodisma yasumatsui*; V₁: *Parapodisma tenryuensis* (Shitara-Town, Aichi Pref.); V₂: *Parapodisma tanzawaensis* (Susono-City, Shizuoka Pref.); V₃: *Parapodisma tanzawaensis* (Yugawara-Town, Kanagawa Pref.); W: *Parapodisma caelestis*; X₁: *Parapodisma setouchiensis* (Mie Pref.); X₂: *Parapodisma setouchiensis* (Mt. Hiei, Shiga Pref.); X₃: *Parapodisma setouchiensis* (Kôzuki-Town, Hyôgo Pref.); X₄: *Parapodisma setouchiensis* (Yakushima Is., Kagoshima Pref.). Scale=1mm.

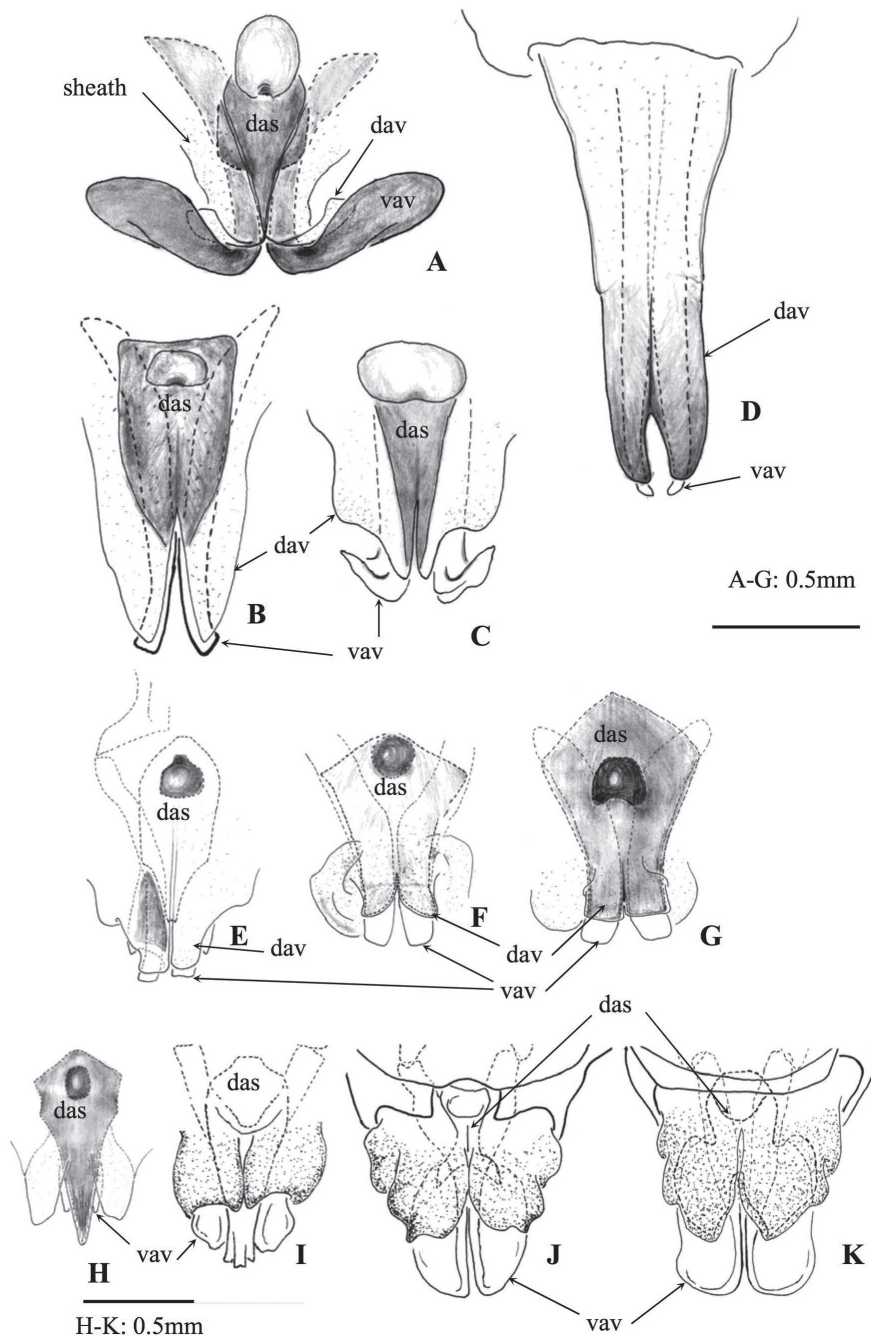


Fig. 1.30. Male aedeagal valves. A: *Prumna hayachinensis*; B: *Zubovskya koeppeni parvula*; C: *Miramella solitaria*; D: *Anapodisma miramae*; E: *Ognevia longipennis*; F: *Podisma sapporensis*; G: *Podisma kanoi*; H: *Sinopodisma punctata*; I: *Sinopodsima aurata*; J: *Tonkinacris ruficerus*; K: *Tonkinacris yaeyamaensis*.

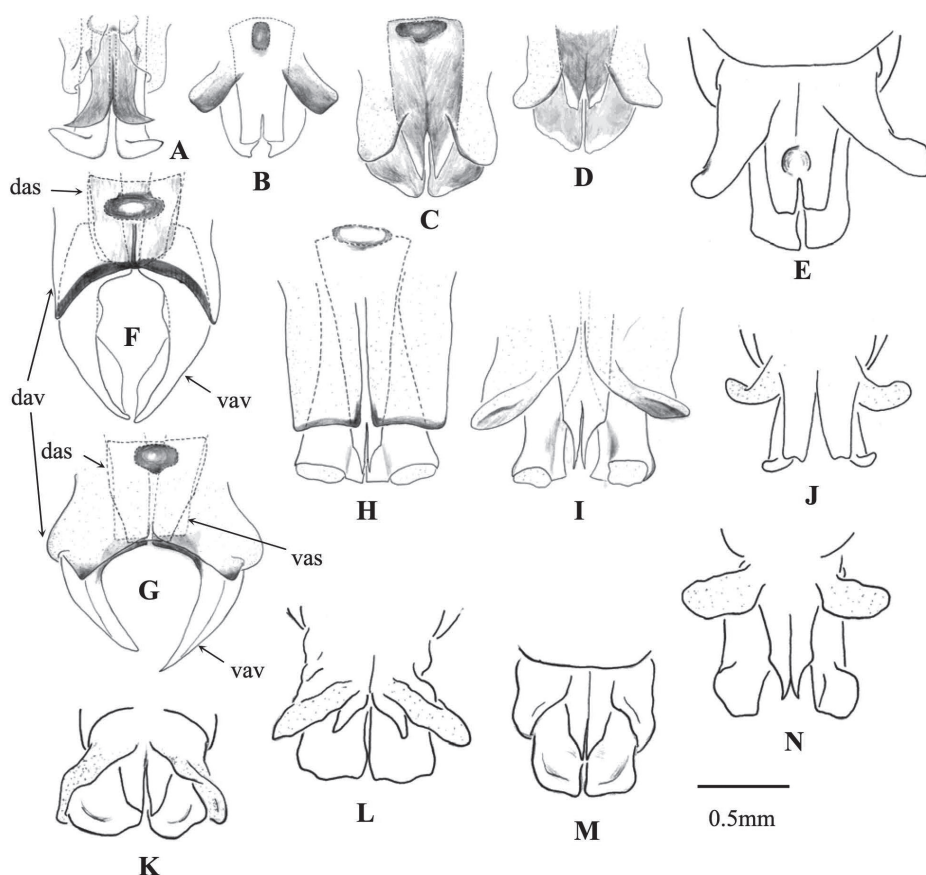


Fig. 1.31. Male aedeagal valves of *Fruhstorferiola*, *Aopodisma* and *Parapodisma*. A: *F. okinawaensis*; B: *A. subaptera*; C: *P. ternryuensis*; D: *P. caelestis*; E: *P. etsukoana*; F: *P. setouchiensis* (Mikazuki-town, Hyogo); G: *P. setouchiensis* (Mt. Hiei, Shiga); H: *P. niihamensis* (Kamiyama-Town, Tokushima); I: *P. hiurai* (Ômiya-Town, Mie); J: *P. subastris*; K: *P. mikao*; L: *P. dairisama*; M: *P. awagatakenis*; N: *P. yasumatsui*.

truncate, fused with the sheath of the cingulum, and this is extended to form the dorsal aedeagal valve. The ventral aedeagal valves of this species are also unique in the genus, being articulated and connected to a slender lamella. In the other *Parapodisma* species (Fig. 1.31B–E, H–N), the dorsal aedeagal valve is formed by the dorsal aedeagal sclerite and the ventral aedeagal valves are not articulated. *Fruhstorferiola* have the aedeagal valves similar to those of most *Parapodisma* species in structure.

Female subgenital plate (Fig. 1.32–34, Table 1.6)

The female subgenital plate of Acrididae possesses a pair of post-vaginal sclerites on the internal surface. These sclerites are connected to the subgenital plate by sclerotic

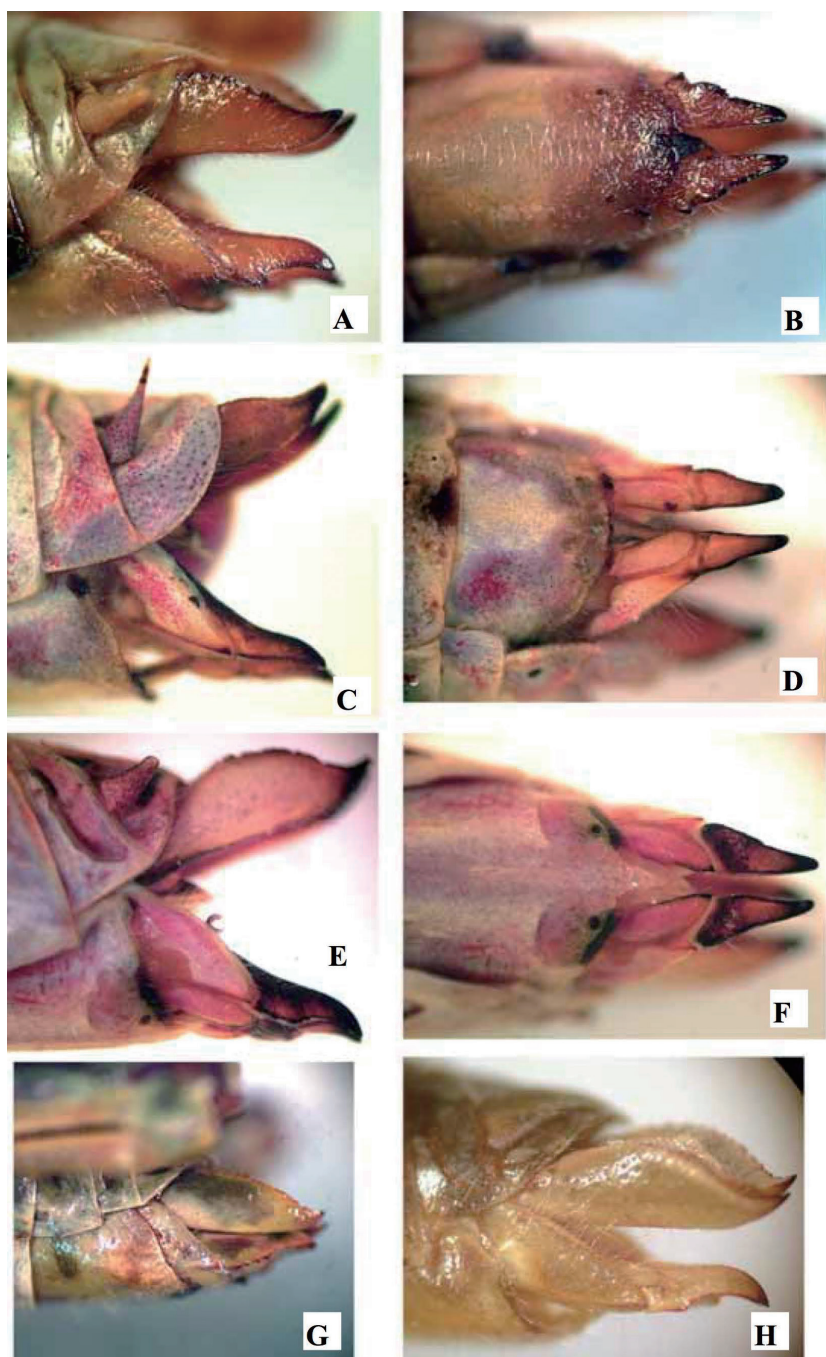


Fig. 1.32. Female subgenital plates. A, B: *Prumna hayachinensis*. C, D: *Ognevia longipennis*. E, F: *Parapodisma mikado*. G: *Zubovskya koeppeni parvula*. H: *Sinopodisma aurata*. A, C, E, G, H: lateral view. B, D, F: ventral view.

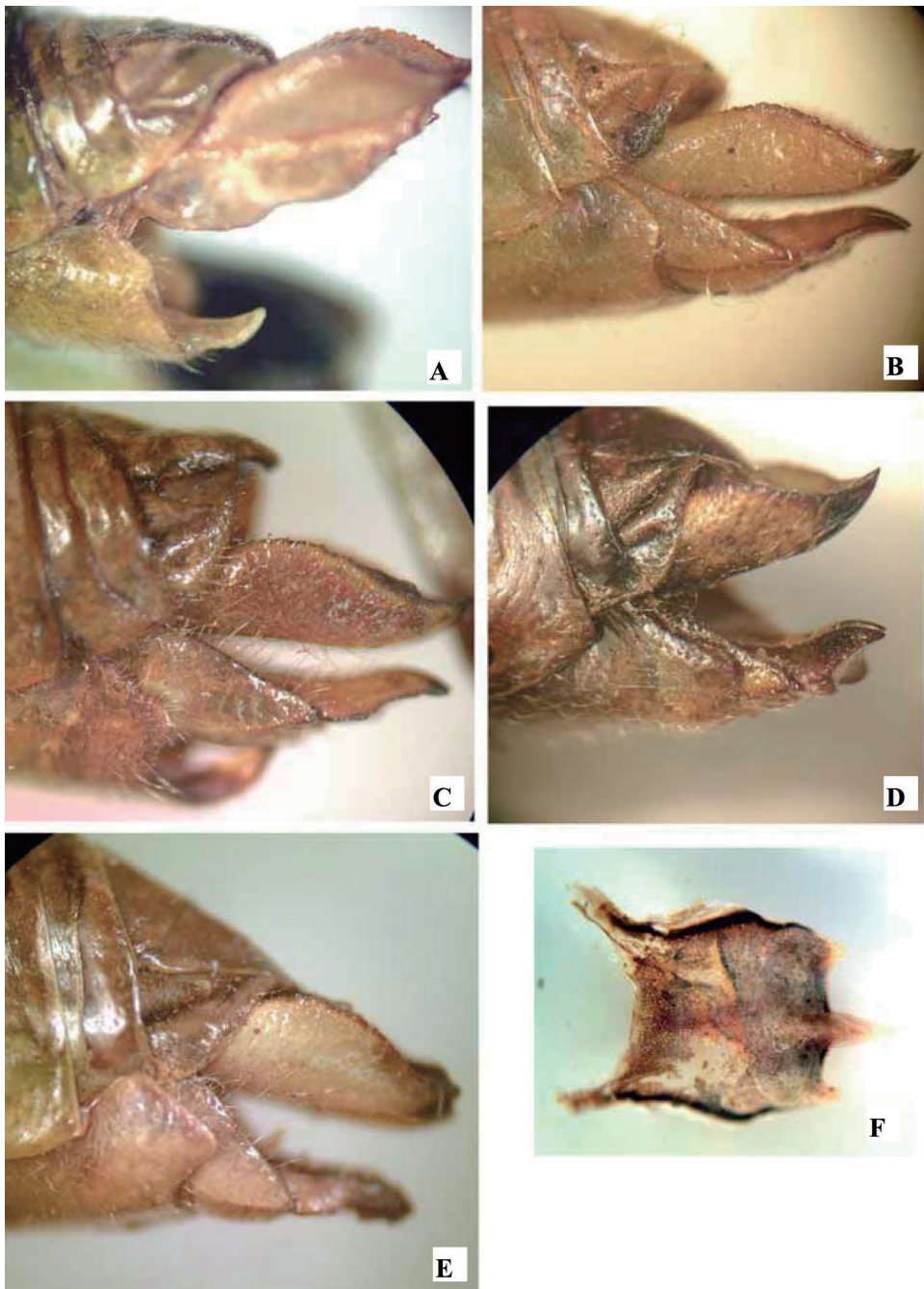


Fig. 1.33. Female subgenital plates. A: *Aopodisma subaptera*. B: *Parapodisma awagatakensis*. C: *Tonkinacris yaeyamaensis*. D: *Parapodisma caelestis*. E, F: *Parapodisma setouchiensis*.

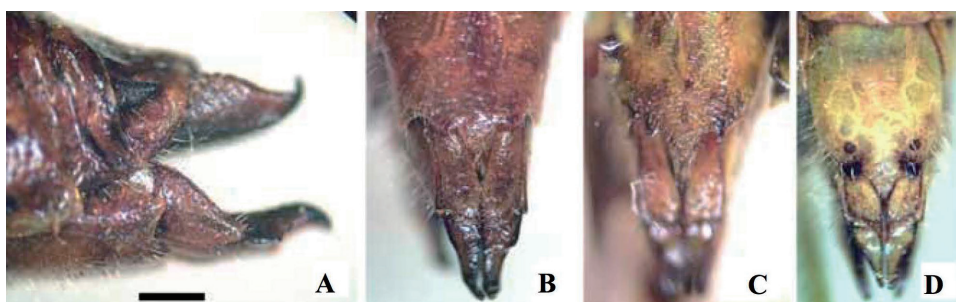


Fig. 1.34. Female subgenital plates of *Fruhstorferiola* spp. A, B: *F. okinawaensis*. C: *F. tonkinensis*. D: *F. viridifemorata*.

connection called the columellae (Rehn & Randell 1963). The columellae are variable in number and shape among generic groups or tribes, but sometimes not easy to observe. More noticeable is the shape of the posterior margin of the subgenital plate. Four types are recognized in this feature as follows:

1. Plate with the median part truncate and serrate. The egg guide extends only from the dorsal part. (Fig. 1.32A–B: *Prumna hayachinensis*; C–D: *Ognevia longipennis*.)

2. Plate gradually curved, the median part produced in a triangle and connected to the egg guide. (Fig. 1.32E–F: *Parapodisma mikado*; G: *Zubovskya koeppenii parvula*; H: *Sinopodisma aurata*.)

3. Plate with the lateral parts slightly produced and the median part produced in a triangle and connected to the egg guide. (Fig. 1.33A: *Aopodisma subaptera*; B: *Parapodisma awagatakensis*; D: *Parapodisma caelestis*, elongated and covering the ventral ovipositor valves.)

4. Plate with the lateral part strongly produced and the median part produced in a triangle and connected to the egg guide. (Fig. 1.33C: *Tonkinacris yaeyamaensis*; E: *Parapodisma setouchiensis*.)

The posterior margin of the subgenital plate in *Fruhstorferiola* is more complicated, with a species-specific emargination. (Fig. 1.34).

Ovipositor (Fig. 1.35, Table 1.6)

The shape of the ovipositor valve is usually used in generic classification. It varies in correlation with oviposition habit among the species of a genus that is variable in oviposition substrate (Cigliano et al 1996). As far as I know, podismini grasshoppers usually oviposit in soil or soil-like substrates. The difference in ovipositor shape therefore should be associated with other factors. In my examination, the following types of the ovipositor have been recognized:

1. Ovipositor with the valves straight and elongate, usually with smooth integument, incised apically. (*Anapodisma* and *Odontopodisma*.)

2. Ovipositor with the valves excurved apically, robuster than type 1, incised apically. (*Miramella*, *Kisella* and *Zubovskya*.)

3. Ovipositor with the valves excurved apically, short and robust, not incised

Table 1.3. Terminology of female genitalia.

Abbreviation	Terms in this study	Packard 1878	Snodgrass 1935	Slifer 1939-1943	Ander 1956	Uvarov 1966	Jones 1981
CK	Comstock-Kellogg gland	-	lateral pocket	glandular pouches of Comstock and Kellogg	glandular pouches	Comstock-Kellogg gland	-
sa	spermathecal aperture	-	spermathecal aperture	-	-	spermathecal aperture	spermathecal aperture
sv	spermathecal vestibule	bursa copulatrix	-	proximal end of the spermathecal duct	-	-	spermathecal vestibule
vsd	valve of spermathecal duct	-	weakly sclerotized heart-shaped sclerite (for <i>Dissosteira</i>)	valve of spermathecal duct	-	-	-
sd	spermathecal duct	-	-	-	-	-	-
sp	ad	spermatheca	sebific gland	spermathecal invagination	spermatheca	spermatheca	spermatheca
	pad	preapical diverticulum apical diverticulum	-	-	-	-	-
ssv	sclerite of spermathecal vestibule *	-	-	-	-	-	-

* Newly named in this study

Table. 1.4. General morphology in 13 genera of Podismini and *Melanoplus* in the Far East.

Genus	1 Male chromosomal number (1)	2 Size of compound eyes (HW / IS in male)	3 Posterior margin of pronotum	4 Tegminal shape	5 Metano- tum (2)	6 Tympanum	7 a spine of hind genicular hood	
<i>Prumna</i>	23	5	emarginate	bamboo-leaf-shaped	0	normal	×	
<i>Zubovskya</i>	21	4-5		×		×		
<i>Anapodisma</i>		6		bamboo-leaf-shaped		normal		
<i>Miramella</i>		4-5		oval	1	small~normal	○ (sometimes absent)	
<i>Sinopodisma</i>		7-12	emarginate or slightly produced	absent~bamboo-leaf-shaped ~oval		small		
<i>Aopodisma</i>		8-10		oval (vestigial)		small~normal		
<i>Parapodisma</i>		7-9	produced	oval~oblong		normal		○, ×
<i>Tonkinacris</i>	?	7-10		elongate				
<i>Fruhstorferiola</i>	21	7-9						
<i>Ognevia</i>	23	6	emarginate or slightly produced	absent~bamboo-leaf-shaped ~oval (rarely oblong)	0			
<i>Podisma</i>		4-5						
<i>Niitakacris</i>	21	6-7	emarginate	oval		○		
<i>Melanoplus</i>	23	6-9	produced	oval~oblong	1-2			

(1) Data from Inoue (1985), Bugrov et al. (1994), Bugrov et al. (2000) and the present author.

(2) Classified degree of development of meso- and metanotal complexity as in Fig. 1.13 and Table 1.2.

Table. 1.5. Male morphology in 13 genera of Podismini *Melanoplus* in the Far East.

Genus	8	9	10	11	12	13	14
	Furculae of 10th abdominal tergite	Tubercle on epiproct near the middle of lateral margin	Near apex of epiproct, lateral margin	Subgenital plate	Cerci	Sheath of aedeagus	Phallus, ventral apical valves
<i>Prumna</i>	○ (present)	spine-like, small, or absent	incised	truncate posteriorly	strongly compressed apically or wholly	fused with <i>das</i> and forming <i>dav</i>	excurred with right angle
<i>Zubovskya</i>		absent or slightly swollen	gradually curved	bow-shaped	slender, compressed apically		simple, slender, long
<i>Anapodisma</i>		spine-like			conical		bent with right angle
<i>Miramella</i>							
<i>Sinopodisma</i>	× (absent or very small)	absent or slightly swollen	gradually curved	bow-shaped	compressed apically	covering around basal part of aedeagal valves	membranous apically, usually spatulate
<i>Aopodisma</i>						partly sclerotized, forming <i>cv</i>	
<i>Parapodisma</i>						partly sclerotized, forming <i>cv</i> or fused	
<i>Tonkinacris</i>						fused with <i>das</i> and forming <i>dav</i>	
<i>Fruhstorferiola</i>						covering around basal part of aedeagal valves	
<i>Ognevia</i>	○		incised		conical	fused with <i>das</i> and covering wholly, forming <i>cv</i>	simple, slender
<i>Podisma</i>			gradually curved				simple, slender
<i>Niitakacris</i>			small, spine-like			?	?
<i>Melanoplus</i>			various type		strongly compressed apically or wholly	?	various shapes

Table. 1.6. Female morphology in 13 genera of Podismini and *Melanoplus* in the Far East.

Genus	15	16	17	18	19	20	
	Subgenital plate, the middle of posterior margin before egg guide	Subgenital plate, lateral side of posterior margin	Ovipositor valves	Comstok-Kellog organ	Spermathecal vestibule, aperture	Spermathecal vestibule, anterior part	
<i>Prumna</i>	truncate	not produced	not incised apically	○	without sclerite	sclerotized	
<i>Zubovskya</i>	triangularly produced		incised apically				without sclerite
<i>Anapodisma</i>		slightly produced	incised apically, straight and elongate	×	without sclerite		
<i>Miramella</i>		not produced	incised apically			○	partly sclerotized
<i>Sinopodisma</i>							
<i>Aopodisma</i>		slightly produced					
<i>Parapodisma</i>		not produced ~strongly produced					
<i>Tonkinacris</i>		produced					
<i>Fruhstorferiola</i>		strongly produced (incised)	not incised apically		without sclerite	without sclerite	
<i>Ognevia</i>		truncate					not produced
<i>Podisma</i>	triangularly produced	not produced ~slightly produced					×
<i>Niitakacris</i>		not produced					
<i>Melanoplus</i>		not produced ~strongly produced	with or without sclerite	with or without sclerite			

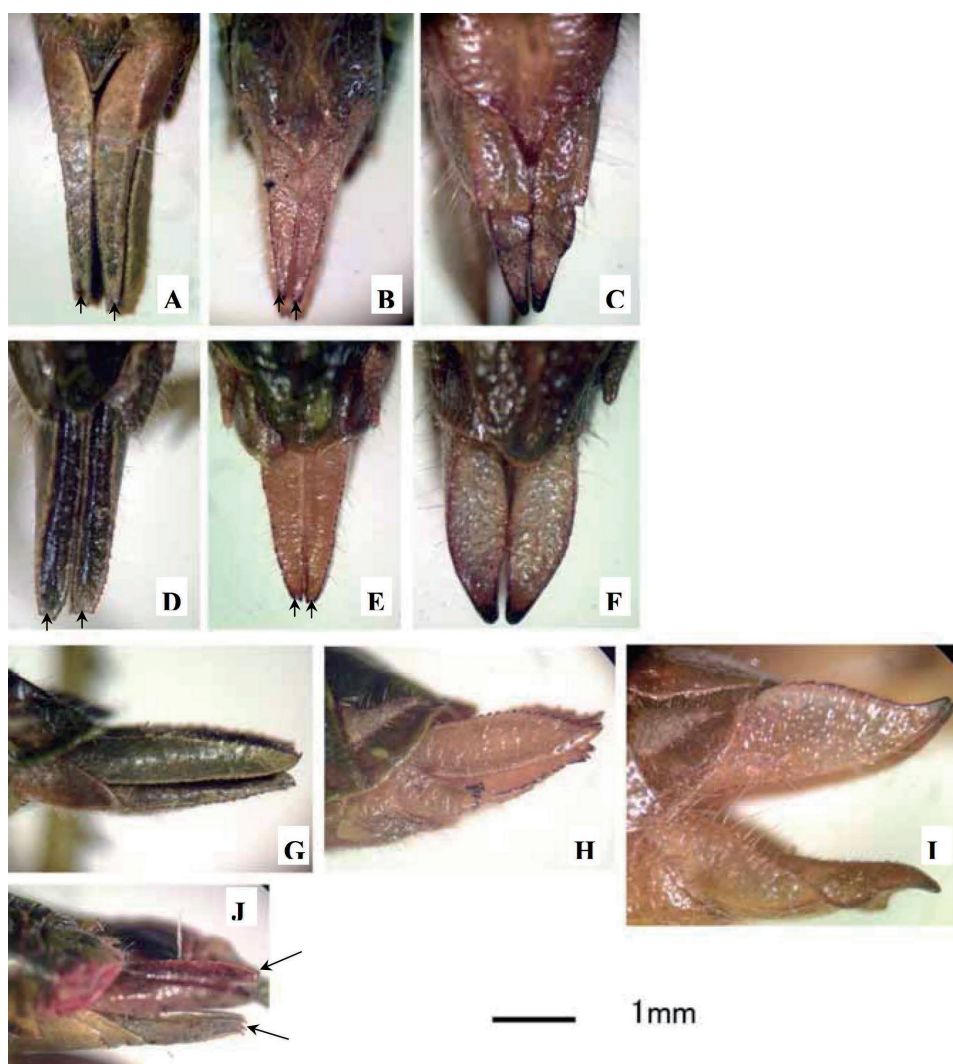


Fig. 1.35. Three types of ovipositors in Podismini. A–F, ventral view, G–J, lateral view. A, D, G (type 1): *Anapodisma miramae*. B, E, H (type 2): *Zubovskya koeppeni parvula*. C, F, I: *Sinopodisma punctata* (type 3, the common type). J (type 1): *Odontopodisma decipiens*. Arrows show the incised point.

apically. (Almost all other genera belong to this type.)

Comstock-Kellogg gland (Fig. 1.36–37, Table 1.6)

The Comstock-Kellogg gland is a pair of pouches lying on the sides of the common oviduct. It is derived from the anterior basivalvular sclerites (*abs*) that form a U- or V-shaped bridge (Fig. 1.37). According to Slifer & King (1936) and my examination,

the pouches have been found in Cyrtacanthacridinae, Catantopinae, Eyprepocnemidinae and several Melanoplinae (*Melanoplus*, *Prumna*, *Nitakacris*, *Sinopodisma*, *Tonkinacris*, *Fruhstorferiola*, *Parapodisma* and *Aopodisma*), while not in Oedipodinae, Acridinae, and some Melanoplinae (*Zubovskya*, *Anapodisma*, *Ognevia* and *Podisma*). The function of the pouches has not been known well. These pouches sometimes can be observed in everted state before copulation and this fact suggests the possibility that they play a role in attracting the male by pheromone (Hubbell & Cantrall 1938).

Female genitalia — Spermatheca (Fig. 1.36–37, 40–45 & Table 1.3, 6)

In grasshopper taxonomy, the female internal genitalia have not usually been used for recognizing species. Taxonomic systems have been based mainly on general morphology and male genital morphology. Almost all authors have regarded characters of the spermatheca as auxiliary ones for subfamily level taxonomy, although the spermathecae of a large number of acridoid species are figured and described by Slifer (1939, 1940a, 1940b, 1943), Dirsh (1957) and Podgornaja (1975). In podismini species, all part of the spermatheca was drawn in *Parapodisma mikado* (Slifer 1940b) and *P. tenryuensis* (Kobayashi 1983), and the apical part of the spermatheca of *P. yasumatsui* was drawn and described by Yamasaki (1980), but the spermathecal vestibule (Sv) was not mentioned in any articles.

However, certain female internal genital organs should be diversified specifically when there are any specific differences in the male aedeagal valves, which are inserted into the female organ during copulation. Ito (1999) has revealed that the spermathecal vestibules are remarkably diversified among three podismini species. In the present study, its sclerites (Fig. 1.38, 43, 44) are studied for the first time in the other Japanese species.

The general structure of the acridid female genitalia is shown in Fig. 1.36. The female copulative organs are composed of external and internal parts. The external part comprises the subgenital plate and the ovipositor. The internal part is the spermatheca. Table 1.3 shows a revision of terms used in this study. “Spermathecal vestibule” was proposed by Jones (1981), and this organ has been called by other names by other authors: “bursa copulatrix” (Packard, 1878), “dilated part of receptaculum” (Fedorov, 1927), and “expanded proximal end of the spermathecal duct” (Slifer, 1939, 1940b). I adopt “spermathecal vestibule” for this part. The bursa copulatrix should be a part for storing spermatophore. The spermathecal vestibule receives the male aedeagal valves, and the spermatophore is not stored there but put into more apical part of the spermathecal duct.

The spermatheca of Podismini usually has an apical and a preapical diverticula (*ad* and *pad*), and length of the apical one is various among genera, species, or populations. The preapical one is usually sac-shaped, functions as a reservoir of the spermatophore. When dissecting, it is often observed that the spermatophore poured in the preapical and apical diverticula, or only in the preapical diverticulum. These diverticula may function dividing spermatophores received through multiple copulations. However, it is still unclear why spermatheca possesses preapical and apical diverticula. In some Podismini the spermathecal vestibule is provided with a sclerite, which is shaped variously as will be described in Chapter 3. I name it “sclerite of spermathecal vestibule”.

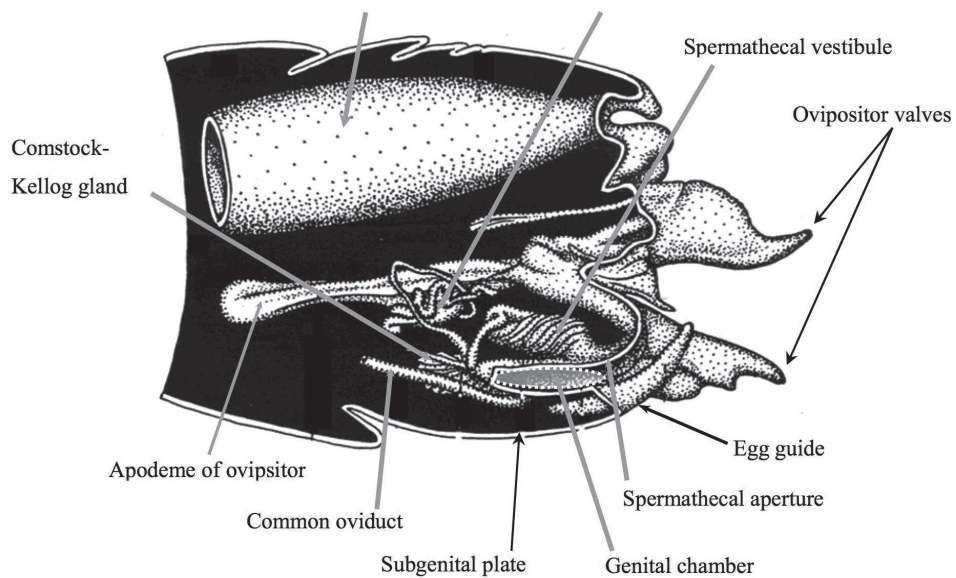


Fig. 1.36. A diagram of lateral section of female abdomen tip, modified after Slifer (1940).

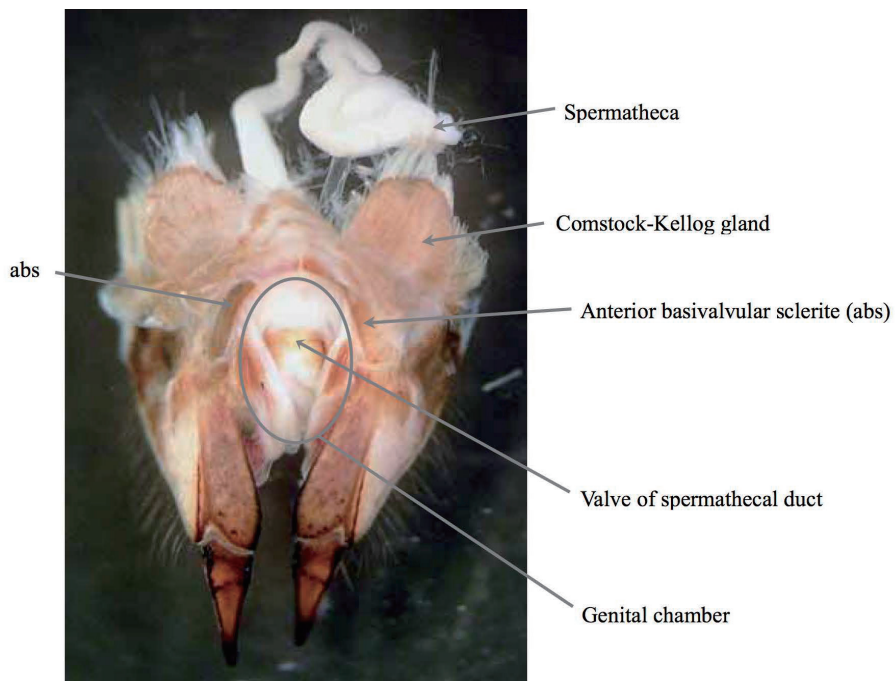


Fig. 1.37. Female ovipositor and copulative organs of *Parapodisma setouchiensis*, ventral view. Subgenital plate was removed with common oviduct.

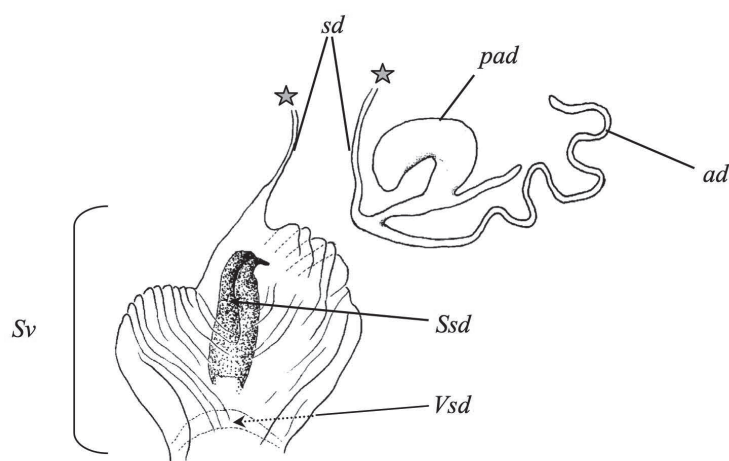


Fig. 1.38. Spermatheca, dorsal view. The exemplar is *Parapodisma etsukoana*. *ad*: apical diverticulum; *pad*: preapical diverticulum; *sd*: spermathecal duct; *Ssd*: Sclerite of spermathecal duct; *Sv*: spermathecal vestibule; *Vsd*: valve of spermathecal duct.

The shape of the spermathecal vestibule is sometimes variable within the same species in many podismini species (Fig. 1.43A). In *Parapodisma*, intraspecific differences of the length of apical diverticulum are large as in *Melanoplus differentialis* (Slifer 1940a). The variation is largest in *P. setouchiensis* (Fig. 1.40.M–N) among the species examined in this study (Fig. 1.39, 42). Secondary diverticulum of preapical diverticulum (*pad*) is observed in the particular group.

1.3. Color

Lateral black stripes (Fig. 1.44)

The body color of grasshoppers quickly changes from green to brown or from other colors to a darker color after death. However, some color patterns are still easily observable, including a pair of lateral black stripes (LS) and red color under the hind femora.

A pair of LS are present in most podismini grasshoppers. They may have no generic value. Sometimes they are remarkably variable in length and width even in the same species (Fig. 1.44A–E in *Parapodisma mikado*, F and H in *P. tenryuensis*), and the ranges of the variation are overlapped among some species (G–I, medium width; J and K, narrow width). However, the pattern of variation is specific to each species. For example, in *P. mikado*, LS in the female are always narrow (A–D) except for some populations in Niigata and Nagano, where LS are well developed over the length of the pronotum (E). In the males of *P. etsukoana* (J) and *P. awagatakensis* (K), LS are always narrow, usually reaching the 3rd transverse sulcus of the pronotum. In this study, LS are classified into three types as follows:

1. LS present only on anterior margin and/or on transverse sulci and/or on posterior

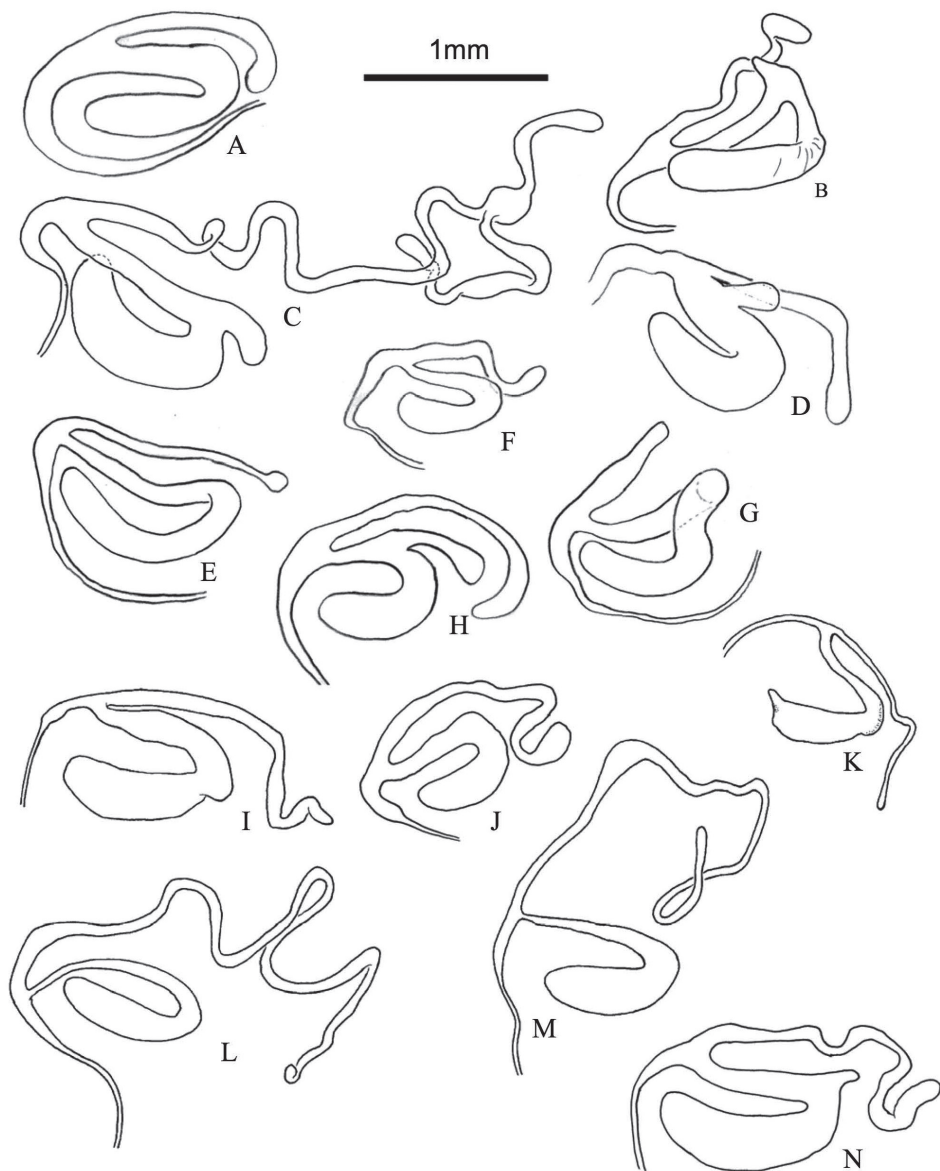


Fig. 1.39. Spermathecae of podismini species. A: *Prumna fauriei*; B: *Miramella solitaria*; C: *Zubovskya koeppeni parvula*; D: *Anapodisma miramae*; E: *Podisma sapporensis*; F: *Ognevia longipennis*; G: *Podisma kanoi*; H: *Fruhstorferiola okinawaensis*; I: *Sinopodsima aurata*; J: *Sinopodsima formosana*; K: *Sinopodsima punctata*; L: *Tonkinacris ruficerus*; M: *Tonkinacris yaeyamaensis*; N: *Tonkinacris sinensis*.



Fig. 1.40. Spermathecae of *Parapodisma* species. A: *Parapodisma takeii*; B: *Parapodisma mikado*; C: *P. dairisama*; D: *P. etsukoana*; E: *P. subastris*; F: *P. hiurai* (Ômiya-Town, Mie); G: *P. niihamensis* (Kamiyama-Town, Tokushima); H: *P. awagataensis*; I: *P. yasumatsui*; J: *P. tenryuensis* (Matsumoto-City, Nagano); K: *P. tenryuensis* (Yugawara-Town, Kanagawa); L: *P. caelestis*; M: *P. setouchiensis* (Mt. Hiei, Shiga); N: *P. setouchiensis* (Totsukawa-Vil., Nara).

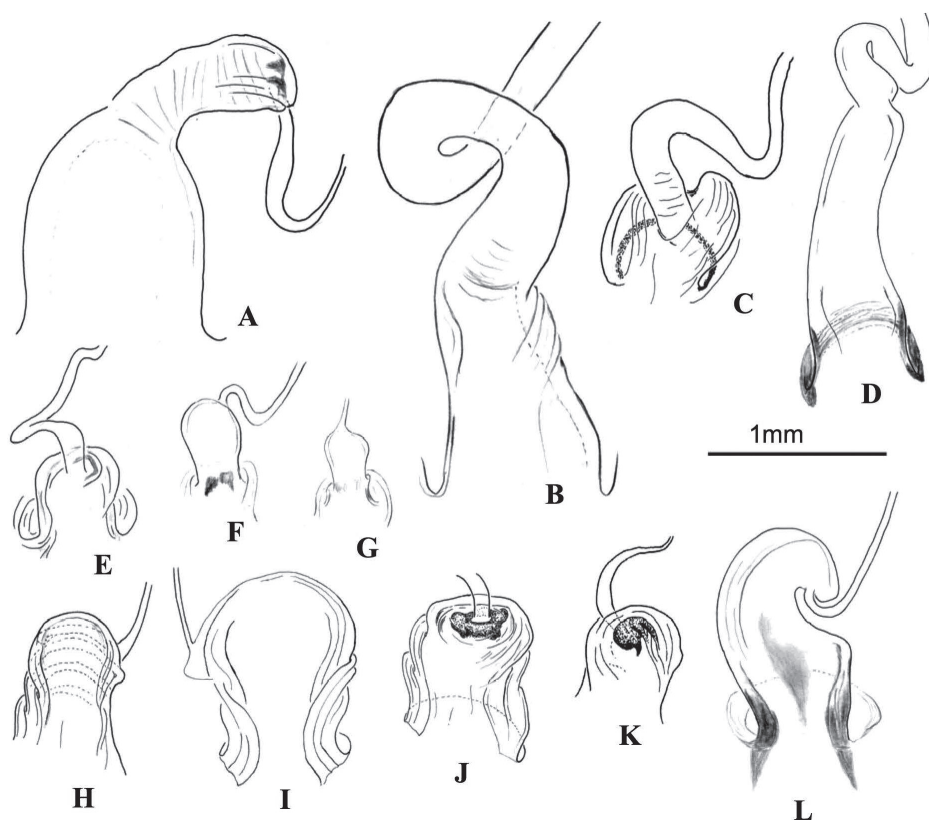


Fig. 1.41. Spermathecal vestibules. A: *Prumna hayachinensis*; B: *Zubovskya koeppeni parvula*; C: *Miramella solitaria*; D: *Anapodisma miramae*; E: *Ognevia longipennis*; F: *Podisma sapporensis*; G: *Podisma kanoi*; H: *Tonkinacris ruficerus*; I: *Tonkinacris yaeyamaensis*; J: *Sinopodisma aurata*; K: *Sinopodisma punctata*; L: *Fruhstorferiola okinawaensis*.

margin.

2. LS reaching the 3rd transverse sulcus, interrupted or continuous, and often present on posterior margin.

3. LS present over length of pronotum.

The LS width on the pronotum is evaluated as ratio of the maximum width (except on the transverse sulci) (LSW) to the approximate height of the pronotum (PH), which was measured where the 3rd transverse sulcus and LS cross (E).

Nymph color
(Fig. 1.45)

I reared 13 species of podismine grasshoppers in the laboratory from eggs laid by adult females. In all these species the number of instars was 5, as usual in Podismini. Nymph morphology and especially the color pattern seemed to be useful for generic or specific level diagnoses.

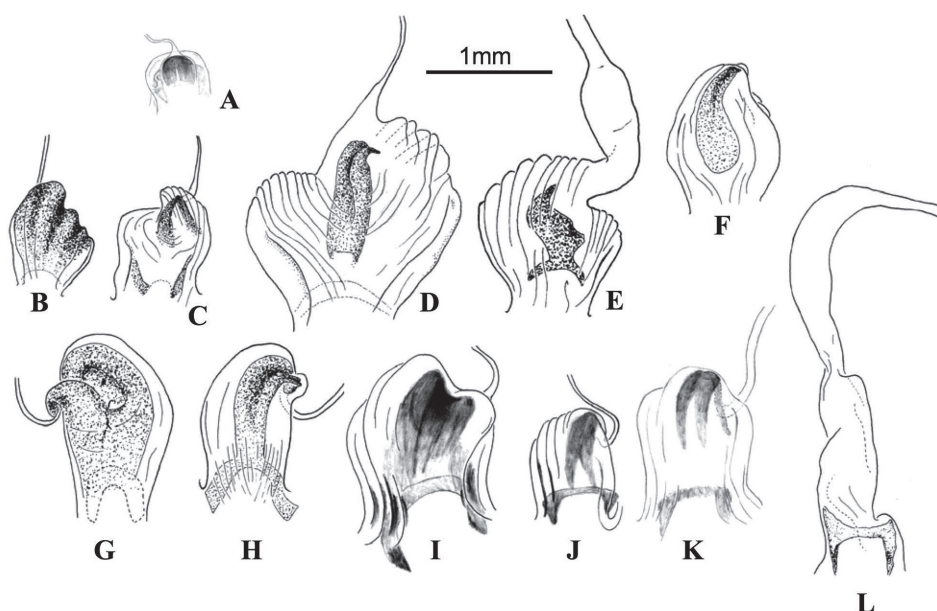


Fig. 1.42. Spermathecal vestibules. A: *Aopodsima subaptera*; B: *P. mikao*; C: *Parapodsima dairisama*; D: *P. etsukoana*; E: *P. subastris*; F: *P. awagatakensis*; G: *P. yasumatsui*; H: *P. niihamensis* (Kamiyama-Town, Tokushima); I: *P. hiurai* (Omiya-Town, Mie); J: *P. caelestis*; K: *P. tenryuensis*; L: *P. setouchiensis*.

In all species examined the integument of the 1st instar is not shining except for the compound eyes. In some species, the integument becomes shining as the body grows, especially in black colored parts (e.g., the lateral black stripes). For example, in *Sinopodisma punctata* the 1st instar nymph (Fig. 1.45E) is not shining, but from the 2nd instar on, its integument becomes shining. In *Parapodsima* species, some individuals were strongly blackish and shining in the 2nd instar (J: *P. mikado*; O: *P. setouchiensis*), but they were not shining in the 1st instar. In *Podisma sapporensis*, the integument is not shining during its nymphal stages, but becomes shining after the final molt. It is unknown what factor in cuticle construction has produced this change.

In the Podismini examined, the body color in the early instars is generally ochre (B, H, K, N), dark brown (A, D, E, G, I, L, M), brown (F) or black (C, J, O) with many small dark spots. The compound eyes are variable in color from brown to ochre. A yellow longitudinal line runs from the vertex to the 9th tergite as usual in Orthoptera; this line corresponds to the split in molting. Behind the compound eyes, a pair of dark stripes extend to the middle of the posterior margin of the pronotum, forming a V-crest. I call this pair of stripes "V-crest" here. In some species the V-crest is obscured. As the grasshopper grows, the V-crest gradually changes into two lateral stripes, and then to the lateral black stripes in the adult. In dorsal view, a pair of pale yellow lines are laid above the V-crest on the head. Sometimes these black and yellow stripes originate from the anterior part of the compound eyes as in *Podisma* species (C, D) and *Fruhstorferiola okinawaensis* (G). Moreover, in some species a pale-colored line is laid under the black stripe extending from the anterior part of the compound eye to the posterior margin of

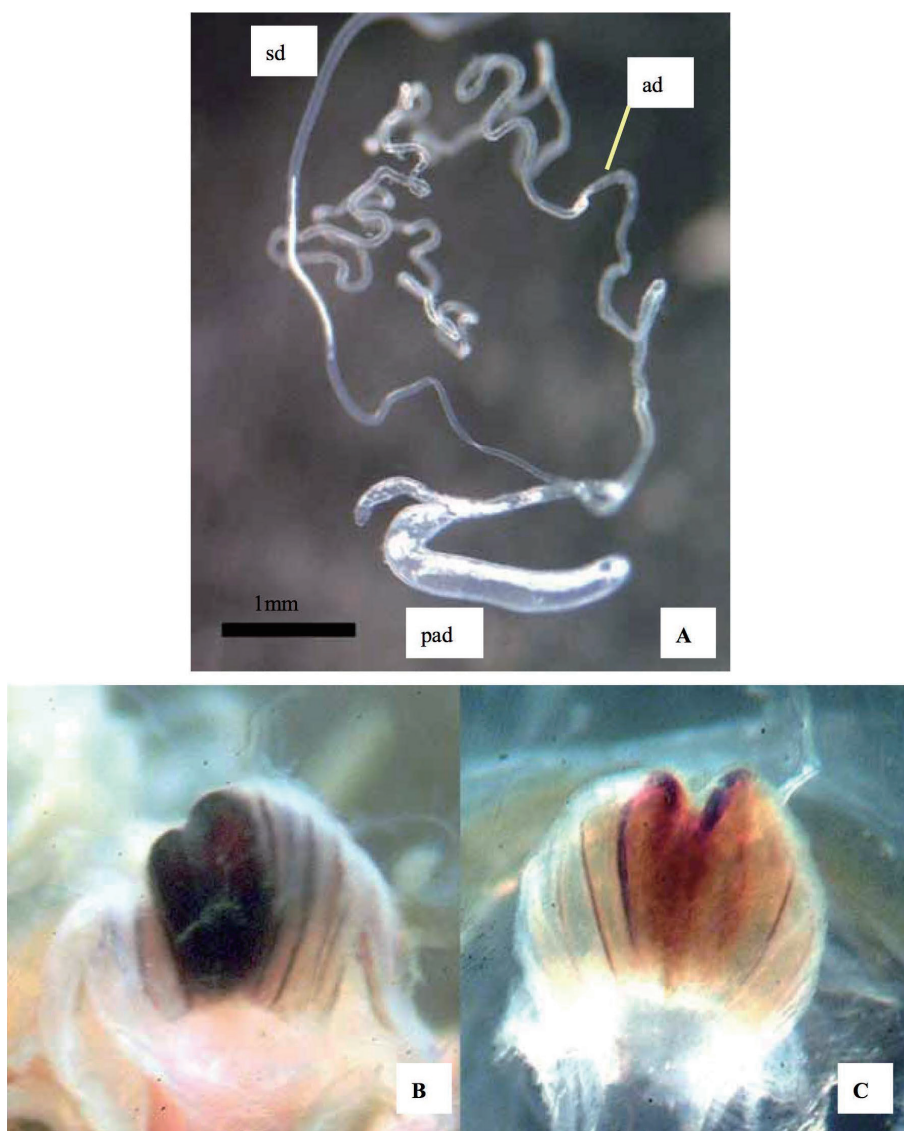


Fig. 1.43. Variation among individuals in female spermathecae. A: Extremely long apical diverticulum of spermatheca of *Parapodsima setouchiensis*. A: Spermathecal vestibule of *Parapodsima mikado* from Kyôwa-Town; B: That from Ôoka-Vil.

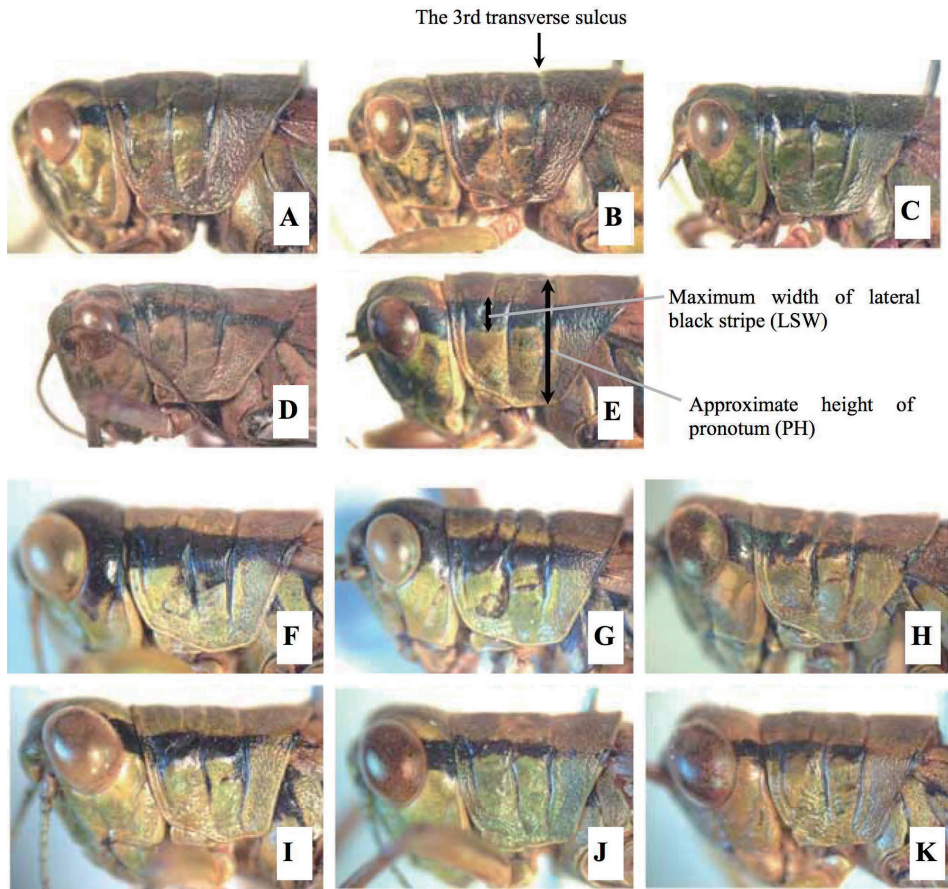


Fig. 1.44. Heads and pronota of *Parapodisma* species, lateral view, showing differences in length and width of lateral black stripe in pronotum. A–E: *Parapodisma mikado*, female (A: Makino-Town, Shiga Pref.; B: Chôkai-Town, Akita Pref.; C: Yuzawa-Town, Niigata Pref.; D: Niiharu-Vil., Gumma; E: Kamikawa-Vil., Niigata Pref.). F–K: *Parapodisma* species, male (F: *P. tenryuensis*; G: *P. caelestis*; H: *P. tenryuensis*; I: *P. hiurai*; J: *P. etsukoana*; K: *P. awagataensis*).

the head (*Podisma* spp.: C, D) or to the middle of the pronotum (*Sinopodisma punctata*: E; some *Parapodisma* spp.: H, K, N). In *Parapodisma* and *Sinopodisma*, a dark line usually black or dark brown, is laid under the pale yellow line (I would like to call this pattern “dark-yellow-dark pattern of stripes”). The hind femora possess 2 or 3 maculae on the outer side, which are usually continuous on to the inner side. The maculae are sometimes fused together (E, O) or obscured (F, K). Similar maculae are present on the outer side, but sometimes quite different in appearance. The inside maculae are fused together in *Tonkinacris ruficerus* (F) and *Parapodisma tenryuensis* (M). A yellow ring is usually present on the tibia near the base as in the adult. The abdomen has a black lateral stripe on each side, sometimes interrupted or obscured.

The body color changes characteristically also in the developmental process. In



A. *Prumna fauriei* (1st).



B. *Ognevia longipennis* (1st).



C. *Podisma sapporensis* (2nd).



D. *Podisma kanoi* (3rd).



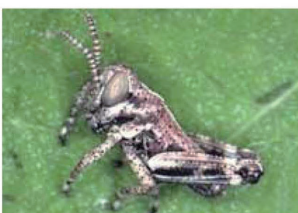
E. *Sinopodisma punctata* (1st).



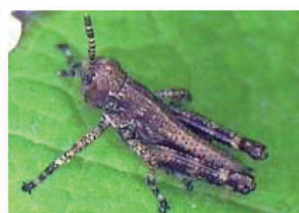
F. *Tonkinacris ruficerus* (1st).



G. *Fruhstorferiola okinawaensis* (1st).



H. *Parapodisma takeii* (1st).



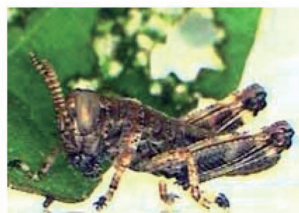
I. *Parapodisma mikado* (1st).



J. *Parapodisma mikado* (2nd).



K. *Parapodisma etsukoana* (1st).



L. *Parapodisma subastris* (1st).



M. *Parapodisma tenryuensis* (1st).



N. *Parapodisma setouchiensis* (1st).



O. *Parapodisma setouchiensis* (2nd).

Fig. 1.45. First to third instar nymphs of Podismini.

Zubovskya, *Ognevia* and *Podisma*, the general body color changes abruptly in the last molt from dark brown, ocher or black to green, while in *Prumna*, *Sinopodisma*, *Tonkinacris*, *Fruhstorferiola*, *Aopdisma* and *Parapodisma* it changes gradually from ocher, dark brown or black to green. The black maculae on the hind femora also become paler, and this process is not the same among taxa. They completely disappear in the adult in *Zubovskya*, *Anapodisma* and *Parapodisma*, and are partly kept in *Sinopodisma*, *Tonkinacris*, and *Fruhstorferiola*.

Although the coloration is useful, it is highly variable. For example, the nymphs of *Parapodisma mikado* are usually colored as in Fig. 1.45I, but in a particular population (Ishinoyu, Nagano Pref.) almost all parts of the body are colored black (J). In *Parapodisma setouchiensis* the nymphal coloration is also variable among local populations (N, O). In *Ognevia longipennis* and *Podisma sapporensis*, the general body color is often variable within and among populations.

1.4. Karyotype

The karyotype is a useful tool for comparing populations or species. The chromosome number is a fundamental property of a genome (Gosalvez et al. 1997). In most acridid grasshopper subfamilies, $2n \text{ ♂}=23$ ($2n \text{ ♂}=22+X$) is a typical number. Based on karyotypic data, Vickery (1977) assigned genera of the Podismini to subtribal groups as follows:

Podismina ($2n \text{ ♂}=23$): *Podisma*, *Cophopodisma*, *Dendrotettix*, *Appalachia*.

Miramellina ($2n \text{ ♂}=21$): *Miramella*, *Parapodisma*, *Sinopodisma*, *Niitakacris*, *Zubovskya*.

In some other subfamilies (e.g., Oxyinae, Cyrtacanthacrididae) $2n \text{ ♂}=23$ is common, and this state is thought to be plesiomorphic. The reduction of chromosomal number may have occurred independently in different lineages. In this interpretation, the number could be a homoplastic character. In fact, the mtDNA tree proposed by Litzenberger & Chapco (2001) suggests that the $2n \text{ ♂}=21$ groups originated paraphyletically from the $2n \text{ ♂}=23$ ancestor. Changes of chromosome number should be resulted from several events such as fusion, fission, inversion or duplication of chromosomes. Further characters of these chromosomal mutations can be obtained from C-banding pattern. This method gives information on the rates and features of chromosome evolution in groups of closely related species (Bugrov et al. 2000). However, only a small part of podismini karyotypes has been studied. In this study, I use only chromosomal number as one character in the generic comparison (Table 1.4) and phylogenetic analysis.

CHAPTER 2. PHYLOGENY

In this chapter, two cladistic analyses on Podismini are presented using morphological characters. These analyses aim to infer not only phylogenetic relationships of melanopline genera in Japan and adjacent regions, but also evolutionary patterns of several characters and, thus to clarify which characters are congruent with each other in the inferred patterns. Some morphological characters used here could be homoplastic (e.g., chromosome number, tegminal length). However, even questionable characters contain useful phylogenetic information and, therefore, should not be excluded entirely (Poe & Wiens 2000).

2.1. Cladistic analysis among Far East Asian melanopline genera

Litzenberger & Chapco (2001) analyzed phylogenetic relationships among Eurasian and North American Podismini and Melanoplineae by mtDNA sequence data, and suggested monophyly was not rejected for Podismini. Litzenberger & Chapco (2003) analyzed phylogeny again adding more genera and species from species of Melanoplineae in the North and South America, and the result suggests paraphyly of Podismini. Currently, monophyly of Eurasian Podismini is suggested by using mtDNA sequence data (Woller, *et al.* 2014) and by using sequence data from ribosomal nuclear and mitochondrial genes (Chintauan-Marquier *et al.* 2014). These results suggest the current subtribes are not monophyletic, too. Thus, the subdivision of Podismini should be critically revised.

All of the Japanese podismine genera except *Parapodisma*, which are endemic to Japan, Kuril Islands, Sakhalin and Cheju Island, are distributed in the Far Eastern part of the Eurasian Continent, having close relatives in this region. In order to infer relationships among the Japanese genera, analysis should include other genera occurring in this region. For my cladistic analyses I have examined specimens of several species from almost all melanopline genera occurring there.

OTUs

For analyzing generic relationships, I have used 17 species from 13 melanopline genera as OTUs. Almost all melanopline genera of the Far East are covered. Each OTU should have its own character set and not overlap entirely in order to avoid meaningless polyphyletic branchings. When several species of the same genus exhibit the same character sets, I have adopted only 1 species as a representative of the genus. I have selected outgroups from *Melanoplus*, a genus belonging to the other tribe Melanoplini.

Characters used in the analysis

In this analysis, I have used characters mainly discussed in the previous chapter. The 18 characters used are listed in Table 2.1. One is cytological (character 1), 4 from non-genital morphology (characters 2–5), 7 from male genitalia (characters 6–12), and 6 from female genitalia (characters 13–18). These characters were summarized in Table 1.4–6. The characters are coded in Table 2.2. Question mark (?) indicates missing data. All multistate characters were treated as unordered. Evolutionary processes cannot be

Table 2.1. Characters used for generic analysis (all of them are "unorder").

No.	Character	0	1	2
1	Male chromosomal number	2n♂=23	2n♂=21	
2	Size of compound eyes	4-5	6-7	7-10
3	Posterior margin of pronotum	produced	emarginate	
4	Tympanum	normal	small	vestigial
5	a spine of hind knee	absent	present	
6	♂Furculae of 10th abdominal tergite	present	absent	
7	♂Tubercle on epiproct near middle lateral margin	absent or small	spine-like	
8	♂Near apex of epiproct, lateral margin	gradually curved	incised	
9	♂Cerci	compressed apically	strongly compressed apically or wholly	conical
10	♂Oval sclerite neaby epiphallus	present	absent	
11	♂Sheath of aedeagus and dorsal aedeagal valve	covering around basal part of aedeagal valves	partly sclerotized, forming cv	fused with dav and forming cv
12	♂Phallus, ventral aedeagal valves	simple, slender	excurved	membranous apically, usually spatulate
13	♀Subgenital plate, the middle of posterior margin before egg guide	triangularly produced	truncate	
14	♀Subgenital plate, lateral side of posterior margin	not produced	slightly produced	strongly produced
15	♀Ovipositor valves	not incised apically	incised apically	
16	♀Comstock-Kellog organ	present	absent	
17	♀Spermathecal vestibule, aperture	without sclerite	sclerotized	
18	♀Spermathecal vestibule, anterior part	without sclerite	sclerotized	

Table 2.2. Character matrix of 17 species of 12 podismini genera and a melanoplina genus in the Far East. All genera distributed in Japan are included.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Melanoplus frigidus</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>Prumna hayachinensis</i>	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1
<i>Zubovskya koeppenii parvula</i>	1	0	1	2	0	0	0	0	1	1	1	0	0	0	1	0	0	0
<i>Anapodisma miramae</i>	1	1	1	0	0	0	1	0	2	1	0	0	0	1	1	1	0	0
<i>Miramella solitaria</i>	1	0	1	0	0	0	0	0	2	1	0	0	0	0	1	1	0	0
<i>Ognevia longipennis</i>	0	1	0	0	0	0	0	1	2	1	0	0	1	0	0	1	0	0
<i>Podisma sapporensis</i>	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	1	0	0
<i>Podisma kanoi</i>	0	0	1	1	0	0	0	0	2	1	0	0	0	0	0	1	0	0
<i>Niitakacris rosacaenum</i>	1	1	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0
<i>Sinopodisma punctata</i>	1	2	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0
<i>Sinopodisma emeiensis</i>	1	2	1	1	1	1	0	0	1	1	1	1	0	0	0	0	1	0
<i>Tonkinacris ruficerus</i>	?	2	0	0	1	1	0	0	1	1	0	0	0	2	0	0	0	0
<i>Fruhstorferiola okinawaensis</i>	1	2	0	0	1	1	0	0	1	1	1	0	0	2	0	0	0	0
<i>Aopodisma subaptera</i>	1	2	1	1	1	1	0	0	1	1	1	0	0	1	0	0	1	0
<i>Parapodisma mikado</i>	1	2	0	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0
<i>Parapodisma tenryuensis</i>	1	2	0	(01)	1	1	0	0	1	1	1	0	0	1	0	0	1	0
<i>Parapodisma setouchiensis</i>	1	2	0	0	1	1	0	0	1	1	0	1	0	2	0	0	0	0

assumed before analysis, when some evidences do not support evolutionary change and some combinations of states of characters are not impossible. All the characters were parsimony-informative.

Cladistic analysis

Parsimony analysis were conducted using the branch-and-bound search option of PAUP* 4.0b10 PPC (Swofford 2002). All the characters were not weighted. Character distributions and alternative topologies were studied using PAUP*, too.

Result and taxonomic consideration

The analysis has yielded 2 most parsimonious trees (Length=44, CI=0.545, RI=0.733). These trees were summarized by strict consensus method (Fig. 2.1). The resulted consensus tree indicates the certainty of holophyly of 2 genus groups. The 1st genus group (Group I) is composed of *Zubovskya*, *Anapodisma*, *Miramella*, *Ognevia* and *Podisma*, and the other group (Group II) comprises *Niitakacris*, *Sinopodisma*, *Tonkinacris*, *Fruhstorferiola*, *Aopodisma* and *Parapodisma*. This result is congruent with a cladogram based on mtDNA sequence data (Litzenberger & Chapco 2001, 2003) and/or another cladogram based on fragments of four genes (Chintauan-Marquier *et al.*, 2014) at the following points: (1) *Zubovskya*, *Anapodisma*, *Miramella*, *Ognevia* and *Podisma* are included in the same clade. However, no synapomorphies support this clade in this study. (2) The clade uniting *Podisma* and *Ognevia* is supported. The clade is supported by a synapomorphy of reversal in the character 1. (3) The topology (*Zubovskya* (*Miramella* (*Ognevia* + *Podisma*))) is the same. However, *Anapodisma* is a sister group of *Miramella* in my result, while it is an outgroup of the clade in the cladogram by mtDNA data. In both the cases, the topology suggests that the chromosome number changed twice in the manner 23 → 21 → 23. (4) *Melanoplus* is an outgroup of podismini genera.

The most conspicuous difference between the consensus tree by morphology and that of mtDNA is the position of *Prumna*. This genus occupied the basal position with *Melanoplus* in my result, but in the mtDNA tree it is a sister group of Group I and *Parapodisma* occupies a more basal position. In this analysis, an important character of the male subgenital plate was not used, because it was not parsimony-informative. The genus *Prumna* is well defined by an autapomorphy that the posterior part of the male subgenital plate is truncate and expanded. Moreover, *Prumna* is distinguished from the other Podismini by the combination of the following characteristics: Male subgenital plate truncate and expanded (autapomorphy); male without a pair of sclerites nearby epiphallus; posterior margin of the female subgenital plate truncate. Identity of the tribe Prumnini Rehn & Randell, 1963 maybe supported by these characters. In order to clarify its phylogenetic position in the subfamily, it is needed to examine members of not only Prumnini and Podismini but also of major tribes belonging Melanoplineae. In this paper I tentatively treat this genus as a member of Podismini.

Paraphyly is suggested for *Parapodisma*, if the genus *Aopodisma* is regarded as a distinct genus. However, *Aopodisma* has no significant differences from *Parapodisma* as will be discussed in Chapter 3.

The available information is still insufficient for revising the tribes and subtribes. I, therefore, make a tentative subtribal division in Table 2.3. Miramellina are paraphyletic

Table. 2.3. Summary of taxonomic affiliations for genera of Podismini in Far East Asia and *Melanoplus*. Subtribal affiliations are in parentheses. Subtribes in "[]" are inferred by chromosome number.

Genus	Rehn & Randell (1963)		Vickery (1977)	Otte (1995)	This study
<i>Melanoplus</i>	Melanoplini		-	Melanoplinae	Melanoplini
<i>Prumna</i>	Podismini	Primnoae	-	Podisminae: All were assigned to Podismini and these were not assigned to any subdivisions.	Podismini
<i>Zubovskya</i>		Podismae	Miramellina		Podismini (Miramellina)
<i>Anapodisma</i>		-	-		
<i>Miramella</i>		Miramellae	Miramellina		Podismini (Podismina)
<i>Ognevia</i>		Podismae	-		
<i>Podisma</i>		Podismae and Miramellae mixed ⁽¹⁾	Podismina		Podismini (subtribe?)
<i>Nitakacris</i>		Podismae	Miramellina		Podismini (Tonkinacridina)
<i>Sinopodisma</i>		Miramellae	-		
<i>Tonkinacris</i>		-	-		
<i>Fruhstorferiola</i>		-	Miramellina		
<i>Parapodisma</i>		- ⁽¹⁾			

(1) Examined "*Parapodisma sapporensis* (Shiraki, 1910)" (= *Podisma sapporensis*) for an exemplar of the genus *Parapodisma* and regarded it as a member of Miramellae, while *Podisma pedestris* was assigned to Podismae.

Table 2.4. Indices of characters used in the cladistic analyses, calculated on the tree shown in Fig. 2.1. Characters bold-faced are RC=1.0.

No.	Character	Steps	CI	RI	RC
1	Male chromosomal number	2	0.50	0.75	0.38
2	Size of compound eyes	4	0.50	0.71	0.36
3	Posterior margin of pronotum	4	0.25	0.50	0.13
4	Tympanum	4	0.50	0.00	0.00
5	a spine of hind knee	1	1.00	1.00	1.00
6	♂Furculae of 10th abdominal tergite	1	1.00	1.00	1.00
7	♂Tubercle on epiproct near middle lateral margin	3	0.33	0.00	0.00
8	♂Near apex of epiproct, lateral margin	2	0.50	0.00	0.00
9	♂Cerci	2	1.00	1.00	1.00
10	♂Oval sclerite neaby epiphallus	1	1.00	1.00	1.00
11	♂Sheath of aedeagus and dorsal aedeagal valve	3	0.67	0.86	0.57
12	♂Phallus, ventral aedeagal valves	3	0.67	0.80	0.53
13	♀ Subgenital plate, the middle of posterior margin before egg guide	2	0.50	0.00	0.00
14	♀ Subgenital plate, lateral side of posterior margin	5	0.40	0.40	0.16
15	♀ Ovipositor valves	2	0.50	0.50	0.25
16	♀ Comstock-Kellog organ	1	1.00	1.00	1.00
17	♀ Spermathecal vestibule, aperture	2	0.50	0.80	0.40
18	♀ Spermathecal vestibule, anterior part	2	0.50	0.75	0.38

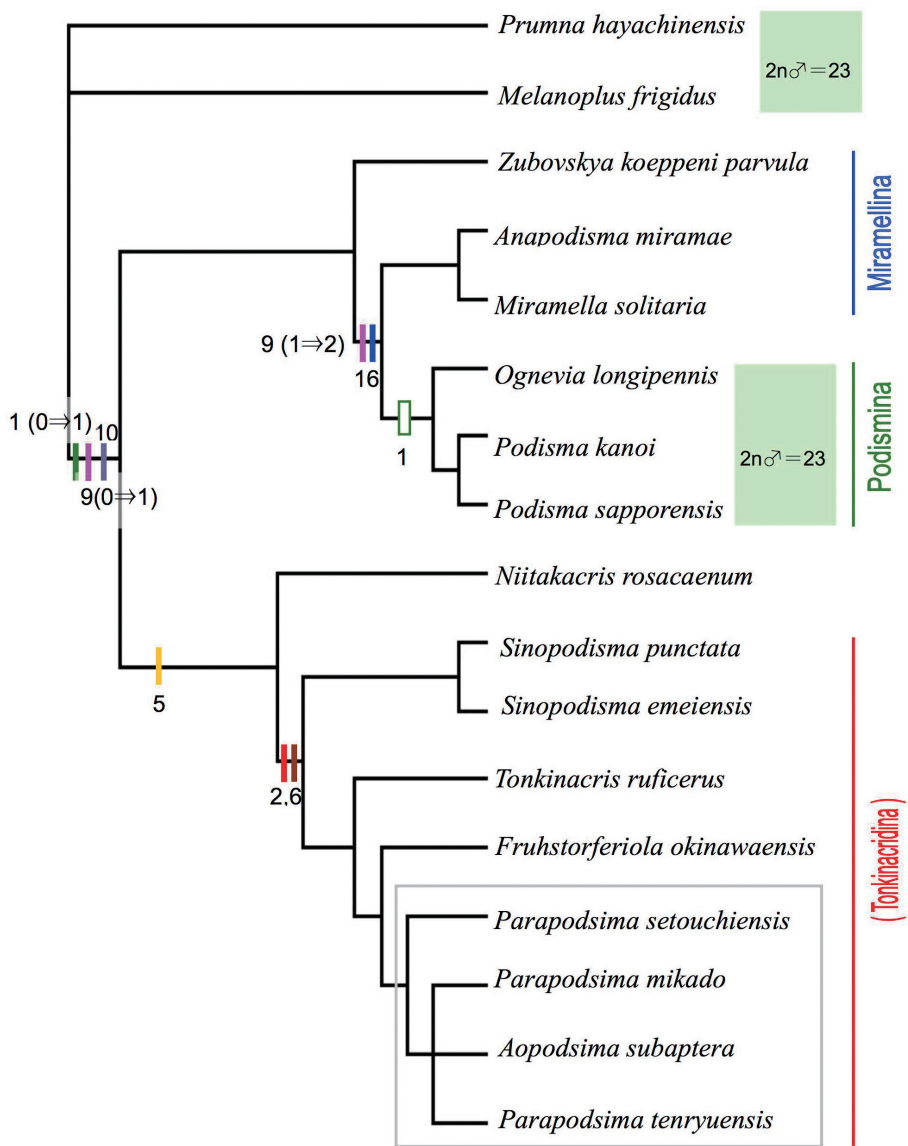


Fig. 2.1. Strict consensus tree of two most parsimonious cladograms of 17 podismini species of 13 genera using 18 characters. Characters of interest mapped. Hashmarks and numbers indicate possible character modifications; filled indicates transformation to the modified state, unfilled indicate reversal.

group comprising *Miramella*, *Zubovskya* and *Anapodisma* among the genera of Group I and excluding Podismina (*Ognevia* and *Podisma*), which are included in that group. A new subtribe Tonkinacridina can be created for the holophyletic group (*Sinopodisma* (*Tonkinacris* (*Fruhstorferiola* (*Parapodisma*+*Aopodisma*))))), all these genera sharing 2 autapomorphies, the large compound eyes (character number 2-code number 2) and the absence of the male furculae on the 10th abdominal tergite (6-1). The position of *Niitakacris* is still unknown. The genus was put into “Podismae” but thought to be atypical one by Rehn & Randell (1963). Morphology of this genus was not well studied in this study, requiring further examinations.

Evaluation of morphological characters

In order to evaluate morphological characters as phylogenetic indicators, rescaled consistency index (RC) was adopted. RC is a product of the consistency index (CI) and the retention index (RI) of a character (Farris 1989). RC=1.0 in characters 5, 6, 9, 10, 16 sharply contrasts with RC=0.0 (CI=0.0 and/or RI=0.0) in characters 4, 7, 8, 13 (Table 2.4). This significant difference of informativeness among characters indicates that evolutionary pattern varies among characters used in this analysis.

2.2. Cladistic analysis among *Parapodisma* species

The genus *Parapodisma* is currently comprised of 14 species. These species are endemic to Japan except *P. mikado*, which is distributed in Japan and Russia (Sakhalin and Kunashiri Island), *P. setouchiensis*, which occurs in Japan and Korea (Cheju Island) and *P. astris*, which is distributed in Yunnan Province, China and is thought to belong to another genus (see Chapter 3). Some species of *Parapodisma* show a large geographic variation in morphology, and the taxonomic status of these species has not been stable. For example, *P. setouchiensis* comprises 4 forms, which were once treated as distinct species but are now considered to be geographical races (Kawakami, 1999), Ichikawa (2006) treated 3 forms as a distinct species, but in this paper I agree with Kawakami (1999) as shown in Chapter 3. This species is variable in the angle of the cercus and the length of the triangular marking of the subgenital plate but its three forms vary in clines (Kawakami, 1999), resulting in difficulty in dividing into discrete forms. The relatively wide distribution range of the species also contributes to the difficulty: it is distributed in most parts of Honshû, Shikoku, Kyûshû, outlying islands around Honshû, Shikoku, and Kyûshû, Japan, and Cheju Island, Korea.

In this genus, male genital characters of the cerci, epiphallus and aedeagal valves are highly diversified and have been used for species diagnosis. Females of this genus have been identified only by appearance or few external characters such as the tegminal length in addition to locality data, since the females of some species are at a glance very similar to each other. As discussed in the preceding chapter, the female internal genitalia are largely different among podismini species, especially of the genus *Parapodisma*, and thus are useful for species identification. In this section, I present a phylogenetic analysis of *Parapodisma* species using morphological characters and investigate evolutionary patterns of some characters.

OTUs and character coding

All the *Parapodisma* species were used for the cladistic analysis. Each geographical form of *P. setouchiensis* was treated as an OTU in this analysis. On the contrary, *P. tanzawaensis* was included in *P. tenryuensis* and *P. hiurai* in *P. niihamensis*, because no differences were found among the character sets of these species pairs. *Aopodisma subaptera* was included into the ingroup. Tominaga & Uchida (2001) erected *Aopodisma* as a division of *Parapodisma* on the basis of only the ratios of a few body parts and the length of the tegmina and wings. *Fruhstorferiola okinawaensis*, *Sinopodisma punctata*, *Tonkinacris ruficerus*, species of genera considerably closely related to *Parapodisma*, were also included in the analysis. Male characters (Characters 3–12, 21, 23), female characters (Characters 13–18, 20) and non-genital characters (Characters 1–2, 19, 22) were coded (Table 2.5). Some multistate characters were treated as ordered, and the other multistate characters as unordered (see Table 2.5). The ordered characters are quantitative and seem to change gradually, on the other hand the unordered characters are qualitative and their transformation patterns are not known. The characters are coded in Table 2.6.

Cladistic analysis

Parsimony analysis and studies of character distributions and alternative topologies were conducted by the same method as in the former section. *Sinopodisma punctata* was set to an outgroup, because it occupied the most basal position in the previous analysis (see Fig. 2.1) among the genera used here.

Results

The analysis obtained 3 most parsimonious trees (Tree length=70, CI=0.529, RI=0.612). These trees were summarized in a strict consensus tree (Fig. 2.2). The topology indicates *Parapodisma* is a paraphyletic group. *P. setouchiensis* is situated outside the main cluster of *Parapodisma* and is more closely aligned with *F. okinawaensis* and *T. ruficerus*. Their affiliation is supported by autapomorphies, the presence of lateral projections on the posterior margin of the female subgenital plate (13-2) and the absence of sclerite in the spermathecal vestibule (18-1). *P. setouchiensis* shares an autapomorphy with *Tonkinacris*, having the male dorsal aedeagal sclerite concealed by the valves of the cingulum (10-1). It is further characterized by two apomorphies: the male valves of the cingulum are fused with the aedeagal valves (8-1) and the male ventral aedeagal valves are thin and membranous (12-2).

A. subaptera, *P. tenryuensis* and *P. caelestis* form a holophyletic group which is supported by the possession of small tympanal organs (2-1). *P. etsukoana* and *P. subastris* form another holophyletic group, which is supported by the male valves of the cingulum strongly sclerotized (9-2) and the spermathecal vestibule very large and shaped like a glove (17-3). The clade ((*subaptera*, *tenryuensis* and *caelestis*)(*etsukoana* and *subastris*)) (*niihamensis*, *hiurai* and *yasumatsui*)) is supported only by a symplesiomorphy, the male valves of the cingulum being slightly sclerotized (9-1). *P. mikado*, *P. dairisama* and *P. awagatakensis* form a holophyletic group, which is supported by the ventral aedeagal valves membranous, widened and thick apically (12-1).

Table 2.5. Characters for cladistic analysis of *Parapodisma*

No.	Character	0	1	2	3	Type
1	Tegminal length	vestigial	oval	oblong		o
2	Tympanal organ	medium	small			
3	Male subgenital plate, distal subsegment	short	medium	projected		o
4	Male subgenital plate, anterior projection on hind margin	absent	present			
5	Male cerci	slightly curved	strongly bent			
6	Male lophus, width	medium	narrow			
7	Male lophus, thickness	moderate-thick	thin			
8	Male valves of cingulum	lobiform	fused with aedeagal valves			
9	Male cv, degree of sclerotized	membranous	slightly sclerotized	strongly sclerotized		o
10	Male dorsal aedeagal sclerite, apex	exposed from cv	concealed by cv			
11	Male dorsal aedeagal sclerite, apex	truncate	acute apically	extending laterally		u
12	Male ventral aedeagal valves	lamellate	thick, membranous	thin, membranous		u
13	Female subgenital plate, posterior margin	gradually curved	lateral part angulate or slightly projected	distinctly projected		o
14	Preapical diverticulum of spermatheca, shape	slender	robust, basal part less than 1/3 width of apical part	robust, basal part thick		o
15	Preapical diverticulum of spermatheca, second diverticulum	absent	present			
16	Preapical diverticulum of spermatheca, length compared to apical one	distinctly shorter	about same	longer		o
17	Spermathecal vestibule (Sv), shape	simply oblong	small, rounded	elongated, simple shaped	large, glove-like	u
18	sclerite in Sv (ssv)	present	absent			
19	Lateral black stripe	narrow	moderate	broad		o
20	Pronotal color (female)	green	red (deep red, pink, orange), dorsally	red, wholly		o
21	Lateral black stripe in abdomen (male)	1st - 3rd tergite	4th - 5th tergite	near tip		o
22	Hind femora, color in ventral part	pale yellowish green	red			
23	Male subgenital plate, distal subsegment, black color	absent	lateral margin	whole part		o

Type of multistate characters. o: ordered; u: unordered;

Table 2.6. Character matrix of *Parapodisma* species and allies.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Sinopodisma punctata</i>	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Tonkinacris ruficrus</i>	1	0	1	0	0	0	0	0	0	1	2	0	2	0	0	0	1	1	1	(12)	0	0	0
<i>Fruhstorferiola okinawaensis</i>	2	0	1	1	0	0	0	0	0	0	2	0	2	1	1	1	0	1	1	(12)	0	0	1
<i>Aopodisma subaptera</i>	0	1	1	0	0	0	0	0	1	0	0	0	0	2	0	2	1	0	1	0	2	0	0
<i>Parapodisma mikado</i>	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	1	0	0	(01)	(12)
<i>dairisama</i>	1	0	1	0	1	0	1	0	0	0	2	1	1	1	0	2	0	0	1	0	0	1	1
<i>awagatakensis</i>	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	1	1	0
<i>etsukoana</i>	1	0	1	1	0	0	0	2	0	1	0	1	1	1	0	3	0	0	(01)	(12)	1	1	1
<i>subastris</i>	1	0	0	0	0	1	0	0	2	0	1	0	1	1	1	0	3	0	0	0	0	1	1
<i>niihamensis</i>	2	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	1
<i>yasumatsui</i>	1	0	2	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	(01)	0	1	1
<i>tenryuensis</i>	1	(01)	(01)	0	0	0	(01)	0	1	0	1	0	1	1	(01)	(12)	0	0	(12)	(012)	(12)	1	(12)
<i>caelestis</i>	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	2	0	0	2	0	2	1	2
<i>setouchiensis</i> (Basic-form)	(12)	0	(12)	1	0	0	(01)	1	0	1	0	2	2	0	1	0	2	1	0	0	0	(01)	1
<i>setouchiensis</i> (Tanba-form)	1	0	(01)	0	1	0	0	1	0	1	0	2	2	0	1	0	2	1	0	0	0	1	1
<i>setouchiensis</i> (Hyonosen-form)	(12)	0	(01)	1	(01)	0	0	1	0	1	0	2	2	0	1	0	2	1	0	0	0	1	1

Evaluation of morphological characters

RC is 1.0 in characters 2, 7–10, 12, 18 (Table 2.7). As shown in the preceding chapter, the transformation pattern of the tympanal organs is not correlated with those of presumably highly plastic parts such as the tegmina, wings and pronotal structures. However, I do not conclude that the development of the tympanal organs is a good phylogenetic character. In some species of *Sinopodisma* the tympanal organ is abbreviated, and this seems to be correlated with the tegminal abbreviation. As shown by many previous studies, the male phallic complex provides useful characters for inferring phylogeny.

Taxonomic consideration and evolutionary pattern

P. setouchiensis is peculiar among Podismini in the structure of the aedeagal valves, and occupies a position isolated from the other *Parapodisma* species in the cladogram. Although the genus *Parapodisma* may be a heterogeneous group, I will treat *P. setouchiensis* as a member of this genus at this time. Above all, *Parapodisma* is still not well defined.

Several subgroups in *Parapodisma* could be well defined. As mentioned by Tominaga (1983) and Kanô (1985), *P. niihamensis*, *P. hiurai* and *P. yasumatsui* are very closely related to each other. Among them, the shape and chitinized pattern of the female spermathecal vestibule are only slightly different the variations overlapping each other, and the structure and shape of the male aedeagal valves are also almost the same. However, the shape of the male cerci and the lophi of the epiphallus are specifically different. These are good characters, but unfortunately I could not evaluate them for cladistic analysis. Tominaga (1983) and Kanô (1985) inferred that *P. subastris* and *P. tenryuensis* should form a holophyletic group with the three species mentioned above. The consensus cladogram strongly supports their opinion when *A. subaptera*, *P. caelestis* and *P. etsukoana* are also included. The latter 2 of these species were described after 1986. Therefore, it is natural that these two were neglected by them. *A. subaptera* has been thought to occupy a more basal position. However, it is very similar to this species

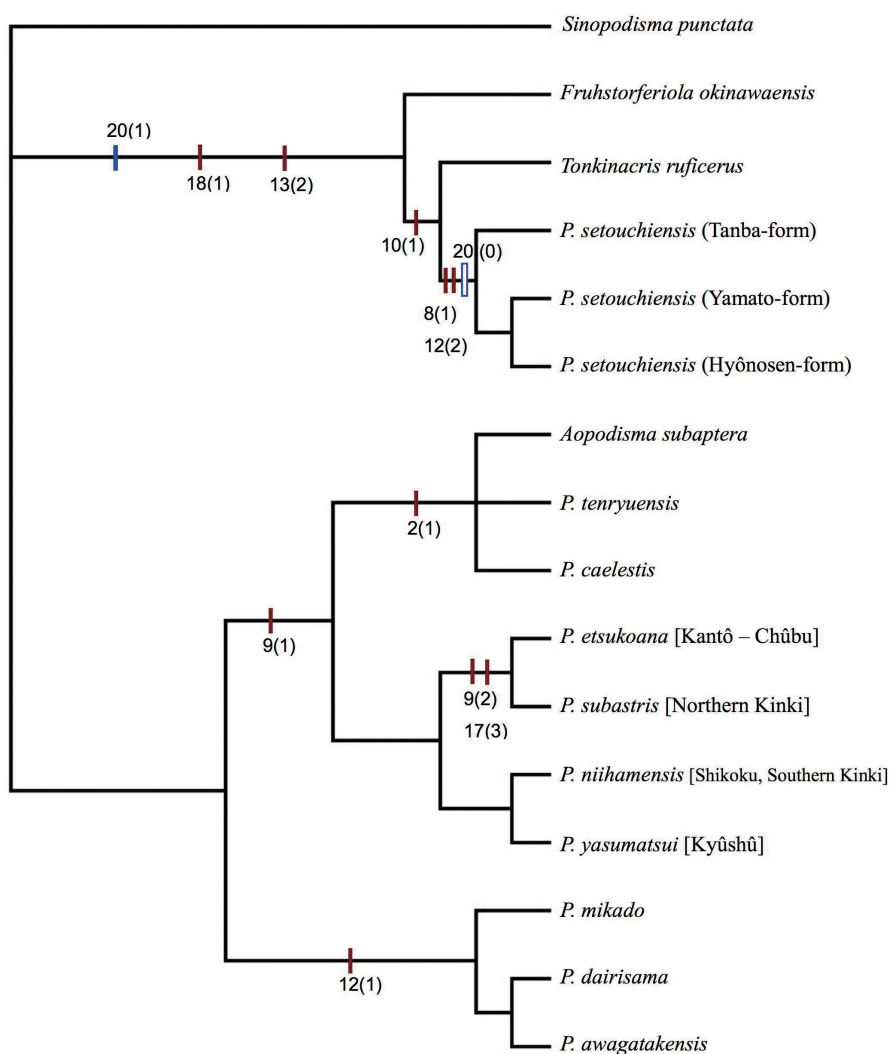


Fig. 2.2. Strict consensus tree of three most parsimonious cladograms of species of *Parapodisma* and allied genera using 23 morphological characters. The numbers under branches are numbers of characters and states which support the holophyly of the branch. “[]” show approximate distribution areas. Characters of interest mapped and their transformations are above branches.

group in the male genital structure. I will move this species to *Parapodisma* in the next chapter.

P. subastris is most closely related to *P. etsukoana*. The clade consisting of these two species with large genitalia is strongly supported as explained above. On the basis of the consensus cladogram, evolutionary changes in the male and female genitalia are inferred. At first the male valves of the cingulum (Cv) became slightly chitinized (9: 01). Then, the male and female genitalia were synchronically expanded and the male Cv became chitinized more strongly (9: 12). This is a mere story without enough evidence, but is

Table 2.7. Indices of characters used in the cladistic analyses, calculated on the tree shown in Fig. 2.2. Characters bold-faced are RC=1.0.

No.	Character	Steps	CI	RI	RC
1	Tegminal length	4	0.75	0.00	0.00
2	Tympanal organ development	1	1.00	1.00	1.00
3	Male subgenital plate, degree of projection of distal subsegment	5	0.40	0.00	0.00
4	Male subgenital plate, presence of anterior projection on hind margin	4	0.25	0.25	0.06
5	Male cerci, degree of bent	2	0.50	0.50	0.25
6	Male lophus, width	2	0.50	0.00	0.00
7	Male lophus, thickness	1	1.00	1.00	1.00
8	Male valves of cingulum (cv), shape and structure	1	1.00	1.00	1.00
9	Male cv, degree of sclerotized	2	1.00	1.00	1.00
10	Male dorsal aedeagal sclerite, relation with cv	1	1.00	1.00	1.00
11	Male dorsal aedeagal sclerite, shape of apex	6	0.33	0.43	0.14
12	Male ventral aedeagal valves, structure	2	1.00	1.00	1.00
13	Female subgenital plate, shape of posterior margin	4	0.50	0.67	0.33
14	Preapical diverticulum of spermatheca, shape	3	0.67	0.75	0.50
15	Preapical diverticulum of spermatheca, presence of second diverticulum	4	0.25	0.40	0.10
16	Preapical diverticulum of spermatheca, length compared to apical one	4	0.50	0.71	0.36
17	Spermathecal vestibule (Sv), shape	5	0.60	0.60	0.36
18	Presence/absence of sclerite in Sv	1	1.00	1.00	1.00
19	Lateral black stripe, width	4	0.50	0.60	0.30
20	Pronotal color (female)	2	0.50	0.00	0.00
21	Lateral black stripe in abdomen, length (male)	4	0.50	0.60	0.30
22	Hind femora, color in ventral part	3	0.33	0.33	0.11
23	Male subgenital plate, distal subsegment, degree of black color	5	0.40	0.00	0.00

interesting in view of sexual selection, particularly sexual conflict. In many podismini, individuals copulate many times, and the male assaults on the female, often copulating by force. In *Podisma sapporensis*, multiple mating makes the female decrease fecundity (Ito, 1997). During copulation, the apical portion of the male aedeagal valves is inserted into the female spermathecal vestibule. Sexual conflict may have been a promoter in the evolution of these genital parts.

Phylogeography

The holophyletic group consisting of *P. etsukoana*, *P. subastris*, *P. hiurai*, *P. niihamensis* and *P. yasumatsui* seems to have evolved allopatrically. Their distribution areas are discrete or nearly so, but overlapping between *P. etsukoana* and *P. subastris* overlapping between *P. etsukoana* and *P. subastris* (Fig. 3.24).

CHAPTER 3. TAXONOMY OF JAPANESE PODISMINI

In this chapter, taxonomic descriptions of 22 species of 9 genera in Japan (Table 3.1) are presented. These descriptions are based on the adult specimens, but in the species for which nymph specimens have been available nymphal characters are also described. The specimen used in this study are listed in Online Appendix (<http://eprints.lib.hokudai.ac.jp/journals/index.php?jname=188>). I have adopted the tabulated description method (Cohn 1994) for all measurements (Table 3.2) and several key characters of *Parapodisma* (Tables 3.3–3.6) in order to describe concisely and to substitute for an identification key. Distribution data are mainly from the examined specimens, and also from the original descriptions, Bey-Bienko (1951), Yasuda (1989), Nagashima (1994) and Ichikawa *et al.* (2006). Terminology of the female genitalia was revised as already mentioned. The following abbreviations for measurements, used in Akimoto *et al.* (1993), are also adopted here—BL: body length; HW: head width; PL: pronotal length; HFL: hind femoral length. Four new abbreviations are adopted here—P/M: ratio of prozonal length to metazonal length which is measured along the median carina; TL: tegminal length. TL values are classified and scored except for two long-winged species, *Fruhstorferiola okinawaensis* and *Ognevia longipennis*, the score increasing by each half tergite length from the posterior margin of the mesonotum (See Fig. 1.12); HW/IS: ratio of head width to width of inter-ocular space, for evaluating size of compound eyes (See Fig. 1.6); LSW/PH: ratio of the maximum width (except on the transverse sulci) to the approximate height of the pronotum, which indicates relative width of lateral black stripes on pronotum (See Fig. 1.44).

Description

Tribe Podismini Jacobson, 1905

Podismini Jacobson, 1905, in Jacobson & Bianki, 1905: 173. Type genus: *Podisma* Berthold, 1827.

Parapodisminae Inoue, 1985: 149. Type genus: *Parapodisma* Mistshenko, 1947. Synonymized by Storozhenko, 1993a: 1.

General morphology. Head slightly oblique; fastigium inclined, slightly depressed; fastigial foveolae absent; frontal carinae distinct, parallel or subparallel; frontal costa slightly or strongly depressed, but sometimes flat; compound eyes large, oval. Antennae filiform, usually composed of 22–25 segments. Prosternal process conical, extended just below or slightly inclined backward; apex acute or obtuse. Mesosternal lobe rounded or obtuse-angled. Pronotum cylindrical or subcylindrical, generally without lateral carinae, with three transverse sulci, of which usually the posterior one is the most distinct; anterior margin sometimes faintly emarginate medially; median longitudinal carina generally present, sometimes distinct only on metazona. Tegmina and wings mostly abbreviated, sometimes apterous. Hind wings, if present, hyalines. Hind femora smooth on dorsal surface; posterior margin of lower genicular lobe not spined. Hind tibiae with 8–12 (mostly 9–11) marginal spines on each of inner and outer sides, without outer apical spine; a small yellow band present near the base. Pronotum cylindrical or subcylindrical; lateral carinae absent or weakly developed. Meso- and metanotum highly

Table 3.1. Podismini species in Japan.

Genus <i>Prumna</i> Motschulsky, 1859 (25)
<i>P. fauriei</i> (Bolívar, 1890) comb. nov.
Genus <i>Zubovskya</i> Dovnar-Zapolsky, 1932 (9)
<i>Z. koeppleri parvula</i> (Ikonnikov, 1911)
Genus <i>Anapodisma</i> Dovnar-Zapolsky, 1933 (4)
<i>A. miramae</i> Dovnar-Zapolskii, 1933
Genus <i>Ognevia</i> Ikonnikov, 1911 (3)
<i>O. longipennis</i> Shiraki, 1910
Genus <i>Podisma</i> Berthold, 1827 (19)
<i>P. sapporensis</i> Shiraki, 1910
<i>P. kanoi</i> Storozhenko, 1993
Genus <i>Sinopodisma</i> Chang, 1940 (53)
<i>S. punctata</i> Mistshenko, 1954
<i>S. aurata</i> Ito, 1999
Genus <i>Tonkinacris</i> Carl, 1916 (6)
<i>T. ruficrus</i> Ito, 1999
<i>T. yaeyamaensis</i> Ito, 1999
Genus <i>Fruhstorferiola</i> Willemse, 1921 (13)
<i>F. okinawaensis</i> Shiraki, 1930
Genus <i>Parapodisma</i> Mistshenko, 1947 (11)
<i>P. mikado</i> (Bolívar, 1890)
<i>P. dairisama</i> (Scudder, 1897)
<i>P. awagataensis</i> Ishikawa, 1998
<i>P. etsukoana</i> Kobayashi, 1986
<i>P. subastris</i> Huang, 1983
<i>P. niihamensis</i> Inoue, 1979
<i>P. niihamensis niihamensis</i> Inoue, 1979
<i>P. niihamensis hiurai</i> Tominaga & Kanô,
<i>P. yasumatsui</i> Yamasaki, 1980
<i>P. tenryuensis</i> Kobayashi, 1983
<i>P. caelestis</i> Tominaga & Ishikawa, 2001
<i>P. takeii</i> (Takei, 1914) comb. nov.
<i>P. setouchiensis</i> Inoue, 1979

Number in parentheses after each generic name is the number of valid species in the each genus in the world.

Table 3.2. Measurements (in mm) of podismine species in Japan.

Species	BL		HW		P/M		PL		TL (1)	HFL	
	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀
<i>Prumna hayachinensis</i>	19.9-23.8	21.6-32.4	3.2-4.0	4.0-4.3	1.6-2.0	1.5-2.0	4.6-5.4	5.6-5.9	3-5	12.9-15.4	15.2-16.3
<i>Zubovskya koeppenii parvula</i>	15.4-17.9	18.6-21.1	2.7-3.0	3.1-3.4	1.9-2.3	2.0-2.3	2.9-3.2	3.2-3.9	0	8.9-9.4	9.4-11.0
<i>Anapodisma miramae</i>	18.7-19.9	24.8-27.1	2.1-2.2	2.3-2.4	2.1-2.5	1.9-2.0	2.7-2.8	3.5	3	10.2-11.6	12.9-13.7
<i>Ognevia longipennis</i>	20.2-24.9	26.9-31.5	3.6-3.8	4.0-4.6	1.0-1.1	0.8-1.0	4.6-4.8	5.4-6.8	♂, 19.9-20.6; ♀, 24.2-28.6	11.3-12.9	13.8-16.2
<i>Podisma sapporensis</i>	15.2-20.7	18.9-27.2	2.8-3.4	3.2-4.1	1.5-1.8	1.2-1.5	3.3-4.4	4.4-6.8	0-6	8.9-11.4	10.8-16.0
<i>Podisma kanoi</i>	15.7-20.0	22.0-26.6	1.9-3.4	3.6-3.9	1.5-1.7	1.4-1.8	3.4-4.1	4.6-5.4	0	9.2-11.3	12.1-14.1
<i>Sinopodisma punctata</i>	20.0-26.9	31.9-35.5	4.6-4.8	5.3-5.7	1.5	1.3-1.6	5.6-5.9	6.5-7.7	5-6	14.0-15.2	16.7-18.7
<i>Sinopodisma aurata</i>	24.5-30.0	33.5-36.5	4.7-5.4	5.9-6.2	1.5-1.8	1.5-1.7	5.7-6.9	7.5-8.4	3-5	13.5-16.0	17.9-19.5
<i>Tonkinacris ruficervus</i>	21.0-24.0	32.5-38.5	4.3-4.6	5.6-6.1	1.3-1.6	1.1-1.3	4.3-5.1	7.0-8.1	4-5	10.3-12.1	15.9-17.5
<i>Tonkinacris yaeyamaensis</i>	26.5	35.0-37.5	4.9	5.8-5.9	1.2	1.3	6.3-6.5	8.3-8.7	5	12.4-14.1	17.0-18.1
<i>Fruhstorferiola okinawaensis</i>	26.2-32.8	31.3-44.8	4.7-5.4	5.5-6.5	1.2-1.4	1.1-1.3	5.6-7.3	8.0-9.2	♂, 10.3-18.1; ♀, 15.6-23.9	14.3-17.3	18.3-21.0
<i>Parapodisma mikado</i>	20.1-26.0	25.5-38.7	3.5-4.3	4.1-5.3	1.3-1.5	1.2-1.6	5.0-6.0	6.0-9.8	3-5	11.0-13.3	13.2-19.0
<i>P. dairisama</i>	18.6-23.8	27.7-28.3	3.6-4.3	4.3-5.0	1.4-1.7	1.4-1.6	4.6-5.1	5.8-7.1	3-4	10.5-12.2	13.0-15.6
<i>P. awagatakensis</i>	21.8-21.9	31.2	4.1-4.4	4.8-4.9	1.4	1.3-1.5	4.8-5.5	5.8-6.4	3-4	11.3-13.0	13.5-15.1
<i>P. etsukoana</i>	20.0-24.8	27.0-32.2	4.0-4.7	4.5-5.1	1.4-1.6	1.2-1.5	4.4-5.4	5.9-7.3	4-6	11.3-14.1	14.4-16.8
<i>P. subastris</i>	23.5-27.8	28.5-32.7	4.3-5.0	4.6-5.6	1.2-1.6	1.2-1.5	5.0-6.4	6.6-8.0	5-7	12.1-15.4	15.2-17.3
<i>P. nilhamensis nilhamensis</i>	24.9-25.8	27.3-32.2	4.2-4.8	4.9-5.4	1.2-1.3	1.3-1.4	5.1-5.6	6.0-6.8	11-16	12.9-14.1	15.6-17.0
<i>P. nilhamensis hiurai</i>	23.8-27.5	26.8-35.4	4.2-4.9	4.6-5.6	1.3-1.5	1.1-1.4	4.7-5.5	5.6-7.4	9-13	12.4-14.6	14.1-18.9
<i>P. yasumatsui</i>	21.2-21.8	29.4-30.7	3.9-4.3	4.8-5.2	1.3-1.7	1.3-1.4	4.3-4.7	5.8-6.6	5-7	11.3-12.4	14.6-16.7
<i>P. tenryuensis</i>	21.3-28.7	26.9-34.8	4.0-4.7	4.6-5.7	1.4-1.6	1.2-1.5	4.6-5.8	5.8-7.5	4-6	11.7-14.6	14.6-19.0
<i>P. caelestis</i>	22.0-25.2	25.0-30.2	3.5-3.8	3.9-4.1	1.3-1.5	1.2-1.3	4.4-5.4	5.4-6.1	3-4	11.3-12.2	12.1-14.0
<i>P. takeii</i>	17.8-23.0	22.8-27.5	3.4-4.0	3.8-4.3	1.5-1.9	1.5-1.9	3.5-4.8	4.7-5.9	1-2	9.5-11.9	11.9-14.6
<i>P. setouchiensis</i>	19.5-29.2	27.0-42.7	3.9-5.1	4.8-6.1	1.3-1.5	1.3-1.5	4.7-6.8	6.6-9.3	5-11	11.1-15.7	14.6-20.2

(1) TL in *Fruhstorferiola okinawaensis* and *Ognevia longipennis*: measurements of the length from the base to the tip (in mm).

TL in the other species: scores for the tegmen length (Fig. 1.12).

variable in correlation with length of tegmina and wings. Tympanal organs usually present, sometimes abbreviated or absent. Abdomen with a fine median carina.

♂. Fore and mid femora slightly expanded. 10th abdominal tergite divided, with or without furculae. Subgenital plate bow-shaped (except for *Prumna*, in which the subgenital plate is abruptly truncate and broadened). Epiproct triangular or pentagonal; median furrow present. Paraprocts with lateral margin slightly swollen. Epiphallus bridged and not divided; ancorae incurved; lophi lobiform with one or two apices, smooth, without tubercle. Ectophallic membrane with a pair of weakly sclerotized areas between epiphallus and phallus. Sheath of aedeagus covering aedeagal sclerites wholly or partly, sometimes elongated and/or sclerotized, forming aedeagal valves.

♀. Epiproct triangular, smooth; median furrow present only on basal half and very shallow, or obscured. Cerci conical, or conical in profile and compressed. Spermathecal vestibule usually dilated, variable in shape, often with sclerotized valve on aperture, sometimes with sclerite internally. Spermatheca with a developed and arcuate preapical diverticulum and one or more apical diverticula; apical diverticulum often elongate, longer than preapical diverticulum.

Remarks. The tribe Podismini still has not been well defined. However, I have prepared the above description from my observations on the species examined (See Materials and Methods). This description is given for avoiding duplicate statements of characters in the descriptions of the genera and species.

Geus *Prumna* Motschulsky, 1859

Primnoa Fischer-Waldheim, 1846: 248, preoccupied by Lamouroux (1812: 188) for a coral genus. Synonymy after Uvarov, 1940: 116. Type species: *Podisma primnoa* Motschulsky in Fischer-Waldheim, 1846: 248.

Prumna Motschulsky, 1859: 11. Type species: *Podisma viridis* Fischer-Waldheim, 1846 by monotypy, a junior synonym of *Primnoa primnoa* Fischer-Waldheim, 1846 (Mistshenko, 1951). Revived by Ito, 2003: 51.

Podisma (Eupodisma) Scudder, 1897a: 200, 205. Type species: *Podisma primnoa* Motschulsky in Fischer-Waldheim, 1846: 248. Synonymized by Mistshenko, 1951: 219[232].

General morphology. Head with frontal carinae parallel or subparallel (Fig. 1.4). Compound eyes relatively small (HW/IS=5). Pronotum relatively small, emarginate posteriorly. Tegmina small and narrow, oblanceolate or narrowly spatulate (Fig. 1.15C), sometimes vestigial (Fig. 1.15D, E). Hind wings absent. Metanotum smooth or with weak scutal grooves and pits. Hind legs slender and long; hind genicular hood without a spine. Abdomen elongate. Tympanal organs present, large (Fig. 1.15A, B) or moderate in size (Fig. 1.15D–E).

♂. 10th abdominal tergite with a pair of furculae. Subgenital plate expanded; posterior margin truncate. Cerci partly or wholly compressed. Epiproct flat, with a pair of tubercles near apex. Beside epiphallus no oval sclerite present. Epiphallus with lateral margins subparallel; ancorae projecting anteriorly; posterior margins of lophi situated with a right angle. Sheath surrounding and fused with dorsal aedeagal sclerite, forming dorsal aedeagal valve. Apical part of ventral aedeagal valves wholly chitinated, compressed, strongly bent and extending laterally, twisted anteriorly in species with longer valves.

♀. Subgenital plate (Fig. 1.32B) with posterior margin truncate. Ovipositor (Fig. 1.32A–B) short and not incised apically. Comstock-Kellogg glands present. Spermathecal vestibule bent strongly, without distinct valve at spermathecal aperture.

Remarks. This genus comprises 25 species from Far East Asia and 1 species is distributed in Japan (Ito, 2003; Mayer, 2004). In this genus the chromosomal number is $2n \text{ ♂}=23$ and the chromosomal morphology is similar to that in the subtribe Podismini. Current phylogenetic analysis using molecular data (Woller *et al.*, 2014; Chintauan-Marquier *et al.* 2014) supports that *Prumna* is a group of Podismini. However, *Prumna* seems atypical in Podismini, having an abruptly truncate male subgenital plate and strongly bent male ventral aedeagal valves and lacking oval sclerite beside the epiphallus as described above. In this paper I treat it as a member of Podismini and do not assign it into any subtribe. I have had no opportunity to examine possibly related genera, *Prumnacris* Rehn & Rehn, 1944 (represented by 1 alpine species in Northeastern USA) and *Pachypodisma* Dovnar-Zapolskii, 1933 (comprising 2 Caucasian species). These genera were included into “subtribe Primnoa Group” by Rehn & Randell (1963) without any comments. Therefore, a critical revision of this group is needed.

In the original description of *Primnoa* Fischer-Waldheim (1846: 248), “*Podisma primnoa* Motsch.” was used in the headline as a new species name, but the other name “*Primnoa viridis*” was also used for the same species under a new genus in the text (“genre nouveau le nom de *Primnoa viridis*”). After 13 years, Motschulsky (1859: 11) described a new genus *Prumna* for *Primnoa viridis*. Since then, the genus has been referred to as *Prumna* until Uvarov (1940) treated *Prumna* as a junior synonym of *Primnoa* Fischer-Waldheim. Unfortunately, he was not aware that *Primnoa* Fischer-Waldheim was a homonym and thus invalid. Ito (2003) revived the name *Prumna* Motschulsky for this genus.

Species examined. *P. fauriei* (Bolívar, 1890), *P. litoralis* Tarbinsky, 1932, *P. primnoa* (Fischer-Waldheim, 1846), *P. ussuriensis* Tarbinsky, 1930.

Prumna fauriei (Bolívar, 1890) comb. nov.

(Figs 1.6AE, 1.9C, 1.10J, 1.15A–C, 1.18A, 1.21, 1.29B, 1.30A, 1.32A–B, 1.45A, 1.39A, 1.41A, 3.1)

Pezotettix fauriei Bolívar, 1890: 322. (Type specimen as in Fig. 3.1C)

Parapodisma fauriei: Mistshenko, 1947: 11.

Primnoa hayachinensis Inoue, 1979a: 54. Syn. nov.

General morphology. Body dark green or yellowish green with many small black maculae, but sometimes maculae obscured. Antennae light brown. Compound eyes brown or reddish brown. Frontal carinae (Fig. 1.6A) parallel and distinct, frontal costa narrow and depressed. Prosternal process acute apically, projecting just below. Pronotum (Fig. 1.10J) shining uniformly, having weak lateral carinae; punctures sparse and slightly rugose on prozona, dense and uniform on metazona; three transverse sulci deep; longitudinal carina indistinct on prozona and distinct on metazona. Tegmina (Fig. 1.15C) blackish brown or brown, spatulate, reaching large tympanal organ (Fig. 1.15A–B), usually covering the latter and slightly bent downward; TL=3–5. Hind femora yellowish brown ventrally; knee red brown. Hind tibiae pale blue; spines with a black tip.

♂. P/M=1.6–2.0. Lateral black stripes on head present behind compound eyes,

but sometimes obscured; on pronotum broad ($LSW/PH=1/4-1/3$), usually reaching 2nd or 3rd abdominal tergite. Furculae of 10th abdominal tergite (Fig. 1.18A) straight, obtuse apically, not in contact with each other. Epiproct (Fig. 1.18A) yellowish green, subquadrate with a shallow median furrow; a small round tubercle at $1/3$ length from apex and near lateral margin; lateral margin emarginate in apical $1/4$; near the middle of each lateral margin slightly constricted, with a small tubercle. Cerci (Fig. 1.21) spatulate, compressed and broadened apically, yellowish brown. Lophi of epiphallus (Fig. 1.29B) in anterior view gradually tapering off with external margin rounded and internal margin straight, and abruptly attenuated apically. Dorsal aedeagal sclerite tapering off and connected to dorsal aedeagal valve. Dorsal aedeagal valve derived from sheath (Fig. 1.30A), membranous and turned forward. Ventral aedeagal valves bent with a right angle and extending laterally.

♀. $P/M=1.5-2.0$. Lateral black stripes on head present behind compound eyes, but often obscured; on pronotum medium to narrow or often almost obsolete (if present, $LSW/PH=1/5-1/7$), when most developed, extending to posterior margin of pronotum but interrupted. Subgenital plate (Fig. 1.32B) posterior margin truncate and serrate. Spermatheca as in Fig. 1.39A; apical diverticulum short; preapical diverticulum almost equally thick, without projection or diverticulum. Spermathecal vestibule (Fig. 1.41A) constricted at apical $1/3$ and strongly bent right- or leftward; very weakly sclerotized at the connection with spermathecal duct.

Nymph color (Fig. 1.45A). Generally dark brown. Pronotum with a distinct dark brown V-crest in dorsal view. Hind femora with three dark maculae. Abdomen with distinct black lateral stripes. Body color gradually changes after each molt.

Type specimen. MNCN Cat. Tipos No 8302, collected in Yeso in 1886 by Dr. Bonnet (MNCN, Madrid).

Distribution. [Hokkaidō] Around Mt. Yûrappu. [Honshû] Around high mountains of Tohoku district – Niigata Prefecture, north of the Agano River (Mt. Iwaki, Mts. Hakkôda, Hachimantai area, Mt. Iwate, Mt. Hayachine, Mt. Kurikoma, Mt. Chôkai, Mt. Gassan, Mts. Zaô, Mts. Asahi). This species is distributed from an altitude of about 500m to mountain peaks (Mt. Yûrappu and Mt. Chôkai, specimens in SEHU; Orobe Tôge, from Hironaga's information; Nagashima (1994)); the population density is relatively high in places where alpine meadows are dominant.

Remarks. Some authors have mentioned characters of *Pezotettix fauriei* Bolívar, 1890, referring only to the original description in which one female individual from “Yeso” (=Hokkaidō) was examined. The holotype specimen of this species is preserved in MNCN, Madrid (Fig. 3.1). After examining photos of the holotype and description, I have concluded that this species is the same with *P. hayachinensis*, having the following characters: Body relatively large (33mm); pronotum shining wholly, with weak lateral carinae; three transverse sulci deep; punctures sparse and rugose on prozona, uniform and dense on metazona; tegmina spatulate.

The name *fauriei* has been used in several taxonomic publications without examination of the type specimen and misunderstood as some other species. Shiraki (1910) identified one male and one female from Gifu Prefecture with “*Podisma fauriei*”. But I have identified these specimens (preserved in Systematic Entomology, Hokkaidô University) with *Parapodisma dairisama* Scudder, 1897. Hebard (1924) regarded *P. fauriei* (*sensu* Shiraki, 1910) as “*Podisma subaptera* Hebard, 1924”, and regarded *P. dairisama* Scudder as a junior synonym of *P. fauriei* Bolívar. Mistshenko (1947)

provisionally moved *P. fauriei* to the genus *Parapodisma* Mistshenko, 1947 without any examination, and used “*Parapodisma fauriei*” for a distinct species different from *P. subaptera* and *P. dairisama* in his two monographs (Mistshenko 1951, 1952). Following Hebard (1924), Tominaga & Uchida (2001) regarded *P. fauriei* (*sensu* Shiraki, 1910) as the same species with *Aopodisma subaptera* (Hebard, 1924).

According to Mistshenko (1974), the genus *Prumna* can be divided into two groups by the shape of cerci as follows. The 1st group has the cerci widened and compressed apically, and the 2nd is characterized by small cerci strongly compressed almost entirely. The ventral aedeagal valves are also different in shape among them. In the 1st group the ventral aedeagal valves are bent with a right angle, thus extending laterally, and in the 2nd the valves are usually long, extending laterally at first and then twisted backwards. *P. fauriei* belongs to the former group. In the species of the latter group, the tip of the abdomen is extraordinarily widened (Fig. 1.18B–D) and the furculae are very small and in contact with each other.

Subtribe Miramellina

Miramellae Rehn & Randell, 1963: 7. Type genus: *Miramella* Dovnar-Zapolskii, 1933.

Diagnosis. The genera of this group are characterised by the combination of the following characters: 1) karyotype $2n \text{ ♂}=21$; 2) Compound eyes small (in male HW/IS=4–6); 3) posterior margin of pronotum emarginate; 4) spine of hind genicular hood absent; 5) male furculae of 10th abdominal tergite present; 6) male epiproct triangular; sometimes with spine-like tubercles; 7) male cerci conical or compressed apically; 8) sheath of aedeagus fused with dorsal aedeagal sclerite and forming dorsal aedeagal valve; 9) ovipositor valves incised apically; 10) spermathecal vestibule without sclerite on anterior part.

Remarks. This subtribe is a sister clade of the subtribe Podismina and comprises 3 genera in the Far East: *Miramella*, *Anapodisma*, *Zubovskya*. Several European genera (*e.g.*, *Kisella*, *Odontopodisma*) are also included in this subtribe, having the diagnostic characters.

Genus *Zubovskya* Dovnar-Zapolskii, 1932

Zubovskya Dovnar-Zapolskii, 1933: 262. Type species: *Podisma parvula* Ikonnikov, 1911.

General morphology. Body small, with integument smooth. Frontal carinae distinct and parallel. Frontal costa depressed almost evenly throughout its length. Compound eyes (Fig. 1.6C–D) relatively small (in male HW/IS=4–5). Prosternal process small and robust (Fig. 1.8A). Pronotum emarginate posteriorly. Apterous. Meso- and metanota (Fig. 1.13E) smooth. Hind genicular hood without a spine. Abdomen smooth. Tympanal organs absent or vestigial (Fig. 1.14E).

♂. 10th abdominal tergite with a pair of furculae; cerci slender and compressed apically; epiproct triangular, with or without a pair of tubercles; dorsal aedeagal sclerite fused with sheath, forming dorsal aedeagal valve; aedeagal valves straight and elongate.

♀. Body very robust compared with male. Posterior margin of subgenital plate gently curved and triangularly produced at the middle. Cerci smaller than in male,

compressed, conical in profile; apex obtuse. Ovipositor valves (Fig. 1.35B, E, H) incised apically. Comstock-Kellogg glands present. Spermathecal vestibule simple; sclerotized valve absent at spermathecal aperture; inner side without sclerite.

Remarks. This genus comprises 9 species now, and these species are distributed in the Far East except for *Z. banatica* Kis, 1965 occurring in Romania. This genus is represented in Japan by only 1 species.

Species examined. *Z. koeppeni parvula* (Ikonnikov, 1911); *Z. mistshenkoi* Storozhenko, 1980.

Zubovskya koeppeni parvula (Ikonnikov, 1911)

(Figs 1.6C–D, 1.8A, 1.10N, 1.13E, 1.14E, 1.19A, 1.22A, 1.29C, 1.30B, 1.32G, 1.35B, E, H, 1.39C, 1.41B, 3.2)

Podisma parvula Ikonnikov, 1911: 260.

Zubovskya parvula: Dovnar-Zapolskii, 1933: 261.

Odontopodisma parvula: Ramme, 1939: 140.

Zubovskia parvula: Mistshenko, 1952: 352[316].

Zubovskia koeppeni parvula: Storozhenko, 1986: 52. (as a subspecies of *Z. koeppeni* Zubovsky, 1900)

General morphology. Body generally dark green or yellowish green. Antennae light brown, composed of 18–20 segments (in Hokkaidô) or 22–24 segments (in Sakhalin and the Maritime Province). Compound eyes brown or light brown. Fastigium slightly produced (Fig. 1.6C, D). Prosternal process short, obtuse apically. Pronotum (Fig. 1.10N) smooth, frosting dorsally and shining laterally, slightly and gradually widened towards posterior margin; three transverse sulci very shallow, in female obscured; longitudinal carina present; lateral black stripes nearly straight, in male distinct from back of eyes to tip of abdomen and in female only reaching posterior margin of pronotum, sometimes obscured. Tympanal organs (Fig. 1.13A, 14A) vestigial or absent. Hind femora green dorsally; ventral part yellowish green in male and red (Hokkaidô populations) or yellowish green (Russian populations) in female; crescent brown; upper and lower genicular lobe yellowish green or dark brown. Hind tibiae yellowish green; spines with a black tip.

♂. Lateral black stripes on head present behind compound eyes; on pronotum very broad ($LSW/PH=1/2.5-1/3$), usually continuously extending to the 10th abdominal tergite. $P/M=1.9-2.3$. Furculae of 10th abdominal tergite (Fig. 1.19A) black, short and obtuse apically, shaped nearly semicircular, not in contact with each other. Epiproct (Fig. 1.19A) triangular, with a deep median furrow; lateral margin black; a pair of tubercles near apex; cerci (Fig. 1.22A) slender, straight, compressed apically but not broadened. Lophi of epiphallus (Fig. 1.29C) in anterior view nearly rectangular, incised apically with the inner apex relatively higher than the outer one. Dorsal aedeagal sclerite (Fig. 1.30B) bifurcated apically, connected to sheath and forming membranous dorsal aedeagal valve. Ventral aedeagal valves thin, slightly excurved.

♀. Lateral black stripes on head present behind compound eyes, but sometimes obscured, broad on pronotum ($LSW/PH=1/4-1/5$), absent on abdomen. $P/M=2.0-2.3$. Subgenital plate (Fig. 1.32G) with posterior margin gradually curved and projected medially. Spermatheca as in Fig. 1.39C; apical diverticulum long, sometimes with one more diverticulum. Preapical diverticulum with a projection; apical half about twice as

thick as basal half. Spermathecal vestibule (Fig. 1.41B) large, elongate, not sclerotized, connected to spermathecal duct without constriction.

Nymph color. Generally dark brown or reddish brown until last instar.

Type specimen. Neotype male (Zoological Institute, St. Petersburg). Russia: Primorskii Distr., 20 km E Spassk-Dalny; 10 vi 1910 (not examined).

Distribution. [Hokkaidô] Mt. Shokanbetsu, Mt. Ashibetsu, Mts. Daisetsu, Mts. Shiretoko, Mt. Rishiri; South and North Korea, North East China (Liaoning and Heilongjiang), Far Eastern Russia (Sakhalin, Amur, South part of Primorskii).

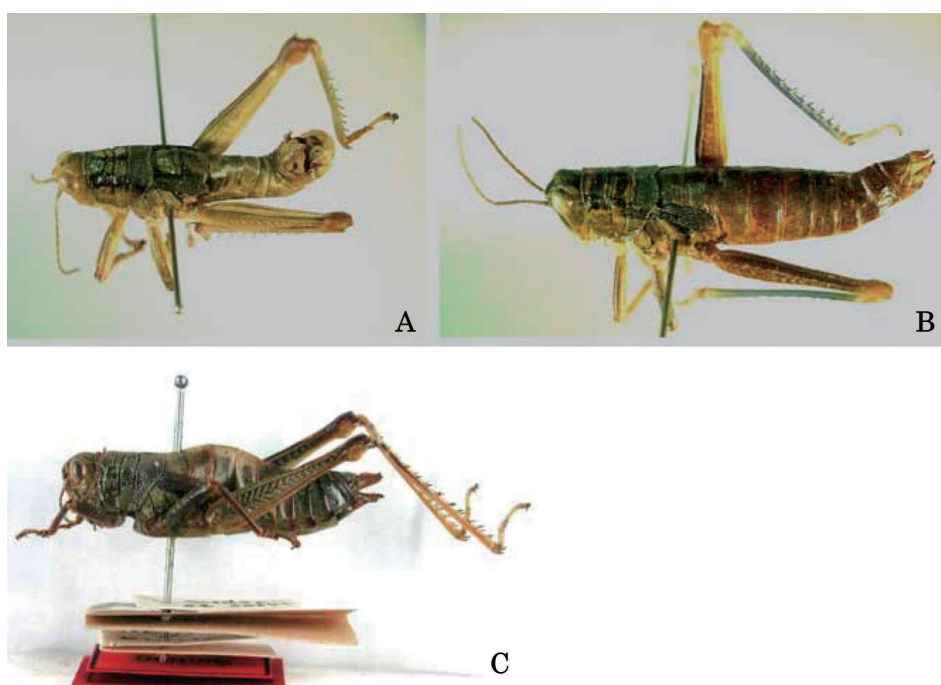


Fig. 3.1. *Prumna fauriei*, male (A) and female (B) from Mt. Yûrappu, holotype of *Pezotettix fauriei* preserved in MNCN, Madrid (C). Photo C was taken by Dra Carolina Martin.



Fig. 3.2. *Zubovskya koeppenii parvula*, male (left) and female (right), from Mt. Shokanbetsu, Hokkaidô.

Remarks. This species is distributed in high altitude areas (usually higher than 1000m) in Hokkaidô. It seems to be associated with some alpine plants (e.g., *Rhododendron aureum*, *Vaccinium* spp., and *Geum pentapetalum*). It can be seen in Shiretoko-Tôge (alt. 738m), where such alpine plants are dominant.

Genus *Anapodisma* Dovnar-Zapolskii, 1933

Anapodisma Dovnar-Zapolskii, 1933: 253. Type species: *Anapodisma miramae* Dovnar-Zapolskii, 1933, by original designation.

Yupodisma Zhang & Xia, 1990: 1. Type species: *Yupodisma rufipennis* Zhang & Xia, 1990, by original designation. Synonymized by Storozhenko, 1993b: 21, cited as “*Yudopodisma*”.

General morphology. Body slender, integument smooth. Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. Compound eyes medium in size (HW/IS=6 in male). Prosternal process slender with an acute apex. Pronotum (Fig. 1.10I) cylindrical, emarginate distinctly in posterior margin; three transverse sulci in conspicuous, the posterior one faint. Tegmina small and narrow, oblanceolate or obovate, red brown. Metanotum smooth, only with a pair of scutal pits and a pair of vestigial scutal grooves. Hind wings absent. Hind genicular hood (Fig. 1.17E) without a spine. Abdomen smooth. Tympanal organs present. Cerci (Fig. 1.22C) conical and straight in both sexes.

♂. 10th abdominal tergite with a distinct pair of furculae (Fig. 1.19B). Epiproct with a pair of spine-like tubercles (Fig. 3.3C) at 1/3 length of lateral margin from base; median furrow deep. Subgenital plate (Fig. 3.3C) short, conical, acute apically. Sheath fused with dorsal aedeagal sclerite, forming aedeagal valves, bifurcate apically, covering most part of slender ventral aedeagal valves.

♀. Subgenital plate elongate. Ovipositor valves (Fig. 1.35A, D, G) long, straight and slender, incised apically, minutely serrate on lateral margin; integument smooth laterally, coarse in the other parts. Comstock-Kellogg glands absent.

Remarks. This genus seems closely related to the European genus *Odontopodisma*, with which it shares the following characters: Body slender; pronotum cylindrical; integument smooth; tegmina small and narrow, and red colored; male cerci straight and slender; ovipositor valves (Fig. 1.35J) straight and elongate with incised apex; and aedeagal valves straightly elongate. *Anapodisma* shares with *Zubovskya* the following characters: Pronotal integument smooth; male cerci straight and slender; and ovipositor valves incised apically. Examinations of further Podismini are necessary to find exact relationship among these genera.

This genus comprises 4 species, all from the Far East, and 1 species occurring in Japan. These species are very similar except for the male genital segments (Storozhenko, 1993b).

Species examined. *A. miramae* Dovnar-Zapolskii, 1933.

Anapodisma miramae Dovnar-Zapolskii, 1933

(Figs 1.10I, 1.17E, 1.19B, 1.22C, 1.29D, 1.30D, 1.35A, D, G, 1.39D, 1.41D, 3.3)

Anapodisma miramae Dovnar-Zapolskii, 1933: 256.

Podisma dairisama: Ikonnikov, 1913: 20 (*nec* Scudder, 1897b)

Miramella sinense Chang, 1940: 54. Synonymized by Storozhenko, 1993b: 22.

Anapodisma rufupenna Zheng, 1989: 71. Synonymized by Storozhenko, 1993b: 22.

General morphology. Body generally dark green, green or yellowish green. Antenna yellowish brown. Compound eyes yellowish brown. Lateral black stripes straight and distinct, running from back of eye to posterior margin of pronotum. Hind femora green or yellowish green; upper genicular lobe and crescent black except for genicular hood yellowish green striped. Lower genicular lobe yellowish green. TL=3. Cerci acute at apex.

♂. LSW/PH= about 1/5. P/M 2.1–2.5. Furculae of 10th abdominal tergite (Fig. 1.19B) in contact with each other, tapering toward apex, black. Epiproct (Figs 1.19B, 3.3C) with a pair of spine-like tubercles at 1/3 length of lateral margin from base; lateral margin black. Subgenital plate (Fig. 3.3C) short, conical; tip and dorsal margin black. Epiphallus (Fig. 1.29D) with large and earlobe-shaped lophi; lophi twisted, rounded apically. Aedeagal valves (Fig. 1.30D) straightly elongate and narrow.

♀. LSW/PH=1/6–1/8. P/M=1.9–2.0. Spermatheca (Fig. 1.39D) with an apical diverticulum; preapical diverticulum with a short projection near base. Spermathecal vestibule (Fig. 1.41D) simple, almost straight, with a valve at spermathecal aperture, and not sclerotized in other parts.

Type specimen. Holotype male (Zoological Institute, St. Petersburg). Russia: Primorskii Krai, Pogranichnaia (not examined).

Distribution. [Kyûshû] Tsushima Is.; South and North Korea (including Cheju Island), North East China (Liaoning and Heilongjiang), Far Eastern Russia (southern part of Primorskii).

Subtribe Podismina

Podismae Rehn & Randell, 1963: 7. Type genus: *Podisma* Berthold. 1827.

Diagnosis. The genera of this group are characterised by the combination of the following characters: 1) karyotype $2n \text{ ♂}=23$; 2) Compound eyes small (in male HW/IS=4–6); 3) spine of hind genicular hood absent; 4) male furculae of 10th abdominal tergite present; 5) male cerci conical; 6) sheath of aedeagus entirely covering dorsal aedeagal sclerite and fused with the latter, forming dorsal aedeagal valve; 7) spermathecal vestibule small, a simple sack in shape.

Remarks. This subtribe comprises 2 genera, *Ognevia* and *Podisma*. Several European genera may also be included in this subtribe, having the diagnostic characters.

Genus *Ognevia* Ikonnikov, 1911

Ognevia Ikonnikov, 1911: 267. Type species: *Ognevia sergii* Ikonnikov, 1911, by original designation.

Eirenephilus Ikonnikov, 1911: 264. Type species: *Eirenephilus debilis* Ikonnikov, 1911, by monotypy. Synonymized by Storozhenko & Kanô, 1992: 3.

Liaoacris Zheng, 1989: 67. Type species: *Liaoacris ochropteris* Zheng, 1989, by original designation. Synonymized with *Ognevia* by Storozhenko & Kanô, 1992: 3.

General morphology. Body slender and integument smooth, with dense long hair. Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. Compound eyes relatively large (HW/IS=6). Prosternal process (Fig. 1.8D) obtuse apically. Pronotum (Fig. 1.10C) shining at almost all parts, flat dorsally on metazona; punctures sparse on prozona, dense and uniform on metazona; posterior margin strongly produced to form a triangular apex; metazona equal to or slightly longer than prozona in length; lateral black stripes straight, distinct in all length of pronotum, but sometimes obscured. Flight organs (Fig. 1.13A) fully developed. Hind femora slender, sometimes with two obscured black maculae; genicular hood without a spine; upper genicular lobe and crescent black except for yellowish green part of hind genicular hood. Lower genicular lobe yellowish green. Meso- and metanota with developed scutum and scutellum. Tympanal organs (Fig. 1.14A) well developed. Cerci (Fig. 1.22D) conical, in both sexes almost same in shape and length, but in male slightly incurved and in female almost straight.

♂. Furculae of 10th abdominal tergite (Fig. 1.19D) in contact with each other, tapering toward apex. Epiproct with two tubercles near the apex. Epiphallus (Fig. 1.29F) with large lophi and long ancorae; anterior projections small. Phallus (Fig. 1.30E) with small aedeagal valves; dorsal aedeagal sclerite covered by sheath and fused with the latter, forming dorsal aedeagal valve.

♀. Subgenital plate (Fig. 1.32D) truncate posteriorly; posterior margin with small serrations. Comstock-Kellog glands absent. Spermathecal vestibule small, simple-shaped.

Remarks. This genus comprises 3 species, and all species distributed in East Asia. As Rehn & Rehn (1939) stated, this genus is closely related to *Podisma*. The result of phylogenetic analysis in the preceding chapter also agrees with their opinion. Hybrids are known between *Ognevia* Ikonnikov and *Podisma* Berthold (Ito, 2004).

Species examined. *O. longipennis* (Shiraki, 1910); *O. sergii* (Ikonnikov, 1911).

Ognevia longipennis (Shiraki, 1910)

(Figs 1.8D, 1.10C, 1.13A, 1.14A, 1.19D, 1.22D, 1.29F, 1.30E, 1.32C, 1.45B, 1.39F, 1.41E, 3.4)

Podisma sapporensis var. *longipennis* Shiraki, 1910: 77. *Eirenephilus debilis* Ikonnikov, 1911: 265. Synonymized by Furukawa, 1939: 169.

Podisma longipennis: Hebard, 1924: 220.

Podisma alpina subsp. *niphona* Furukawa, 1929: 171. Synonymized by Furukawa, 1939: 169.

Eirenephilus longipennis: Furukawa, 1939: 166.

Ognevia longipennis: Storozhenko & Kanô, 1992: 2.

General morphology. Body relatively slender, dark green, green or yellowish green. Antennae light brown. Compound eyes brown or light brown. Lateral black stripes straight and usually distinct, running from back of eye to posterior margin of pronotum. Tegmina uniformly ocher. Hind femora green, yellowish green or yellow. Outer lower genicular lobe with ventral margin sinuate; crescent brown; upper and lower genicular lobe yellowish green or dark brown. Hind tibiae yellowish green; spines with a black tip. Abdomen with a broad dorsal dark purple band continuous on segments. Cerci (Fig.

1.22D) in both sexes slender, 2.6–3.0 times as long as its greatest width, tapering toward acute apex.

♂. LSW/PH=1/4–1/5. P/M=1.0–1.1. Furculae of 10th abdominal tergite (Fig. 1.19D) black, short and nearly regular-triangular in outline. Epiproct generally black except for apical triangular part in yellowish green, with a deep median furrow on basal half, with a pair of tubercles near apex; lateral margin emarginate at apical 1/4. Lophi of epiphallus (Fig. 1.29F) in anterior view near rectangular, weakly incised apically. Dorsal aedeagal sclerite (Fig. 1.30E) tapering off, connected to sheath and forming membranous dorsal aedeagal valve. Ventral aedeagal valves slender, straight in apical half, truncate apically.

♀. LSW/PH=1/5–1/7. P/M=0.8–1.0. Paraproct large, exceeding posterior margin of epiproct, covering about half length of dorsal ovipositor valves. Subgenital plate (Fig. 1.32G) with posterior margin gradually curved and truncate, minutely serrate medially. Spermatheca (Fig. 1.39F) small and simple. Preapical diverticulum without projection, slightly longer than apical diverticulum; apical half about twice as thick as basal half. Spermathecal vestibule (Fig. 1.41E) small, not distinctly sclerotized except for connection to spermathecal duct with a weak semicircular sclerite.

Nymph color (Fig. 1.45B). Generally dark brown, ocher or gray until last instar; body color changing drastically after last molt. Pronotum with distinct dark brown V-crest. Hind femora with three dark maculae. Abdomen with distinct black lateral stripes; each segment with a pair of symmetrical weak brown oblique stripes dorsally.

Type specimen. Syntype (SEHU): 1 ♂, “ハ キ 8/10” (=Hagi, Kumamoto Pref., collected in Aug. 10) in handwriting. This species was described based on specimens from Hagi and Sapporo. But any specimens from Sapporo are not found.

According to Tomokuni (1994), S. Matsumura used this kind of handwritten labels until 1904 or so. Besides the type specimen, some other specimens of this species are found in the Matsumura Collection. However, the information available from the labels are not sufficient to determine that they belong to the type material.

Distribution. [Hokkaidô] Widely distributed. [Honshû] Widely distributed. In western Honshû, Shikoku and Kyûshû, distributed in high altitude areas. In northern to central Japan, this species inhabits the hilly to montane zone, and in Western Japan occurs only in the montane zone.

Remarks. *Ognevia* were revised by Storozhenko & Kanô (1992), who, however, did not mention some important characters. The following characters should be added to *O. sergii* in their descriptions: body relatively robust; outer ventral genicular lobe of hind femora with ventral margin straight; tegmina brown, with a broad yellowish green stripe along hind margin; cerci relatively short and robust, in both sexes 2.0–2.4 times as long as its greatest width; male epiproct with four tubercles, the two near apex and the other two near middle of lateral margin; male lophi of epiphallus rounded apically; female paraproct relatively small, not exceeding posterior margin of epiproct, covering base of dorsal ovipositor valves.

Genus *Podisma* Berthold, 1827

Podisma Berthold. 1827: 411. Type species: *Gryllus pedestris* Linnaeus, 1758.

General morphology. Integument smooth. Frontal carinae distinct and parallel. Frontal costa depressed almost evenly throughout its length. Compound eyes relatively

small (HW/IS=4–5 in male). Pronotum (Fig. 1.10H) shining at almost all parts, punctures sparse on prozona, dense and uniform on metazona; three transverse sulci deep; longitudinal carina distinct only on metazona; posterior margin rounded and in some species emarginate medially. Hind genicular hood without a spine. Tegmina small, oval, oblanceolate, or narrowly obtrullate, sometimes apterous. Metanotum with flattened scutellum, scutal grooves and a pair of pits, but sometimes these structures more vestigial. Tympanal organs (Fig. 1.14D) present, medium or small in size. Cerci (Fig. 1.22E–F) conical, almost straight.

♂. Furculae of 10th abdominal tergite present. Dorsal aedeagal sclerite (Fig. 1.30F, G) bifurcated apically, fused with sheath and forming dorsal aedeagal valve.

♀. Comstock-Kellogg glands absent. Spermatheca with an apical diverticulum; preapical diverticulum narrow, without projection; spermathecal vestibule small, membranous, a simple sac in shape.

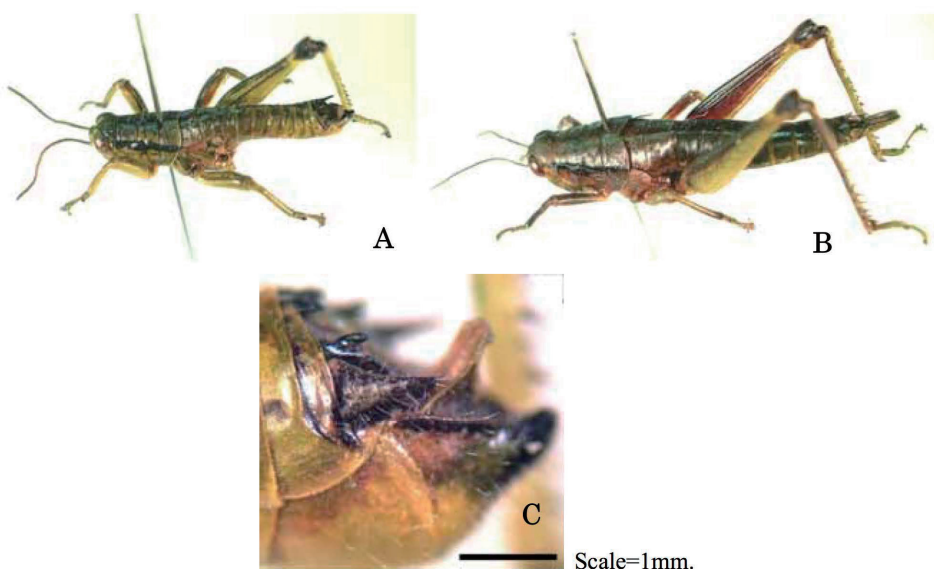


Fig. 3.3. *Anapodisma miramae*. A: male; B: female; C: tip of male abdomen, from Maritime Province, Russia.

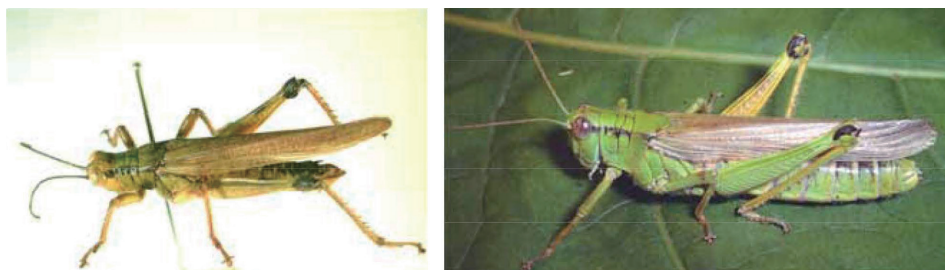


Fig. 3.4. *Ognevia longipennis*, male (left) and female (right) from Sapporo-City.

Species examined. *P. kanoi* Storozhenko, 1993; *P. sapporensis* Shiraki, 1910; *P. pedestris* (Linnaeus, 1758).

Podisma sapporensis Shiraki, 1910

(Figs 1.10H, 1.13D, 1.14D, 1.19J, 1.22F, 1.29H, 1.30F, 1.45C, 1.39E, 1.41F, 3.5)

Podisma sapporensis Shiraki, 1910: 76.

Parapodisma sapporensis: Mistshenko, 1952: 390[351]. *Miramella sapporensis*: Hiura, 1979: 5.

Podisma sapporensis: Kanô, 1986: 5.

Podisma tyatiensis Bugrov and Sergeev, 1997: 48. Syn. nov.

General morphology. Body generally dark green, yellowish green, or sometimes yellow laterally and dorsally, pale gray ventrally. Antennae brown. Head with a black macula dorsally, which is fused with the black lateral stripes but sometimes obscured or absent; gena pale yellow or pale bluish green. Prosternal process short, projecting just below, or slightly inclined backward. Pronotum (Fig. 1.10H) with a pair of broad lateral black stripes, distinct and running from back of compound eyes to tip of abdomen, but sometimes reaching only posterior margin of pronotum or wholly obscured. Hind femora yellowish green or yellow; crescent brown; upper and lower genicular lobe yellowish green or dark brown. Hind tibiae pale blue or pale yellowish green; spines cream-colored with a black tip. Tegmina dark brown or yellowish brown, sometimes with a black stripe on ventral margin, small and narrow, oblanceolate or narrowly obtrullate, sometimes apterous; TL=0–6. Tympanal organs medium in size.

♂. LSW/PH=1/2.5–1/3. P/M=1.5–1.8. Furculae of 10th abdominal tergite (Fig. 1.19J) black, obtusely triangular, not in contact with each other. Epiproct (Fig. 1.19J) triangular with sides swollen and apex obtuse; median length longer than basal width; median furrow deep or shallow. Cerci (Fig. 1.22F) short; ratio of length to basal width 1.9–2.3. Lophi of epiphallus (Fig. 1.29H) in anterior view trapezoid with an obtuse apex; apical margin gradually curved. Dorsal aedeagal valve (Fig. 1.30F) acute apically. Ventral aedeagal valves slightly excurved apically.

♀. LSW/PH=1/3–1/4. P/M=1.2–1.5. Subgenital plate with posterior margin gradually curved and projected medially. Spermatheca as in Fig. 1.39E; preapical diverticulum twice as long as apical diverticulum, without projection, apical half twice as thick as basal width. Spermathecal vestibule (Fig. 1.41F) small, simple, not sclerotized except for weakly sclerotized area in spermathecal aperture, connected to spermathecal duct with constriction.

Nymph color (Fig. 1.45C). Generally black or dark brown until last instar. Integument smooth, not shining. Head reddish brown, with lateral black stripes; a cream-colored band under compound eyes. Pronotum with many longitudinal short yellow stripes on posterior margin. Hind femora yellowish brown or brown, with two large black bands; hind knee black; several small cream-colored maculae on posterior margin of each abdominal tergite.

Type specimens. Syntypes (SEHU): 1♀, 定山溪 8/ 上 (=Jôzankei, early Aug.) // *Pezotettix pedestris* L.; 2♂, 定山溪 8/ 上.

The labels suggest that these specimens were used for preparing the original description, in which the collection localities are stated as follows: “Zahlreiche Exemplare aus Ziosankei (August) und Sapporo (August) in der Sammlung von Herrn Dr. S. Matsumura und in meiner Sammlung”.

“Ziosankei” is spelled “Jôzankei” or “Zyôzankei” now, a place south of Sapporo-City. Although only the three specimens have been determined as Syntypes, Shiraki (1910) examined many other specimens, which are not found in the collection at SEHU.

Distribution. [Hokkaidô] Widely distributed; Kunashiri Isl., Etorofu Isl., Sakhalin. In north and east of Sapporo, this species is distributed in the hilly to subalpine (Mts. Hidaka and Mt. Yûbari) or montane zone (the other areas). West of Sapporo, this species is usually found on the montane to subalpine zone.

Remarks. Studies on geographic variation of this species by Akimoto et al. (1993), Ito (1997) and Tatsuta et al. (2000) have revealed that the morphological variation pattern is not correlated with the geographic distance and that the tegminal length is highly variable within and among populations. This species comprises two chromosomal races. One is the race with $2n \delta=23$ chromosomes, distributed in north, central and southern part of Hokkaidô and in Sakhalin. The other has $2n \delta=20+\text{neoX}+\text{neoY}$ chromosomes and distributed in eastern part of Hokkaidô and in Kunashiri. These two races are thought to be different biological species, because hybrids between them have very low viability (Sugano, personal communication). However, morphological differences are not accordant with the chromosomal differences (Tatsuta et al. 2000). *P. sapporensis* is a very complex species, not simply divisible into geographical subspecies.

P. sapporensis is divided into 3 subspecies: *P. s. ashibetsuensis* in Shikaribetsu, central Hokkaidô, *P. s. kurilensis* Bey-Bienko, 1949 in Kuril Islands and *P. s. krylonensis* Storozhenko, 1983 in Sakhalin. The latter two are distinguished from Hokkaidô populations by the body shape, the relative width of frontal costa to eye distance and shape of valves of cingulum in male phallus (Storozhenko 1993a). According to Storozhenko (1993a), *P. s. ashibetsuensis* is distinguished from nominal subspecies by valves of cingulum being relatively acute apically. But this character and other characters (e.g., tegminal length, shape of lophi of epiphallus) are overlapped in other populations.

Bugrov & Sergeev (1997) described *P. tyatiensis* from a high altitude area of Mt. Tyata. This species has $2n \delta=23$ chromosomes and is distinguished by unique morphology in a few chromosomes. So far as the chromosomes are concerned, *P. tyatiensis* may be a good biological species, because they can be reproductively isolated even crossed artificially. However, Tatsuta et al. (2000) have revealed that in morphology *P. tyatiensis* is not different from *P. sapporensis*. *P. tyatiensis* has been geographically isolated and is differentiated in the chromosomal number from the Golovnin population of *P. sapporensis* in the same island ($2n \delta=20+\text{neoX}+\text{neoY}$). *P. sapporensis* is a complex of several biological races or species, which are not discrete in morphology. *P. tyatiensis* is one of such races, may be treated as a junior synonym of *P. sapporensis*.

P. kanoi Storozhenko, 1993 and *P. aberrans* Ikonnikov, 1911 are closely related to *P. sapporensis*. *P. kanoi* is distinguished by some characters discussed below. *P. aberrans* can be distinguished from *P. kanoi* by the following characters: 1. Relatively wide tegmina; 2. Pronotum with posterior margin slightly produced. However, these characters are so plastic in *P. sapporensis* that the species status of *P. aberrans* is still unclear.

Podisma kanoi Storozhenko, 1993
(Figs 1.19K, 1.22E, 1.29G, 1.30G, 1.45D, 1.39G, 1.41G, 3.6)

Podisma kanoi Storozhenko, 1993a: 3.

General morphology. Body generally bright green or yellowish green laterally and dorsally, and pale gray or cream-colored ventrally. Antennae brown. Head without black macula dorsally; gena pale bluish green. Prosternal process short, projecting just below. Lateral black stripes distinct, running from back of compound eyes to posterior margin of pronotum. Pronotum cylindrical, transverse sulci relatively shallow. Fore and mid legs yellow, yellowish green or yellowish brown. Hind femora yellowish green or yellowish brown; crescent brown; upper and lower genicular lobe yellowish green or dark brown. Hind tibiae pale blue, pale bluish purple or pale yellowish green, with several parts darkish; spines cream-colored with a black tip. Apterous.

♂. LSW/PH=1/2.5–1/3 P/M=1.5–1.7. Furculae of 10th abdominal tergite (Fig. 1.19J) black, obtusely triangular, not in contact with each other. Epiproct (Fig. 1.19K) triangular; median length longer than basal width; median furrow shallow. Cerci (Fig.

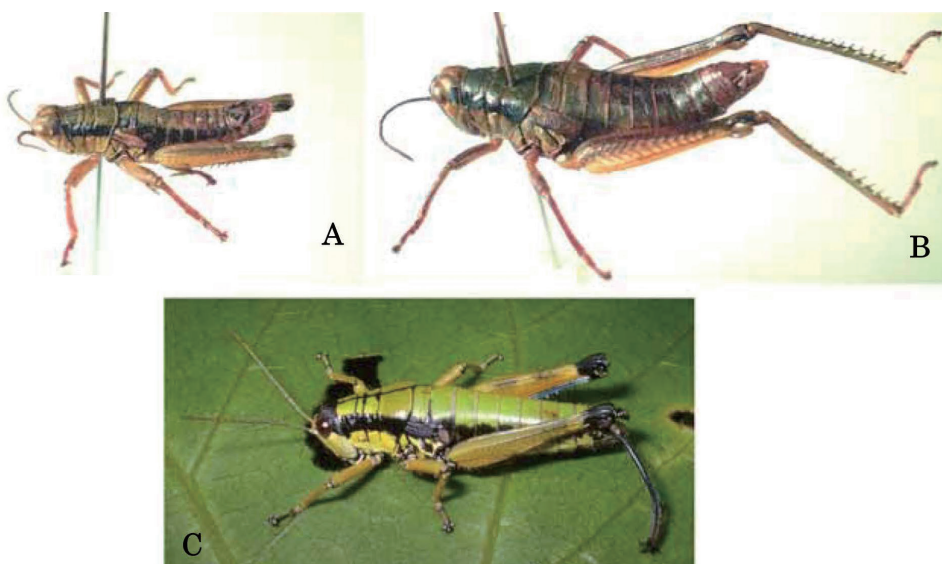


Fig. 3.5. *Podisma sapporensis*, male (A) and female (C) from Sapporo-City, female (B) from the peak of Mt. Yōtei, Kutchan-Town.



Fig. 3.6. *Podisma kanoi*, male (left) and female (right) from Tenjindaira, Gumma.

1.22E) short, ratio of length to basal width about 1.8. Lophi of epiphallus (Fig. 1.29G) in anterior view triangular with obtuse apex, outer margin slightly swollen. Dorsal aedeagal valve (Fig. 1.30G) truncate. Ventral aedeagal valves slightly excurved in apical half; apex truncate.

♀. LSW/PH=1/3–1/4. P/M=1.4–1.8. Subgenital plate with posterior margin gradually curved and projected medially. Spermatheca as in Fig. 1.39G; apical diverticulum 1/3–1/2 as long as preapical diverticulum. Preapical diverticulum slender, without projection; apical half about twice as thick as basal width. Spermathecal vestibule (Fig. 1.41G) small, simple, not sclerotized except for a very weakly sclerotized area in spermathecal aperture, connected to spermathecal duct with constriction.

Nymph color (Fig. 1.45D). Generally dark brown until last instar. A cream-colored band laid under compound eyes. Lateral black stripes distinct, running from anterior margin of compound eyes to posterior margin of head. Pronotum with an obscure brown V-crest. Hind femora with two large black bands; knee dark brown.

Type specimen. Holotype: male (NIAES). Japan, Shibu-Tôge 12. X. 1951 (K. MATSUSHIMA).

Distribution. [Honshû] High altitude areas around Mt. Aizu-komagatake, Mts. Nikkô, Mts. Mikuni and Mts. Echigo. According to Nagashima (1994), this species inhabits only the montane and subalpine zones of mountains higher than about 1600m. In my collection, Tenjindaira (an altitude of 1200m) is the lowest.

Remarks. Morphology of this species was studied by Wada & Ukawa (1983), who concluded that this species is closely related to *P. sapporensis*. Differences of the two species are observed in the nymph color, pronotal shape, size of the tympanal organs, etc.

Subtribe Tonkinacridina, n.

Type genus: *Tonkinacris* Carl, 1916.

Diagnosis. The genera of this group are characterised by the combination of the following characters: 1) karyotype $2n \text{ ♂}=21$; 2) compound eyes large (HW/IS in male 7–12); 3) posterior margin of pronotum usually produced; 4) spine of hind genicular hood present; 5) male furculae of 10th abdominal tergite absent; 6) male cerci compressed at least in apical half; 7) sheath of aedeagus usually forming valves of cingulum; 8) female subgenital plate, posterior margin projected in lateral sides; 9) spermathecal vestibule with or without distinct sclerite anteriorly.

Remarks. This subtribe comprises 4 genera occurring in the Far East: *Sinopodisma*, *Tonkinacris*, *Fruhstorferiola* and *Parapodisma*. These genera were once treated as members of Miramellina, but the phylogenetic hypothesis in the previous chapter suggests that they should represent another subtribe, which is established above.

Genus *Sinopodisma* Chang, 1940

Sinopodisma Chang, 1940: 68 (as subgenus under the genus *Indopodisma* Dovnar, 1933). Type species: *Indopodisma* (*Sinopodisma*) *pieli* Chang, 1940.

Sinopodisma: Mistshenko, 1951: 253 (as genus).

Pedopodisma Zheng, 1980: 336, 347. Type species: *Pedopodisma microptera* Zheng, 1980 (= *Micropodisma emeiensis* Yin, 1980), by original designation. Synonymized by Storozhenko,

General morphology. Compound eyes large and inter-ocular space narrow (Fig. 1.7; HW/IS=7–12 in male). Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. Antennae yellowish brown. Pronotum nearly cylindrical; posterior margin slightly produced and weakly emarginate or not. Tegmina small, oblanceolate, oval or absent. Metanotum smooth, with scutal grooves and a pair of scutal pits. Hind femora with a small apical spine on the genicular hood; knees black or dark brown. Tympanal organs small to medium in size.

♂. 10th abdominal tergite without furculae. Epiproct triangular with a subacute apex, distinct median furrow in basal half, and a pair of tubercles near apex; lateral margin slightly swollen near base; basal width proximately same as median length. Cerci slightly incurved, compressed apically. Aedeagal valves surrounded by sheath except for apical part. Dorsal aedeagal sclerite tapering off, produced to form dorsal aedeagal valve and its apex bifurcated, trifurcated or not incised. Ventral aedeagal sclerites connected to membranous lobe, forming ventral aedeagal valves which extends along the dorsal aedeagal valve.

♀. Subgenital plate with gradually curved posterior margin. Cerci much smaller than male, compressed, conical in profile; apex obtuse. Comstock-Kellogg glands present. Spermathecal vestibule abruptly dilated; internal surface with a sclerite in anterior connection to spermathecal duct. Apical diverticulum of spermatheca sometimes with secondary diverticula. Preapical diverticulum of spermatheca relatively narrow, sometimes with a small diverticulum.

Remarks. *Sinopodisma*, including “*Pedopodisma*”, has been represented by 53 described species. Several species are divided by only slight differences (Huang *et al.*, 2013) which seems to be intraspecific differences, and taxonomic revision of this genus is needed.

Species examined. *S. aurata* Ito, 1999; *S. emeiensis* (Yin, 1980); *S. formosana* (Shiraki, 1910); *S. houshana* Huang, 1982; *S. kawakamii* (Shiraki, 1910); *S. kelloggii* (Chang, 1940); *S. kodamae* (Shiraki, 1910); *S. lofaoshana* (Tinkham, 1936); *S. punctata* Mistshenko, 1954; *S. rostellocera* You, 1985; *S. shirakii* (Tinkham, 1936); *S. splendida* (Tinkham, 1936); *S. yingdensis* Liang 1988.

Sinopodisma punctata Mistshenko, 1954

(Figs 1.6C, 1.19E, 1.24B, 1.29I, 1.35C, F, I, 1.45E, 1.39K, 1.41K, 3.7)

Sinopodisma punctata Mistshenko, 1954: 30.

General morphology. Integument coarse. Body shining, generally green, yellowish green or brownish green. Compound eyes yellowish brown. Pronotum (Fig. 1.10G) punctate densely, deeply and uniformly; longitudinal carina indistinct, sometimes distinct on metazona; anterior and posterior margins weakly notched, yellowish green laterally. Tegmina elongate oval, light brown; TL=5–6. Tegmina narrowly oval, yellowish brown. Fore and middle legs yellowish green or yellowish brown. Hind femora yellowish green or yellowish brown, ventral part red; upper part with two black maculae, which are often obscured in the female; lateral genicular lobes black or dark brown; genicular hood black or yellowish green. Hind tibiae yellowish green, ventral area darkened; spines black.

Tympanal organs medium in size.

♂. Lateral black stripes present from the posterior margin of eyes to the middle of abdomen (LSW/PH=1/4–1/5). P/M=1.5. Cerci (Fig. 1.24B) gradually and slightly tapering off, obtuse apically, slightly bent upward. Epiphallus (Fig. 1.29I) with lophi ear-lobe-like and bridge narrowed. Lophi uniformly rounded in inner apical margin; outer margin straight and transparent. Dorsal aedeagal sclerite (Fig. 1.30H) marged with sheath, tapering off and elongate. Dorsal aedeagal valve membranous in upper part and sclerotized in lower part; upper part subacute apically and lower part with a very acute apex. Ventral aedeagal valves small; apex not exceeding dorsal aedeagal valve.

♀. Lateral black stripes often obscured (LSW/PH=1/5–1/6). P/M=1.3–1.6. Spermatheca as in Fig. 1.39K; preapical diverticulum as long as apical diverticulum, slightly widened in apical half, subacute apically; spermathecal vestibule (Fig. 1.41K) small, with a hemispheric sclerite in the inner connection to spermathecal duct.

Nymph color (Fig. 1.45E). Generally dark brown, but body color gradually changing. A broad cream-colored band laid under dark brown V-crest, distinct, running from posterior margin of compounds to middle of pronotum. Hind femora with a broad black band on inner side and also on outer side; knee black.

Type specimen. Holotype male (St. Petersburg). Ryūkyū Isl., Amami-Ōshima, Koniya; 16–19 XII 1926 (not examined).

Distribution. [Ryūkyū] Amami Islands and Tokara Islands.

Remarks. *S. kodamae* in Taiwan is closely related to this species, having the body generally green colored, the integument coarse and the male cerci with an obtuse apex. However, it is easily distinguished from *S. punctata* by the male aedeagal valve with an obtuse apex. Habitats of this species are usually light areas around the forest edge of 0–600m altitude in Amami Island.

Sinopodisma aurata Ito, 1999

(Figs 1.4B, 1.7, 1.10G, 1.19F, 1.24A, 1.29J, 1.30I, 1.39I, 1.41J, 3.8)

Sinopodisma aurata Ito, 1999: 504.

General morphology. Integument coarse. Body yellow, yellowish green, or yellowish brown, often aureate. Pronotum (Fig. 1.10G) densely and uniformly punctate; longitudinal carina indistinct, sometimes distinct on metazona; anterior and posterior margins weakly notched. Tegmina oblanceolate, obtuse apically, yellow or yellowish brown; TL=3–5. Fore and middle legs yellowish green or yellowish brown. Hind femora yellowish green or yellowish brown, red ventrally; upper part with two black maculae, which are often obscured in the female; genicular lobes almost black, partly dark brown or partly black. Hind tibiae yellowish green, darken ventrally; tips of spines black. Tympanal organs medium in size.

♂. Lateral black stripes present from posterior margin of eyes to middle of abdomen, on pronotum often extending below along transverse sulci (LSW/PH=1/2.5–1/3). P/M=1.5–1.8. Posterior margin of subgenital plate with a small right-triangular process protruding forward. Cerci (Fig. 1.24A) tapering off and flattened on apical half. Lophi of epiphallus (3.29J) large, trapezoidal. Phallus (Fig. 1.30I) with developed valves of cingulum; dorsal aedeagal sclerite trifurcate apically; ventral aedeagal valves spatulate apically.

♀. Lateral black stripes almost absent, only small maculae present on pronotum. P/M 1.5–1.7. Apical diverticulum of spermatheca (Fig. 1.39I) prolonged, as long as preapical diverticulum, without secondary diverticulum. Sclerite in spermathecal vestibule (Fig. 1.41J) shaped like a glove.

Type specimen. Holotype male (SEHU). Ishigaki Island, Mt. Banna, 26-xi-1997, ITO Gen leg.

Distribution. [Ryûkyû] Yaeyama Islands: Ishigaki Island, Iriomote Island, Kohama Island, Yonaguni Island.

Remarks. *S. punctata* is easily distinguished from *S. aurata* by the green body, the relatively broad tegmina, and dorsal aedeagal sclerite not bifurcate apically. All the known species of the genus from Taiwan are also green- or yellowish green-colored, and thus easily distinguished from *S. aurata*. The species once referred to *Pedopodisma* are characterized by the subapterous or apterous condition and the slightly degenerated tympanal organs. Most of the continental species of *Sinopodisma* (including those of “*Pedopodisma*”) are distinguished from *S. punctata* and *S. aurata* by the shallow transverse sulci, the weak punctures on the pronotum, and the specifically shaped male cerci.

Genus *Tonkinacris* Carl, 1916

Tonkinacris Carl, 1916: 485. Type species: *Tonkinacris decoratus* Carl, 1916, by original designation.

General morphology. Compound eyes large, with a narrow inter-ocular space (Fig.



Fig. 3.7. *Sinopodisma punctata*, male (left) and female (right), from Amami-Ôshima.



Fig. 3.8. *Sinopodisma aurata*, paratype male (left) and paratype female (right), from Ishigaki Island.

1.6A–B; HW/IS=7–10 in male). Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. Pronotum produced posteriorly, sometimes not well produced; punctures sparse on prozona, dense and uniform on metazona; dorsal part of metazona slightly flattened. Tegmina oval or oblong. Hind femora with a small apical spine on the genicular hood. Tympanal organs medium in size.

♂. Furculae absent. Epiproct triangular, longer than wide; median furrow deep in basal half. Cerci tapered off and compressed apically. Lophi of epiphallus quadrilateral, sometimes incised apically. Dorsal aedeagal sclerite bifurcate apically, covered wholly or partly by developed sheath of aedeagus. Ventral aedeagal sclerites bent like a spoon apically and forming ventral aedeagal valves which extend along the dorsal aedeagal valve.

♀. Subgenital plate (Fig. 1.33C) slightly or moderately produced at lateral sides of posterior margin. Cerci much smaller than in male, compressed, conical in profile; apex obtuse. Comstock-Kellogg glands present. Spermathecal vestibule (Fig. 1.41H–I) abruptly narrowed anteriorly, with or without a sclerotized plate, and connected to spermathecal duct; valve in spermathecal aperture present or absent. Spermatheca (Fig. 1.39L–N) with a prolonged apical diverticulum; preapical diverticulum without secondary diverticulum but sometimes with a small projection (*Tonkinacris sinensis*: Fig. 1.39N).

Remarks. This genus contains 6 described species: 2 from the Ryûkyû Archipelago, Japan, 1 from Vietnam, and 3 from continental China. The 2 species from Ryûkyû are relatively isolated within the genus in having the following characters: tegmina strongly abbreviated; pronotum weakly produced; black stripe on longitudinal carina of pronotum indistinct. These characters, however, are not regarded as of generic value, because the tegminal length is variable even within species in Melanoplinae and the other characters mentioned are also often variable within a genus.

Species examined. *Tonkinacris ruficerus* Ito, 1999; *T. sinensis* Chang, 1937; *T. yaeyamaensis* Ito, 1999.

Tonkinacris ruficerus Ito, 1999

(Figs 1.6A, B, 1.19H, 1.24D, 1.29K, 1.30J, 1.45F, 1.39L, 1.41H, 3.9)

Tonkinacris ruficerus Ito, 1999: 506.

General morphology. Antennae red. Lateral black stripes straight, almost continuous from back of compound eyes to hind margin of pronotum (LSW/PH=1/4). Pronotum weakly produced posteriorly; longitudinal carina indistinct on prozona and distinct on metazona; dorsal part of metazona flattened; lateral black stripes present from caudal margin of eyes to 1st abdominal tergite. Metaepimeron yellowish white. Tegmina short and narrow, never overlapping each other; TL=4–5; length / maximum width 2.1–2.7; dark brown below radial vein; upper part almost same as dorsal part of pronotum in color. Hind femora with two black maculae, which are sometimes obscure; narrowest part near femoral flange sometimes becoming yellow by gradually; femoral flange and genicular hood black. Tympanal organs medium in size.

♂. P/M=1.3–1.6. Median furrow of supra-anal plate deep. Posterior margin of subgenital plate (Fig. 1.19H) obtusely rounded. Cerci (Fig. 1.24D) relatively broad,

rounded apically. Lophi of epiphallus (Fig. 1.29K) with two apices. Dorsal aedeagal valve (Fig. 1.30J) small, bifurcate apically, acute apically, wholly covered by sheath of aedeagus; ventral aedeagal valves spatulate and membranous apically.

♀. P/M=1.1–1.3. Body much larger and stouter than in male. Spermathecal vestibule (Fig. 1.41H) without a sclerotized plate, small and narrow, maximum width / width between basal points of anterior basivalvular plate about 1/3. Anterior part of spermathecal duct as in Fig. 1.39L; preapical diverticulum slender, about 1/3 length of apical diverticulum.

Color morphs. In male, body yellowish green laterally and greenish brown dorsally. In female, body variable in color, showing three color patterns as follows: 1. laterally green, dorsally pale brown (morph-1); 2. laterally pale brown, dorsally reddish brown (morph-2); 3. wholly reddish brown (morph-3). In male and morph-1 female, fore and middle legs yellowish green; hind femora green; hind tibiae yellowish green. In morph-2 and -3 females, fore and middle legs reddish brown; hind femora reddish brown; hind tibiae dark blue or dark green.

Nymph color (Fig. 1.45F). Generally brown. Pronotum without distinct V-crest. Hind femora black internally, dark brown externally; knee brown. Body color gradually changing in each molt.

Type specimen. Holotype: male (SEHU). Okinawa-Island, Kunigami-Vil., Oku, 5-xii-1997, ITO Gen leg.

Distribution. [Ryūkyū] Okinawa Island.

Remarks. This species is usually found at the edge of *Pinus luchuensis* (Pinaceae) forests. I observed that some individuals lived on the leaves of *P. luchuensis* for more than three weeks (Ito, 1999). On the other hand, in the laboratory it feeds on some other plants, *Petasites japonicus* var. *giganteus*, *Polygonum sachalinense*, *Plantago asiatica*, and *Aegopodium podagraria*, all these being not distributed in Ryūkyū but having relatives in the archipelago. In the field, this species may feed on various plants in addition to *Pinus luchuensis*.

This species is very similar to *T. yaeyamaensis*, but distinguished by the following characters: sexual dimorphism in body size outstanding; antennae red; tegmina narrow; median furrow of supra-anal plate narrow and deep; cerci short and rounded apically; posterior margin of subgenital plate obtusely rounded in male; dorsal aedeagal sclerite very small; terminal dilation of spermathecal duct narrow; lateral black stripes on head and pronotum distinct in both sexes.

Tonkinacris yaeyamaensis Ito, 1999

(Figs 1.10D, 1.17C, 1.19H, 1.24E, 1.29L, 1.30K, 1.33C, 1.39M, 1.41I, 3.10)

Tonkinacris yaeyamaensis Ito, 1999: 509.

General morphology. Antennae yellowish brown. Pronotum almost same as in *T. ruficerus* in shape. Tegmina brown, short and broad (1.7–1.9 times as long as maximum width), covering tympanal organ, sometimes overlapping each other; TL=5. Hind femora with two black maculae, which are sometimes obscured; upper and lower genicular lobe and genicular hood (Fig. 1.17C) black.

♂. Lateral black stripes narrow (LSW/PH=1/6). P/M=1.2. Body yellowish green, dorsal side faintly reddish; lateral black stripes narrow, occurring from anterior margin

to posterior part of pronotum; fore and mid legs yellowish green; hind femora yellowish green; hind tibiae bluish green with black tipped spines. Supra-anal plate (Fig. 1.19H) with shallow median furrow. Posterior margin of subgenital plate relatively acute. Cerci (Fig. 1.24E) slightly acute apically. Lophi of epiphallus (Fig. 1.29L) with two apices. Dorsal aedeagal sclerite (Fig. 1.30K) bifurcate, broadened medially, acute apically, wholly covered by sheath; ventral aedeagal valves spatulate and membranous apically.

♀. P/M=1.3. Body brown; lateral black stripes obscured; fore and middle legs brown; hind femora brown; hind tibiae dark green with black tipped spines. Spermathecal vestibule (Fig. 1.41I) weakly sclerotized anteriorly, small, relatively broad, maximum width / width between basal points of anterior basivalvular plate about 1/2. Anterior part of spermathecal duct as in Fig. 1.39M; preapical diverticulum slender, about 1/2 length of apical diverticulum.

Type specimen. Holotype: male (SEHU). Iriomote Island, Ôtomi, 5-viii-1996, S. Azuma et al. leg.

Distribution. [Ryûkyû] Yaeyama Islands: Ishigaki Island and Iriomote Island.

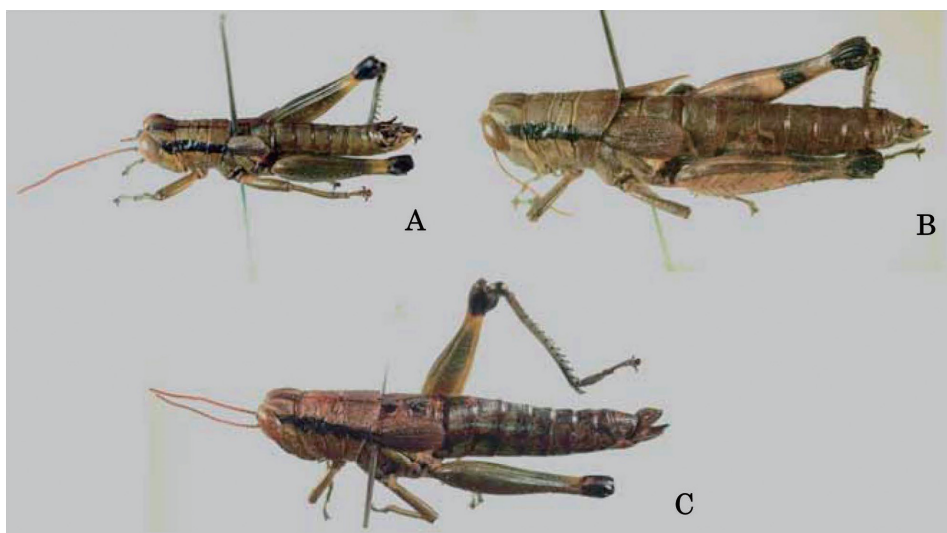


Fig. 3.9. *Tonkinacris ruficerus*, holotype male (A) and paratype females (B, C) from Okinawa Island.



Fig. 3.10. *Tonkinacris yaeyamaensis*, holotype male (left) and paratype female (right) from Iriomote Island.

Genus *Fruhstorferiola* C. Willemse, 1921

Fruhstorferiola Willemse, C., 1921: 3. Type species: *Fruhstorferia tonkinensis* Willemse, C., 1921.

Caudellacris Rehn & Rehn, 1939: 67. Type species: *Caudellacris omei* Rehn & Rehn, 1939, by original designation. Synonymized by Ramme, 1939.

General morphology. Compound eyes large, with a narrow inter-ocular space (HW/IS=7–9 in male). Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. Pronotum produced posteriorly; punctures relatively deep; metazona flattened dorsally. Tegmina oblong, exceeding half length of abdomen. Hind femora with a small apical spine on genicular hood; two faintly black maculae present dorsally. Tympanal organs medium in size.

♂. Furculae absent or very small. Lophi of epiphallus quadrilateral, sometimes incised apically. Sheath of aedeagus covering basal part of aedeagal valves. Dorsal aedeagal sclerite bifurcate apically. Ventral aedeagal sclerites projecting to form ventral aedeagal valves.

♀. Subgenital plate (Fig. 1.33C) weakly or moderately produced at lateral sides of posterior margin. Cerci small, compressed, conical in profile; apex obtuse. Comstock-Kellogg glands present. Spermatheca (Fig. 1.39H) robust; preapical diverticulum robust, as long as apical diverticulum, with a distinct secondary diverticulum. Spermathecal vestibule (Fig. 1.41L) with a weakly sclerotized valve; inner part without distinct sclerite; anterior part abruptly narrowed and bent right- of leftward.

Remarks. This macropterous genus is represented by 9 described species: 8 from continental China and 1 from the Ryūkyū Archipelago, Japan.

Species examined. *F. okinawaensis* Shiraki, 1930; *F. omei* (Rehn & Rehn, 1939); *F. tonkinensis* (Willemse, C., 1921); *F. viridifemorata* (Caudell, 1921).

Fruhstorferiola okinawaensis Shiraki, 1930

(Figs 1.2A, 1.19C, 1.23A, 1.31A, 1.34A, B, 1.45G, 1.39H, 1.41L, 3.11)

Melanoplus okinawaensis Shiraki, 1930: 330.

Fruhstorferiola okinawaensis: Ramme, 1939: 150.

General morphology. Antennae red. Integument coarse. Head and pronotum brown or dark brown dorsally, yellowish green, yellow or ochre laterally. Lateral black stripes on head present behind compound eyes distinctly, on pronotum straight and relatively broad but sometimes obscured in female, continuous to anterior part of 2nd abdominal segment. Abdomen same-colored as lateral part of head and pronotum. Pronotum triangularly produced posteriorly, slightly obtuse apically; punctures sparse on prozona, dense and uniform on metazona; longitudinal carina distinct only on metazona, sometimes distinct on prozona. Lateral black stripes present from posterior margin of eyes to posterior margin of pronotum, straight. Tegmina well developed, yellowish brown or dark brown. Fore and middle legs yellowish green. Hind femora yellowish green or ochre, with two black maculae ventrally; genicular lobes almost black. Hind tibiae pale blue, darken ventrally and basally, with small yellow band near base; spines black.

♂. LSW/PH=1/4. P/M=1.2–1.4. Posterior margin of subgenital plate with a right-triangular process protruding forward. Cerci (Fig. 1.23A) widened and flattened in apical

half; apical margin rounded. Lophi of epiphallus (Fig. 1.29M) trapezoidal, with inner apex slightly projected. Phallus (Fig. 1.31A) with dorsal aedeagal sclerite bifurcate and excurved apically; ventral aedeagal valves membranous and bent toward outside.

♀. LSW/PH=1/4–1/6 (when the black stripes is distinct). P/M=1.1–1.3. Subgenital plate (Fig. 1.34A, B) moderately produced at lateral sides of posterior margin. Preapical diverticulum of spermatheca (Fig. 1.39H) as long as apical diverticulum; secondary diverticulum about 1/3 as long as preapical diverticulum. Spermathecal vestibule (Fig. 1.41L) with a distinct valve, very weakly sclerotized dorsally.

Nymph color (Fig. 1.45G). Generally ocher. Head with very thin lateral black stripes; a cream-colored longitudinal band present on lower internal margin and center of compound eyes. Pronotum with obscure dark brown stripes. Hind femora ocher with three black maculae dorsally, two large black maculae on inner and also outer side; knee black. Abdomen with broad lateral black stripes; a few small rectangular maculae on posterior margin of each abdominal tergite dorsally.

Type specimen. Holotype: female (ENTU). Okinawa, col. T. Shiraki; (another circle label) 684.

Distribution. [Ryûkyû] Okinawa Island, Iheya Island, Amami Islands.

Remarks. This species has relatives in continental China, but is distinguishable by the male cerci (Fig. 1.23) and the female subgenital plate (Fig. 1.34).

Genus *Parapodisma* Mistshenko, 1947

Parapodisma Mistshenko, 1947: 10. Type species: *Pezotettix mikado* Bolívar, I., 1890.

Pseudoparapodisma Inoue, 1985:130. Type species: *Pseudoparapodisma niihamensis* Inoue, 1979, by original designation. Synonymized by Storozhenko, 1993a: 20.

Callopodisma Kanô, 1996: 25. Synonymized by Ishikawa, 1998: 173.

Aopodisma Tominaga & Uchida, 2001: 9. Type species: *Podisma subaptera* Hebard, 1924, by monotypy. Syn. nov.

General morphology. Antennae yellowish brown. Compound eyes large, yellowish brown or dark brown; inter-ocular space narrow (HW/IS=7–10 in male). Frontal carinae distinct and parallel. Frontal costa relatively narrow, depressed almost evenly throughout its length. A pair of lateral black stripes usually extending from hind margin of compound eyes to pronotum or abdomen, and sometimes obscure or absent. Pronotum punctate sparsely on prozona, densely and uniformly on metazona; longitudinal carina distinct only on metazona, sometimes also on prozona; posterior margin triangularly produced or rounded, and sometimes incised; dorsal part usually rounded on prozona and slightly flattened on metazona. Tegmina oval or oblong, not reaching tip of abdomen. Hind femora with a small apical spine on genicular hood; ventral surface usually with a red line (except *P. takeii*). Tympanal organs medium to small.

♂. 1st abdominal segment with a longitudinal carina more distinct than that in the posterior segments. Furculae of 10th abdominal tergite absent or very small. Cerci usually well compressed in apical half, slightly, moderately or strongly incurved. Lophi of epiphallus quadrilateral, trapezoid or sometimes triangular. Sheath of aedeagus covering basal part of aedeagal valves. Dorsal aedeagal sclerite extending to form dorsal aedeagal valve, bifurcate apically. Ventral aedeagal sclerites projecting to form ventral aedeagal valves.

♀. 1st abdominal segment with a longitudinal carina as distinct as that on 2nd segments. Subgenital plate weakly or moderately produced or not produced at lateral sides of posterior margin. Cerci small, compressed, conical in profile; apex obtuse. Comstock-Kellogg glands present. Spermathecal vestibule (Fig. 1.41L) with a sclerite at the aperture forming a valve; inner part with or without a distinct sclerite.

Remarks. *Aopodisma* Tominaga & Uchida (2001) was established by monotypy, excluding *subaptera* from *Parapodsima*. However, all of the characters mentioned by them (enclosed by double quotation marks “ ”) are ambiguous by the following reasons:

- “Size smaller”: This is true, but *subaptera* is not especially small, see the measurements in Table 3.2.

- “Head / pronotal width larger”: No explanation of this ratio was provided, but the measurements in the original description suggest that the value indicates the ratio of the anterior width to the posterior width of the pronotum. However, the authors examined only three *Parapodsima* species of which the pronotum is distinctly widened posteriorly. If species with a slightly widened pronotum (e.g., *P. yasumatsui*) are added to the comparison, *subaptera* will be included in the range of *Parapodisma*.

- “Tegmina degenerated and short, not overlapping with posterior portion of 1st abdominal tergite”: As shown in Chapter 1, the tegminal length is highly plastic and the sizes of some other body parts, for example, the meso- and metanotum, are variable in correlation with the tegmina. In *subaptera* the mesonotum has a pair of grooves, the scutellum and the scutum are not raised, and the metanotum is smooth, with the grooves and scutal pits small and vestigial. In other *Parapodisma*, the mesonotum (Fig. 1.13B) has deep grooves, the scutellum and the scutum are distinctly raised, the metanotum (Fig. 1.13B) has distinct scutal ribs, and the scutum and the scutellum are not raised.

- “Posterior margin of pronotum incised medially. (*Parapodisma* species never or seldom incised)”: Not all *subaptera* individuals show this character, and the occurrence of the incision is connected with the tegminal condition as discussed in Chapter 1. The variation in the shape of the posterior margin of the pronotum is continuous in *Parapodisma*.

- “Structures of nymphs. Particularly color of the body”: As shown in Fig. 1.45, no differences are observed between *subaptera* and the other *Parapodsima* in the color of the nymph. In some individuals from certain populations, nymphs of *subaptera* are darkish color throughout the body, but this condition can often be observed in some other *Parapodsima*, too.

These comparisons and the phylogenetic analysis in the previous chapter suggest that *Aopodisma* should be a synonym of *Parapodsima*. However, *Aopodisma* is somewhat similar to *Sinopodisma* in the characters of female spermathecal vestibule as follows: small; rounded like a ball; semispherical small sclerite situated on inner surface of median part of anterior margin, and connected to thin spermathecal duct.

Parapodisma astris Huang, 2006 was described in Li *et al.* (2006) from Yunnan Province, continental China. Judging from the figures in Li *et al.* (2006), this species apparently belongs to another genus by the following characters:

- Tegmina narrowly spatulate. In *Parapodisma* obovate or oblong.
- Outside of the hind femora with distinct dark maculae. In *Parapodisma* absent. This maculae are often conspicuous in other genera (e.g., *Sinopodisma*).
- Cingulum of male phallus absent or not developed. In *Parapodisma* developed and sometimes forming valves.

Table 3.3. Characters of *Parapodisma* species (1).

Species	Lateral black stripe			Pronotum			Abdomen		
	width in pronotum	development in pronotum (*)		Shape	Dorso-lateral	Color	Color, generally	Lateral black stripe reaching	
		Male	Female					Male	Female
<i>mikado</i>	♂ 1/4-1/6; ♀ 1/5-1/10	2-3	1-3	slightly expand posteriorly	faintly angled in metazona			1st or 2nd tergite	
<i>dairisama</i>	♂ 1/7-1/10	1		nearly cylindrical	rounded	yellowish green or dark green	same as pronotum	2nd or 3rd tergite	present only on 2nd tergite
<i>awagatazensis</i>	♂ 1/6-1/7	2-3						4th or 5th tergite	— (absent)
<i>etsukoana</i>	♂ 1/6-1/7	1-2	1	slightly expand posteriorly	faintly angled in metazona	dark green, sometimes redish green dorsally	yellowish green, dark green or reddish green	4th-10th tergite	3rd-5th tergite
<i>subastris</i>	♂ ♀ 1/7-1/10	1-2				yellowish green or dark green	yellowish green or cream-colored	1st or 2nd tergite	
<i>niihamensis</i> <i>niihamensis</i> <i>niihamensis hiurai</i>	♂ 1/4-1/5; ♀ 1/5-1/8	2-3	1-3		weakly angled in metazona		brownish green	2nd tergite	almost absent
<i>yasumatsui</i>	♂ ♀ 1/5-1/6		1	slender, very slightly expand posteriorly		yellowish green or dark green, rarely red dorsally		2nd tergite	
<i>tenryuensis</i>	♂ ♀ 1/3-1/5	3	2-3	slightly expand posteriorly	faintly angled in metazona	Many color patterns as mentioned in the text	same as pronotum	3rd-10th tergite	2nd-4th tergite
<i>caelestis</i>	♂ ♀ 1/3-1/4			robust, distinctly expand posteriorly		yellowish or dark green laterally and dark green dorsally		10th tergite	6th-8th tergite
<i>takeii</i>	♂ 1/4	3	1-2	nearly cylindrical	rounded			5th-10th tergite	— (absent)
<i>setouchiensis</i>	usually obscured	1-3		slightly expand posteriorly	faintly angled in metazona	yellowish green or dark green	yellowish or brownish green, sometimes pale yellow or reddish green	1st or 2nd tergite (present only in anterior margins)	

(*) Classified as in Chapter 1.

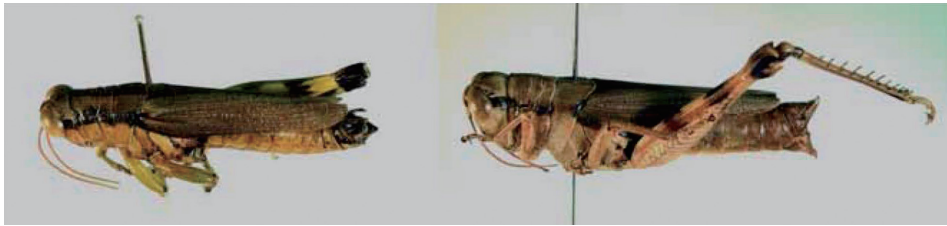


Fig. 3.11. *Fruhstorferiola okinawaensis*, male (left) and female (right) from Okinawa Island.

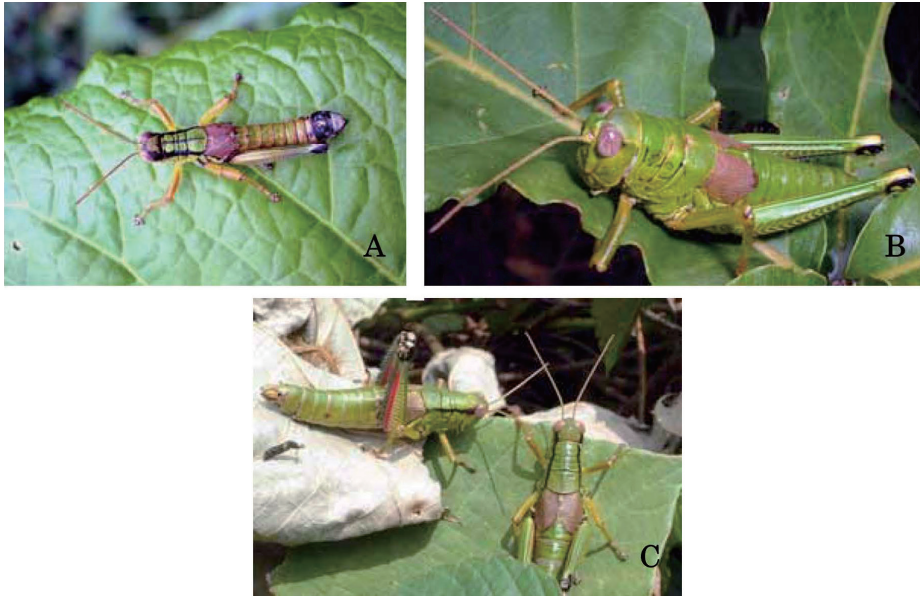


Fig. 3.12. *Parapodisma mikado*. A: male in Tenjindaira, Gunma; B: female in Sapporo; C: females “sun-burning” in Doai, Gumma. Note variation of lateral black stripes, compare females on B and C.

In this paper I exclude *P. astris* from *Parapodisma* but postpone determination of genus it belongs until when specimens of this species are examined well.

Species examined. All 11 species distributed in Japan and adjacent region. Characters of these species are shown in Tables 3.3–6.

Parapodisma mikado (Bolívar, 1890)

(Figs 1.2E, 1.8B, 1.9B, 1.12, 1.13B, 1.14B, 1.17A, 1.20B, 1.25B, 1.29O, 1.31K, 1.32E–F, 1.44A–E, 1.45I–J, 1.40B, 1.42B, 1.43, 3.12, 3.23)

Pezotettix mikado Bolívar, 1890: 323.

Podisma mikado: Rehn, 1902: 637.

Parapodisma mikado: Mistshenko, 1947: 10.

General morphology. Body generally yellowish green or dark green in dorsal and

Table 3.4. Characters of *Parapodisma* species (2).

Species	Tegmina		Tympanal organ	Hind femora		♂ epiproct
	Shape	Color		Color in general	Color of ventral part	Shape
	Figs. 3.12-22					Figs. 1.20
<i>mikado</i>	oval; apex rounded or subacute	yellowish or dark brown	medium	yellowish green	bright red, sometimes pale red or pale green	pentagonal
<i>dairisama</i>	oval, relatively narrow; apex rounded	yellowish or reddish brown			bright red	triangular
<i>awagataensis</i>						
<i>etsukoana</i>	oval; apex rounded or subacute	reddish brown				
<i>subastris</i>		yellowish brown				
<i>niihamensis</i> <i>niihamensis</i>	tapered, rounded at apex					
<i>niihamensis</i> <i>hiurai</i>	only slightly tapered, rounded at apex					
<i>yasumatsui</i>	oval; apex rounded or subacute					
<i>tenryuensis</i>	oval, sometimes more abbreviated	medium or small	yellowish green, sometimes slightly blackish internally			
<i>caelestis</i>	oval, relatively narrow; apex rounded	small	black in depressed part and yellowish green in convex part	bright red, sometimes with darkish stripe		
<i>takeii</i>	vestigial	yellowish or reddish brown	small	yellowish green	pale green	
<i>setouchiensis</i>	oval~oblong, if tegmina developed, tapered; apex rounded or subacute	yellowish brown	medium		bright red, sometimes pale red or pale green	

lateral parts, pale gray or cream-colored in ventral part. Pronotum subcylindrical; dorso-lateral part rounded on prozona and faintly angled on metazona; hind margin (Fig. 1.12) slightly produced and rounded, or triangularly produced. Tegmina oval, subacute or rounded at apex, covering tympanal organs, sometimes overlapping each other, brown, yellowish brown or reddish brown; TL=3–5. Hind wings exceeding posterior margin of metanotum but not reaching posterior margin of 1st abdominal tergite. Hind femora yellowish green with a ventral red line, but in some populations (e.g., from around Toyama Pref.) with the red color weakened and turned into pale yellowish-green. Hind tibiae pale bluish green; spines black. Metanotum (Fig. 1.13B) with distinct scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Tympanal organs (Fig. 1.14B) medium in size.

♂. P/M=1.3–1.5. Lateral black stripes on head present behind compound eyes distinctly or obscured; on pronotum moderate in width (LSW/PH=1/4–1/6), developed continuously in whole length of pronotum, but sometimes obscured on metazona; in abdomen interrupted, present on 1st or 2nd segment. Epiproct (Fig. 1.20B) pentagonal or sometimes nearly right-triangular, black on lateral margins or wholly black; basal width longer than median length; median groove shallow and broad, present on basal half. Distal subsegment of subgenital plate short, black on lateral margins or on entire surface; posterior margin without a triangular process protruding forward. Cerci (Fig.

Table 3.5. Characters of *Parapodisma* species (3).

Species	♂ subgenital plate, distal subsegment			♂ cerci	♂ lophi, in anterior view		
	Length	Black color	Anterior projection on hind margin		Width, comared to epiphallus	Thickness	Shape
				Figs. 1.25-27	Figs. 1.29		
<i>mikado</i>	short	lateral margin or whole part	— present	robust; gradually narrowed in basal 2/3; widened in apical 1/3; obliquely truncate at apex	1/4	thin	trapezoid, with rounded corners
<i>dairisama</i>	medium	lateral margin		gradually and strongly narrowed in basal half; strongly incurved in apical 1/3; obtuse apically			outer margin gradually curved, apical margin straight, inner margin straight
<i>awagatakenensis</i>		—		gradually and strongly narrowed in basal half; incurved in apical 2/5; broadly rounded apically			quadrilateral, with apical margin emarginate
<i>etsukoana</i>		posterior half		gradually narrowed in basal half, incurved in apical half; broadly rounded apically			
<i>subastris</i>	short	lateral and anterior margin	—	slender; gradually narrowed in basal 2/3; slightly compressed and incurved in apical 1/3	1/8	moderate	strongly constricted and bent inward in apical 1/3
<i>niihamensis niihamensis</i>		lateral margin		slender; gradually narrowed in basal 2/3; apical 1/3 compressed, widened, slightly incurved, rounded or sometimes truncate at apex	1/7-1/6		triangular (sometimes elongate), apical margin acute or subacute
<i>niihamensis hiurai</i>				slender; gradually narrowed in basal 2/3; apical 1/3 compressed, narrowed, slightly incurved, subacute at apex			trapezoid or excurved, apical margin rounded
<i>yasumatsui</i>	project strongly and sharply		—	strongly and gradually narrowed in basal half; incurved in apical half; obtuse apically	1/4		earlobe-shaped, apical inner corner slightly projected acutely
<i>tenryuensis</i>	medium	lateral and anterior margin		gradually narrowed in basal half or 2/3; slightly incurved in apical 1/3; the apical part narrowed or slightly widened with obtuse apex	1/4 - 1/3	thin - thick	
<i>caelestis</i>	short	whole part		gradually narrowed in basal half; rounded or subacute apically	1/5	thick	earlobe-shaped, apical margin rounded
<i>takeii</i>	medium	—		short and robust; gradually narrowed in basal half; obtuse apically	1/4	moderate	outer margin gradually curved, inner margin straight
<i>setouchiensis</i>	short ~ project	lateral margin	absent ~ present	gradually narrowed in basal half; apical half slightly widened or strongly incurved	1/5 - 1/4	thin - moderate	trapezoid, with rounded rounded outer corner and slightly projected inner corner

1.25B) short and robust, gradually narrowed from base to basal 2/3, and then widened in apical 1/3; the most narrowest point about a half width of the base; tip obliquely truncate. Lophi of epiphallus (Fig. 1.29O) thin, about 1/4 times as wide as epiphallus, trapezoid with corners rounded or only outer margin gently curved. Apical part of phallus as in Fig. 1.31K; valves of cingulum surrounding aedeagal valves, not sclerotized; dorsal aedeagal valve gradually attenuate, acute apically; ventral aedeagal valves membranous, widened apically.

♀. P/M=1.2–1.6. Lateral black stripes present (Figs 1.44A–E, 3.13C) or absent (Fig. 3.13B), and if present, on pronotum broad, medium or narrow in width (LSW/

Table 3.6. Characters of *Parapodisma* species (4).

Species	♂ valves of cingulum (cv)	♂ dorsal aedeagal valve (dav), apical part	♂ ventral aedeagal valves (vav)	♀ subgenital plate, posterior margin	Preapical diverticulum of spermatheca		Apical diverticulum length compared to preapical one	Spermathecal vestibule (Sv)			
					Shape	Second diverticulum		Shape	Sclerite	spermathecal duct is connected to	
	Figs. 1.31			Figs. 1.32-33	Figs. 1.41			Figs. 1.43			
<i>mikado</i>	surrounding aedeagal valves	gradually attenuate, acute apically, extending lateral sides	membranous, widened apically	gradually curved	robust, basal part less than 1/3 width of apical part	absent	shorter	fist-like	almost whole part strongly sclerotized	right- or leftside of anterior part, ventral surface	
<i>dairsama</i>		near apex abruptly narrowed, apex	nearly truncate	lateral part angulate or slightly projected				present	emarginate right or leftside of anterior margin		diverged narrow sclerite in anterior half
<i>awagatakensis</i>			membranous, truncate apically						flattened pyriform		medially, 1/3 as wide as Sv
<i>etsukoana</i>	lobiform, strongly sclerotized	gradually attenuate and truncate apically, with a rounded protuberance dorsally	thick, obliquely truncate apically	x 2		extraordinary large, glove-like, with many wrinkles	medially, about 1/5 as wide as Sv				
<i>subastris</i>	lobiform, moderately sclerotized	gradually attenuate and truncate apically	thick, apex slightly bent upward	about same length		glove-like, with anterior sac and many wrinkles	shaped like profile of claw	right- or leftside of anterior part, ventral surface			
<i>niihamensis</i>	lobiform, slightly sclerotized	near apex abruptly narrowed, apex very acute	thick, truncate and membranous apically				absent (sometimes present)		anterior part strongly bent downward in right- or leftside, concave medially		sclerotized medially, 1/3 to 1/2 width of Sv
<i>niihamensis</i>											
<i>niihamensis hiurai</i>						sclerotized in almost all part except lateral margins					
<i>yusumatsui</i>						gradually attenuate, acute apically					
<i>tenryuensis</i>						shorter					
<i>caelestis</i>											
<i>takeii</i>	lobiform, slightly sclerotized	attenuate and truncate apically	lamellate, rounded, subacute apically	gradually curved	robust, basal part thick	absent		small and rounded	small, ball-like	median part of anterior margin	
<i>setouchiensis</i>	fused with das, vas and weakly sclerotized vav	cv triangularly produced as dav	bent inward and upward, acute apically	lateral part distinctly projected	slender	present	x 2 or much longer	elongated, gradually narrowed to spermathecal duct	—	median part of anterior margin	

PH=1/5–1/10); development highly variable: sometimes present only on posterior part of compound eyes and some grooves, sometimes continuously over pronotum and 1st or 2nd abdominal segments. Subgenital plate (Fig. 1.32E, F) gradually curved on posterior margin. Spermatheca as in Fig. 1.40B; preapical diverticulum robust; basal part relatively thick; 2nd diverticulum usually absent, but rarely present and small; apical diverticulum shorter than preapical one. Spermathecal vestibule (Fig. 1.42B) shaped like a fist, with a few longitudinal grooves; sclerite black, dark brown or brown, 1/2–2/3 as wide as spermathecal vestibule, with a deep medial groove, usually asymmetrical (Fig. 1.42B, 3.43B) but sometimes nearly symmetrical (Fig. 1.43C); thin spermathecal duct connected to ventral surface of right or left side of anterior part.

Nymph color (Fig. 1.45I, J). Generally greenish brown, rarely wholly black. The dark-yellow-dark pattern of stripes indistinct. Femora with two large black maculae on each lateral surface, which are sometimes continued.

Type specimen. Holotype male (Museo Nacional de Ciencias Naturales, Madrid), with 6 labels as follows: (1) Yeso 86 / Japon [handwritten]; (2) 3 [printed on yellow label]; (3) Pezotettix Mikado Bol Dr. Bonnet; (4) Prunna mikado Bol. [handwritten by Bolívar]; (5) Sintipo [printed on red label]; (6) MNCN Cat. Tipos / 8301 [printed on red label].

Distribution (Fig. 3.23). [Hokkaidô] Widely distributed. [Honshû] Tôhoku district and Tochigi, Gumma, Niigata, Nagano, Gifu, Toyama, Ishikawa, Fukui, Shiga; Kunashiri Is.; Sakhalin.

Remarks. Geographic variations have been observed in the development of the lateral black stripes, the coloration on the ventral part of the hind femora and the male aedeagal valves. In Hokkaidô, the lateral black stripes are not well developed and sometimes almost entirely absent (Fig. 3.13B), while in Honshû, they are well developed in almost all the individuals examined (Fig. 3.13A, C). According to Negoro (1991), geographic variations are found in the color of the ventral surface of the hind femur: around Toyama Prefecture, it is pale yellowish-green and the red line is weaker.

Parapodisma dairisama (Scudder, 1897)
(Figs 1.20C, 1.25C, 1.29P, 1.31L, 1.40C, 1.42C, 3.13)

Podisma dairisama Scudder, 1897b: 112.

Podisma fauriei Shiraki, 1910: 73. (*nec* Bolívar, 1890)

Miramella dairisama: Dovnar-Zapolskii, 1933: 266.

Odontopodisma dairisama: Ramme, 1939: 139.

Parapodisma dairisama: Mistshenko, 1951: 225.

Callopodisma dairisama Kanô, 1996: 27.

Parapodisma dairisama: Ishikawa, 1998: 173.

General morphology. Body generally yellowish green or dark green in dorsal and lateral parts, yellow or cream-colored in ventral part. Pronotum subcylindrical; dorso-lateral part rounded; hind margin slightly produced and rounded, or slightly emarginate. Tegmina oval, rounded at apex, covering tympanal organ, never overlapping each other, yellowish or reddish brown; TL=3–4. Hind wings vestigial, reaching or slightly exceeding hind margin of metanotum. Metanotum flat, only with vestigial scutal pits and grooves. Hind femora yellowish green with a ventral red line. Hind tibiae pale bluish green; spines black. Tympanal organs medium in size.

♂. P/M=1.4–1.7. Lateral black stripes on head present behind compound eyes; on pronotum absent or, when present, very narrow, reaching 1st transverse sulcus (LSW/PH=1/7–1/10); on abdomen distinct and broad only on 2nd segment, present but faint and narrow on the several posterior segments. Epiproct (Fig. 1.20C) triangular, black on lateral margins or on entire surface; basal width equal to median length; median groove deep, present on basal half or in almost whole length. Distal subsegment of subgenital plate medium in length, black on lateral margin; posterior margin without a triangular process protruding forward. Cerci (Fig. 1.25C) strongly narrowed on basal half and width of apical half less than half width of the base; strongly incurved on apical 1/3; obtuse apically. Lophi of epiphallus (Fig. 1.29P) thin, about 1/4 times as wide as epiphallus; outer margin gradually curved; apical and inner margins straight. Apical part of phallus as in Fig. 1.31L; valves of cingulum surrounding aedeagal valves, not sclerotized; dorsal aedeagal valve extending laterally, acute apically; ventral aedeagal valves membranous, truncate apically.

♀. P/M=1.4–1.6. Lateral black stripes on head present behind compound eyes; absent on pronotum; on abdomen broad on anterior margin of 2nd segment, faint or absent on several posterior segments. Subgenital plate with posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40C; preapical diverticulum robust and basal part less than 1/3 width of apical part, without 2nd diverticulum; apical diverticulum shorter than preapical one. Spermathecal vestibule (Fig. 1.42C) emarginate

near apex, with several furrows dorsally; sclerite reddish brown, shaped like a reversed V; thin spermathecal duct connected to ventral surface of right- or left-side of anterior part.

Type specimen. Syntypes: 1 male and 1 female (United States National Museum of Natural History, Washington, USA). Japan: (U.S.N.M. [No. 729], through L. Bruner) (not examined).

Distribution (Fig. 3.23). [Honshû] Nagano, Aichi, Gifu, Ishikawa, Shiga, Kyôto, Mie, Nara, Ôsaka, Hyôgo, Tottori, Okayama.

Remarks. This species is closely related to *P. awagatakensis* so far as based on the cladistic analysis and the shape of the male cerci and aedeagal valves. In this species the male cerci have the apical part narrower than in *P. awagatakensis*, the dorsal aedeagal valve not extending laterally at the apex, and the male subgenital plate provided with no anterior process on hind margin.

Parapodisma awagatakensis Ishikawa, 1998

(Figs 1.20D, 1.25G, 1.29Q, 1.31M, 1.33B, 1.44K, 1.40H, 1.42F, 3.14)

Parapodisma awagatakensis Ishikawa, 1998: 173.

General morphology. Body generally yellowish green. Pronotum subcylindrical; dorso-lateral part rounded on prozona, slightly angulate on metazona; hind margin slightly produced and rounded. Tegmina oval, rounded at apex, covering tympanal organ, never overlapping each other, yellowish brown; TL=3–4. Hind wings vestigial, slightly exceeding hind margin of metanotum. Hind femora yellowish green with a ventral red line. Hind tibiae pale bluish green; spines black. Tympanal organs medium in size.

♂. P/M about 1.4. Lateral black stripes (Fig. 1.44K) on head present behind compound eyes; on pronotum narrow (LSW/PH=1/6–1/7), reaching 3rd transverse sulcus or interrupted and reaching posterior margin; on abdomen broad, running from 1st to 4th or 5th segment, absent in the posterior segments. Metanotum flat; shallow scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Epiproct (Fig. 1.20D) triangular, black on lateral margins; basal width equal to median length; median groove deep and narrow, present in almost whole length. Distal subsegment of subgenital plate medium in length, black part absent; posterior margin with a small triangular process protruding forward. Cerci (Fig. 1.25G) strongly narrowed in basal 3/5; strongly incurved in apical 2/5; rounded apically. Lophi of epiphallus (Fig. 1.29Q) thin, about 1/4 times as wide as epiphallus; quadrilateral, with apical margin emarginate. Apical part of phallus as in Fig. 1.31M; valves of cingulum surrounding aedeagal valves, not sclerotized; dorsal aedeagal valve abruptly narrowed near apex, acute at apex; ventral aedeagal valves membranous, truncate apically.

♀. P/M=1.3–1.5. Lateral black stripes on head present only in posterior half between hind margin of compound eyes and posterior margin of head; on pronotum only on anterior margin; on abdomen absent. Metanotum flat, only with vestigial scutal pits and grooves. Subgenital plate with posterior margin (Fig. 1.33B) angulate or slightly projected laterally. Spermatheca as in Fig. 1.40H; preapical diverticulum robust and basal part less than 1/3 width of apical part, with 2nd diverticulum; apical diverticulum slightly longer than preapical one. Spermathecal vestibule (Fig. 1.42F) flattened pyriform; sclerite reddish brown, 1/3 as wide as spermathecal vestibule; thin spermathecal duct connected to ventral surface of right or left side of anterior part.

Type specimen. Holotype male (OMNH). Mt. Awagatake, Kakegawa-City, Shizuoka Pref. 14,

vii, 1997, H. Ishikawa leg.

Distribution (Fig. 3.23). [Honshû] Shizuoka. The distribution of this species is limited to an area between the Ôi River and the Tenryû River.

Remarks. This species is closely related to *P. dairisama*, as stated under the preceding species.

Parapodisma etsukoana Kobayashi, 1986

(Figs 1.20E, 1.25J, 1.29R, 1.31E, 1.44J, 1.45K, 1.38, 1.40D, 1.42D, 3.15)

Parapodisma etsukoana Kobayashi, 1986: 513.



Fig. 3.13. *Parapodisma dairisama*, male (left) and female (right) from Inabu, Aichi Pref.

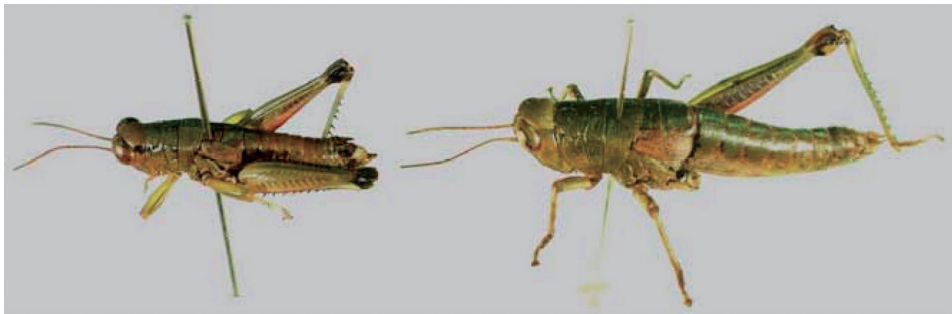


Fig. 3.14. *Parapodisma awagataensis*, male (left) from Mt. Awagatake, Kakegawa-City and female (right) from Kanaya-Town.



Fig. 3.15. *Parapodisma etsukoana*, male (left) and female (right) from Shitara-Town, Aichi Pref.

General morphology. Body generally yellowish green or dark green in dorsal and lateral parts, cream-colored or pale green in ventral part. Pronotum subcylindrical, usually green but sometimes only dorsal part reddish green; dorso-lateral part rounded on prozona, slightly angulate on metazona; dorsal part slightly flattened; hind margin slightly produced and obtusely acute medially. Tegmina oval, usually subacute but sometimes rounded at apex, covering tympanal organ, never overlapping each other, reddish brown or brown; TL=3–4. Hind wings vestigial, slightly exceeding hind margin of metanotum. Hind femora yellowish green with a ventral red line. Hind tibiae pale bluish green or dark yellow; spines black. Tympanal organs medium in size.

♂. P/M=1.4–1.6. Lateral black stripes (Fig. 1.44J) on head present behind compound eyes; on pronotum narrow (LSW/PH=1/6–1/7), present on anterior and posterior margins, or interrupted and reaching 3rd transverse sulcus; on abdomen distinct and broad, running from 1st segment to near tip of abdomen. Metanotum with distinct scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Abdominal tergites generally yellowish green, but sometimes reddish green. Epiproct (Fig. 1.20E) triangular, without black part or black on lateral margins; basal width equal to median length; median groove deep or shallow, narrow or broad, present in almost whole length. Distal subsegment of subgenital plate medium in length, black on posterior half; posterior margin usually with a distinct triangular process protruding forward. Cerci (Fig. 1.25J) gradually narrowing in basal half; strongly incurved in apical half; broadly rounded apically. Lophi of epiphallus (Fig. 1.29R) moderately thick, about 1/4 times as wide as epiphallus; quadrilateral, with apical margin emarginate. Apical part of phallus as in Fig. 1.31E; valves of cingulum lobiform, strongly sclerotized; dorsal aedeagal valve gradually attenuate and truncate apically, with a rounded protuberance dorsally; ventral aedeagal valves thick, membranous and obliquely truncate at apex.

♀. P/M=1.2–1.5. Lateral black stripes on head present behind compound eyes, on pronotum only at anterior margin and sometimes also at posterior margin, on abdomen running from 2nd to 3rd, 4th or 5th segment. Metanotum with shallow scutal grooves incompletely dividing scutum+scutellum from the other parts; scutal ribs obscured. Abdominal tergites generally dark pink green or dark orange green, but sometimes yellowish green. Subgenital plate with posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40D; preapical diverticulum robust and basal part less than 1/3 times wide of apical part, with 2nd diverticulum; apical diverticulum about twice length of preapical one. Spermathecal vestibule (Fig. 1.42D) extraordinary large, glove-like, with many wrinkles; sclerite reddish brown, 1/5 as wide as spermathecal vestibule; thin spermathecal duct connected to ventral surface of right or left side of anterior part.

Nymph color (Fig. 1.45K). Generally pale brown. The dark-yellow-dark pattern of stripes present, the dark stripes being pale brown. Femora usually with two large pale brown maculae on each lateral surface, which are sometimes continuous.

Type specimen. Holotype male (OMNH). Hashiba, Nagiso-Town, Nagano Pref., 8, viii, 1980, M. Kobayashi leg.

Distribution (Fig. 3.24). [Honshû] Gumma, Tochigi, Saitama, Tôkyô, Yamanashi, Niigata, Nagano, Shizuoka, Aichi, Gifu, Toyama, Ishikawa, Fukui, Shiga, Mie, Kyôto.

Remarks. In general coloration this species is divisible into 3 types as follows. Type 1: both pronotum and abdominal tergite green; type 2: pronotum green, abdominal tergite reddish green; type 3: both dorsal part of pronotum and abdominal tergite reddish

Table 3.7. Coloration of *Parapodisma etsukoana*.

Prefecture	City, Town, Vil.	♂			♀		
		Type 1	Type 2	Type 3	Type 1	Type 2	Type 3
Niigata	Tsunan-Town (Mikura)	6	-	-	-	5	-
Niigata	Tsunan-Town (Maekura)	10	-	-	-	2	-
Niigata	Muikamachi-Town	2	-	-	-	3	-
Gumma	Niiharu-Vil. (Sarugakyô)	5	-	-	1	6	-
Gumma	Niiharu-Vil. (Hôshi)	5	-	-	1	8	1
Gumma	Onishi-Town	1	-	2	1	1	-
Saitama	Hannô-City	2	-	2	-	1	-
Saitama	Ogano-Town	-	-	-	-	1	4
Aichi	Kamiyahagi-Vil.	-	-	-	-	2	-
Aichi	Shitara-Town	7	-	-	-	14	-
Gifu	Miyagawa-Vil.	-	-	-	1	-	-
Shiga	Makino-Town	2	-	-	2	5	-

Type 1: both pronotum and abdominal tergite green; type 2: pronotum green, abdominal tergite reddish green; type3: both dorsal part of pronotum and abdominal tergite reddish green.

green. When the pronotum is reddish, the abdomen is always reddish, that is, there are no individuals in which the pronotum is reddish and the abdomen is green. Females usually have reddish abdominal tergites, and in most males, only the posterior margin of each tergite is reddish. Only in the eastern part of its distribution (Saitama Pref. And Gumma Pref.), I found individuals with the dorsum of the pronotum and the abdominal tergite are reddish green (Table 3.7).

This species is closely related to *P. subastris* as discussed in the previous chapter. It is easily distinguished from the other members of *Parapodisma* by the shape of extraordinary large male phallic complex.

Parapodisma subastris Huang, 1983

(Figs 1.20F, 1.25H, 1.29S, 1.31J, 1.45L, 1.40E, 1.42E, 3.16)

Parapodisma subastris Huang, 1983: 457.

General morphology. Body generally yellowish green or dark green in dorsal and lateral parts, cream-colored or pale green in ventral part, seldom black wholly. Pronotum subcylindrical; dorso-lateral part rounded on prozona, slightly angulate on metazona; hind margin slightly produced and obtusely acute medially. Tegmina oval, subacute or rounded at apex, covering tympanal organ, often overlapping each other, yellowish brown; TL=5–7. Hind wings almost reaching or slightly exceeding hind margin of 1st

abdominal segment. Metanotum with distinct scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Hind femora yellowish green with a ventral red line. Hind tibiae pale yellowish green or dark yellow; spines black. Tympanal organs medium in size.

♂. P/M=1.2–1.6. Lateral black stripes on head present behind compound eyes; on pronotum narrow (LSW/PH=1/7–1/10), on anterior and posterior margins, or reaching 3rd transverse sulcus; on abdomen broad only on 1st and 2nd segments. Epiproct (Fig. 1.20F) triangular and flat, black on lateral margins or entirely cream-colored; basal width longer than median length; median groove narrow and shallow, in half to almost whole length of epiproct. Distal subsegment of subgenital plate short or medium in length, broadly black on lateral margins (and often on anterior margin, too) and forming a triangle zone in cream-colored ground, sometimes black more extensively or wholly; posterior margin without a triangular process protruding forward. Cerci (Fig. 1.25H) slender; basal 2/3 gradually narrowed; apical 1/3 compressed and incurved; apex obliquely truncate. Lophi of epiphallus (Fig. 1.29S) moderately thick, about 1/8 times as wide as epiphallus; apical 1/3 strongly constricted and bent inward. Apical part of phallus as in Fig. 1.31J; valves of cingulum lobiform, inner part moderately sclerotized; dorsal aedeagal valve gradually and slightly attenuate and truncate apically, with a longitudinal carina at exposed part; ventral aedeagal valves compressed, constricted near apex, and outcurved at apex.

♀. P/M=1.2–1.5. Lateral black stripes on head present behind compound eyes; on pronotum sometimes limited to 1st and 3rd transverse sulci, but usually present on posterior margin, and sometimes interrupted and reaching 3rd transverse sulcus, narrow if distinct, LSW/PH=1/7–1/10; on abdomen almost absent. Subgenital plate with posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40E; preapical diverticulum robust and basal part less than 1/3 width of apical part, with 2nd diverticulum; apical diverticulum about twice length of preapical one. Spermathecal vestibule (Fig. 1.42E) extraordinary large, glove-like, with many wrinkles; sclerite reddish brown, shaped like a claw in profile, 1/3–1/4 as wide as spermathecal vestibule; right or left side of anterior part connected to thick spermathecal duct. Spermathecal duct strongly bent, slightly widened, and then strongly narrowed.

Nymph color (Fig. 1.45L). Generally greenish brown or yellowish brown. The dark-yellow-dark pattern of stripes indistinct, or sometimes distinct, the dark stripes being dark brown. Femora usually with two large dark brown maculae on each lateral surface, which are sometimes continuous.

Type specimen. Holotype male (Beijing. Not found during my visit, thus not examined). Japan, Kyôto, 1931. VIII. 16, K. Eki leg.

Distribution (Fig. 3.24). [Honshû] Nagano, Gifu, Fukui, Shiga, Mie, Nara, Wakayama, Kyôto, Ôsaka, Hyôgo.

Remarks. This species is closely related to *P. etsukoana* as discussed in the previous chapter.

Parapodisma niihamensis Inoue, 1979

(Figs 1.10E, 1.20G–H, 1.25D–E, 1.29T₁₋₂, 1.31H–I, 1.40F–G, 1.42H–I, 3.17A–B)

Parapodisma niihamensis Inoue, 1979b: 61.

Pseudoparapodisma niihamensis: Inoue, 1985: 130.

Parapodisma niihamensis: Tominaga & Kanô, 1987: 35; Kanô, 1990: 45.

General morphology. Body generally yellowish green or slightly brownish green in dorsal and lateral parts, cream-colored or pale green in ventral part; abdominal tergite sometimes yellowish brown. Pronotum (Fig. 1.10E) subcylindrical; dorso-lateral part rounded on prozona, angulate on metazona; dorsum flattened on metazona; hind margin produced and obtusely acute medially. Tegmina oblong, covering tympanal organ, overlapping each other, rounded at apex, yellowish brown; TL=9–16. Hind wings almost as long as tegmina. Hind femora yellowish green with a ventral red line. Hind tibiae dark yellow or pale bluish green, sometimes darkened partly or entirely; spines black. Metanotal scutum+scutellum divided from the other parts with deep scutal grooves; scutal ribs forming a triangular shape. Tympanal organs medium in size.

♂. P/M=1.2–1.5. Lateral black stripes on head present behind compound eyes; on pronotum moderate in width (LSW/PH=1/4–1/5), reaching 3rd transverse sulcus and present on posterior margin; on abdomen in anterior part of 2nd segment and almost absent on the posterior segments. Epiproct (Fig. 1.20G–H) triangular, flat; basal width



Fig. 3.16. *Parapodisma subastris*, male (left) and female (right) from Kyoto-City.

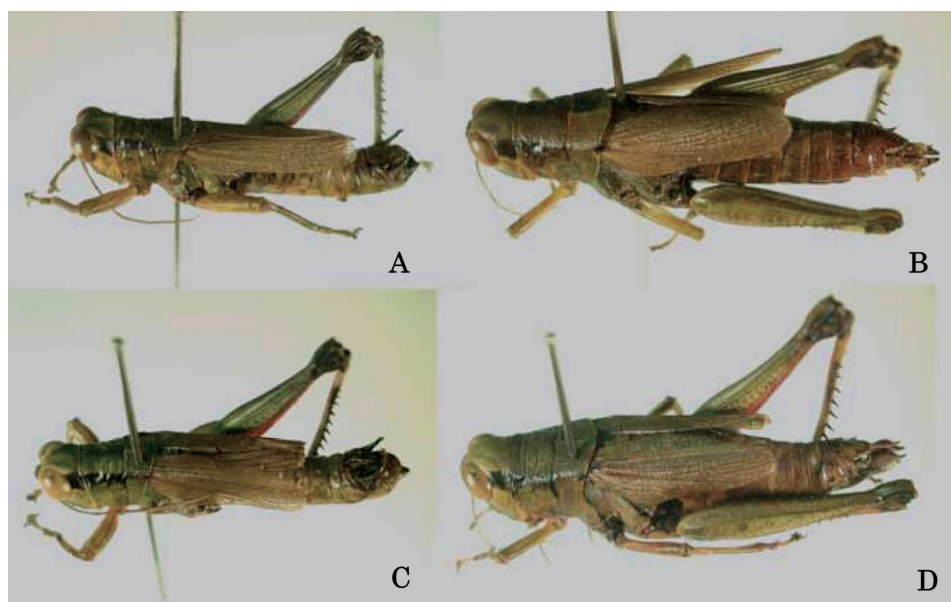


Fig. 3.17. *Parapodisma niihamensis niihamensis*, male (A) and female (B) from Kamiyama-Town, Tokushima Pref. *P. niihamensis hiurai*, male (C) and female (D) from Ômiya-Town, Mie Pref.

equal to or exceeding median length; median groove shallow or deep, and narrow or broad, present in almost whole length. Distal subsegment of subgenital plate very short, black laterally; posterior margin without a small triangular process protruding forward. Cerci slender; basal 2/3 gradually narrowed; apical 1/3 compressed, slightly incurved and widened (Fig. 1.25D) or narrowed (Fig. 1.25E), rounded at apex. Lophi of epiphallus moderately thick, about 1/6–1/7 times as wide as epiphallus, triangular (Fig. 1.29T₁) or quadrilateral (Fig. 1.29T₂); apical margin subacute or rounded. Apical part of phallus as in Fig. 1.31H–I; valves of cingulum lobiform, slightly sclerotized; dorsal aedeagal valve abruptly narrowed near apex, acute at apex; ventral aedeagal valves with a truncate and membranous apex.

♀. P/M=1.1–1.4. Lateral black stripes on head present behind compound eyes; on pronotum moderate in width (LSW/PH=1/5–1/8), sometimes present only on anterior and posterior margins, but sometimes reaching 3rd transverse sulcus; on abdomen absent. Abdominal tergites pale brown. Subgenital plate posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40F–G; preapical diverticulum robust and basal part less than 1/3 width of apical part, with 2nd diverticulum; apical diverticulum as long as preapical one. Spermathecal vestibule (Fig. 1.42H–I) with anterior part strongly bent downward in right or left side, concave medially; sclerite reddish brown, 1/2–1/3 as wide as spermathecal vestibule; thin spermathecal duct connected to ventral surface of right or left side of anterior part.

Type specimen. Holotype male (ELEU). Kawamata (500m alt.), Niihama-City, Ehime Pref., VIII-16 1972, M. INOUE leg.

Distribution (Fig. 3.24). [Honshû] Mie, Nara, Wakayama, Ôsaka. [Shikoku] Kagawa, Tokushima, Ehime, Kôchi; Awaji Island.

Remarks. The concept of *P. niihamensis* adopted in this paper includes *P. hiurai*, which was formerly supposed to be a distinct species. I treat *hiurai* as a subspecies of this species. Each subspecies are distinguished by the following characters: 1) groove width of male epiproct; 2) degree of protruding of male subgenital plate; 3) male cercal shape; 4) shape of lophi of epiphallus; 5) shape of valves of cingulum in male; 6) slight difference in tegminal shape.

Similar differences, however, are usually observed among populations of *P. tenryuensis* and also of *P. setouchiensis*. In the female *niihamensis* and *hiurai* are indistinguishable even in characters of the spermathecal vestibule (Fig. 1.41H–I). There may be some difference in the length of the 2nd diverticulum of the preapical diverticulum of the spermatheca (Fig. 1.39F–G), but it is usually variable among conspecific individuals in *Parapodisma*. All this suggests that the differences among *niihamensis* and *hiurai* are conspecific variations. These populations are discretely distributed and thus I recognize them as subspecies.

Parapodisma niihamensis niihamensis Inoue, 1979

Diagnosis. Groove of epiproct relatively broad (Fig. 1.20H). Male subgenital plate not protrude (Fig. 1.25D). Male cerci widened apically (Fig. 1.25D). Lophi of male epiphallus triangular, acute or subacute at apex (Fig. 1.29T₂). Valves of cingulum of phallus truncate at apex (Fig. 1.31H). Tegmina relatively broad, only slightly tapered (Fig. 3.17A, B).

Distribution (Fig. 3.24). [Honshû] Awaji Island. [Shikoku] Kagawa, Tokushima,

Ehime, Kôchi.

Parapodisma niihamensis hiurai Tominaga & Kanô, 1987

Parapodisma hiurai Tominaga & Kanô, 1987: 29.

Diagnosis. Groove of epiproct relatively narrow (Fig. 1.20G). Male subgenital plate slightly protrude (Fig. 1.25E). Male cerci slightly tapered, not widened apically (Fig. 1.25D). Lophi of male epiphallus quadrilateral, rounded or subacute at apex (Fig. 1.29T₁). alves of cingulum of phallus slightly tapered, subacute at apex (Fig. 1.31I). Tegmina tapered and relatively narrow (Fig. 3.17C, D).

Distribution (Fig. 3.24). [Honshû] Kii Peninsula.

Type specimen. Holotype male (OMNH). Chihaya-jôshi, Kurotogadani, Mt. Kongô, Chihayaakasaka-Vil., Ôsaka Pref. 23, viii, 1977. I. Hiura leg.

Parapodisma yasumatsui Yamasaki, 1980

(Figs 1.20I, 1.25F, 1.29U, 1.31N, 1.40I, 1.42G, 3.18)

Parapodisma yasumatsui Yamasaki, 1980: 50.

General morphology. Body generally yellowish green or slightly brownish green dorsally and laterally, pale green ventrally. Dorsal part of pronotum and abdominal tergites seldom bright red. Pronotum subcylindrical; dorso-lateral part rounded on prozona, slightly angulate on metazona; dorsal part rounded on prozona, but slightly flattened on metazona; hind margin slightly produced and obtusely acute medially. Tegmina oval, covering tympanal organ, sometimes overlapping each other, yellowish brown; TL=5–7. Hind wings almost reaching or slightly exceeding hind margin of 1st abdominal segment. Metanotum with distinct scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Hind femora yellowish green with a ventral red line. Hind tibiae pale bluish green or dark yellow; spines black. Tympanal organs medium in size.

♂. P/M=1.3–1.7. Lateral black stripes on head present behind compound eyes; on pronotum narrow (LSW/PH=1/5–1/6), reaching 3rd transverse sulcus and present on posterior margin, or continuously present in whole length; on abdomen distinct, running from 1st tergite to anterior part of 2nd segment, absent in posterior segments. Epiproct (Fig. 1.20I) triangular; basal width slightly exceeding median length; median groove distinct and shallow on basal half, strongly converged near median transverse suture, subparallel and obscured apically. Distal subsegment of subgenital plate strongly projected; lateral margin black; posterior margin without a small triangular process protruding forward. Cerci (Fig. 1.25F) strongly narrowed on basal half, strongly incurved in apical half; apex obtuse. Lophi of epiphallus (Fig. 1.29U) moderately thick, about 1/4 times as wide as epiphallus; earlobe-shaped; apical inner corner slightly projected. Apical part of phallus as in Fig. 1.31N; valves of cingulum lobiform, slightly sclerotized; dorsal aedeagal valve abruptly narrowed near apex, acute at apex; ventral aedeagal valves at apex membranous and truncate.

♀. P/M=1.3–1.4. Lateral black stripes on head present behind compound eyes; on pronotum only at anterior and posterior margins, or reaching 3rd transverse sulcus (when stripes continuously present, LSW/PH=1/5–1/6); on abdomen almost absent. Subgenital

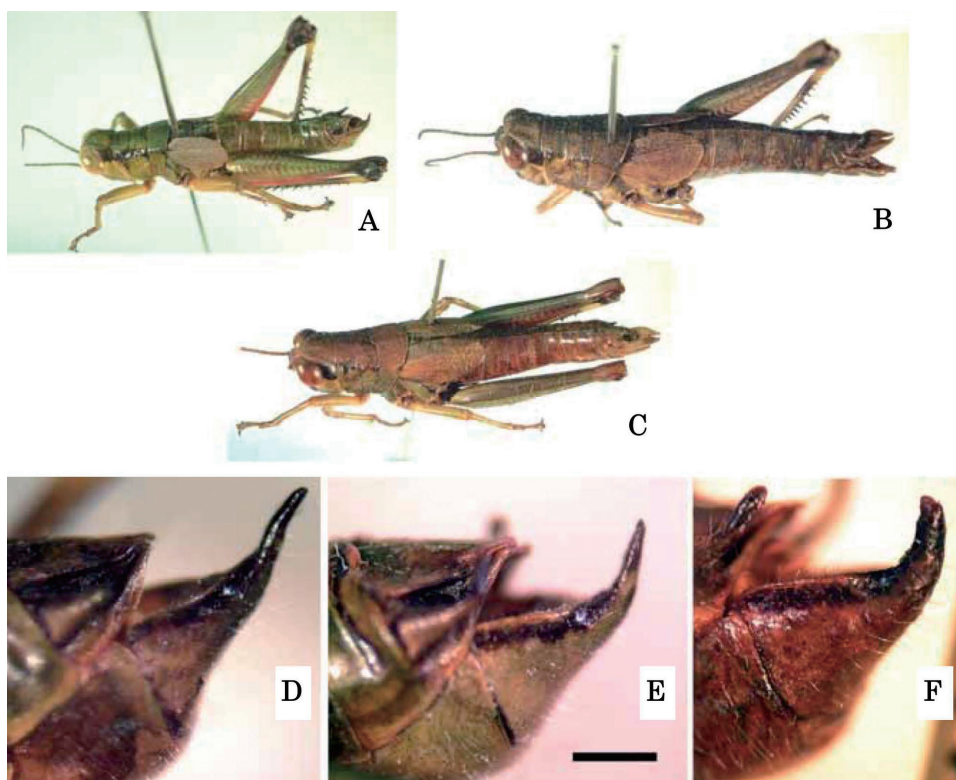


Fig. 3.18. *Parapodisma yasumatsui*, male (A) and female (B) from Mt. Hikosan, Fukuoka. Female (C) from Haki, Kumamoto. Various shapes of the subgenital plate in specimens collected at the same locality, Mt. Hikosan. The tip shape is as follows. D, excurved; E, straight; F, incurved. Scale: 1mm.

plate with posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40I; preapical diverticulum robust and basal part less than 1/3 width of apical part, with 2nd diverticulum; apical diverticulum almost as long as preapical one. Spermathecal vestibule (Fig. 1.42G) with a reddish brown sclerite, as wide as spermathecal vestibule except its lateral margins; thin spermathecal duct connected to ventral surface of right or left side of anterior part.

Type specimen. Holotype male (ENSM). Top of Mt. Hiko-san, Soeda-Town, Fukuoka Pref., 15. x. 1979, T. Yamasaki leg.

Distribution (Fig. 3.24). [Kyûshû] Fukuoka, Saga, Nagasaki, Miyazaki, Ôita, Kumamoto, Kagoshima.

Remarks. This species is closely related to *P. niihamensis*.

Parapodisma tenryuensis Kobayashi, 1983

(Figs 1.9C–D, 1.10F, 1.11, 1.13C, 1.14C, 1.20J₁–J₂, 1.27, 1.28C, 1.29V₁–V₃, 1.31C, 1.45M, 1.40J–K, 1.42K, 3.19)

Parapodisma ternryuensis Kobayashi, 1983: 647.

General morphology. Body color highly variable (See “Remarks”). Pronotum subcylindrical; dorso-lateral part rounded on prozona, slightly angulate on metazona; hind margin slightly produced and obtusely acute medially. Tegmina oval, obtuse or subacute apically, covering tympanal organ, seldom overlapping each other, yellowish brown or dark brown; TL=4–6. Hind wings vestigial, exceeding hind margin of metanotum, but never reaching that of 1st abdominal tergite. Metanotum with distinct but relatively shallow scutal grooves dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Hind femora yellowish green or salmon-pink with a ventral red line, sometimes inner surface darken. Hind tibiae pale bluish green or dark yellow; spines black. Tympanal organs medium to small in size.

♂. P/M=1.4–1.6. Lateral black stripes on head present behind compound eyes; on pronotum broad or moderate in width (LSW/PH=1/3–1/5), reaching 3rd transverse sulcus or posterior margin; in abdomen distinctly present and broad, reaching to the 3rd–10th segment. Epiproct (Fig. 1.20 J₁–J₂) triangular; basal width equal to or slightly exceeding median length; median groove deep, present in almost whole length. Distal subsegment of subgenital plate medium in length, black on lateral and anterior margin; posterior margin without a small triangular process protruding forward. Cerci (Fig. 1.27) gradually narrowed on basal half or 2/3; slightly incurved in apical 1/3; apical part narrowed or slightly widened with an obtuse apex, but highly variable. Lophi of epiphallus (Fig. 1.29V) thin to thick, about 1/3–1/4 times as wide as epiphallus; earlobe-shaped, with apical margin rounded. Apical part of phallus as in Fig. 1.31C; valves of cingulum surrounding aedeagal valves, slightly sclerotized; dorsal aedeagal valve gradually attenuate, acute at apex; ventral aedeagal valves lamellate, rounded laterally, subacute apically.

♀. P/M=1.2–1.5. Lateral black stripes on head present behind compound eyes; on pronotum reaching the 3rd transverse sulcus interrupted or continuous, often present on posterior margin, wide (LSW/PH=1/3–1/5), on abdomen reaching 2nd–4th tergite. Subgenital plate with posterior margin angulate or slightly projected laterally. Spermatheca as in Fig. 1.40J, K; preapical diverticulum robust and basal part less than 1/3 width of apical part, without 2nd diverticulum (sometimes present); apical diverticulum shorter than preapical one. Spermathecal vestibule as in Fig. 1.42K; lateral sides almost straight and parallel; anterior part strongly bent downward in right or left side of the anterior margin; sclerite reddish brown, usually dichotomous in posterior part, 1/4 as wide as spermathecal vestibule; thin spermathecal duct connected to ventral surface of right or left side of the anterior part.

Nymph color (Fig. 1.45M). Generally reddish brown. Dark-yellow-dark pattern of stripes distinct or indistinct, the dark stripes being black. Femora usually with two large black maculae on each lateral surface, which are sometimes continued. Dorsal color gradually changes according to development.

Type specimen. Holotype male (OMNH). Himemiya (700m alt.), Kamisato-Town (presently Iida-City), Nagano Pref., 23, vii, 1980, M. Kobayashi leg.

Distribution (Fig. 3.25). [Honshû] Gumma, Saitama, Chiba, Tōkyō, Kanagawa, Yamanashi, Nagano, Shizuoka, Aichi, Gifu.

Variations. This species is highly variable in color, having three principal female color morphs as follows. 1: Red (salmon-pink or reddish brown) in the whole body; 2: Red (pink, orange or deep red) dorsally, green (dark green, yellowish green, or rarely yellow) laterally; 3: Green (dark green or yellowish green) in the whole body. Male

individuals belong to type 2 or type 3. However, so many individuals are intermediate between the types. Moreover, the body color can change with age. In my collection, the distribution pattern of each color morph agrees with the record by Tominaga & Wada (2001). Type 1 female and type 2 male are distributed in the western part of the distribution range of this species (Gifu, Aichi, western part of the Tenryû River). Between the Tenryû River and the foot of Mt. Fuji, type 2 and 3 are mixed. Type 2 and 3 occur also east of Mt. Fuji, and the proportion of type 3 individuals gradually increases eastward. However, even in western part of Tôkyô (Mt. Takao) and western part of Kanagawa (Tsukui-Town), type 1 female is rarely found. In my observation, a type 2 female (colored red dorsally and yellow laterally) collected from Tsukui-Town produced individuals of all these types. Thus, the coloration does not correspond to specific division.

Tominaga & Wada (2001) described *P. tanzawaensis* dividing eastern populations (east of the foot of Mt. Fuji) from *P. tenryuensis*. The diagnostic characters for *P. tanzawaensis* from *P. tenryuensis* are as follows:

- (1) “Metazona of pronotum with coarse punctures.”
- (2) “Apical half of male cerci ‘narrower’ than that of its base.” (Incorrect statement ‘broader’ has been given in the description in English, but the state observed in specimens is ‘narrow’ and the correct expression has been given by their descriptions in Japanese version in the same article.)
- (3) “Male dorsal aedeagal valve with butterflies with open wings.”
- (4) “Females have Green Type, and its percentage being high in lowlands and eastern part.”

However, all of these characters are incredible by the following reasons and, therefore, *P. tanzawaensis* is synonymized with *P. tenryuensis*.

(1) Coarse punctures on metazona can be seen in *P. tenryuensis* and fine punctures on metazona can be seen in *P. tanzawaensis*.

(2) Geographic variation pattern in the male cerci is as shown in Fig. 1.27. Western populations (D, J–L) have the cerci with a narrow apex and widened halfway (E–H, M–Q), but eastern populations (I, R–V) also have the apex narrowed.

(3) When dried, the aedeagal valves often change their original shape. The male genitalia of the type specimens of *P. tanzawaensis* have been preserved dry, and this may be responsible for the condition “butterfly wing”. The aedeagal valves of all individuals examined in this study are as in Fig. 1.31C.

(4) Western populations do not have the green female and eastern populations do not have the red female. However, in intermediate populations the proportion of the color morphs gradually changes. The pattern of geographic variation in color is thus continuous.

Parapodisma caelestis Tominaga & Ishikawa, 2001
(Figs 1.20K, 1.25I₁–I₂, 1.29W, 1.31D, 1.33D, 1.40L, 1.42J, 3.20)

Parapodisma caelestis Tominaga & Ishikawa, 2001: 27.

General morphology. Body generally dark green with many dark colored parts dorsally and laterally, cream-colored ventrally. Compound eyes relatively small. Pronotum subcylindrical; dorso-lateral part rounded; hind margin slightly produced

and rounded. Tegmina oval, not reaching tympanal organ, never overlapping each other, yellowish brown or reddish brown; TL=3–4. Hind wings vestigial, not exceeding hind margin of metanotum. Hind femora yellowish green with a ventral red line, darkened strongly and extensively on inner surface and weakly on outer surface. Hind tibiae dark yellow with many black areas; spines black. Tympanal organs small.

♂. P/M=1.3–1.5. Lateral black stripes on head present behind compound eyes; on pronotum wide or moderate in width ($LSW/PH=1/3-1/4$), present in whole length; on abdomen distinct and broad, running from 2nd segment (almost black) to 10th tergite. Metanotum with distinct but shallow scutal grooves; scutum+scutellum slightly raised. Epiproct (Fig. 1.20K) triangular; basal width slightly exceeding median length; median groove deep and wide, present on basal half, obscured and narrowed on posterior 1/4. Distal subsegment of subgenital plate very short, entirely black; posterior margin without a small triangular process protruding forward, but sometimes with a vestigial one. Cerci (Fig. 1.25I₁–I₂) gradually narrowed on basal half; rounded or subacute apically. Lophi

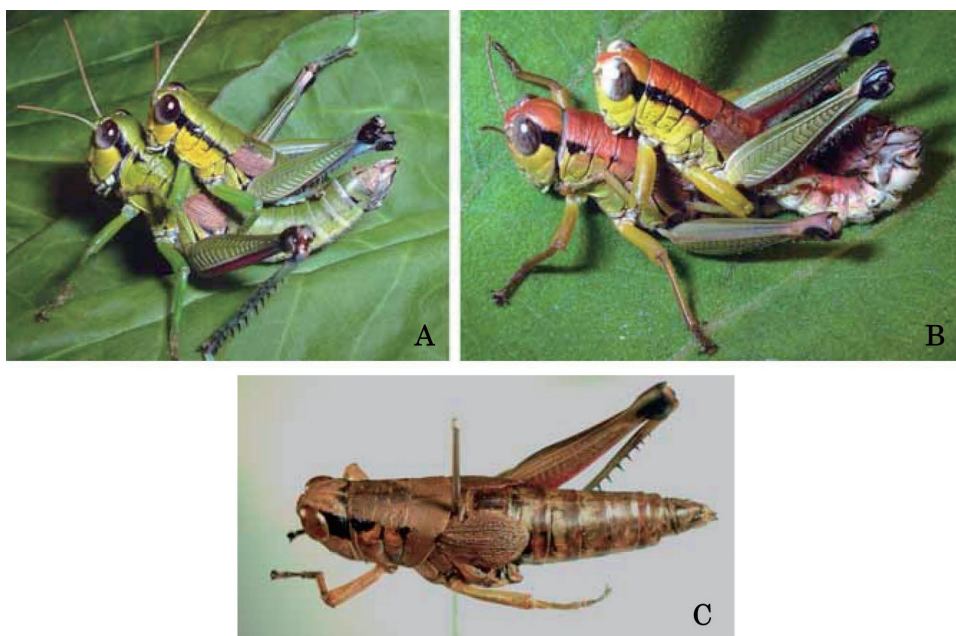


Fig. 3.19. *Parapodisma tenryuensis*. A & B: Mt. Enkaizan, Yokohama-City, Kanagawa Pref. C: Kawamuki, Shitara-Town, Aichi Pref.

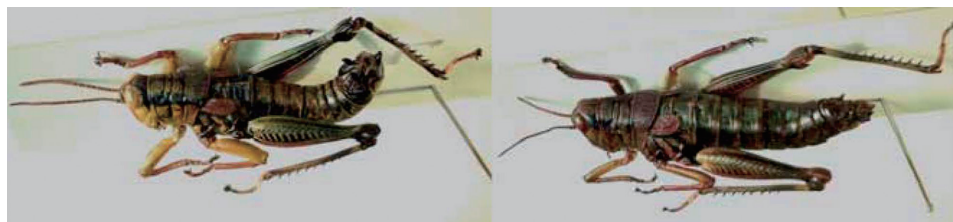


Fig. 3.20. *Parapodisma caelestis*, male (left) and female (right) from Mt. Tekari, Shizuoka City.

of epiphallus (Fig. 1.29W) thick, about 1/5 times as wide as epiphallus; earlobe-shaped, with apical margin rounded. Apical part of phallus as in Fig. 1.31D; valves of cingulum lamellate, rounded laterally, subacute apically.

♀. P/M=1.2–1.3. Lateral black stripes on head present behind compound eyes; on pronotum reaching the 3rd transverse sulcus continuously, and sometimes reaching the posterior margin; on abdomen reaching 2nd to 4th tergite. Metanotum flat, only with vestigial scutal pits and grooves. Subgenital plate elongate, posterior margin (Fig. 1.33D) angulate laterally. Spermatheca as in Fig. 1.40L; preapical diverticulum robust and basal part less than 1/3 width of apical part, without 2nd diverticulum; apical diverticulum shorter than preapical one. Spermathecal vestibule as in Fig. 1.42J; lateral sides almost straight and parallel; anterior part strongly bent downward on right or left side of anterior margin; sclerite reddish brown, usually dichotomous in posterior part, 1/4 as wide as spermathecal vestibule; thin spermathecal duct connected to ventral surface of right or left side of the anterior part.

Type specimen. Holotype male (OMNH). About alt. ca 2500m, Tekari-dake, Southern Alps, Shizuoka Pref., 13. ix. 1998, leg. H. Ishikawa.

Distribution (Fig. 3.25). [Honshū] High elevation area (2000–2500m) around Mt. Tekaridake, the Southern Alps mountains.

Remarks. This species is very closely related to *P. tenryuensis*, and especially similar to the western populations of *P. tenryuensis* in the lophi of male epiphallus and both the apical part of the hind tibiae and the inner surface of the hind femora darkened. The male phallus is almost the same in shape in the two species. However, this species has the following specific characters: 1) relatively small compound eyes; 2) prolonged female subgenital plate; 3) shortened distal subsegment of male subgenital plate; 4) more darkish coloration.

Among the characters given by Tominaga & Ishikawa (2001), “minimum size of *Parapodisma* species” is not correct, because this species is moderate or only slightly small in body size (Table 3.2).

Parapodisma takeii (Takei, 1914) comb. nov.

(Figs 1.2D, 1.10M, 1.20A, 1.25A, 1.29N, 1.31B, 1.33A, 1.45H, 1.40A, 1.42A, 3.21)

Podisma takeii Takei, 1914: 123.

Podisma subaptera Hebard, 1924: 221. Syn. nov.

Parapodisma subaptera: Bey-Bienko & Mistshenko, 1951: 224.

Aopodisma subaptera: Tominaga & Uchida, 2001: 9.

General morphology. Body generally yellowish green or dark green dorsally and laterally and yellow ventrally. Pronotum (Fig. 1.10M) nearly cylindrical, rounded dorso-laterally; hind margin slightly emarginate in middle (Fig. 3.12C) or slightly rounded (Fig. 3.12D); P/M=1.5–1.9. Tegmina vestigial, yellowish brown or reddish brown; TL=1–2. Hind wings vestigial, like a small lobe. Hind femora yellowish green in general, pale yellowish-green ventrally. Hind tibiae pale green; spines cream-colored on basal half, black on apical half. Metanotum nearly flat, only with a pair of small scutal pits and vestigial grooves. Tympanal organs relatively small.

♂. Lateral black stripes on head behind compound eyes present distinctly; on pronotum relatively broad (LSW/PH=1/4), developed continuously in whole length of

pronotum; on abdomen interrupted, reaching middle of abdomen or more backward. Epiproct (Fig. 1.20A) triangular, black on lateral margins; basal width almost equal to median length; median groove relatively narrow, present on basal half. Subgenital plate yellow; distal segment slightly projected posteriorly; posterior margin without a triangular process protruding forward. Cerci (Fig. 1.25A) short and robust, gradually narrowed on basal half, obtuse apically, entirely pale yellow. Lophi of epiphallus (Fig. 1.29N) moderately thick; about 1/4 times as wide as epiphallus; outer margin gradually curved, inner margin straight; tip slightly projecting internally. Apical part of phallus as in Fig. 1.31B; valves of cingulum lobiform, truncate apically, slightly sclerotized on inner surface; dorsal aedeagal valve attenuate and truncate in apical portion; ventral aedeagal valves lamellate, rounded and subacute apically.

♀. Lateral black stripes on head present behind compound eyes; on pronotum usually present only on anterior margin; on abdomen absent. Subgenital plate (Fig. 1.33A) gradually curved on posterior margin. Spermatheca as in Fig. 1.40A; preapical diverticulum thick basally, robust, 2nd diverticulum absent; apical diverticulum distinctly shorter than preapical one. Spermathecal vestibule (Fig. 1.42A) small and rounded; semispherical small sclerite brown or dark brown, situated on inner surface of median part of anterior margin, connected to thin spermathecal duct.

Nymph color (Fig. 1.45H). Generally pale brown, sometimes wholly darkish. The dark-yellow-dark pattern of stripes distinct; dark stripes black or dark brown. Femora usually with two large black maculae on each lateral surface and both of them sometimes continued.

Type specimen. Syntypes: 1 male and 1 female (SEHU). Japan: Gumma. 26, IX 1913.

Distribution (Fig. 3.25). [Honshū] Iwate, Miyagi, Fukushima, Yamagata, Tochigi, Gumma, Ibaraki, Saitama, Tōkyō, Kanagawa, Yamanashi, Niigata, Nagano, Aichi, Gifu.

Remarks. The name has been used in no article since the original description, and a junior synonym, *subaptera* Hebard, 1924, has been applied for this species. Tominaga & Uchida, 2001 suppressed *P. takeii*, the senior synonym of *A. subaptera*, as *nomen oblitum*, but they did not mention the type material. Moreover, their treatment is apparently invalid.

The cladistic analysis in the previous chapter and the shape of the aedeagal valves suggest that this specie is a close relative of *P. tenryuensis* and *P. caelestis*.

Parapodisma setouchiensis Inoue, 1979

(Figs 1.2F, 1.20L₁–L₃, 1.26, 1.29X₁–X₄, 1.31F–G, 1.33E, 1.37, 1.45N–O, 1.40M–N, 1.42L, 3.22)

Parapodisma setouchiensis Inoue, 1979: 59.

Parapodisma tanbaensis Tominaga, 1989: 1. Synonymized by Kawakami, 1999: 56.

Parapodisma yamato Tominaga & Storozhenko, 1996, in Tominaga, Storozhenko & Kanô, 1996: 1. Synonymized by Kawakami, 1999: 56.

Parapodisma hyonosenensis Tominaga & Kanô, 1996, in Tominaga, Storozhenko & Kanô, 1996: 11. Synonymized by Kawakami, 1999: 56.

Parapodisma tanbaensis: Ichikawa, 2006: 28. Syn. nov.

Parapodisma hyonosenensis: Ichikawa, 2006: 28. Syn. nov.

Synonymies in detail see Kawakami (1999).

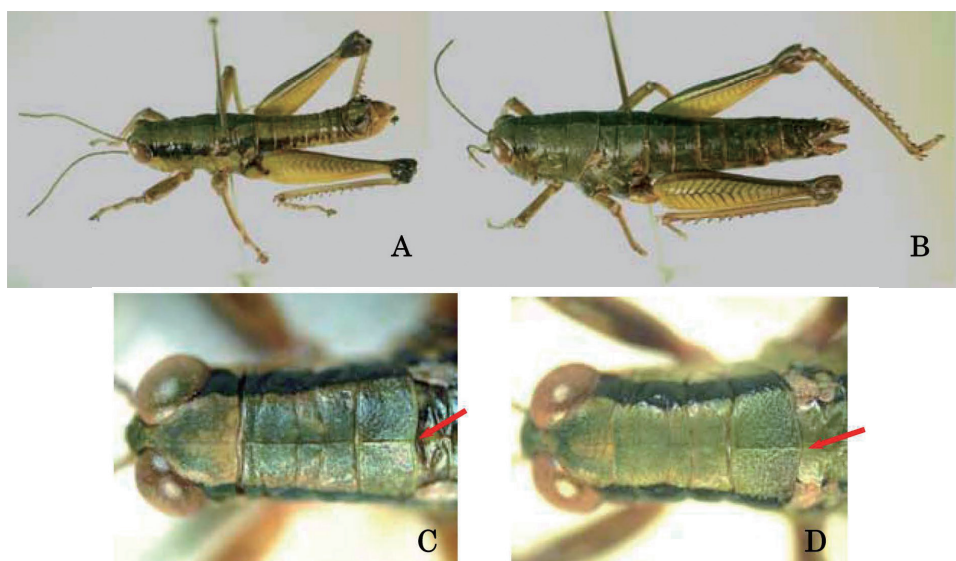


Fig. 3.21. *Parapodisma takeii*. A: male; B: female (right); C: male with pronotum emarginate posteriorly; D: male with pronotum slightly produced posteriorly. All from Hôshi, Gumma Pref.

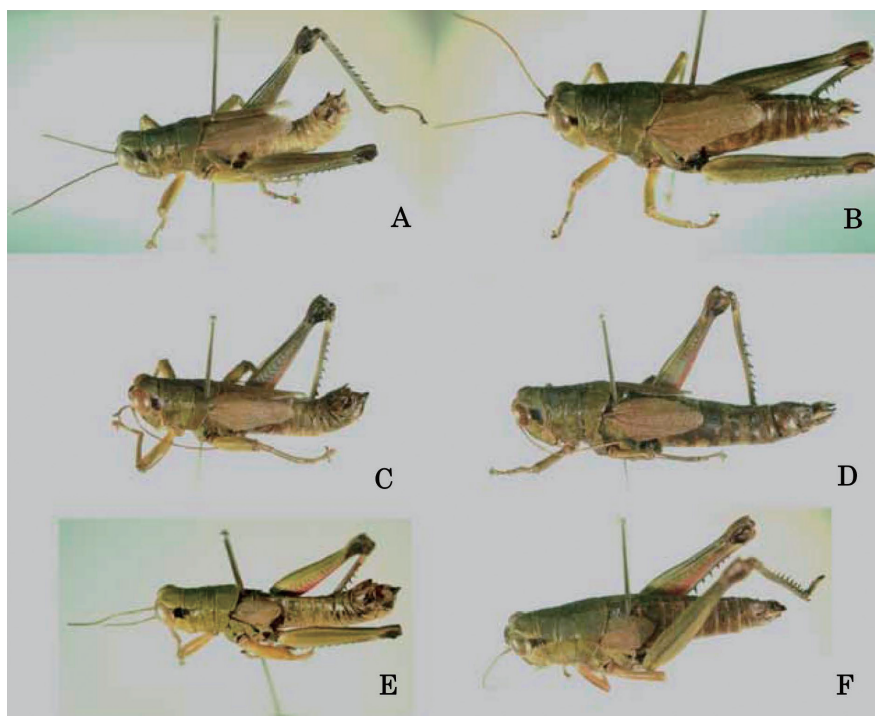


Fig. 3.22. *Parapodisma setouchiensis*, male (A, C, E) and female (B, D, F) from Yawata-City, Kyôto Pref.(A, B), Kôduki-Town, Hyôgo (C, D) and Ôtsu-City, Shiga Pref. (E, F).

General morphology. Body color highly variable (see Remarks); ventral part cream-colored or pale green. Lateral black stripes on head present behind compound eyes, sometimes obscured; on pronotum only on anterior margin and/or posterior margin, rarely more developed; on abdomen absent. Pronotum subcylindrical, generally yellowish green or dark green; dorso-lateral part rounded on prozona, slightly angulate on metazona; hind margin produced and obtusely acute medially; P/M=1.3–1.5. Tegmina oval or oblong, covering tympanal organ, usually overlapping each other, reddish brown; TL=5–11. Hind wings as long as tegmina. Metanotum with distinct scutal grooves

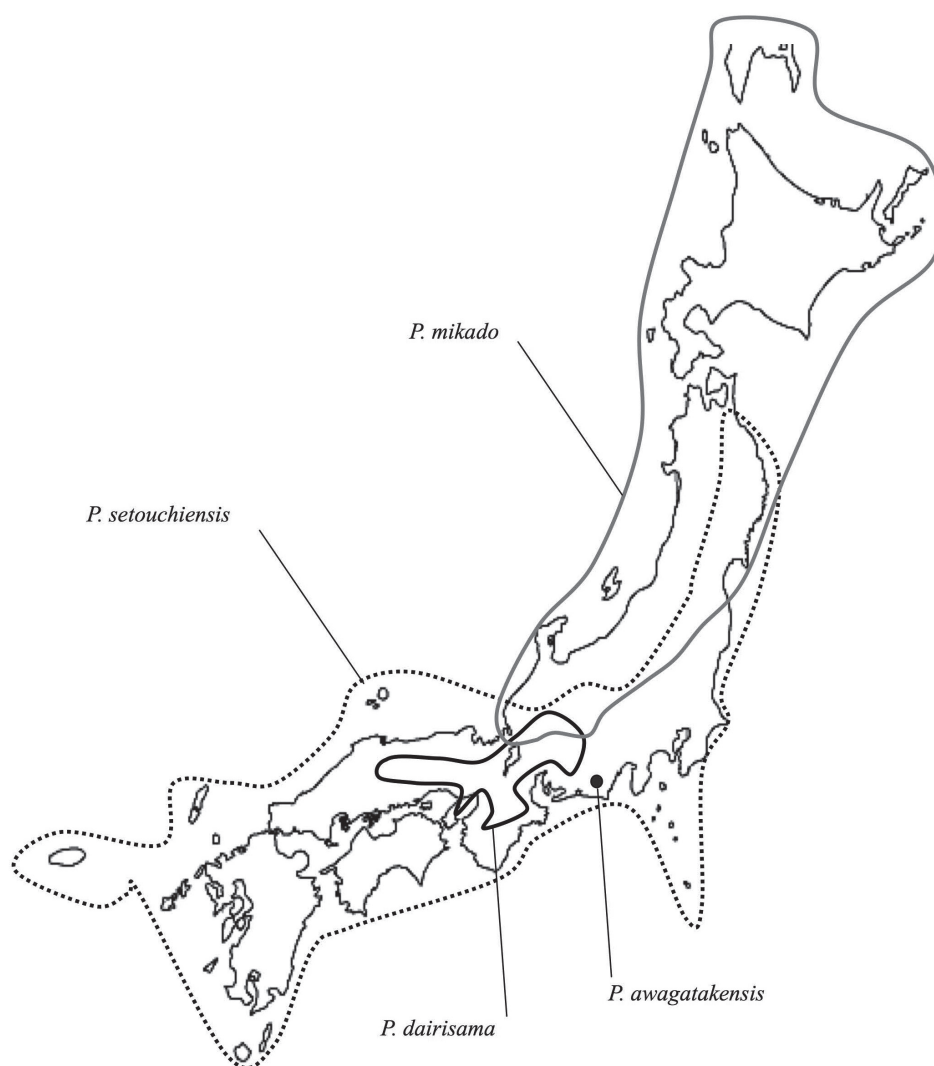


Fig. 3.23. Distribution map of *Parapodisma* species (1).

dividing scutum+scutellum from the other parts; scutal ribs forming a triangular shape. Hind femora yellowish green with a ventral red line, which is sometimes obscured or lacked. Hind tibiae pale blue or pale bluish green; spines black. Tympanal organs medium in size.

♂. Lateral black stripes usually distinct only on head behind compound eyes, but sometimes present on pronotum, $LSW/PH=1/5-1/7$. (in individuals with well-developed lateral black stripes). Epiproct (Fig. 1.20L₁-L₃) triangular; basal width equal to or slightly exceeding median length; median groove deep, narrow or moderate in width, present

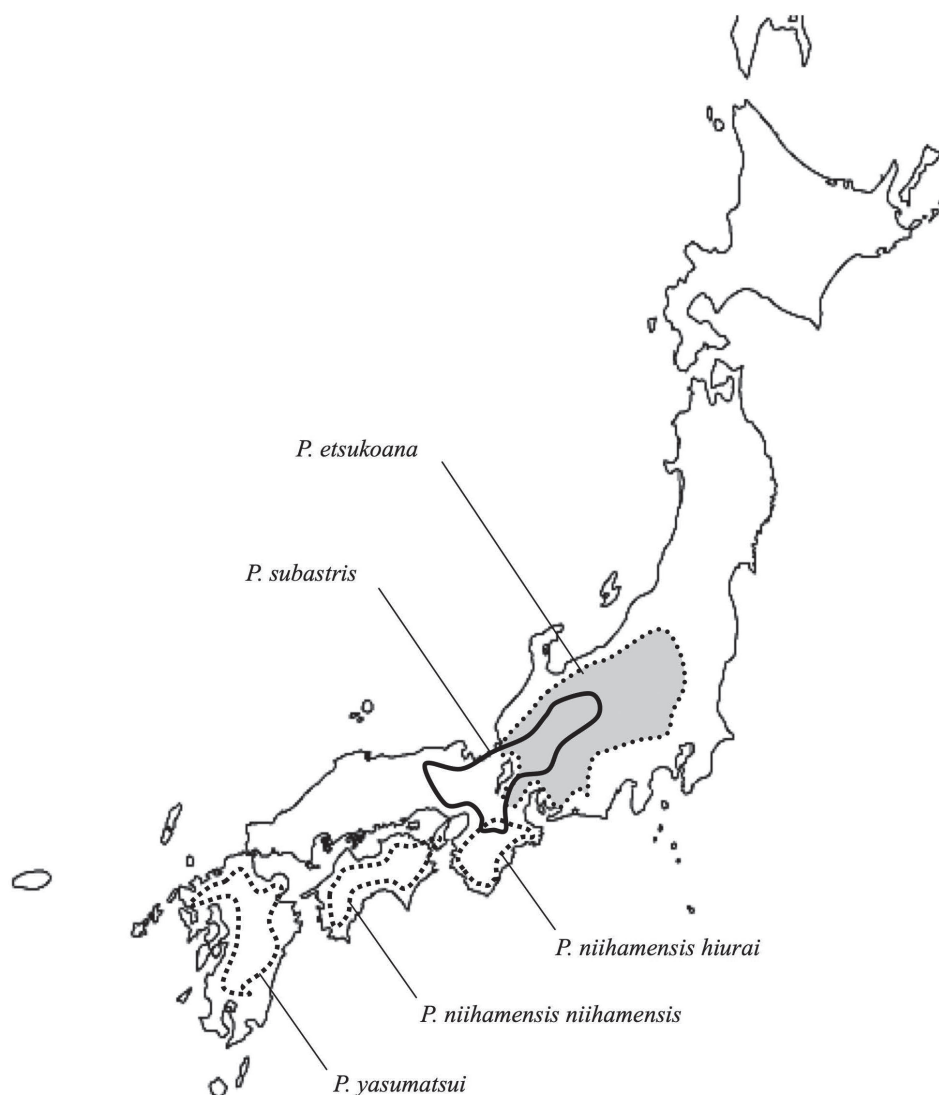


Fig. 3.24. Distribution map of *Parapodisma* species (2).

on basal 1/2–3/4. Distal subsegment of subgenital plate short to long, black on lateral margin; posterior margin with or without a triangular process protruding forward. Cerci (Fig. 1.26) gradually narrowed on basal half; apical half slightly widened or strongly incurved, highly variable (see Remarks). Lophi of epiphallus (Fig. 1.29X₁–X₄) thin or moderately thick, about 1/4–1/5 times as wide as epiphallus; trapezoid, with a rounded outer corner and a slightly projected inner corner. Apical part of phallus as in Fig. 1.31F–G; sheath of aedeagus fused with dorsal aedeagal sclerite and ventral aedeagal sclerites, forming aedeagal valves, which are not strongly sclerotized; dorsal aedeagal valves

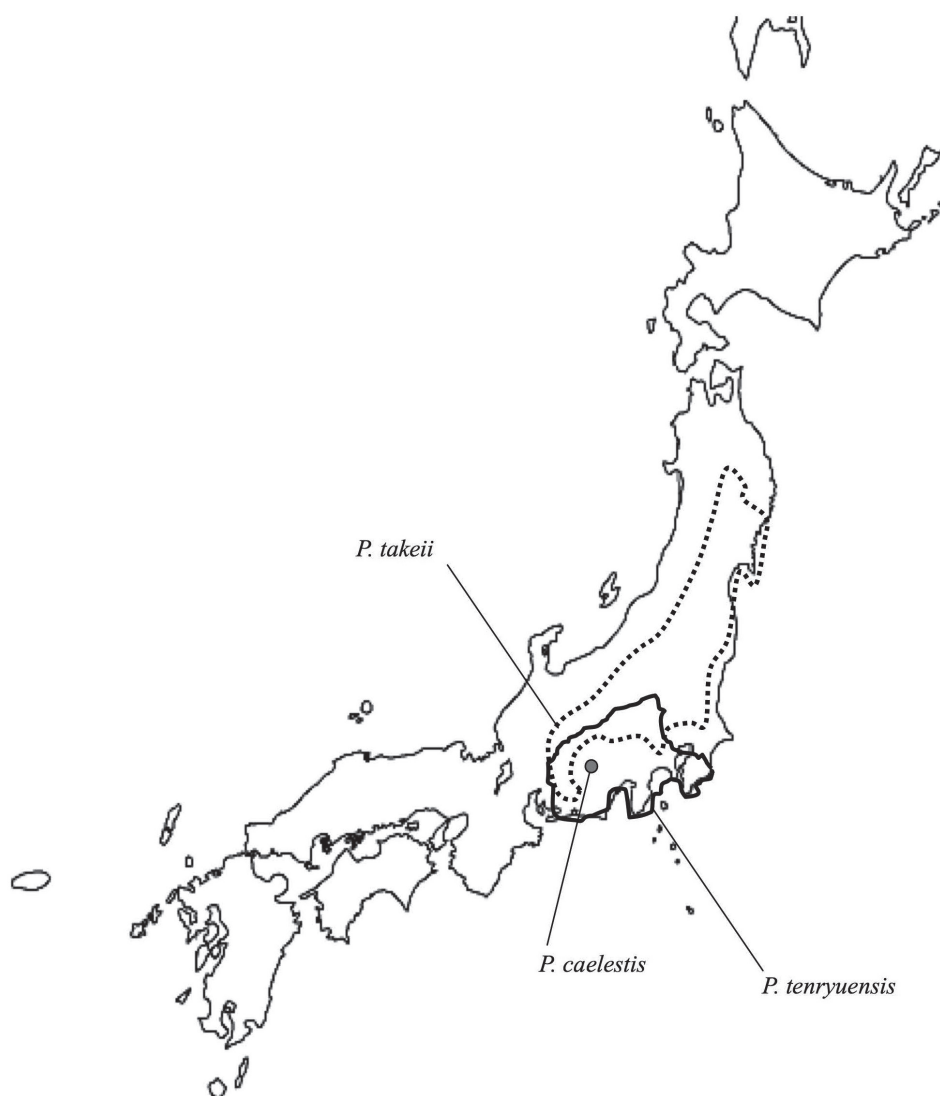


Fig. 3.25. Distribution map of *Parapodisma* species (3)

subacute at apex; ventral aedeagal valves membranous, also subacute apically.

♀. Lateral black stripes usually present only on head behind compound eyes. Subgenital plate with posterior margin (Fig. 1.33E) distinctly projected laterally. Spermatheca as in Fig. 1.40M–N; preapical diverticulum slender; width of apical part less than 3 times of basal part, with distinct 2nd diverticulum; apical diverticulum twice as long as or longer than preapical one. Spermathecal vestibule (Fig. 1.42L) elongate, with a sclerite forming a valve, but without any sclerite in the other parts; anterior part gently narrowed, twisted once and then continued to spermatheca with a duct.

Nymph color (Fig. 1.45N–O). Nearly as in *P. takeii* or *P. etsukoana*. Generally pale brown, sometimes wholly darkish. Dark-yellow-dark pattern of stripes distinct, the dark stripe being pale brown, brown or black. Femora usually with two large black maculae on each lateral surface, which are sometimes continues.

Type specimen. Holotype male (ELEU). Kawamata (500m alt.), Niihama-City, Ehime Pref., VIII-16 1972, M. INOUE leg.

Distribution (Fig. 3.23). [Honshû] Widely distributed except for Western Tôhoku district. [Shikoku] widely distributed. [Kyûshû] widely distributed; Cheju Island (Korea).

Remarks. This species has the widest range of distribution among the Japanese Podismini except for *Ognevia longipennis*. Large variations have been observed in body size, tegminal length, male cercal shape and shape of male subgenital plate. However, this species is recognized by its peculiar structure of the male aedeagal valves (sheath of aedeagus completely fused with aedeagal sclerites and forming dorsal and ventral valves) and the female spermathecal vestibule (absence of a strong constriction and anterior sclerite, usually found in the other *Parapodisma* species).

Kawakami (1999) studied geographic variation in morphology of this species. He recognized 4 geographic forms, which are connected by intermediate individuals in the transitional zones in Kinki District in his morphometric study on the body size, the anterior projection of the male subgenital plate, the cercal angle, the degree of projection of the subgenital plate, and the tegminal length. Ichikawa (2006) revived *tanbaensis* and *hyonosenensis* as distinct species from *setouchiensis* without discussion on morphology and thus I accept Kawakami (1999) in this paper.

Color of ventral part of the hind femur is variable among populations. The color is green in many populations in northern Chûgoku district (Kawakami, 2007) and some part of Kii peninsula (e.g., Susami-Town in SEHU collection). Color of the female abdominal tergite is also variable. Females usually have an abdomen yellowish green or brownish green. Females from around Kyôto often have an abdomen reddish green dorsally, and this color type has not been found in other localities.

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REFERENCES

- Akimoto, S., Sakurai, Y. & Tatsuta, H. 1993. Geographic variation in the shape and allometry of the brachypterous grasshopper *Podisma sapporensis*. Japanese Journal of Entomology 61(3): 625–640. (In Japanese, with English summary.)
- Ander, K. 1956. Orthoptera Saltatoria. In: Tuxen, S. L. (ed.) Taxonomists Glossary of Genitalia in Insects. 2nd edition, pp. 61–71. Ejnar Munksgaard, Copenhagen.
- Bolívar, I. 1890. Dianosis de Ortopteros Nuevos. Anales de la Sociedad Española de Historia Natural 19: 299–334.
- Bugrov, A. G. & Sergeev, M. G. 1997. A new grasshopper species of the genus *Podisma* Berthold (Orthoptera: Acrididae) from the Southern Kuril Islands and its karyotypic features. Acta Zoologica Cracov 40(1): 47–52.
- Bugrov, A. G., Warchalowska-Sliwa, E. & Maryanska-Nadachowska, A. 1994. Karyotype evolution and chromosome C-banding patterns in some Podismini grasshoppers (Orthoptera, Acrididae). Caryologia 47(2): 183–191.
- Bugrov, A. G., Warchalowska-Sliwa, E., Ito, G. & Akimoto, S. 2000. C-Banded karyotypes of some Podisminae grasshoppers (Orthoptera, Acrididae) from Japan. Cytologia 65: 351–358.
- Carl, J. 1916. Acridides nouveaux ou peu connus du Muséum de Genève. Revue Suisse de Zoologie 24(6): 461–518.
- Chang, K. S. F. 1940. The group Podismae from China. Notes d'Entomologie Chinoise 7(2): 31–97.
- Chintauan-Marquier, I. C., Jordan, S., Berthier, P., Amédégato, C. & Pompanon, F. 2011. Evolutionary history and taxonomy of a short-horned grasshopper subfamily: The Melanoplinae (Orthoptera: Acrididae). Molecular Phylogenetics and Evolution 58: 22–32.
- Chintauan-Marquier, I. C., Amédégato, C., Nichols, R. A., Pompanon, F., Grandcolas, P. & Desutter-Grandcolas, L. 2014. Inside the Melanoplinae: New molecular evidence for the evolutionary history of the Eurasian Podismini (Orthoptera: Acrididae). Molecular Phylogenetics and Evolution 71: 224–233.
- Cigliano, M. M., Ronderos, R. A. & Kemp, W. P. 1996. Phylogenetic relationships of *Scotussa* and *Leiotettix* (Orthoptera: Acrididae). Cladistics 21: 125–138.
- Cohn, T. J. 1994. A plea for tabulated descriptions, keys and illustrations. Journal of Orthoptera Research 3: 55–57.
- Dirsh, V. M. 1956. The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. Transactions of the Royal Entomological Society, London 108: 223–356.
- Dirsh, V. M. 1957. The spermatheca as a taxonomic character in Acridoidea. Proceedings of the Royal Entomological Society of London (A) 32: 107–114.
- Dirsh, V. M. 1975. Classification of the Acridomorpha Insects. E. W. Classey Ltd., 171 pp.
- Dovnar-Zapolskii, D. P. 1932 [1933]. Zur kenntnis der palearktischen Podismini

- (Orthoptera, Acridoidea). Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 1(3–4): 253–268. (In Russian with German summary.)
- Eades, D. C. 1961. The terminology of phallic structures in the Cyrtacanthacridinae (Orth. Acrididae). Entomological News 72: 141–149.
- Eades, D. C. 2000. Evolutionary relationships of phallic structures of Acridomorpha (Orthoptera). Journal of Orthoptera Research 9: 181–210.
- Farris, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.
- Federov, S. M. 1927. Studies in the copulation and oviposition of *Anacridium aegyptium*. 1. (Orthoptera, Acrididae). The Transactions of the Entomological Society of London 75: 53–61.
- Fischer-Waldheim, G. 1846. Orthopteres de la Russie. In: Entomographie de la Russie, Moscou, Russia, pp. 1–443, 37 pls.
- Fontana, P. G. & Vickery, V. R. 1976. Cytotaxonomic studies on the genus *Boonacris*. I. The 'eastern' taxa and a comparison with the related genera *Dendrotettix* and *Appalachia* (Orthoptera: Catantopinae: Podismini). Canadian Journal of Genetics and Cytology 18: 625–652.
- Furukawa, H. 1929. Some alpine Orthopterans from Mt. Ogahana, with description of a new subspecies. Kontyû 3: 165–178, plate v.
- Furukawa, H. 1939. Superfamily Acridoidea. in Report of the first scientific expedition to Manchoukuo, Section V, Division I, Part V, Article 16: 1–180, i–xii, 20 pls. (In Japanese and English.)
- Gosalvez, J., Mason, P. L. & Lopez-Fernandez, C. 1997. 16. Differentiation of individuals, populations and species of Orthoptera: The past, present and future of chromosome markers. In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds.) The Bionomics of Grasshoppers, Katydid and Their Kin, pp. 355–383. CAB International, Oxon, UK.
- Gupta, P. D. 1950. On the structure, development and homology of the female reproductive organs in orthopteroid insects. Indian Journal of Entomology 10: 75–123.
- Harz, K. 1975. The Orthoptera of Europe II. Dr W. Junk Publishers, The Hague, 939 pp.
- Hebard, M. 1924. Studies in Japanese Acrididae (Orthoptera). Transactions of the American Entomological Society 50: 209–224.
- Hiura, I. 1979. Entomology on insects of more than 1cm. 8. Grasshoppers (2). Nature Study 25(1): 5–10. (In Japanese.)
- Huang, C.-m. 1983. One new species of *Parapodisma* from Japan (Orthoptera: Acrididae, Catantopinae). Acta Entomologica Sinica, 26(4): 457–458.
- Huang, J.-h., Zhang, A.-b., Mao, S.-l. & Huang, Y. 2013. DNA Barcoding and species boundary delimitation of selected species of Chinese Acridoidea (Orthoptera: Caelifera). Plos One 8(12): e82400. doi:10.1371/journal.pone.0082400.
- Hubbell, T. H. & Cantrall, I. J. 1938. A new species of *Appalachia* from Michigan (Orthoptera, Acrididae, Cyrtacanthacrinae). Occasional Paper, Museum of Zoology of University Michigan (389): 22 pp., 1 pl, 1 fig.
- Ichikawa, A., Ito, F., Kanô, Y., Kawai, M., Tominaga, O. & Murai, T. (eds.) 2006. Orthoptera of the Japanese Archipelago in color. Hokkaido University Press, Sapporo, xxxvi + 687 pp.
- Ichikawa, A. 2006. New status, combinations, synonymy and records of Orthoptera from Japan and Korea [Contributions to the knowledge of Orthoptera III]. Tettigonia (8): 23–29.
- Ikonnikov, N. 1911. Zur kenntnis der Acridoideen Sibiriensis. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg 16: 242–270.

- Ikonnikov, N. 1913. Über die von P. Schmidt aus Korea mitgebrachten Acridiideen, Kuznetzk, 1–22.
- Inoue, M. 1979a. A new species of the genus *Primnoa* unknown from Japan (Orthoptera: Acrididae). Proceedings of the Japanese Society of Systematic Zoology 16: 53–57.
- Inoue, M. 1979b. Two new species of the genus *Parapodisma* from Western Japan (Orthoptera: Acrididae). Proceedings of the Japanese Society of Systematic Zoology 16: 58–64, 1 pl.
- Inoue, M. 1985. A taxonomic revision of Japanese Acridoidea (Orthoptera) with special reference to their karyomorphology. Transactions Shikoku Entomological Society 17(1–2): 103–183.
- Ishikawa, H. 1996. Mesuaka-fukibatta shugun no bunrui no tame no ichishiryô. Battarigisu (108): 28–35. (In Japanese.)
- Ishikawa, H. 1998. A new *Parapodisma* species (Orthoptera, Acrididae, Catantopinae) from Shizuoka Prefecture, central Honshu, Japan. The Japanese Journal of Systematic Entomology 4(1): 173–178.
- Ito, G. 1997. Mate selection in *Podisma sapporensis*. MSc thesis in Hokkaido University.
- Ito, G. 1999. Descriptions of three new species of Podismini (Orthoptera: Acrididae) from the Ryukyu Archipelago, Southern Japan. Entomological Science 2(4): 503–510.
- Ito, G. 2003. *Prumna* Motshulsky, a revived name for a grasshopper genus, *Primnoa* Fischer-Waldheim (Orthoptera: Acrididae). Tettigonia (5): 51–52.
- Ito, G. 2004. An intergeneric hybrid between a *Podisma sapporensis* female and an *Ognevia longipennis* male (Orthoptera: Acrididae). Tettigonia (6): 5–10.
- Jacobson, G. G. 1905 [1902–1905]. Orthoptera. In: Jacobson, G. G. & Bianchi, V. L. Insects of Russian Empire and adjacent countries, pp. 6–466. (In Russian.)
- Jones, J. C. 1981. The Anatomy of the Grasshopper (*Romalea microptera*). Charles C Thomas Publisher, 281 pp.
- Kanô, Y. 1985. *Parapodisma* grasshoppers around Nabari-City (3). Hirakura 20(4): 51–64. (In Japanese.)
- Kanô, Y. 1986. Podismini in Tôhoku district and adjacent region. Tôhoku no Shizen (15): 2–9. (In Japanese.)
- Kanô, Y. 1990. Encyclopedia of Japanese Podismini. Battarigisu (86): 18–47. (In Japanese.)
- Kanô, Y. 1996. A new genus of the tribe Melanoplina (Orthoptera, Acrididae) from Japan. Tettigonia 1(1): 25–28.
- Kanô, Y., Okada, M., Kawai, M. & Ichikawa, A. 1992. Caelifera. In: Miyatake, Y. and Kano, Y. (eds.), [Colored illustrations of the Cicadas and grasshoppers], pp. 46–137. Hoikusha, Ôsaka. (In Japanese.)
- Kawakami, Y. 1999. Geographic variation of the brachypterous grasshopper *Parapodisma setouchiensis* group in Western Honshu, with its taxonomic revision. Species Diversity 4: 43–61.
- Kawakami, Y. 2007. The transitional zones found between areas characterized by the four geographic forms of the brachypterous grasshopper *Parapodisma setouchiensis* and their historical formation processes. Taxa, Proceedings of the Japanese Society of Systematic Zoology (22): 15–19.
- Kobayashi, M. 1983. A new species of the genus *Parapodisma* (Orthoptera, Acrididae) from Central Japan. Kontyu 51(4): 647–652.
- Kobayashi, M. 1986. A new *Parapodisma* species (Orthoptera, Acrididae) from Central Honshu, Japan. Kontyu 54(3): 513–518.
- La Greca, M. 1987. Some characters in meso- and metanotum of Acridoidea (Orthoptera) and their utilization in taxonomy. In: Baccetti, B. (ed.). Evolutionary Biology of

- Orthopteroid Insects, pp. 325–332. Ellis Horwood Ltd., Chichester, England.
- Lamouroux, J. V. F. 1812. Extrait d'un memoire sur la classification des polypiers coralligenes non entierement pierreux. Nouveau Bulletin des Sciences, par la Societe Philomatique de Paris 3 (63): 181–188.
- Li, H.-c., Xia K.-l., Bi, D.-y., Jin, X.-b., Huang, C.-m., Yin, X.-c., Zheng Z.-m., Lian, Z.-m., You, Q.-j., Zhang F.-l. & Li, T.-s. (eds.) 2006. Fauna Sinica. Insecta 43. Science Press, Beijing. 736 pp.
- Litzenberger, G. & Chapco, W. 2001. Molecular phylogeny of selected Eurasian Podismine Grasshoppers (Orthoptera: Acrididae). Annals of the Entomological Society of America 94(4): 505–510.
- Litzenberger, G. & Chapco, W. 2003. The North American Melanoplinae (Orthoptera: Acrididae): A molecular phylogenetic study of their origins and taxonomic relationships. Annals of the Entomological Society of America 96(4): 491–497.
- Mayer, F. L. 2004. *Primnoa* Fischer-Waldheim 1846, *Sharovia* Otte 1997, *Parahagla* Lin 1982, *Phyllophora erosifolia* Piza 1981 and *Archibrunnea* Otte 1997: naming issues resolved. Journal of Orthoptera Research 13(1): 161–165.
- Mistshenko, L. L. 1947. Two new genera of the Tribe Podismini (Orthoptera, Acrididae) from the old world. Proceedings of Royal Entomological Society of London (B) 16: 10–12.
- Mistshenko, L. L. 1951. Subfamily Catantopinae. In: Bey-Bienko, G. Ja. & Mistshenko, L. L. Locusts and grasshoppers of the USSR and adjacent countries, pp. 131–270. [Translated from Russian. Israel program for scientific translations, Jerusalem, published in 1963, pp. 138–286.]
- Mistshenko, L. L. 1952. Fauna of the USSR. Orthoptera. IV. 2. Locusts and grasshoppers (Catantopinae). USSR Academy Publisher, Leningrad, 610 pp. [Translated from Russian. Israel program for scientific translations, Jerusalem, published in 1965, 558 pp.]
- Mistshenko, L. L. 1954. New representatives of the tribe Podismini (Orthoptera, Acrididae) from Eastern Asia. Proceedings of the Zoological Institute, USSR Academy of Science, Leningrad 15: 27–34. (In Russian.)
- Mistshenko, L. L. 1974. Revision of the genus *Primona* F.-W. (Orthoptera: Acrididae, Catantopinae). Trudy Russkogo entomologicheskogo Obschestva 57: 7–37. (In Russian)
- Motschulsky, V. 1859. Voyages et excursions entomologiques. Etudes Entomologiques 8: 6–15.
- Nagashima, Y. 1994. Podismini in Niigata Prefecture. Essa Entomological Society Special Report (2): 97–108. (In Japanese.)
- Negoro, H. 1991. Geographical variation of *Parapodisma mikado* (Bolivar, 1890) (Orthoptera, Acrididae). Bulletin of the Toyama Science Museum (14): 49–62. (In Japanese.)
- Otte, D. 1995. Orthoptera Species File 4. Grasshoppers [Acridomorpha] C. The Orthopterists' Society and the Academy of Natural Sciences of Philadelphia. USA.
- Packard, A. S. 1878. Chapter 9. Anatomy and embryology. In: First annual report of the United States Entomological Commission for the year 1877: relating to the Rocky Mountain locust and the best methods of preventing its injuries and of guarding against its invasions, in pursuance of an appropriation made by Congress for this purpose, pp. 257–279. U.S. Government Printing Office, Washington.
- Podgornaja, L. I. 1975. Anatomical peculiarities of the grasshoppers *Melanoplus frigidus* (Boh.) and *Podisma pedestris* (L.) (Orthoptera, Acrididae). Entomologicheskoe Obozrenie 65(2): 346–351. (In Russian.)
- Poe, S. & Wiens, J. J. 2000. Character selection and the methodology of morphological

- phylogenetics. In Wiens, J. J. (ed.) *Phylogenetic Analysis of Morphological Data*, pp. 20–36. Smithsonian Institution Press, Washington and London.
- Ramme, W. 1939. Beitrage zur Kenntnis der palaearktischen Orthopterenfauna (Tettig. U. Acrid.). III. Mitteilungen aus dem Zoologischen Museum in Berlin 24: 41–150.
- Randell, L. R. 1963. On the presence of concealed genitalic structures in female Caelifera (Insecta; Orthoptera). *Transactions of the American Entomological Society* 88: 247–260.
- Rehn, J. A. G. 1902. Contributions towards a knowledge of the Orthoptera of Japan and Korea. I. Acridiidae. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 54: 629–637
- Rehn, J. A. G. & Rehn, J. W. H. 1939. Studies of certain cyrtacanthacridoid genera (Orthoptera: Acrididae). Part I. The *Podisma* complex. *Transactions of the American Entomological Society* 65: 61–96 + pls. vi, vii.
- Rehn, J. A. G. & Randell, R. L. 1963. A preliminary analysis of the lines of the supertribe Melanoplini (Orthoptera; Acrididea; Cyrtacanthacridinae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 115(1): 1–32.
- Roberts, H. R. 1941. A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the basis of their phallic structures. *Proceedings of the Academy of Natural Sciences of Philadelphia* 93: 201–246.
- Scudder, S. H. 1897a. The Genera of North American Melanopli. *Proceedings of the American Academy of Arts and Sciences* 32: 195–206.
- Scudder, S. H. 1897b. Revision of the Orthopteran group Melanopli (Acrididae), with special reference to North American forms. *Proceedings of the U.S. National Museum* 20: 1–421.
- Sergeev, M. G. 1999. Distribution and biological diversity of the melanopline grasshoppers (Orthoptera: Acrididae: Catantopinae) in the holarctic kingdom. *Journal of the Entomological Research Society* 1(1): 1–12.
- Shiraki, T. 1910. *Acrididen Japans*. 90 pp., 2 pls. Keiseisha, Tokyo.
- Shiraki, T. 1930. Some new species of Orthoptera. *Transactions of the Natrural History Society of Formosa* 20(111): 327–355.
- Skareas, S. D. & Hsiung, C. C. 1998. Male genitalia of selected genera of the subfamily Melanoplinae (Orthoptera: Acrididae). *Journal of Orthoptera Research* 8: 125–145.
- Slifer, E. H. 1939. The internal genitalia of female Acridinae, Oedipodinae and Pauliniinae (Orthoptera, Acrididae). *Journal of Morphology* 65(3): 437–467.
- Slifer, E. H. 1940a. Variations in the spermatheca of two species of grasshoppers (Orthoptera, Acrididae). *Entomological News* 51 (1): 1–3. 2 plates.
- Slifer, E. H. 1940b. The internal genitalia of female Ommexechinae and Cyrtacanthacridinae (Orthoptera, Acrididae). *Journal of Morphology* 67(2): 199–239.
- Slifer, E. H. 1943. The internal genitalia of female Acrididae (Orthoptera). *Journal of Morphology* 72: 225–237.
- Slifer, E. H. & King, R. L. 1936. An internal structure in the Cyrtacanthacrinae (Orthoptera, Acrididae) of possible taxonomic value. *Journal New York Entomological Society* 44: 345–348.
- Snodgrass, R. E. 1928. Morphology and evolution of the insect head and its appendages. *Smithonian Miscellaneous Collections* 81: 1–158.
- Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithonian Miscellaneous Collections* 82(2): 1–111.
- Snodgrass, R. E. 1935. The abdominal mechanisms of a grasshopper. *Smithonian Miscellaneous Collections* 94(6): 1–89.
- Storozhenko, S. 1986. Revision of the genus *Zubovskya* Dov.-Zap. (Orthoptera,

- Acrididae). Proceedings of the Zoological Institute, Leningrad 143: 47–58. (In Russian)
- Storozhenko, S. 1993a. To the knowledge of the tribe Podismini (Orthoptera, Acrididae) of the Eastern Palearctica. *Articulata* 8: 1–22.
- Storozhenko, S. 1993b. Revision of the genus *Anapodisma* Dov.-Zap. (Orthoptera, Acrididae). *Russian Entomological Journal* 2(3–4): 21–25.
- Storozhenko, S. & Kanô, Y. 1992. A review of the genus *Ognevica* Ikonn. of the eastern Palearctic region (Orthoptera: Acrididae). *Akitu* 128: 1–16.
- Swofford, D. 2001. PAUP*: Phylogenetic Analysis Using Parsimony Version 4. Sinauer, Sunderland, MA.
- Takei, T. 1914. A few insects from Gumma. *The Insect World* 18: 123–124. (In Japanese.)
- Tarbinsky, S. P., 1932. A contribution to our knowledge of the Orthopterous insects of USSR. *Bulletin of the Leningrad Institute for Controlling Farm and Forest Pests* 2: 181–205 (in Russian, partly in English).
- Tatsuta, H., Ito, G., Bugrov, A. G., Tchernykh, A. A. & Akimoto, S. 2000. Multivariate morphometrics of two *Podisma* species (Orthoptera: Acrididae) in Kunashiri Island. *Applied Entomology and Zoology* 35(1): 1–8.
- Tominaga, O. 1983. *Parapodisma* information 26. *Battarigisu* 50: 1472. (In Japanese.)
- Tominaga, O. 1989. A new *Parapodisma* species (Orthoptera: Catantopidae) from Japan. *Akitu*, new series 102: 1–10.
- Tominaga, O. 1996. Tanzawa-fukibatta demodori no scandal. *Battarigisu* 107: 70–77. (In Japanese.)
- Tominaga, O. & Kanô, Y. 1987. A new *Parapodisma* species (Orthoptera, Acrididae) from the Kinki District, Japan. *Essa Entomological Society Journal* 64: 29–38. (Description in Japanese and English.)
- Tominaga, O., Storozhenko, S. Y. & Kanô, Y. 1996. Two new species and a new subspecies of the genus *Parapodisma* (Orthoptera, Acrididae) from Japan. *Tettigonia* 1(1): 1–23.
- Tominaga, O., & Uchida, M. 2001. A new genus of tribe Melanoplinae (Orthoptera, Acrididae) from Japan. *Tettigonia* (3): 9–15.
- Tominaga, O. & Wada, I. 2001. A new *Parapodisma* species (Orthoptera, Acrididae) from central Honshu, Japan. *Tettigonia* (3): 17–25.
- Tominaga, O. & Ishikawa, H. 2001. A new alpine species of the genus *Parapodisma* (Orthoptera: Acrididae) from Honshu, Japan. *Tettigonia* (3): 27–32.
- Tomokuni, M. 1994. Type materials of several Japanese and Korean Tingidae (Heteroptera), with designation of lectotypes and notes on Matsumura's collection. *Japanese Journal of Entomology* 62 (4): 839–844.
- Uvarov, B. P. 1940. Twenty-four new generic names in Orthoptera. *Annual Magazine of Natural History* 11 (6): 112–117.
- Uvarov, B. P. 1966. *Grasshoppers and Locusts*. Vol. 1. 481pp. Cambridge University Press, Cambridge, UK.
- Uvarov, B. P. 1977. *Grasshoppers and Locusts*. Vol. 2. 613 pp. Centre for Overseas Pest Research, London, UK.
- Vickery, V. R. 1977. The value of cytology in taxonomy with particular reference to the Podismini (Acridoidea: Acrididae: Melanoplinae). *Revista de la Sociedad Entomologica Argentina* 36: 89–95.
- Vickery, V. R., 1997. Classification of the Orthoptera (sensu stricto) or Caelifera. In: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. Eds.) *The Bionomics of Grasshoppers, Katydid and their Kin*, pp. 5–40. CAB International, New York.
- Wada, I. & Ukawa, S. 1983 *Miramella* sp. collected at Mt. Kusatsu-Shirane. *Kontyû to Shizen* 18(11): 15–19. (In Japanese.)

- Willemse, C. 1921. Bijdrage tot de kennis der Orthoptera s. s. van den Nederlandsch Indischen Archipelen Omliggende Gebieden. Zoologische Mededelingen 6: 1–44.
- Woller, D. A., Fontana P., Mariño-Pérez, R. & Song, H. 2014. Studies in Mexican Grasshoppers: *Liladownsia fraile*, a new genus and species of Dactyloini Acrididae: Melanoplinae) and an updated molecular phylogeny of Melanoplinae. Zootaxa (3793): 475–495.
- Yamasaki, T. 1980. A new *Parapodisma* species (Orthoptera, Catantopidae) from Kyushu, Japan. Annotationes Zoologicae Japonenses 53(1): 50–55.
- Yasuda, N. 1989. Distribution of high altitude apterous and brachypterous Podismini (Orthoptera) on the high mountains, Hokkaidô. Kamikawa-Chô no Shizen 14: 47–55.
- Yin, X.-c. 1980. Notes on two new species of grasshoppers from Emeishan of Sichuan Province. Entomotaxonomia 2(3): 229–232. (In Chinese, with English summary.)
- Yin, X.-c., Shi, J.-p. & Yin, Z. 1996. A synonymic catalogue of grasshoppers and their allies of the world (Orthoptera: Caelifera). 1266 pp. China publishing house, Beijing.
- Zhang, X.-j. & Xia, K.-l. 1990. A new genus and species of grasshoppers (Acridoidea: Catantopidae) from Henan Province, China. Entomotaxonomia 12(1): 1–4.
- Zheng, Z.-m. 1980. New genera and new species of grasshoppers from Sichuan, Shaanxi and Yunnan. Entomotaxonomia 2(4): 335–349. (In Chinese, with English summary.)
- Zheng, Z.-m. 1989. A preliminary survey of grasshoppers from Liaoning Province (Orthoptera). Journal of Hubei University (Natural Science) 11(4): 67–75.

