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A Comparative Histology of Male Gonads in Some Cerambycid Beetles with Notes on the Chromosomes¹⁾

By

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(With 1 Plate and 30 Text-figures)

Since a comparative study of the spermatogenesis in some cerambycid beetles was published in 1951 by the author, a considerable amount of data has been accumulated to furnish further morphological criteria for the taxonomy of this group of insects. In the present paper it is proposed to describe the comparative histology of male gonads in fifty-three species, with an additional account on the chromosomes of twenty-three species which will supplement the histological data. Previously the chromosomes of related cerambycids have been reported by Stevens (1909), Snyder (1934), Smith (1950, 1953) and Yosida (1952).

Before proceeding further, the author wishes to acknowledge his indebtedness to Professor Tohru Uchida for his kind guidance. His hearty thanks are also due to Professor Sajiro Makino, Drs. Eiji Momma and Tosihide H. Yosida and to Messrs. Hiroshi Nakahara and Masayasu Konishi for their valuable suggestions rendered during the course of this work. Moreover, the author is indebted to Dr. Masao Okada for taking photomicrographs, and to Mr. Kazuo Ohbayashi for sending material.

Material and method

The beetles concerned in this paper were collected in Hokkaido within a period from 1949 to 1954, with the one exception of *Spondylis buprestoides* which was collected in Gifu Prefecture, Honshu, by Mr. Kazuo Ohbayashi. The testes of adult specimens were removed in living state, and fixed in Allen-Bouin's solution. Sections made by the usual paraffin process were stained with Heidenhain's iron-haematoxylin.

The fifty-three species used for histological observations cover the five subfamilies, Prioninae, Aseminae, Lepturinae, Cerambycinae and Lamiinae, as listed below. Based on that material, the chromosomes were investigated in twenty-three species from among them.

1) Contribution No. 350 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

Jour. Fac. Sci. Hokkaido Univ. Ser. VI, 12, 1956.

List of species investigated¹⁾

1. Subfam. Prioninae
Megopsis (Aegosoma) sinica sinica White *Prionus insularis* Motschulsky
2. Subfam. Aseminae
Distenia gracilis (Blessig) *Spondylis buprestoides* (Linné)
3. Subfam. Lepturinae
* *Gaurotes (Paragaurotes) doris* Bates *Anoplodera (Anoplodera) rubra dichroa*
Anoplodera (Pachytodes) cometes (Bates) (Blanchard)
Anoplodera (Anoploderomorpha) cyanea *Leptura (Podostrangalia) xanthoma* Bates
(Gebler) *Leptura (Leptura) aethiops* Poda
Anoplodera (? Kanekoa) azumensis *Leptura (Leptura) latipennis* (Matsushita)
(Matsushita et Tamanuki) *Leptura (Leptura) ochraceofasciata*
Anoplodera (Anoplodera) scotodes (Bates) (Motschulsky)
Anoplodera (Anoplodera) sequensi (Reitter) *Leptura (Leptura) obliterateda vicaria* Bates
4. Subfam. Cerambycinae
* *Leontium viride* Thomson *Clytus melaenus* Bates
* *Rosalia (Rosalia) batesi* Harold * *Cyrtoclytus caproides* Bates
* *Rhopalopus (Prorrhopalopus) signaticollis* *Brachyclytus singularis* Kraatz
Solsky * *Plagionotus pulcher* (Blessig)
Callidium (Callidium) violaceum (Linné) *Chlorophorus japonicus* (Chevrolat)
Phymatodes (Poecilium) maaki (Kraatz) *Paraclytus excultus* Bates
Xylotrechus clarinus Bates * *Purpuricenus spectabilis* Motschulsky
Clytus auripilis Bates
5. Subfam. Lamiinae
Plectrura (Phlyctidola) metallica (Bates) * *Xenolea nubila* (Matsushita)
Monochamus urussovi (Fischer) * *Pterolophia jugosa* (Bates)
Monochamus grandis Waterhouse * *Pterolophia rigida* (Bates)
Monochamus saltuarius Gebler *Sydonia divaricata* Bates
* *Monochamus beloni* Pic * *Pogonocherus (Pogonocherus) dimidiatus*
* *Dihammus luxuriosus* (Bates) Blessig
* *Dihammus fraudator* (Bates) * *Acanthocinus (Acanthocinus) griseus*
* *Anoplophora (Anoplophora) chinensis* (Fabricius)
macularia (Thomson) * *Agapanthia daurica* Ganglbauer
* *Mesosa myops* var. *japonica* Bates *Saperda octomaculata* Blessig
* *Mesosa hirsuta* Bates * *Eutetrappa sedecimpunctata* (Motschulsky)
* *Mesosa longipennis* Bates * *Eutetrappa ocelota* (Bates)
* *Apalimna liturata* Bates *Stenostola niponensis* Pic

Histological account

The cerambycid beetles generally possess a pair of testes in each side of the abdomen. The testicular follicles show a radial arrangement as usually observed in the other forms of the Coleoptera, and contain germ-cells which are

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in successive stages of development, with younger germ-cells in the apical part. The structural details are described in the following according to the subfamily.

Prioninae and Aseminae

In general, the adult testes of *Prionus insularis* were primarily filled with both spermatozoa and spermatids, with certain numbers of spermatocytes sometimes observable in the apical part (Pl. IX, Fig. 1). The adult testes of *Megopis sinica sinica*, *Distenia gracilis* and *Spondylis buprestoides* were the same as those of *Prionus insularis* in general features of germ-cells (Pl. IX, Figs. 2-3).

Lepturinae

The adult testes of *Anoplodera rubra dichroa* showed numerous spermatozoa and spermatids (Pl. IX, Fig. 5). The testicular structure of twelve species of the Lepturinae so far studied was apparently identical with that of *A. rubra dichroa*. Occasionally there occurred some primary and secondary spermatocytes in the testes of *Gauvotus doris* and *Anoplodera azumensis*, some of them undergoing the meiotic divisions (Pl. IX, Fig. 4).

Cerambycinae

In fourteen species of the Cerambycinae here studied the testicular structure was similar to that observed in the Lepturinae (Pl. IX, Figs. 6-8). In addition, even some young individuals probably just after emergence possessed testes in which the spermioteleosis was generally highly advanced. However, it seems to be a general feature of the Cerambycinae that the apical parts containing spermatocytes are proportionately larger than those of the Lepturinae. It is not infrequent that the 1st and 2nd meiotic divisions proceed actively.

Lamiinae

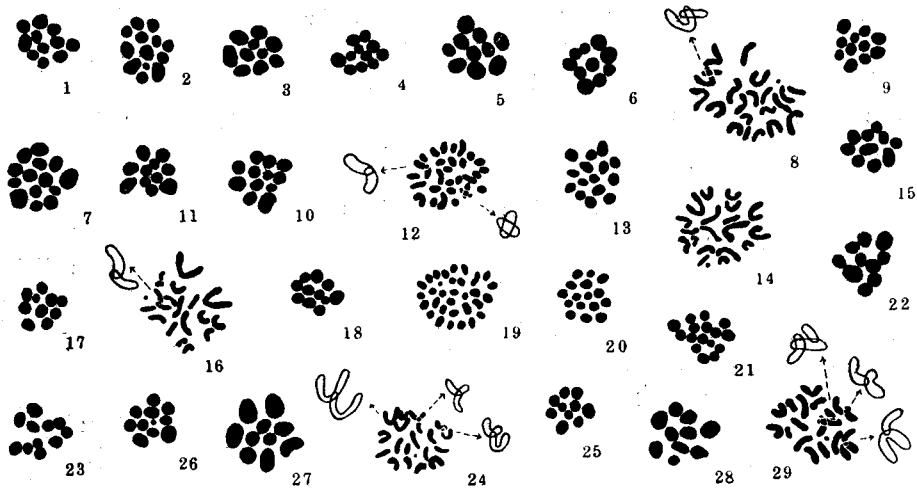
Twenty-three species of the Lamiinae here examined showed adult testes which were unique in their developmental features. The apical portions of the testicular follicles furnished a considerable number of primary spermatocytes in various stages of the growth period. Noticeable is the fact that a number of spermatogonia are frequently observable in the very end of the apical portion. The testicular follicles were provided with germ-cells in successive stages of development ranging from primary spermatocytes to secondary spermatocytes, in order of developmental stages, together with spermatids and spermatozoa (Pl. IX, Figs. 9-12).

The parts provided with spermatogonia and spermatocytes are generally smaller in size than those with spermatozoa and spermatids. But some specimens showed the former area of considerable large size (Pl. IX, Fig. 9). Even the specimens which were in copulation or old in age nearing death also often furnished in their testes a number of spermatocytes, some of them being in process of meiotic divisions.

Account on the chromosomes

The chromosome constitution of twenty-three species covering the following

three subfamilies, Lepturinae, Cerambycinae and Lamiinae was studied in male germ-cells.



Figs. 1-29. Chromosomes at metaphase. Camera-lucida drawings ; approximately $\times 1600$. The outlines of some overlapping chromosomes are shown in certain metaphases by hand drawings. 1-7, 9-11, 13, 15, 17-18, 20-23, 25-28. Primary spermatocyte chromosomes. 8, 12, 14, 16, 19, 24, 29. Spermatogonial chromosomes. 1. *Gauvotus doris*. 2. *Leontium viride*. 3. *Rosalia batesi*. 4. *Rhopalopus signaticollis*. 5. *Cyrtoclytus caproides*. 6. *Plagionotus pulcher*. 7. *Purpuricenus spectabilis*. 8-9. *Monochamus beloni*. 10. *Dihammus luxuriosus*. 11. *Dihammus fraudator*. 12-13. *Anoplophora chinensis macularia*. 14-15. *Mesosa myops* var. *japonica*. 16-17. *Mesosa hirsuta*. 18. *Mesosa longipennis*. 19-20. *Apalimna liturata*. 21. *Xenolea nubila*. 22. *Pterolophia jugosa*. 23. *Pterolophia rigida*. 24-25. *Pogonocherus dimidiatus*. 26. *Acanthocinus griseus*. 27. *Agapanthia daurica*. 28. *Eutetrappa sedecimpunctata*. 29. *Eutetrappa ocelota*.

Spermatogonial chromosomes: The spermatogonial chromosomes were available for investigation in seven species belonging to the Lamiinae for the confirmation of the diploid number and the sex-chromosome mechanism. The results are given in Table 1, together with some account of the primary spermatocytes. In most species the chromosomes seem to be of metacentric nature, except the Y-chromosome which is acrocentric. All the species here studied uniformly showed an XY-type of the sex-determining mechanism. The Y-chromosome is always represented by a small-sized element, whereas it was difficult to identify the X-chromosome because of lack of adequate configuration.

Primary spermatocyte chromosomes: The primary spermatocytes observed in twenty-two species furnished data on the haploid numbers which varied from 10 to 16. It is a general feature that the higher the chromosome number is, the

Table 1. Species studied and their chromosome numbers established in this study

Species †	Locality	Chrom. number		Sex-chrom. (♂)
		2n (spermatogonium)	n (primary spermatocyte)	
Subfam. Lepturinae				
<i>Gauvotus doris</i>	Sapporo		11	
Subfam. Cerambycinae				
<i>Leontium viride</i>	Jōzankei		13	
<i>Rosalia batesi</i>	Jōzankei		10	
<i>Rhopalopus signaticollis</i>	Sapporo		11	
<i>Cyrtoclytus caproides</i>	Sapporo		10	
<i>Plagionotus pulcher</i>	Jōzankei		10	
<i>Purpuricenus spectabilis</i>	Sapporo		14	
Subfam. Lamiinae				
<i>Monochamus beloni</i>	Sapporo	22	11	X-Y
<i>Dihammus luxuriosus</i>	Mt. Soranuma		12	
<i>Dihammus fraudator</i>	Mt. Tarumaé		11	
<i>Anoplophora chinensis macularia</i>	Nopporo	30	15	X-Y
<i>Mesosa myops</i> var. <i>japonica</i>	Sapporo	20	10	X-Y
<i>Mesosa hirsuta</i>	Sapporo	20	10	X-Y
<i>Mesosa longipennis</i>	Sapporo		11	
<i>Apalimna liturata</i>	Mt. Moiwa	32	16	X-Y
<i>Xenolea nubila</i>	Sapporo		16	
<i>Pterolophia jugosa</i>	Mt. Moiwa		10	
<i>Pterolophia rigida</i>	Sapporo		11	
<i>Pogonocherus dimidiatus</i>	Sapporo	20	10	X-Y
<i>Acanthocinus griseus</i>	Nukabira		11	
<i>Agapanthia daurica</i>	Sapporo		10	
<i>Eutetrappa sedecimpunctata</i>	Nopporo		10	
<i>Eutetrappa ocelota</i>	Jōzankei	20		X-Y

† For the subgeneric names of species, refer to p. 310.

smaller the chromosome-size is. The actual confirmation of the XY-complex was difficult in most species, due to the unsuitable state of preservation.

Discussion

In the former paper the author (1951) suggested that the members of the Lamiinae are differentiated in the histological structure of the testes from those of the Lepturinae and Cerambycinae. The results of the present study which was supplied with sufficient and additional material furnished supplementary evidence for the former view, showing that the adult testes of the members of the Lamiinae are provided with germ-cells in various developmental stages ranging from the spermatogonia to the primary and secondary spermatocytes, together with mature spermatozoa. In striking contrast to that feature of the Lamiinae the adult testes of the Prioninae, Aseminae, Lepturinae and Cerambycinae show a considerable advance in spermioteleosis, with a few spermatocytes occurring in a few restricted portions. The results of the present histological study seem to be supported by the

fact that the investigations of the spermatogonial chromosomes have exclusively been carried out in the Lamiinae in the past, including this study, due probably to the easy availability of material for cytological study.

It is generally accepted by most coleopterologists that the members of the Lamiinae alone are highly different from all other members of the Cerambycidae in several taxonomic characteristics. The same has been said on the basis of some other morphological and biological studies, such as from the structure and habits of larvae by Craighead (1923), from the structure of the wing veins by Saalas (1936), and from the structure of the male genitalia by Ehara (1954). The results of this histological study serve to strengthen the above belief.

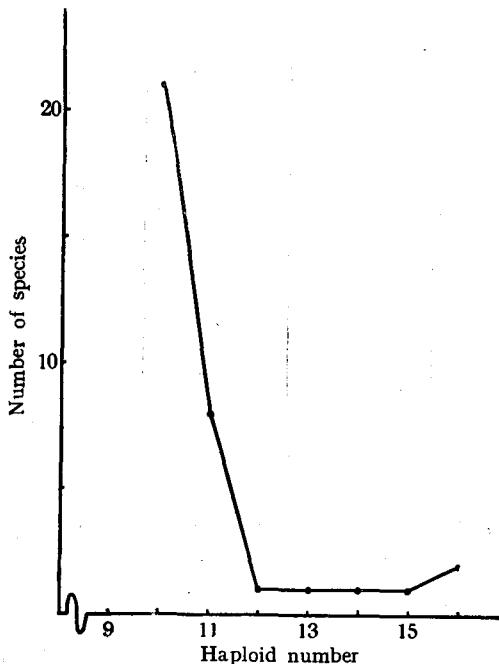


Fig. 30. Distribution of the chromosome numbers in the Cerambycidae, based on the data so far recorded.

Referring to the lists of Makino (1951) and Smith (1953) it is understood that the chromosomes of the Cerambycidae have so far been studied in thirteen species by Stevens (1909), Snyder (1934), Smith (1950, 1953) and Yosida (1952).¹⁾ According to these past work, the sex-determining mechanism is represented by an XY-type in all cases, and the haploid chromosomes were 10 in number, with one exceptional species having 11.

Thus the number of species in which the chromosomes have been reported is thirty-six in total (Fig. 30). As shown in the foregoing pages seven species belonging to the Lamiinae provided the spermatogonial chromosomes with the sex-determining mechanism of an XY-type. The haploid chromosome number here established for twenty-three species varies within the range from 10

to 16, the numbers of 10 and 11 being predominant. There occurs no constancy in the number of chromosomes within the same subfamily. It has also been shown that the species within the same genus are not always constant in number

1) Yosida (1952) reported the chromosomes of *Pterolophia caudata* (Bates). According to the author's observation, the specimen used by Yosida should be classified as *P. jugosa* (Bates).

of chromosomes. For instance, the haploid number of *Mesosa longipennis* is 11, whereas it is 10 in both *M. myops* var. *japonica* and *M. hirsuta*. A similar situation is known to occur in the genera *Dihammus* and *Pterolophia*.

It may not be of insignificance in reference to taxonomy that all the members of the family Cerambycidae uniformly show an XY sex-determining mechanism in males. In striking contrast, the species of the family Chrysomelidae which are closely related to the family Cerambycidae carry sex-chromosomes of both XO- and XY-types in males and show a number of chromosomes considerably differing from species to species (cf. Makino 1951). From the anatomy of the male genitalia, Sharp and Muir (1912), Zia (1936) and Ehara (1954) have proposed the view that there is a relative uniformity in structural type among the species of the Cerambycidae, in contrast with the diversity occurring in the Chrysomelidae. Based on the results of both cytological and anatomical studies so far presented, the author should like to conclude that the family Cerambycidae are probably an oligotrepic (or monotrepic) group, in comparison with the evidence occurring in the family Chrysomelidae.

Summary

1. The course of spermatogenesis was compared on the basis of the histological structure of adult gonads in fifty-three species belonging to the Cerambycidae which cover the following five subfamilies, Prioninae, Aseminae, Lepturinae, Cerambycinae and Lamiinae.

2. It was shown that in histological features the members of the Lamiinae are well differentiated from those of the other subfamilies.

3. The chromosomes of twenty-three species were investigated in male germ-cells. The number of chromosomes shows a range of variation according to species, ranging from 10 to 16 in haploid, the cases showing the numbers 10 and 11 being most frequent. There is no constancy in the number of the chromosomes within the same subfamily but this not always the case within the same genus.

4. An XY-type of the sex-determining mechanism was established in seven species of the Lamiinae.

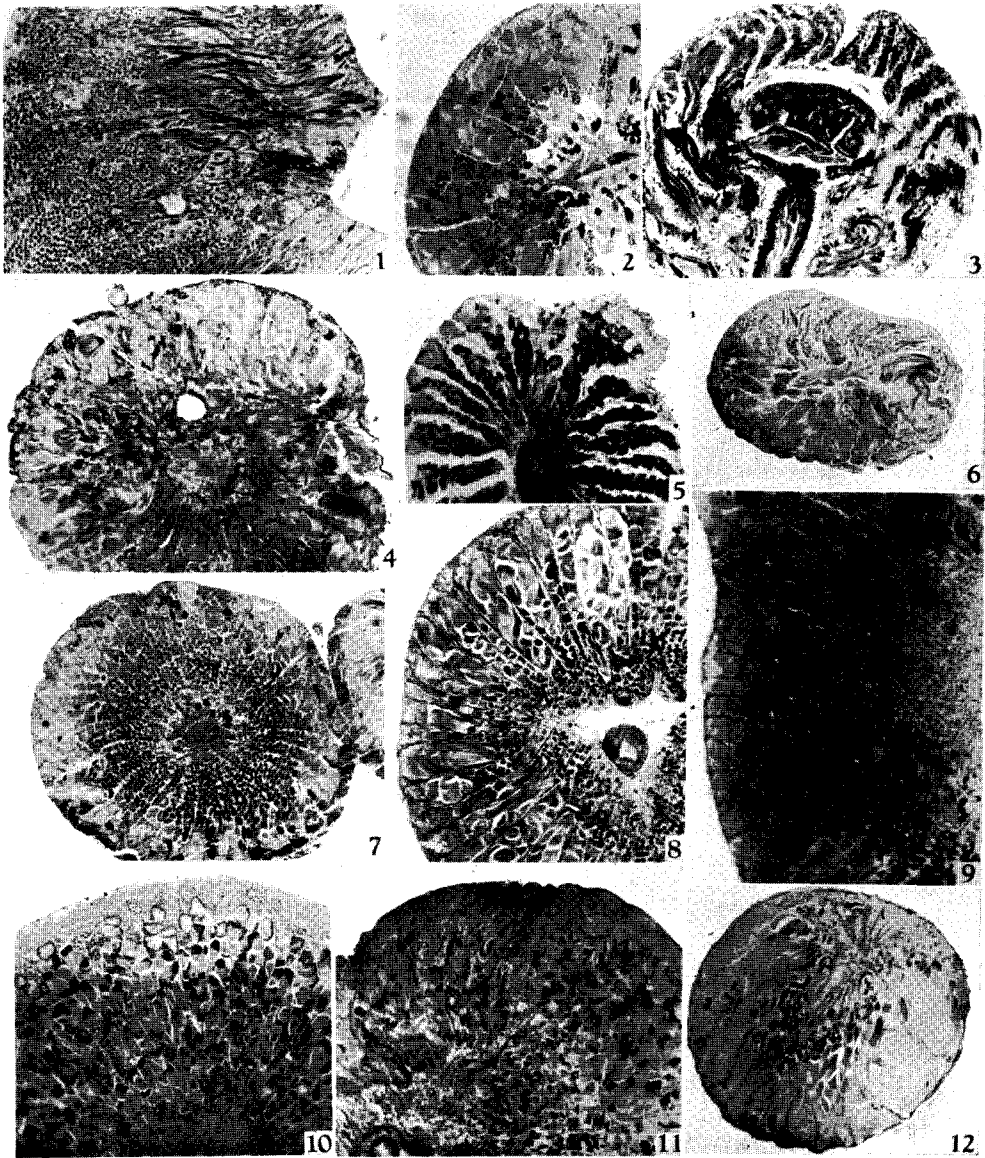
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Explanation of Plate IX

Figs. 1-12. Cross sections of testes. $\times 49$. (Photo by Dr. M. Okada) 1. *Prionus insularis*, showing the testicular follicles filled with spermatozoa and spermatids. 2. *Distenia gracilis*. The same, showing the occurrence of some colonies of spermatocytes. 3. *Spondylis buprestoides*. The testis is provided exclusively with spermatozoa. 4. *Gaurotes doris*. The testis is occupied with spermatozoa, showing a colony of dividing primary spermatocytes in the peripheral portion. 5. *Anoplodera rubra dichrou*, showing the testicular follicles filled with spermatozoa. 6. *Phymatodes maaki*, showing the testicular follicles occupied with spermatozoa. 7. *Plagionotus pulcher*, showing the testicular follicles provided with spermatozoa and spermatids. In the peripheral parts there occurs a good number of primary spermatocytes, in growth period and in division. 8. *Purpuricenus spectabilis*, showing the testicular follicles occupied with spermatozoa and spermatids. Some secondary spermatocytes can be seen in the peripheral portion. 9. *Monochamus grandis*. There is the expanding area with spermatogonia and primary spermatocytes, together with a number of spermatozoa. 10. *Mesosa myops* var. *japonica*. In the peripheral part there occur primary and secondary spermatocytes, in various developmental stages. 11. *Mesosa longipennis*. In the peripheral region the primary spermatocytes in growth period occur. 12. *Eutetrappa ocelota*. The spermatocytes are scarcely found in the testis. This is rather exceptional in the Lamiinae.



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Lamiinae

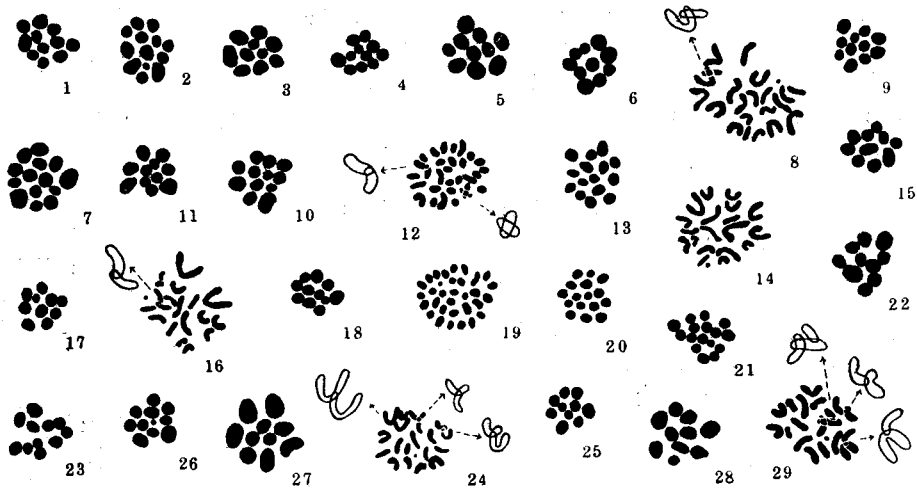
Twenty-three species of the Lamiinae here examined showed adult testes which were unique in their developmental features. The apical portions of the testicular follicles furnished a considerable number of primary spermatocytes in various stages of the growth period. Noticeable is the fact that a number of spermatogonia are frequently observable in the very end of the apical portion. The testicular follicles were provided with germ-cells in successive stages of development ranging from primary spermatocytes to secondary spermatocytes, in order of developmental stages, together with spermatids and spermatozoa (Pl. IX, Figs. 9-12).

The parts provided with spermatogonia and spermatocytes are generally smaller in size than those with spermatozoa and spermatids. But some specimens showed the former area of considerable large size (Pl. IX, Fig. 9). Even the specimens which were in copulation or old in age nearing death also often furnished in their testes a number of spermatocytes, some of them being in process of meiotic divisions.

Account on the chromosomes

The chromosome constitution of twenty-three species covering the following

three subfamilies, Lepturinae, Cerambycinae and Lamiinae was studied in male germ-cells.



Figs. 1-29. Chromosomes at metaphase. Camera-lucida drawings ; approximately $\times 1600$. The outlines of some overlapping chromosomes are shown in certain metaphases by hand drawings. 1-7, 9-11, 13, 15, 17-18, 20-23, 25-28. Primary spermatocyte chromosomes. 8, 12, 14, 16, 19, 24, 29. Spermatogonial chromosomes. 1. *Gauvotus doris*. 2. *Leontium viride*. 3. *Rosalia batesi*. 4. *Rhopalopus signaticollis*. 5. *Cyrtoclytus caproides*. 6. *Plagionotus pulcher*. 7. *Purpuricenus spectabilis*. 8-9. *Monochamus beloni*. 10. *Dihammus luxuriosus*. 11. *Dihammus fraudator*. 12-13. *Anoplophora chinensis macularia*. 14-15. *Mesosa myops* var. *japonica*. 16-17. *Mesosa hirsuta*. 18. *Mesosa longipennis*. 19-20. *Apalimna liturata*. 21. *Xenolea nubila*. 22. *Pterolophia jugosa*. 23. *Pterolophia rigida*. 24-25. *Pogonocherus dimidiatus*. 26. *Acanthocinus griseus*. 27. *Agapanthia daurica*. 28. *Eutetrappa sedecimpunctata*. 29. *Eutetrappa ocelota*.

Spermatogonial chromosomes: The spermatogonial chromosomes were available for investigation in seven species belonging to the Lamiinae for the confirmation of the diploid number and the sex-chromosome mechanism. The results are given in Table 1, together with some account of the primary spermatocytes. In most species the chromosomes seem to be of metacentric nature, except the Y-chromosome which is acrocentric. All the species here studied uniformly showed an XY-type of the sex-determining mechanism. The Y-chromosome is always represented by a small-sized element, whereas it was difficult to identify the X-chromosome because of lack of adequate configuration.

Primary spermatocyte chromosomes: The primary spermatocytes observed in twenty-two species furnished data on the haploid numbers which varied from 10 to 16. It is a general feature that the higher the chromosome number is, the

Table 1. Species studied and their chromosome numbers established in this study

Species †	Locality	Chrom. number		Sex-chrom. (♂)
		2n (spermatogonium)	n (primary spermatocyte)	
Subfam. Lepturinae				
<i>Gaurotes doris</i>	Sapporo		11	
Subfam. Cerambycinae				
<i>Leontium viride</i>	Jōzankei		13	
<i>Rosalia batesi</i>	Jōzankei		10	
<i>Rhopalopus signaticollis</i>	Sapporo		11	
<i>Cyrtoclytus caproides</i>	Sapporo		10	
<i>Plagionotus pulcher</i>	Jōzankei		10	
<i>Purpuricenus spectabilis</i>	Sapporo		14	
Subfam. Lamiinae				
<i>Monochamus beloni</i>	Sapporo	22	11	X-Y
<i>Dihammus luxuriosus</i>	Mt. Soranuma		12	
<i>Dihammus fraudator</i>	Mt. Tarumaé		11	
<i>Anoplophora chinensis macularia</i>	Nopporo	30	15	X-Y
<i>Mesosa myops</i> var. <i>japonica</i>	Sapporo	20	10	X-Y
<i>Mesosa hirsuta</i>	Sapporo	20	10	X-Y
<i>Mesosa longipennis</i>	Sapporo		11	
<i>Apalimna liturata</i>	Mt. Moiwa	32	16	X-Y
<i>Xenolea nubila</i>	Sapporo		16	
<i>Pterolophia jugosa</i>	Mt. Moiwa		10	
<i>Pterolophia rigida</i>	Sapporo		11	
<i>Pogonocherus dimidiatus</i>	Sapporo	20	10	X-Y
<i>Acanthocinus griseus</i>	Nukabira		11	
<i>Agapanthia daurica</i>	Sapporo		10	
<i>Eutetrappa sedecimpunctata</i>	Nopporo		10	
<i>Eutetrappa ocelota</i>	Jōzankei	20		X-Y

† For the subgeneric names of species, refer to p. 310.

smaller the chromosome-size is. The actual confirmation of the XY-complex was difficult in most species, due to the unsuitable state of preservation.

Discussion

In the former paper the author (1951) suggested that the members of the Lamiinae are differentiated in the histological structure of the testes from those of the Lepturinae and Cerambycinae. The results of the present study which was supplied with sufficient and additional material furnished supplementary evidence for the former view, showing that the adult testes of the members of the Lamiinae are provided with germ-cells in various developmental stages ranging from the spermatogonia to the primary and secondary spermatocytes, together with mature spermatozoa. In striking contrast to that feature of the Lamiinae the adult testes of the Prioninae, Aseminae, Lepturinae and Cerambycinae show a considerable advance in spermioteleosis, with a few spermatocytes occurring in a few restricted portions. The results of the present histological study seem to be supported by the

fact that the investigations of the spermatogonial chromosomes have exclusively been carried out in the Lamiinae in the past, including this study, due probably to the easy availability of material for cytological study.

It is generally accepted by most coleopterologists that the members of the Lamiinae alone are highly different from all other members of the Cerambycidae in several taxonomic characteristics. The same has been said on the basis of some other morphological and biological studies, such as from the structure and habits of larvae by Craighead (1923), from the structure of the wing veins by Saalas (1936), and from the structure of the male genitalia by Ehara (1954). The results of this histological study serve to strengthen the above belief.

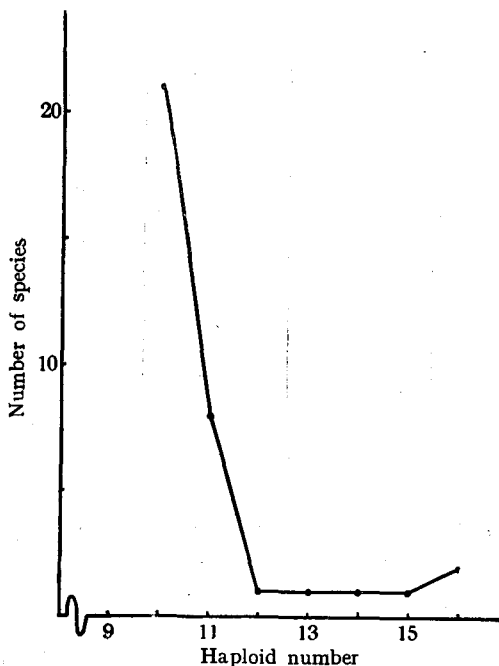


Fig. 30. Distribution of the chromosome numbers in the Cerambycidae, based on the data so far recorded.

Referring to the lists of Makino (1951) and Smith (1953) it is understood that the chromosomes of the Cerambycidae have so far been studied in thirteen species by Stevens (1909), Snyder (1934), Smith (1950, 1953) and Yosida (1952).¹⁾ According to these past work, the sex-determining mechanism is represented by an XY-type in all cases, and the haploid chromosomes were 10 in number, with one exceptional species having 11.

Thus the number of species in which the chromosomes have been reported is thirty-six in total (Fig. 30). As shown in the foregoing pages seven species belonging to the Lamiinae provided the spermatogonial chromosomes with the sex-determining mechanism of an XY-type. The haploid chromosome number here established for twenty-three species varies within the range from 10

to 16, the numbers of 10 and 11 being predominant. There occurs no constancy in the number of chromosomes within the same subfamily. It has also been shown that the species within the same genus are not always constant in number

1) Yosida (1952) reported the chromosomes of *Pterolophia caudata* (Bates). According to the author's observation, the specimen used by Yosida should be classified as *P. jugosa* (Bates).

of chromosomes. For instance, the haploid number of *Mesosa longipennis* is 11, whereas it is 10 in both *M. myops* var. *japonica* and *M. hirsuta*. A similar situation is known to occur in the genera *Dihammus* and *Pterolophia*.

It may not be of insignificance in reference to taxonomy that all the members of the family Cerambycidae uniformly show an XY sex-determining mechanism in males. In striking contrast, the species of the family Chrysomelidae which are closely related to the family Cerambycidae carry sex-chromosomes of both XO- and XY-types in males and show a number of chromosomes considerably differing from species to species (cf. Makino 1951). From the anatomy of the male genitalia, Sharp and Muir (1912), Zia (1936) and Ehara (1954) have proposed the view that there is a relative uniformity in structural type among the species of the Cerambycidae, in contrast with the diversity occurring in the Chrysomelidae. Based on the results of both cytological and anatomical studies so far presented, the author should like to conclude that the family Cerambycidae are probably an oligotrepic (or monotrepic) group, in comparison with the evidence occurring in the family Chrysomelidae.

Summary

1. The course of spermatogenesis was compared on the basis of the histological structure of adult gonads in fifty-three species belonging to the Cerambycidae which cover the following five subfamilies, Prioninae, Aseminae, Lepturinae, Cerambycinae and Lamiinae.

2. It was shown that in histological features the members of the Lamiinae are well differentiated from those of the other subfamilies.

3. The chromosomes of twenty-three species were investigated in male germ-cells. The number of chromosomes shows a range of variation according to species, ranging from 10 to 16 in haploid, the cases showing the numbers 10 and 11 being most frequent. There is no constancy in the number of the chromosomes within the same subfamily but this not always the case within the same genus.

4. An XY-type of the sex-determining mechanism was established in seven species of the Lamiinae.

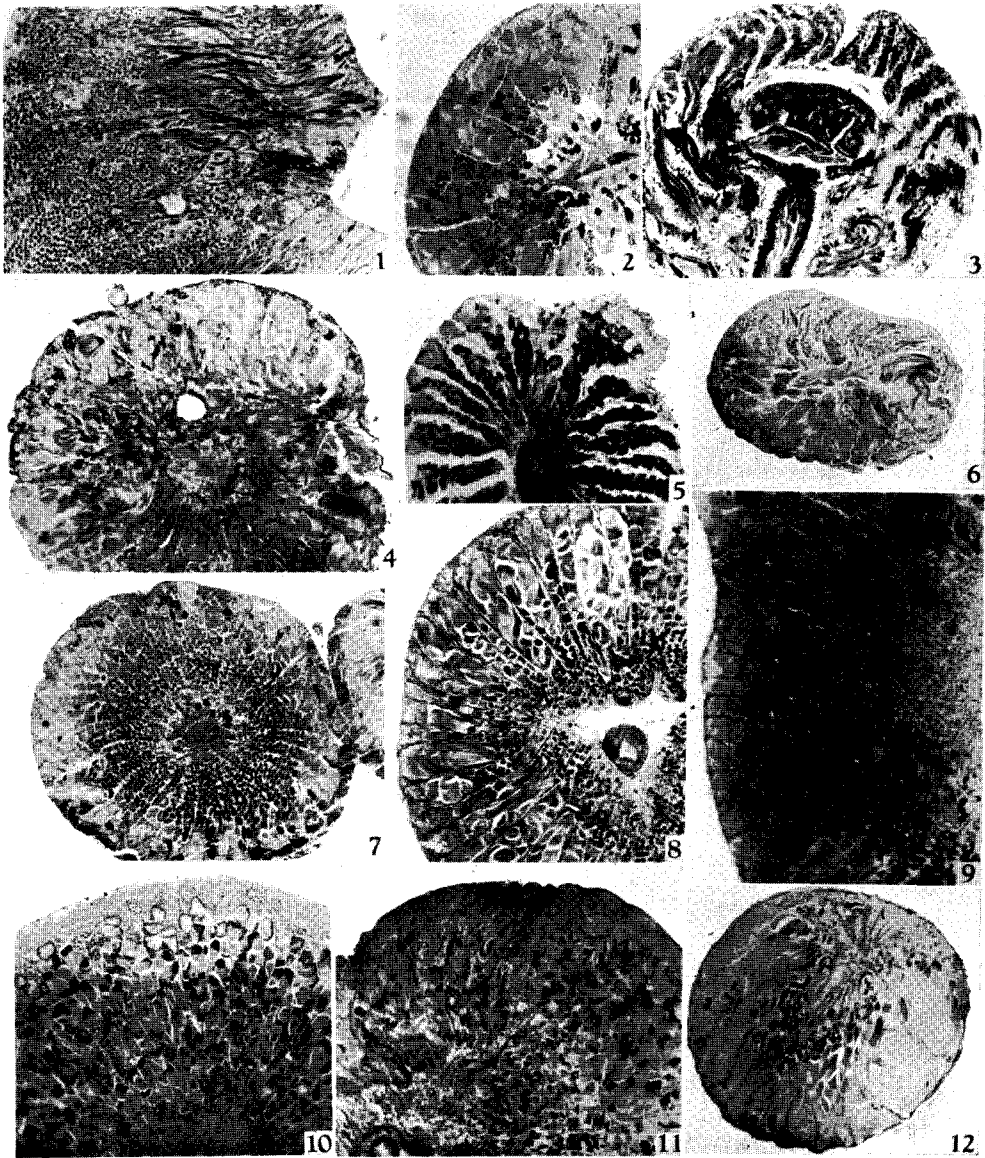
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Explanation of Plate IX

Figs. 1-12. Cross sections of testes. $\times 49$. (Photo by Dr. M. Okada) 1. *Prionus insularis*, showing the testicular follicles filled with spermatozoa and spermatids. 2. *Distenia gracilis*. The same, showing the occurrence of some colonies of spermatocytes. 3. *Spondylis buprestoides*. The testis is provided exclusively with spermatozoa. 4. *Gaurotes doris*. The testis is occupied with spermatozoa, showing a colony of dividing primary spermatocytes in the peripheral portion. 5. *Anoplodera rubra dichrou*, showing the testicular follicles filled with spermatozoa. 6. *Phymatodes maaki*, showing the testicular follicles occupied with spermatozoa. 7. *Plagionotus pulcher*, showing the testicular follicles provided with spermatozoa and spermatids. In the peripheral parts there occurs a good number of primary spermatocytes, in growth period and in division. 8. *Purpuricenus spectabilis*, showing the testicular follicles occupied with spermatozoa and spermatids. Some secondary spermatocytes can be seen in the peripheral portion. 9. *Monochamus grandis*. There is the expanding area with spermatogonia and primary spermatocytes, together with a number of spermatozoa. 10. *Mesosa myops* var. *japonica*. In the peripheral part there occur primary and secondary spermatocytes, in various developmental stages. 11. *Mesosa longipennis*. In the peripheral region the primary spermatocytes in growth period occur. 12. *Eutetrappa ocelota*. The spermatocytes are scarcely found in the testis. This is rather exceptional in the Lamiinae.



S. Ehara: A Comparative Histology of Male Gonads in Cerambycid Beetles

A Comparative Histology of Male Gonads in Some Cerambycid Beetles with Notes on the Chromosomes¹⁾

By

Shôzô Ehara

(Zoological Institute, Hokkaido University)

(With 1 Plate and 30 Text-figures)

Since a comparative study of the spermatogenesis in some cerambycid beetles was published in 1951 by the author, a considerable amount of data has been accumulated to furnish further morphological criteria for the taxonomy of this group of insects. In the present paper it is proposed to describe the comparative histology of male gonads in fifty-three species, with an additional account on the chromosomes of twenty-three species which will supplement the histological data. Previously the chromosomes of related cerambycids have been reported by Stevens (1909), Snyder (1934), Smith (1950, 1953) and Yosida (1952).

Before proceeding further, the author wishes to acknowledge his indebtedness to Professor Tohru Uchida for his kind guidance. His hearty thanks are also due to Professor Sajiro Makino, Drs. Eiji Momma and Tosihide H. Yosida and to Messrs. Hiroshi Nakahara and Masayasu Konishi for their valuable suggestions rendered during the course of this work. Moreover, the author is indebted to Dr. Masao Okada for taking photomicrographs, and to Mr. Kazuo Ohbayashi for sending material.

Material and method

The beetles concerned in this paper were collected in Hokkaido within a period from 1949 to 1954, with the one exception of *Spondylis buprestoides* which was collected in Gifu Prefecture, Honshu, by Mr. Kazuo Ohbayashi. The testes of adult specimens were removed in living state, and fixed in Allen-Bouin's solution. Sections made by the usual paraffin process were stained with Heidenhain's iron-haematoxylin.

The fifty-three species used for histological observations cover the five subfamilies, Prioninae, Aseminae, Lepturinae, Cerambycinae and Lamiinae, as listed below. Based on that material, the chromosomes were investigated in twenty-three species from among them.

1) Contribution No. 350 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

Jour. Fac. Sci. Hokkaido Univ. Ser. VI, 12, 1956.

List of species investigated¹⁾

1. Subfam. Prioninae
Megopsis (Aegosoma) sinica sinica White *Prionus insularis* Motschulsky
2. Subfam. Aseminae
Distenia gracilis (Blessig) *Spondylis buprestoides* (Linné)
3. Subfam. Lepturinae
* *Gaurotes (Paragaurotes) doris* Bates *Anoplodera (Anoplodera) rubra dichroa*
Anoplodera (Pachytodes) cometes (Bates) (Blanchard)
Anoplodera (Anoploderomorpha) cyanea *Leptura (Podostrangalia) xanthoma* Bates
(Gebler) *Leptura (Leptura) aethiops* Poda
Anoplodera (? Kanekoa) azumensis *Leptura (Leptura) latipennis* (Matsushita)
(Matsushita et Tamanuki) *Leptura (Leptura) ochraceofasciata*
Anoplodera (Anoplodera) scotodes (Bates) (Motschulsky)
Anoplodera (Anoplodera) sequensi (Reitter) *Leptura (Leptura) oblitterata vicaria* Bates
4. Subfam. Cerambycinae
* *Leontium viride* Thomson *Clytus melaenus* Bates
* *Rosalia (Rosalia) batesi* Harold * *Cyrtoclytus caproides* Bates
* *Rhopalopus (Prorrhopalopus) signaticollis* *Brachyclytus singularis* Kraatz
Solsky * *Plagionotus pulcher* (Blessig)
Callidium (Callidium) violaceum (Linné) *Chlorophorus japonicus* (Chevrolat)
Phymatodes (Poecilium) maaki (Kraatz) *Paraclytus excultus* Bates
Xylotrechus clarinus Bates * *Purpuricenus spectabilis* Motschulsky
Clytus auripilis Bates
5. Subfam. Lamiinae
Plectrura (Phlyctidola) metallica (Bates) * *Xenolea nubila* (Matsushita)
Monochamus urussovi (Fischer) * *Pterolophia jugosa* (Bates)
Monochamus grandis Waterhouse * *Pterolophia rigida* (Bates)
Monochamus saltuarius Gebler *Sydonia divaricata* Bates
* *Monochamus beloni* Pic * *Pogonocherus (Pogonocherus) dimidiatus*
* *Dihammus luxuriosus* (Bates) Blessig
* *Dihammus fraudator* (Bates) * *Acanthocinus (Acanthocinus) griseus*
* *Anoplophora (Anoplophora) chinensis* (Fabricius)
macularia (Thomson) * *Agapanthia daurica* Ganglbauer
* *Mesosa myops* var. *japonica* Bates *Saperda octomaculata* Blessig
* *Mesosa hirsuta* Bates * *Eutetrappa sedecimpunctata* (Motschulsky)
* *Mesosa longipennis* Bates * *Eutetrappa ocelota* (Bates)
* *Apalimna liturata* Bates *Stenostola niponensis* Pic

Histological account

The cerambycid beetles generally possess a pair of testes in each side of the abdomen. The testicular follicles show a radial arrangement as usually observed in the other forms of the Coleoptera, and contain germ-cells which are

1) The species names and their arrangement in this list have mainly followed Mitono's catalogue (1940) and Gressitt's articles (1951, 1953). The species in which the chromosomes were reported in this paper are marked with an asterisk.

in successive stages of development, with younger germ-cells in the apical part. The structural details are described in the following according to the subfamily.

Prioninae and Aseminae

In general, the adult testes of *Prionus insularis* were primarily filled with both spermatozoa and spermatids, with certain numbers of spermatocytes sometimes observable in the apical part (Pl. IX, Fig. 1). The adult testes of *Megopis sinica sinica*, *Distenia gracilis* and *Spondylis buprestoides* were the same as those of *Prionus insularis* in general features of germ-cells (Pl. IX, Figs. 2-3).

Lepturinae

The adult testes of *Anoplodera rubra dichroa* showed numerous spermatozoa and spermatids (Pl. IX, Fig. 5). The testicular structure of twelve species of the Lepturinae so far studied was apparently identical with that of *A. rubra dichroa*. Occasionally there occurred some primary and secondary spermatocytes in the testes of *Gauvotus doris* and *Anoplodera azumensis*, some of them undergoing the meiotic divisions (Pl. IX, Fig. 4).

Cerambycinae

In fourteen species of the Cerambycinae here studied the testicular structure was similar to that observed in the Lepturinae (Pl. IX, Figs. 6-8). In addition, even some young individuals probably just after emergence possessed testes in which the spermioteleosis was generally highly advanced. However, it seems to be a general feature of the Cerambycinae that the apical parts containing spermatocytes are proportionately larger than those of the Lepturinae. It is not infrequent that the 1st and 2nd meiotic divisions proceed actively.

Lamiinae

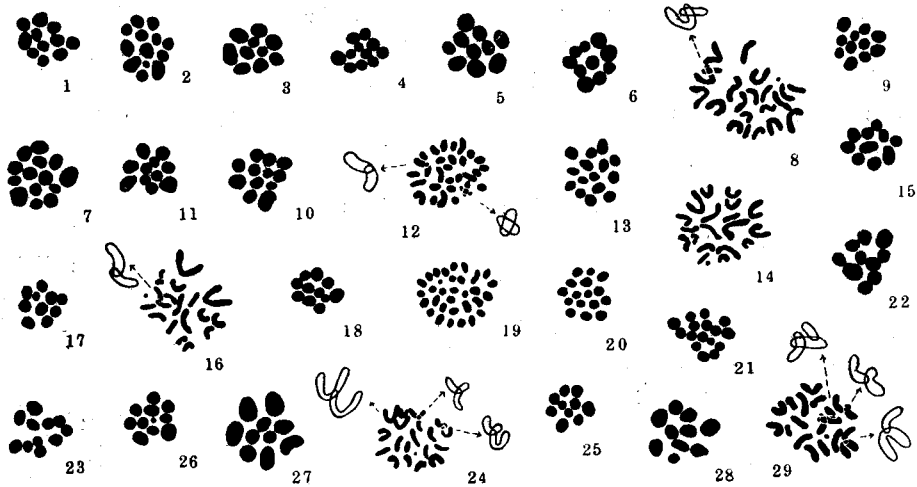
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Primary spermatocyte chromosomes: The primary spermatocytes observed in twenty-two species furnished data on the haploid numbers which varied from 10 to 16. It is a general feature that the higher the chromosome number is, the

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Species †	Locality	Chrom. number		Sex-chrom. (♂)
		2n (spermatogonium)	n (primary spermatocyte)	
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<i>Gauvotus doris</i>	Sapporo		11	
Subfam. Cerambycinae				
<i>Leontium viride</i>	Jōzankei		13	
<i>Rosalia batesi</i>	Jōzankei		10	
<i>Rhopalopus signaticollis</i>	Sapporo		11	
<i>Cyrtoclytus caproides</i>	Sapporo		10	
<i>Plagionotus pulcher</i>	Jōzankei		10	
<i>Purpuricenus spectabilis</i>	Sapporo		14	
Subfam. Lamiinae				
<i>Monochamus beloni</i>	Sapporo	22	11	X-Y
<i>Dihammus luxuriosus</i>	Mt. Soranuma		12	
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<i>Anoplophora chinensis macularia</i>	Nopporo	30	15	X-Y
<i>Mesosa myops</i> var. <i>japonica</i>	Sapporo	20	10	X-Y
<i>Mesosa hirsuta</i>	Sapporo	20	10	X-Y
<i>Mesosa longipennis</i>	Sapporo		11	
<i>Apalimna liturata</i>	Mt. Moiwa	32	16	X-Y
<i>Xenolea nubila</i>	Sapporo		16	
<i>Pterolophia jugosa</i>	Mt. Moiwa		10	
<i>Pterolophia rigida</i>	Sapporo		11	
<i>Pogonocherus dimidiatus</i>	Sapporo	20	10	X-Y
<i>Acanthocinus griseus</i>	Nukabira		11	
<i>Agapanthia daurica</i>	Sapporo		10	
<i>Eutetrappa sedecimpunctata</i>	Nopporo		10	
<i>Eutetrappa ocelota</i>	Jōzankei	20		X-Y

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smaller the chromosome-size is. The actual confirmation of the XY-complex was difficult in most species, due to the unsuitable state of preservation.

Discussion

In the former paper the author (1951) suggested that the members of the Lamiinae are differentiated in the histological structure of the testes from those of the Lepturinae and Cerambycinae. The results of the present study which was supplied with sufficient and additional material furnished supplementary evidence for the former view, showing that the adult testes of the members of the Lamiinae are provided with germ-cells in various developmental stages ranging from the spermatogonia to the primary and secondary spermatocytes, together with mature spermatozoa. In striking contrast to that feature of the Lamiinae the adult testes of the Prioninae, Aseminae, Lepturinae and Cerambycinae show a considerable advance in spermioteleosis, with a few spermatocytes occurring in a few restricted portions. The results of the present histological study seem to be supported by the

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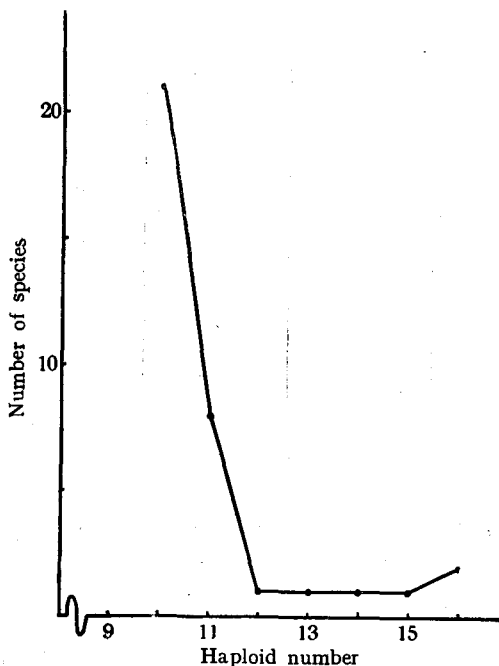


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Referring to the lists of Makino (1951) and Smith (1953) it is understood that the chromosomes of the Cerambycidae have so far been studied in thirteen species by Stevens (1909), Snyder (1934), Smith (1950, 1953) and Yosida (1952).¹⁾ According to these past work, the sex-determining mechanism is represented by an XY-type in all cases, and the haploid chromosomes were 10 in number, with one exceptional species having 11.

Thus the number of species in which the chromosomes have been reported is thirty-six in total (Fig. 30). As shown in the foregoing pages seven species belonging to the Lamiinae provided the spermatogonial chromosomes with the sex-determining mechanism of an XY-type. The haploid chromosome number here established for twenty-three species varies within the range from 10

to 16, the numbers of 10 and 11 being predominant. There occurs no constancy in the number of chromosomes within the same subfamily. It has also been shown that the species within the same genus are not always constant in number

1) Yosida (1952) reported the chromosomes of *Pterolophia caudata* (Bates). According to the author's observation, the specimen used by Yosida should be classified as *P. jugosa* (Bates).

of chromosomes. For instance, the haploid number of *Mesosa longipennis* is 11, whereas it is 10 in both *M. myops* var. *japonica* and *M. hirsuta*. A similar situation is known to occur in the genera *Dihammus* and *Pterolophia*.

It may not be of insignificance in reference to taxonomy that all the members of the family Cerambycidae uniformly show an XY sex-determining mechanism in males. In striking contrast, the species of the family Chrysomelidae which are closely related to the family Cerambycidae carry sex-chromosomes of both XO- and XY-types in males and show a number of chromosomes considerably differing from species to species (cf. Makino 1951). From the anatomy of the male genitalia, Sharp and Muir (1912), Zia (1936) and Ehara (1954) have proposed the view that there is a relative uniformity in structural type among the species of the Cerambycidae, in contrast with the diversity occurring in the Chrysomelidae. Based on the results of both cytological and anatomical studies so far presented, the author should like to conclude that the family Cerambycidae are probably an oligotrepic (or monotrepic) group, in comparison with the evidence occurring in the family Chrysomelidae.

Summary

1. The course of spermatogenesis was compared on the basis of the histological structure of adult gonads in fifty-three species belonging to the Cerambycidae which cover the following five subfamilies, Prioninae, Aseminae, Lepturinae, Cerambycinae and Lamiinae.

2. It was shown that in histological features the members of the Lamiinae are well differentiated from those of the other subfamilies.

3. The chromosomes of twenty-three species were investigated in male germ-cells. The number of chromosomes shows a range of variation according to species, ranging from 10 to 16 in haploid, the cases showing the numbers 10 and 11 being most frequent. There is no constancy in the number of the chromosomes within the same subfamily but this not always the case within the same genus.

4. An XY-type of the sex-determining mechanism was established in seven species of the Lamiinae.

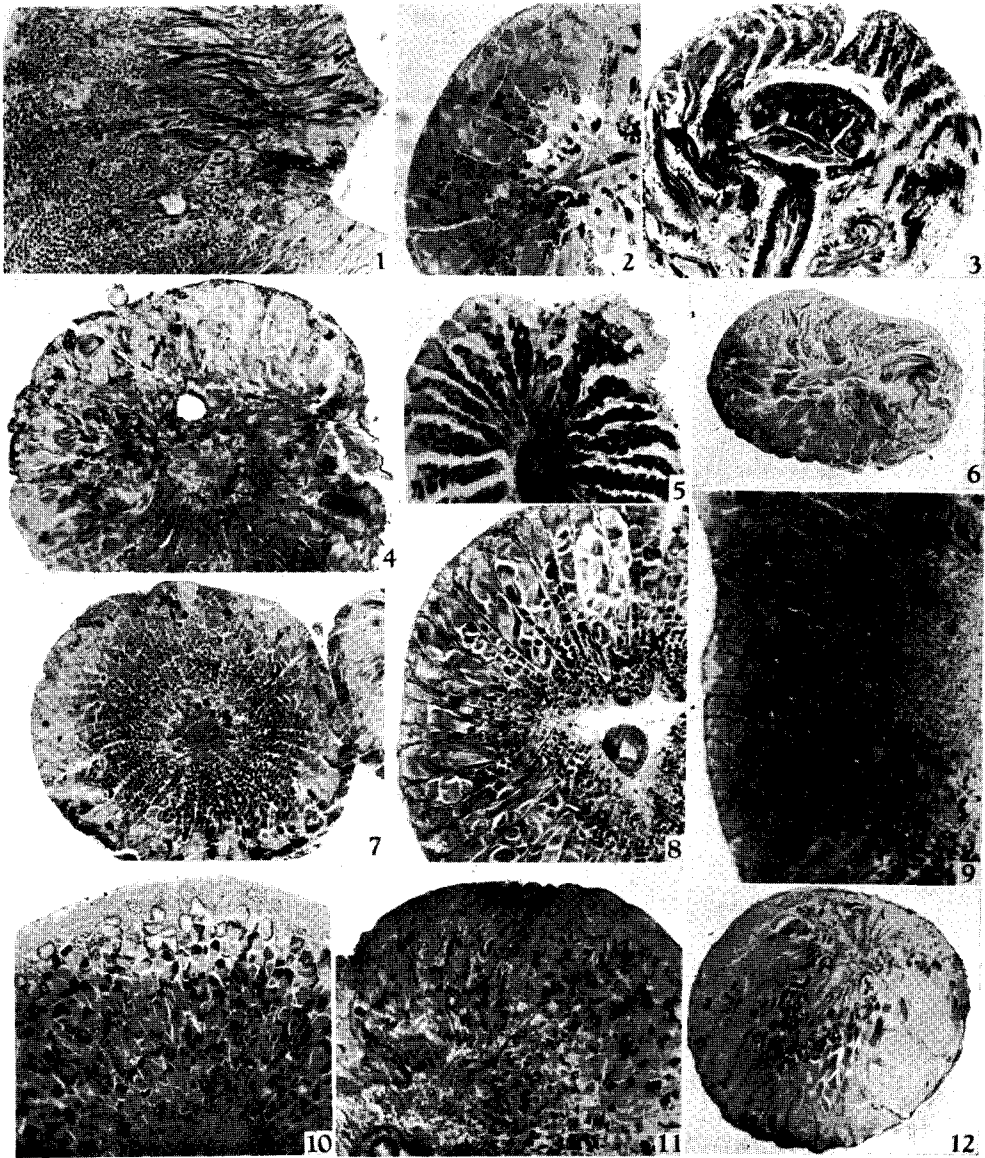
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Explanation of Plate IX

Figs. 1-12. Cross sections of testes. $\times 49$. (Photo by Dr. M. Okada) 1. *Prionus insularis*, showing the testicular follicles filled with spermatozoa and spermatids. 2. *Distenia gracilis*. The same, showing the occurrence of some colonies of spermatocytes. 3. *Spondylis buprestoides*. The testis is provided exclusively with spermatozoa. 4. *Gaurotes doris*. The testis is occupied with spermatozoa, showing a colony of dividing primary spermatocytes in the peripheral portion. 5. *Anoplodera rubra dichrou*, showing the testicular follicles filled with spermatozoa. 6. *Phymatodes maaki*, showing the testicular follicles occupied with spermatozoa. 7. *Plagionotus pulcher*, showing the testicular follicles provided with spermatozoa and spermatids. In the peripheral parts there occurs a good number of primary spermatocytes, in growth period and in division. 8. *Purpuricenus spectabilis*, showing the testicular follicles occupied with spermatozoa and spermatids. Some secondary spermatocytes can be seen in the peripheral portion. 9. *Monochamus grandis*. There is the expanding area with spermatogonia and primary spermatocytes, together with a number of spermatozoa. 10. *Mesosa myops* var. *japonica*. In the peripheral part there occur primary and secondary spermatocytes, in various developmental stages. 11. *Mesosa longipennis*. In the peripheral region the primary spermatocytes in growth period occur. 12. *Eutetrappa ocelota*. The spermatocytes are scarcely found in the testis. This is rather exceptional in the Lamiinae.



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