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Author(s)	NIIYAMA, Hidejiro
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AN XX-Y SEX-MECHANISM IN THE MALE OF A DECAPOD CRUSTACEA

CERVIMUNIDA PRINCEPS BENEDICT

Hidejiro NIYAMA

Faculty of Fisheries, Hokkaido University

On the subject of the sex-chromosomes in decapod Crustacea, several papers have been published by Fasten ('14), Delpino ('34), Leopoldseder ('34) and Niyama ('37, '38, '41). Niyama stated on the basis of his own studies that the sex-chromosomes reported by the former three authors are certain ordinary chromosomes which were displaced mechanically from their ordinary position, due probably to distortion of spindle fibres influenced by fixation. In males of three species of the family Grapsidae (Brachyura: Reptantia), there was reported by the present author clear-cut evidence showing the sex-chromosomes of an X-Y type (Niyama '37, '38). The X-O sex-mechanism was found to occur in the male of *Ovalipes punctatus* belonging to the family Portunidae (Brachyura: Reptantia) also by the author (Niyama '41).

Recently the present author has found a clear-cut example of an XX-Y sex-determining mechanism in *Cervimunida princeps* BENEDICT, a species of the family Galateidae (Anomura: Reptantia); the data of which will be given in this paper. Reference to the literature indicates that this type of sex-mechanism seems to be the first and a unique example in the Crustacea.

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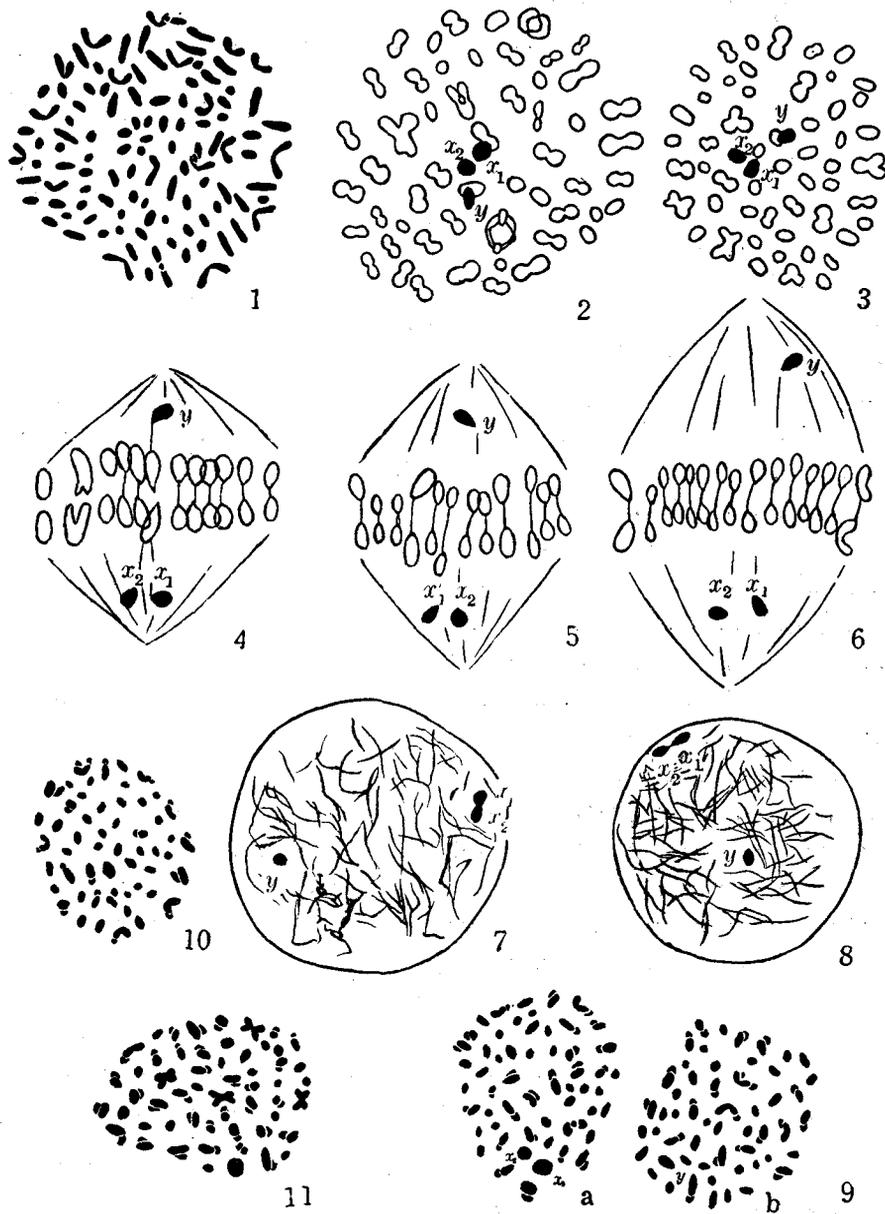
Cervimunida princeps BENEDICT is a deep-sea crab. The specimens for the present work were obtained in April, 1937 from Suruga Bay, to the west of Izu Peninsula, at depths of 200 to 400 meters. Identification of the species was made by Dr. Ken Yokoya, to whom the author wishes here to express his cordial thanks.

The testes were fixed with the modified weak Flemming's solution immediately after having been removed from the living bodies. Sections were cut 10 micra in thickness. For staining, the iron-haematoxylin method after Heidenhain was employed.

Observations

General morphology of the chromosomes

Dividing figures of spermatogonia were observable among cells constituting the inner walls of testicular cysts. Fig. 1 is an example of excellent metaphase equatorial plates of spermatogonia. It was found that the diploid complex consisted of 18 V-shaped metacentric elements plus 91 rod- and dot-shaped acrocentric ones. The diploid number of this species was determined as 109 in the male. The odd number, 109, suggests the existence of sex-chromosomes. Since the acrocentric chromosomes vary in size gradually

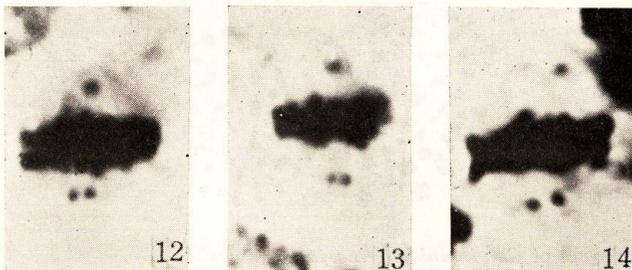


Figs. 1-11. Chromosomes of *Cervimunida princeps* BENEDICT

1. Metaphase plate of spermatogonium, 109 chromosomes. 2-3. Polar view of metaphase chromosomes of primary spermatocytes, 53 bivalents and X_1X_2Y chromosomes in each. 4-6. Side views of metaphase chromosomes of primary spermatocytes, indicating distance pairing of X_1X_2-Y . 7-8. Nuclei in leptotene stage, exhibiting heteropycnotic bodies consisting of X_1X_2 and Y in deep black. 9 a-b. Two daughter complexes of an equatorial plate of a primary spermatocyte at anaphase. 10. Metaphase of a secondary spermatocyte, containing 54 chromosomes. 11. The same, with 55 chromosomes. $\times 3700$

from rod to dot, it is impossible to identify any unpaired chromosome.

The division takes place synchronously in all spermatocytes within a cyst. The dividing figures of spermatocytes, therefore, could be observed in large number. Every primary spermatocyte under study showed in side-view three univalent chromosomes, two being at one side and the other one at the other side of the equatorial plate: the three lie considerable distance apart from the remaining chromosomes which arrange themselves in an equatorial plate. The evidence will be well understood by referring to Figs. 4 to 5 and 12 to 14. The number of bivalents lying in the equatorial plate was found to be 53. Size differences are noted among them in a rather remarkable degree: some larger ones exhibit the type of ring- and cross-tetrads, while the remaining ones are of dumbbell shape. By changing the focus of the microscope from the equatorial plate up and down, two chromosomes at one side and one chromosome at the other side, or *vice versa*, could be observed in every metaphase plate (Figs. 2-3). According to the general rule of the sex-determining mechanism, it is apparent that these three univalent chromosomes constitute a compound sex-chromosome complex composed of X_1X_2 and Y elements. The X_1 and the X_2 are nearly identical in size, while the Y is slightly larger than either of the two X's (Figs. 2-6). The Y is joined separately at one end with each of the two X's. At metaphase, the compound sex-chromosome is situated always considerably off the equatorial plate without exception. It seems therefore that the distance pairing of the sex-trivalent is established by a pairing mechanism during the diakinetic stage, but is not due to the mechanism of precession at metaphase. A comparable case was reported in a neuropteran, *Plethosmylus decoratus* by Hirai ('56). The chromosome formula of the primary spermatocyte is represented by $53 + X_1 + X_2 + Y$. At anaphase, the two X's and Y separate from each other and migrate to opposite poles together with daughter halves of ordinary chromosomes. The number of chromosomes in the two daughter complexes after division is 54 and 55, respectively (Figs. 9 a-b).



Figs. 12-14. Microphotographs of side views of metaphase chromosomes of a primary spermatocyte, showing the distance pairing of X_1X_2 and Y. Figs. 12, 13, 14 correspond to 4, 5, 6 respectively. $\times 2400$

The secondary spermatocyte consequently produced are of two sorts: the one possesses 54 chromosomes and the other 55 (Figs. 10-11). In the secondary spermatocytes it is difficult to distinguish the sex-chromosomes due to the absence of any character to enable distinction of them from the autosomes.

Further, there are no precocious chromosomes in the second division.

Behaviour of the sex-chromosomes during meiotic prophase

In the leptotene nucleus of the meiotic prophase the sex-chromosomes made their appearance distinguishable from the autosomes. In this stage, two compact chromatic masses which are positively heteropycnotic could be observed among lightly stained spireme threads in the nucleus. One of them is composed of two parts of nearly equal size; they connect with each other transversely. The other one is about 1/2 the size of the above double mass having no connection with the latter (Figs. 7-8). In view of the heteropycnotic character in the leptotene stage and from their shape and size observed at metaphase, it seems most probable that the double mass consists of the X_1 and X_2 in association whilst the smaller one is the Y. Since there is no nucleolus in any stage of the meiotic prophase, the association of the sex-chromosomes with the nucleolus was not observed. With the advance in the stage of meiotic prophase, there appear many chromatic bodies indistinguishable in size from the X_1 , X_2 and Y in the nucleus; this makes impossible the distinction of the sex-chromosomes from the autosomal chromatic bodies. Though there is no positive evidence, the establishment of the distance pairing of the sex-elements might have taken place in late diakinetik stage, as it was reported to occur in *Plethosmylus decoratus* (Hirai '56).

Remarks

As described in the foregoing pages, *Cervimunida princeps* BENEDICT belonging to the family Galateidae (Anomura: Reptantia) is characterized by the existence of three peculiar chromosomes, two of which lie always at one side of the equatorial plate and one on the other side. The peculiar elements are quite comparable in their behaviour and other morphological features to the sex-trivalent showing distance pairing in the male of a neuropteran, *Plethosmylus decoratus* (Hirai '56). The diploid number of chromosomes attained in the spermatogonial division is 109. Further, the number of chromosomes is 54 and 55 in the secondary spermatocytes. The evidence presented leads to the conclusion that the three peculiar chromosomes which arrange themselves off the metaphase plate of the primary spermatocyte are no other than the sex-trivalent showing a distance pairing. Though there is no positive proof, the distance pairing of the sex-trivalent may be established by a certain pairing mechanism in the diakinetik stage, but may not be due to the process of precession at metaphase.

Excepting some doubtful cases, the sex-determining mechanism in the Crustacea is of XO- or XY-type (Table 1). In certain species of Decapoda, Amphipoda, Isopoda, and Phyllopoda, the XO- or XY-mechanism was found to occur in the male (Niiyama '37, '38, '41, '50, '56, Baker & Rosof '27, 28a,b). In Copepoda, male heterogamety of XO-type was reported by Heberer ('32), while Beervaun ('54) observed female heterogamety of XO-type. In Ostracoda, on the other hand, a compound sex-chromosome was reported in males of three species, such as *Heterocypris incongruens* (Bauer '40),

Table 1. Sex-determining mechanism so far reported in the Crustacea

Species	2n	Sex-chrom.	Author
Phyllopoda			
<i>Branchipus vernalis</i>	23	X-O ♂	Baker & Rosof '27, '28a, b.
Ostracoda			
<i>Cyprinotus incongruens</i>		Multiple X ♂	Bauer '34
<i>Heterocypris incongruens</i>	20 ♀ 15 ♂	X ₁ -6Y ♂	Bauer '40
<i>Notodromas monacha</i>		X ₁ X ₂ -O ♂	Dietz '54
Copepoda			
<i>Centropagis typicus</i>		X-O ♂	Heberer '32
<i>Cyclops affinis</i>		*X-O ♀	Matschek '10
<i>Cyclops fuscus</i> var. <i>distinctus</i>		*X-O ♀	Matschek '10
<i>Cyclops phaleratus</i>	13	*X-O ♀	Braun '09
<i>Cyclops phaleratus</i>		*X-O ♀	Matschek '09, '10
<i>Cyclops prasinus</i>	11	*X-O ♀	Braun '07, '09
<i>Cyclops prasinus</i>		*X-O ♀	Matschek '10
<i>Cyclops serrulatus</i>		*2X-O ♀	Matschek '10
<i>Cyclops vernalis</i>		*X-O ♀	Matschek '09, '10
<i>Ectocyclops strenzki</i>		X-O ♀	Beervan '54
Isopoda			
<i>Asellus aquaticus</i>	17	*X-O ♂	Dworak '35
<i>Jaera marina forsmanni</i>		*X-Y ₁ Y ₂	Steiger & Bocquet '54
<i>Jaera marina ischiosetosa</i>		*X-X ₁ Y ₂	Steiger & Bocquet '54
<i>Tecticeps japonicus</i>	63	X-O ♂	Niiyama '56
Amphipoda			
<i>Annisogammarus annandalei</i>	54	X-Y ♂	Niiyama '50
<i>Gammarus chevreuxi</i>	26	*X-Y ♂	Palmer '25, '26
Decapoda			
<i>Cambarus immunis</i> (?)		*8X-O ♂	Fasten '14
<i>Eriocheir japonicus</i>	148	X-Y ♂	Niiyama '37
<i>Hemigrapsus sanguineus</i>	128	X-Y ♂	Niiyama '38
<i>Ovalipes punctatus</i>	103	X-O ♂	Niiyama '40
<i>Pandalus borealis</i>	34	*2X-O ♂	Leopoldseder '34
<i>Plagusia dentipes</i>	106	X-Y ♂	Niiyama '37a, b
<i>Telphusa fluviatilis</i>	78	*2X-O ♂	Delpino '34

*The data marked with asterisks are considered to be doubtful at the present standard of cytology. For reference, see Makino's list, 1956.

Cyprinotus incongruens (Bauer '34) and *Notodromas monacha* (Dietz '54). The sex-mechanism of X₁X₂Y-type as found in *Cervimunida princeps* is therefore quite unique in the Class Crustacea, so far as the investigations have gone.

It has repeatedly been claimed that the X₁X₂Y-mechanism was secondarily derived from either an originally XO- or an XY-condition by translocation involving an autosome and sex-chromosomes (White '40, '41, '54, Cooper '46, '51, Hughes-Schrader '47, '50). Most likely the X₁X₂Y-mechanism of *Cervimunida princeps* originated from an XY- or XO-type, since the latter types are have been found in Decapoda. On the basis of the

number of chromosomes, the present species having $53 + X_1X_2Y$ in haploid has closer relationship to some species of Decapoda which have a large number, for example $41(n)$ in *Gebia major* (Oka '41), than to some species of Ostracoda.

Summary

The X_1X_2Y -mechanism of sex-chromosomes was found in male germ cells of *Cervimunida princeps* BENEDICT (Galateidae: Anomura: Reptantia: Decapoda: Crustacea). The diploid number was found to be 109. In the primary spermatocyte, 53 bivalents and X_1X_2Y -trivalent were observed. There are two kinds of secondary spermatocytes having 54 and 55 chromosomes respectively. During the meiotic prophase, two X's and one Y make their appearance as distinct chromatic bodies in the auxocyte. The X_1X_2Y -trivalent displays a distance pairing in the spindle of the primary spermatocyte metaphase.

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