**The Chromosomes of the Sticklebacks, *Pungitius tymensis*
(Nikolsky) and *P. pungitius* (Linnaeus) ***

By

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(With 6 Text-figures and one Plate)

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Notwithstanding the extensive studies on chromosomes of the vertebrates in recent years, those of Pisces seem to have been neglected. Many important problems in the morphological aspects of chromosomes, associated with the question of sex determination, remain unsolved in this group of animals. At the present time, chromosome studies of vertebrates have a practical value to breeders and are of scientific importance to biologists, especially in the case of useful animals. For these reasons, a complete knowledge of chromosomes of fishes is highly desirable. In a series of investigations the author wishes to contribute to the chromosome study in various kinds of fishes. Chromosomes of two common teleost fishes only, however, will be dealt with in the present paper.

The work has been carried out under Professor OGUMA to whom the author wishes to express his sincere thanks.

Material and Method

Pungitius tymensis and *P. pungitius*¹⁾, with which the present paper is concerned are small gasterosteiid fishes. They are the most common teleosts in small fresh-water streams in the neighbourhood

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1) The author is greatly indebted to Prof. KAHEI IKEDA of the Niigata High School, for his effort of identifying the scientific names of these fishes. According to him, *P. tymensis* occurs only in Hokkaido and Sakhalin, and *P. pungitius* is distributed through Siberia to Europe.

of Sapporo. They are called 'stickleback', as they have several spines in both dorsal and ventral sides of the body and they are well known by their nest-building habit in the breeding season. These two species inhabit the same stream and breed during spring time to early summer.

The fishes for the present investigation were collected from various streams in the vicinity of Sapporo, at different times from summer to autumn of 1931 and 1932. Those captured from the end of July to the beginning of August were favourable for the study of the maturation division. The animals were dissected and the testes were taken out immediately after captivity. The testes of both adult and young specimens are used: the former is favourable for the maturation division and the latter for the spermatogonial division. Of various fixing reagents employed for preservation, CHAMPY's mixture was the best for spermatocyte chromosomes and BENDA's fluid diluted with equal volume of water for spermatogonial chromosomes. Sections were cut 5 to 6 micra in thickness. Iron haematoxylin was the stain chiefly employed.

The figures were drawn with the aid of an ABBE drawing apparatus at the level of the desk on which the microscope was set, a ZEISS 1.5 mm. Apochr. Obj. and a K 20 × Oc. being used.

Observations

I. *Pungitius tymensis* (NIKOLSKY)

1. *The spermatogonium.*

Two kinds of spermatogonia, early and late, can be demarkated; they are clearly distinguishable by their size (Figs. 2-3). The early spermatogonia are found in small rounded cysts in only a few cells in a section. They gradually become smaller in size by repeated divisions, giving rise finally to the late spermatogonia. The cells contained in a cyst are of the same phase of development but are different from other cysts, thus all successive stages of the maturation process are found in a single section.

The early spermatogonium in the resting stage is characterized by the presence of clear, large-sized nucleus containing a huge nucleolus of spherical shape in its central region (Fig. 2). The nucleus appears almost spherical or oval in shape and is quite smooth in outline. It is filled with nuclear sap and no trace of chromatin is

visible. The late spermatogonia vary much in shape, because of their close aggregation; some are elongated oval and others almost square. Their nuclei are generally oval-shaped and clear in the resting stage, showing no other features different from the early spermatogonia except that they contain several round nucleoli, usually 5 to 6 in number (Fig. 3). In both kinds of spermatogonia numerous small bodies of dense consistency, stained black and various in form, are always found distributed in the cytoplasm (Figs. 2-3). They are considered to be the GOLGI bodies, as frequently observed in germ cells of other animals.

As the cell prepares for division the fine chromatin reticulum appears throughout the nucleus. In the early prophase the chromatin threads, of which the reticulum is composed, thicken and become densely stained, distributing irregularly along the nuclear wall (Fig. 4). As the condensation proceeds these threads become shortened and finally assume a definite outline of chromosomes, lying just below the nuclear wall for a short time before their arrangement on the spindle (Fig. 5). The nucleolus which remains apparent during these prophase stages becomes first obscure when the nuclear wall disappears at the end of the prophase.

In the polar view of the metaphase equatorial plate the chromosomes are seen in radial arrangement, showing a typical rosette form (Text-fig. 1, *a-d*). Text-fig. 1, *a* to *c* are polar views of early spermatogonial metaphase, *a* and *c* being drawn from young animals, and Text-fig. 1, *d* represents a late spermatogonial plate. The

Text-fig. 1, *a-d*. *Pungitius tymensis*. Spermatogonial metaphases, 42 chromosomes in each. $\times 4200$.

chromosomes are all telomitic rod-shaped, some straight, some more or less curved. Each chromosome of the early is longer than the cor-

responding one of the late spermatogonial metaphase. Occasionally, in the longer chromosomes for instance, the curving takes place so strongly that they appear as V's. Such a curving, however, seems to be merely a temporal occurrence, as it is not observed constantly in any definite chromosomes. The individual chromosomes possess no other distinctive features than length. They show gradual difference in length, from extremely long to short, as is obviously demonstrated in the serial arrangement of chromosomes (Text-fig. 2). No dot-like chromosomes, commonly known in teleosts hitherto studied, occur in the present case.

In every case without exception when good polar views of the spermatogonial equatorial plates have been examined 42 chromosomes have been counted. There are found no particular chromosomes which can be considered as the heterochromosomes. When spermatogonial chromosomes are aligned in pairs in the approximate order of their size and shape, all the chromosomes can be arranged into 21 homologous pairs and no unpaired elements can be identified (Text-fig. 2).

Text-fig. 2. *Pungitius tymensis*. Paired alignment of spermatogonial chromosomes from Text-figure 1, a.

Though extremely rare, the giant spermatogonium-like cells were found in the testis of the young specimen, imbedded among the spermatogonial cysts (Fig. 1, g). The cell is solitary and devoid of follicle cells. The nucleus is enormous in size and smooth in outline, and filled with colourless nuclear sap. A conspicuous, huge nucleolus round in shape is seen situated in the central part of the oval nucleus. There is no visible evidence of any chromatin reticulum or any other like structure in the nucleus. Numerous black granular bodies of various size and shape are attached to the outside of the nuclear wall. In cytoplasm too, several larger black bodies are distributed. The giant cell

resembles therefore the early spermatogonium in general structure, except for a great difference in size. The size relation between the former (g) and the latter (p) may become clear if one compares their dimensions in Fig. 1.

All the structures and conditions of the giant cell, however, remind us of the feature of the egg-cell which has been described by previous authors as the ovum in the testis of other fishes. But the author has no positive proof at present in taking this giant cell as the egg-cell, for its fate and behavior still remain in question.

2. *The growth period of the spermatocyte.*

Following the telophase of the last spermatogonial division, the chromosomes begin to disintegrate and convert into irregular bodies with vague outline (Fig. 6). In the meantime several round nucleoli of various size reappear in the nucleus. As the diffusion process advances in chromosomes, the nucleus becomes cloudy. This stage is followed by the appearance of leptotene threads which are very thin and entangled with one another (Fig. 7). The nucleoli, which appeared in the preceding stage, are lost from sight in this stage. The nucleus grows by and by and the threads become spread along the inner side of the nuclear membrane (Fig. 8). Then, they begin to contract in such a way that every thread directs its two ends towards the pole of contraction (Fig. 9). The threads thus polarized eventually assume loop-shape and grow shorter by gradual thickening (Fig. 10). After having grown sufficiently thicker and shorter to be in the pachytene condition, they give up their polarization and become scattered about through the nucleus (Fig. 11). The number of the pachytene threads seems to be much less than that of the leptotene threads although exact counting has not succeeded. The pachytene stage is followed by the diplo-strepsitene stage in which the threads begin to assume the appearance of tetrads owing to longitudinal breaking of a single thread into two thinner ones often twisted with each other (Fig. 12). By the time diakinesis is reached, the long dual threads of the diplotene contract and gradually assume the complete tetrad form (Fig. 13). VAUPEL ('29) observed in *Lebistes* that following the pachytene stage, the confused stage in which the nucleus appears as a pale homogeneous ball by disintegration of chromatin threads, occurs just before the diakinesis. In the present case, however, no such stage can be noticed. In early diakinesis when the bivalents begin to come in contact with the

nuclear wall, the characteristic tetrad structure becomes quite obvious (Fig. 13); rings, crosses and V's of various sizes are observable. During late diakinesis, however, concentration continues further on until they are converted into the compact bivalent form as seen in metaphase as illustrated in Figs. 14 and 15.

Throughout these stages of growth period, a small distinct body appears without exception in the cytoplasm, which is considered to be the chromatoid body from its behavior in the maturation divisions (Figs. 7-14, *c*). The shape of this body is not exactly round in outline, as is frequently the case in some animals, but is somewhat oblong. It is stained intensely by haematoxylin and appears of a compact nature. Usually it is found so closely attached to the nuclear surface that, at first sight, it looks like a heteropycnotic karyosome underneath the nuclear membrane.

3. *The first spermatocyte division.*

As shown in Text-fig. 3, *a-h*, the primary spermatocyte chromosomes in metaphase are observed in absolute distinctness; they show a radial arrangement as most cases, the larger ones surrounding the

Text-fig. 3, *a-h*. *Pungitius tymensis*. Primary spermatocyte-metaphases, 21 tetrads in each. $\times 4200$.

smaller ones. They are well apart from one another. Therefore the counting, is very easy in this division. A garniture of chromosomes is constituted of 21 tetrads of various sizes as counted without any question. The individual chromosomes show distinct and constant size differences, at least two or three at the periphery being conspicuously large in size, in strong contrast to the facts hitherto observed

in some other teleosts, such as *Lebistes* (WINGE, '22; VAUPEL, '29; IRIKI, '32), *Aplocheilus* (= *Oryzias*) (GOODRICH, '27; IRIKI, '32) and *Gambusia* (GEISER, '24) etc., in which all the chromosomes of this division are represented by round bodies of nearly equal size and irregularly arranged. When the chromosomes are highly destained, the bivalent nature becomes clear to a considerable degree; three large tetrads appear in the form of a horizontal ring and of the remainder, some are V-shaped and some rings or horse-shoes (Fig. 16). In such case, the polar granules form a distinct structure, as they are stained intensely with haematoxylin, each taking position at the inner end of every chromosome. These tetrads are probably comprised in the type of the diaschistic tetrads with telomitic fibre attachment (WILSON, '25), similar in principle to those generally found in the grasshopper.

In division, the tetrads are all separated into two equal halves along the plane parallel to the equatorial plate (Figs. 17-19); there are no elements showing asymmetrical separation. The large horizontal ring tetrads are split into two single V-shaped dyads by the plane of conjugation, representing lozenge-shape in the early stage of separation (Fig. 20). In the remaining smaller ones the separation process is obscure merely showing dumbbell-shape in side view; marked dual nature is hardly observable in each separating half (Figs. 17-18). In the polar view of the anaphase, there can be found two sister sets of chromosomes, quite homologous in the garniture, both of which contain 21 dyads (Text-fig. 4, *a-a'*: *b-b'*); the secondary spermatocytes thus produced receive an equal number of the chromosomes.

The separation of chromosomes seems to be synchronous and no chromosome showing particular behavior as the sex chromosomes can be discovered.

The chromatoid body fails to separate in the present division, as occurred in the case of *Pentatoma* (WILSON, '13) and migrates to one pole (Figs. 17-19, *c*). Thus one half of the secondary spermatocytes receives this body.

Text-fig. 4, *a-a'*; *b-b'*. *Pungitius tymensis*.
Sister chromosome groups in anaphases
of the first division. $\times 4200$.

4. *The second spermatocyte division.*

After the telophase of the first division, the cell enters the resting stage, the interkinesis; enclosed by the newly formed nuclear wall the chromosomes become distributed about, in the form of slightly elongated rods or dots with diffused contour (Figs. 21–22). There is no visible evidence of nucleolus or of any other like body in the nucleus. Some of the secondary spermatocytes contain a chromatoid body in the cytoplasm (Fig. 21, *c*), while the others are entirely free from it (Fig. 22).

As may be expected from the mode of division of chromosomes in the primary spermatocyte, there is produced only one kind of chromosome garniture in the resulting secondary spermatocytes. Every metaphase without exception shows 21 dyads; the chromosomes as-

sume condensed rod-shape, which may correspond in form and size to those observable in the spermatogonial metaphase, though their number is reduced (Text-fig. 5, *a-e*). They lie, in the equatorial plate, directing their ends of spindle fibre attachment toward the center, the larger ones being arranged in the peripheral region surrounding the smaller ones in the central part.

There is nothing unusual about the second division; each dyad is so separated that it becomes two equal telomitic daughter halves (Fig. 23), and every spermatid acquires no doubt an equal set of chromosomes.

Text-fig. 5, *a-e*. *Pungitius tymensis*.
Secondary spermatocyte-metaphases,
21 dyads in each. $\times 4200$.

The chromatoid body migrates again to one pole without division (Fig. 23, *c*); either one of the spermatid thus resulted therefore contains this body in the cytoplasm (Fig. 24, *c*).

II. *Pungitius pungitius* (LINNAEUS)

Another species of stickleback, *Pungitius pungitius* comes next under notice. The investigation in this allied species reveals that the chromosomes show nothing different in their form, number and

behavior from those observed in the foregoing species, *P. tymensis*, so far as the scope of the present study is concerned. The detailed description of observed facts will therefore be abbreviated.

As shown in Text-fig.

6, the haploid number of chromosomes is 21 as was clearly counted in both the primary and secondary spermatocytes. The spermatocyte chromosomes of this species do not show any marked features different in form and arrangement from those of the preceding (compare Text-fig. 6 with Text-figs. 3 and 5). The author

could not succeed in accurate count of the spermatogonial chromosomes due to the lack of material, but the diploid number may consequently be 42 in this species.

Text-fig. 6. *Pungitius pungitius*. a-c: Primary spermatocyte-metaphases, 21 tetrads in each. In c, polar granules are shown. d-f: Secondary spermatocyte-metaphases, 21 dyads in each. $\times 4200$.

Historical

Generally speaking, the chromosome study on fishes has been in a poor state up to the present time, compared with the remaining groups of Vertebrata (see OGUMA and MAKINO, '32). The pioneer investigators in this field had chiefly dealt with the spermiogenesis or egg development in the Elasmobranchs and Cyclostomes, and the morphological research of chromosomes was therefore of secondary importance to them. Thus their results, from the standpoint of chromosome morphology, are not sufficient to be discussed with knowledge of the recent cytology.

The literature on the chromosome study of teleosts is very limited. The work has chiefly been confined to the material with which genetic experiments were made. Previously, MOENKHAUS ('04), and PINNEY ('18) have given the diploid chromosome number observed in cleavage eggs of *Fundulus*, *Menidia* and *Ctenolabrus*. TURNER ('19) in his study of seasonal cycle of germ cells, reported the diploid chromosome number in the perch. Recently several authors as WINGE

('22), GEISER ('24), FOLEY ('26), GOODRICH ('27), VAUPEL ('29) and IRIKI ('32), have undertaken the cytological study with improved technique on *Lebistes*, *Aplocheilus* (= *Oryzias*), *Gambusia*, and *Umbra*, with the particular purpose to discover data in parallel to those formerly found by genetic experiments.

So far as the author is aware, the chromosomes of the gastero-steiid fishes have never been studied by any authors up to the present time. As has been stated in the descriptive part of the present paper, the chromosomes of *Pungitius* are all rod-shaped of intergrading size and the spindle fibre attachment is conclusively telomitic. In this respect therefore, they are quite different from those commonly found in the teleosts so far studied, in which dot-like chromosomes of no size differences are found though FOLEY ('26) reported an exceptional case in *Umbra*, with V-shaped chromosomes. Apparently the chromosome complex of *Pungitius* very much resembles those in some higher vertebrates such as certain rodents or lizards, in many points, i.e. in their number, form and mode of arrangement.

The history of chromosomes during the spermatogenesis has been insufficiently studied in the teleosts in general. So far as the present observation shows the chromosome behavior of *Pungitius* follow the usual course of maturation having no features worthy of special notice. In this respect, the author cannot agree with WINGE's ('22) statements in *Lebistes* that "a very characteristic feature is the absolute lack of stages which may be called synapsis and diakinesis."

Some Remarks on the Sex Chromosome

The discovery of sex-linked inheritance in some teleosts, male heterogamety established by AIDA ('21)¹⁾ in *Aplocheilus* and by WINGE ('22)²⁾ in *Lebistes*, and female heterogamety adduced by BELLAMY ('23)³⁾ and GORDON ('27)⁴⁾ in *Platypoecilus*, suggests the presence of heterochromosomes in the fishes. Efforts have been made by cytologists to obtain the cytological demonstration for these genetic data. WINGE ('22) reached the conclusion that an X-Y pair of chromosomes may possibly occur in the male of *Lebistes*, though no conclusive evidences can be given cytologically. GEISER ('24) expressed a similar

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- 1) Genetics, 6 (1921).
 - 2) Journ. Genet., 12 (1922).
 - 3) Anat. Rec., 24 (1923).
 - 4) Genetics, 12 (1927).

opinion in discussion on this problem in *Gambusia*, saying that "if one were to trust to the uncertain help of analogy, it might be claimed that *Gambusia* has one heterochromosome." FOLEY ('26) suggested in working on the spermatogenesis of *Umbra* that, a pair of large L-shaped chromosomes, relatively constant in size and shape, are to be the sex chromosomes and then inclined to conclude that if so the male of *Umbra* should have a pair of X-chromosomes. In the study of *Lebistes*, VAUPEL ('29) found one pair of chromosomes which migrate to the pole precosiously in the first division, and then stated that there may be some evidence for the presence of an X-Y pair. As he interpreted so, however, this evidence is never conclusive for the identification of the sex chromosome, since such displaced chromosomes are often encountered in the material fixed improperly. In the present study, as already given, the author failed to find out any characteristic chromosomes to be identified as the sex chromosome. No unpaired elements occur in the spermatogonial chromosomes. In the meiosis too, there is no indication of heteropycnosis, no lagging or precession of particular chromosome, or any other features suggesting the existence of heterochromosomes of any kind. Recently similar results have been attained by IRIKI ('32) in the studies of *Lebistes* and *Aplocheilus*. Looking over these facts as referred to above, there is seemingly no room to deny that the sex chromosomes of the teleosts show no characteristic features distinguishable morphologically from the other autosomes, or in short, it is impossible to identify the sex chromosomes among the autosomes. The conclusion represented by IRIKI ('32) on this subject in *Lebistes* and *Aplocheilus* is as follows: "the sex chromosomes which are homologous to those of the other animals is also present in these fishes and they are homomorphic, i.e., XX-type, but it is impossible to distinguish them from the other autosomes." At present, however, the present author hesitates to accept his conclusion without modifications. In fact, in the teleost fishes dealt with at least, whatever the results of genetic experiments may be, there cannot be distinguished any particular chromosomes. Still this fact can be accounted for otherwise than the presumption of existence of two X's. It seems to the author that the sex chromosomes of fish are not so much differentiated that they acquire characteristic behavior or form to be distinguished from the other autosomes, and accordingly the type of the sex chromosome is impossible to be determined morphologically. A similar evidence has

been discovered by the present author ('33) in the Amphibian Urodele, *Hynobius retardatus*, in examination of the male and female chromosomes. And it emphasizes the view that the sex chromosomes of the Amphibian Urodele and Pisces are in state of the lowest differentiation in vertebrates in evolution of the sex chromosomes.

Summary

Pungitius tymensis

1. Two kinds of spermatogonia, early and late, are distinguished morphologically. The giant spermatogonium-like cells are infrequently found in the testis of the young male. Their significance and destiny are now unexplainable.

2. The chromosome number is 42 in diploid and 21 in haploid. The spermatogonial chromosomes are all arranged into 21 homologous pairs, representing no heteromorphic elements in either tetrad or dyad sets.

3. The spermatogonial chromosomes are all telomitic rod-shaped, straight or slightly curved, ranging in shape from long rods to short ones. They form the equatorial plate with 21 tetrads of horizontal ring and horse-shoe shape in the primary spermatocyte division. The secondary spermatocyte chromosomes all appear in the form of rods.

4. The behavior of the chromosomes during meiosis corresponds to that generally described in other vertebrates. The chromatoid body is traced through the whole meiotic phases.

5. Throughout the dividing stages during spermatogenesis the author could not find any particular chromosomes in heterotropic behavior characteristic to the sex chromosome. The sex chromosomes of fish must be in the lowest state of differentiation from the autosomes, as compared with those of other vertebrates.

Pungitius pungitius

So far as the form and number of chromosomes are concerned, *P. pungitius* shows no marked morphological difference from *P. tymensis*. Only brief accounts concerning the primary and secondary spermatocyte chromosomes are given.

May, 1933.

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Explanation of Plate 3

Pungitius tymensis (NIKOLSKY)

All the figures, except Fig. 1, were drawn with the aid of a camera lucida, a ZEISS Apochr. Obj. 1.5 mm. and a K 20× Oc. being used, and were reproduced in about 3500 diameters. c, chromatoid body.

- Fig. 1. Part from a section of the testis, showing a gaint spermatogonium-like cell (g). Photomicrograph, ×380. Relative size of the nucleus is suggested by comparison of the giant cell (g) and early spermatogonia (p); 0.018 mm. in diameter across long axis of the nucleus of the giant cell. s, cysts of late spermatogonia, in resting and dividing stages.
- Fig. 2. Early spermatogonium in resting stage; 0.007 mm. in diameter across long axis of the nucleus.
- Fig. 3. Late spermatogonium in resting stage.
- Fig. 4. Nucleus of early spermatogonium in early prophase.
- Fig. 5. The same in late prophase.
- Fig. 6. Last spermatogonial telophase nucleus. Several nucleoli are seen.
- Fig. 7. Nucleus of primary spermatocyte in early leptotene stage.

- Fig. 8. The same in more advanced stage.
Fig. 9. The same in late leptotene stage.
Fig. 10. The same in pachytene stage.
Fig. 11. The same in late pachytene stage.
Fig. 12. The same in diplo-strepsitene stage.
Fig. 13. The same in early diakinesis.
Fig. 14. The same in late diakinesis.
Fig. 15. Various kinds of tetrads found in the nucleus of later diakinesis.
Fig. 16. Polar view of primary spermatocyte metaphase plate, 21 tetrads, from well destained preparation. Polar granules are seen densely stained at the inner ends of individual chromosomes.
Figs. 17-19. Side views of primary spermatocyte chromosomes in earlier and later anaphases (not all elements shown in each). Note the migration of chromatoid body.
Fig. 20. Separation of 3 large tetrads in first division anaphase.
Fig. 21. Secondary spermatocyte in interkinesis, with chromatoid body.
Fig. 22. The same without chromatoid body.
Fig. 23. Side view of secondary spermatocyte chromosomes in early anaphase (not all elements shown). Note the migration of chromatoid body.
Fig. 24. Two sister spermatids resulted from secondary spermatocyte division. One receives chromatoid body.
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S. Makino del.

Makino: The chromosomes of the sticklebacks.