THE GROWTH PERIOD IN THE
SPERMATOGENESIS OF
ANAX JUNIUS.

by

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I. INTRODUCTION

During the formation of the functional germ cells, the ova and the spermatozoa, from the primordial germ cells, a definite series of changes occur in all animals and plants. In spermatogenesis, the following events take place. The primitive germ cells form the spermatogonia by ordinary mitoses. These divide until they are very numerous, and finally enter on a period during which they do not divide but increase in size. At the close of this growth period, the cells are known as preimary spermatocytes and enter on the first maturation division. The secondary spermatocytes, formed by the above division, divide again to form the spermatids, which are transformed directly into the spermatozoa.

The process of maturation reduces the characteristic, or spermatogonial, number of chromosomes to one-half. This reduction is believed to be initiated by a pairing or synapsis of like chromosomes during the growth period. The term synapsis is here used, as defined by Wilson ('12), to mean "the conjugation of chromosomes two by two". The word was first introduced by Moore ('95), but ambiguity arose thru a misunderstanding of his use of the term. The meaning was cleared up by Farmer and Moore ('05) when they stated (p.490) that: "The synapsis represents that series of events which are concerned in causing the temporary union in pairs of pre-maiotic chromosomes".

There are two contrasted views as to how synapsis takes place, namely (1) by end to end union or telosynapsis, and (2) by side to side union or parasynapsis.

This problem was undertaken to determine the nature of synapsis in *Anax junius*, a dragonfly belonging to the family Aeschnidae of the order Odonata.

The spermatogonial number of chromosomes in *A. junius* is twenty-seven. These do not vary greatly in size, and the X cannot be identified, but there is one pair which is somewhat larger than the others. It was pointed out by Lefevre and McGill ('08) that this size-difference marks off this pair during the growth period, and, since it very often lies near the nuclear membrane away from the general mass of chromosomes, it is favorable for study. The observations recorded in this paper are for the most part on this particular pair as it is the only one that has been studied carefully at all stages.

The fact that there is no seriation of spermatogenetic stages in the testes of *A. junius* makes it difficult to determine the sequence of stages accurately. However, there are very frequently crypts where transformation from one stage to another is taking place, and there one can usually be fairly sure of the sequence of events.

The writer is indebted to Professor George Lefevre, under whose direction the work was done, for criticism and advice, and, also, for the use of material which he had obtained during the course of his work on *A. junius*.

II. MATERIAL AND METHODS

The large nymphs were collected from ponds near Woods Hole in the summer of 1917, by Mr. George Gray of the Supply Department of the Marine Biological Laboratory. They were, as

a rule, ready to transform, altho a few young nymphs were used.

The insects were pinned down thru the thorax, and a mid-dorsal incision made. The testes lay on either side, surrounded by large masses of fatty tissue. In some cases they were dissected out in .75% sodium chloride solution; in others in the fluid in which they were to be fixed; but in the majority of cases in the body fluid.

Three fixing fluids were used, Bouin's, Flemming's, and a modified Bouin's which has been used by McClung and his students in their work. Bouin's fluid gave the best results. Flemming's, when the fatty tissue had been carefully dissected away, gave good results, but most of this material was badly fragmented in transportation. The picro-formol-acetic plus urea solution was used on only two specimens, and they were too young to show growth stages. The fixation obtained on the spermatogonial groups with this fluid was very good.

All observations have been made on sectioned material, stained with iron haematoxylin with no counter stain. It would be very desirable to see these stages in smear preparations where one would always be sure that the entire chromosome was seen, but no material has been obtainable at Columbia.

III. OBSERVATIONS AND INTERPRETATIONS

As has been described by Lefevre and McGill ('08) the spermatogonial number of chromosomes is twenty-seven, twenty-six autosomes, or euchromosomes, and one accessory chromosome. Figure 1 shows an equatorial plate of one of the early spermatogonial divisions. The chromosomes can be rather well paired

off according to size, and the largest pair is the one which has been followed. During the spermatogonial divisions, the cells become smaller and more numerous in the crypts, and the chromosomes seem to become diffuse between each division.

If crypts containing cells which are entering on the growth period are examined, the following pre-leptotene stages can be determined. In the telophase of the last spermatogonial division, the chromosomes become irregular in outline (fig. 2), and finally are seen to ^{be} very diffuse masses (fig. 3). This is stage "a" as Wilson ('12) describes it for a wide range of forms.

Figure 4, which is considered a later stage, the stage "b" of Wilson ('12), on account of the great increase in the size of the nucleus, and because it, with others of the same stage, was separated from those of the preceding stage by intergrading conditions, shows the condensation of the chromatin into masses. It will be noticed in figures 5, 6 and 7 that these "blocs" (Janssens, '01) become spirally elongated, and this process continues until a single leptotene thread is formed from each one. This is Wilson's stage "c", and is shown in figure 8. Since all of these stages occur in a single crypt, it seems that they are not of long duration.

It is impossible to be sure that no fusion of the chromosomes has occurred during this process because all of the "blocs" are never seen in any one section. No evidence of the telophase masses occupying separate vesicles has been found, but, since only a single leptotene thread is derived from one "bloc" and these leptotene threads finally form the chromosomes of the

spermatocyte, it seems reasonable to assume that the "blocs" correspond to the spermatogonial chromosomes. I have been unable to find any means of identification of the largest pair of chromosomes during the foregoing stages, but the size difference distinguishes it in the following stages.

In the latter part of the leptotene stage, the slender threads come to lie side by side in twos (fig. 7). Then these pairs of threads begin their conjugation, coming in contact at first at only one end. As the amphitene stage progresses, the threads twist closely about each other. This twisting may take place continuously from one end to the other (figs. 9 and 10), or it may proceed from both ends (fig. 11). Wenrich ('17), in describing the union of the threads in the Acrididae on which he worked, says (p. 497): "However, I am inclined to believe that the progress of pairing may not always be uniform along the whole length of the threads, but that chance association of the distal ends of a pair would result in their union, even if the region between the ends and apices had not completely united." It is this latter case, of twisting from both ends, that I think was interpreted by Lefevre and McGill ('08) as a late diplotene stage. This chromosome pair lies near the nuclear membrane, and is very often cut in the middle where it lies nearest the plane of section. Figure 13 shows such a thread cut on one side. My material does not show any threads cut on both sides, as the sections were cut relatively thick. Smear preparations would determine this condition with accuracy.

Figure 14 shows the amphitene stage in several other chromosomes. The twisting and side by side union of the threads is seen to be characteristic of *Anax junius*.

At about this stage, the large pair of chromosomes begins to lag behind the others. The closely coiled pachytene threads, which are now beginning to condense, become oriented toward one side of the nucleus, and form the "bouquet" of the pachytene stage. The observed pair lies outside this "bouquet" and is often still in the amphitene condition (fig. 13 and 15). The pachytene thread formed by the large chromosome does not seem to ever become part of the bouquet.

During the pachytene stage, due to the twisting and condensation, all trace of the plane of union between the threads is lost sight of. This is what Wenrich ('16) has called the primary longitudinal split. In the forms which he studied, where no twisting occurred in the amphitene, this line of union was visible thruout the pachytene stage.

At the end of the "bouquet" period of the pachytene, the condensed, heavily staining threads become scattered thruout the nucleus (fig. 16). It is now that the separation of the threads, the diplotene stage, begins. It has been thought that, in the diplotene, the separation of the threads takes place along the line of their union. However, Wenrich ('16) demonstrates clearly that such is not the case in *Phrynotettix magnus*. A line of division, to which he has given the name of secondary longitudinal split, occurs at right angles to the primary split, or line of union, and the threads separate along that line. The chromosomes, as mentioned above, do not twist dur-

ing the amphitene in this case, and observation would therefore be easier than in *A. junius*.

I have, however, been able to find several cases of early diplotene threads which seem to show a separation along a secondary split. The twisted condition of the threads makes a clear demonstration very difficult, but figure 17 (a, b, and c) show what I have observed. This stage was the most difficult to find of any in the series, which may mean that it is of short duration, or only that the material was unfavorable.

During the diplotene period, the threads exhibit the secondary twisting (fig. 17d). My interpretation of this stage will be given in the following pages.

Condensation of the chromatin, resulting in the shortening and thickening of the threads, is a very conspicuous change which begins during the early pachytene. Figure 17(e, f, and g) show this progressive change, until finally the tetrad is formed and taken up on the equatorial plate of the primary spermatocyte.

If one grants that the separation of the pachytene threads is along a secondary split, the long axis of the tetrad represents the division between the allelomorphic chromosomes (text figure 1, p. 9). The tetrad lies on the first maturation spindle with its long axis parallel to the long axis of the spindle. Therefore, if one assumes that the chromosomes separate after synapsis as the original chromosomes, the first division is the equational one in this chromosome pair.

The accessory chromosome can be distinguished from

about the time the leptotene threads begin to be formed by the fact that it remains as a condensed, rounded chromatin-mass. There is also a plasmosome seen during the growth period. The accessory and the plasmosome are shown in several of the figures, but, of course, are not seen in all sections.

Text figure 1. Showing, schematically, the stages from the pachytene to the first maturation division. One member of the pair is stippled to distinguish it from the other. A, pachytene stage; B and C, successive stages in separation along secondary split; D and E, stages in condensation, showing the secondary twisted condition; F and G, tetrad formation; H, separation of tetrad in the first maturation division.

IV. SUMMARY

The observations made seem to show that the following stages occur during the growth period.

- 1) The spermatogonial chromosomes become diffuse after the telophase of the last division.

- 2) These diffuse masses condense, and each begins to unwind spirally to form a single, delicate, chromatin strand, the leptotene threads.

- 3) The leptotene threads become associated in pairs,

and conjugate side by side in parasynapsis. This is known as the amphitene stage, and twisting of the threads occurs.

4) At the close of the amphitene stage, the pachytene stage begins. During this stage the chromatin commences to condense. The large pair of chromosomes does not join the others in the characteristic "bouquet" of this period.

"Synizésis", as a stage, does not occur.

5) The diplotene stage is initiated by a splitting of the pachytene thread at right angles to the plane of synapsis.

6) The tetrad lies on the spindle in such a way as to make the first maturation division equational for the large pair under observation.

The spermatogonial number of chromosomes is twenty-seven.

Parasynapsis is clearly demonstrated as occurring in the largest pair of chromosomes, and indicated in a number of others.

V. GENERAL CONSIDERATIONS

In 1883, Van Beneden stated for the first time the theory of the individuality of the chromosomes, and determined that only half of the normal number of chromosomes were present in the mature germ cells. Since then these two points have been given much attention by cytologists, and many different views have received support.

The literature is very extensive and I have not attempted to review all of it in the original. Montgomery ('11),

Wilson ('12), Kornhauser ('14), Robertson ('16), and Wenrich ('16), have discussed the literature extensively, and I shall present only a summary of the ideas obtained from their papers.

Montgomery ('11, p. 749) has tabulated "the chief opinions relating to the phenomena of the reduction of the autosomes" which I give below.

"I. The actual reduction of the number of the chromosomes is during the prophases of the maturation mitoses, and both of these divisions are equational. This was originated by Boveri ('87), and Brauer ('93). Today it is held in two forms: (A) Meves ('96, '07a), Fick ('07, '08), and Duesburg ('08) argue that a continuous spireme is produced, that this segments into half the normal number of chromosomes, the cleft along such a bivalent chromosome being a true longitudinal split; they reason there is neither metasyndetic nor parasyndetic conjugation of chromosomes.* (B) Bonnivie ('06, '08) and Vejdoský ('07) hold there is a parasyndetic union of chromosomes, but that this conjugation leads to complete and persisting fusion.

"II. The reduction of the number of the chromosomes is effected by the maturation mitoses, one at least of which is a reduction division. There are several variants of this, as follows:

"A. The univalent chromosomes, without conjugation or pseudoreduction, double their number during the prophases;

*Note: Syndesis is used synonymously with synapsis.

then become quartered in number by two successive reduction divisions. This view was founded especially by O. Hertwig ('90) and Wilcox ('95).

"B. The univalent chromosomes undergo neither conjugation nor pseudoreduction during the prophases, but conjugate first in the equator of the first maturation spindle, and there separate reductionally. Founded by Henking ('91) and Korschelt ('95).

"C. The univalent chromosomes undergo pseudoreduction in the prophases by a continuous spireme segmenting into half the normal number of segments; these divide equationally in the first mitosis, and reductionally in the second; Ruckert ('93, '94), Hacker ('95), Vom Rath ('95).

"D. There is no continuous spireme produced in the prophases, but the univalent chromosomes conjugate to form pairs or gemini and these undergo a reductional and an equational division. This view, now shared by a great majority of students, exhibits itself under these aspects:

"D.1. The chromosomes conjugate metasynetically.

(a) The reduction in number of the chromosomes is effected by the first maturation mitosis (Montgomery, '00; Farmer and Moore, '03).

(b) The reduction in number of chromosomes is effected by the second maturation mitosis, McClung ('00) and his students.

"D.2. The chromosomes conjugate parasynetically, and the first maturation mitosis is reductional; Winiwarter ('00),

Grégoire ('04), Berghs ('04), A. and K.E. Schreiner ('04, '05)."

Of these views, the one expressed under IID has received the support of the more recent workers, but a new division in the classification under IID may now have to be made. In the work of Wenrich ('16) and this work on Anax, the chromosomes are shown to conjugate parasynaptically, but the first division is equational. McClung ('14) has pointed out that other things being equal, the position of the spindle-fiber attachment of the chromosomes determines which division is equational and which reductional. It may, therefore, differ in different chromosomes of the same animal. Since the method of synapsis and the consequent tetrad formation govern the reductional division, let us consider that point.

Wilson ('13, p. 392) states that: "The cytological problem of synapsis and reduction involves four principal questions, as follows: (1) Is synapsis a fact? Do the chromatin-elements actually conjugate or otherwise become associated two by two? (2) Admitting the fact of synapsis, are the conjugating elements chromosomes, and are they individually identical with those of the last diploid or pre-meiotic division? (3) Do they conjugate side by side (parasynapsis, parasyn-desis), end to end (telosynapsis, metasyn-desis), or in both ways? (4) Does synapsis lead to partial or complete fusion of the conjugating elements to form 'zygosomes' or 'mixochromosomes', or are they subsequently disjoined by a 'reduction-division'? Upon these questions depends our answer to a fifth and still more important question, namely, (5) Can the Mendelian segre-

gation of unit-factors be explained by the phenomena of synapsis and reduction?"

As regards the first question-"Is synapsis a fact?". The theory of a true conjugation of chromosomes was advanced by Montgomery ('00), and Winiwarter brought forth the idea in the same year. Since then it has received confirmation from many observers, and has, also, been severely criticised. The chief line of criticism has been that the amphitene threads are divided longitudinally from the beginning and therefore do not represent union of two different threads. However, when in numerous cases there is a definite number of pairs of autosomes in the primary germ cells, and only half that number of bivalent chromosomes at the time of the first maturation division, it seems very sure that synapsis is a fact, and that the chromosomes conjugate in pairs. This conviction is strengthened by the pairing of unequal chromosomes where there can be no question of previous splitting. Robertson ('16, p. 247) says: "A second line of evidence that synapsis takes place is afforded by the behavior of the V's in *Jamaicana*, where one individual showed in its first spermatocyte cells a single unequal-armed V autosome paired with, and separating from, rod autosome mates (pp. 221-222, 246-247). In germ-cell divisions preceding synapsis the V autosome existed separate from the rod autosomes, but in divisions succeeding synapsis it separated again from them, passing into one-half of the spermatids while the rod autosomes passed into the other half." Similar evidence could be obtained

from the heteromorphic chromosomes described by Carothers ('17).

The question of the identical individuality of the conjugating elements with those of the last diploid division of course does not exist for those who hold that the chromosomes are not morphological characters. But the fact that chromosomes always come out of a diffuse condition with the same peculiarities of number, size and shape indicates that they do not lose their individuality. If an abnormality occurs, as, for example, in the occurrence of supernumerary chromosomes of various forms, it is constant for all the cells and for all divisions. The size differences in many forms are very evident and perfectly characteristic, and the same is true of the variations in shape among the chromosomes. The latter point is strikingly illustrated in the case of hybrid forms such as Moenkhaus ('04) and Tennent ('08) have described. In many cases, beginning with Boveri's account of *Ascaris*, the chromosomes pass from one division to the next in what are called chromosome vesicles. Richards' work ('17) on *Fundulus* is the most recent account of this occurrence. Wenrich ('16) has presented a striking case of persistent organization of chromosomes which bears directly on the question of the individuality of the pairing chromosomes. In *Phrynotettix*, he has been able to trace three pairs of autosomes from the spermatogonia to the spermatids, giving conclusive evidence of their individuality and persistent organization at all stages. From this case, direct evidence is

gotten, and from the other evidence given above, we must assume that the conjugating elements are chromosomes and that they are identical with the chromosomes of the last diploid division.

As to the method of conjugation of the chromosomes, there are two views. On the one hand, it is held that the chromosomes conjugate end to end (telosynapsis); on the other, that they conjugate side by side (parasynapsis). Parasynapsis has been described for many different forms.

In 1913, de Saedeleer described side by side conjugation in *Ascaris*.

Kornhauser ('15) found parasynapsis in a copepod, and Fasten ('14) described a like condition for two species of *Cambarus*.

The insects have probably been more fully studied than any other group. Among the Orthoptera, the greater number of investigators have described telosynapsis, but more recently the conditions in that group are being brought into line with other groups. McClung ('14) has admitted the possibility of parasynapsis in Acrididae. Miss Stevens was another worker whose opinion on synapsis in the Orthoptera changed. However, she held that both extremes may occur in a single group. In her 1912 paper, p. 227, she says: "Indeed I should not be surprised if the range of variation should prove to extend from (a) cases where there is nothing that could be called conjugation, but merely such a pairing, without contact even, as will secure segregation of homologous maternal and paternal chromo-

comes to different daughter cells, through (b) an intermediate condition of telosynapsis and less intimate parasynapsis, to (c) cases where homologous chromosomes are so completely fused in parasynapsis that it is impossible to tell whether the resulting chromosomes which are segregated in mitosis are identical with those that went into synapsis or not;". While one must, of course, grant the possibility of such an occurrence, Wilson ('12) points out that: "We should certainly expect a phenomenon so fundamental to follow everywhere the same type;" and we should seek to find a more uniform method of behavior.

Very few of the Odonata have been studied cytologically. The papers of McGill ('04) and of Lefevre and McGill ('08) described the spermatogenesis of *Anax junius* and suggested that a condition of parasynapsis obtained in that form. Smith ('16) has described parasynapsis for *Sympetrum semicinctum* (Say), and her notes and figures on *Libellula basalis* indicate that a side to side union of the leptotene threads occurs in that form.

Montgomery ('11), Wilson ('12), and Kornhauser ('14) have pointed out the widespread occurrence of parasynapsis in the Hemiptera.

The Diptera exhibit parasynapsis in a marked degree. Metz ('14) in describing conditions in *Drosophila* says (p.55): "But the most remarkable feature of the whole study is the discovery that the chromosomes not only exhibit a close association in pairs at nearly all times, but that before every

cell division the members of each pair become so intimately united that they may be said actually to conjugate. Each pair, with the possible exception of the sex-chromosomes, goes through with what amounts to a synapsis in every cell generation, so that in many cases the figures closely resemble those of haploid groups". Miss Stevens ('10a) found the same condition in *Culex*.

The Schrieners have found parasynapsis in birds, reptiles, fishes, molluscs, and annelids. Among the vertebrata, parasynapsis has also been described for several amphibians, and indicated for the opossum and the pig.

Montgomery's acceptance of parasynapsis was a complete reversal of opinion on his part. He says ('11, p. 753): "My original conclusion was right in that in the species examined by me the chromosomes are paired end to end in the first maturation spindle and in the late prophase, whereas in most other cases they lie in these stages in parallel juxtaposition. But I made my error, as Grégoire has pointed out, in overlooking or giving scant attention to most of the stages preceding the pachytene condition, which are necessarily the decisive ones; I also employed too low powers of magnification for such delicate determinations". This would probably explain many of the supposed cases of telosynapsis. If only the late prophases are studied, the stages can certainly be explained on the basis of telosynapsis. Lefevre and McGill ('08) pointed this out with reference to *Anax* in discussing a break in one of the chromosome ribbons. They say (p. 474): "It may represent, of

course, the line of suture between two univalent chromosomes conjugating end to end, or it may equally well be interpreted as the point of contact between the ends of two chromosomes which have previously undergone a parallel conjugation and subsequently opened out to form a loop or ribbon". It is only in studying the entire growth period with its typical pre-leptotene, leptotene, amphitene, pachytene, and diplotene stages, that one sees what actually takes place. The earlier stages make the later ones intelligible, and it is the earlier stages which have been neglected. Most of the recent work in which the earlier stages have been studied show parasynapsis.

In passing, I want to mention the chiasmotype theory of Janssens ('09). The theory holds that a secondary twisting of the chromatin threads occurs in the late diplotene, or strepsitene, as Janssens calls it, and that large segments of one thread may become fused to the other and disjoin with it. Morgan used this theory for a time to explain the "crossing-over" phenomena observed in the breeding experiments on *Drosophila*. It has now been abandoned because it would call for great numbers of factors crossing over and that does not occur. The amphitene twisting has been taken over as the place where the crossing-over might better occur.

However, I wish to present another objection to the theory. While I was modeling the various stages in the growth period, and making the changes from one to the other, I found that a secondary twisting is part of the mechanics of transforming a twisted pachytene thread into a tetrad. Wenrich ('16)

figures no secondary twisting in the diplotene. It will be recalled that the amphitene threads in *Phrynotettix* do not twist. Therefore, I wish to suggest that this secondary twisting in the diplotene is dependent on the condition in the amphitene stage, and not necessarily a typical condition of the growth period. See text figure 1 for these stages.

As regards the fourth question of Wilson, there can be no doubt, from recent work like that of Wenrich and Robertson, that the conjugating chromosomes are not fused completely, but disjoin in one of the maturation divisions.

Morgan has presented the evidence for believing that the chromosomes are the carriers of Mendelian factors so many times that a further discussion here is superfluous. The work by Carothers ('17) on segregation and recombination of chromosomes is the most significant piece of corroborative evidence that has been brought forward recently. The main fact that the opponents of the theory cannot gainsay is that it offers an adequate explanation of the facts as brought out by breeding experiments.

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VII. EXPLANATION OF DRAWINGS

All drawings were outlined, at table level, with a camera lucida, under a 2 mm. Zeiss apochromatic objective and compensation ocular 12, with draw-tube set at 160 mm. They were corrected from the objects, enlarged with a drawing camera two and a half times and corrected again by comparison with the objects. A reduction of about one third was made during the photographing of the plates, so that the magnification as they appear here is about 4300 diameters.

Figures 1 to 16 show the nucleus, but no attempt has been made to represent all the chromosomes. Figure 17 shows only the large pair of chromosomes.

The following abbreviations are used:

A designates the large pair of chromosomes.

X designates the accessory chromosome.

P designates the plasmosome.

Plate 1

- 1 Spermatogonial group.
- 2 Last spermatogonial telophase.
- 3 Diffuse condition of chromatin after telophase.
- 4 Chromatin again condensing.
- 5 Pre-leptotene stage.
- 6 Pre-leptotene stage.

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Plate 2

- 7 Pre-leptotene, and pairing of leptotene threads.
- 8 Typical leptotene nucleus.
- 9 Early amphitene stage.
- 10 Amphitene stage.
- 11 Amphitene stage.
- 12 Typical "bouquet" of pachytene.

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Plate 3

- 13 Amphitene stage.
- 14 Amphitene stage.
- 15 Pachytene stage.
- 16 Late pachytene stage.
- 17 Diplotene stages and tetrad formation.

GROWTH PERIOD IN ANAX

PLATE 3

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Scanning system software	Omni scan v. 12.8 SR2 (2675)
Optical resolution	600 dpi
Color settings	grayscale, 8 bit and color, 24 bit
File types	tiff

Source information

Format	Book
Content type	Text [with images]
Source ID	010-100727199
Notes	Pages typed and single-sided. Title page has signature and perforated property stamp. Some pages have handwritten marginalia and corrections. Photographs are pasted in. 58 blank pages at end were not scanned.

Derivatives - Access copy

Compression	Tiff compressed with LZW before conversion to pdf
Editing software	Adobe Photoshop CS5
Resolution	600 dpi
Color	Grayscale and color
File types	pdf
Notes	Grayscale pages cropped, canvassed, and images brightened. Color pages cropped and canvassed. Blank pages removed.