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Recombination in Male and Female Meiocytes Contrasted [and Discussion]

H. G. Callan, P. E. Perry, R. B. Nicklas, K. Jones and K. R. Lewis

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Recombination in male and female meiocytes contrasted

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[Plates 1–4]

For technical reasons studies of chiasma frequency and distribution, and hence of intra-chromosomal recombination, have mostly been confined to male meiosis. However, there is now sufficient comparative data on male and female meiosis, in both plants and animals, to show that the extent of intra-chromosomal recombination in some organisms may be much the same on the female as on the male side, whereas other organisms show extreme sexual divergence in this regard. The evolutionary significance of such diversity remains enigmatic.

Meiosis fulfils two primary functions in the lives of eukaryotic organisms, and both are connected with sexual reproduction. One function is to ensure the orderly production of haploidy, haploid generations in plants, haploid gametes in animals, these being pre-requisites for the orderly repetition of syngamy from generation to generation. The second function is to provide for genetic recombination, without which sexual reproduction would lose all biological meaning.

In the great majority of eukaryotic organisms, overwhelmingly so in the case of plants, rather less so in the case of animals, both functions are served by the same mechanism. In such organisms, as Darlington first stressed in 1932, chiasmata, which achieve genetic recombination between homologous chromosomes, are also essential for the orderly disjunction of homologous chromosomes to form haploid sets. When for one reason or another chiasmata fail to form between homologous chromosomes, not only does intra-chromosomal recombination lapse, but regular disjunction is impaired.

Figure 1 (plate 1) shows 1st meiotic metaphase in a spermatocyte of the newt *Triturus vulgaris*. This animal had been subjected to a 24 h heat shock 13 days before its testes were fixed. As a consequence of the treatment, which came 7 days after the termination of the premeiotic S-phase and just at the beginning of zygotene (Callan & Taylor 1968), two pairs of homologous chromosomes failed to form chiasmata; they can be seen as the four univalents, and their prospects of regular disjunction are evidently poor. The failure of chromosomes to associate by chiasmata is a well-known outcome of heat-shock treatment during synapsis. What is less well known is that this treatment frequently induces chromosome interlocking during synapsis, and provided chiasmata form at appropriate places, interlocked bivalents can be seen at 1st meiotic metaphase. Figure 1 shows two such interlocked ring bivalents. It is easy enough to account for interlocking; the real puzzle is how interlocking is normally avoided by chromosomes which start their synapsis at *both* telomeres. This particular problem, however, is not our primary concern in the present paper.

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The association between the two functions of chiasmata, to ensure regular disjunction and to achieve intra-chromosomal recombination, in so many eukaryotes, including higher plants and chordates (and one could hardly look for a wider evolutionary divergence than between these) is a powerful argument for the antiquity of the mechanism. Indeed in the 1920s and 1930s the relationship appeared well nigh ubiquitous, and that is why the problem of *Drosophila* appeared so enigmatic. As was already well established at the time, no intra-chromosomal recombination occurs in male *Drosophila*, nevertheless the disjunction of homologues during male meiosis is at least as regular in this as in other sexually reproducing eukaryotes.

The *Drosophila* male meiosis problem remains an enigma; no satisfactory explanation has yet been advanced for the continued association of homologous chromosomes up to first meiotic anaphase in the absence of chiasmata. Moreover both genetical and cytological studies over the past forty years have shown that *Drosophila* is by no means unique among animals in achieving regular meiotic disjunction without chiasmata. This topic has been well reviewed by White (1973) in the 3rd edition of his comprehensive text *Animal cytology and evolution*. The list of organisms with achiasmate meiosis in one sex (generally the male) is long: it includes a few protozoa, a mollusc, a few oligochaet worms, some mites and scorpions, several copepods (in which the female sex is heterogametic and female meiosis achiasmate), many mantids, a couple of grasshoppers, the scorpion flies, some (possibly all) Trichoptera and Lepidoptera (in which again the female sex is heterogametic and female meiosis achiasmate), some of the Diptera Nematocera and most of the Diptera Brachycera (including of course *Drosophila*).

The diversity of the animals in this list, and the sporadic occurrence of achiasmate species in groups where chiasmate meiosis is the general rule, strongly suggests that achiasmate meiosis has evolved on many different occasions. At one time there was speculation that the evolution of achiasmate meiosis was connected in some way with the phenomenon of somatic pairing, so characteristic of the Diptera. While somatic pairing may have predisposed the Diptera to engage in achiasmate meiosis in the male sex, and it is certainly true that achiasmate meiosis is more widespread in the Diptera than in any other group of animals, the fact remains that achiasmate meiosis has successfully evolved in many animals which do not exhibit somatic pairing. Why it should have evolved is another matter, and another enigma.

When *Drosophila* was considered unique amongst eukaryotes in having achiasmate male meiosis, it was argued that this evolutionary step might have taken place to permit the retention of inversions within the species (White 1973, p. 489). There exists in *Drosophila*, in *Sciara*, and perhaps in other organisms too, a simple mechanism operating in female meiosis whereby in paracentric inversion heterozygotes any chromatids which partake in recombination within the inverted segment, and which as an outcome of this event form a dicentric bridge at first meiotic anaphase, are shunted off to the polar bodies leaving an unrecombined chromatid for the egg pronucleus (Sturtevant & Beadle 1936; Carson 1946). Such inversions are of course the cytological concomitants of crossover suppressors, which were recognized genetically several years before their peculiar cytology was comprehended. As on the contrary all four products of a male meiosis will in the ordinary course of events give rise to functional spermatozoa, achiasmate male meiosis guarantees that defective genotypes are not produced by inversion heterozygotes, for intrachromosomal recombination is suppressed altogether.

However, this line of reasoning came to grief once it was realized that inversion heterozygosity on a large scale can co-exist with chiasmate meiosis in both sexes. Perhaps the most striking example of this condition is to be found in *Chironomus tentans*, where Beermann (1956)

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came to the conclusion that spermatid nuclei which are linked to one another by an inversion bridge do not differentiate into functional spermatozoa. The reduction in the number of spermatozoa formed by an inversion heterozygote male *Chironomus* does not lead to any overall loss of fertility, because at least three times as many spermatozoa are available at copulation as there are eggs to fertilize. In inversion heterozygote plants the male gametophyte sieve ensures a similar outcome; deficient and unbalanced genomes resulting from recombination within relatively inverted segments do not, in the ordinary course of events, survive to engage in syngamy. Furthermore, if one argues that achiasmate meiosis evolved so as to stabilize and perpetuate inversion heterozygosity, it is distinctly odd that this mechanism should operate on the female side, not on the male, in Trichoptera and Lepidoptera; for as has already been mentioned, the adverse consequences of recombination between mutually inverted segments in the meiosis of oocytes can be otherwise circumvented.

Beginning with the work of Meyer (1964) several ultrastructural studies have been carried out on the zygotene/pachytene stage of meiosis in animals which do not form chiasmata in one sex or the other, and comparisons made between the two sexes, also with related organisms which do form chiasmata in both sexes. The outcome of these studies has again proved enigmatic. As might have been anticipated, Meyer found that synaptonemal complexes are absent from the male meiosis of *Drosophila*, *Tipula caesia* and *Phryne fenestralis*, all these species being achiasmate, but that complexes are present in the chiasmate male meiosis of *Tipula oleracea*. So far so good; at first glance it looked as though there might be a direct correlation between the presence of synaptonemal complexes and intrachromosomal recombination, the absence of synaptonemal complexes and no intrachromosomal recombination. However, it was soon found that there is no such general correlation. The male scorpion fly *Panorpa* is achiasmate but nevertheless forms synaptonemal complexes (Gassner 1967), so do two achiasmate male mantids (Gassner 1969; J. Wahrman, quoted by White 1973), so too do several female Lepidoptera in which the oocytes are achiasmate (G. F. Meyer, quoted by Moses 1968; Rasmussen 1967). Therefore while one can almost certainly assume that synaptonemal complexes are a *sine qua non* for intrachromosomal recombination, the converse assumption: that chiasmata will occur provided a synaptonemal complex is formed, is manifestly untrue.

Within the animal kingdom it will be evident that many successful species have dispensed with intrachromosomal recombination in one sex, whatever selective advantage this may have conferred upon them, while relying on a sufficiency of recombination occurring in the other sex. This being so, it is perhaps surprising that several of the early studies on meiosis in organisms which show limited intrachromosomal recombination (localized chiasmata) in male meiosis should have led to quite false conclusions regarding the selective advantage of restricted recombination (Darlington & Mather 1949). Meiosis in the female sex was disregarded, it being more difficult to study, and it being assumed that what held for one sex would apply equally to the other. More recent work on organisms which show localized chiasma distribution in the one sex have revealed a quite different chiasma distribution in the other.

Male meiosis in the grasshopper *Stethophyma grossum* is a classical example of procentric chiasma localization (White 1936; see figure 2, plate 2). A single chiasma, occasionally two chiasmata very close together, form near the centromeres of each bivalent, and chiasmata are not normally present in intercalary regions. An occasional bivalent may form a single distal chiasma, but the general picture is one of extremely restricted chiasma distribution in close proximity to the centromeres. More than thirty years later oocyte meiosis was investigated

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(White 1973; Perry & Jones 1974) and it was found that in the female sex chiasmata are not procentrically localized; less than 6% of chiasmata occur close to the centromeres, all the rest being interstitial or distal (see figure 3, plate 2). Chiasma distribution in the one sex of *Stethophyma* is therefore complementary to that in the other.

Precisely parallel observations have been made on plants. Thus in 1930 Newton & Darlington described the extreme procentric localization of chiasmata in male meiosis of *Fritillaria meleagris*. The situation is just as in male meiosis of *Stethophyma*, except that whereas all the chromosomes of *Stethophyma* are acrocentric, *Fritillaria* has two pairs of metacentric chromosomes and ten pairs of chromosomes with subterminal centromeres. However, nearly thirty years later when Fogwill (1958) examined female meiosis in *Fritillaria meleagris* she found considerably higher chiasma frequencies in the embryo sac mother cells, with plentiful chiasmata occurring in intercalary chromosome regions where in pollen mother cells chiasmata are rarely if ever located.

When comparisons were made between the chiasma distributions in male and female newts (Watson & Callan 1963) a similar picture emerged. Meiosis in the male palmate newt *Triturus helveticus* affords a striking example of proterminal chiasma localization; essentially all chiasmata are restricted to the ends of the chromosomes, far removed from the centromeres (see figure 4, plate 3). In oocytes of this species, quite to the contrary, although chiasma frequency is much the same as in male meiosis, all chiasmata occupy intercalary positions (see figure 5, plate 3); just as in *Stethophyma* the two sexes complement one another in regard to intrachromosomal recombination, with the female sex playing by far the more significant role. Sex differences in grouse locusts precisely parallel the situation in *Triturus helveticus*. In two species with proterminal chiasma localization in male meiosis there is little recombination between colour pattern genes in this sex, whereas in females the crossover frequencies may reach 50% (Henderson 1961).

In other newts the reverse applies. All subspecies of the Great Crested Newt *Triturus cristatus* have male meiosis in which chiasmata are liberally distributed throughout the lengths of the chromosomes (see figure 6, plate 4). The females of these newts, on the other hand, show a grade of procentric chiasma localization that is nearly as strict as that found in male *Stethophyma* (see figure 7, plate 4). Again the two sexes play complementary roles in regard to intrachromosomal recombination, but here the male's role dominates.

At one time it was thought that chiasma localization is a consequence of incomplete synapsis, and that the gross type of localization – procentric or proterminal – is therefore an indicator of where synapsis starts, at the centromeres or at the telomeres. Nowadays it is generally conceded that synapsis is complete even in forms where chiasmata are localized, though here one runs into semantic as well as observational problems. Studies on newt meiosis reveal, however, that chiasma distribution is unrelated to the sequential character of synapsis, for in both male and female synapsis starts at chromosome ends, whether the outcome be procentrically or proterminally or unlocalized chiasmata.

The existence of procentric chiasma localization in the females of *Triturus cristatus* was of great practical advantage when the lampbrush chromosomes of these animals were being scrutinized for the locations of the centromeres, because attention could be concentrated on the regions between zones where chiasmata most frequently form (Callan & Lloyd 1960). This fact is mentioned in passing because it allows us to introduce an observation which, though not directly relevant to the main concern of the present paper, is certainly relevant to the general

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FIGURE 1. 1st meiotic metaphase in a spermatocyte of *Triturus vulgaris*, showing 4 univalents and 10 bivalents. Two of the ring bivalents are interlocked. The newt had been kept at 31.5 °C for 1 day, then at 17.5 °C for 13 days before its testes were fixed.

(*Facing p.* 230)

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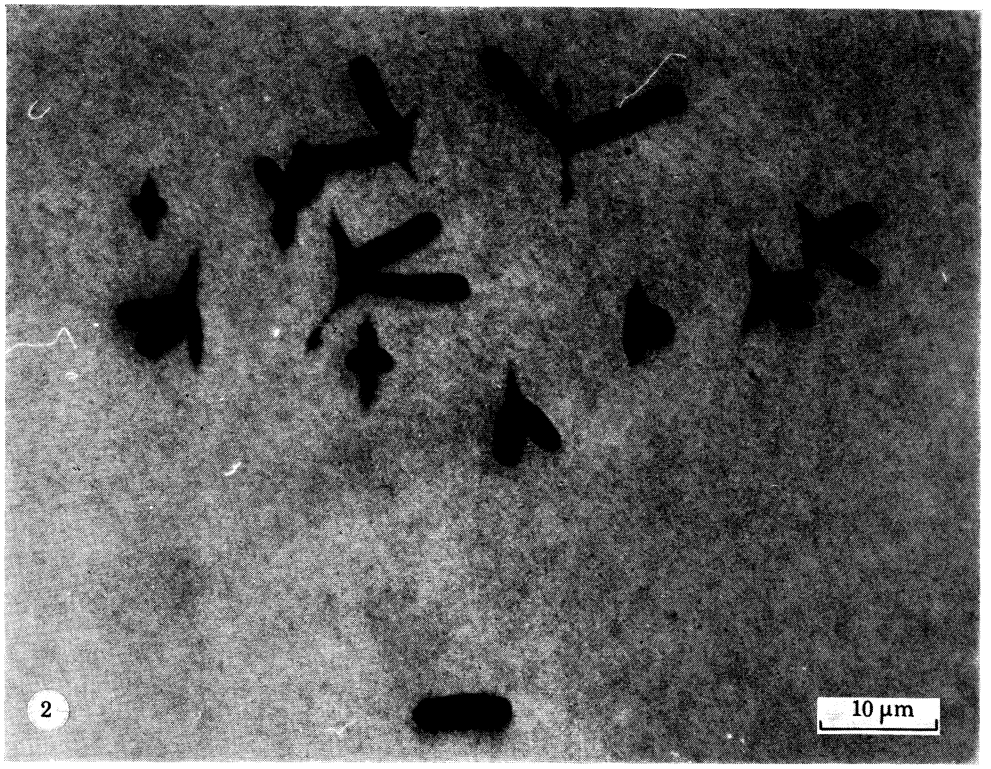

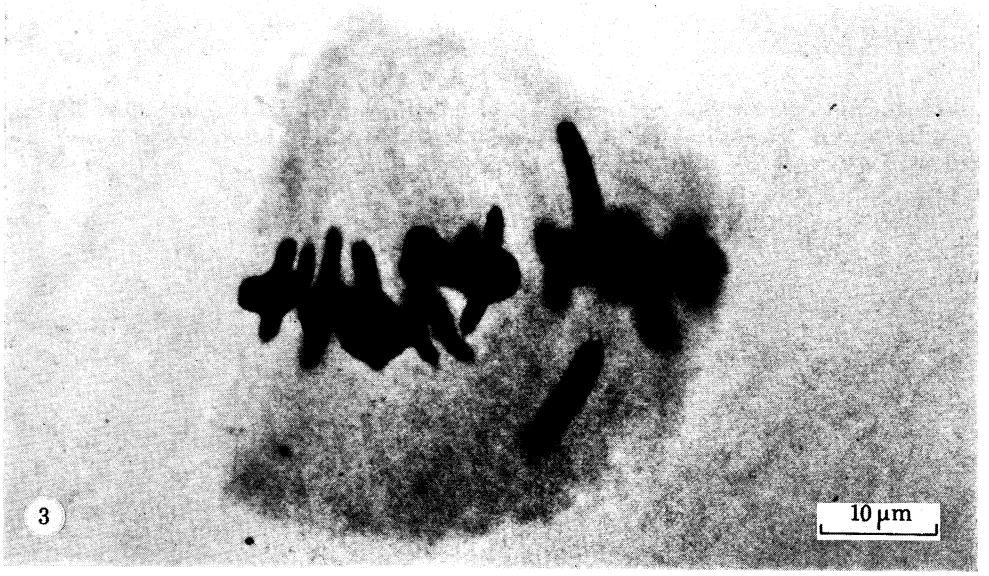

FIGURE 2. 1st meiotic metaphase in a spermatocyte of *Stethophyma grossum*. The univalent sex chromosome lies towards the bottom of the photograph. (From Perry & Jones 1974.)

FIGURE 3. 1st meiotic metaphase in an oocyte of *Stethophyma grossum*.

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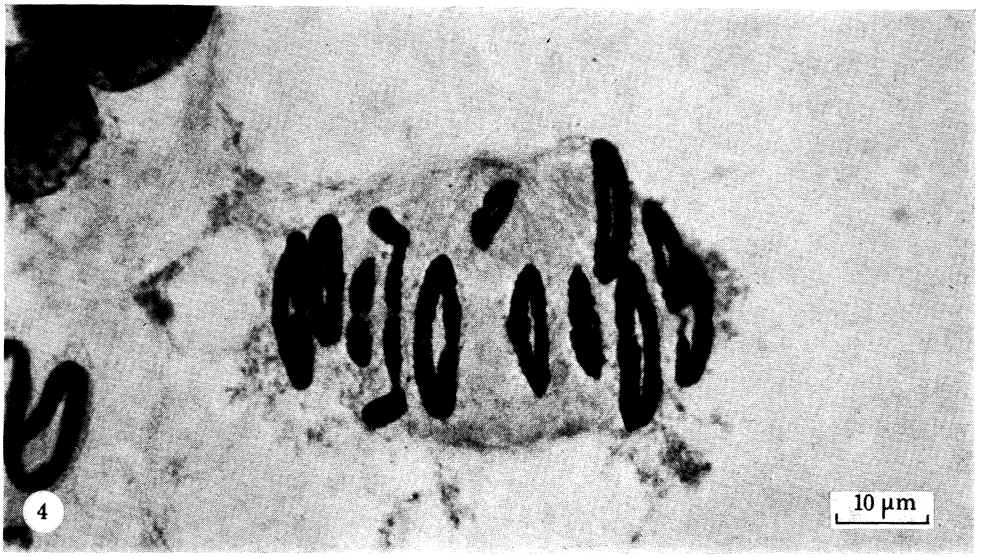

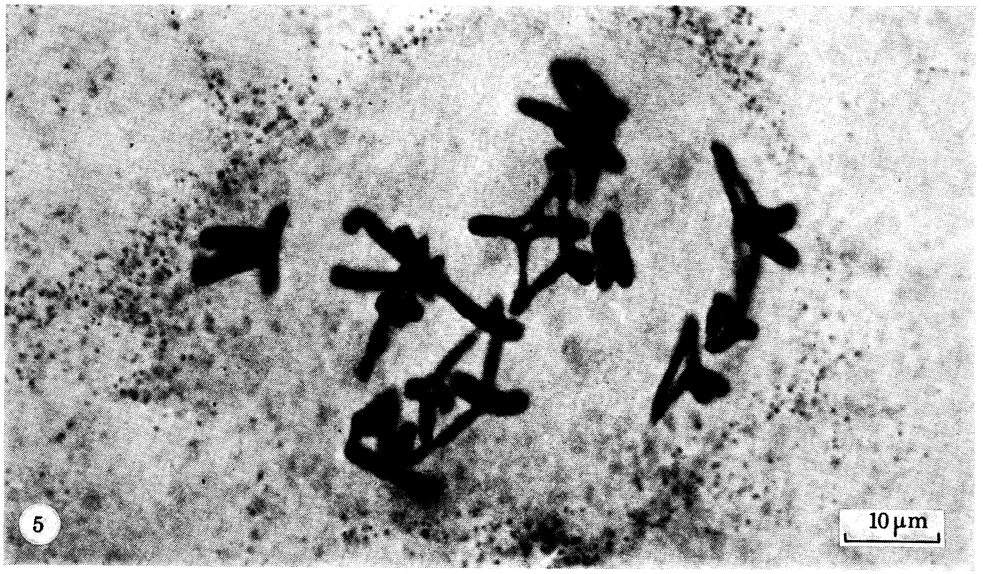

FIGURE 4. 1st meiotic metaphase in a spermatocyte of *Triturus helveticus*. (From Watson & Callan 1963.)
FIGURE 5. 1st meiotic metaphase in an oocyte of *Triturus helveticus*. (From Watson & Callan 1963.)

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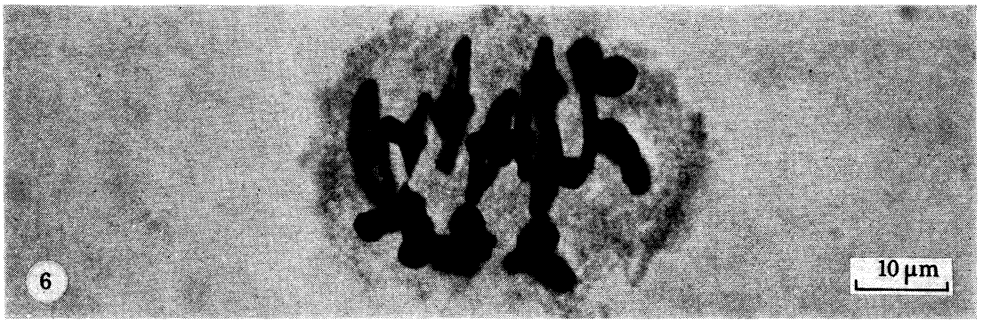

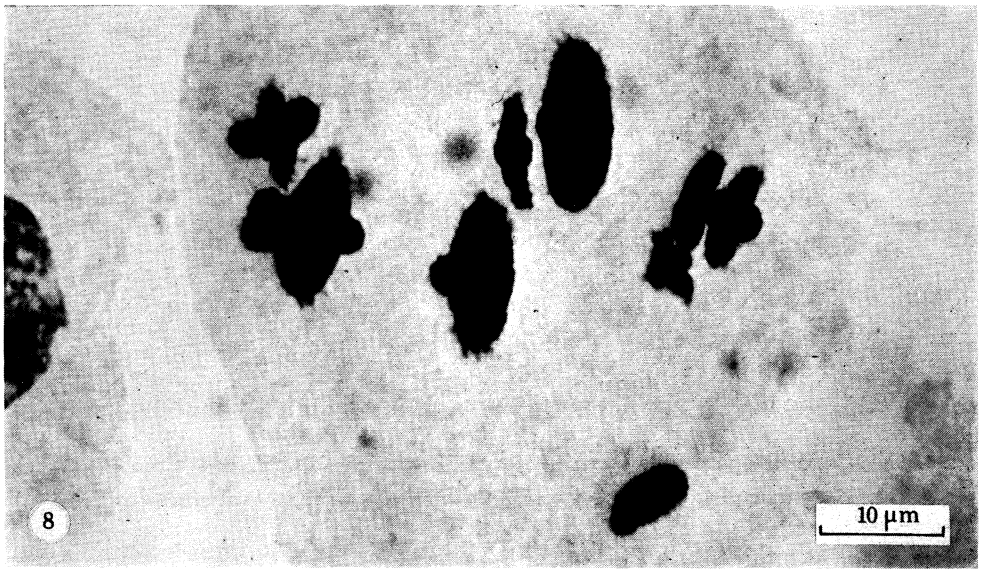

FIGURES 6–9. For description see opposite.

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topic of this discussion meeting. *Chiasmata in lampbrush chromosomes always involve the main chromosome axis, i.e. the interchromomeric strands or chromomeres themselves, they never involve the lateral loops.* If recombination ever occurred within the lengths of the lateral loops, this would be immediately apparent in preparations of lampbrush chromosomes, for the homologues would lie far apart and connected only by lateral loops. Such configurations have never been seen. Knowing as we do that the lateral loops represent intermittently distributed, RNA-transcribing regions along a DNA double helix that is continuous within each chromatid, evidently recombination must be restricted to those segments of the DNA which do not engage in RNA transcription in oocytes. The implications of this observation are not as generally appreciated as they should be, for lampbrush chromosomes are widely distributed in the meiotic cells of both male and female animals, and this restriction on recombination is therefore likely to be equally widespread.

The organisms which we have so far considered all represent breeding systems where there is extreme divergence between the sexes in regard to intrachromosomal recombination. There are, however, many other creatures, probably the great majority of both plants and animals, which do not display any such clear-cut differences. To take an animal case that has recently been investigated (Jones, Stamford & Perry 1975), the common field grasshopper *Chorthippus brunneus* forms much the same number of chiasmata in male as in female meiosis (the slightly higher chiasma frequency in the female is attributable to the X-chromosome bivalent that is confined to this sex), and there is no obvious difference between the sexes as regards chiasma distribution (see figures 8 and 9, plate 4). The same is true of such plants as barley (Bennett. Finch, Smith & Rao 1973) and rye (Davies & Jones 1974). Where there are sex differences on a minor scale, it is commonly found that chiasma frequency and/or rate of crossing-over is higher in female than in male meiosis, even when both processes occur in the same hermaphroditic organism (Pastor & Callan 1952). However, such a sweeping statement should not blind us to the possibility, indeed the probability, that in regard to specific portions of any particular genome crossover frequency may well differ markedly between the two sexes (and not always in the same direction) even though the overall impression from cytology suggests similarity, More than thirty years ago Rhoades (1941) made this point in regard to maize.

Until we have a better understanding of the intimate details of synapsed homologues, of the mechanisms responsible for chiasma formation and chiasma interference, thorough-going explanations for differences in intrachromosomal recombination rates between the sexes will continue to elude us.

Description of plate 4

Figure 6. 1st meiotic metaphase in a spermatocyte of *Triturus cristatus karelinii*. (From Watson & Callan 1963.)

Figure 7. 1st meiotic metaphase in an oocyte of *Triturus cristatus karelinii*. (From Watson & Callan 1963.)

Figure 8. 1st meiotic metaphase in a spermatocyte of *Chorthippus brunneus*. The univalent sex chromosome lie towards the bottom of the photograph. (From Jones *et al.* 1975.)

Figure 9. 1st meiotic metaphase in an oocyte of *Chorthippus brunneus*. (From Jones *et al.* 1975.)

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Discussion

R. B. Nicklas, (*Zoology Department, Duke University, Durham, N. Carolina, U.S.A.*). The significance of achiasmate meiosis is certainly very interesting especially since achiasmate meiosis has arisen independently in such diverse groups. If, as Professor Callan suggested, achiasmate meiosis is *not* an adaptation permitting inversions to persist, would you care to speculate on its significance ? Evidently it would seem an awkward way (requiring many genetic changes, presumably) simply to regulate recombination frequency.

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K. Jones, (*Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey*). On the subject of 'chiasmate meiosis' it is of interest to note that a virtual absence of crossing over could be achieved by distal localization as well as by loss of chiasmata. However, since we have seen in Professor Callan's paper several good examples of proximal and distal localization we may ask whether in fact chiasmata are formed in the places where we *see* them. If this is so, if there is no movement, then can we believe in random crossing over as population geneticists do?

H. G. Callan. I do not understand the significance of achiasmate meiosis. However the fact that achiasmate meiosis (and for that matter extreme chiasma localization too) has arisen independently in one or other sex in several diverse groups suggests that the generality of organisms may have considerably higher rates of intrachromosomal recombination than they really 'need' for adequate genetic flexibility.

K. R. Lewis, (*University of Oxford*). With regard to the question raised by Keith Jones, I would suggest that chiasma movement between the time of formation and scoring is not an important consideration in the case of procentric localization, especially where a single chiasma is involved. To my knowledge 'negative terminalization' has never been proposed.

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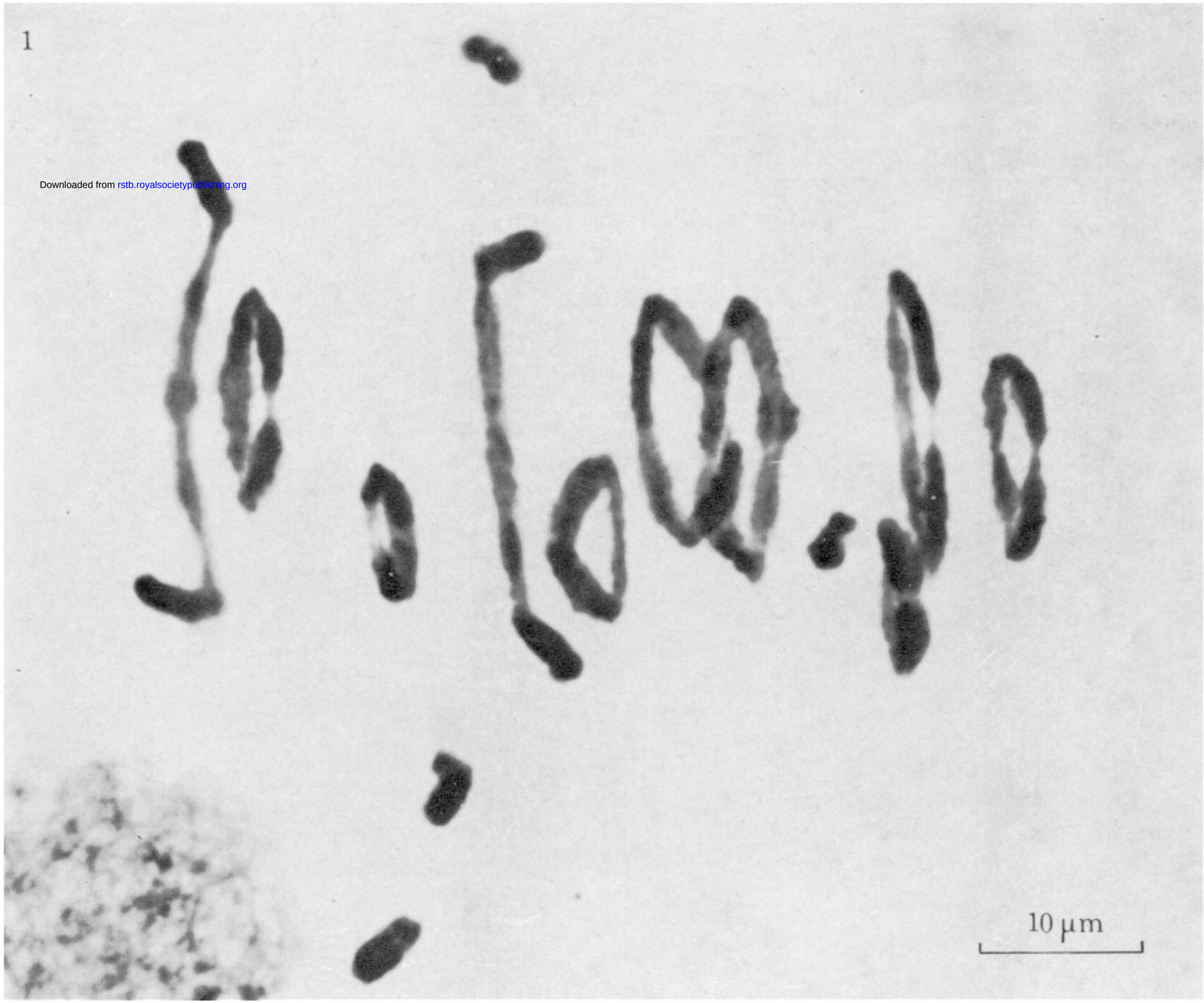

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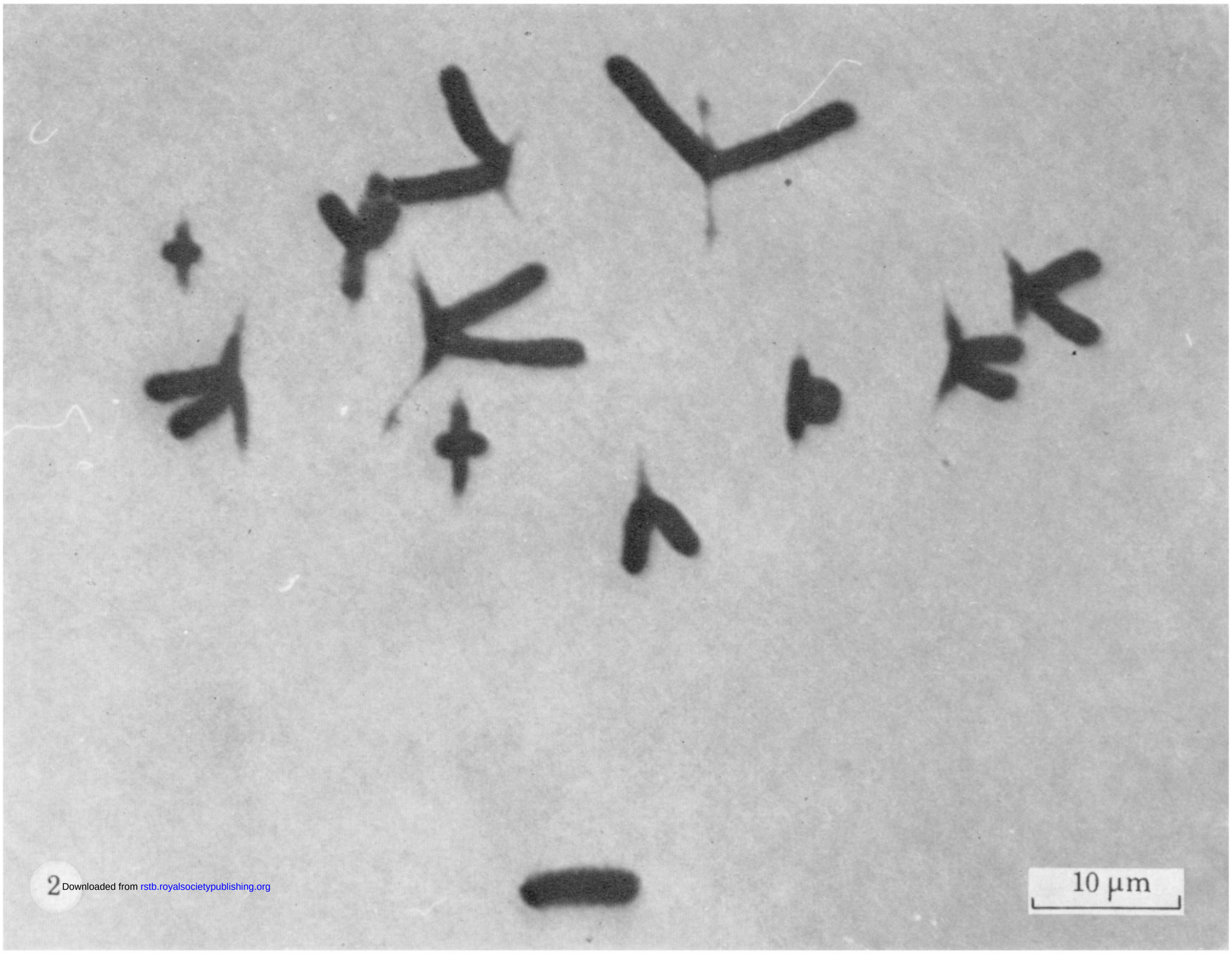

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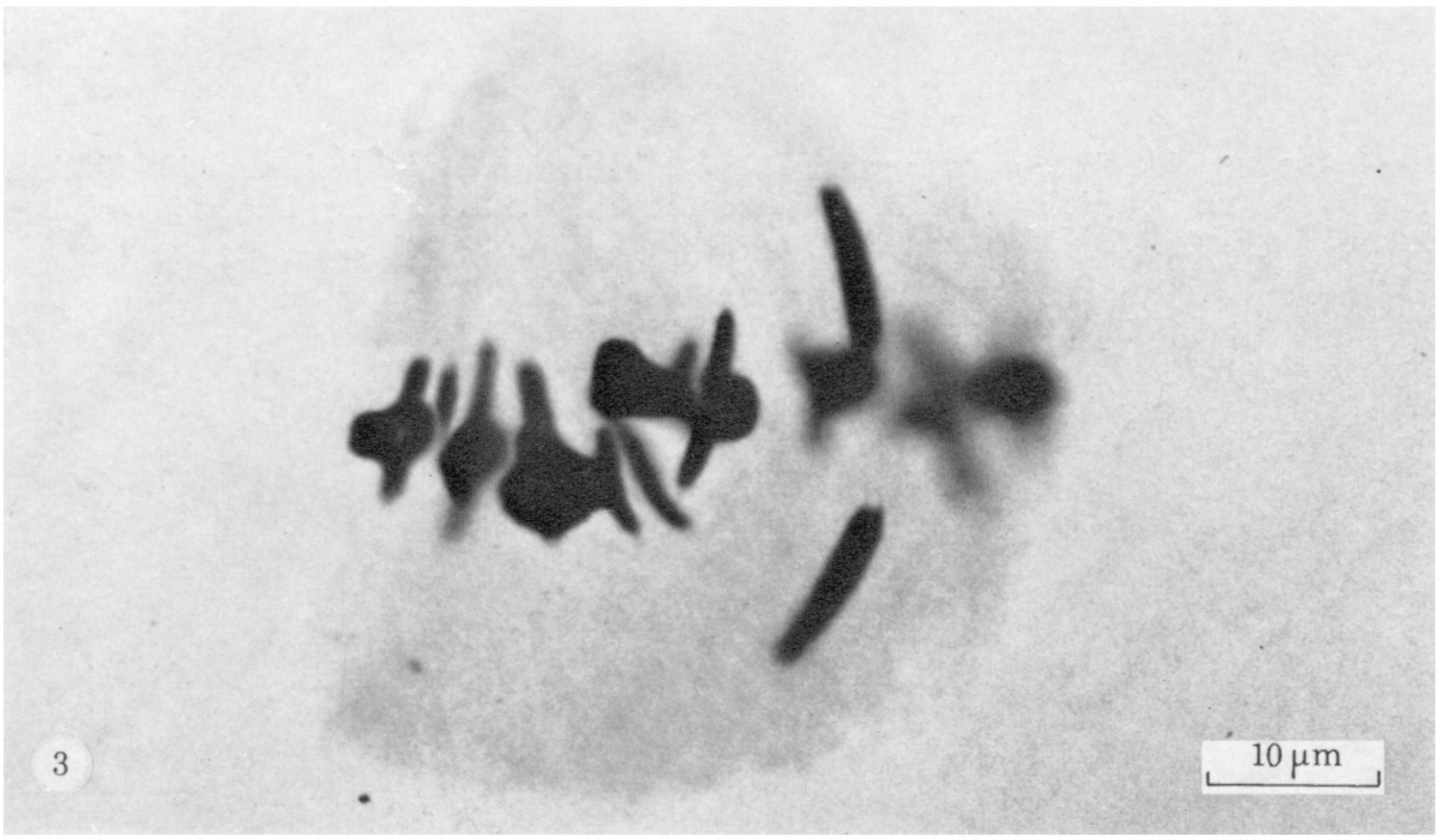

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FIGURE 2. 1st meiotic metaphase in a spermatocyte of *Stethophyma grossum*. The univalent sex chromosome lies towards the bottom of the photograph. (From Perry & Jones 1974.)

FIGURE 3. 1st meiotic metaphase in an oocyte of *Stethophyma grossum*.

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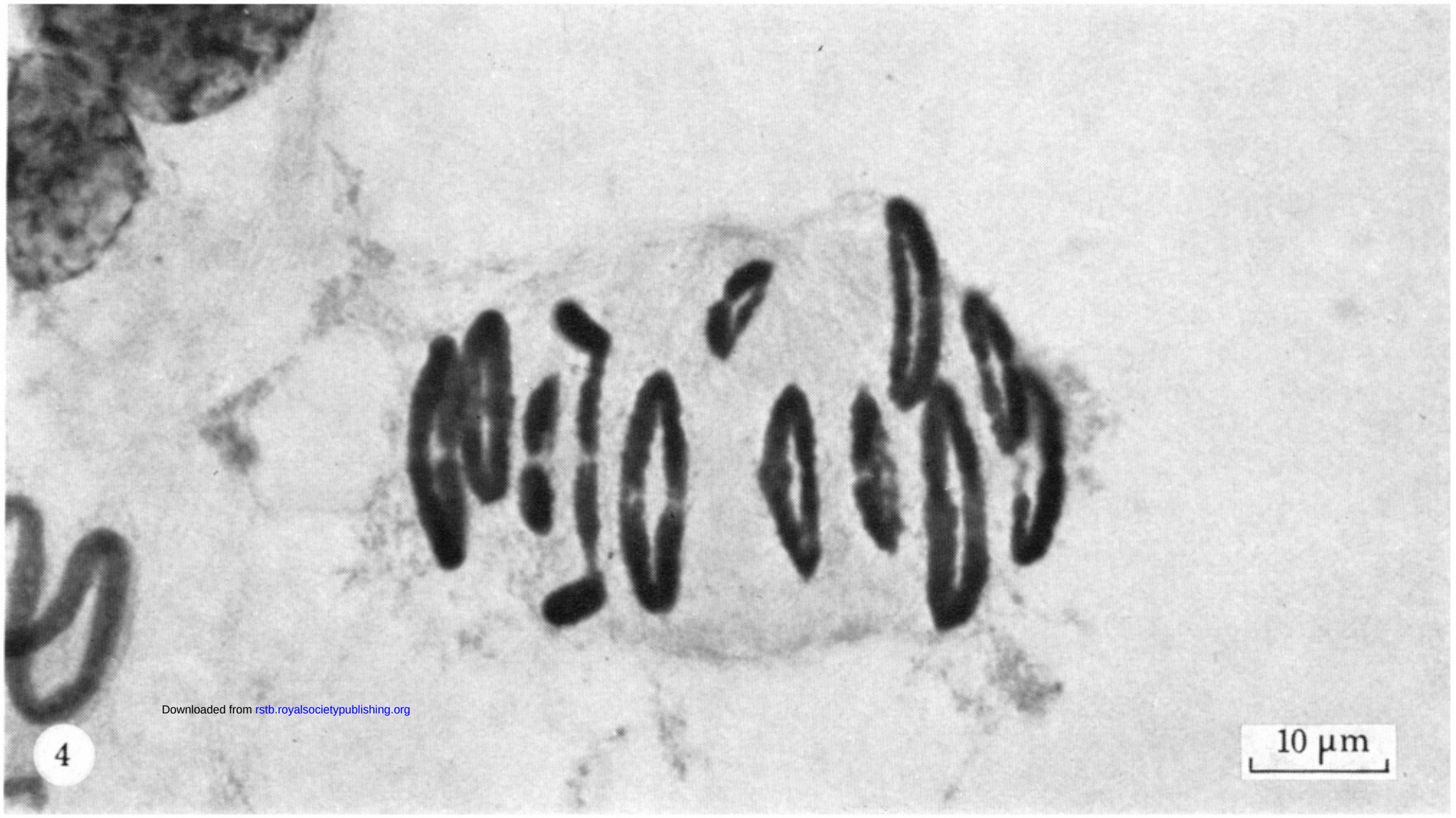

FIGURE 4. 1st meiotic metaphase in a spermatocyte of *Triturus helveticus*. (From Watson & Callan 1963.)

FIGURE 5. 1st meiotic metaphase in an oocyte of *Triturus helveticus*. (From Watson & Callan 1963.)

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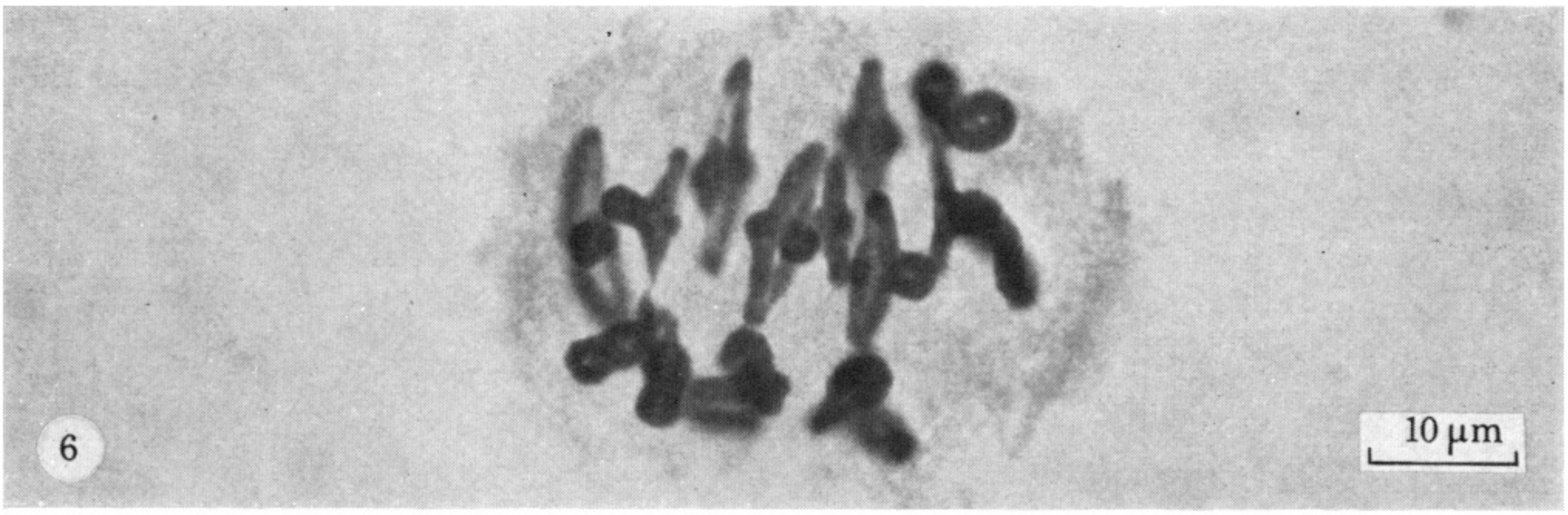

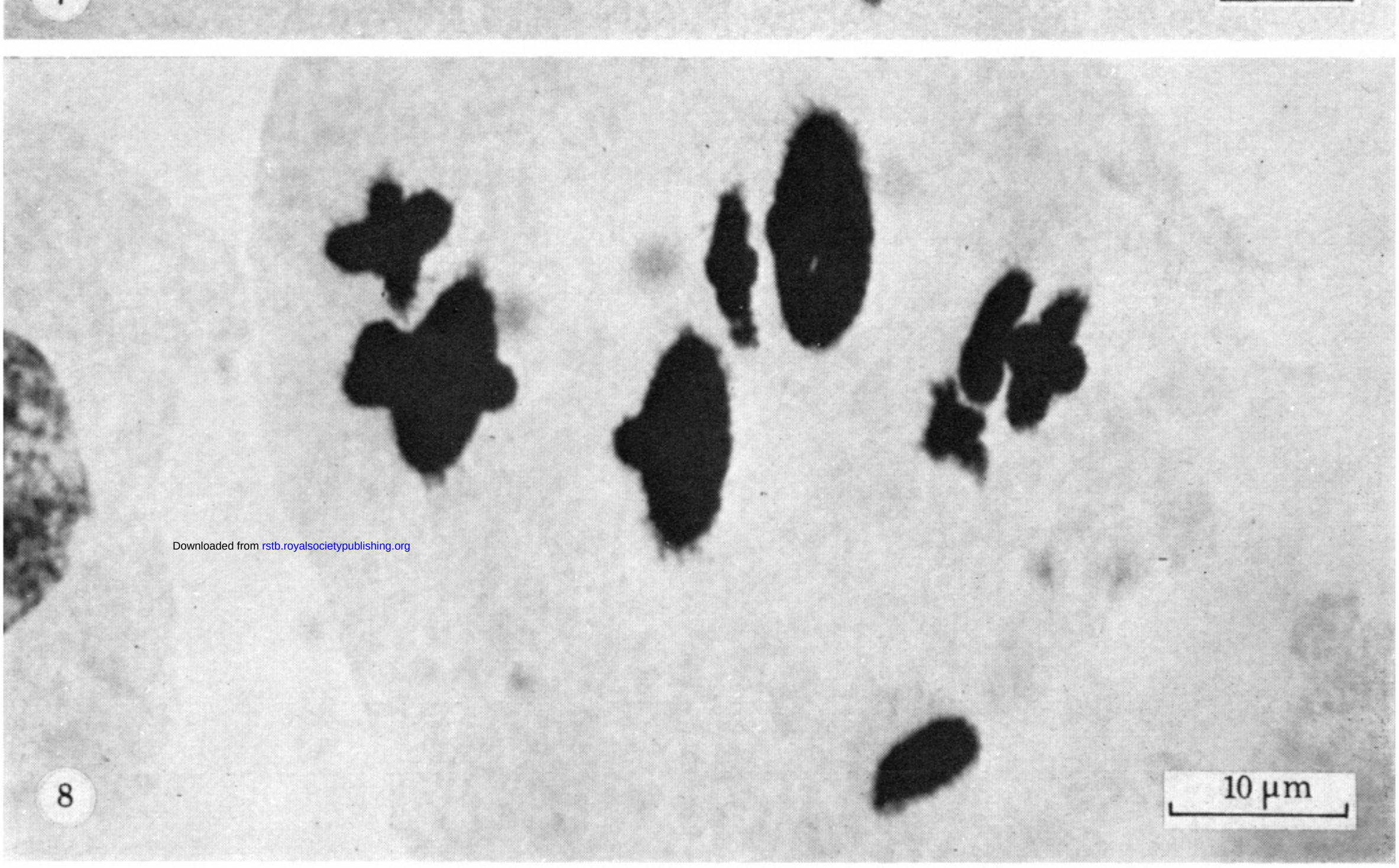

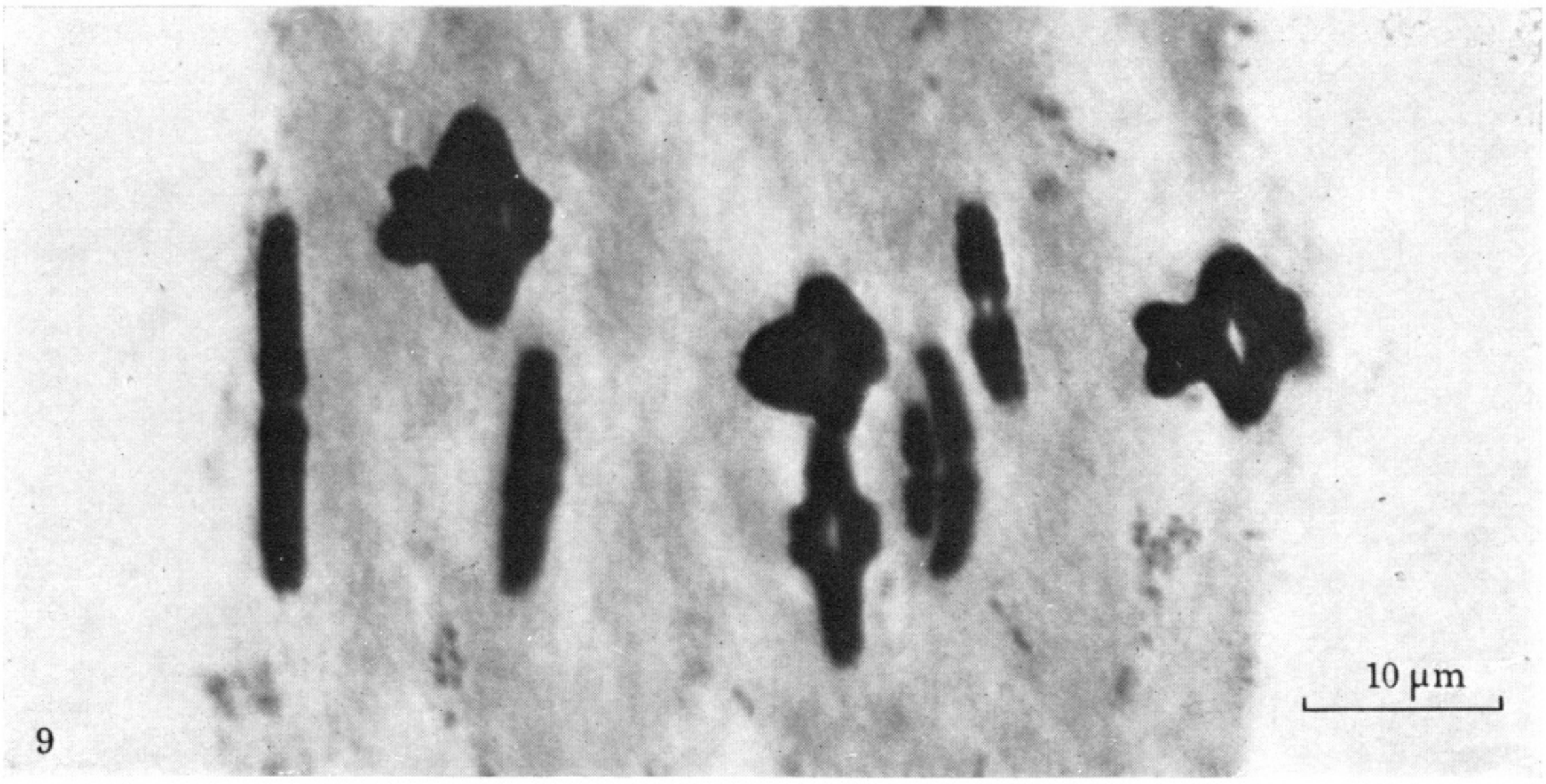

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FIGURES 6–9. For description see opposite.