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Transcription in the interbands of *Drosophila*

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[Plate 1]

Many interbands of *Drosophila* contain morphological evidence for transcription. Decondensed band material makes no detectable contribution to certain transcriptionally active interbands.

I have some evidence from electron microscopy of the polytene chromosomes in the nuclei of salivary glands of *Drosophila melanogaster* that transcription starts in, and may in some cases be confined exclusively to, the interbands. The possibility of interband transcription was suggested by Crick (1971).

In a typical puff (figure 1) one can see very large numbers of perichromatin granules, 35–40 nm in diameter. It is well known that these granules contain RNA (Bernhard 1969) and regions containing them are quite rapidly labelled with tritiated uridine (Lakhotia & Jacob 1974). The presence of these granules in puffs, in Balbiani rings, on lampbrush loops and in chromatin seems to be highly correlated with transcription. Although figure 1 is of a fairly large puff, there are numerous fragments of band material present. Fragments of uncondensed band material normally occur in both large and small puffs. In large puffs these frequently lose their lateral register one with another. A loss of lateral register, associated with an increase in volume of the puff, will contribute to the disappearance of the band in the light microscope as a puff develops.

In smaller puffs there are still large numbers of perichromatin granules but the band material is in lateral register (Skaer 1977).

In still smaller puffs (figure 2), which incidentally are very common, the perichromatin granules occur as a single row across the centre of a normal sized interband (arrowed). This interband is approximately 0.1 μm thick. On either side are unbroken bands. Although this is a normal sized interband it is possible that before it became transcriptionally active it was an exceptionally small interband; decondensation of band material, associated with transcriptional activity, might have changed the interband from a very small one to a normal sized one. The perichromatin granules, however, are arranged down the centre of the interband, and are not packed tightly against the band as might be expected if it were decondensed band material that was being transcribed.

Moreover, transcription products can be found in interbands so small that it is difficult to believe that decondensation of band material has contributed anything to the transcriptionally active interband. Figure 3 shows a fairly large puff (P); further down the chromosome are perichromatin granules in an interband (arrowed) that is only 50 nm or so wide. No interbands smaller than this, whether transcriptionally active or not, have been found by me or described in the literature.

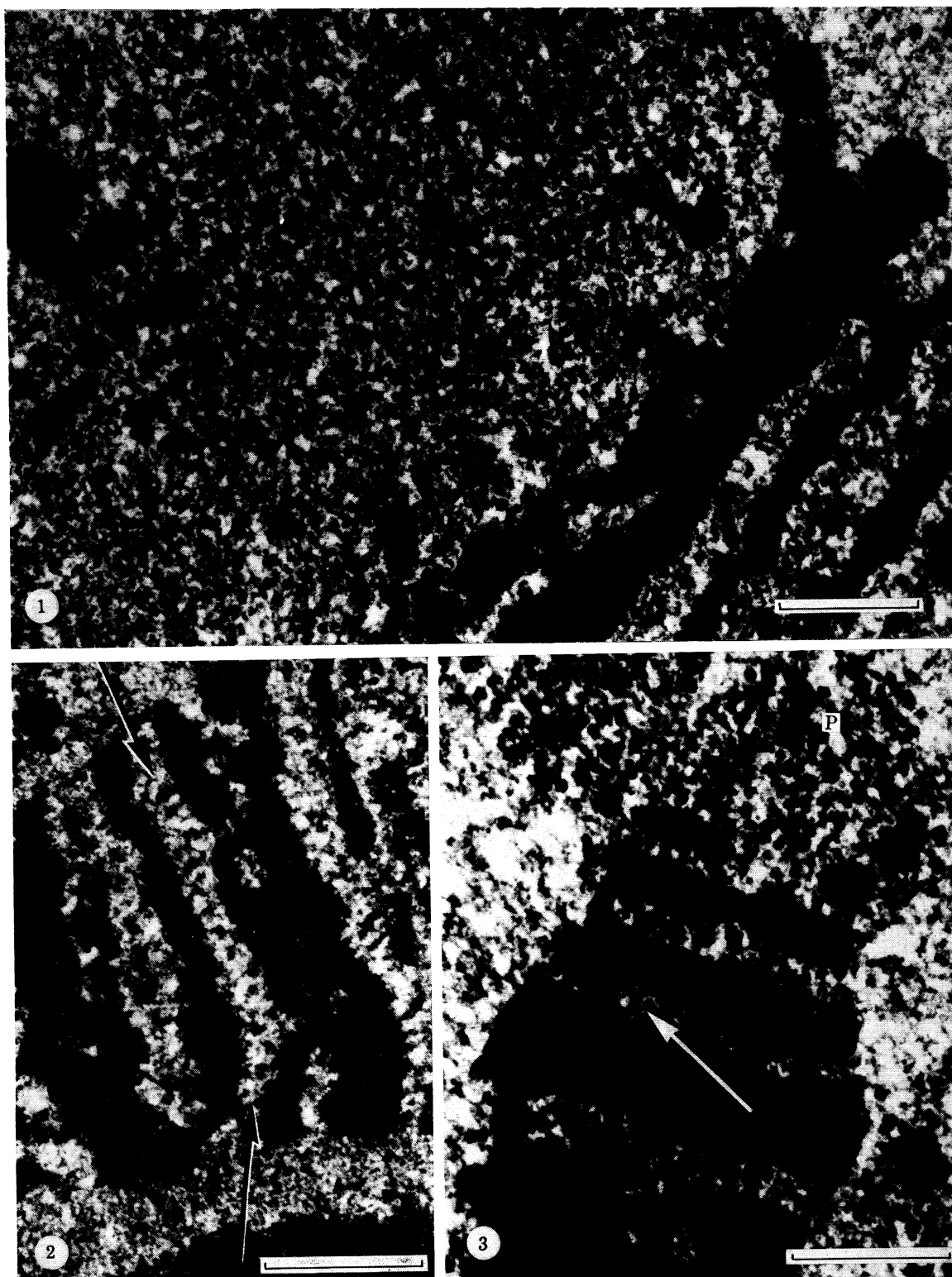
As can be seen in figure 3, interbands containing perichromatin transcription products are very common. Up to $\frac{1}{3}$ of all interbands in a nucleus contain perichromatin granules. This is a much greater number of transcriptionally active sites than the number of puffs seen in the light microscope, so only a few interbands can be developing into puffs that could be detected by that method. The number is also greater than the 500 or so regions that in the autoradiographic work of Pelling (1964) had grain counts significantly above background levels. These matters are dealt with in greater detail in Skaer (1977).

I should now like to speculate on the significance of the presence of pieces of condensed band material in even large puffs. Clearly it could be due to the spread of the puff to bands not involved in transcription. The band material, however, is fairly randomly scattered all over the puff (figure 1). Its existence raises the question of the contribution that band material makes during transcription. This is a particularly pertinent question coming after Daneholt's demonstration in this volume (Danaholt *et al.* 1978) that the transcription products in *Drosophila*, and particularly in the Balbiani rings of *Chironomus*, are very large. Whether even a giant 75S mRNA could come just from interband material remains to be discovered. It depends on how much DNA is accommodated in particular interbands. This is determined by the length of the chromatin fibres, and, as a measure of the DNA packing ratio, on their thickness, in known interbands.

If, and only if, there is no decondensation of band material during puffing do we need to postulate that the pattern of bands and interbands has to be strictly related to DNA sequences. We know that the pattern of bands and interbands is constant from tissue to tissue in *Drosophila* and *Chironomus* (Beermann 1972). On the other hand the pattern of chromomeres in interphase cells that are not polytene varies throughout the cell cycle by a complex pattern of fusion and decondensation. This has been shown, for example in mammalian cells (Röhme 1974), by premature chromosome condensation. The fact that the pattern in the polytene tissue of *Drosophila* is constant suggests that polytenization begins only at a very precise moment in the cell cycle. Since polytenization is characterized by DNA synthesis, the polytene pattern may be an S-phase pattern. If polytenization occurred at a different time in the cell cycle, the pattern would presumably be different. The pattern as it exists, happens to give, in those regions where it has been tested, what may be a 1:1 relation between units of the pattern and complementation groups.

If in addition to loss of lateral register during puffing, band decondensation also occurs, the DNA sequences transcribed may change as a puff develops. On such a view the precise placing of the interband in relation to particular DNA sequences that are to be transcribed would not necessarily be of crucial importance.

If a band decondenses to a position just beyond a particular DNA sequence that is to be transcribed, one would expect some band material to remain condensed even at maximum activity of the puff - except in those cases where the sequence was at the far distal end of the band. On the other hand, if a band can become decondensed and contains tandem sequences one would expect the quantity of condensed band material to be inversely related to transcriptional activity. I am at present attempting to study the quantity of band material in known puffs under varying conditions of stimulation.



In all figures the bar represents 0.5 μm .

FIGURE 1. Section through a large puff showing abundant perichromatin granules and condensed band material that has lost its lateral register across the chromosome.

FIGURE 2. Section showing an interband (arrowed) with perichromatin granules arranged as a single row across its centre. The structure at the bottom of the picture is part of the nucleolus.

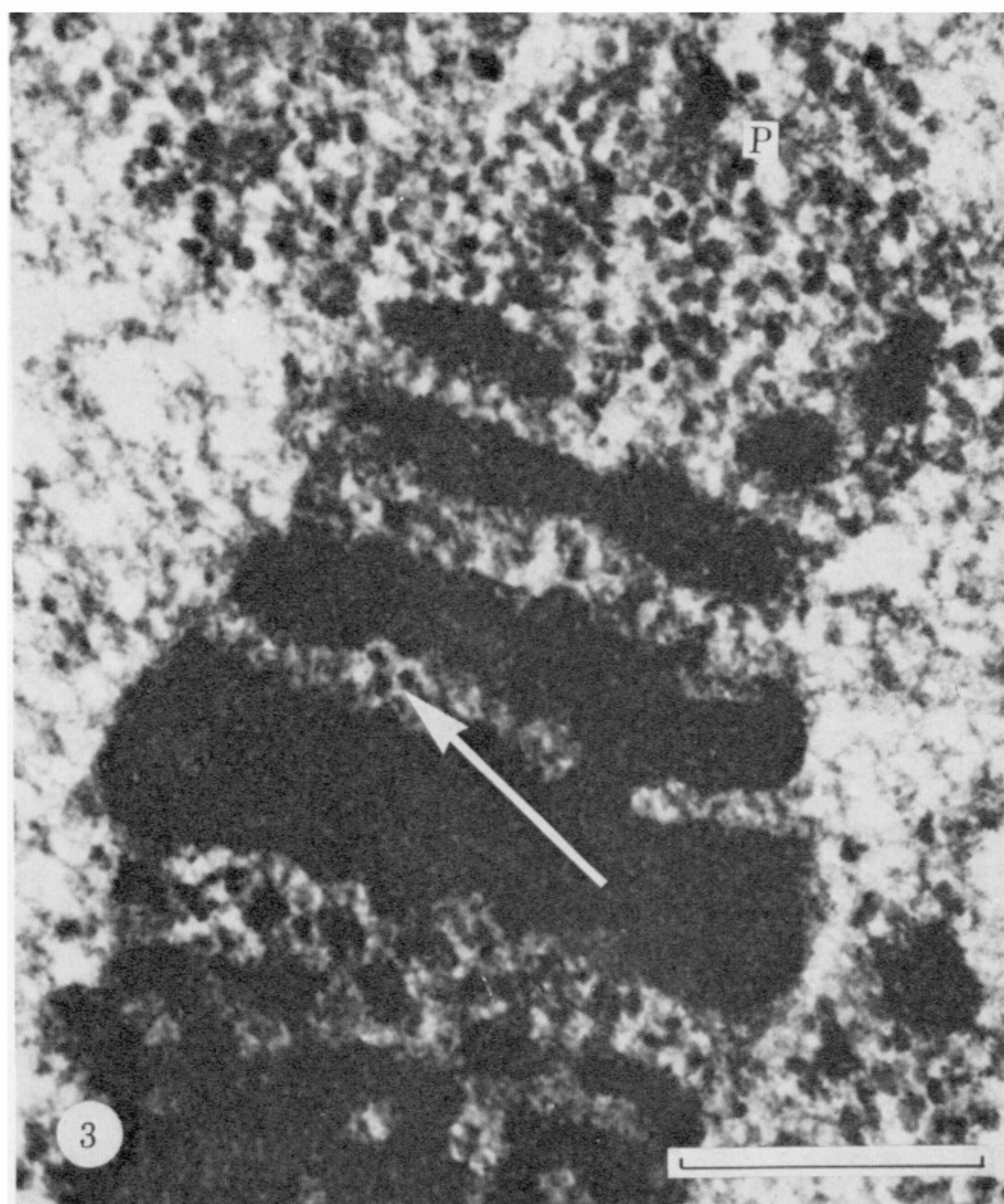
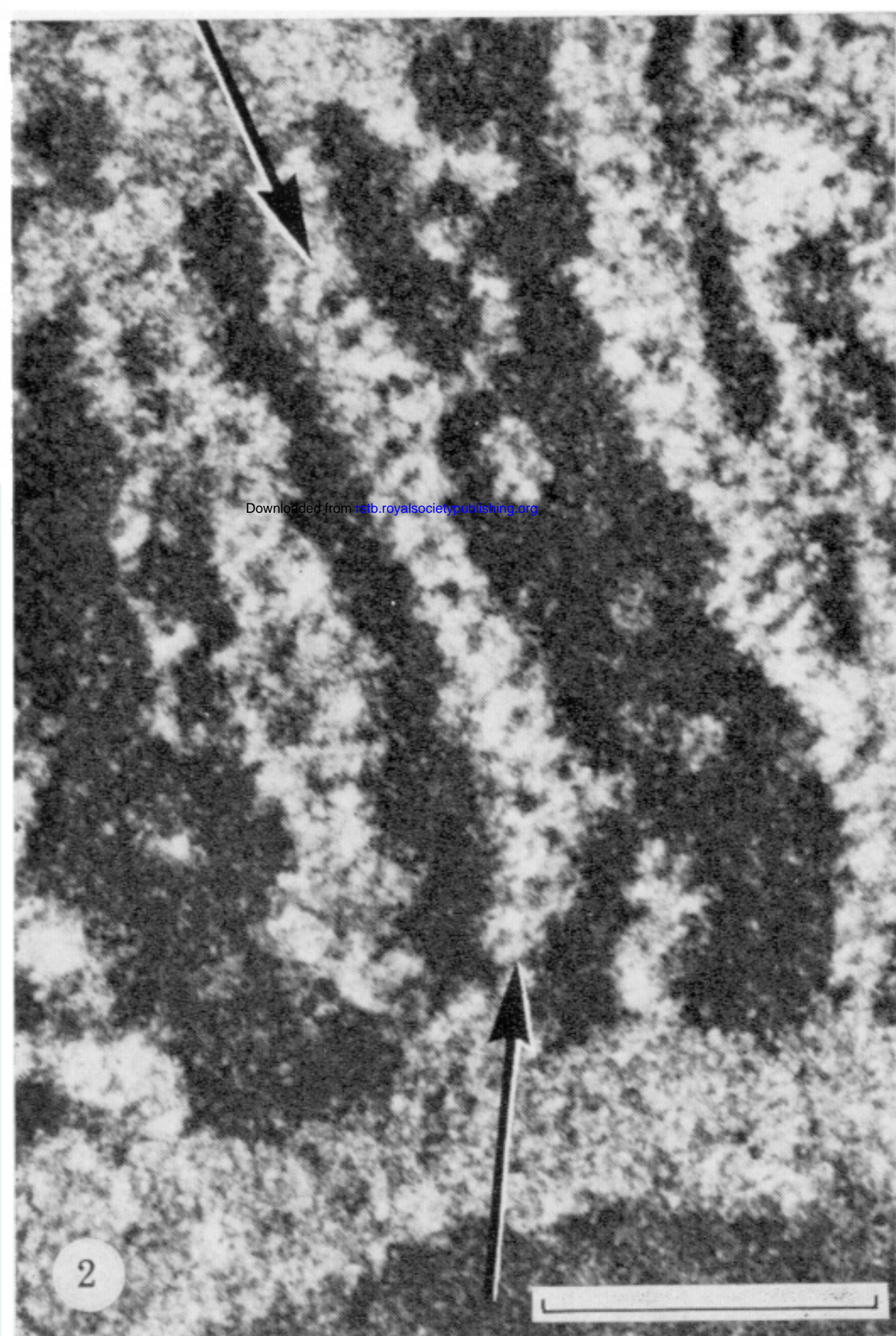
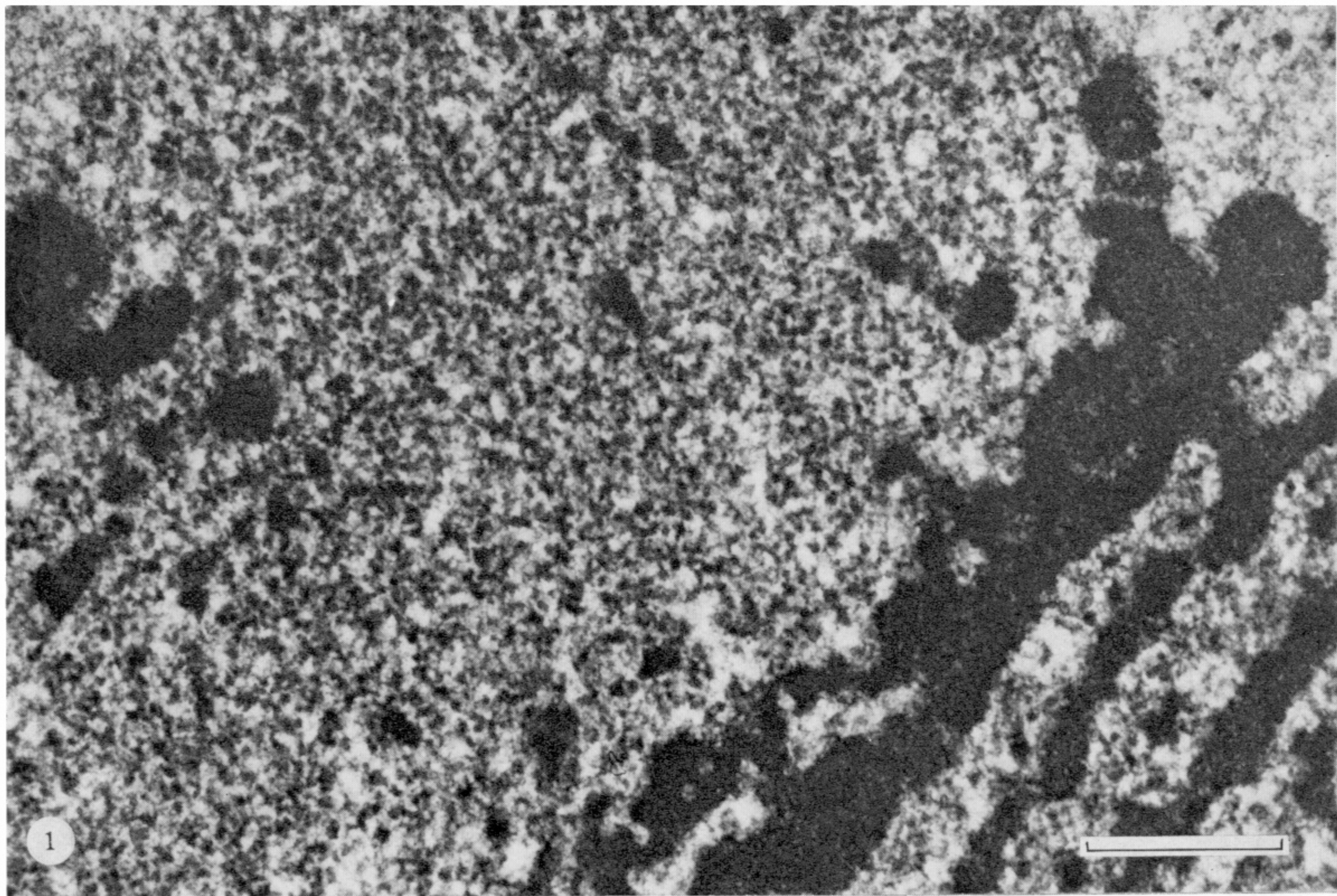
FIGURE 3. Longitudinal section through a length of chromosome showing perichromatin granules (arrowed) in a very narrow interband. A fairly large puff (P) is shown at the top of the picture; a small puff is shown in the interband below that with the arrow.

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