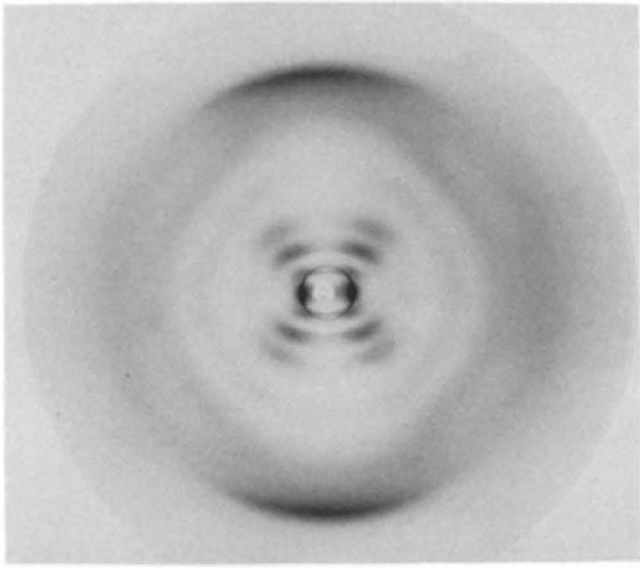

FIG. 4 Pattern of the highly concentrated DNA phase recorded on station D16 at LURE (Université Paris-Sud) using the synchrotron source at wavelength 0.1553 nm and a sample–film distance of 85 mm. The pattern is characteristic of DNA in the B form with a strong meridional arc at 0.333 nm (full width at half-maximum (FWHM) = 5×10^{-2} nm^{-1} and a double helix pitch of 3.33 nm). The strong equatorial reinforcement of the sharp arc (FWHM = 7×10^{-3} nm^{-1}; reticular spacing 2.57 nm) reveals the hexagonal lateral order with interhelix distances of 2.97 nm. A DNA concentration of ~380 mg ml^{-1} can be estimated from the interhelix spacing. To prepare the sample, a 250 mg ml^{-1} solution of 50-nm DNA molecules in 0.25 M ammonium acetate, 0.5 mM EDTA, 10 mM sodium cacodylate, pH 7.0, was allowed to slowly evaporate, and flow-aligned in a quartz-capillary of 1 mm diameter.

the capillary axis. In the inner part, the intensity is located on layers corresponding to the helix pitch periodicity (3.33 nm). The first three layers above the equatorial layer are the three most intense, the fourth one is missing. In the outer part, a strong meridional arc located at 0.333 nm is observed. Such a pattern is characteristic of B-DNA chains with ten base pairs per helix turn, oriented perpendicular to the helix axis and separated, on average, by 0.333 nm (refs 15 and 16). A sharp arc with a strong equatorial reinforcement is also present. This arc reveals a long-range periodic lateral arrangement of the DNA chains which characterizes a hexagonal lattice of parameter length 2.97 nm. Higher order reflections of the hexagonal lattice are barely visible, revealing a significant displacement of the molecules around their average position (~0.15 nm). A more ordered structure is observed for higher concentrations and revealed by the appearance of several additional reflections which become visible when the interhelix spacing reaches 2.8 nm. This value can be compared with the data of Franklin and Gosling[16] in which B-DNA fibres show interhelix spacings of 2.84 and 2.55 nm, attributed to the coexistence in the structure of two different hydration states. We never observed such a coexistence, although a progressive decrease of the interhelix spacing was apparent. This discrepancy could be attributed to the state of the specimen, which is mesophase rather than fibre. Complementary experiments, performed on samples whose textures were controlled optically, showed that the hexagonal parameter depends on the water concentration, with values ranging from 2.8 to 4.0 nm.

The longitudinal order of the DNA chains has been investigated with the SAXS station D24. The wavelength was 0.1608 nm and the sample-to-film distance was 1,850 mm. The film does not display any scattering maximum within the reticular range (7.5–7.0 nm), which thus excludes the possibility of a smectic-type layer arrangement.

The polyelectrolyte structure of DNA implies that water surrounds the whole area of the cylinder and the decrease in interhelix spacing with increasing polymer concentration agrees with the hypothesis of a hexagonal phase. The structure remains liquid crystalline for molecular separations of up to ~2.8 nm (that is ~0.6 nm greater than the DNA helix diameter). Our results are consistent with previous X-ray experiments on DNA samples of different origin[17,18]. In ψ-type DNA aggregates, which are short-range ordered structures, interhelix spacings were shown to be in the same range (2.92–4.38 nm)[19]. An ultimate degree of compaction of DNA is obtained when DNA is crystallized in the form of hexagonal platelets in which intermolecular distances are 2.76 nm (ref. 20) and 2.77 nm (ref. 21). Such structures present similarities with the dense packing of DNA that exists in virus capsids, where the DNA is also packed hexagonally with interdistances of 2.73–2.75 nm (ref. 22). However, in most biological structures the compaction of nucleic acids is not so great. In this case, the highly concentrated liquid-crystalline phase of DNA seems a more appropriate model than crystallized DNA to the understanding of *in vivo* DNA packing. For instance, the hexagonal order of the columnar phase can be compared with that in certain sperm heads[17,18,23]. The value of such comparisons has already been demonstrated in the case of the cholesteric phase[6]. The hexagonal structure of the highly concentrated phase of 50 nm DNA molecules is consistent with previous results with longer DNA molecules[11] and suggests that the nature of this phase does not depend on the length of the molecules. We can assume that extremely long molecules, such as those found *in vivo*, behave in the same way. □

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ERRATUM

Multiscale periodic structure in the Io wake

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