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THE QUESTION OF POLYPLOIDY IN THE SALMONIDAE

By

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With 3 Figures in the Text

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I. Introduction

Species within the *Salmonidae* fall into three cytological groups with, approximately, 60, 80 and 100 somatic chromosomes (see Table 1). This numerical sequence strongly suggests a polyploid series and SVÄRDSON (1945) has argued strongly in favour of a polyploid evolution. He suggests a basic haploid number of 10 for the group so that the Atlantic salmon, the brown trout and the grayling, for example, would be hexaploid, octaploid and decaploid respectively. In support of his case SVÄRDSON points out that the chromosome complements of the 60 group contain 6 metacentric chromosomes whereas those of the 80 group contain 8 metacentrics — exactly what would be expected in a polyploid series based on a haploid set of 10.

Table 1. *Chromosome numbers in the Salmonidae*

Species	2n	Author
Osmerus eperlanus (The Smelt)	58	SVÄRDSON, 1945
Salmo salar (Atlantic salmon)	60	SVÄRDSON, 1945
Salmo irideus (Rainbow Trout)	60	WRIGHT, 1955
Salmo clarki lewisi (Cut throat Trout) . . .	64	SIMON and DOLLAR, 1963
Salmo trutta (Brown and sea trout).	80	SVÄRDSON, 1945
Salmo alpinus (The Char)	80	SVÄRDSON, 1945
Salmo fontinalis (The Speckled Trout) . . .	84	SVÄRDSON, 1945
Coregonus lavaretus (The Gwyniad)	80	SVÄRDSON, 1945
Coregonus albula (The Small Gwyniad) . . .	80	SVÄRDSON, 1945
Thymallus thymallus (The Grayling)	102	SVÄRDSON, 1945

On the face of it there seems no good reason to question the polyploidy theory or for suggesting that the arithmetic series is fortuitous. There are however certain cytological observations described by SVÄRDSON himself which are difficult to reconcile with a chromosome evolution simply in terms of polyploidy. In particular two of the metacentric chromosomes in the Atlantic salmon (*S. salar*, $2n = 60$) are distinctly hook shaped and completely unlike any of the metacentrics found in the complement of the brown trout (*S. trutta*, $2n = 80$). While polyploidy

could explain the change in number it is clear that we have to invoke structural change to explain the change in form. Given, as seems certain, that structural change is involved the question then arises as to whether structural change, through "fusion" or "fragmentation", may not in itself explain the numerical as well as the morphological

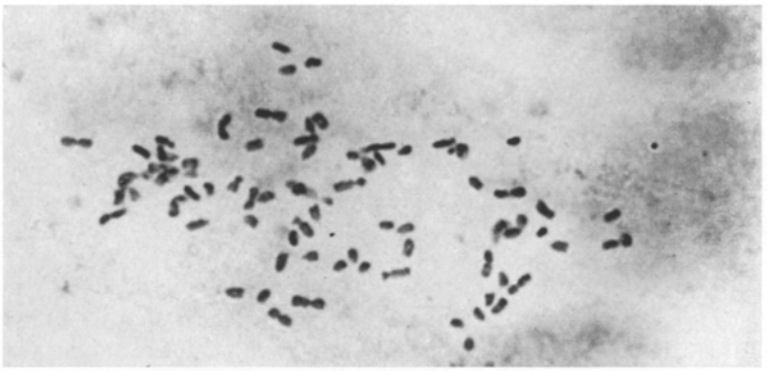

Fig. 1

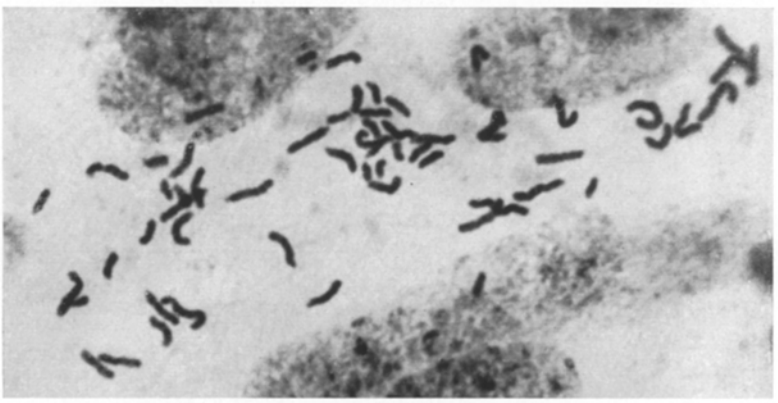

Fig. 2

Figs. 1 and 2. Mitotic metaphase in 1. *S. trutta* (sea trout), 2n = 80 and 2. *S. salar* (salmon), 2n = 60. × ca. 2250

variation in salmonoid chromosomes, to the exclusion, that is, of polyploidy.

One useful way of confirming whether or not the numerical series is indeed a polyploid series is to compare the nuclear *DNA* content of the different species. If it is we should expect an increase in *DNA* proportional to the increase in chromosome number. For example we should expect the nuclear *DNA* content to be one third greater in *S. trutta* (2n = 80) than in *S. salar* (2n = 60). The following is an account of the results of such comparisons and of their significance to the chromosome evolution of salmonoid species.

II. Materials and Methods

Embryos of three kinds were investigated. They were derived from eyed ova of salmon (*S. salar*), sea trout and brown trout (*S. trutta*) at 6 to $7^1/_2$ weeks after fertilisation.

For the counting and examination of chromosomes well spread mitotic metaphases were obtained following the immersion of embryos in 0.2% colchicine for 4 hours. The chromosomes were stained in propionic orcein.

DNA estimates in nuclei were made on an integrating microdensitometer following the Feulgen staining procedure of McLeish and Sunderland (1961).

III. Results

1. Chromosomes. The somatic complement of the salmon is 60, that of both brown trout and sea trout 80. The salmon chromosomes, as will be seen from Figs. 1 and 2, are very much larger than those of the trout. These observations with regard to both number and size completely confirm those of Svärdson (1945).

Table 2. *The mean DNA amounts (in arbitrary units) in 2C nuclei of S. salar (salmon) and S. trutta (brown trout and sea trout)*

Species	Replicate 1	Replicate 2
S. trutta		
Brown trout .	10.7 ± 0.26	10.4 ± 0.16
Sea trout . .	10.7 ± 0.15	10.4 ± 0.16
S. salar		
Salmon. . . .	10.8 ± 0.20	10.7 ± 0.22

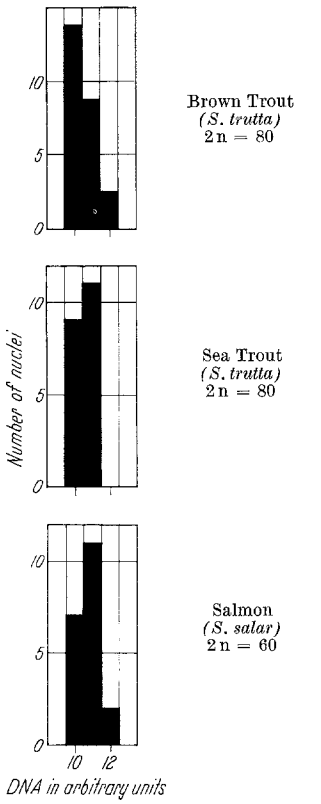

Fig. 3. The distributions of *DNA* values in 2 C nuclei. Data are from pooled replicates, twenty nuclei in each type

2. Nuclear DNA. In Table 2 are the *DNA* estimates in 2 *C* nuclei of trout and sea trout (*S. trutta*) and of the salmon (*S. salar*). The results are also plotted in Fig. 3. As will be seen there is excellent agreement between replicates. From these data it will also be observed that there is no significant variation between the two forms of *S. trutta*. Neither is there significant variation in *DNA* content between *S. trutta* and *S. salar*. The expectation, with polyploidy, of a one third increase in *DNA* in *S. trutta* as compared with *S. salar* is not realised.

That the *DNA* content is the same in the 60 and the 80 chromosome forms means, obviously, that the *DNA* per chromosome is greater in the

former than the latter. This, in fact, is precisely what might have been expected in view of the greater size of the salmon chromosomes. Rough estimates of *total* chromosome lengths give a ratio of 1,00 to 0,96 in salmon and trout nuclei respectively. The close similarity in *total* length indicates as one might expect that the *DNA* content is proportional to chromosome length. It means furthermore that the difference in the average size of salmon and trout chromosomes cannot be entirely due to genotypic control (cf. Svärdson *loc. cit.*). In part at least the size difference must reflect a difference in structure.

IV. Polyploidy versus Structural Change

The similarity in *DNA* amount in salmon and trout nuclei is difficult to reconcile with a polyploid evolution. In the vast majority of cases investigated nuclear *DNA* amount increases in proportion with increasing ploidy and if the 80 chromosome *S. trutta* were derived by the addition of two haploid sets of 10 from the 60 chromosome form we should certainly have expected a corresponding increase in *DNA*. The case for polyploidy can be sustained only by postulating a chromosomal diminution in *DNA* with increasing chromosome number. Convincing evidence in favour of such diminution is exceptional although it may well occur in rare instances (see Hughes-Schrader and Schrader 1956). Because of the differences in chromosome morphology one must, in any case, as has already been mentioned, invoke structural change in conjunction with polyploidy to explain satisfactorily the evolution of the 80 from the 60 chromosome type. Finally, with polyploidy, the very large difference between the salmon and the trout chromosomes must be attributed entirely to genotypic control in which case the approximate equality of total chromosome lengths in the two species must be regarded as nothing more than a coincidence.

In contrast to the "if and but" type of case in favour of polyploidy a very straight forward explanation based on "fusion" or "fragmentation" would appear to account completely for the cytological variation between these species. The case may be summarized as follows:

1. The nuclear *DNA* content is similar in both trout ($2n = 80$) and salmon ($2n = 60$). The amount per chromosome is consequently greater in the latter and, as would be expected, the salmon chromosomes are larger than those of the trout. Indeed the nuclear *DNA* amount is approximately proportional to total chromosome length which, it will be recalled, is much the same in the two species.

2. "Fusion" or "fragmentation" accounts for the change in number without appreciable change in chromosome length or in nuclear *DNA* content. This accounts perfectly for the equivalence both with regard to *DNA* amount and to total chromosome lengths in trout and salmon.

3. "Fusion" or "fragmentation" also accounts for the change in shape as well as in number that distinguish the chromosomes of the two species investigated. And here it is worth pointing out that there is very good evidence to show that fusion or fragmentation of this kind does indeed occur in other salmonoid species (SIMON and DOLLAR 1963).

Both the cytological and the cytochemical evidence are very satisfactorily explained by chromosome "fragmentation" or "fusion". While polyploidy is not completely ruled out by this evidence it would appear that polyploidy, at best, is unlikely.

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