ABSTRACT

The distribution and effects of the 1/29 translocation in cattle, defined with chromosome banding techniques, are described. Findings in different parts of the world are reported, and the origin of the translocation in some cases is explained. Geographical distribution as known at present reflects the areas in which chromosome investigations have been carried out rather than the true distribution. It is not known whether the occurrence of the 1/29 translocation in different geographical areas and breeds is due to recurrent mutation or distribution of an ancient mutation, but many observations point to the latter.

Although direct observations of an increased embryonic mortality are lacking, reduced fertility of males and females heterozygous for 1/29 is established. No correlations of the 1/29 translocation with other characteristics have been found, and variability in incidence between different populations is probably due to genetic drift. The importance in animal breeding of introducing eradication programs is emphasized, and it is stressed that cattle populations using artificial insemination should undergo routine cytogenetic investigations.

INTRODUCTION

Chromosome studies of domestic animals applying modern techniques have been in effect for 20 yr. Since the introduction of new staining techniques, the normal cattle karyotype of 58 telo- or acrocentric autosomes and two submetacentric sex chromosomes is well known even in its minor details. For a variety of reasons, however, few chromosome aberrations have been found hitherto (85). The overwhelming preponderance of aberrations so far are translocations of Robertsonian or centric fusion type, and the best known of these is the 1/29 translocation.

The first description of 1/29 originated from the Swedish Red and White cattle breed (SRB) in 1964 (43) and was followed in 1966 with an investigation of the general dairy cattle population of Sweden (28). That same year, the translocation was described in Norway (2), in the USA (54), and in the late sixties also in Italy (94, 95) and West Germany (93). In the seventies, findings of the 1/29 have been reported in several countries and various cattle breeds all over the world.

CYTOLOGICAL DEFINITION

OF THE 1/29 TRANSLOCATION

The 1/29 Robertsonian or centric fusion translocation (Fig. 1) is the result of a "fusion" in the centromere region of two autosomes, 1 and presumably 29, when the autosomes are arranged in decreasing size (29). The somatic chromosome number consequently is reduced from 60 to 59 in the heterozygous and from 60 to 58 in the homozygous condition. For similar translocations in other breeds and countries, the same conclusions about the cytological origin were drawn either subjectively or after measuring the chromosomes (6, 13, 78).

For many years the cytological origin of 1/29 remained unknown; even the application of autoradiographic techniques (31, 45) failed to provide the necessary information. The introduction of the Q-banding technique (44) was of little help to identification (Fig. 2A) and the G-banding technique (6, 44, 61, 69) was only successful with top quality preparations (Fig. 2B). However, with the application of T- and R-banding (40, 44), conclusions at last could be definite (Fig. 2C, D). The 1/29 translocation also was characterized by having a single centromeric block (Fig. 2E) of C-banded constitutive heterochromatin (6, 44,
Although chromosome homologies of the various cases of 1/29 described have been established with the help of banding patterns only in a few instances, it is presumed that most of the 1/29 translocations described in the literature have the same cytological origin.

**DISTRIBUTION**

Despite reports of a number of the 1/29 translocation in the literature, little is known about its geographical distribution. As foreseen by me as early as 1970 (30), the translocation appears to have world-wide distribution (Table 1). It has been described in roughly 30 different breeds, particularly the European ones, but I presume that these descriptions reflect the areas in which cattle chromosomes have been investigated (Fig. 3) rather than give an accurate picture of the true distribution of 1/29. The findings have been summarized in (35, 36, 85, 88).

The international trade in cattle provides one explanation for many of the cases described in different countries. Exports from Sweden have spread 1/29 at least to Norway (1) and Hungary (41) and probably also to Czechoslovakia (65). In several countries, many of the breeds have been imported not for the improvement of the native cattle breeds but for the establishment of the breed(s) in question in the importing country. Such breeds are Simmental, Swiss Brown, Charolais, Aquitaine Blond, and others. There are also a few cases of 1/29 described in non-European breeds such as Siamese cattle (21), Brown Atlas (22), Kuri (76, 90), Baoulé (85), and crosses between N'Dama and Zebu (87).

Since cytogenetic analysis is a laborious process, little is known of the incidence of the 1/29 translocation in different cattle populations (Table 2). The most accurate and unbiased estimations of incidence are probably those concerning the British White (not included in Table 2), the Hungarian Grey, the Swedish Red and White, and the Norwegian Red cattle breeds. This is due to the fact that
the British White and the Hungarian Grey are numerically small breeds comprising just 495 (18) and 1200 (58) cattle at the time of cytogenetic investigations and all or most of the AI (artificial insemination) bulls of the Swedish Red and White (34, 38) and the Norwegian Red (1) are cytogenetically known. Although only a few animals of the Italian breed Romagna have been investigated, the incidence of 1/29 appears high among them (71). There are great variabilities in incidence not only between breeds but also within breed in different parts of the same country. Thus, Harvey (53) found that in seven breeds demonstrating 1/29 in Great Britain, there was a variability in incidence between .5 and 20%. Variability was similar in French breeds (82), and in southwestern France (90) Aquitaine Blond demonstrated an incidence of 21% which appeared to be considerably higher than the incidence in other parts of the country (82).

**OCCURRENCE IN DIFFERENT BREEDS: RECURRENT MUTATION OR A COMMON ORIGIN?**

The occurrence of 1/29 in different breeds and countries can be explained by recurrent mutation or distribution of an ancient mutation, but in neither case is there any definite proof. In spite of some indications to that effect (3), no proven case of de novo formation of 1/29 has been described, and in all cases in which ancestors and progenies can be traced, hereditary patterns have been found. Nor has the formation of 1/29 in vitro been described (e.g. 73). It is true that at the interphase of mitosis (29) and meiosis (68) there are centromere associations of nonhomologous chromosomes. However, there is still no conclusive explanation for these associations; it has been assumed that they result from the nonrandom pairing of centromeres with similar DNA sequences (9). Hybridization experiments with

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**FIG. 2.** Various staining techniques (5, 10, 13, 14, 94, 100) applied to the 1/29 translocation and its homologues. Most often chromosome 29 cannot be recognized with certainty in the Q-banded (A) and G-banded (B) karyotypes. With the application of the T-banding (C) and R-banding (D) techniques, definite identification is possible. The 1/29 translocation demonstrates a single structure of the centromere region by T-banding (C) and C-banding (E), and the translocation, and its homologues have no nucleolar organizing regions as revealed by the Ag-As technique (F).
TABLE 1. Distribution of the 1/29 translocation according to geographical area and breed (67).

<table>
<thead>
<tr>
<th>Geographical area</th>
<th>Breed(s)</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australia</td>
<td>Red Poll</td>
<td>24</td>
</tr>
<tr>
<td>Austria</td>
<td>Austrian Simmental (?)</td>
<td>68</td>
</tr>
<tr>
<td>Brazil</td>
<td>Charolais</td>
<td>72</td>
</tr>
<tr>
<td>Canada</td>
<td>Guernsey</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Simmental</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>Charolais</td>
<td>47</td>
</tr>
<tr>
<td>Chad (?)</td>
<td>Kuri</td>
<td>76, 90</td>
</tr>
<tr>
<td>Cuba</td>
<td>Holstein-Friesian × Criollo</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Santa Gertrudis</td>
<td>4</td>
</tr>
<tr>
<td>Czechoslovakia</td>
<td>Czechoslovakian Red Pied</td>
<td>65</td>
</tr>
<tr>
<td>France</td>
<td>Charolais</td>
<td>23, 79, 90</td>
</tr>
<tr>
<td></td>
<td>Limousin</td>
<td>14, 88, 90</td>
</tr>
<tr>
<td></td>
<td>Aquitaine Blond</td>
<td>88, 90</td>
</tr>
<tr>
<td></td>
<td>Montbeliard</td>
<td>78, 79</td>
</tr>
<tr>
<td></td>
<td>Vosges</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>Gascony</td>
<td>90</td>
</tr>
<tr>
<td>Great Britain</td>
<td>Charolais</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>Limousin, Simmental</td>
<td>49, 50</td>
</tr>
<tr>
<td></td>
<td>Red Poll</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>British White</td>
<td>18</td>
</tr>
<tr>
<td>Hungary</td>
<td>Hungarian Simmental, German Simmental</td>
<td>59, 75</td>
</tr>
<tr>
<td></td>
<td>Hungarian Grey</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Swedish Red and White</td>
<td>41</td>
</tr>
<tr>
<td>Italy</td>
<td>Romagna</td>
<td>71, 94, 95, 103</td>
</tr>
<tr>
<td></td>
<td>Chiana, Marche, Modica</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>Pisa</td>
<td>96</td>
</tr>
<tr>
<td></td>
<td>Swiss Brown</td>
<td>27</td>
</tr>
<tr>
<td>Ivory Coast</td>
<td>Baoulé</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>Zebu × N’Dama</td>
<td>87</td>
</tr>
<tr>
<td>Morocco</td>
<td>Brown Atlas</td>
<td>22</td>
</tr>
<tr>
<td>New Zealand</td>
<td>Aquitaine Blond</td>
<td>10</td>
</tr>
<tr>
<td>Norway</td>
<td>Norwegian Red</td>
<td>1, 2</td>
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<tr>
<td>Poland</td>
<td>Charolais, Polish Red</td>
<td>107</td>
</tr>
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<td>Romania</td>
<td>Charolais</td>
<td>62, 97</td>
</tr>
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<td>Sweden</td>
<td>Swedish Red and White</td>
<td>28, 29, 34</td>
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<tr>
<td>Switzerland</td>
<td>Simmental</td>
<td>89, 108</td>
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<tr>
<td>Thailand</td>
<td>Siamese</td>
<td>21</td>
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<tr>
<td>USA</td>
<td>Holstein-Friesian</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>American Brown Swiss</td>
<td>6, 19</td>
</tr>
<tr>
<td>USSR</td>
<td>Russian Black Pied (?)</td>
<td>26</td>
</tr>
<tr>
<td>West Germany</td>
<td>German Red Pied</td>
<td>93</td>
</tr>
<tr>
<td></td>
<td>Simmental</td>
<td>55</td>
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<tr>
<td></td>
<td>Brown Mountain</td>
<td>100, 102</td>
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<tr>
<td></td>
<td>Chiana</td>
<td>56</td>
</tr>
<tr>
<td>Yugoslavia</td>
<td>Simmental</td>
<td>104</td>
</tr>
</tbody>
</table>

different DNA satellites have not demonstrated any distinctive properties for chromosome 1, while the presumptive chromosome 29 demonstrated an absence of satellites III and IV (60, 66). Nor do chromosomes 1 and 29 organize common nucleoli (Fig. 2F). As far as we know, there is no increased cytological risk that chromosomes 1 and 29 will undergo centric fusion, a conclusion which also is supported strongly by evolutionary evidence (11).

Since the 1/29 translocation appears to be more common in beef than in dairy cattle (77) and beef cattle carrying the 1/29 originate from central Europe, it has been proposed that all cases derive from a common stock (49). Such a theory finds support in the complete or almost complete absence (Tables 1 and 2) of the translocation in breeds such as Hereford.
and Holstein-Friesian. If the theory of a monophyletic origin is valid, there are observations in more primitive breeds pointing to an ancient origin. Some of the latter cases may be explained by crossing with modern breeds. Such is the case of the Hungarian Grey, into which chromosome material was introduced, particularly from the Romagna and the Maremma (58), and the Brown Atlas into which chromosome material has been introduced from several French breeds. Maybe future studies on the occurrence in karyotypes of other bovines of chromosomes similar to 1/29 can adduce support to the theory of an ancient origin. Some people (e.g. 74) also consider the monocentric appearance of a centromere to be indicative of an ancient origin.

**PHENOTYPIC EFFECTS**

In the meiosis of the heterozygous carrier, the translocation and its homologues build up a (hetero)trivalent, and the segregation, which is dependent on factors such as the relative size of the chromosomes, the location of centromeres and chiasmata, proceeds in a fairly regular way with the production of chromosomally balanced gametes. The 1/29 appears to be inherited in Mendelian fashion; half of the offspring become normal while the other half are balanced carriers (1, 5, 6, 19, 50, 101). Nevertheless, it is presumed that to a certain degree the heterotrivalent segregates nondisjunctionally at the first meiotic division (39, 63, 64), but direct evidence of this in the form of unbalanced gametes (25) or embryos is lacking.

There are, however, convincing indirect proofs of the occurrence of cytogenetically unbalanced zygotes which give the heterozygous carriers reduced fertility. In the investigation of the Swedish Red and White cattle breed, encompassing several thousand female offspring of translocation heterozygous bulls, a 3% reduced fertility for the 56-day nonreturn and 6% for the 273-day nonreturn could be demonstrated as being attributable to an increased embryonic mortality (29). The observation of a reduced fertility in daughters of bulls with 1/29 was supported fully by an investigation of daughters of five heterozygous bulls of the Norwegian Red cattle breed (91). The daughter groups, comprising a total of

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FIG. 3. Geographical distribution of the 1/29 translocation. The black points indicate the findings of 1/29 reported in the literature. (For the details see Table 1.)
<table>
<thead>
<tr>
<th>Geographical area</th>
<th>Breed</th>
<th>No. of cattle investigated</th>
<th>No. of translocation carriers</th>
<th>% 1/29</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australia</td>
<td>Holstein-Friesian</td>
<td>174</td>
<td>0</td>
<td>0</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>Hereford</td>
<td>602</td>
<td>0</td>
<td>0</td>
<td>46</td>
</tr>
<tr>
<td>France</td>
<td>Limousin</td>
<td>231</td>
<td>13</td>
<td>5.6</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Aquitaine Blond</td>
<td>228</td>
<td>47</td>
<td>20.6</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Normandy</td>
<td>249</td>
<td>0</td>
<td>0</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>Limousin</td>
<td>124</td>
<td>6</td>
<td>4.8</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>Charolais</td>
<td>314</td>
<td>12</td>
<td>3.8</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>F.F.P.N.</td>
<td>215</td>
<td>0</td>
<td>0</td>
<td>82</td>
</tr>
<tr>
<td>Great Britain</td>
<td>Holstein-Friesian</td>
<td>586</td>
<td>0</td>
<td>0</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Charolais</td>
<td>185</td>
<td>1</td>
<td>.5</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Simmental</td>
<td>113</td>
<td>3</td>
<td>2.7</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Holstein-Friesian</td>
<td>330</td>
<td>0</td>
<td>0</td>
<td>77</td>
</tr>
<tr>
<td>Hungary</td>
<td>Hungarian Grey</td>
<td>106</td>
<td>4</td>
<td>3.8</td>
<td>59</td>
</tr>
<tr>
<td>Italy</td>
<td>Romagna</td>
<td>122</td>
<td>39</td>
<td>32.0</td>
<td>71</td>
</tr>
<tr>
<td>Norway</td>
<td>Norwegian Red</td>
<td>430</td>
<td>18</td>
<td>4.2</td>
<td>1</td>
</tr>
<tr>
<td>Sweden</td>
<td>Swedish Red and White</td>
<td>944</td>
<td>120</td>
<td>12.4</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Swedish Holstein-Friesian</td>
<td>1173</td>
<td>164</td>
<td>14.3</td>
<td>29</td>
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<tr>
<td>Switzerland</td>
<td>Simmental</td>
<td>654</td>
<td>21</td>
<td>3.2</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td>Swiss Brown</td>
<td>430</td>
<td>1</td>
<td>.2</td>
<td>108</td>
</tr>
<tr>
<td>USA</td>
<td>Holstein-Friesian</td>
<td>743</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>American Brown Swiss</td>
<td>224</td>
<td>3</td>
<td>1.3</td>
<td>19</td>
</tr>
<tr>
<td>West Germany</td>
<td>German Simmental</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>56</td>
</tr>
</tbody>
</table>
21,212 head, were compared with a control population of 610,714 animals. There was a rapid, statistically significant increase in the nonreturn percentage from 0 to 30 to 60 to 90 days, indicating that most of the embryonic loss occurred in this period.

The reduced fertility in females of the Swedish Red and White cattle breed is reflected in increased culling rates (32) and the incidence of 1/29 in repeat breeders of both the Swedish Red and White (33) and the Norwegian Red cattle (92) are higher than expected. The first investigation of bulls heterozygous for the 1/29 translocation failed to demonstrate any reduced fertility (29). This was presumed to be due to the fact that the bulls investigated had been selected according to fertility. Subsequently, therefore, 67 unselected bulls, 45 of them chromosomally normal and 12 carrying the 1/29 translocation, were investigated concerning sexual functions, semen characteristics, and fertility (17, 37). Translocation bulls demonstrated reduced fertility. The true reduction due to the 1/29 translocation was estimated 3.0 to 3.5% for the 28-day nonreturn and 4.5% for the 56-day nonreturn. The deviations were statistically significant at .99%.

There is convincing information attesting to a reduced fertility in cattle heterozygous for 1/29. For these conclusions, it has been necessary to investigate large numbers of cattle. Furthermore, as has been pointed out on several occasions (6, 52), it is also necessary to investigate animals not selected according to fertility. Consequently, no conclusions about fertility can be drawn from restricted materials (56, 70, 109), and the annotation often given “no reduced fertility” regarding a few selected animals (e.g. 103) is of no use and should be disregarded.

No correlation has been found between 1/29 and other characteristics in artificial selection (29), and a correlation with high meat production (14) later was shown to be coincidental (90). Any relationship between 1/29 possession and increased milk production (1, 109), three-colored exterior (93), sterility (1, 2), leukemia (43), crooked forelegs (23), hydrocephalus, and spina bifida (55) is probably coincidental, or if any connection exists, it must be tenuous (29).

**POPULATION DYNAMICS**

The mere occurrence of 1/29 in different breeds and countries easily can be explained by recurrent mutation or a common ancient origin, but these causes alone hardly can explain the extensive distribution in some breeds. For well-defined characteristics in artificial selection, possession of the translocation is of no advantage (1, 29). Nor has it been possible to ascertain what the translocation signifies in natural selection. Some advantage in selection when the translocation first appeared (36) is reasonable. It is possible that artificial selection was capable of reducing those subtle adaptations which resulted from changes in chromosomes, but with the introduction of artificial insemination, the population structure was changed radically, and random factors became increasingly capable of influencing population dynamics. By extensive use in an AI association of a few bulls which often have different reproductive capacities, the effective population becomes small. Since the 1/29 translocation acts more or less as a neutral character, its incidence is influenced greatly by chance variations. The ability of random factors to influence the population structure is exemplified in the British White breed consisting of 495 specimens at the time of investigation in which the incidence of 1/29 had increased to 60% (18). The same chance factors are at work in other populations; with decreasing size of the effective population, the importance of chance factors will increase. This apparently explains some variabilities mentioned above.

**ERADICATIONAL WORK AND ITS IMPORTANCE IN CATTLE BREEDING**

The importance of introducing eradication programs in cattle breeding has been demonstrated clearly for the Swedish Red and White cattle breed. Since the translocation meant an annual loss of approximately 2 million Swedish crowns (30) for Swedish agriculture, measures to eliminate the translocation and prevent its spread were taken soon after discovery (38, 57, 106). All bulls with 1/29 were eliminated from AI, and it was decided that only bull calves free from 1/29 should be recruited. The cytogenetic analysis of the Swedish AI population was started at the end of 1969 (34), and since that time all SRB bull calves are investigated before being recruited to AI (38). In this eradication program more than 2600 bulls have so far been checked and approximately 6000 SRB cattle have been investigated since 1963, which makes
the Swedish Red and White breed most thoroughly investigated, accounting for one-third of all cattle hitherto investigated in the world (87) cytogenetically.

The introduction of an eradication program for AI bulls carrying the 1/29 translocation soon was reflected in increasing fertility for the entire SRB population of Sweden (106). For several years the fertility of SRB had been declining and for the 3 yr prior to the introduction of the eradication program the decrease had been 1%. For the next 3 yr (after the program was introduced) fertility increased by .5%, and this increasing tendency still prevails.

Routine investigations are now the rule in several other countries, including Norway, Great Britain (51, 52, 77), France (82), Hungary (59, 75), and West Germany (100). Most often they are voluntary by AI stations and several other countries, including Norway, Great Britain (51, 52, 77), France (82), Hungary (59, 75), and West Germany (100). Most often they are voluntary by AI stations and sometimes also are under national auspices (65). Some countries, such as Australia, have imposed restrictions on breed societies (53) but sometimes also are voluntary. For AI bulls carrying the 1/29 translocation the decrease by .5%, and this increasing tendency still prevails.

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