Secular Changes of Twinning Rates in Nordic Populations[*]

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INTRODUCTION

In each species, natural selection has resulted in an optimal litter size, to ensure the largest average number of surviving offspring and the lowest maternal mortality. The terrestrial insectivores from which the primates evolved had large litters. It has been argued that in primates adaptation to an arboreal mode of life led to a reduction of litter size to a single offspring because of the difficulty of producing and caring for a large litter in a tree [6]. A recent critical survey of the literature indicates that twinning frequency in most nonhuman primates is lower than in man [20].

There are clear ethnogeographic differences in the incidence of human twinning. Among peoples of Eastern Asia, multiple maternities are rare; in Japan for instance, the twinning rate is only 3-7 per mill, according both to the official statistics and hospital records. These low rates seem not to be caused by the facts that it is customary in Japan to have children very early in life or that twin births were at one time viewed with displeasure and concealed, or sometimes twins were even killed in some areas [21].

In hospital series among some Negro tribes almost 10 times higher twinning frequencies than among Japanese have been reported e.g. the Yorubas in western Nigeria with values above 60 per mill [24]. However, where national birth statistics of Blacks are available, twinning is lower, e.g. in U.S.A. 13-15 per mill [1].

The twinning rate seems to be low among the ancient European populations – Saamis and Basques. In Europe there is a progressive decrease in incidence of twinning from North to South, reaching minimum values on the Iberian Peninsula [6]. By European standards the twinning rate is low among the Latins, medium among the Slavs and rela-

tively high among the Germanic peoples, particularly among the Nordic peoples, including the Finns. It is of interest to note that populations of different origin such as Scandinavians, Finns, Estonians, and Latvians in and around the Baltic Sea basin, all seem to have had high twinning rates [13]. The Finns have a considerable amount of "eastern", non-European, ancestry that has been estimated at 25 to 30%. Some insular isolates in the Baltic Sea – where eastern (Finno-Ugric) and western (Scandinavian) genes meet (Åland and Åboland archipelago, Gotland) – have had some of the highest rates of twin and triplet maternities among Whites [13, 16].

Partly unexplained secular changes in rates of multiple maternities have occurred in Sweden and Finland [9-10, 13-16]. Trends over shorter periods of time have been described from Denmark [25, 27, 30, 31]. High frequencies of twinning have been reported in isolated Norwegian peasant families [4].

Unexplained worldwide changes have occurred in the pattern of twinning in recent decades [8, 22]. To gain a proper perspective, these variations in multiple maternities should be seen in their historical context. The majority of studies have neglected the longitudinal view, and most studies are limited to looking only at the last few decades. The only truly secular series on twinning outside Fennoscandia are the 110 years series based on Italian data [28] and the 130 years series from Australia [7]. In Nordic countries some long term studies have been conducted dating back to the middle of the 17th century [9-10, 13-14].

No constant pattern can be seen in the temporal changes of the twinning rate. Most countries show a marked decline in the incidence of twin maternities at various times during the last 2 generations. Where zygosity can be ascertained the downward trend has been attributed to the fall in the dizygotic (non identical) twinning rate (DZTR). The monozygotic (identical) twinning rate (MZTR) has up to recently been remarkably constant (around 3.5 per mill). However, during the last decades almost all northwestern European populations demonstrate an unexpected increase in MZTR [5]. The etiology of MZ twinning is unclear. There is an excess of congenital malformations in twins. There is no agreement on whether this is entirely due to their increased incidence in MZ twins [2]. However, since MZ twinning can itself be regarded as a developmental "malformation", an unexplained increase in incidence requires further investigation. The increased incidence is not necessarily due to a malign influence (as toxic or teratogenic substances, pelvic infection diseases and oral contraceptives). The apparent increase of MZTR may also be caused by an artefact from a defect in Weinberg's differentiation method or – at least in some countries – a reflection of changes in registration or of improved maternal health and a consequent decline in spontaneous abortions and perinatal deaths.

For Italy it has been shown that the decline in twinning rate cannot be explained by changes in maternal age or parity alone [17, 22, 28]. In other words, the decline was intrinsic to twinning; the decline was real. By using different standardization methods, it was noted that, irrespective of standardization method, changes in maternal age alone cannot explain temporal or regional variations in the twinning rate [14, 17-18].

The purpose of this study is to compare the temporal changes of twinning rates in Nordic populations and to elucidate to what degree longitudinal variations can be explained by changes in population structure, maternal age and/or parity.

MATERIAL AND METHODS

The oldest continuous population statistics for a whole nation are in Sweden and Finland. The Church archives with details on births, including twins or higher multiple maternities, started as early as the 17th century [13]. From the national statistical offices in Nordic countries we have obtained numbers of multiple and total maternities. The numbers for Finland for the 18th century were collected from Wargentin's tables and for the 19th century from partly unpublished sources (Prosterilängder 1841-1860). Attempts have been made to get numbers of like-sexed and unlike-sexed pairs of twins as well as numbers of live- and still-born, children. Using Weinberg's differential rule we estimated the MZTR and the DZTR. When possible, age-specific rates and parity distribution of all maternities have been documented. Maternities with maternal ages under 15 and over 40, which constitute less than 5 to 10% of births, have been excluded from the standardization of age and parity with linear regression analyses [17].

Twinning rates are expressed as the number of twin in maternities (confinements, deliveries) per 1000 maternities (not births; 1 twin maternity = 2 twin births).

RESULTS AND DISCUSSION

Finland

Secular trends

For Finland the yearly twinning rates (Fig. 1) between 1754 and 1773 show strong fluctuations between 13.3 to 19.7 per mill with an average for this period of 16.2 ± 4.3 per mill. Between 1841-54 the rates are mainly below 14 per mill but between 1855-1871 the values flucutated around 15 per mill. During this period there were several years with crop failure and famine. The years 1862, 1865, and 1867 were particularly severe. In 1868, when starvation and other privation was rampant, almost 8% of the population of Finland died and there was a strong decrease in the birth rate. Neither for Finland as a whole, nor for the severest hunger areas, was noted any significant decrease in twinning rate during any of the years from 1866 to 1869. On the contrary, there was an unexpected catch-up peak in the twinning rate in 1868 [16].

From 1880 the whole of Finland showed a downward trend in twinning rate until the turn of this century. In the 1910s the fertility transition with the limitation in family size spread to most parts of Finland [29]. But in spite of a decreasing mean maternal age and a decreasing number of children per mother the twinning rate was increasing up to the 1960s, being above 15 per mill 1936-46 and 1952-58. In the 1950s the twinning in Finland was the highest noted for a whole nation, 15.5 per mill. After 1963 there was a steep downward trend lasting to around 1975 when a levelling out and even a slight increase of the trend between 10.3-11.2 per mill can be noted.
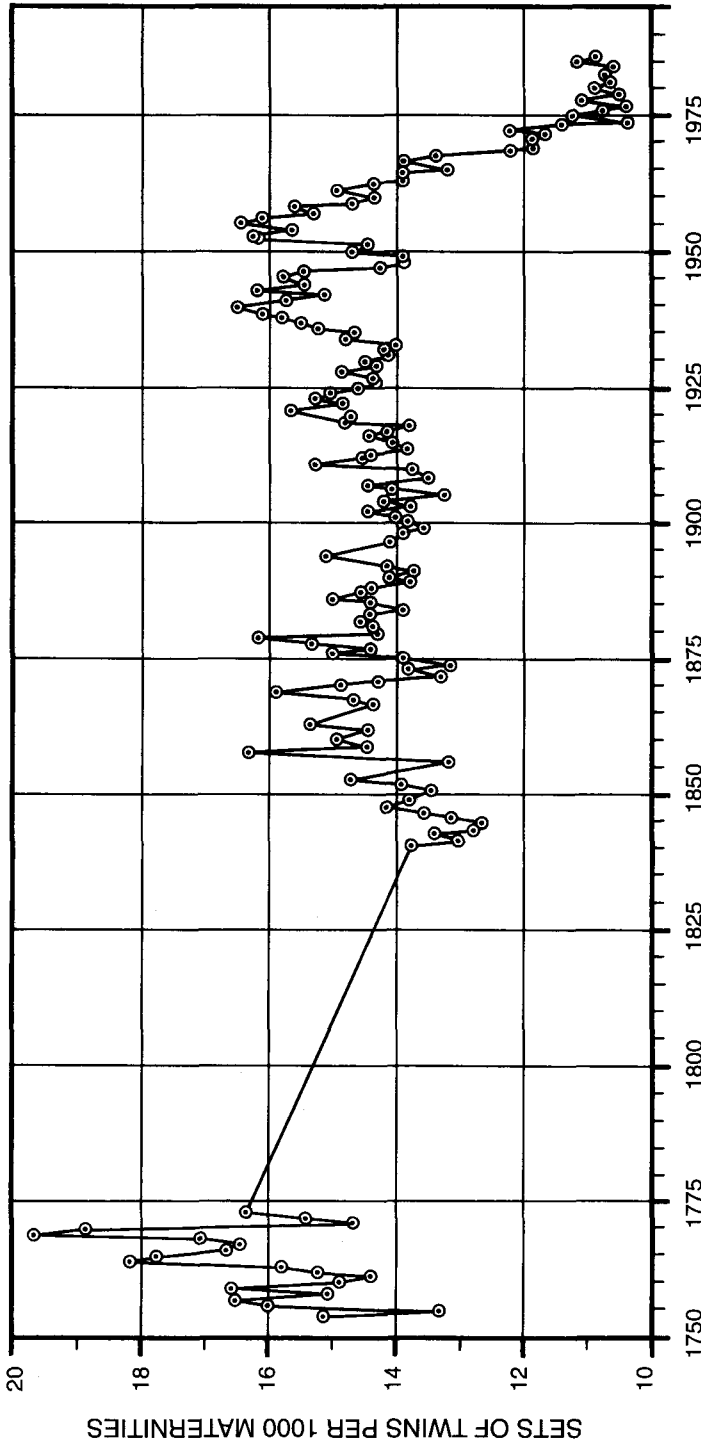
Fig. 1 - Secular changes in twinning rate in Finland, 1754-1773 and 1841-1986. The values from 18th century are compiled from Wargentin's tables.
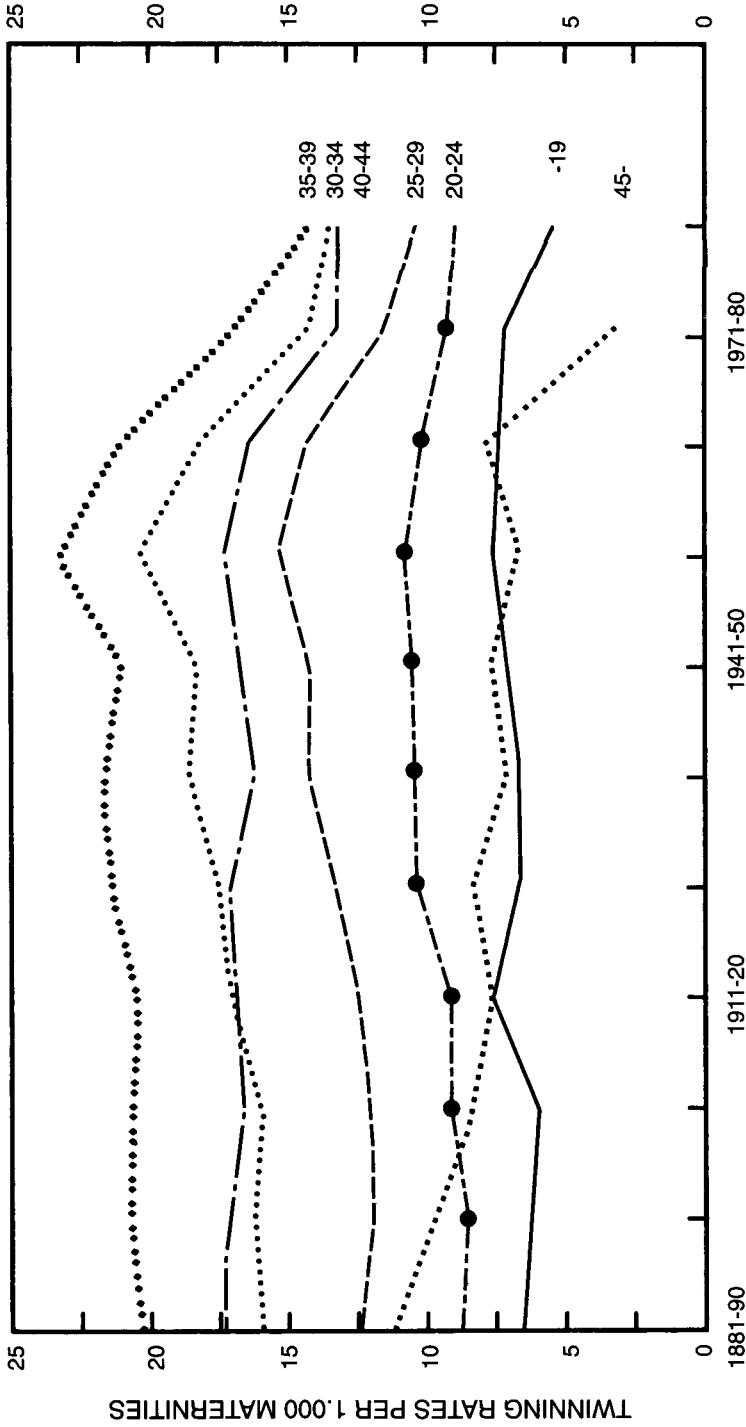
Fig. 2 - Age specific twinning rates in Finland, 1881-1984. Up to the 1960s the rise in twinning rates affects all age groups up to 40 years. The decrease in the twinning rate after the 1950s is most marked in the most twinning-prone age-groups between 30-39 years.

Age specific twinning rates, 1881-1984

To examine the effect of changes in maternal age on twinning rates, age-specific rates were calculated in 10-year age groups (Fig. 2). The importance of the role of maternal age is clearly demonstrated. The lowest rates were found in teenage mothers and mothers of the oldest age group. Sampling variation causes fluctuations, due to small numbers of strata, especially at the oldest age group of mothers. The decline from the peak level in 1951-60 was considerably steeper in mothers over 25 years and most marked in those between 30 and 39 years of age.

Completed family size and the mean age of mothers have decreased strongly in Finland since the beginning of this century. Not only the mean age of the mother at first birth decreased but also the mean age of mothers at the last birth. This effectively shortened the span and thus considerably decreased the repro-duction during the most twinning prone ages around 37 years of age. All these facts suggest that the increase of the twinning rate in Finland up to the 1960s was influ-cenced by other factors than changes in maternal mean age and number of previous children.
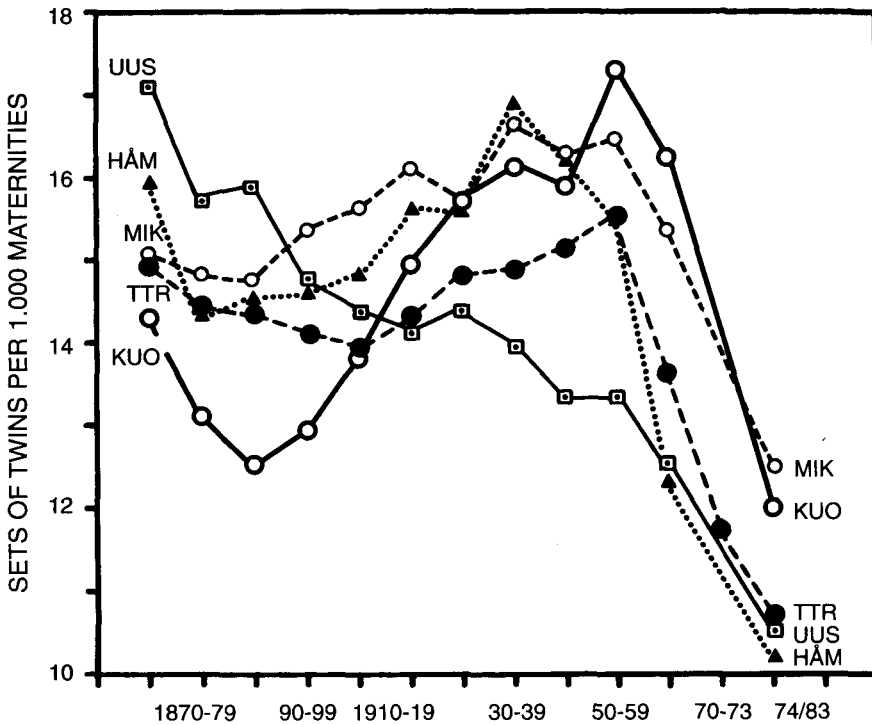

Fig. 3 - The twinning rates, 1860-1983, in Finland as a whole (TTR), in the adjacent counties of Kuopio, Mikkeli (St. Mickel) and Häme (Tavastehus), and in the southern and most urbanized county Uusimaa (Nyland).

Differences between counties in temporal trends of twinning

The "melting pot" Uusimaa (Nyland), with the capital Helsinki and with the highest density of the population, shows a distinct decrease in the gross twinning rate from 17.1 per mill to 10.4 per mill i.e. a decrese of about 40% during the observation period of 123 years (Fig. 3). In contrast to that and in spite of a decrease in parity and mean maternal age, the counties of Mikkeli and particularly Kuopio show marked increases in the twinning rate from the 1880s to the 1950s, when the twinning rate among the East Finns in these counties was the highest known among Whites.

Standardization according to maternal age, with the aid of the age-specific twinning rates, shows that the low twinning rate in the 1960s in the counties of Uusimaa and Häme seems mainly to be a consequence of a decrease in mean maternal age. This does not seem to be the case in the counties of Kuopio and Mikkeli, however. When the total twinning rate for the county of Kuopio was estimated according to the age-specific twinning rate from 1900-1909, the total twinning rate for 1960-1969 should have been only 11.8, but that actually observed was 16.3. This in spite of the fact that parity had also declined markedly during the 50-year period [14]. Hence, there seem to be factors other than maternal age and parity that can increase the twinning rate considerably. The population of the county of Kuopio had up to the last World War a high rate of endogamous marriages. In a recent paper [18] we noted that the standardization according to maternal age does not reduce the regional heterogeneity in the twinning rate for the period 1974-1983.
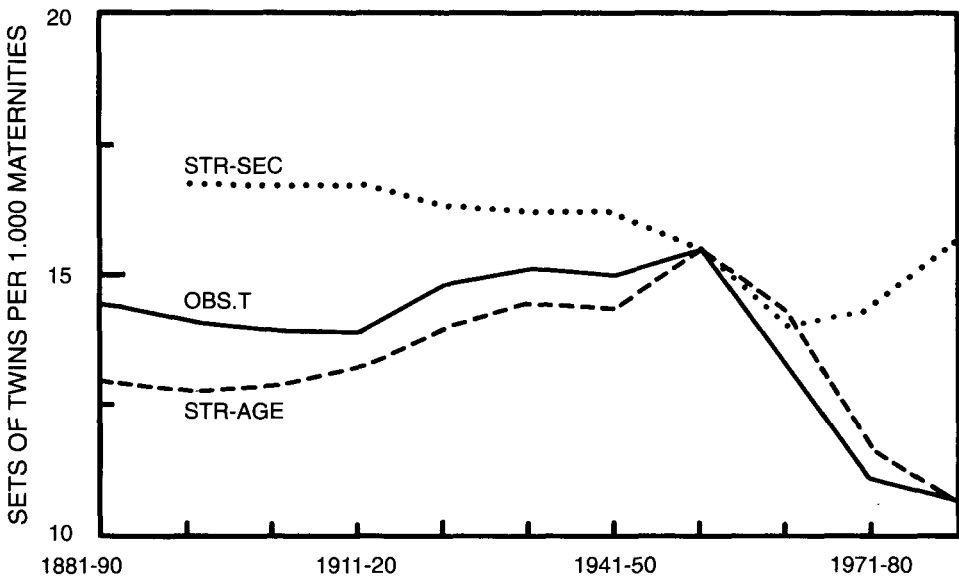

Fig. 4 - Observed twinning rate (OBS.TR) and standardized twinning rates in Finland, 1881-1984. STR-SEC (secular effect on twinning rate) is the frequency of twin maternities estimated as if the age-specific twinning rates had been the same as during 1951-60. STR-AGE (maternal age effect on twinning rate) is the estimated frequency of twin maternities if the distribution of maternal age had been the same as during the period 1951-60.

Standardized twinning rates

Figure 4 shows estimated and observed twinning rates in Finland. Curve STR-SEC shows the trends in twinning rates when standardized according to age specific twinning rates (i.e. the extent to which maternal age has influenced the twinning rates). The downward trend up to the 1960s and the rise thereafter are in good agreement with the temporal development of the maternal mean age that decreased by 2.5 years between the 1880s and the 1950s.

Curve STR-AGE shows that elimination of the influence of maternal age accentuates the rise in the twinning rate up to the 1950s. This rise is paradoxical. Hence, there must
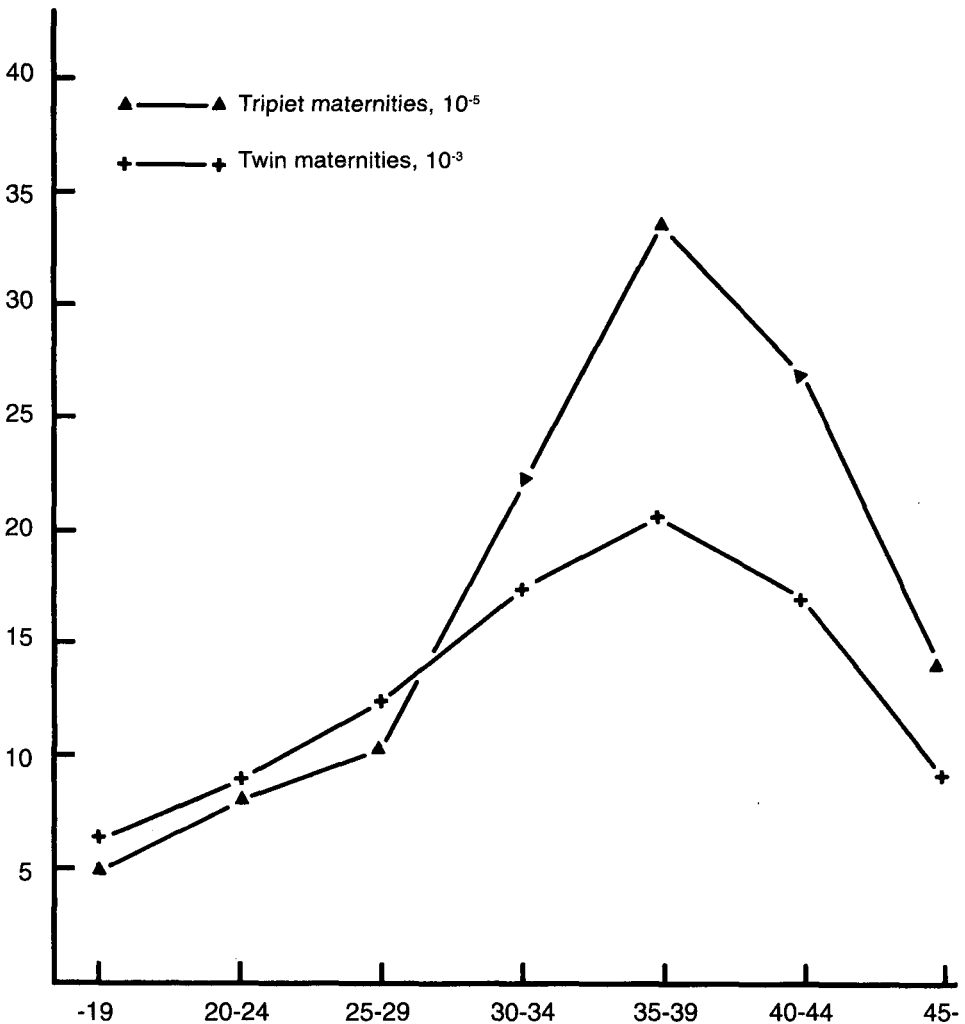

Fig. 5 - Comparison of age-specific twinning and triplet rates in Finland, 1878-1916.

be some factors that outweigh the fall in the maternal mean age and average number of children per mother [17].

Comparison of age specific twinning and triplet rates

It has been stated that the triplet rate in Finland was among the highest noted [13]. For the period 1881-1952 the frequency of sets of triplets was 17.0 per 100000 maternities being in Sweden 15.7 per 100000 (1881-1940). Figure 5 shows that the triplet rate shows a much stranger relative increase with maternal age than the twinning rate, being 6-7 times higher in the age group 35-39 years than below 20 years of age.

Sweden

Temporal changes in twinning rate in relation to mean maternal age

The total twinning rate for Sweden (Fig. 6) showed an increasing trend from values below 15 per mill in the mid-1750s to average values above 17 per mill during the period 1776 to 1797. After the mid-1810s there was a downward trend. In 1836-55 the twinning rate was only 13.61 ± 0.08 per mill.

This strong decline in the twinning rate is surprising. During the first part of the 19th century there were many improved socio-economic conditions (vaccination against smallpox, favourable climate, peace after 1814). An increase in the average height of soldiers indicates a clear improvement on the average nutritional status of the population, probably influenced by the spread of potato cultivation and lower prices for corn and other commodities. Furthermore after 1810 there was an increase in fertility among women in the most twinning-prone ages [16]. In terms of these changes, one would expect increasing – not declining – twinning rates.

At the same time, however, Sweden experienced a subsistence crisis. During 1801-1850 the increase in the population was the highest recorded for Sweden. The cohorts born between 1811 and 1835 were particularly large. The rapid increase in population, particularly in the number of landless crofters, led to a subsequent proletarianization with about 10 times higher stillbirth rates than today, the longterm decline in child mortality reversed, and the five-year moving averages of height of cohorts of Swedish men at ages 25-49 born between 1840-1850 went down by no less than about 6 cm [16]. The period around 1850 is pointed out as a period of crisis and especially so in the western part of south Sweden. However, low values in the twinning rate in the past were not consistently associated with periods of nutritional stress or similar privations [16]. The causes of the paradoxically low twinning rates in Sweden around 1835-1855 remain a mystery and need further studies.

After 1855, when emigration to the U.S.A. begun, there was a slight upward trend which after the turn of this century reaches values around 15 per mill. From the 1930s a marked decrease in the twinning rate took place in Sweden with a minimum of 7.9 ± 0.3 per mill in 1969. In the 1980s there has been an increase to values around 10 per mill.

During the periods 1751-1800 and 1801-50 the average ages of all mothers in Sweden were 31.4 and 31.6, respectively, which is considerably lower than in 1851-1900,
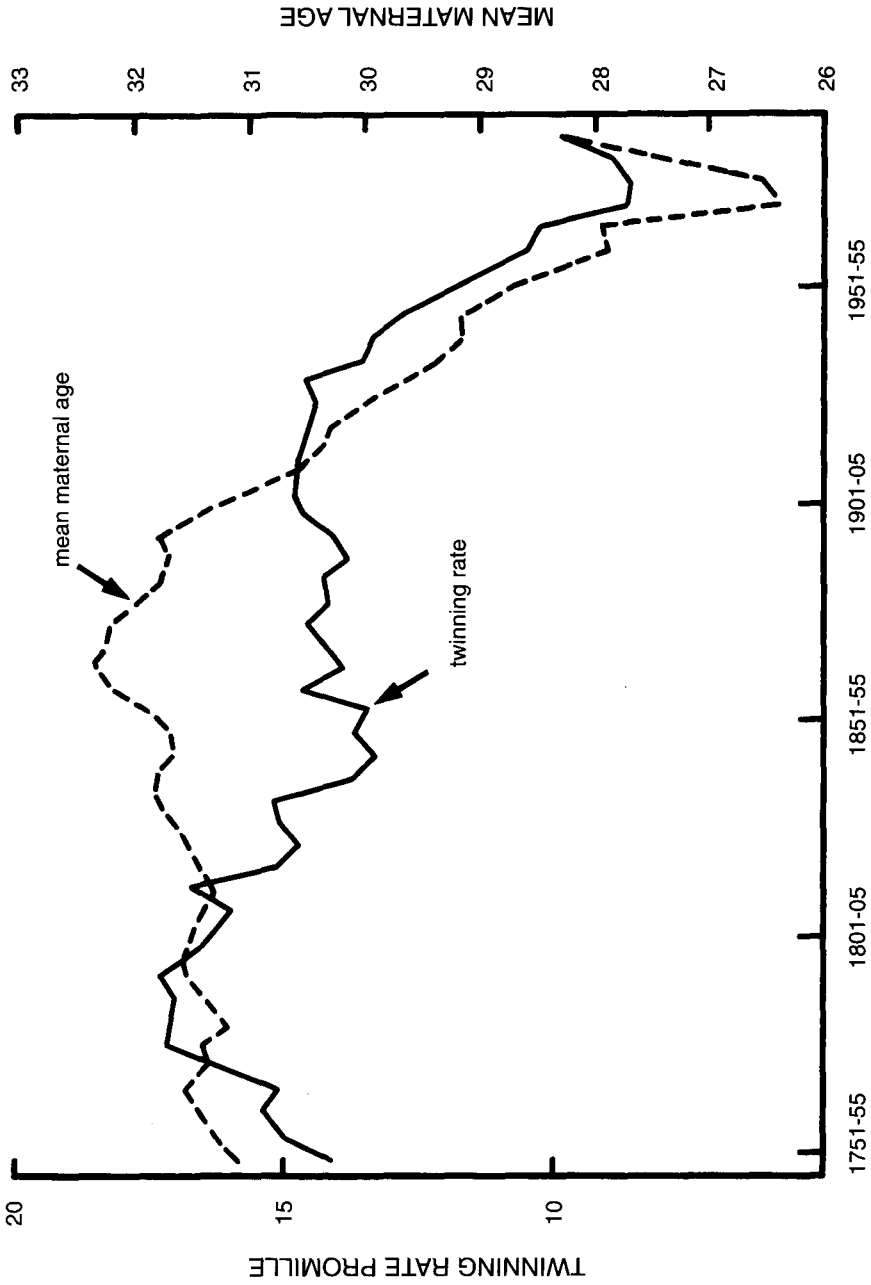
Fig. 6 - Twinning rate in relation to mean maternal age in Sweden 1751-1985.
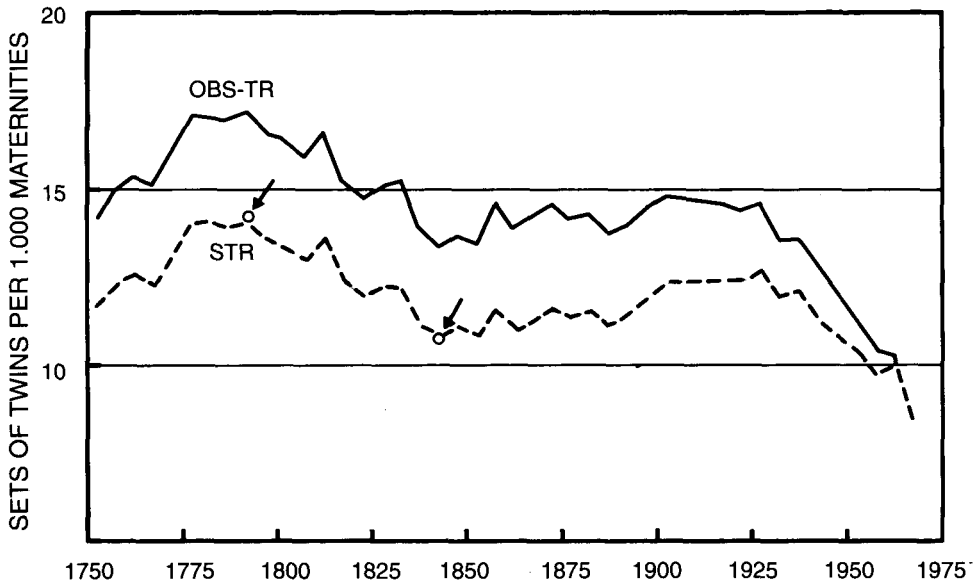
Fig. 7 - Observed (OBS-TR) and for maternal age standardized (STR) twinning rates in Sweden, 1750-1970. STR shows the extent to which maternal age has influenced the twinning rate. As reference population was used Sweden, 1971-75 (1973). The two points, indicated by arrows, for 1971-95 and 1836-40 are standardized according to Hill's indirect method of standardization (Fellman and Eriksson 1990).

when the corresponding figure was 32.0. Nevertheless twinning rates were significantly higher (p < 0.0005) during the first two periods [13]. During the period 1856-1875 the maternal mean age was the highest recorded (over 32.2). In spite of this relatively high mean maternal age the twinning rate was not particularly high during this period (Fig. 6).

Since the beginning of this century the proportion of mothers under 25 years of age has increased markedly. Up to the 1970s over 45% of maternities in Sweden occurred in women of the age groups with the lowest twinning rates, whereas a century ago the corresponding figure was only 15%. In the age groups with the highest twinning rates (30-39 years) maternities have decreased from about 45% to about 20%. Seen in relation to these figures, the marked decline in the twinning rate that set in after the 1920s in Sweden is perhaps not surprising. However, even after standardization for maternal age (Fig. 7) the downward trend in the twinning rate is still steep. During the 1950s and 1960s the highest age specific twinning rates, in women between 35-39 years of age, was lower (below 16 per mill) than the average twinning rate in the latter half of the 18th century.

Standardization of twinning rate

Figure 7 shows that irrespective of standardization method, changes in maternal age only to about 50% explain the strong temporal variations in the twinning rate [18].

Comparison of secular changes in twinning, triplet and quadruplet rates

Figure 8 shows that the secular decrease of rates of multiple maternities is much more strongly accentuated in maternities of triplets and quads than of twins. Before the introduction of ovulation inducers in the treatment of infertility the triplet rate was in this
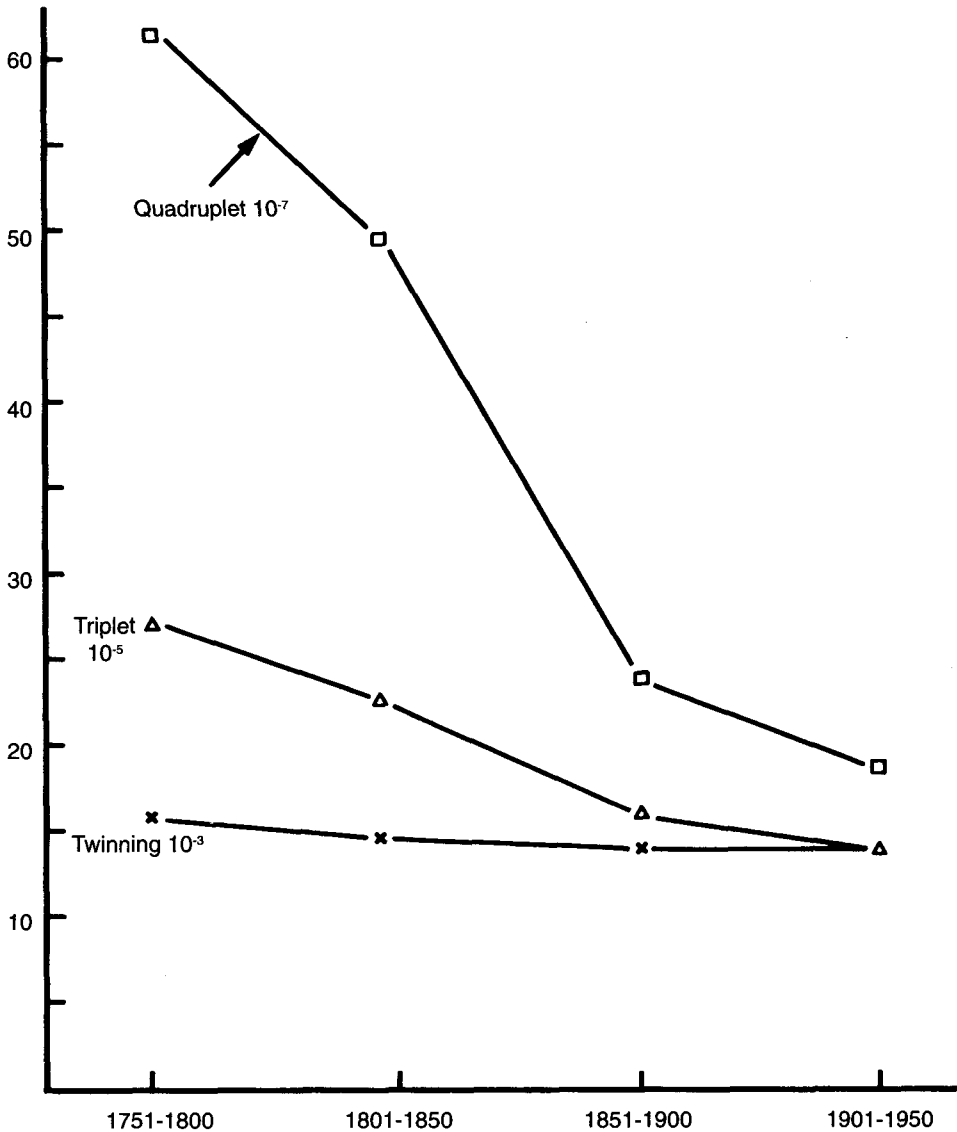

Fig. 8 - Secular changes of rates of maternities of twins (1000), triplets (100000) and quadruplets (10000000) in Sweden, 1751-1950.

century only about 1/2 and the quadruplet rate only 1/3 of what they were in the second part of the 18th century. Thus it seems that biocultural changes have had a much stronger effect on the triplet and quadruplet rates than on the twinning rates. This may partly be explained by the decreased mean maternal age that seems to have a stronger effect on triplet rates than on the twinning rate (Fig. 5). A high mean parity in the past may also have contributed to high rates of multiple maternities and recurrent twinning [18].

Zygotic rates

The MZTR for the decades between 1901 and 1930 was above 3.6 per mill but then decreased to 3.1 per mill in the 1950s. Since the beginning of the 1970s there was a strongly significant increase to 5.1 per mill in 1984 [5]. In the first decade of this century the DZTR was 11.2 per mill but decreased to minimum values below 5 per mill in the 1970s.

Denmark

Temporal changes

Denmark had up to the 1910s a twinning rate mainly below 15 per mill (Fig. 9). However, between 1911 and 1925 the average twinning rates were around 15.5 per mill peak-

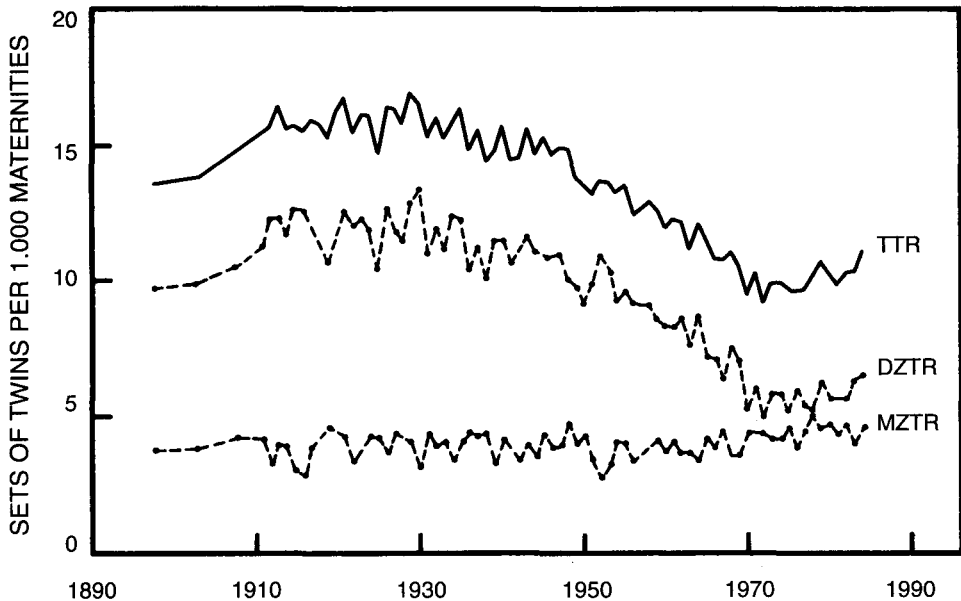Fig. 9 - **Twinning rates in Denmark, 1896-1984. For the period 1896-1910 the twinning rates are averages for five-year periods. From 1911 onwards, the twinning rates are given for each year. The rise in the monozygotic twinning rate (MZTR) during the period 1960-1984 was highly significant (p < 0.0001) [5].**
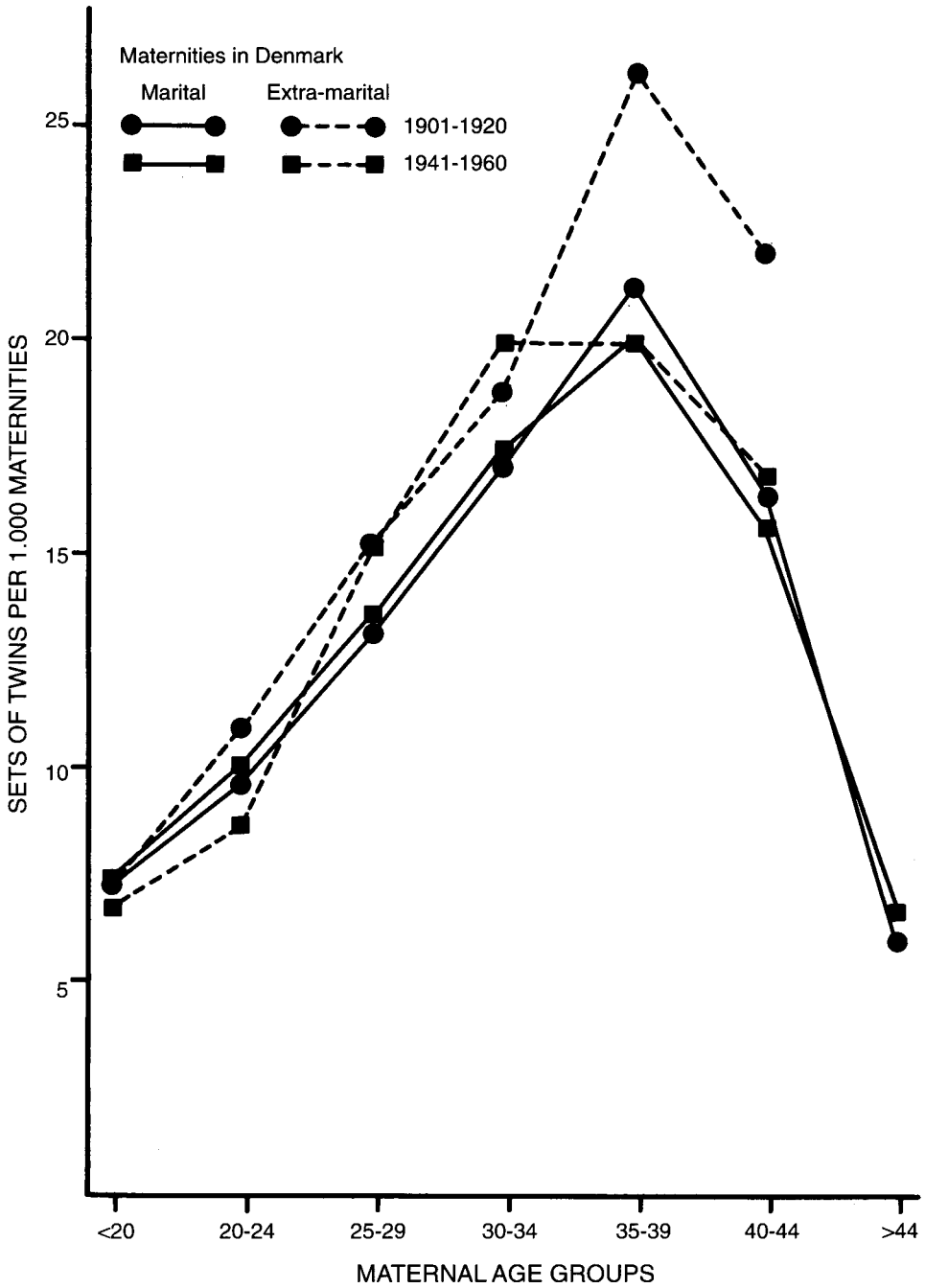
Fig. 10 - Twinning rates in Denmark, 1901-20 and 1941-60, according to legitimacy and maternal age.

ing in 1921 (16.5 per mill). During 1926-30 a quinquennial maximum was reached with a twinning rate no less than 16.1 ± 0.2 per mill. This is the highest value noted in this century for a whole nation. After that there is a downward trend that accentuated (after the World War II) reaching in the 1970s average values below 10 per mill, with a minimum of 9.4 ± 0.4 per mill in 1970.

Zygotic rates

Figure 9 shows that since the beginning of the 1950s the MZTR has shown a slight but significant increase. The DZTR shows a trend more or less parallel with the total TR. Both appear to have stabilized in the mid-1970s and have even begun to rise slightly in the 1980s.

Marital status and twinning

Between 1901-1920 unmarried Danish mothers had considerably higher twinning rates than married moters in all age groups from the age of 20 to 44 (Fig. 10). The difference in the age-specific twinning rates between marital and extramarital maternities is most pronounced between the ages of 35 and 45 years, where unmarried mothers show a peak: the twinning rate is a good 25% higher for unmarried than for married mothers.

For the period 1941-1960 the twinning peak among the extramarital mothers had disappeared and only the extramarital mothers between the ages of 25-34 have higher twinning rates than the marital mothers. In Denmark 1973-1984 no marital status effect could be found [17].

The higher twinning rate of unmarried mothers in the beginning of this century is in many respects a paradoxical phenomenon. The socio-economic status of the unmarried mother was anything but easy. Even in the beginning of this century there were not seldom cruel and awful Church punishments employed to throw light on the role of the sexual offender in the peasant society. It was also believed that a prostitute had the ability to evoke rickets also in unborn children. She was a peril in homes with infant children. If she were given employment, her duties were often located in the out-sphere, which was the same as the male sphere. She had to perform heavy tasks that were otherwise left to men. Women who expected or had given birth to an illegitimate child were exploited through heavier work for less pay [19].

Furthermore, the majority of pregnant unmarried women were young and primigravidae in which risk of toxemia and other complications is greatly enhanced, particularly in gestations with multiple embryos or fetuses. Because of the low mean parity and the low mean age, unmarried mothers tend to have higher rates of spontaneous abortions and stillbirths of both singletons and twins than married mothers. And an increased prenatal selection affects twin maternities to a higher degree than singleton maternities [10, 23]. Considering all the above-mentioned antenatal selective factors, it appears that the majority of unmarried mothers of twins who in the past completed a pregnancy belonged to an elite, as far as reproduction performance is concerned. We know very little about interindividual differences in reaction to sexual stimuli in the complex chain of events in women leading to ovulation, including polyovulation. The hypothesis that the ovulation

rate is higher among unmarried mothers than among married ones is supported by the fact that the higher twinning rate among the former seems to involve only DZ twin maternities [10-11].

Apart from a high polyovulation rate, the requisite qualifications for high rate of multiple maternities are high rates of fertilization, implantation and embryonic survival. It is estimated that as many as 50% of conceptions end in spontaneous abortions (many of which are so early as to be unrecognized) and that 25% of all conceptions are afflicted whith major chromosome abnormalities. The likelihood of the presence of lethal factors with prenatal selection is greater in two zygotes than one. Intrauterine fetal death occurs more often in twin pregnancies than in singleton pregnancies. Pregnancies with multiple embryos make particularly heavy demands on the mother's capacity to increase her uterine blood-circulation for which good health and a good physical condition may be of great importance [10]. Recent studies suggest that at least 73% of natural single conceptions have no real chance of surviving 6 weeks gestation and that pregnancies with multiple embryos may constitute more than 12% of all natural conceptions, of which number only 2% survive to term as twins and about 12% result in single births [2].

A high rate of recurrent twinning, and a high rate of extramaritally or premaritally conceived firstborn children indicate that twin – and triplet – prone mothers are more fecund, i.e. they polyovulate and conceive with greater ease or are less able to avoid becoming pregnant and have the capacity to carry through a gestation with multiples – also under poor and uncertain socio-economic conditions [10-12] .

Norway

Temporal changes

With some exceptions for values above 15 per mill in the years 1918, 1926 and 1931 the twinning rate is mainly between 13 and 14 per mill up to the beginning of the 1940s (Fig. 11). During 1942-45 the average rate was below 12 per mill but rises above 14 per mill in 1950. After that there is a clear downward trend reaching a minimum with 8.7 ± 0.4 per mill in 1972. From then there seems to be an end to the drop in the twinning rate, which even shows an increasing trend.

Zygotic rates

The MZTR has an unexplained downward peak, 2.1 per mill, in 1957. After that a slight but significant increasing trend can be noted [4]. The DZTR is mainly parallel to the total twinning rate having a minimum in 1979 of 4.6 per mill.

Comparisons of twinning in Swedes and Finns

Up to the 1930s, the twinning rates were roughly the same in Sweden and Finland but after that a marked drop occurred in Sweden, whereas in Finland there was an upward trend up to the end of the 1950s. In the 1950s Finland had a twinning rate of 4.5 per mill units (over 40%) higher than Sweden. It is a strange phenomenon that the twinning rate
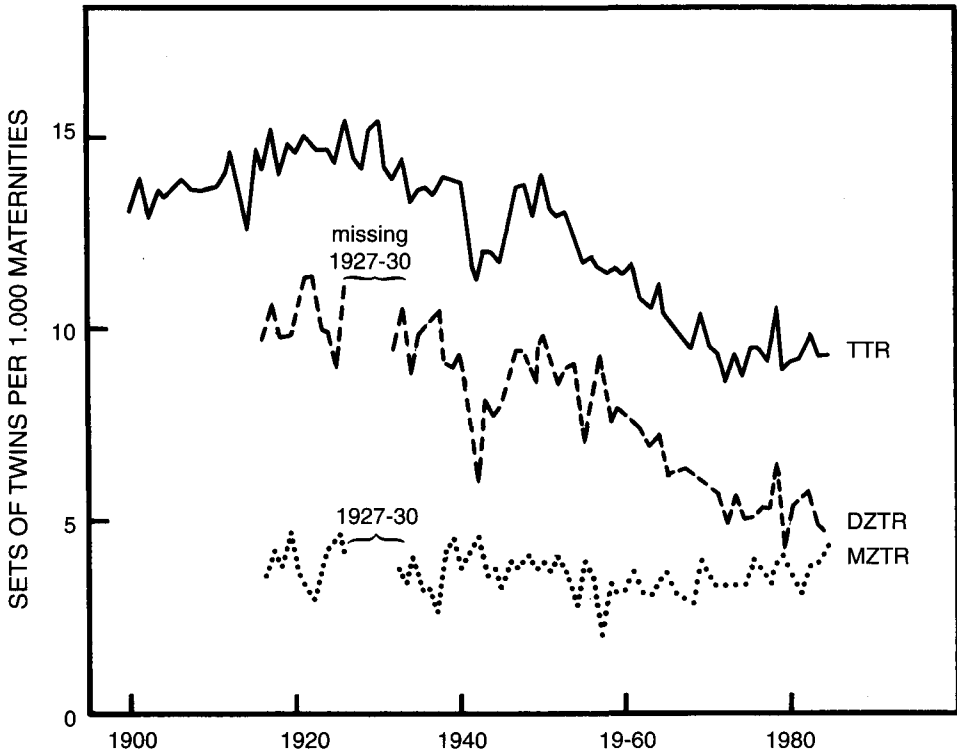
Fig. 11 - Variations in total twinning rate (TTR), dizygotic twinning rate (DZTR) and monozygotic twinning rate (MZTR) in Norway, 1900-1984. The DZTR and MZTR are missing for the period 1927-1930. During the period 1960-1984 there was a highly significant increase of MZTR (p < 0.001) [5].

in Finland increased from 13.0 per mill in 1901-10 to 15.5 per mill in 1951-60 in spite of the fact that the mean maternal age decreased by 2.0 years [14] and the mean parity went strongly down after the 1910s when the practice of family limitation spread rapidly to most parts of Finland [29].

Standardized twinning trends

The divergent trends of observed twinning rates in Sweden and Finland between the 1920s and the 1960s have been studied [14]. When the twinning rates were standardized according to age-specific twinning rates (thus showing the extent to which age had influenced the twinning rates during the period 1881-1960) it was shown that the curves for the two countries were almost parallel but the level of the twinning rate in Finland was 4 to 5 per mill units higher than in Sweden. This is in good agreement with the fact that the maternal age had decreased in a similar way in the two countries (from 31.7 to 28.1 years in Sweden and from 31.3 to 28.8 years in Finland).

The frequency of twin maternities was estimated as if the distribution of maternal

age had been the same as during the period 1954-62. These frequencies diverge after the 1920s, but for Finland the frequency increases markedly in spite of the fact that the average number of children per mother and childbearing in the most twin-prone maternal age groups between 30-44 years decreased. However, in the 1950s the Finnish mothers had an approximately 30% higher mean parity than their counterparts in Sweden, where there was also a higher frequency of primiparae. These facts do not explain the divergent trends, but to a certain degree they do match the differences in twinning rate [14]. The twinning rate in Finnish mothers (1954-63) increases by only about 1 per mill unit per birth order (parity) [11-12, 17-18].

The decrease in twinning rate in Sweden cannot be explained totally by the decrease in maternal age. Figures 6 and 7 show the extent to which maternal age has influenced the twinning rates in Sweden. For standardization for maternal age different methods have been used and they all give very similar standarized twinning rates [18]. Figure 7 indicates that up to about 1920 the maternal age factor is strong but during the last two generations the influence of the maternal age on the twinning rate has decreased markedly.

Changes in population structure

There must have been other factors that decreased the twinning rate, such as declining mean parity and probably increased urbanization. The industrialization process with breaking up of isolates took place about one generation earlier in Sweden than in Finland [14]. In this century there have been many improvements in communications (steam ships, trains, bicycles, cars, motor boats, mopeds, etc.). The average distances between birth places (origin) of marriage partners (matrimonial migration distances) have increased considerably. All this has been interpreted as an evidence for the hypothesis that degree of relationship between parents of the mothers of the twins (and not between the parents of twins) is important for the manifestation of dizygotic twinning [10, 13].

The Finnish genetic pool has a unique pattern not to be found in any other European population [26]. In rural Finland there are a great number of isolated subpopulations with local enrichments of rare genetic markers and diseases. The Finnish disease heritage consists of about 30 rare diseases found to be unusually common in Finns but rare elsewhere. On the other hand there has also been a loss of genes. Some hereditary disorders that are quite common elsewhere are very rare in Finns, e.g. cystic fibrosis and phenylketonuria.

Up to the 1500s the main parts of eastern and northern Finland were not permanently settled. Newcomers to the mainly uninhabited areas often caused a strong founder effect and genetic drift that is still reflected in clusters of rare genes. The isolation has been accentuated by both long distances between villages and a low population density. Up to the last World War Finland was a typical agrarian country with little need of internal migration. The country progressed from an agricultural society to a post-industrial one very rapidly. In 1860 about 80% of the population was working in agriculture, in 1940 around 54%, but no more than 9% in 1980. Industrialization and the rise in wealth associated with it began in Finland around 1870, i.e. some 30-40 years later than in Sweden [14].

The unique assortment of some genes among Finns has been accentuated by national

isolation, too. Few immigrants have been tempted by Finland's outlying, subarctic position. As a non-Indo-European language, Finnish is completely different from both Scandinavian and Russian. Furthermore, another religion, a contrasting culture and acts of war have restrained exchange of marriage partners in an easterly direction.

The differences in the onset of the dramatic decline in the twinning rates that set in during the 1930s in Sweden but not until the 1960s in Finland seem mainly to depend on differences in population structure changes. Industrialization and urbanization with breaking up of isolation in rural areas took place about one generation later in Finland than in Sweden [14].

Sociodemographic factors

A factor not to be neglected is that gestations with multiple embryos make particularly heavy demands on the mother's capacity to increase her heart volume and maintain an optimal blood supply to the uterus [10, 13]. Studies with ultrasonic scanning in an early phase of gestation indicate that one or both twins vanish more often than singletons [23]. Furthermore, age standardized twinning rates are significantly higher in rural than in urban areas. Higher order multiple maternities, such as triplets and quadruplets, have considerably higher frequencies in rural than in urban regions [14]. Some rural isolates show very high twinning rates, e.g. in Norwegian valleys [4], in the archipelagos of Åland, Åboland, (Turunmaa), Stockholm (Roslagen) and Gotland [13]. Mainly rural counties show a much later onset of the decline in the twinning rates than urbanized ones (Fig. 3). In such rural isolates there may be a complex interplay between maternal (sex-limited) recessive genetic factors and physical condition of the mother. In the countryside in the past mainly only healthy, physically fit women were married. There are indications that gestations with multiple embryos demand a good physical condition of the mothers [10].

Stature and twinning

A positive association appears to hold for mammals that within species average litter size is largest in the larger races. In man too there seems to be some similar evidence from rates of DZ twinning. Very high rates of twinning are found in Nigeria where women are tall, and low in Oriental populations where women are small [21, 24]. Tall stature may at least partly reflect anterior pituitary function, e.g. level of growth hormon (somatotrophin) and gonadotrophins, inter alia the follicle-stimulating hormone (FSH), but also occupational class, since tall women are more common among upper social classes.

The peoples of Northern countries are among the tallest in the world. Particularly the insular populations on Åland and Gotland and in the Åboland archipelago are among those with the tallest average stature in the world [13], and have had among the highest twinning rates among White populations [13].

It has been noted that twinning rates were high in eastern and central Norway, where the average stature of the population was greatest [32]. Among Saamis of Finland, stature is short and the DZ twinning rate has been only about half of that in other Nordic populations. Among the East-Finns, on the other hand, stature is shorter than among West-Finns and Swedes, but up to recently the twinning rate has been among the highest known in Europe (Fig. 3).

Recent studies indicate that Danish mothers of DZ twins had significantly higher pre-pregnancy weight, height and body mass index (weight in grams over height in centimeters) than mothers of singletons [3]. The differences remained after adjustment for potential differences in maternal age, parity and social class. Maternal weight appeared to be the critical variable associated with the occurrence of DZ twinning.

A correlation between twinning and stature may be coincidental and they may have no direct connection with each other. This conclusion is supported by the fact that although stature has increased in Nordic populations by about 10 cm in a century, the twinning rate has shown a dramatic decline. The association between maternal body weight and DZ twinning, however, emphasizes the importance of the constitution of women for completing a gestation with multiples.

Recurrent twinning

The frequency of recurrent twinning, i.e. the repeat frequency of twinning among mothers who already had one set of twins, was about twice as high among the women in Åland than elsewhere. In the period 1750-1949, about 8.5 percent of the mothers in Åland had twin or triplet maternities and no less than 8.2 per cent of the mothers with multiple maternities had a recurrent twinning. The fecundity in mothers in Åland with recurrent twinning was high, 7.7 maternities, i.e. almost 10 offspring per mother, and a high proportion (almost 50%) of opposite-sexed twins. This indicates that polyovulation is the chief cause of recurrent twinning. The overall frequency of twinning was estimated to be about twice that in the general population. The twinning rate among mothers with triplets was a good four times (80 per mill) that of mothers in general (19.2 per mill). It seems that the chance of one further multiple maternity is approximately constant and independent of the number of previous multiple maternities. A mathematical model based on these assumptions has been worked out and the proportion of mothers in Åland with different numbers of multiple maternities follows Fellman's law [13, 18]. The repeat frequency of twinning seems to be a good parameter for testing the variability of twinning proneness in a population, even if it does not tell us anything about the cause (genetic or environmental) of this variability.

CONCLUSIONS

It is commonly agreed that variations in age and parity standardized twinning rates in different populations are mainly caused by genetic factors. Populations in and around the Baltic Sea basin have the highest twinning rates among Whites, e.g. in Sweden above 17 per mill at the end of the 18th century and in some insular isolates twinning rates between 20-25 per mill have been noted.

Up to the 1920s the Nordic countries Denmark, Finland, Norway and Sweden had similar twinning rates. Denmark had in the 1920s and 1930s the highest yearly twinning rates with values above 16 per mill. After the 1930s and up to the 1950s the twinning rate increased in Finland in spite of decrease in maternal mean age and mean parity, whereas in other Nordic countries it declined. The downward trend in twinning started in

Finland about one generation later than in other Nordic countries. No final explanation can as yet be given for the different twinning trends, but it may be noted that industrialization and urbanization with breaking up of isolates started considerably later in Finland than in the other Nordic countries. The high twinning rates in Finland during 1945-59 are mainly caused by higher rates in rural regions, particularly in the relatively isolated core area of the East-Finns where the twinning rate in 1930-59 was extremely high, actually among the highest known among Whites in the 20th century. However, at the end of the 1950s a strong downward trend was setting in also in Finland, but the twinning rate did not reach such low values as in Denmark, Norway, and Sweden. In the 1970s and 1980s a rising tendency of twinning is noted in all four Nordic countries. This increase is caused not only by the DZTR but also by the MZTR. Variations in the DZTR seem to be only partially explained by changes in the maternal age. It is hypothesized that mothers in rural (endogamic) regions may have a stronger genetic disposition for twinning and/or that mothers in the countryside with a good physical condition have better possibilities than women in urban and industrialized areas (with much sedentary work) for completing a gestation with multiple embryos. It is increasingly evident that the explanation of the variability of twinning rates is very complex and is not just of interest per se, but may disclose new insights into the role of genetic versus environmental factors in the reproduction of man.

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