II. *The Inheritance of Sinistrality in* Limnæa peregra (*Mollusca, Pulmonata*).*

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[Plate 10.]

Tables 1–35 are tables in the text.
Tables I–X are pedigree tables.

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* Summaries of the conclusions reached here were published in *Proc. Roy. Soc. B.*, 1929, vol. 104, p. 152, and in *Proc. Royal Institution*, May 10, 1929.

*Limnœa peregra** is one of the commonest British fresh-water molluscs. Like other aquatic Pulmonates, it is hermaphrodite and breeds either by self- or cross-fertilisation. Normally the shell and body are coiled in a right-handed spiral ("dextral"). Very rarely a reversed ("sinistral") form occurs in which the whole symmetry is completely inverted: the shell and body are coiled in a left-handed spiral, the heart and kidney are reversed; the rectum, penis and vagina open on the left-hand side of the neck instead of the right; the osphradium is on the left and the consequent asymmetry of the nervous ganglia is reversed. A sinistral snail is a complete mirror image of a dextral. The difference involves the whole development of each individual: it is apparent in the first division of the egg and obvious in the second.

To be twisted either to the right or to the left seem to be the only available morphological possibilities. A shell which is not dextral is not necessarily sinistral, nor *vice versa;* the shells might be coiled on the flat, something like a *Planorbis.* We have had a few of these monsters (fig. 8, Plate 10), of which the animals have been sinistral: if fertile they have normal dextral or sinistral young and appear to play no particular part in the genetic scheme. But a spiral mode of cleavage in the egg and a spiral twist in the soft parts of the adult seem to be essential qualities of gastropod mollusca, and an animal which is neither dextral nor sinistral is presumably impossible: the twist being obligatory there is no third alternative.

A small proportion of sinistrals has been known to occur in a pond near Leeds (NELSON 1901; Plate 10, fig. 10) since 1901, and we began our breeding experiments in 1920 with four sinistral specimens derived from this source, which were kindly given to us by Mr. J. W. TAYLOR. We published a preliminary account (BOYCOTT and DIVER, 1923) and a full discussion (DIVER, BOYCOTT and GARSTANG, 1925) of the results obtained up to the end of 1923.

Since then our observations have been considerably extended, partly by line-breeding the progeny of our original specimens to the ninth and tenth generations and partly by making crosses with material of known composition which we felt justified in beginning in 1925. Our data now include records of more than 6,000 broods and about a million snails.

From our preliminary data we concluded (1923, 1925) that the twist of any individual is determined not by its own chromosomes, but by the nuclear composition of its parent, and all our subsequent observations have confirmed this deduction. Dextrality and sinistrality furnish a complete example of the kind of inheritance often referred to as "maternal inheritance" but which may be better distinguished as "delayed inheritance." The twist of an individual is predetermined in the unfertilised egg and is not affected by anything the sperm brings with it; the effect of the sperm is felt in

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* The *Buccinum peregrum* of O. F. MÜLLER, 1774. A. S. KENNARD and B. B. WOODWARD (1926, p. 48) and others prefer *Limnœa pereger* on the ground that "*pereger*" is known only as a noun; the argument is not convincing. The earliest spelling of *Limnœa* is *Lymnœa* in LAMARCK, 1799.

the next succeeding generation. A sinistrally-determined egg fertilised by a dextral-determining sperm produces a sinistral snail in F_1 which, self-fertilised, produces a brood of dextrals in F_2 ; in F_3 some of these dextrals produce dextral broods and some produce sinistral broods. Correspondingly from a dextrally-determined egg fertilised by a sinistral-determining sperm we get dextrals in F_1 and F_2, and a mixture of dextral and sinistral broods in F_3. The scheme is Mendelian but, compared with the ordinary sequence, there is a delay of one generation and segregation is by broods in F_3 and not by individuals in F_2. This has one unfortunate consequence, for while it is easy enough to breed 5,000 snails to determine a segregation ratio it is with our establishment quite impossible to get anything like that number of broods, and our ratios are necessarily based on numbers that are not always adequate.

We know of no other character in *Limnœa* which has been examined genetically. It is, therefore, fortunate that an albino mutant sinistral turned up in our line breeding in 1925 (BOYCOTT and DIVER, 1927) and allowed us to demonstrate that albinism in *L. peregra* follows the usual lines and behaves as a simple Mendelian recessive with normal inheritance and segregation in F_2. Another albino strain appeared in 1926 and behaved in the same way. We also found that when an Irish lake form (" Stelfox ")* with a characteristic shell-shape was crossed to our stock, this character was modified in F_1 towards the ordinary shape (fig. 9, Plate 10). Delayed inheritance is, therefore, not a general feature of this particular mollusc.

Our original interpretation of the dominance relationship between dextrality and sinistrality requires some modification. The earlier results from line breeding gave no definite evidence that either twist was dominant to the other, and we had an unduly large number of results that were anomalous on any hypothesis of simple dominance : we, therefore, suggested a rather vague hypothesis of a balanced reaction which, in the absence of simple dominance and owing to the impossibility of a neutral position, gave rise to two classes of heterozygote. But our subsequent experience from cross-breeding experiments shows that this view is not tenable. Dextrality is dominant, at any rate under the conditions in which the question can be reduced to critical experiments, and we agree that STURTEVANT (1923) was right in his inspired guess (for with the data at his disposal it certainly reached that degree) that the essential facts could best be explained by dextral dominance and delayed inheritance, an interpretation that has been adopted and very clearly set out by E. B. WILSON (1925, p. 1109) and T. H. MORGAN (1927, p. 261) in their text-books.

The anomalies, however, still remain and their reality has been clearly demonstrated by our increased experience. They fall into two classes :—

(*a*) The production in self-fertilised lines of broods of a coil opposite to that shown by the line. Thus, we have wholly dextral broods (" *dextral break-throughs* ")

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* From Lough Rea, South Galway, kindly given us by Mr. A. W. STELFOX.

appearing in sinistral lines in such a way that they cannot be explained by the phenomena of segregation.

(*b*) The production from *single* snails of broods containing both phenotypes, *i.e.*, dextral broods with one or two sinistrals (" F broods ") and sinistral broods with anything from one to quite a large proportion of dextrals (" E broods "). Such broods cannot fit into the simple system of delayed inheritance outlined above.

It was largely the presence of these anomalies that led us to suppose that simple dominance was not the rule ; and we suggested that E broods were genotypically dextral broods whose normal phenotypic expression had been in some way suppressed, while the dextral break-throughs associated with them were those broods that had broken through this suppression and reverted to the normal expression of their genotype. Similarly F broods were regarded as suppressed sinistral broods. It was thought possible that these two types of suppression might be associated with the two types of heterozygote, though the possibility that the phenomena might be the expression of genetic factors was recognised.

The establishment of the fact of dextral dominance necessitates some modification of these views. In particular the interpretation previously offered of dextral break-throughs and with them of E broods falls to the ground. The simplest way of regarding dextral break-throughs is as reverse mutations. Our previous view that F broods are " suppressed " or converted sinistral broods still holds, but it seems probable that they are only special cases of dextral break-throughs. The tendency to give E broods is now definitely known to be inherited and strains showing this tendency in a high degree can be extracted from sinistral stocks by selective line breeding. There is no evidence that E broods are due to extra-nuclear (*i.e.*, cytoplasmic) factors and broadly speaking our results are compatible with the idea that they are caused by nuclear factors or genes, though some non-factorial unknown is not excluded.

The majority of these discrepant facts can be brought under one heading by saying that there is a general tendency for dextrals—some genotypic, some only phenotypic—to appear where sinistrals are expected. The reverse does occasionally occur, but in our material at any rate it is relatively very rare.

I. Cross- and Self-Fertilisation.

The greater part of our work has been done with single snails, isolated when quite small and breeding by self-fertilisation : it is to be assumed that this procedure has been followed unless pairing is specified.

It has been abundantly proved by others (see 1925, p. 123) and by our own experience that self-fertilisation occurs quite readily in *L. peregra* and some other hermaphrodite snails. Indeed, so intimate is the association between eggs and spermatozoa in the gonad and the upper part of the genital ducts, that the difficulty has been rather to imagine how self-fertilisation can be avoided. The whole question has recently been reviewed in detail in the allied American species *L. stagnalis appressa* by CRABB (1927, 1928), and he concludes by doubting whether cross-fertilisation ever occurs. That it can and does happen is shown without any doubt by the results we have obtained on crossing pigmented with albino, and dextral with sinistral, snails. It seems too to be the method of choice, for, starting with similar full grown specimens, eggs and young will on the whole be obtained quicker if the snails are put together in pairs than if they are kept singly. What is remarkable is that the same snail will use both methods : if it cannot pair it will, somewhat later, proceed to self-fertilise.

Experiments in crossing albino and pigmented snails show that the foreign sperms have the advantage : an albino fertilised by a pigmented produces at first only pigmented young. But it may afterwards (without further copulation) produce albinos showing that it is quite prepared to use its own spermatozoa when it has exhausted those received from the pigmented snail. The same phenomenon is also clearly demonstrated for a shell-shape character when "Stelfox" (fig. 9, Plate 10) is crossed to our stock. The use of the two lots of sperms may for a short time actually overlap, showing that there is little hesitation in changing from one to the other. Thus, an albino was paired with a pigmented on April 8 and separated on May 9 ; on June 13, 63 pigmented, 11 albino and 9 dead young were found and the parent was moved to a fresh jar, in which on October 20 78 albinos and 1 pigmented were found. There is presumably in *L. peregra* as in some other hermaphrodite animals some degree of incompatibility between the eggs and sperms of the same individual which discourages self-fertilisation. Experiments with the ascidian *Ciona* have shown (see MORGAN, 1927, p. 64) that this tendency to self-sterility may be partly overcome by increasing the relative concentration of sperms to eggs, and it is possible that *L. peregra* self-fertilises when it has accumulated a sufficient excess of its own sperms.

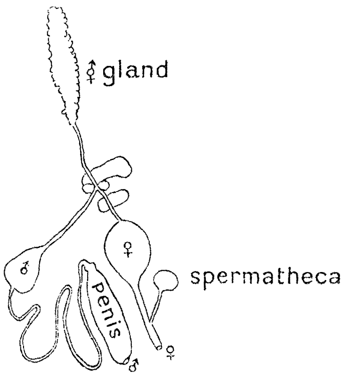

FIG. 1.—Diagram of genitalia of *Limnæa*.

II. METHODS.

Our earlier breeding was done at a variety of places (1925, p. 122). The greater part has always been at University College Hospital Medical School ("U.C.H.") in Central London, and since 1925 the only other places used have been gardens at the South-Eastern Fever Hospital at New Cross in South London, at Pembroke Square in West London, and at Radlett in Hertfordshire : relatively little has been done at the two last.

We have continued to use jars (known commercially as "4 lb. sticks") of coarse greenish glass with loose glass stoppers, 8 inches high by 5½ inches wide, holding about 2,000 c.c. or rather less, weeded with *Elodea* and without any sand or earth. With one or more snails to provide the necessary CO_2 these aquaria will often run without attention for 12 months or more : the less they are interfered with the better they will do. Our customary routine, especially in the earlier years, aimed at one brood in the year. The young of one year are kept in their jar through the winter : if there are more than about a dozen they will not grow much, and if they are fewer than about 200 there will not be any great mortality from overcrowding. In the following spring, any time from February to May, they are planted out singly or in pairs into fresh jars, and the broods will mostly be complete and ready to count in August and September, though they come to no harm if left until November or later.* Our previous experience that the jars should be filled with water and weeded about a fortnight before any *young* snails are placed in them has been fully confirmed. For the first few years we kept the jars indoors : in 1923 some, and since then all, of them have been kept out of doors,† on the flat roof of the Medical School or in a garden, and this has proved to be far more satisfactory. The only necessary precaution is to protect them from the sun on the few days in each year on which an average London summer will heat the water to a dangerous level (*i.e.*, about 35°—40° C.).

The eggs are laid at intervals over a period of a month or six weeks‡ in gelatinous capsules fixed to the glass or weed or, more rarely, loose. A capsule may contain anything from one to 100 eggs ; generally the average is 30—40 : we have hardly ever seen in our jars the long capsules with 200—300 eggs which *L. peregra* often lays in nature. When egg laying is finished, the parents do not grow much more and presently die : in the ordinary routine most of them are dead by October, though if they are moved to a fresh jar and protected from the competition of the young they may produce more eggs and sometimes make more growth. Those which lay no eggs or only a few go on growing and will generally live through the winter if they are given the chance.

There is a considerable mortality among the young, not so much immediately after birth as at an age of two or three weeks, when, we presume, overcrowding begins to have an effect. The larger the brood the greater the proportionate mortality : of 100 nearly all may survive ; of 800, three-quarters may be represented by tiny empty shells. The best technique for finding the whole brood in one of our jars is this :—

> Swirl round the jar with its weed so as to brush off most of the young which are sitting on the glass. Pour the whole contents into a white enamelled tray, about 15 inches by 12 inches and 3 inches deep. Search the jar carefully,

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* Some of the small dead shells may possibly dissolve and disappear if the jars are left too long.

† Bachrach and Cardot (1924) find experimentally that the eggs of *Limnæa stagnalis* and of the slug *Agriolimax agrestis* develop more quickly if they are cooled each day for half an hour. Cooling also has a stimulating effect on tissue cultures (Spear, 1929).

‡ Interesting details of the egg laying of *Limnæa luteola* in India are given by Sechaiya (1927) and of *Planorbis* in America by Cole (1923).

> brush off any snails with the help of some fresh water and a soft brush and add them to the tray. Fill another tray with clean water, transfer the weed to it *en masse* and search each piece separately, brushing off any young snails into the tray and returning the clean weed to the jar. Most of the young snails will fix themselves on to the bottoms of the trays in a few minutes. Pour off the contents of the first tray, containing accumulated dirt and *débris* and dead young, through a piece of soft muslin supported in the mouth of an empty jar, and gently wash the tray with a little fresh water. Take the piece of muslin and, holding it like a bag, wash it thoroughly with a good stream of water under the tap, by which means the dirt can be got rid of. Wash off what remains into a tray of clean water by inverting the muslin, and when the shells have settled to the bottom carefully pour away the water. By this means all the shells, alive and dead, are presented spread out clean on a white background, and by bare eye or with lenses they can be thoroughly scrutinised and enumerated. We have found magnifying spectacles* very useful. If it is desired to obtain the whole brood alive, the egg capsules should be taken as they are laid and moved to jars where the young will have ample room.

In a small proportion of cases, when jars have been urgently needed for other snails, we have not waited for the whole brood to hatch, but have been satisfied when 100 young could be counted: these broods appear in the records as "100 +."

The number of young which are obtained depends on following this standard routine or something like it. If the parent is moved to a fresh jar after it has laid about 100 eggs and again to another jar after laying another batch, and so on, the total number of eggs and young may far exceed what would have been produced in our routine: one such snail, for example, was induced to lay more than 3,000 eggs by successive moves to fresh jars, whereas about 500 is the average figure for our prolific strains, and about 1,500 the maximum. Our data for brood sizes therefore are significant only in relation to the conditions under which they have been obtained. At U.C.H., as far as we have been able to secure, these conditions have been uniform since 1924, and we have excluded from consideration in respect of brood size any instances where exceptional circumstances may be suspected to have influenced the number of young. Little importance should be attached to brood sizes before 1924 (*i.e.*, in gens. 1 to 5 of the line breeding).

By taking a little more trouble and by having abundance of jars two generations may be had in one season. This technique has been generally followed by TURNER, and in the experimental crosses from 1926 onwards. Without waiting for the brood to be finished the earliest hatched young are taken and planted out into well-ripened jars as soon as may be, up to about the first week in July. Most of these will grow up and produce normal broods by October: the shortest generation time which has been

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* Made by Messrs. W. Watson & Sons, 313, High Holborn, London, W.C.

actually observed is 57 days. If the infants are planted out in July and August only a few will achieve a brood that year, though something may be done by moving the jars indoors to warmer conditions in the autumn, and in this way it is sometimes possible to get three generations in a year. On the whole, however, breeding is poor outside May to October. Similarly there seems to be little advantage in growing up the young during the winter so that they are full-grown in March : the best results seem to be obtained if maturity is reached at the time of year which is appropriate for breeding.*

One of our standard jars used in the way we have described is enough to allow two snails to grow up and breed : they will, however, be distinctly smaller than corresponding single snails with the same accommodation. More than two snails will in most instances fail to reach sexual maturity except with a long delay. The limiting factor is food,† which for *L. peregra* is naturally algæ, growing on the weed or on the glass : the snails never eat green *Elodea,* though they feed on the decayed stalks and leaves. In smaller jars (2 lb. jam jars holding about 400 c.c.) the young will grow up only very slowly with *Elodea,* though animals which have matured under better conditions will lay in them : they are also very useful for storing young snails through the winter and at other times when no growth is desired.‡ But if the food supply is altered these rules no longer apply, and with enough feeding a young snail can be reared to maturity and will lay eggs in a $\frac{5}{8}$th-inch test-tube in about 15 c.c. of water. Lettuce and cabbage (especially when yellowing to decay) are good foods and their use is very helpful when it is desirable to grow individual snails up quickly for pairing. They seem to act partly by being directly eaten and partly by encouraging the growth of algæ. The disadvantage of their routine use is that the water is liable to become so foul that the eggs fail to hatch and broods may be lost, unless the jars are under constant supervision.

Pairing may be effected by planting out two young snails in the same jar and separating them when the first eggs are laid. But it is better to grow the parents up separately, either in large jars or in jam pots with extra feeding, so that they are adult about March or April. They are then put together. If they are anxious to copulate a few days' association is enough for reciprocal mating, or they may be left together for a month or more, or (which is perhaps best) until some eggs are laid. They are then separated into fresh individual jars. If it is desired to carry on to the next generation, it is important to use the first young born after separation, before the effect of the cross-fertilisation has had any chance of wearing off : later progeny may be the result of self-fertilisation. In the pairing in our line-breeding the parents were not as a rule

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* The natural breeding season of most lowland wild *L. peregra* is from March to June : it differs in different places, and exceptionally eggs may be found in early February or in November, the latter probably a second generation.

† See Turner (1926, 1927) and Crabb (1929).

‡ Snails, kept dwarfed for two or even three years, will quickly grow up and produce normal broods when they are given room and food enough : the capacity for growth is exhausted by growth, not by lapse of time (T. B. Osborn and L. B. Mendel, 1914, 1915).

separated. The treatment of any individual pair may be seen from the way the entries are made in the pedigree tables.

III. NOMENCLATURE AND DEFINITIONS.

The word " single " in reference to a snail is used to denote that the snail was isolated in early youth before sexual maturity and has been allowed to breed by self-fertilisation : " DS " = dextral single, " SS " = sinistral single. The word " pair " (" DP " or " SP ") denotes that two full sibs have been allowed to breed together and mutual cross-fertilisation is assumed. The word " cross " is used only where the two parents are derived from different lines, strains, etc.

A " *brood* " is the product of a single parent (or pair), a " *group* " the product of a single grandparent (or pair).

When the manifestation of a character is delayed for a generation (delayed inheritance), it is the phenotype of the brood (*brood-type*) that becomes of importance in determining the genotype of its parent snail. We designate the various brood-types by capital letters, as follows :—

A = broods in which all the snails hatched are dextral.
K = broods in which all the snails hatched are sinistral.*
E = broods in which sinistrals predominate but one or more dextrals are present.
F = broods in which dextrals predominate but one or more sinistrals are present.

When a snail that gives an A or F brood is paired with a snail that gives an E or K brood and both parents are allowed to lay in the same bottle, a mixed brood results, containing both dextrals and sinistrals : for descriptive purposes we call this a " C " brood, but the term has no genetic significance. The " B " broods (3 dextrals to 1 sinistral) of the 1925 paper we now regard as fortuitous mixtures of this kind.

For the different types of groups we have used the small Greek letters corresponding to the capital Roman letters applied to the brood-types, thus :—

An α group is one composed of A broods only.
A κ group is one in which K broods predominate but occasionally an E brood may occur.
An ε group is one in which E broods predominate but some K broods may be present.

When an individual self-fertilised grandparent is heterozygous for factors determining brood-type it gives rise in the process of segregation to a mixed group of dextral and sinistral broods, which we call a γ group.

The word "*family*" is used only for the whole progeny derived from one of the original pairs with which these experiments were started, *i.e.*, the " London family " and the " Radlett family."

The word " *strain* " is used loosely for the smaller branches of the families and does not imply genetic homogeneity, while " *line* " is restricted to the supposedly

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* By an unfortunate choice formerly called " D " broods.

homogeneous series of generations extracted from the various strains; for these we use the same Greek letters as for the corresponding groups.

In the crossing experiments we use the term "A-dextral" to denote a snail from an α line that will produce an A brood, and similarly an "E-dextral" is a dextral from an ε line that will give an E or K brood. The terms "E-sinistral" and "K-sinistral" are used in the same way.

The terms "A-ness," "K-ness" and "E-ness" are used to express the qualities which give respectively A, K and E broods.

IV. Dextral and Sinistral (A × K) Crosses.

From a careful examination of their attempts at copulation and influenced by the analogy of land pulmonates, we concluded (1925, p. 120) that it was impossible to cross snails of opposite twist.* When, however, in 1927, we put the matter to the test of experiment we found that mating was certainly possible and apparently not much more difficult than between two dextrals or two sinistrals. Turner succeeded, at any rate partially, in all of four trials; we had 8 failures and 9 successes, which is about the same result as we had, using the same technique, in crossing A-dextrals with E-dextrals.

In these experiments each snail to be used as a parent was grown up alone and when adult was put together with its mate into the same bottle. After sufficient time to allow of reciprocal mating each parent was again isolated. In the F_2 and subsequent generations the snails to be used as parents were isolated in early youth and allowed to self-fertilise (in a few cases pairs were made up between full sibs in F_1).

On the sinistral side we have used the albino line† established by the 1925 mutant in the brood 1629 (Table II): it is a strongly sinistral strain and breeds well (average brood size 273, 7 E broods in 74, 8 dextrals in 20,126 snails). With it we can be assured that crossing has taken place in F_1 on the sinistral side and in F_2 on the dextral side, without waiting for the change of twist to appear in F_2 and F_3.

The dextrals have been taken from several sources:—

(1) Lines derived from "dextral break-throughs" which from their behaviour were judged to be homozygous for dextrality (α lines):

  (*a*) from 4511 (1922) bred for 6 generations, giving 24 A broods with 2,425 dextral snails (Table I):

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* According to Büchner (Pelseneer, 1920, p. 743) dextral and sinistral *Helix pomatia* can copulate with one another, but the general experience is that they cannot.

† These are, as is usual in pulmonate mollusca (*e.g.*, *Planorbis corneus*: Oldham, 1928) partial albinos. At birth there is no melanin, but as the animal grows up the eyes develop a certain amount and they are dark grey when the snail is full-grown: they are never as black as in normally pigmented *peregra*. This eye-pigmentation appears earlier in 1929 than it did in 1926. The rest of the body remains without any melanin, but there is plenty of the diffuse golden pigment which most races of *peregra* have, so that it looks bright yellow. The shell is normal, *i.e.*, pale horn-coloured. Genetically, the albinism behaves as would be expected: it is a simple Mendelian recessive and the segregation ratio in F_2 is 3 to 1, as near as may be, *e.g.*, in one series 3,392 pigmented to 1,126 albinos against an expectation of 3,389 to 1,129.

(*b*) From 4532 (1923) bred for 6 generations, giving 41 A broods with 4,888 dextrals (Table I).

Both these lines arose in the London family and are closely related, and in both (especially in 4532) the body-colour of the snails is pale but not albino: they both breed rather badly.

(*c*) From 968 (1924) in the Radlett family, bred for 5 generations with 55 broods and 17,544 dextrals (Table V).

(2) Wild strains with no known history previous to the crossing:

(*a*) From a pond at Downham, near Catford in Kent: the breeding with this has been carried out by TURNER at the South-Eastern Hospital at New Cross:

(*b*) From the river Colne, between Colney Street and Munden, in Hertfordshire. A large flood deposit of snail shells obtained here in November, 1925, gave an opportunity of examining this population extensively. At present 104,248 shells have been sorted with the kind help of Dr. H. CHICK, Mrs. GIBBS, and Mr. L. E. ADAMS, and a single young sinistral has been found by Capt. G. C. C. DAMANT, R.N. Under our conditions it breeds badly but we have insufficient data to define a brood size.

The results show that sinistrality (using the term in a broad sense and including K, E and F broods) is inherited as a Mendelian recessive character, with a delay of one generation, albinism behaving as usual:

P_1		pigmented dextral		×		albino sinistral	
F_1		pigmented dextrals				pigmented sinistrals	
F_2		dextral broods each containing 3 pigmented to 1 albino				dextral broods each containing 3 pigmented to 1 albino	
F_3		γ groups				γ groups	
	3 dextral broods	to	1 sinistral brood		3 dextral broods	to	1 sinistral brood
F_4	dextral groups and further γ groups,		sinistral groups		dextral groups and further γ groups,		sinistral groups

Working with this material we have (Table VII) :—

Sinistral side.—12 crosses verified in F_1, 9 of which were carried to F_2, 3 to F_3 and 3 to F_4.

Dextral side.—4 crosses verified in F_2 ; 4 were taken on to F_3 and 3 to F_4.

The brood sizes are subject to a certain amount of qualification, since a good many of the F_2 and F_3 broods were obtained late in the summer under indifferent conditions ; no particular stress can therefore be laid on small broods. The crosses with the Catford strain of wild dextrals were bred in a garden at New Cross, the others on the roof of the Medical School, U.C.H.

F_1 dextral side.

In the four verified crosses three of the F_1 broods (containing respectively 128, 76 and 271 dextrals) do not obviously differ from what might have been obtained if no crossing had occurred.

TURNER, however, obtained two anomalous broods from wild Catford dextrals. One consisting of three pigmented sinistrals was not carried on any further. The other contained 162 dextrals and 3 sinistrals, all pigmented, and in F_2 and F_3 these unexpected sinistrals behaved like the product from either side of the cross, though in this actual cross the fully-pigmented brood of 270 sinistrals and 3 dextrals from the albino sinistral parent was not taken on.

It is impossible to give a certain explanation of this vagary. It is almost incredible that this wild dextral would by itself have produced three sinistrally-determined eggs, or that albino sinistral spermatozoa should have imposed immediate sinistrality upon dextrally-determined eggs without imposing albinism too. The most likely explanation seems to be that the sinistral parent transferred some of its eggs as well as its sperm to the dextral parent. COLTON (1912) makes the significant observation that he has often found eggs in the spermatheca of *Limnœa columella*, and CRABB (1927) working with *Limnœa stagnalis appressa* found that eggs not infrequently pass down the male passages and are ejected through the penis along with the spermatozoa. If this is really the explanation the three sinistrals and their progeny should be assigned to the sinistral rather than the dextral side of the cross : their transference, however, makes no difference in the final results.

F_1 sinistral side.

The 12 broods obtained were all pigmented (Table 1).

The series is probably homogeneous ($P = 0 \cdot 13$). The broods are rather smaller than those obtained by line-breeding the albino parent strain, but the breeding conditions of the two are not quite similar ; there are also rather more dextrals, the similarity of the two populations in this respect being expressed by $P = 0 \cdot 00072$. But in view of the possible transference of dextral eggs this difference can be neglected, so that apart from the pigmentation the sperm has had no obvious effect.

TABLE 1.—F_1 broods from the sinistral parents in A × K crosses.

Sinistral.	Dextral.	Sinistral.	Dextral.
222	—	127	—
270	3	162	—
142	—	142	—
80	—	242	—
331	1	116	—
337	—		
64	—	Total 2,235	4

Mean brood size = 195

F_2.

On the *sinistral side* nine crosses have been taken to F_2. Albino young, produced after the effect of crossing had been exhausted, were carried on in several instances, and as was expected produced sinistral albino broods of normal type. From the pigmented sinistral F_1 young we have (Table 2) 75 F_2 broods (74 singles, 1 pair) containing something more than 9,208 young (the exact number is not known as some of the broods were not counted out) : all the snails are dextral and, with the exception of two broods of one each, all the broods are mixtures of albinos and pigmenteds.

TABLE 2.—F_2 from A × K : all A broods.

Dextral parent in cross.	Dextral side.			Sinistral side.		
	No. of crosses.	No. of broods.	Mean brood size.	No. of crosses.	No. of broods.	Mean brood size.
From 4511	2	10	142	2	11	129
From 4532	—	—	—	1	2	305
From 968	—	—	—	3	6	270
Colne wild	1	2	55	2	9	62
Catford wild ...	1	9	64	1	47	(106 ?)
Total	4	21	—	9	75	—

On the *dextral side* four crosses were taken on, and gave 21 broods with more than 2,116 snails : all the snails are dextral and (with one exception, where there is no record) all the broods were mixtures of albinos and pigmenteds.

F_3.

Six of the crosses were carried to F_3 ; one on both sides, three only on the dextral side, and two only on the sinistral side. In all there are 340 broods. The results are given in detail in Table VII, and are summarised by crosses and groups in Table 3, under A, K, E and F broods.*

There is some uncertainty as to what E and F broods truly represent, but our view is (pp. 72 and 120 below) that both types are modified sinistral broods. We have, therefore, expressed the proportions in terms of A broods, and have regarded the K, E and F broods taken together as representing the sinistral element in the cross.

TABLE 3.—F_3 groups from A × K crosses.

A : wholly dextral broods. K : wholly sinistral broods. E : mainly sinistral with a few dextrals. F : mainly dextral with a few sinistrals.

Dextral parent.	Dextral side.						Sinistral side.					
	A.	K.	E.	F.	Total.	A per cent.	A.	K.	E.	F.	Total.	A per cent.
4511...	7	1	—	—	8	87·5	18	2	4	—	24	75·0
	14	1	3	—	18	77·7	22	—	2	—	24	91·7
	12	4	1	—	17	70·6	—	—	—	—	—	—
Total	33	6	4	—	43	76·7	40	2	6	—	48	83·3
4511...	12	6	2	—	20	60·0						
Colne	17	—	1	—	18	94·4						
Colne							17	2	1	—	20	85·0
Catford	13	2	1	—	16	81·2						
	4	1	—	—	5	80·0						
	5	1	—	—	6	83·3						
	9	1	—	1	11	81·7						
	8†	4	—	1	13	61·5						
	10†	5	—	—	15	66·7						
	3†	—	—	—	3	100·0						
Total	52	14	1	2	69	75·3						
Catford							7	4	1	—	12	58·3
							3	3	—	—	6	50·0
							33	7	1	1	42	78·6
							5	—	1	—	6	83·3
							13	7	—	1	21	61·9
							26	7	1	1	35	74·3
Total	—	—	—	—	—	—	87	28	4	3	122	71·3
Total ...	114	26	8	2	150	76·0	144	32	11	3	190	75·8

---

* In the Catford series some E broods are probably included under K, since they were not all counted out.

† From aberrant sinistrals in F_1, probably belonging to sinistral side.

Taking all the results together, the agreement with a 3 to 1 ratio is very close, and there can be little doubt that it is what the figures represent.

	Observed.			Expected.	
	A.	KEF.	Total.	A.	KEF.
Dextral side	114	36	150	112·5	37·5
Sinistral side	144	46	190	142·5	47·5
Both sides	258	82	340	255·0	85·0

The dextral side does not differ from the sinistral side in the proportion of A broods, and it makes no significant difference on which side the doubtful groups from 5911 (above, p. 62) are included.

Doubtful groups included on	Dextral side.				Sinistral side.			
	A.	KEF.	Total.	A per cent.	A.	KEF.	Total.	A per cent.
Dextral side	114	36	150	76·0	144	46	190	75·8
Sinistral side	93	26	119	78·2	165	56	221	74·7

Among the individual groups the ratio is naturally more variable: in one group of 20 broods there were only 12 A (ratio 1·5 to 1) instead of 15, and in another of 18 broods, 17 A (ratio 17 to 1) instead of 13·5. Such figures are, however, compatible with a 3 : 1 ratio, using the mild statistical criterion of a 20 : 1 chance; and the other groups are all, on one side or the other, within a likely range of random samples.

Nor are the results obtained from one dextral clearly different from those obtained with another, and the proportions obtained at University College Hospital Medical School ("U.C.H.") and by TURNER at New Cross are nearly the same, the chief difference being that all five F broods were found at New Cross.

Dextral parent.	Dextral side.				Sinistral side.				Both sides.			
	A.	KEF.	Total.	A per cent.	A.	KEF.	Total.	A per cent.	A.	KEF.	Total.	A per cent.
4511 ...	45	18	63	71·4	40	8	48	83·8	85	26	111	76·6
Colne ...	17	1	18	94·4	17	3	20	85·0	34	4	38	89·5
Catford	52	17	69	75·3	87	35	122	71·3	139	52	191	72·8
Total ...	114	36	150	76·0	144	46	190	75·8	258	82	340	75·9

Place.	Dextral side.				Sinistral side.				Both sides.			
	A.	KEF.	Total.	A per cent.	A.	KEF.	Total.	A per cent.	A.	KEF.	Total.	A per cent.
U.C.H.	62	19	81	76·5	57	11	68	83·8	119	30	149	79·9
New Cross	52	17	69	75·3	87	35	122	71·3	139	52	191	72·8

The only groups in which there is any substantial suspicion of a departure from a 3 to 1 ratio are those derived from Colne wild dextrals, in both of which there is an excess of dextral broods—17 out of 18 on the dextral side and 17 out of 20 on the sinistral side, in all 34 compared with an expectation of 28·5. It is true that these numbers do not differ from a 3 : 1 ratio by more than twice the standard deviation and by the χ^2 test P is 0·04 : they are also compatible with the other groups, though if they are compared with the group showing the largest defect in A broods the difference is $2\frac{1}{2}$ times its standard error and P is only 0·01. But it may be remarkable that, of three groups showing a considerable deficiency of sinistral broods, two should have come from Colne pairings, though there is (below, p. 103) no similar deficiency in the F_3 groups derived from pairing Colne wilds with E dextrals. The facts are suspicious, but it is impossible to be sure that they indicate anything definite. The results described below (p. 99) may also support the suggestion that Colne wilds are different from the others.

Of the 340 F_3 broods, 234 came from pigmented and 106 from albino parents. There is no apparent association between shell twist and albinism (Table 4).

TABLE 4.—Association between shell-twist and albinism.

Dextral parent.	Pigmented.		Albino.	
	Broods.	A per cent.	Broods.	A per cent.
4511	70	75·9	41	78·0
Colne	28	89·3	10	90·0
Catford	136	71·3	55	76·4
Total	234	74·8	106	78·3
All on dextral side	107	77·6	43	72·1
All on sinistral side	127	72·4	63	82·5

F_4 *broods.*

Twelve sinistral broods were tested, some on a very small scale, and all bred true, giving in all 36 K, 20 E and two of the aberrant broods (one A and one F) which we know as dextral break-throughs (below, p. 116).

Of sixteen dextral broods carried on, 5 gave dextral broods only and 11 mixed (γ) groups of A with E and (or) K. Adding the heterozygous groups together we have :—

Original dextral parent.	A.	K.	E.	F.	Total.
Catford	43	12	1	1	57
Colne	51	15	2	—	68
4,511	25	2	2	—	29
Total	119	29	5	1	154

giving 77·3 per cent. of A broods, or 119 against a 3 : 1 expectation of 115·5.

We have as confirmatory evidence of a 3 : 1 segregation ratio two other series, one derived from the heterozygous groups in the line-breeding (below, Table 35, and p. 127), the other from crosses between E (which are in effect sinistrals) and A (below, Tables 24 and 25 and p. 101). So that in all there are :—

	Number of broods.	A.	KEF.	A per cent.
A dextral × K sinistral F_3 and F_4	494	377	117	76·3
Line breeding	742	552	190	74·4
A × E : F_3 and F_4	357	263	94	73·7
Total	1,593	1,192	401	74·8
3 to 1 expectation	1,593	1,194·75	398·25	75·0

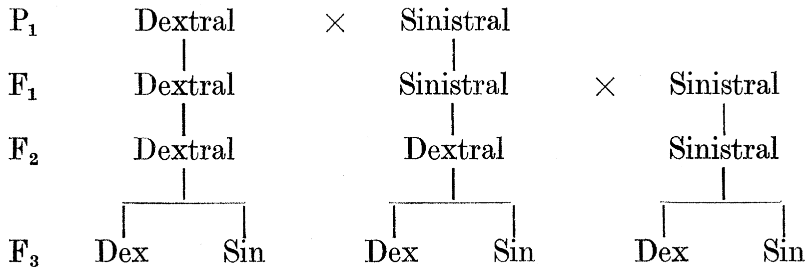
V. DELAYED INHERITANCE.

It seems clear, at any rate under the conditions of these observations, that

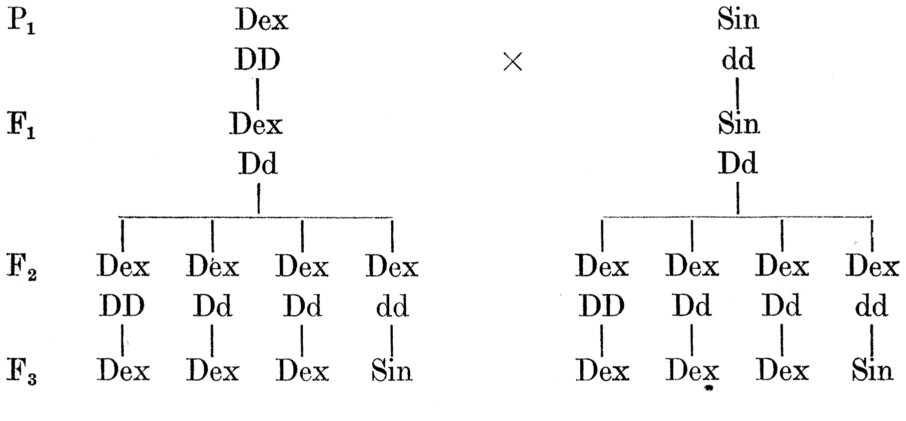
1. dextrality and sinistrality are simple allelomorphs :
2. dextrality is dominant and sinistrality recessive :
3. the manifestation of any change of twist imposed by crossing is delayed a generation.

The egg of a K-sinistral snail fertilised by the sperm of a homozygous A-dextral snail develops into a sinistral snail, as if nothing had happened. In the ordinary process of gametic assortment this snail has eggs which carry either the dextral-determining or the sinistral-determining factor. These eggs are fertilised by its own spermatozoa, also carrying either the one factor or the other. Again no immediate effect follows this rearrangement of the factors ; the F_2 brood is entirely dextral instead of a 3 : 1 mixture of dextrals and sinistrals ; each egg has been dextrally determined, prior to gametogenesis, by the dextral-determining factor introduced by the sperm at the original cross. But the rearrangement of the factors that took place at the fertilisation of the F_2 eggs becomes apparent in the F_3 broods ; thus of the resulting F_2 dextral snails three in every four produce dextral broods and one produces a sinistral brood. Again this result depends upon the fact that the final determination of the twist of the eggs of a snail takes place prior to gametogenesis, and the type of coil exhibited by its young depends on the presence or absence of a dominant dextral determining factor in its nucleus.

That this delay is not due to any general abnormality in the behaviour of the chromosomes is practically certain, from the normal behaviour of albinism in the same snails ; and that the nuclear changes *qua* twist are also normal is further supported by back-crossing, which gives this result :—*



Our scheme, therefore, of the appearance and the genetic constitution of our snails is :—



It is a clear and typical example of what has been called " maternal inheritance," " pre-inheritance," or " deferred nuclear action." The term " maternal inheritance "

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* This was actually obtained (below, p. 106) with crosses between A-dextrals and E-dextrals, the latter being (below, p. 91) genetically sinistrals.

has been used in a loose and irregular way to cover a variety of phenomena, and further confusion has been introduced by failing to distinguish between those parts of the young which are derived directly from the somatic tissues of the mother and those which are formed by the fertilised egg cell. " Delayed inheritance " seems on the whole the most suitable term, but, whichever expression is used, it would be well to restrict it, as we do here, to a form of inheritance in which both sexes contribute factors in the normal manner and in which phenotypical expression of the resulting character is delayed for a generation.

It seems a little uncertain whether any precise parallel has been established in animals. The classical examples are voltinism (number of broods *per annum,* in effect the rate at which the eggs develop and hatch) and egg colour in silkworms. Unfortunately, we cannot examine in detail the basis for the categorical statements in some of the text-books (MORGAN, 1919: MORGAN, STURTEVANT, MULLER and BRIDGES, 1926: MORGAN, 1927, pp. 596, 654) that the inheritance of these characters follows a plan entirely similar to the *Limnæa* scheme, because we cannot read Japanese; they are hardly borne out by such evidence as is available in English.

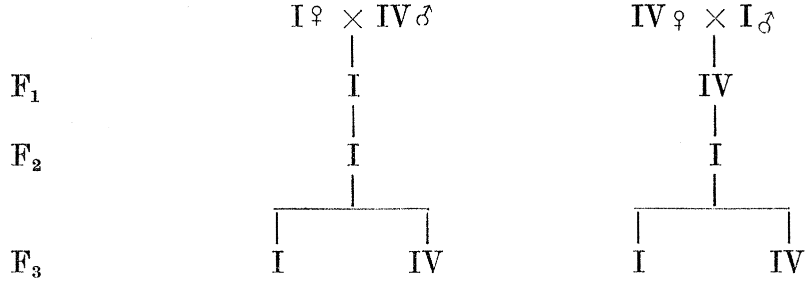
TOYAMA'S original observations (1913) on egg colour are confused, and he did not clearly distinguish between colours which are due to the egg shell (which is part of the mother) and those which are in the serosa of the actual embryo: it is obviously only these latter which need consideration. As PELLEW (1925) points out in her clarifying commentary, he found that three egg colours—blue, brown and crimson—are all recessive to the normal slate. The data for crimson are particularly clear and show simple mendelian inheritance with segregation in F_2; those for blue are less satisfactory, but as far as they go they indicate delayed inheritance with segregation in F_3; those for brown are inconsistent, some showing delayed, others ordinary inheritance. Crimson and brown are real embryo colours, but according to TANAKA (1924) blue is an egg-shell colour and its apparently delayed inheritance has no significance. UDA (1923) has published some remarkable results from a series of slate × brown crosses, in which the egg colour in F_1 follows the female, while in F_2 each brood consists of a 3 : 1 mixture of slates and browns. TANAKA (1924) explains this strange combination of delayed and normal inheritance by the hypothesis that there are two brown factors, one maternally, the other ordinarily inherited; he does not give the details of any experiments demonstrating either. But in the same paper he says :—

> " The characteristics of maternal inheritance may be summed up as follows :—
>
> (1) F_1 individuals are like the female parent, regardless of the dominance or recessiveness of her character.
>
> (2) Dominant characters appear only in F_2.
>
> (3) Segregation occurs, apparently for the first time, in F_3, between different batches, but never in the same batch.

> (4) *Both* the dominant *and the recessive* F_3 batches may, when inbred, give rise to both characters in the next generation.
>
> I have repeated experiments similar to Toyama's and have got the same results. The only difference is that Toyama (1913) gave the F_3 ratio as 2D : 1R, whilst it is evident, from my experimental results, that the ratio is actually 3D : 1R, as is theoretically expected."

In view of this statement, which is not accompanied by any detailed results, there seems no reason to doubt that some embryo colour (probably a brown) follows a system of delayed inheritance in the silkworm, though it is at least equally clear that another (crimson) is inherited in the ordinary fashion. Tanaka's summary of the criteria of "maternal" inheritance fits our *Limnœa* results precisely, except for the inexplicable words we have italicised: if he really means what he says there is substantial divergence.

We are in much the same uncritical position with regard to *voltinism*. The earlier results of I. McCracken (1909), with the comments of W. E. Castle (1910) and M. L. Cleghorn (1918) are not clear beyond F_1, but they appear to show that voltinism depends on the mother, irrespective of the father, that the univoltine condition is dominant to the multivoltine and that some sort of segregation occurs. Toyama (1913, p. 401) mentions voltinism only casually, saying that he believes from his results that it is inherited "maternally" and segregates. In 1923 Uda, when on a visit to this country, gave Bateson this diagram (I representing univoltine and IV tetravoltine) :—



and a similar scheme for crosses between bivoltine (dominant) and tetravoltine races. Tanaka (1924, p. 480) has no observations of his own, but says that Watanabe has published results in Japanese which "are exactly comparable with those of the four characteristics of maternal inheritance mentioned above," which we have already quoted.

It seems, therefore, fairly certain that in silkworms a brown colour of the serosa of the egg and the number of broods per annum (*i.e.*, the rate at which development proceeds) are inherited on the same plan as we have shown to prevail with the shell-twist of *Limnœa*. We regret that we have not been able to examine the original data in greater detail. The only other instance that we know of which seems analogous to our own is H. Redfield's (1926) sex-limited recessive lethal effect in *Drosophila*, which, in reciprocal crosses with normal, follows the mother in F_1, gives all normal in F_2, and segregates in some undetermined ratio in F_3.

It is hardly necessary to bring the results of interspecific crosses into the discussion. It has been known since BOVERI (1889) that the embryos and larvæ obtained by crossing different species of echinoderms and fish generally show characters which are exclusively maternal or more maternal than paternal, and that paternal characters may appear in a hybrid which was originally purely maternal (see the accounts in T. H. MORGAN (1927, Chap. XXV) and E. B. WILSON (1925, Chap. XIV)). In some of these experiments the sperm nucleus acts merely as a stimulus to what is in effect artificial parthenogenesis, in others some of the paternal chromosomes are eliminated, with an effect on inheritance which is not known and cannot be predicted. In some instances it is known that the cytological events following fertilisation proceed in the normal manner, but we do not know what the genetical result of this is, because none of the hybrids have been raised to maturity and carried on to subsequent generations.

The features which these four instances of maternal inheritance have in common is that the character which is involved appears at an early stage of development. The serosa of the silkworm egg is differentiated soon after the embryo begins to grow ; voltinism depends on the rate of embryonic development* ; REDFIELD'S lethal factor in *Drosophila* operates chiefly before the eggs hatch, and the twist of *Limnæa* is determined at the first division of the egg. It is an obvious suggestion (*cf.* UDA, 1923) that the effect of the sperm is deferred because it has not had time† to influence the behaviour of the zygote in respect of characters which appear at an early stage. In the elegant contrast between albinism and twist which they exhibit our snails are from the very start irrevocably committed for the rest of their lives to dextrality or sinistrality, whereas the choice between developing pigment or remaining without it might be left undecided almost indefinitely.‡ We may surmise that any other character with these qualities would show a similar system of inheritance. It is indeed possible that some delay in sperm influence is normal and that every embryo starts by being maternal, and that we expect the parental chromosomes to show their effects in F_1 because the appearances of such characters as have been examined are not determined at the earliest stages of development. If this is so, "delayed" inheritance differs from

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* In interspecific crosses between species having different rates of egg segmentation the hybrid eggs divide at the rate characteristic of the mother.

† We do not actually know, in *Limnæa*, the interval between the entrance of the sperm and the beginning of segmentation, which commences immediately the eggs are laid. Eggs giving rise to young which show paternal characters may be laid as soon as 2 days after copulation, but exactly when and where fertilisation occurs is still unknown.

‡ Actually the eye pigment appears some time before hatching ; the mantle and body pigment is fully developed only in snails about one-third grown. Our albino strains produce a little melanin in the eyes when they are adult.

normal inheritance, not in its mode, but in the nature of the characters which give it phenotypic expression. It may be more correct to attribute the phenomena in *Limnœa* to " accelerated character determination " than to " deferred nuclear action."

VI. ANOMALIES.

We have shown that the quality of sinistrality is the product of a gene, that this gene is a simple recessive to its normal allelomorph which produces dextrality, and that the phenotypic product of this allelomorphic pair is delayed for one generation, so that segregation appears among the broods in a group and not, as in direct inheritance, among the individuals in a brood. This definitely implies that all the snails in any one brood should be of the same twist. If, as we believe, this simple system provides a reasonable explanation of the primary facts of our line-breeding and crossing, then the occurrence of single broods containing both phenotypes or of dominant broods in recessive lines is anomalous and implies either a breakdown in the system or the presence of other factors that modify its expression.

There are three main groups of occurrences which are thus apparently anomalous, and owing to the extra attention which has been paid to them they figure in the pedigree tables of the line-breeding with disproportionate frequency :—

(1) E broods, mainly (and genetically) sinistral with a varying proportion of dextrals, are quite common ;

(2) F broods, mainly dextral with a few sinistrals, are much less frequent ;

(3) we have had a number of dextral broods (" dextral break-throughs ") leading to pure or heterozygous dextral lines which have arisen in pure recessive groups, sometimes after two or three generations of self-fertilising sinistrals.

We attempt to show below that F broods (p. 120) and dextral break-throughs (p. 116) represent an actual breakdown in the system, *i.e.*, they are the produce of new mutation which under our conditions occurs rather commonly. Since we know (*e.g.* DEMEREC, 1928) that reverse mutations of this type do sometimes occur with very high frequency, it might be reasonable to suppose that the dextrals in E broods were attributable to the same cause or to an anomaly involving direct segregation within a brood. This is in fact not the case : E broods are sinistral broods containing phenotypic dextrals, and they represent not a breakdown, but a modification of the system.

Between the three types of anomaly there is this common bond, that dextrals, some genotypic, some phenotypic, tend to appear where sinistrals would be expected.

(1) *E Broods and ε Groups and Strains.*

By definition a K brood consists entirely of sinistral snails. An E brood is a mixed brood of sinistrals and dextrals obtained from a self-fertilising single,* in which sinistrals

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* Or from a pair in an ε strain of established constitution.

predominate and which is (as we shall show) essentially a sinistral brood genetically. The proportion of dextrals varies widely : it does not often exceed 25 per cent., and there may be anything from one dextral in several hundred sinistrals to equal numbers. Occasionally the dextrals may be in excess and by strict definition these broods should be graded as F,* but the test of their essential E-ness is their genetic behaviour. A brood of five dextrals to one sinistral is the most extreme case we have verified in this way. We may by the same means be able to identify the rare brood of one or two dextrals as an E brood. This method is possible because *the dextrals are equivalent to their sinistral sibs*, *i.e.*, they are phenotypic, not genotypic. Their appearance is associated with irregularities in development and an excess embryonic mortality which leads to small broods, the dextral components of which are to be regarded as viable monsters.

E broods appear only in the presence of sinistrality, and no analogous abnormality appears in pure dextral lines. The tendency to produce them is definitely heritable, and it might be brought about by :—

(*a*) Environmental factors.
(*b*) Extra-nuclear factors (*e.g.* cytoplasmic).
(*c*) Nuclear factors or genes.

Environmental circumstances have some effect, but the results cannot be explained solely by them. The assumption of cytoplasmic factors does not satisfy the facts any better, and on the whole the most likely explanation seems to be that E-ness is the product of genes which do not themselves produce a type of sinistrality, but effect a pull towards dextrality when they are in the presence of the sinistral determining gene.

E broods occur more or less abundantly in all our sinistral strains which have been bred to any considerable extent.† To some degree, therefore, the quality which we may call " E-ness " is present in all our sinistral strains, though groups such as—

——	——									Total.	K broods.	E broods.	Average brood size.
Sinistrals	5	37	13	11	12	13	21	27	33	172			
Dextrals	4	13	5	6	10	2	7	8	7	62=26·6 per cent.	0	9	26
Sinistrals	30	49	34	17	10	2	19	74		235			
Dextrals	4	9	7	2	2	0	5	7		36=13·3 per cent.	1	7	34

---

* We thought in 1925 that F broods might prove to be the dextral analogue, but we can now show that this is not the case ; their genetic behaviour is quite different.

† We have one extensively bred strain (the heterozygous A K from 706, Table II) in which no dextral has appeared in its sinistral broods from generation 5 onwards for six generations, the recessives adding up to 95 K broods with 16,216 sinistrals.

are in definite contrast with groups such as—

Sinistrals	178	164	213	208	119	174	168	209	1,433	6	2	179
Dextrals	0	1	1	0	0	0	0	0	2=0·1 per cent.			
Sinistrals	117	108	385	299	313	200	303	85	1,810	8	0	226
Dextrals	0	0	0	0	0	0	0	0	0=0·0 per cent.			

The first two are ε groups (though one contains a K brood), the second two we should call κ groups (though one contains two E broods). Between these two kinds of groups (and the examples include about the extremes which have occurred) we can arrange a series of intermediates. Starting with extreme K-ness, as the proportion of E broods to K broods increases, so the proportion of dextrals to sinistrals in each brood tends to rise till E-ness reaches its most complete expression in groups in which about 20 per cent. of the snails are dextrals and all, or nearly all, the broods are E broods. ε and κ groups breed approximately true, giving rise to ε and κ strains.

In trying to solve the fundamental question whether E-ness is really qualitatively different from K-ness, it is convenient to have some simple quantitative expression of these varying degrees of E-ness. The percentage of dextrals in the group or strain is fairly adequate. It does not, however, take into consideration the relative number of K and E broods,* nor the number of snails which have been bred, so we have used the formula

$$k = \frac{\text{total number of young in hundreds} \times \text{total number of broods}}{\text{number of dextral young} \times \text{number of E broods}}.$$

k being a measure either of K-ness (*i.e.*, pure sinistrality) or of E-ness: the more purely sinistral the group or strain, the higher the value of k. The four examples given above have $k = 0{\cdot}037$, $0{\cdot}086$, $28{\cdot}7$ and $144{\cdot}8$ respectively. There is no natural upper limit, the figure depending on the numbers of broods and young: experience puts the lower limit near 0·02, the figure for a group of E broods with 50 per cent. of dextrals.† Obviously the lower values of k are reliable only when the breeding has been fairly ample.

If we put together all our κ and ε groups which are large enough to give fairly accurate figures, we get a graded series of which some of the members are shown in Table 5.

The whole series of 223 groups is shown in fig. 2. We have a complete gradation of k values from 0·03 to 1722, *i.e.*, from intensely ε groups to almost purely κ groups. There are no obvious gaps in the series, and it is difficult to draw a sharp distinction

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* As a matter of fact the dextrals in an ε group are seldom concentrated in one or two broods so that k and the percentage of dextrals generally give much the same relative results.

† The actual lowest and highest are 0·027 and 15,000.

TABLE 5.—Series of κ and ε groups.

No. of broods.	No. of E broods.	No. of snails.	No. of dextrals.	k.	Dextrals per cent.
14	13	599	108	0·05	18·1
31	30	1,521	178	0·09	11·7
15	9	385	39	0·16	10·1
11	10	976	32	0·34	3·3
12	8	1,198	17	1·06	1·4
11	6	1,853	9	3·77	0·5
20	8	2,223	11	5·05	0·5
14	4	3,834	19	7·06	0·5
14	4	2,242	4	19·6	0·18
28	3	2,123	5	39·6	0·24
12	1	952	1	114	0·11
10	0	4,030	0	403	0·0
28	2	7,916	2	554	0·025
16	1	6,055	1	969	0·017

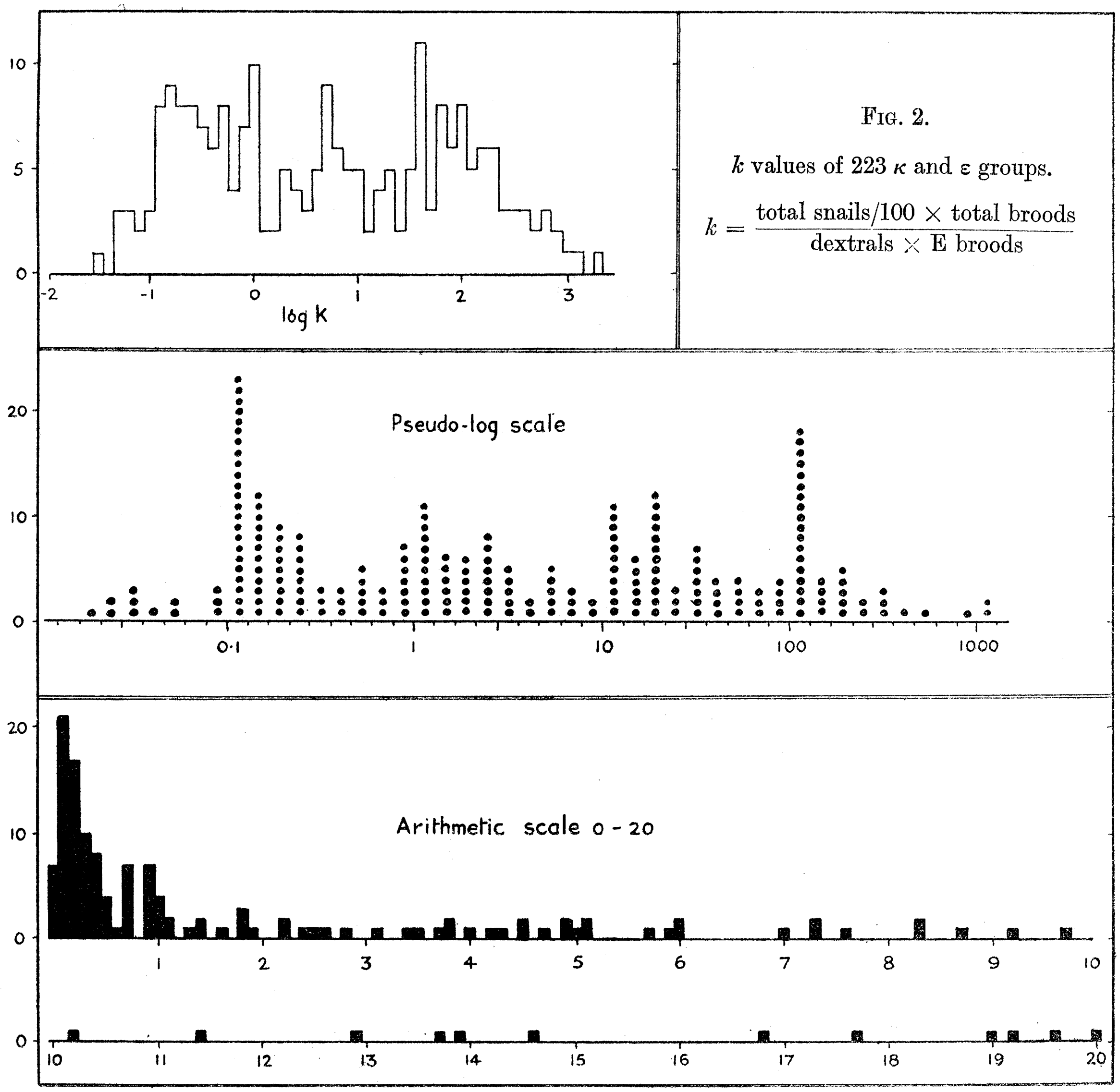

FIG. 2.

k values of 223 κ and ε groups.

$$k = \frac{\text{total snails}/100 \times \text{total broods}}{\text{dextrals} \times \text{E broods}}$$

between ε and κ. In general, however, and with the proviso that the known ancestry of any strain must be taken into consideration, we classify groups and strains as follows :—

k less than 1 : definite ε.
k between 1 and 10 : indeterminate.
k more than 10 : κ.

The significance of the peaks in fig. 2 is difficult to be sure of, because the numerical abundance of different values of k is so much affected by (1) our choice of what strains should be carried on and to what extent, and (2) our judgment as to what may fairly be called separate strains. Certain strains and their substrains have been bred much more extensively than others, and in closely-related strains it is difficult to be consistent in deciding what degree of difference constitutes distinction. We cannot be sure that the peaks represent anything more than selective breeding. The evidence as a whole is consistent with the view that the most completely κ and ε strains are the end terms of a graded series ; on the other hand, established κ and ε strains are very distinct from one another and the border-line groups (k between 1 and 10) occur mostly in places in the pedigrees where it is not unreasonable to suppose that heterozygous K E groups might be present.

The main facts about the occurrence and behaviour of ε strains will be best apprehended by a study of the pedigree tables, especially I and VI. The data have been pretty thoroughly analysed in a variety of ways, of which it is impossible to give a full discussion. The following summary covers the chief points :—

(*a*) *Origin and progress of* ε *strains.*—E broods may occur anywhere in sinistral lines or as the recessive component of heterozygous dextrals. In both our line-bred families sinistral strains have sooner or later given E broods among K broods. A number of these E broods when bred on have established ε groups and strains composed exclusively or predominantly of further E broods ; others have established κ lines. Heterozygous dextrals may break up into A and E (*e.g.*, Table IV) as well as into A and K, and ε groups have also been extracted from A × K and A × E crosses (below, p. 111).

Well-marked ε strains commonly arise from an E brood with a large proportion of dextrals occurring as a heterogeneous member of a sinistral group, *e.g* :—[*]

London family (Table I) gen. 4 : 153/0, 2/0, **35/4**, 172/0, 72/0, 51/0.
Radlett family (Tables IV and VI) gen. 4 : 12/0, 6/0, 64/0, 19/0, **9/4**.

The incidence of this phenomenon might be called sporadic, and with our data cannot be proved to be systematic : it is, however, compatible with the view that E separates off from K much as a recessive segregates from a heterozygote. It has occurred only in the earlier generations of our line-breeding (mostly gens. 3 and 4) and no fresh ε strains have arisen in the established κ strains in gens. 6 to 10.

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[*] 153/0 = 153 sinistrals and no dextrals ; 9/4 = 9 sinistrals and four dextrals, and so on throughout.

The proportion of dextrals in a strain varies roughly with the proportion in its primary brood of origin (Table 6), though a very small κ brood (*e.g.*, 5/0) may have a progeny appropriate to its real nature, *i.e.*, an E brood from which dextrals are absent by accident. A high percentage tends to fall in subsequent years, and we have not succeeded in maintaining a strain with as much as 20 per cent. of dextrals. A low percentage in the primary brood may subsequently rise somewhat. In the first group produced from the primary brood there may also be further separation into distinctive substrains, the percentage of dextrals in which follows roughly the percentage in the brood from which it came : *e.g.* (Table 6, Table VI, fig. 3) :—

Reference number	..	331
Primary brood	..	9/4

Reference number	..		672	671	677	678	
Primary group	..	326/93 containing broods of	17/16	20/4	54/3	31/0	carried on
Mean percentage of dextrals in six following years	..		14·4	10·6	7·1	2·3	

But in later generations, in stabilised ε strains, this relation between parent and offspring does not hold. The proportion of dextrals in each strain remains much the same (fig. 3), *e.g.*, the high ε strain from 672 (Table VI, Table 26) remains quite distinct

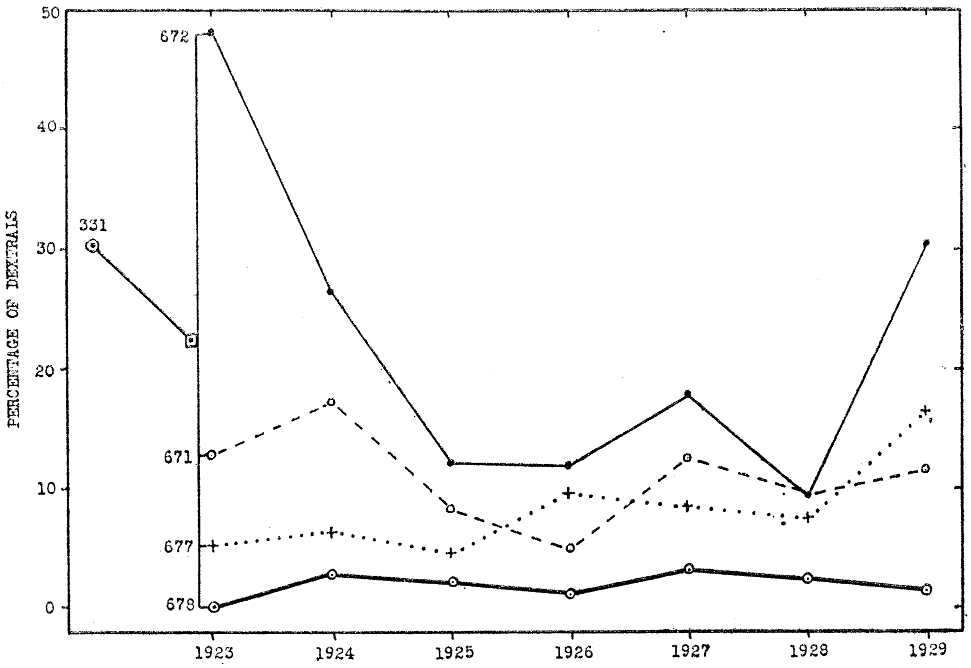


FIG. 3.—E Strains—Inheritance of Percentage of Dextrals.

TABLE 6.—Mean brood size and percentage of dextrals by years in ε and κ strains: arranged in order of brood size. Strains with k = under 10 are classed as ε.

Table.	Origin.	Primary brood.		1923.		1924.		1925.		1926.		1927.		1928.		1929.		Weighted mean.		
		Sin.	Dex.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	Brood.	Per cent. D.	*k*.
ε strains	(29).																			
II	1580	88	0	—	—	—	—	—	—	179	**0·6**	(339	**0·1**)	(150	**1·0**)	(191	**0·3**)	201	**0·46**	6·6
II	711	352	1	—	—	112	**1·8**	304	**0·5**	—	—	—	—	—	—	—	—	193	**0·93**	1·6
IV	2254	300	9*	—	—	—	—	148	**2·5**	—	—	—	—	—	—	—	—	148	**2·5**	0·4
I	939	624	29	—	—	—	—	197	**2·1**	124	**1·5**	136	**1·4**	64	**2·0**	103	**5·7**	141	**2·4**	0·6
IV	2361	175	10	—	—	—	—	188	**1·4**	153	**0·6**	111	**0·5**	(121	**1·2**)	149	**0·9**	139	**0·80**	2·4
IV	2174	5	0	—	—	26	**2·9**	167	**0·5**	—	—	—	—	—	—	—	—	130	**0·61**	3·1
IV	2115	10	0	—	—	—	—	122	**0·4**	—	—	—	—	—	—	—	—	122	**0·41**	4·9
II	1859	358	2	—	—	—	—	—	—	119	**0·5**	—	—	—	—	—	—	119	**0·50**	4·0
IV	2361 het. ...	—	—	—	—	—	—	—	—	—	—	167	**2·4**	91	**1·7**	—	—	109	**1·98**	0·7
IV	2814	98	5	—	—	—	—	—	—	(37	**1·8**)	100	**1·4**	—	—	—	—	87	**1·5**	1·1
I	749 U.C.H. ...	39	4	—	—	62	**4·4**	91	**2·4**	—	—	—	—	—	—	—	—	80	**3·0**	0·5
II	1004	—	—	—	—	—	—	—	—	70	**0·9**	98	**0·6**	—	—	(54	**1·2**)	79	**0·84**	3·2
II	565	150	2	—	—	75	**1·1**	—	—	—	—	—	—	—	—	—	—	75	**1·1**	1·5
V	114	32	4	—	—	64	**0·4**	83	**1·2**	—	—	—	—	—	—	—	—	74	**0·87**	3·2
II	1004 seg. dex. ...	—	—	—	—	—	—	—	—	73	**0·9**	—	—	—	—	—	—	73	**0·92**	2·2
IV	2811	160	1	—	—	—	—	—	—	(32	**3·0**)	86	**3·3**	(33	**2·0**)	—	—	71	**3·1**	0·4
III	1943	125	0	—	—	—	—	—	—	122	**0·9**	(12	**0**)	(46	**0**)	50	**2·7**	71	**1·5**	1·6
IV	2210	19	1	—	—	—	—	63	**5·0**	—	—	—	—	—	—	—	—	63	**5·0**	0·1
V	684	43	1	—	—	58	**4·3**	57	**4·8**	78	**8·3**	—	—	—	—	—	—	61	**5·2**	0·3
IV	7262 het. ...	—	—	—	—	—	—	—	—	—	—	123	**0·8**	40	**1·1**	—	—	58	**0·99**	2·4
III	726	11	3	—	—	32	**3·7**	66	**4·2**	25	**6·8**	20	**5·1**	(20	**15·0**)	—	—	47	**4·6**	0·3
VI	671	20	4	—	—	31	**17·4**	36	**8·5**	52	**5·0**	66	**12·8**	29	**9·7**	34	**11·6**	42	**10·6**	0·1
VI	678	31	0	—	—	29	**3·0**	45	**2·5**	36	**1·3**	48	**3·3**	18	**2·8**	24	**1·6**	37	**2·3**	1·0
VI	670	30	8	—	—	43	**8·0**	27	**2·8**	—	—	—	—	—	—	—	—	37	**6·5**	0·2
VI	677	54	3	—	—	37	**6·8**	34	**4·9**	39	**9·9**	28	**8·8**	13	**7·7**	19	**16·8**	32	**7·1**	0·2
VI	672	17	16	—	—	26	**26·5**	27	**12·1**	49	**12·0**	40	**18·0**	16	**9·5**	6	**30·7**	29	**14·4**	0·1
I	749 P. Sq. ...	39	4	—	—	—	—	—	—	67	**10·5**	17	**6·1**	16	**7·5**	35	**5·2**	24	**7·4**	0·2
III	1613	4	2	—	—	—	—	—	—	19	**0·9**	15	**12·9**	(4	**0**)	—	—	14	**5·8**	0·7
VI	668	5	0	—	—	12	**10·4**	—	—	—	—	—	—	—	—	—	—	12	**10·4**	0·2

κ strains (19).

IV	1185	322	0	—	—	—	—	321	**0·09**	—	—	—	—	—	—	—	—	321	**0·09**	41
III	945	155	1	—	—	—	—	403	**0**	288	**0·17**	330	**0**	(200	**0**)	—	—	319	**0·08**	109
II	1307	159	0	—	—	—	—	275	**0·21**	—	—	—	—	—	—	—	—	275	**0·21**	11
II	301	77	0	261	**0·03**	76	**0**	157	**0·24**	407	**0·03**	226	**0**	283	**0·08**	239	**0**	273	**0·05**	266
II	970	367	0	—	—	—	—	441	**0·05**	151	**0**	228	**0**	108	**0**	—	—	227	**0·02**	940
II	706	—	—	—	—	187	**0**	42	**0**	100	**0**	285	**0**	168	**0**	243	**0**	209	**0**	3,180
IV	2177	107	0	—	—	—	—	209	**0**	—	—	—	—	—	—	—	—	209	**0**	103
II	4103	195	0	—	—	198	**0·03**	243	**0·06**	196	**0**	201	**0**	—	—	—	—	208	**0·03**	566
IV	2255	624	8*	—	—	—	—	195	**0·31**	—	—	—	—	—	—	—	—	195	**0·31**	11
II	4108	25	0	175	**0**	251	**0·04**	—	—	—	—	226	**0**	(191	**0**)	(46	**0**)	189	**0·01**	2,580
II	192 het. ...	—	—	—	—	95	**0·04**	170	**0**	291	**0·01**	147	**0·17**	—	—	—	—	186	**0·02**	1,190
VI	1645	23	0	—	—	—	—	—	—	204	**0**	201	**0·04**	118	**0·50**	(78	**0**)	179	**0·08**	109
II	297	88	0	—	—	144	**0·06**	212	**0**	—	—	—	—	—	—	—	—	165	**0·04**	422
III	1623	138	0	—	—	—	—	—	—	181	**0·21**	200	**0**	(61	**0**)	(141	**0**)	163	**0·12**	122
II	943	47	0	—	—	—	—	258	**0·11**	120	**0·04**	165	**0**	(134	**0**)	—	—	151	**0·06**	326
VI	7269	277	0	—	—	—	—	—	—	—	—	165	**0**	(84	**0·59**)	—	—	151	**0·05**	218
II	4102	88	0	122	**0·05**	84	**0**	283	**0**	79	**0**	97	**0·51**	71	**0**	101	**0**	145	**0·04**	470
VI	7270 seg. ...	—	—	—	—	—	—	—	—	—	—	174	**0**	139	**0·10**	85	**0**	128	**0·07**	154
II	1412	86	1	—	—	—	—	117	**0**	—	—	—	—	—	—	—	—	117	**0**	75

* Pairs. Figures based on inadequate numbers are bracketed.

	Mean brood size.	Mean per cent. dextrals.	Mean dextrals per brood.
ε strains (29)	81·2 $\sigma = 47{\cdot}8$	3·510 $\sigma = 3{\cdot}527$	1·744 $\sigma = 1{\cdot}132$
κ strains (19) ...	197·7 $\sigma = 56{\cdot}75$	0·105 $\sigma = 0{\cdot}076$	
ε and κ strains (48)	129·75 $\sigma = 79{\cdot}0$	2·148 $\sigma = 3{\cdot}16$	

Coefficients of correlation : brood size and percentage of dextrals :	48 ε and κ strains	— 0·67 ± 0·08
” ” ”	29 ε strains	— 0·68 ± 0·10
” ” ”	19 κ strains	+ 0·20 ± 0·27
” ” ”	29 ε and κ in 1925	— 0·60 ± 0·14
” ” ”	27 ε and κ in 1927	— 0·67 ± 0·11
” dextrals per brood :	29 ε strains	— 0·21 ± 0·18
percentage of dextrals and dextrals per brood :	29 ε strains	+ 0·62 ± 0·11

from the low ε strain from 678 (Table VI). And within such a strain the E-ness of a group does not correspond with the E-ness of the brood from which it comes, but with the E-ness of the strain to which it belongs (Table 7).

TABLE 7.—Percentage of dextrals in parent broods and offspring groups in 672 line (Table VI).

Parent.	Offspring.	Parent.	Offspring.
55·5	13·1	20·8	12·3
48·5	26·5	18·3	21·1
44·4	12·5	15·0	16·9
35·4	10·5	11·8	18·5
34·2	13·3	11·4	17·0
26·0	13·7	8·5	20·0
26·0	17·4	7·5	11·1
22·8	5·9	7·0	12·2
		5·3	3·8

$r = +0{\cdot}179 \pm 0{\cdot}235.$

Our tendency has been to carry on from high percentage broods, but this has certainly not led to any general increase in the proportion of dextrals. The characteristic of the strain is reproduced rather than the characteristic of the individual brood.

Within one of these stable strains the variation in the number and percentage of dextrals in the broods is considerable. If we apply the statistical test for homogeneity (FISHER, 1928, p. 89) we find that groups, and all the groups of a strain in one year taken together, are more often than not compatible with the broods being random samples of the same population. Thus for the 31 broods obtained in the 672 strain (Table VI) in 1926 P = 0·28, for the 49 broods in 1925 P = 0·01 : the distribution of this last series is summarised in Table 8. The range is from 24/0 to 4/5 and the broods which tend to disturb the homogeneity of the series are those with an excessive proportion of dextrals, *i.e.* 4/5 and 27/14. And it is to this type of aberrant brood that the persistent lack of homogeneity shown by some strains (*e.g.*, strain from 671, Table VI) is nearly always due. These aberrant high E broods have been frequently tested and do not in a stabilised strain give rise to groups of more than average E-ness. Only very occasionally is it a large K brood which is outside the reasonable range of chance distribution.

(*b*) *Emergence of other brood types from ε strains.*—ε strains normally continue as such, qualitatively and approximately quantitatively, except for the homozygous or heterozygous dextral mutants which we know as "dextral break-throughs." These have a special tendency to appear in ε rather than κ strains, especially at or about the initiation of ε strains and from dextrals in E broods : their incidence is fully discussed below (p. 119).

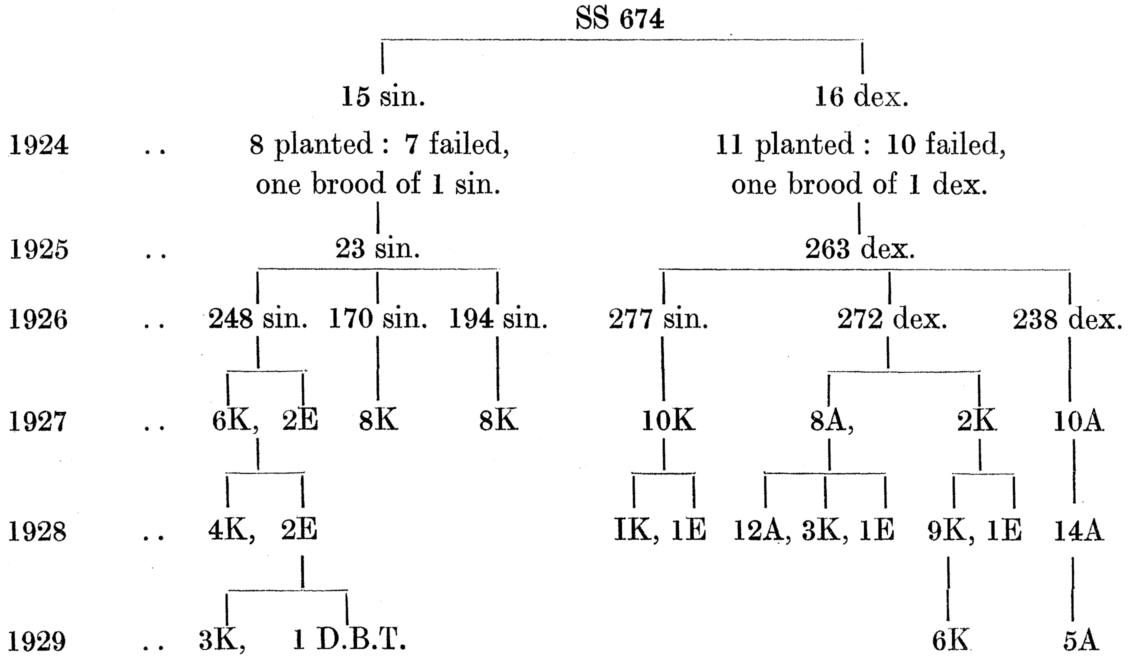
TABLE 8.—ε strain from 672 : 49 broods in 1925. They satisfy the test (P = 0·01) that they may be random samples of a population containing 12·1 per cent. of dextrals.

Sin.	Dex.	Sin.	Dex.	Sin.	Dex.	Sin.	Dex.	Sin.	Dex.
79	14	4	5	10	3	3	1	6	0
27	14	60	4	17	2	3	1	5	0
52	13	60	4	14	2	24	0	4	0
51	9	35	4	9	2	16	0	3	0
34	9	31	4	8	2	15	0	3	0
44	8	30	4	7	2	15	0	2	0
92	7	37	3	18	1	11	0	1	0
54	7	30	3	10	1	10	0	1	0
49	5	26	3	8	1	8	0	1	0
20	5	11	3	5	1	7	0	—	

Mean brood size = 27.

Mean percentage of dextrals = 12·1.

One instance is of a rather special character. The progeny of SS 331 gave well-marked E broods, and those which have been carried on have remained ε except for two dextral break-throughs, and the young of SS 674 (Table VI), which, after a convulsion which proved nearly fatal, broke up into ordinary large-brooded K and heterozygous AK broods, and no further small-brooded E appeared.



Average brood size : A 247, K 164 (see Table 10).

We have no "explanation" to offer: presumably the agent, whatever it was, that nearly killed the whole strain was also responsible for the change in type. It is the only proved example in our line-breeding in which κ has come from ε, though in our crossing experiments tolerably complete κ has been derived from A × high E crosses (below, p. 112).

(*c*) *Brood Size.*—ε strains are characteristically smaller brooded than the immediately related α and κ strains. Table 9 shows the brood sizes in the strains from SS 331 compared with those of representative segregating dextral and sinistral groups bred alongside under the same conditions: 96 per cent. of the broods in the ε strains (which may be called shortly ε broods) are under 100, compared with 36 per cent. of the κ broods and 18 per cent. of the A broods. On the average the κ broods are four times as large as the ε broods and the A broods six times.

Some of the small broods are due to environmental causes: odd jars in a series become overgrown with algæ, or the weed for some reason dies, or the jar is overheated in hot weather, and as a result the snail does not lay or the eggs do not hatch.

TABLE 9.—Distribution of brood sizes in 1924–1927 for 291 dextral and 319 sinistral broods from SP 36 (Table II) and for 368 broods in ε groups descended from SS 331 (Table VI). All bred under the same conditions: singles only. The distributions of the totals are shown as percentages.

—	No. of broods.	Under 50	Brood size.												Mean brood size.
			50–	100–	150–	200–	300–	400–	500–	600–	700–	800–	900–	1,000	
1924 dex. ...	64	10	7	3	10	12	7	8	3	1	1	1	0	1	283
sin. ...	52	18	11	2	10	5	5	1	—	—	—	—	—	—	122
ε	96	72	21	1	2	—	—	—	—	—	—	—	—	—	30
1925 dex. ...	70	4	8	6	2	27	19	1	2	0	1	—	—	—	246
sin. ...	89	9	15	12	10	21	11	4	3	2	1	1	—	—	221
ε	179	134	38	5	2	—	—	—	—	—	—	—	—	—	38
1926 dex. ...	74	3	11	20	11	16	11	2	—	—	—	—	—	—	188
sin. ...	119	13	35	26	23	13	6	2	1	—	—	—	—	—	141
ε	52	35	15	2	—	—	—	—	—	—	—	—	—	—	48
1927 dex. ...	83	5	2	6	7	27	16	11	3	5	0	1	—	—	304
sin. ...	59	10	5	10	10	12	10	1	1	—	—	—	—	—	189
ε	41	25	14	2	—	—	—	—	—	—	—	—	—	—	46
Total—		per cent.													
dex. ...	291	8	10	12	10	28	18	8	3	2	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{3}$	256
sin. ...	319	15	21	16	17	16	10	2	2	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{3}$	—	—	169
ε	368	72	24	3	1	—	—	—	—	—	—	—	—	—	38

Largest A brood ... ... 1,085.
,, K brood ... ... 831.
,, ε brood ... ... 186 (184 sin., 2 dex.).

> Dextral A broods of less than 50 are apparently almost always due to this, and presumably about the same proportion (5–10 per cent.) of the small broods in κ and ε strains should be attributed to the same cause.

This relationship generally holds good, but there are some strains which clearly fall in the ε category ($k = <1 \cdot 0$), which have an average brood size equal to that of κ strains. Thus the well-bred strain from SS 939 (Table I) started with a unique brood of 624 sinistrals and 29 dextrals, and in successive years had average brood sizes of 197, 124, 136, 64 and 103, with altogether 2·4 per cent. of dextrals and $k = 0 \cdot 6$. We have also strains, not extensively bred, with brood size 148 and $k = 0 \cdot 4$ (Table IV, 2254) and with 109 and $k = 0 \cdot 7$ (Table IV, 2361), but the other definite ε strains all have average brood sizes of less than 100 (Table 6).

As a whole, as is shown in the examples in Tables 9 and 10, A broods are larger than comparable K broods, though we have two A strains ("dextral break-throughs" from 4511 and 4532* : Table I) with mean brood sizes as low as 115 and 113, and κ strains may go as high as 300. Generally, however, κ strains (see Table 6) average about 200, while we expect something like 250 or 300 for α groups (Table 11).

TABLE 10.—Brood sizes in dextral (A) and sinistral (κ) broods.

——	F3 broods from A × K crosses (Table VII).		A and κ broods in segregating strains from 674 (Table VI).	
Brood size.	A broods.	κ broods.	A broods.	κ broods.
Under 50 ...	11	8	1	4
50 ...	9	9	3	8
100 ...	14	5	2	11
150 ...	13	2	6	15
200 ...	33	5	21	16
300 ...	25	1	14	4
400 ...	9	—	—	—
500 ...	1	—	—	—
600 ...	0	—	—	—
700 ...	2	—	—	—
800 ...	1	—	—	—
Total	118	30	47	58
Mean	245	112	247	164
Largest	805	322	388	342

The precise relationship between the percentage of dextrals (or the degree of E-ness measured by k) and brood size is not very easy to determine, because it is difficult to

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* In both these strains there is some deficiency of black pigment and the snails' bodies are pale and yellow, so that when young they may be difficult to distinguish from albinos. This is the sort of change which is often associated with some lethality.

TABLE 11.—Brood sizes in α groups and strains.

Table.	——	Number of broods.	Mean brood size.	Largest brood.
I	D.B.T. from 958	32	305	769
III	Pure line from 45	47	334	818
II	Segregating 1928 from 706	40	314	653
II	Pure line 1928 from 706	48	240	498
V	D.B.T. from 968	35	341	948
IV	D.B.T. from 2819	39	226	503
IV	Seg. from 2209...	28	165	343
IV	Seg. from 2361...	22	253	665

decide what should be called "separate" strains, and if our correlation table is overweighted with substrains from one line in which small-broodedness and high E-ness happen to coincide we shall be apt to find a spurious relationship. Table 6 shows a series of κ and ε strains worked out with this danger in mind. It seems clear that, comparing one strain with another, E-ness and brood size are inversely related to one another, though the intensity of the association indicated by the coefficient of correlation of − 0·65 must be qualified by the fact that the relationship is not linear (fig. 4). Among the available κ strains the relationship is not demonstrable.

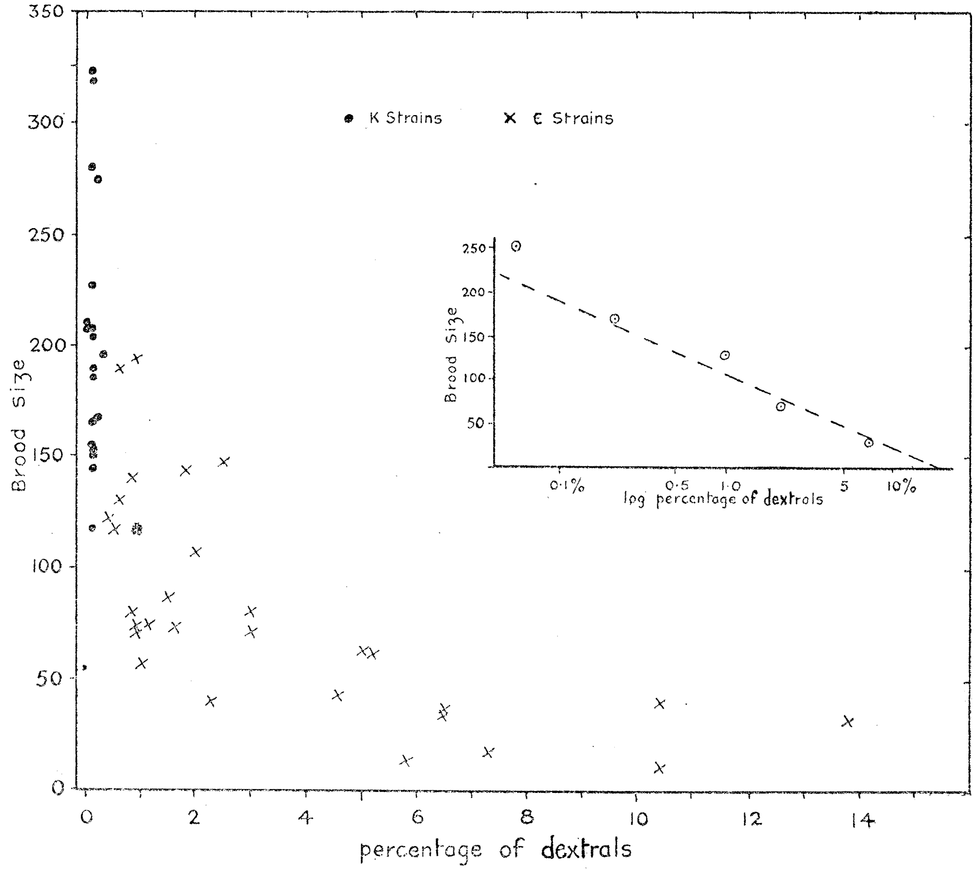

FIG. 4.—Brood Size and Percentage of Dextrals.

TABLE 12.—The percentage of dextrals in the 48 κ and ε strains of Table 6 grouped by brood size.

Brood size groups.	Mean brood size.	Mean dextrals per cent.	No. of strains.
Under 50	31	7·5	9
50–99	72	2·2	11
100–149	130	0·96	9
150–199	173	0·22	10
200–321	251	0·056	9

If, using these grouped figures, we plot brood size against the logarithm of the percentage of dextrals, we get a tolerably straight line (fig. 4), the quantitative meaning of which is, approximately, that the percentage of dextrals is doubled for every drop of 25 snails in brood size,* giving the scale (interrupted line in fig. 4) :—

Percentage of dextrals.	Brood size.
20	0
10	25
5	50
2·5	75
1·25	100
0·08 (1 in 1,250)	200
1 in 20,000	300
1 in 5 millions	500

Which fits pretty well with the facts that there is a limiting value of about 20 per cent. dextrals and that no sinistral strain is quite free from a chance of producing a dextral. These data unfortunately throw little further light on the question whether κ and ε are qualitatively or only quantitatively different : they are obviously compatible with the latter view, but they are not inconsistent with the other interpretation.

For the broods within an ε strain this relation does not hold (Table 13), nor does it necessarily apply (though it may do so) to the substrains within an ε strain nor to the fluctuations within a substrain from year to year. Nor are the E broods in stable κ strains smaller than the K broods. Like the proportion of dextrals, brood size is a heritable character of strains, not of individuals or broods. This is what we should expect on the chance distribution of dextrals among the broods of a group. If, on the other hand, some real change in the constitution of a strain leads to a rise or fall in the proportion of dextrals, we should expect a corresponding decrease or increase in brood size, and *vice versa* : this appears to happen.

These differences in brood size between A, K and E broods are due to differences in *embryonic mortality* rather than in the numbers of eggs laid. The number of young in

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* *i.e.*, for every increase of 5 per cent. in embryonic mortality (below, p. 87).

TABLE 13.—Relation between brood size and percentage of dextrals within an ε strain (strain from 672, Table VI).

Percentage of dextrals.	Brood size.												
	1–9	10–	20–	30–	40–	50–	60–	70–	80–	90–	100–	110–	Total.
0	12	6	1	—	—	—	—	—	—	—	—	—	19
0·1–4·9	—	—	1	—	—	1	—	1	—	—	—	—	3
5·0–9·9	—	2	—	2	4	2	2	—	1	2	—	1	16
10–	1	5	2	6	1	—	4	1	—	—	1	—	21
15–	1	3	2	—	5	2	2	1	—	1	1	—	18
20–	1	3	2	3	1	1	—	—	—	1	—	—	12
25–	4	1	1	1	—	1	—	—	—	—	—	—	8
30–	1	—	—	—	1	—	—	—	—	—	—	—	2
35–	—	1	—	—	—	—	—	—	—	—	—	—	1
40–	1	—	—	—	—	—	—	—	—	—	—	—	1
45–	—	—	1	—	—	—	—	—	—	—	—	—	1
50–	—	—	—	—	—	—	—	—	—	—	—	—	0
55–	1	—	—	—	—	—	—	—	—	—	—	—	1
Total	22	21	10	12	12	7	8	3	1	4	2	1	103
Without K broods ...	10	15	9	12	12	7	8	3	1	4	2	1	84

Mean brood size 34·25.

Mean percentage of dextrals, 12·66.

r for 103 E and K broods = + 0·012 ± 0·10.

r for 84 E broods = − 0·38 ± 0·09 ; it is not legitimate to exclude small broods because they happen to contain no dextral.

a brood depends on the number of eggs laid and the proportion of those which develop in a normal way and hatch. Of the number of eggs laid we have no exact quantitative information : to collect and examine all the capsules extruded over a period of six or eight weeks involves more labour than we have been able to undertake ; such disturbance is also very bad for the snails. We know that some snails grow up to full size and more under favourable conditions and lay no eggs : on histological examination some of them have no gonads and others apparently normal eggs and spermatozoa. At the other end of the scale we have several times counted some 30 capsules, with an average of 30 eggs in each, and an even larger number of eggs is necessary to account for the largest broods (1085, 1091 and 1157 : all A broods) which have been obtained from singles.

On the mortality between laying and hatching we made a number of observations in 1925 and 1928 by taking capsules, counting the eggs under the microscope, and isolating each with a scrap of weed in a 6 × 1-inch test-tube, in which development and hatching go on at least as well as in the breeding jar. In more advanced capsules the egg shells of the young which have hatched may be recognised and counted. There is practically always some embryonic mortality, which in some instances involves more than 90 per cent. of the eggs. Death takes place at any stage : we have in our counts roughly distinguished between " young dead," which appear as unsegmented eggs or granular morulæ, and " big dead," which represent advanced larvæ, most of which are abnormal. Young dead are most abundant, but after this mortality is distributed about evenly through the other stages of growth, and we cannot distinguish any difference in this respect between the three main brood types.

Knowing the percentage mortality from the examination of a sample of the eggs and afterwards counting up the total snails hatched, we can calculate the number of eggs laid.*

TABLE 14.—Examples of the determination of hatching rate and number of eggs laid.

Brood type.	Capsules examined.	Eggs examined.	Young dead.	Big dead.	Hatched = per cent.	Brood.		Eggs laid calculated.
						Dex.	Sin.	
A	17	305	11	28	266=87 per cent.	374	—	430
A	13	402	106	48	248=62 per cent.	269	—	430
K	10	518	259	83	176=34 per cent.	—	187	550
K	24	763	419	146	198=26 per cent.	—	262	1,010
E	15	450	421	23	6= 1·3 per cent.	4	5	680
E	26	1,269	1,126	89	56= 4·4 per cent.	50	8	1,310

The whole series are summarised in Table 15 and fig. 5.

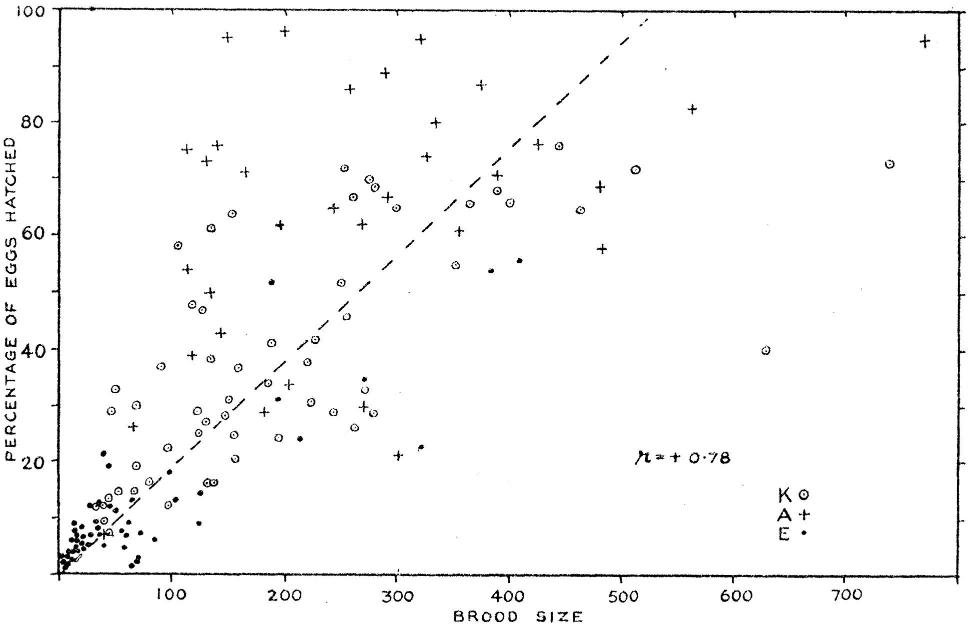

FIG. 5.

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* JEFFREYS (1862, p. 107) says that in nature *L. peregra* " lays about 1,300 eggs in a season, contained in clusters of from 12 to 180." As has been pointed out above (p. 57), the number of eggs obtained in captivity depends on the breeding technique.

TABLE 15.—Proportion of eggs which hatch in relation to brood size.

Brood size.	A broods (33).			K broods (56).			E broods (44).			All broods (133).		
	No. of broods.	Mean hatching rate per cent.	Mean calculated eggs laid.	No. of broods.	Mean hatching rate per cent.	Mean calculated eggs laid.	No. of broods.	Mean hatching rate per cent.	Mean calculated eggs laid.	No. of broods.	Mean hatching rate per cent.	Mean calculated eggs laid.
Under 50 ...	1	7	660	5	10	442	26	7	356	32	7·6	379
50– ...	1	26	250	9	22	401	8	8	868	18	16·1	600
100– ...	12	64	265	19	35	504	5	19	820	36	42·4	469
200– ...	7	62	479	13	47	620	2	29	826	22	49·9	592
300– ...	7	70	589	4	63	548	2	38	1,012	13	63·1	650
400– ...	3	68	693	3	69	637	1	56	728	7	66·6	674
500– ...	1	83	680	1	72	710	—	—	—	2	77·5	795
600– ...	—	—	—	1	40	1,580	—	—	—	1	40·0	1,580
700– ...	1	94	820	1	73	1,000	—	—	—	2	83·5	910
Mean ...	268	63·6 p. cent.	460	205	38·7 p. cent.	546	75	12·1 p. cent.	564	178	36·1 p. cent.	531

All broods : coefficients of correlation :—

brood size and hatching rate + 0·78 ± 0·03.
brood size and eggs laid + 0·41 ± 0·07.
hatching rate and eggs laid — 0·15 ± 0·08.

coefficient of variation :—

brood size 87 per cent.
hatching rate 71 ,,
eggs laid 54 ,,

There is no doubt a good deal of natural variation, but on the whole it seems clear that differences in embryonic mortality account for a large part of the variations in brood size. It also appears that the parents in small brooded ε lines lay on the average at least as many eggs as dextral or sinistral strains, and that the small brood size is essentially due to an excessive embryonic mortality. Among 26 ε broods of less than 50 snails which were tested, only 5 gave a hatching rate of more than 10 per cent., the highest being 21 per cent. The difference in brood size between large-brooded E and small-brooded E may be wholly accounted for by the mortality in the latter being half as large again as in the former ; in 1925, for instance, under as nearly comparable conditions as possible, we got :—

——	Broods.	Eggs examined.	Hatched per cent.	Brood size.	Calculated eggs laid.
Small brooded E : 331 strain (Table VI) ...	18	6,738	8·0	54	680
Large brooded E : 939 strain (Table I) ...	8	3,745	33·4	231	694

The small-brooded ε strain from 674 (above, p. 81), which almost died out and then suddenly broke into ordinary α and κ groups showed the corresponding changes in embryonic mortality and brood size, the A broods tested giving on the average 294 snails with a hatching rate of 81 per cent., the K broods 165 and 62 per cent.

Dextral broods show the least embryonic mortality, though under our conditions even in them it averages nearly two-fifths of the eggs, and among the A broods the brood size seems to depend on the number of eggs laid more than in K and E broods. K broods occupy an intermediate position, with a mortality of about two-thirds; the larger broods are associated with a lower mortality, as in the albino strain from 1629 (Table II) with a brood size of 308 and a hatching rate of 62 per cent.

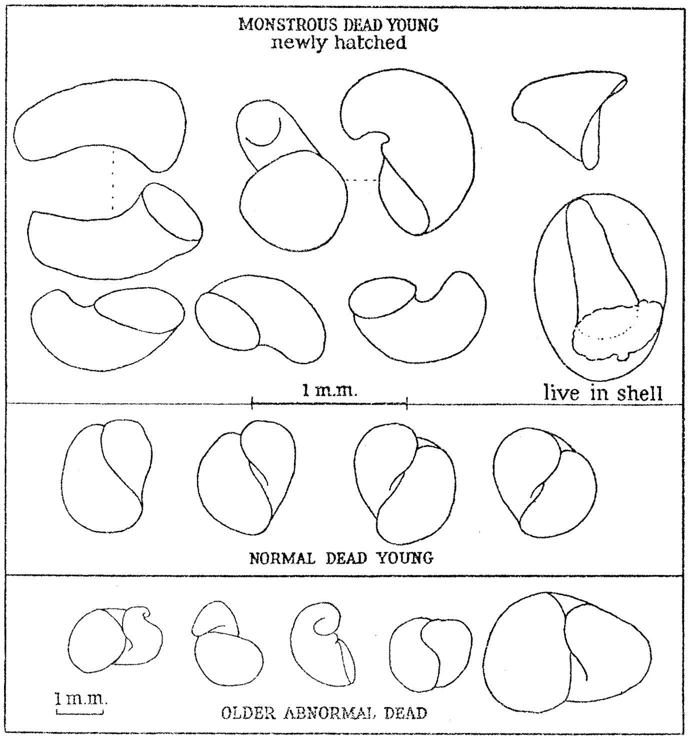

Fig. 6.

Embryos which die in the egg at the stages of development when they may be classed as "larvæ" or "young snails" are practically always obviously abnormal. We have not examined the histological details which are worth further study. The commonest gross error in the soft parts is the formation of vesicular protuberances and a general tendency to be amorphous. Abnormalities in the shell usually appear as partial or complete failures to twist, giving rise to cones which may be bent at the tip. The great majority of these monsters die in the egg, but a few are born alive (fig. 6), nearly always sinistral if the twist is determinate: of these, most die soon after hatching, but a small proportion grow up into flat, half-flat or scalariform adults (Plate 10, fig. 8): from these we have obtained a number of broods of normal snails* with no more monsters than would be expected in the strain to which they belong. They are non-heritable monstrosities, as are the viable dextrals in E broods. The tendency to produce monsters of one kind and another is, however, evidently heritable and closely associated with a high embryonic mortality. Monsters viable enough to hatch are very rare in A broods, not uncommon in κ strains, and commonest in ε strains, especially in large-brooded ε strains in which the threshold of viability is raised and monsters which would otherwise have died young can reach the hatching stage. Our counts of them are probably not very accurate, for the tiny shells are liable to be overlooked, and we suspect that they may sometimes dissolve and disappear before the contents of the jar are examined. But the examples of their occurrence shown in Table 16 may be taken as fairly representative.

TABLE 16.—Incidence of hatched monsters in A, K and E broods.

	Broods.	Snails.		Mean brood size.	Monsters.	
		Dextrals.	Sinistrals.			p. mille.
A. Dextral break-through from 4532 (I)	41	4,888	0	119	15 in 8 broods	3
Dextral break-through from 680 (VI)	55	17,544	0	311	2 in 2 „	0·1
Segd. dextral pure line (III) from 45	47	15,718	0	334	3 in 3 „	0·2
Segd. dextral pure line (II) 1928 from 706	48	11,356	0	237	1 in 1 „	0·1
Het. dextral broods (II) 1927 from 706	40	12,586	0	315	2 in 1 „	0·2
A × K crosses : A broods	118	28,892	0	245	4 in 4 „	0·1
K. A × K crosses : KE broods... ...	30	38	2,067	70	30 in 12 broods	14
E × K crosses : KE broods F_2 ...	38	32	6,620	175	48 in 14 „	7
Sinistral segregates (II) 1925 from 192	19	0	3,227	170	21 in 11 „	6
Sinistral segregates (II) 1926 from 192	41	8	6,036	147	18 in 9 „	3
Sinistral albino strain 1926 (II) ...	25	2	10,108	404	41 in 16 „	4
E. 672 strain (VI) 1926	32	178	1,309	47	45 in 12 broods	29
677 strain (VI) 1925	35	67	1,090	33	13 in 6 „	11
939 strain (I) 1925	26	111	7,567	295	148 in 18 „	19
ε strain from F brood 1945 (III) ...	31	37	1,894	62	27 in 10 „	14

Gross abnormalities of the soft parts are presumably incompatible with life. The only one which we have been able to identify in adult snails is absence of the penis—a not uncommon deficiency in hermaphrodite mollusca (PELSENEER, 1894 and 1920, pp. 222 ff ; and 1925 paper, p. 125). This was found in 14 out of 110 ε snails dissected,

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* See ‘Proc. Malac. Soc. Lond.,’ 1930, vol. 19, p. 141. The albino sinistral strain from 1629 (Table II) appeared in a group from the half-flat 960 figured in our previous paper (1925, Plate V, fig. 1).

in 1 of 93 K, and in 2 of 87 A. Most of the defective snails had been isolated as singles, and had produced ordinary broods, disposing of the suggestion that self-fertilisation is achieved by self-copulation.

Egg capsules laid by wild *L. peregra* under natural conditions show practically nothing of this maldevelopment and mortality. We have specially examined a number from several ponds and streams in Hertfordshire : the capsules were generally much larger (200 eggs and thereabouts) and showed only an occasional blighted egg, though one sometimes finds a capsule in which all the eggs have died at an early stage. PELSENEER (1920, pp. 314 ff.) records a few abnormal embryos in wild *Limnœa stagnalis*, and CONKLIN (1897, p. 42) says that in captivity *Crepidula* produces many monstrous embryos, in nature none. In some mollusca (*Neritina, Purpura*) only 1 to 5 per cent. of the eggs develop normally and hatch under natural conditions. BACHRACH and CARDOT (1924) note that abnormal embryos of *L. stagnalis* and *Agriolimax agrestis* are more frequent towards the end of the breeding season and under unfavourable environmental circumstances.

We see, therefore, that—

proportion of dextrals,
brood size,
embryonic mortality,
monsters,

are all associated together in the E–K series ; a high percentage of dextrals, small broods, high mortality and many monsters being connected together to constitute what we call E-ness. Evidently something goes seriously wrong with the development of the eggs, which leads to the appearance of the phenotypic dextrals of E broods. The error is present to some extent in sinistral strains of all complexions : its smallest manifestations lead to our most completely K strains. E grades into K in these respects, just as it does in the proportion of dextrals.

(*d*) *Equivalence of dextrals and sinistrals in E Broods.*—As far as we can make out, the dextrals and sinistrals in E broods differ only in their twist. They both produce E broods, and those arising from dextrals are not essentially different in brood size or the proportion of dextrals from those which come from their sinistral brothers or cousins. The nine broods, for example, obtained from 672 (Table VI) gave—

	Dextral parents.		Sinistral parents.	
	Sinistrals.	Dextrals.	Sinistrals.	Dextrals.
	5	4	12	10
	37	13	13	2
	13	5	21	7
	11	6	27	8
			33	7
Total	66	28	106	34
Dextrals, per cent.	30		24	
Average brood size	24		28	

Similarly, the 16 broods from 1323 (Table I) were—

	Dextral parents.		Sinistral parents.	
	Sinistrals.	Dextrals.	Sinistrals.	Dextrals.
	233	2	269	2
	80	1	103	3
	75	1	97	1
	72	1	85	4
	63	4	81	1
	25	0	74	0
	19	1	63	0
			33	9
			40	0
Total	567	10	845	20
Dextrals, per cent.	1·7		2·3	
Average brood size	82		96	

The figures may be analysed in a variety of ways ; the groups with more than one or two broods from dextral parents are summarised in Table 17 ; the others correspond (fig. 7).

TABLE 17.—Progeny of dextrals and sinistrals in E broods.

Table.	Ancestor.	Year.	Dextral parents.				Sinistral parents.			
			No. of broods.	Broods with no dextrals.	Percentage of dextrals.	Brood size.	No. of broods.	Broods with no dextrals.	Percentage of dextrals.	Brood size.
VI	672	1924	4	0	29·8	24	5	0	24·1	28
	672	1925	16	6	9·7	27	29	10	12·8	27
	672	1926	11	0	12·4	67	20	1	10·9	30
	672	1927	4	0	20·9	63	10	1	15·9	35
VI	671	1924	3	1	23·9	32	8	1	14·4	30
	671	1925*	6	0	13·8	48	10	5	4·4	38
V	1442	1925	5	0	3·6	62	9	3	6·7	56
I	1323	1925	7	1	1·7	82	9	3	2·3	96
I	939	1925	4	0	1·7	257	16	2	2·3	186
	939	1926	9	6	0·7	146	9	3	2·7	101
			69	14= 20 per cent. of all broods.	11·8 per cent.	81	124	29= 23 per cent. of all broods.	9·6 per cent.	62

* The difference in percentage of dextrals in this instance is statistically significant, being 4·4 times its standard error. But it seems very doubtful whether this indicates a difference between dextral and sinistral parents. The strain has a persistent tendency to give a few high-percentage broods, which may make the groups in which they occur heterogeneous by the χ^2 test. In this group two such broods happened to arise from dextrals and none from sinistrals. If the whole progeny of 671 for 1924–1929 are added together we get—

	Broods.	Snails.	Dextrals per cent.	Brood size.
Dextral parents ...	25	1,022	10·7	41
Sinistral parents ...	27	1,190	11·7	44

In low ε strains and in κ strains with a few E broods it is not possible to make this exact comparison between the dextrals and sinistrals of single broods ; but the same equivalence evidently prevails. Thus in the progeny of SP 36 (Table II) 13 broods were obtained from odd dextrals in E broods in κ strains ; comparing them with the 54 broods from related sinistrals we have—

	Broods.	E broods.	Sinistrals.	Dextrals.	Dextrals per cent.	Brood size.
Dextral parents ...	13	4	1,412	6	0·42	109
Sinistral parents ...	54	13	5,406	28	0·51	101

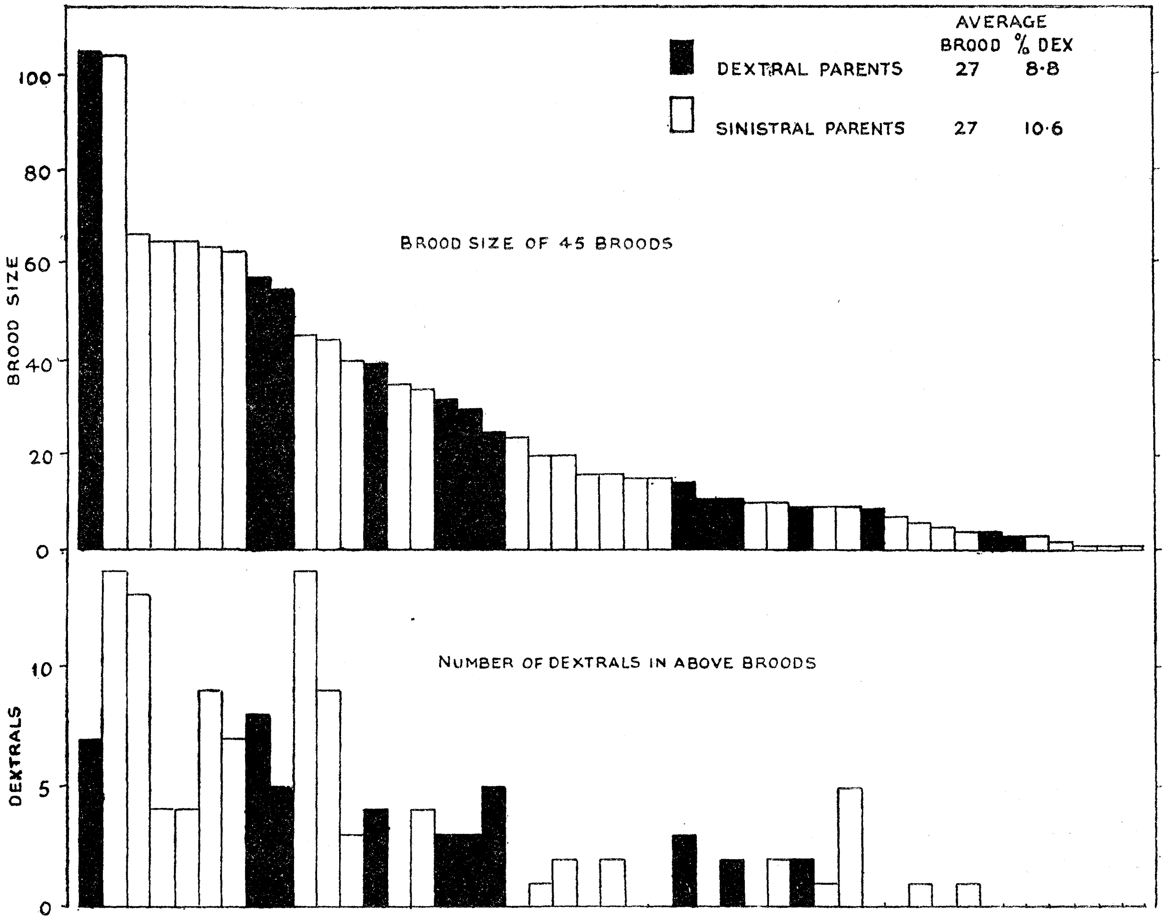

FIG. 7.—Progeny of dextrals and sinistrals in E Broods. 672 Strain : 1925.

There is a suggestion in the figures that dextrals might prove on further enquiry (and especially by persistent breeding through dextrals : *cf.* strain 671, Table VI) to yield rather larger broods with relatively more dextrals. But this is quite indefinite. Such differences as appear are not consistently on one side or the other, and are a good deal less than those between different ε strains or the annual fluctuations which, *e.g.*, in the 672 strain, affect dextrals and sinistrals in the same sense and roughly to the same degree. The only difference we know of is that the reverse mutations to α (" dextral break-throughs ") come more frequently from the dextrals than from the sinistrals in E brood (below, p. 119).

The dextrals and sinistrals are equally viable and at no stage in their lives has there been any evidence of a differential mortality. TURNER identified the determination of the twist in a number of eggs by observing the first two divisions, and afterwards followed the embryos through individually till they died (as most of them did) or hatched. The observations are troublesome and tedious and more are needed. Besides establishing the important points that the abnormalities of later embryonic development are not represented by anything grossly wrong in the earliest segmentation and that the dextrals and sinistrals of E broods are not half embryos, TURNER found (as far as he went) that the mortality of embryonic dextrals is approximately the same as that of embryonic sinistrals.

Similarly in later life the vitality of the two twists seems to be equal. We have had some suggestions that dextrals perished more easily. Thus of the progeny of 670 (VI) 17 dextrals and 13 sinistrals were planted out simultaneously to breed : 6 of the dextrals died young and all the sinistrals grew up, and 11 bred satisfactorily. And in the next generation of the same family, under bad conditions, 2 of 13 dextrals and 5 of 12 sinistrals produced young. But these differences seem to be accidental, and taking the results as a whole the dextrals show no inferiority in vitality to the sinistrals : in the 672 (VI) strain, for instance, 36 of 55 (65 per cent.) dextrals bred and 68 of 100 (68 per cent.) sinistrals. Other monsters, such as those shown in fig. 8, plate 10, are, if they survive infancy, about as healthy and prolific as normal snails.

By the time the breeding season is over and the jars are turned out and counted, a variable proportion of the young (greater with large and less with small broods) are dead from overcrowding. Analysing our records of E broods, we find no great difference in this death-rate during the first one to three months of life (Table 18) : we give for comparison similar data from jars where, in consequence of pairing in γ groups, dextrals and sinistrals from separate parents were living in the same jar.

TABLE 18.—Mortality of young snails in E broods.

—	No. of broods.	Dextrals.				Sinistrals.			
		Total.	Dead.	= per cent.	Average percentage of dead.	Total.	Dead.	= per cent.	Average percentage of dead.
E broods : 1924	56	224	67	30*	33†	2,909	900	31	27
E broods : 1925	62	228	55	24	26	5,344	2,260	42	27
Broods of more than 100	10	54	16	30	36	2,937	1,743	59	50
Broods of less than 100 ...	52	174	39	22	23	2,407	517	21	24
Broods with 5 or more dextrals	16	130	30	23	24	1,432	316	22	21
Pairs in γ groups	16	2,463	1,367	55	50	1,992	1,097	55	53

* Weighted mean. † Unweighted mean.

The survival of dextrals and sinistrals in " nurseries " (2 lb. jam-jars) is also the same. In 30 broods which had been crowded in this way for about 10 months, 57 per cent. of 83 dextrals were dead and 65 per cent. of 612 sinistrals.

When the broods are examined in detail, it sometimes happens that a few of the snails are conspicuously larger than the rest.‡ This may occur in a batch of snails

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‡ This was noticed and figured by POPOVICI-BASNOSANU (1921, p. 501) ; and see TURNER (1927, p. 50).

all hatched at the same time, but it is naturally suggestive of differences in age. We thought at one time that the dextrals in E broods were particularly liable to be bigger than their sinistral brothers and that this might be due to the dextral-producing eggs being laid earlier, but a survey of the details of the broods in which extra large individuals were noted showed that 134 of 712 sinistrals (19 per cent.) and 23 of 143 dextrals (16 per cent.) were so classed. We know, too, that both twists may come out of the same capsule, so that there is no evidence that they are unequally distributed in the egg-laying process.[†]

(*e*) *Environmental effects.*—Our data about the effect of *pairing* (*i.e.*, by putting two young snails together in a jar, without subsequent separation) are inadequate, but they do not suggest that it influences E-ness in any marked way. None of the comparisons in Table 19 are numerically significant.

TABLE 19.—Effect of pairing on E-ness.

Strain.	Year.	Singles.					Pairs.				
		Broods.	Sinistrals.	Dextrals.	= per cent.	Brood size.	Broods.	Sinistrals.	Dextrals.	= per cent.	Brood size.[*]
671 (VI)	1925	8	405	47	10·4	57	8	460	63	12·0	65
672 (VI)	1927	5	163	37	18·5	40	3	82	9	9·9	30
939 (I) ...	1925	13	2,830	46	1·6	213	7	3,650	24	0·7	525
939 (I) ...	1926	18	2,190	34	1·5	124	9	1,345	39	2·8	154
939 (I) ...	1927	14	1,879	27	1·4	136	4	904	17	1·8	230
939 (I) ...	1928	7	437	9	2·0	64	5	626	16	2·5	128
939 (I) ...	1929	8	967	59	5·7	103	8	913	58	6·0	121

[*] Broods from pairs obtained in this way are larger than the parallel broods from singles, but they are not double. The snails breed when they are smaller.

In 1924 we had what seemed to be fairly good evidence that the *date of planting out* the young snails to grow up and breed had an influence on brood size and percentage of dextrals (Table 20). Broods in recognised ε lines were divided up and in each case later planting gave proportionately fewer dextrals (statistically significant in those marked *) and a larger brood size.

In the following year we tried to confirm this result, planting out broods from the same and similar strains, partly on February 24 and partly on May 15. The results were wholly negative, the former giving 5·8 per cent. of dextrals with an average brood size of 41, the latter 6·3 per cent. and 38. The effect obtained in 1924 was, therefore,

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[†] Except in the unique instance 2819 (Table IV), which laid dextrals first and afterwards an E brood; (p. 118 below).

TABLE 20.—Influence of time of breeding on E-ness, 1924.

Grand-parent.	Early planting (25th March).					Later planting (15th April).				
	Broods.	Sinis-trals.	Dex-trals.	= per cent.	Brood size.	Broods.	Sinis-trals.	Dex-trals.	= per cent.	Brood size.
670 ...	12	436	43	9·0	40	15	630	49	7·2	45
*679 ...	6	100	22	18·0	20	4	197	8	3·9	51
678 ...	9	147	7	4·5	17	6	276	6	2·1	47
*677 ...	15	296	39	11·6	22	6	436	14	3·1	75
*Total...	42	979	111	10·2	26	31	1,539	77	4·8	452

presumably due not to the date of planting *per se*, but to some environmental factor which we have not identified.

We have also tried a few experiments to see whether *delaying* the broods for a year would make any difference: broods born in 1924 were partly planted out in 1925 and partly kept dwarfed in small jars till 1926, when they were grown up and bred. The 21 delayed broods so obtained do not suggest that postponement of the natural breeding season for a year of itself makes any significant difference in E-ness.

TABLE 21.—Effect of place of breeding on E-ness.

Strain.	Grand-parent.	U.C.H.					Radlett.				
		Broods.	Sinis-trals.	Dex-trals.	= per cent.	Brood size.	Broods.	Sinis-trals.	Dex-trals.	= per cent.	Brood size.
671 ...	1,216	12	540	54	9·1	50	4	74	3	3·9	19
678 ...	1,357	13	784	8	1·0	61	6	402	10	2·4	69
677 ...	1,246	10	334	18	5·1	35	7	224	19	7·8	35
330 ...	1,442	9	507	21	4·0	59	6	256	24	8·6	47
*939 ...	939	13	2,830	46	1·6	221	7	1,026	38	3·6	152
*Total		57	4,995	147	2·9	90	30	1,982	94	4·5	70

Some broods were also bred out (Table 21) in parallel in 1925 under standard conditions at U.C.H., in London tap water, and in a garden at Radlett, in the local tap water.* Though only the totals and one of the strains (939) show statistically significant differences, the differences are in the same sense, except in strain 671, which is apt to give heterogeneous groups and of which the Radlett sample is poor. The change

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* This is lime-softened chalk water, containing about 45 mg. calcium per litre against about 100 mg. in London: it is not in general so good an aquarium water.

of conditions seems, therefore, to have had some effect, though not a large one. Further breeding of the large-brooded 939 strain at Radlett led to a more considerable change : and in 1927–1929 broods such as 62/25, 10/10, 32/26 and 15/10 were obtained there —in all 11 broods averaging 34 snails, with 24 per cent. of dextrals. The controls at U.C.H. continued as before, and in the corresponding years gave average broods of 136, 64 and 103, with 1·5, 1·4 and 5·7 per cent. dextrals.

We also tried to make comparisons at Merton (London tap water) and Leeds (soft moorland water), but breeding was unsatisfactory in both places : so far as they go, the data show no effect on E-ness.

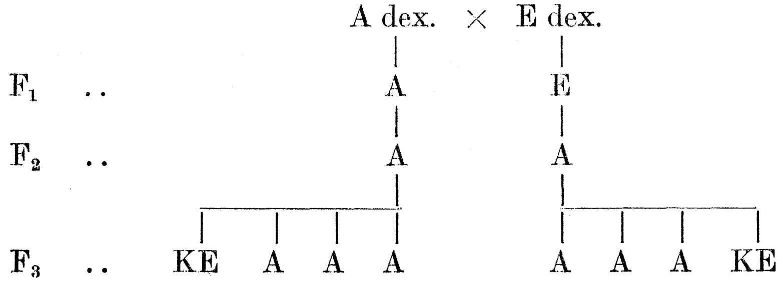
We have, too, the fact that annual fluctuations (statistically real) in brood size and percentage of dextrals occur in ε strains which we should class as pure lines. Thus in 672 (Table VI) we have—

——	Total snails.	Dextrals per cent.	Brood size.
1924	234	26·5	26
1925	1,217	12·1	27
1926	1,487	12·0	49
1927	599	18·0	40
1928	145	9·5	16
1929	127	30·7	6

In 1927 there was a parallel rise in the strain 671 (fig. 3, p. 77), in 1929 in 677 (Table VI), and in 939 (Table I) strains. The obvious environmental characteristic of 1928 and 1929 was excessive heat.

There is, therefore, a considerable body of evidence that significant differences in E-ness may be brought about by changes in circumstances which we have failed to analyse. It is difficult to detect small effects because we cannot guarantee that a group will necessarily be homogeneous, even if it is bred under conditions which are as far as possible uniform.

(*f*) *Crossing experiments with snails in E broods.*—An ε dextral, fertilised by a pure α dextral, produces an E brood in F_1, which, self-fertilised or paired, gives dextral broods in F_2, which break up into a mixture of A and E or K broods in F_3. Reciprocally, an α dextral fertilised by an ε dextral gives A broods in F_1 and F_2 and a mixture of A with E or K in F_3 :—



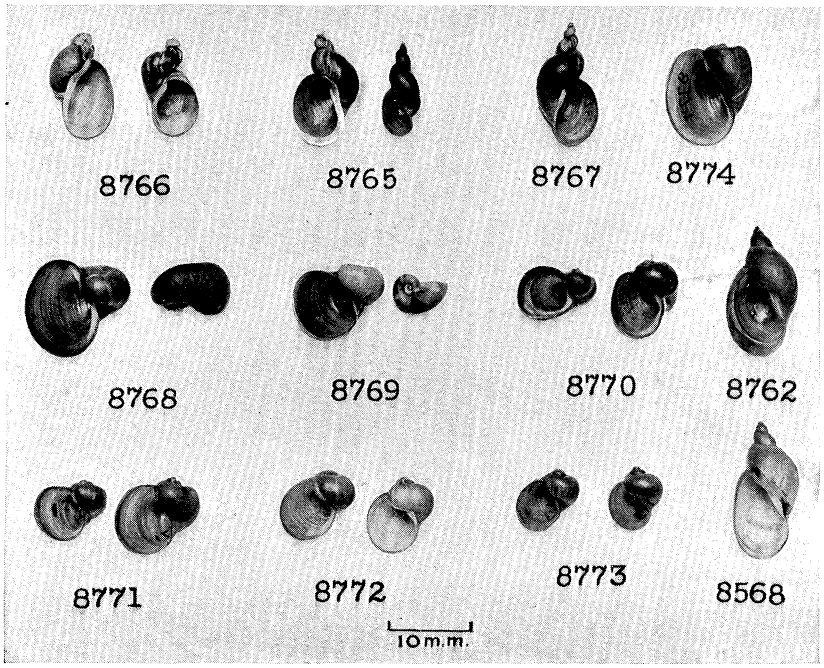


Fig. 8.

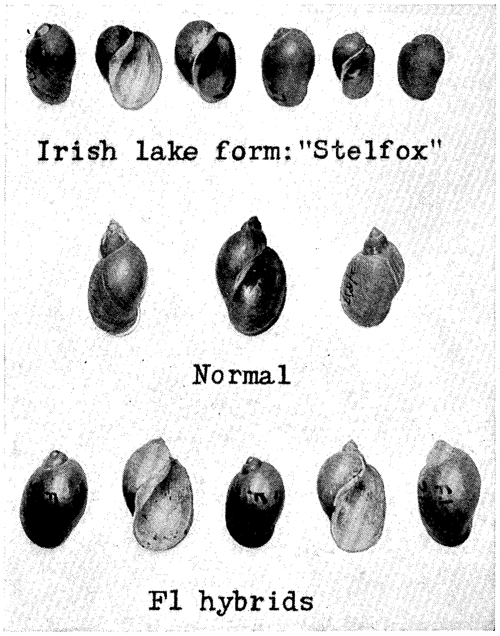


Fig. 9.

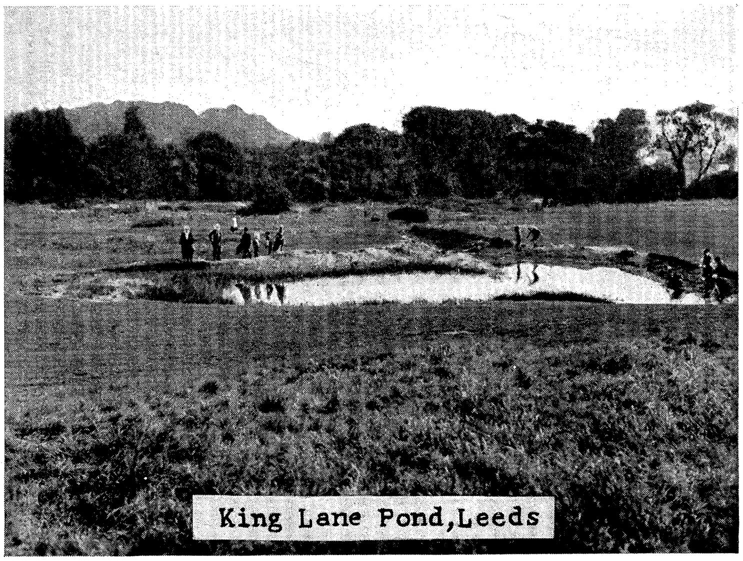


Fig. 10.

Similarly, an ε sinistral, fertilised by a typical κ sinistral, has an E brood in F_1, and K and E broods in F_2 and F_3 :—

	K sin.	×	E sin.
F_1	K		E
F_2	KE		KE
F_3	KE		KE

With the other crosses we have been much less successful, but we know that (1) a κ sinistral fertilised by an ε dextral gives K in F_1 and K or E in F_2 and F_3, and (2) an ε sinistral fertilised by an α dextral gives E in F_1 and A in F_2, and in F_3 a mixture of A and K or E, and (3) an α dextral fertilised by an ε sinistral gives A in F_1 and F_2, and a mixture of A and K or E in F_3.

From which it follows that both dextrals and sinistrals in E broods are genetically ε or κ, *i.e.*, essentially sinistral : there is no evidence that they contain any real dextrality. E-ness has the same relation in A × E as K-ness has in A × K.

(1) *E dextral × A dextral crosses* (Tables VIII and IX).—For the E parent we have used dextrals from a variety of ε strains, mostly from the 331 family : for the A parent dextrals from our pale-bodied dextral break-throughs (4511 and 4532), two lots of wild dextrals from Hertfordshire (Colne and pond 27), and the Irish form given us by Mr. A. W. STELFOX, which has a characteristic shell shape and breeds true under our experimental conditions (Plate 10, fig. 9). Of these, 4511, 4532 and Colne were used in the A × K crosses (above, p. 60). The STELFOX dextrals are particularly convenient for these experiments, since the characteristic shell shape is modified in F_1 ; the hybrids are intermediate and can generally be recognised as such ; we can, therefore, tell at once whether crossing has taken place on one or both sides. We began these crosses before the albino ε mutant had appeared in the 331 strain ; it would, of course, have been more convenient than its pigmented relatives.

F_1 and F_2.—On the E side we have 19 crosses verified by A broods in F_2 (Table 22) and on the A side 7 crosses verified by a mixture of A and EK broods in F_3 (Table 23.) In each case the F_1 product is what might be expected from the self-fertilised uncrossed parent. Using the criterion of STELFOX shell-shape, we have on the A side seven more instances of the failure of the sperm to cause any immediate change in twist. In F_2 on the E side 59 A broods (16 from dextral, 43 from sinistral F_1 parents) yielded nearly 20,000 dextrals without a single sinistral. On the A side in F_2 we have 36 A broods and 1 F brood in which we judge the sinistral to be a mutant (see below, p. 122).

There are also four crosses where we thought that crossing had taken place on the A side, owing to an apparent segregation of dark and light body pigmentation in F_2. They gave 150, 159, 405 and 201 dextrals respectively in F_1 and a total of 19 A broods with 9,461 dextrals in F_2. But it is uncertain whether they had really crossed. In two, Colne wild dextrals were involved; one of these which was taken on gave 11 A broods in F_3 and 13 A broods in F_4, the other 37 A broods in F_3 (Table VIII).

TABLE 22.—α dextral × ε dextral. Product of E parent in F_1 and F_2.

Strain of α parent.	Strain of ε parent.	Table of ε parent.	F_1.		F_2.	
			Sin.	Dex.	Broods.	Dextrals.
4511	672	VI	27	17	1	147
4532	672		148	34	9	2,717
4532	672		61	7	2	1,283
4532	672		3	1	1	62
4532	677	VI	25	17	2	1,182
4532	677		55	10	4	2,758
4532	677		31	6	7	2,107+
4532	677		30	0	2	507
4532	678	VI	107	7	3	1,756
4532	678		8	2	1	138
Colne	672	VI	22	6	1	11+
,,	672		4	0	1	617
,,	684	V	49	0	2	1,222
,,	684		53	9	2	1,062
Pond 27	939	I	173	24	1	225
,,	939		23	0	2	642
,,	684	V	68	1	2	863
Stelfox	671	VI	61	?	10	1,525
,,	749	I	11	1	6	280
Total ...	—	—	—	—	59 A broods	19,364+ dextrals.

TABLE 23.—α dextral × ε dextral. Product of A parent in F_1 and F_2.

Strain of α parent.	Strain of ε parent.	F_1 dextrals.	F_2.
4532	672	158	8 A broods : 2,083 dextrals.
4532	677	164	5 A ,, : 3,167 ,, 1 F brood : 189 dextrals, 1 sinistral.
Pond 27	684	126	3 A broods : 468 dextrals.
Stelfox	671	36	10 A ,, : 2,172 ,,
,,	749	5	2 A ,, : 77 ,,
,,	749	144	4 A ,, : 223 ,,
,,	672	89	4 A ,, : 994 ,,
—	—	—	36 A broods, 1 F brood : 9,184 dextrals, 1 sinistral.

Just as the effect of crossing an albino with a pigmented may wear off (p. 55) and the albino produce first pigmented and later albino young, so may the Stelfox-shape effect disappear. Thus an E dextral, after mating with a Stelfox dextral, produced (Table IX) :—

F_1 ..	11 sinistrals 1 dextral	hybrid shape, followed by	73 sinistrals 5 dextrals	normal shape
F_2 ..	6 A broods		4 EK broods	
F_3 ..	7 A, 10 K E and F		7 EK broods	

One very anomalous result (Table IX) turns on the identification of the hybrid shape. A cross between a Stelfox dextral and an E dextral gave (the parents not being separated) a brood of 36 dextrals and 61 sinistrals, all judged to be of hybrid shape. All that were carried on (14 sinistrals and 10 dextrals) were shown to be hybrids except one sinistral, which was back-crossed to an E sinistral (672 strain), with the result :—

AE sinistral × E sinistral

F_1 ..	45 sin. 9 dex.	69 sin. 12 dex.	14 sin. 3 dex. laid before separation.
F_2 ..	6 ε broods	7 ε broods	2 ε broods
F_3 ..		10 ε broods	6 ε broods
F_4 ..		10 ε broods	

No signs of Stelfox dextrality emerged. There are three possibilities :—(1) that the parent was not a hybrid, but an uncrossed E sinistral, though its shell seems on critical inspection to be more hybrid than normal in shape, and as the original parents were both fertile and not separated there is no reason to suspect selfing ; (2) that the E sinistral overwhelmed the dextrality of the AE hybrid in some way of which we have no parallel ; (3) that, which is almost incredible, in the back-cross the AE hybrid had no progeny of its own, but laid eggs which, after fertilisation, had been passed into it by the E sinistral.

F_3.—The data of segregation in F_3 are summarised in Table 24. As before, we treat K, E and F broods as together forming the recessive element. Taken as a whole we have :—

	A side.		E side.		Both sides.	
	A	KEF	A	KEF	A	KEF
Observed	91	26	80	33	171	59
3 : 1 expectation ...	87·75	29·25	84·75	28·25	172·5	57·5

which is in reasonably good correspondence with a 3 : 1 ratio. There is an excess of recessives on the E side and a defect on the A side, but the difference is not numerically significant.

The groups, however, give irregular results, some of which are on the verge of incompatibility with a 3 : 1 ratio, and it is possible that the concordance shown by the summed figures is due to a mixture of counterbalancing ratios. The most suggestive discrepancy is in the comparison between the A and E sides of the Stelfox crosses bred at Pembroke Square (Table IX). Adding these together, we have :—

——	A side.	E side.	Total.
A broods	29	12	41
KEF broods ...	6	15	21
Total ...	35	27	62

By the usual statistical tests the two sides are different, the difference being 3·2 times its standard error and P = 0·0016. The E side, too, is hardly consistent with a 3 : 1 ratio, the extreme acceptable numbers of recessives in a sample of 27 being 0 and 13 : P on the χ^2 test works out as 0·0003. The A side by itself and both sides together might well be samples of a 3 : 1 ratio. If one adds in the 37 broods on the A side obtained from another Stelfox cross, bred at U.C.H., the difference between the two sides is increased (diff./s.e. = 3·6). On the other hand, the incompatibilities become less if we transfer the F broods from the KEF category to the A broods ; and we are not quite certain that this would not be justifiable. Further, from the F_3 groups on the E side, which gave 12A and 15KEF, F_4 groups were obtained, totalling 16A and 4KEF, and taking F_3 and F_4 together we have :—

——	A side.	E side.	Total.
A broods	67	28	95
KEF broods ...	17	19	36
Total ...	84	47	131

and the difference between the two sides is no longer significant (diff./s.e. = 2·5). It is evident, too, that an excess of KEF is not characteristic of the E side as a whole. The only conclusion which seems to be justified is that our data do not prove conclusively that there is a definite departure from a 3 : 1 ratio, but there may be.

TABLE 24.—Segregation in F_3 of α dextral × ε dextral crosses.

Strain of A parent.	Strain of E parent.	A side.						E side.					
		A.	K.	E.	F.	Total.	A per cent.	A.	K.	E.	F.	Total.	A per cent.
4532	672	*25	1	5	0	31	81	*13	0	1	0	14	93
4532	677	—	—	—	—	—	—	*31	5	2	1	39	79
4532	677	* 1	0	1	0	2	50	—	—	—	—	—	—
Colne	672	—	—	—	—	—	—	* 5	2	0	0	7	71
"	672	—	—	—	—	—	—	*17	3	3	0	23	74
Pond 27	684	7	3	2	0	12	58	2	1	0	0	3	67
Stelfox	671 P. Sq.	9	0	1	0	10	90	* 4	3	1	0	8	50
"	749 P. Sq.	—	—	—	—	—	—	* 8	4	5	2	19	42
"	749 P. Sq.	*14	3	0	0	17	82	—	—	—	—	—	—
"	749 P. Sq.	* 6	1	1	0	8	75	—	—	—	—	—	—
"	672 U.C.H.	*29	1	7	0	37	78	—	—	—	—	—	—
Total ...	—	91	9	17	0	117	77·8 per cent.	80	18	12	3	113	70·8 per cent.
Both sides ...		171	27	29	3	230	74·3 per cent.						

* Carried on to F_4.

F_4.—In F_4 the KE broods breed true. Some of the A broods break up into mixed groups of A and KE, some do not. The number tested is inadequate to establish any ratio : actually 6 have appeared to be homozygous, 11 heterozygous and 5 doubtful. The broods obtained in the heterozygous groups (excluding two in each of which the only evidence of heterozygosity is an F brood) are summed in Table 25. The results are compatible with a 3 : 1 ratio :—

	A broods.	K E F broods.	Total.
Observed	70	29	99
3 : 1 expectation ...	74·25	24·75	99

(2) ε *sinistral* × α *dextral crosses* (Table X).—Using the pigmented dextral breakthrough, 4532, and E sinistrals from an albino mutation (which appeared in the 677 strain from 331 in 1926 and breeds badly (Table VI)), we got :—

E side : F_1 (*a*) five albino snails and one pigmented sinistral which failed to breed, (*b*) six albino and two pigmented sinistrals, one of which gave a brood of 772 pigmented and albino dextrals, from which in F_3 we had 10A, 2K and 1E broods, the KE broods containing 839 sin. and 1 dex.

TABLE 25.—Segregation in F_4 of α dextral and ε dextral crosses.

Strain of A parent.	Strain of E parent.	A side.						E side.					
		A.	K.	E.	F.	Total.	A per cent.	A.	K.	E.	F.	Total.	A per cent.
4532	672	—	—	—	—	—	—	23	—	7	3	33	70
4532	677	—	—	—	—	—	—	6	3	1	—	10	60
4532	677	4	1	1	—	6	67	—	—	—	—	—	—
Colne	672	—	—	—	—	—	—	8	2	1	—	11	73
,,	672	—	—	—	—	—	—	4	2	1	—	7	57
Stelfox	671	—	—	—	—	—	—	10	2	—	—	12	83
,,	749	—	—	—	—	—	—	6	—	2	—	8	75
,,	749	6	2	—	—	8	75	—	—	—	—	—	—
,,	749	3	1	—	—	4	75	—	—	—	—	—	—
Total ...	—	13	4	1	0	18	72 per cent.	57	9	12	3	81	70 per cent.
Both sides ...		70	13	13	3	99	71 per cent.	—	—	—	—	—	—

A side : F_1 were dextral broods of 46 and 27 : F_2 15 dextral broods (pigmented and albino) with 5,858 snails : F_3 12A with 2K and 1E brood adding up to 532 sin. and 2 dex.

(3) ε *sinistral* × κ *sinistral crosses* (Table X). For this we used E sinistrals from the high ε strain 672 and K sinistrals from the albino strain 1629.

F_1.—On the E side we have four crosses verified by mixed broods of albino and pigmenteds in F_2 :—

Sin. .. 25 55 28 11 : 119
Dex. .. 14 15 5 5 : 39 = 24·7 per cent. $k = 0{\cdot}04$

which is much what might be expected from self-fertilised parents : the total product does not differ statistically from the control singles in the 672 strain bred in the same year (1927) (diff./s.e. = 1·9).

On the K side six crosses are verified by F_1 being pigmented, the broods being :—

Sin. .. 28 117 171 74 163 60 : 613
Dex. .. 0 0 1 0 0 1 : 2 $k = 9{\cdot}2$

and corresponding to those obtained in parallel from uncrossed controls.

F_2.—Five of the crosses were carried on and gave in all :—

——	Broods.	E broods.	Sinistrals.	Dextrals.	= percentage.	Brood size.*	*k*.
E side	24	13	5,122	23	0·45	214	4·1
K side	21	8	4,101	13	0·32	196	8·3
Total ...	45	21	9,223	36	0·39	205	5·5

* These are liable to some qualification, since some were obtained late in the summer as second broods.

The dextrals in the F_1 E broods from the E parents giving the same progeny as their sinistral brethren. A few which were bred to F_2 in the same year (1927) are not different from the majority, which were bred in 1928. The two sides do not differ from one another (diff./s.e. = 1·0).

Though 21 of the 45 broods are classed as E because each contains some dextrals, it is evident that they are of an E-ness quite different to that of the 672 component of the cross. There is indeed only one brood (57 sin., 1 dex.) which would be natural in the 672 strain, the E-est of the others being 219 sin., 1 dex. The E-ness of 672, therefore, has not appeared in F_2. On the other hand, the F_2 product is probably not identical with the controls bred in the parent K strain 1629 :—

——	Broods.	Sinistrals.	Dextrals.	= percentage.	Brood size.	*k*.
E × K { E broods ...	21	4,159	36	0·8	215	1·26
K broods ...	24	4,704	0	0·0	196	—
672 strain : 1926–1928 ...	54	1,931	300	13·4	41	0·08

——	Broods.	E broods.	Sinistrals.	Dextrals.	= percentage.	Brood size.	*k*.
F_2 E×K crosses	45	21	9,223	36	0·389	205	5·5
Control K 1629	13	2	3,377	2	0·059	260	110

Difference/standard error = 3·0.

But it is much nearer the K than the E parent.

F_3.—One cross was taken on extensively in F_3 and three others on a small scale, giving in all :—

——	Broods.	E broods.	Sinistrals.	Dextrals.	= percentage.	Brood size.	*k*.
E side	34	7	3,494	24	0·68	103	7·1
K side	33	9	6,787	16	0·23	206	15·4
Total ...	67	16	10,281	40	0·39	154	10·8
E broods only	—	16	2,580	40	1·53	218	0·65

The E side has smaller broods and more dextrals (diff./s.e. $= 3\cdot5$) than the K side. The possible segregation ratio of E-ness and K-ness cannot be properly examined, since small K broods which are really ε cannot be identified: 16 in 67 is a fair approximation to 1 in 4, and if we add the 9 K broods of less than 50 to the E broods we have: K 42, E 25. Whatever the ratio (if any) may be, it is clear that what reappears in F_3 is not the small-brooded E-ness characteristic of the E parent: only one brood is possibly characteristic of the 672 strain (170 sin., 11 dex.).

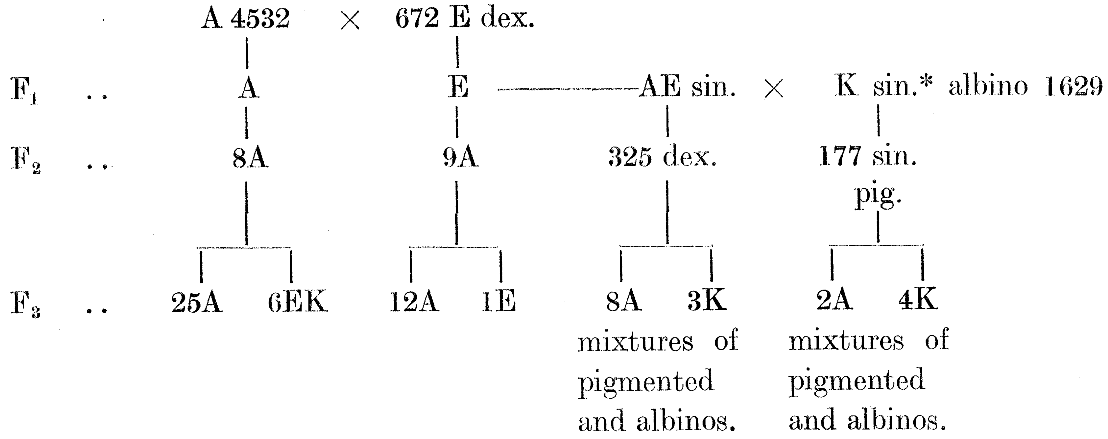
F_4.—Four E and 2 K broods were taken on, but only to a small extent, giving in all 11 K and 9 E broods. One group, from the best E brood in F_3, had $2\cdot9$ per cent. dextrals and $k = 0\cdot52$.

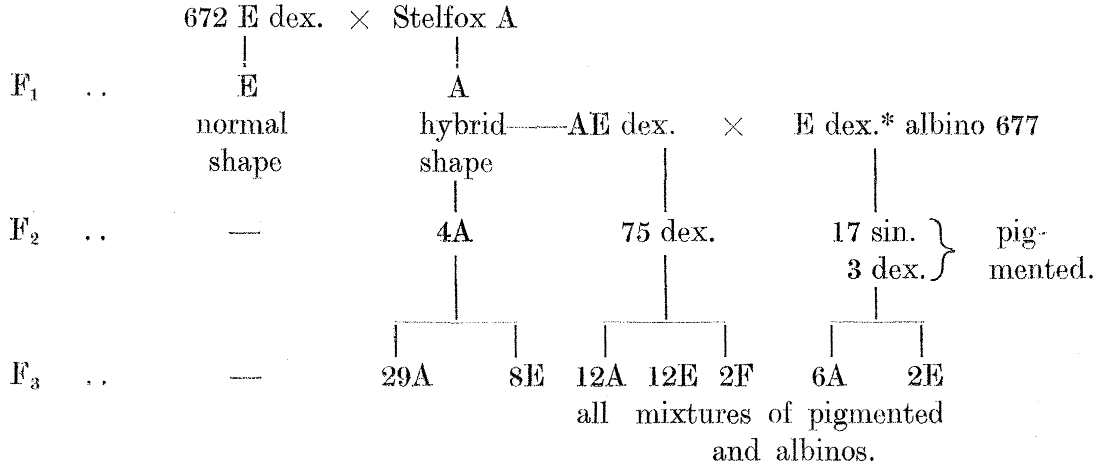
We made also two crosses between K sinistrals (ultimately derived from an F brood: 1572, Table II) and albino E sinistrals from 677. They succeeded only on the K side and in F_1, F_2 and F_3 produced 9 K and 6 E broods, the E broods together having $1\cdot1$ per cent. dextrals and $k = 0\cdot9$.

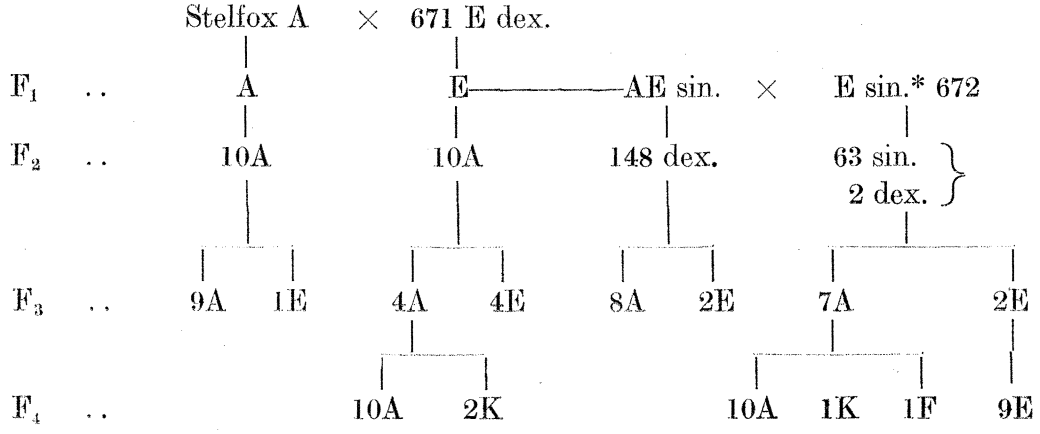
The total result, therefore, of these E sinistral × K sinistral crosses is 157 K and E broods without the appearance of any genetical dextrality.

(4) *ε Dextral and κ Sinistral Crosses.*—Two crosses succeeded (on the K side only) between ε dextrals of the 672 strain and albino sinistrals 1629. F_1 were K broods of 14 and 314 sinistrals; in F_2 we have 7 K broods and 1 E brood, totalling 634 sin. and 2 dex. The dextral parent has not introduced any genetical dextrality. In F_3 there are 10 K broods and 8 E, the latter totalling 892 sin. and 26 dex., with one brood of 73 sin., 18 dex.

(5) *Back-crosses with ε Snails* (Tables VIII and IX).—Three sorts of back-crosses have been made. They are chiefly of interest as showing that zygotic segregation actually occurs in F_1 of A × E (and therefore presumably in A × K) crosses. In each instance the progeny of the fresh snail brought in (marked *) have segregated in their F_2 instead of F_3 because their eggs were fertilised by segregated sperm. The segregation ratios are in the expected sense (43 A to 27 KEF), but the number of broods is too small to be of any great significance.







The summary of the facts of these crossing experiments with ε snails is then

(1) E-ness has a similar relation to A-ness as K-ness, *i.e.*, E-ness behaves as a recessive;

(2) E-dextrals are genetically equivalent to E-sinistrals and have no genetic dextrality.

(*g*) *The character of the E and K broods which appear in F_3, F_4 and F_5 of α × ε and ε × κ crosses.*—The precise character of the segregating recessive in A × E crosses is of considerable importance in trying to come to some conclusion as to the nature of E-ness. The chief question is—Does the E-ness put into the cross reappear as such?

During the progress of the crossing experiments we have continued in most instances to breed the components in the usual routine way as self-fertilising singles, and these broods form the control for what emerges from the crossings.

(1) *A × E crosses involving the ε strain* 672 (*Tables VIII and IX*).—We have most information about the crosses in which we used E snails from the characteristic ε strain from 672. Our routine control breeding of this strain is shown in Table 26 (Table VI).

TABLE 26.—Control breeding of ε strain 672 used in crosses.

Year.	Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	k.
1924 ...	9	9	172	62	26·5	26	0·04
1925 ...	49	32	1,070	147	12·1	27	0·13
1926 ...	31	30	1,309	178	12·0	49	0·09
1927 ...	14	13	491	108	18·0	40	0·06
1928 ...	9	3	131	14	9·5	16	0·15
1929 ...	21	11	88	39	30·7	6	0·06
Total ...	133	98	3,261	548	14·4	29	0·09

The products of the different years are not the same (though the broods of each year are homogeneous among themselves), but the strain consistently produces a high proportion of dextrals and k is below 0·2. The crossings were made in 1926 and 1927 and the recessive broods obtained in 1927, 1928 and 1929. Unfortunately the breeding of the controls was unsatisfactory in 1928 and 1929, and it is a little difficult to be sure what comparisons may most justly be made. The nature of the results, however, make it unnecessary to discuss this at length, for the E and K broods which emerged mostly failed to reproduce the E-ness of the 672 strain at any time.

(*a*) Taking first the well-bred crosses with the dextral strain 4532, we had

F_3 (1927) .. brood of 4/1*.
|
F_4 (1928) .. broods of 56/6, 84/20.
|
F_5 (1929) .. group of 6 broods with 215/98 : $k = 0{\cdot}04$

which, except that the brood size is rather large, would pass for 672 itself.

But the rest of the EK broods are quite unlike 672. Adding them together we have :—

TABLE 27.—Segregate recessive groups in $\alpha \times \varepsilon$ crosses.

——	Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	k.
F_3 ...	6	5	514	20	3·7	89	0·32
F_4 ...	42	21	2,934	44	1·5	71	1·33
F_5 ...	32	12	1,814	27	1·5	57	2·3
A side ...	61	27	4,487	66	1·4	75	1·58
E side ...	19	11	775	26	3·2	42	0·53
Total ...	80	38	5,262	92	1·7	67	1·23

---

* *i.e.*, 4 sinistrals and 1 dextral.

The E side has more dextrals than the A side (diff./s.e. = 3·7) and smaller broods, but neither reproduces the E-ness which was put into the crosses. Even the E broods by themselves fall short of 672 in E-ness :—

——	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	*k*.
A side	27	1,968	66	3·3	75	0·31
E side	11	379	26	6·4	37	0·16

And there are a number of broods (K broods of 210, 118 and 102, E broods of 268/1, 238/1, etc.) which are very unlikely members of the 672 strain.

(*b*) Crosses with Colne wild dextrals (Table VIII) gave similar results (E side only obtained) with a better approximation to 672, while a Stelfox cross (on the A side only : Table IX) gave four groups, one in F_3 and three in F_4, any of which would pass for uncrossed 672.

Dextral parent.	Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	*k*.
Colne ...	23	12	629	37	5·6	29	0·35
Stelfox ...	27	18	375	54	12·6	16	0·08

(2) *E × K crosses involving the ε strain* 672 (Table X).—We have E-sinistral × K-sinistral and E-dextral × K-sinistral. Of 33 E broods, only two show high E-ness, notably 73/18 ; from another F_3 brood of 170/11 a good ε group ($k = 0·52$) was obtained in F_4. As a whole the emergent E broods have little resemblance to what was put into the original crosses (Table 28).

TABLE 28.—Segregate E broods from ε × κ crosses.

——	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	*k*.
E sin. × K : F_3 K side	9	1,799	16	0·9	202	1·1
E sin. × K : F_3 E side	7	781	24	3·0	115	0·3
E sin. × K : F_4 E side	9	892	26	2·8	102	0·4
Total	25	3,472	66	1·9	141	0·5
E dex. × K : F_3 K side	8	892	26	2·8	115	0·3

(3) *A × E crosses between Stelfox dextrals and the ε strain* 749 (Table IX).—These crosses were made in 1926 and the ε strain and the progeny of the crosses were bred side by side at Pembroke Square. The control annual totals gave the following results :—

——	Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	*k*.
1927 ...	15	6	245	16	6·1	17	0·41
1928 ...	16	9	235	19	7·5	16	0·24
1929 ...	6	3	202	11	5·2	35	0·39
Total ...	37	18	682	46	6·3	20	0·32

The segregating broods, on the E side in one instance, on the A side in the two other crosses, were *en masse* :—

——		Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood size.	*k*.
F_3	A side	5	1	179	8	4·3	37	1·2
	E side	9	5	243	20	7·6	29	0·24
F_4	A side	12	7	473	16	3·3	41	0·44
	E side	48	38	1,342	276	17·1	34	0·07

And the degree of E-ness emerging is in F_3 about equal to and on the E side in F_4 distinctly greater than what was put in. The F_4 groups differ among themselves and show (as did the original 331 strain at its initiation : see p. 77) an exceptional correspondence between the proportion of dextrals in a brood and the E-ness of the group bred from it. One group contained four broods out of 20 in which dextrals predominated (21/31, 13/18, 22/28, 18/40), and is about as high in E-ness ($k = 0·04$) as any group we have had.

Parent brood.	Derived group.
33 sin. 0 dex. ...	2·4 per cent. dex., brood size 41, *k* = 0·48
24 ,, 1 ,, ...	4·1 ,, ,, ,, 21 ,, 0·46
88 ,, 8 ,, ...	17·6 ,, ,, ,, 60 ,, 0·06
20 ,, 8 ,, ...	29·0 ,, ,, ,, 34 ,, 0·04

(4) *Other A × E and A × K crosses* (Tables VIII, IX and X).—We have a few other results from crosses in which various ε strains were used. The results may be summarised :—

——	Broods.	E broods.	Sinistrals.	Dextrals.	Dex. per cent.	Brood.	*k.*	ε strain uncrossed.	
								Average dex. per cent.	Average brood size.
E dex. 677 × A dex. 4532 ...	12	5	713	7	1·0	60	2·47	7·1	32
E dex. 677 × K sin.	3	3	508	7	1·4	172	0·74	7·1	32
E sin. 677 × A dex. 4532 ...	4	1	1,047	1	0·1	262	42·0	7·1	32
E dex. 684 × A dex. pond 27	6	2	167	5	2·9	29	1·03	5·2	61
E dex. 671 × A dex. Stelfox...	7	2	169	7	4·0	25	0·88	10·6	42

The E-ness of the emerging broods is distinctly less than that of their ultimate parent.

(5) *Back-crosses* (Table IX).—Two A × E back-crosses (above, p. 107) have been bred to F_3 and F_4 (on the scale of the original cross) : in both the original A parent was of the Stelfox strain. (*a*) A × E dex. of 671 strain (controls = 10·6 per cent. dex.) ; an F_1 sinistral on the E side was then crossed with an E sinistral from 672 (controls = 14·4 per cent. dex.) and bred on from the progeny of the latter. (*b*) A × E dex. from 672 ; an F_1 dextral on the A side was then crossed with an albino E dextral from 677 (7·1 per cent.) and the progeny of the former carried on. The summary results of the recessive broods are :—

	Broods.	E broods.	Sinistrals.	Dextrals.	Dextral percentage.	Brood.	*k.*
(*a*)	34	13	1,880	34	1·8	56	1·47
(*b*)	32	28	1,129	151	11·0	40	0·097

The groups are various, including in (*a*) 257/16 and 1200/2 : in (*b*), where a direct comparison is possible, the E-ness does not differ from that of F_3 and F_4 which are not back-crossed.

The chief conclusion which can be drawn from this series of facts is that a high ε strain does not usually come out as such in F_3, F_4 and F_5 of crosses with A dextral or K sinistral snails. Occasionally it may do so, especially in F_4 and F_5, and this E-ness may often be enhanced by selecting a brood with many dextrals to carry on : high E-ness can in this way emerge from a cross in which the original E parent came from a heterogeneous strain (p. 80) of only moderate E-ness. There is some inconclusive evidence that E-ness comes out higher on the E side of the cross than on the A side, and it seems almost certain that high E-ness comes out better from a cross with a Stelfox dextral than from those in which other brands—line-bred or wild—of dextrals were used. But, broadly speaking, it is true that in A × E and E × K crosses less E-ness emerges than was put in.

On the other hand, we have obtained only one good-sized group which can be classed as frank κ (*i.e.*, with $k = 10$ or more), though we have deliberately carried on large sinistral broods as well as those showing most dextrals. The nearest we have are :—

——	Brood of origin.	Broods.	E broods.	Sinistrals.	Dextrals.	Dex. per cent.	Brood.	k.
A 4532 × E 672 F_4	118/0	16	8	2,180	16	0·73	137	2·7
A 4532 × E 672 F_5	210/0	14	6	1,197	18	1·48	87	1·6
A Stelfox × E 671 : back-cross	60/0	12	2	1,200	2	0·17	100	36·1

The only explanation available seems to be that the lowering of the degree of E-ness is due to an increase in brood size caused by the crossing. It is clear that such an increase takes place on both the A and E sides. Thus the small-brooded α strain from 4532 (normal mean brood = 113) emerges about twice as big : 43 A broods in F_2 and F_3 average 232 snails. The ε strain 672 selfed has an average brood size of about 30 : the segregating KE broods from the crosses are two to four times as big, except when they approach 672 in E-ness, when they are about the same as the controls. If the same relation holds as obtains between the different ε and κ strains (above, p. 85) we should expect a rise in brood size to 100 to be associated with a fall in the dextrals to about $1\frac{1}{2}$ per cent. The proportion of dextrals (which in our descriptions we have commonly treated as the more important feature) could hardly be altered directly by hybrid vigour (heterosis) : it is probably more correct to think of the tendency to monstrous development and the consequent small broods as the primary event. In this way it is possible to imagine that the general improvement in healthiness produced by the cross is also responsible for the fall in the proportion of dextrals.* Pairing within an ε strain, where there should be no heterosis, does not alter the proportion of dextrals (above, p. 96), nor, as far as we know, the brood size, though we have no controls of this kind in which the parents were grown up, put together and then separated as in the crosses between different types.

On the other hand, from the *A-dextral* × *K-sinistral crosses* (above, p. 60) more E-ness emerges than was put in, and the size of the recessive segregate broods is smaller than those of the uncrossed K parent (Table 29), which was in all instances an albino sinistral from 1629 of very low E-ness. In the U.C.H. series the segregates evidently have more E-ness than the parent strain. In F_3 this is not of a very high order, the

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* It may be significant that the Stelfox strain, through which high E-ness emerges most successfully, is a specialised wild form of *peregra* produced presumably by isolation in a lake.

E broods by themselves giving $k = 0{\cdot}54$ with a best brood of 69/9. In F_4, however, we have broods of 9/13, 29/10 and 53/15 and groups with $k = 0{\cdot}23$ and $0{\cdot}06$. The Catford series (bred at New Cross with the same K, but other A, parents) are less satis factory for detailed analysis : many of the broods were small, and of 10 of the 47 K E broods we know only that they contained at least 100 sinistrals ; only 5 E broods were identified. As far as they go, they give a result in the same sense, though they do not differ statistically from the 1928 series of 1629 (diff./s.e. = 1·8). In none of the crosses is there a detectable difference between the dextral and sinistral sides.

TABLE 29.—K and E segregates in F_3 and F_4 of A × K crosses compared with the strain from which the K parents came.

——				Broods.	E broods.	Sinistrals.	Dextrals.	Dex. per cent.	Brood size.	*k*.
K parents : 1629 albino			1926	18	2	7,360	2	0·03	409	331
,, ,, ...			1927	6	0	1,422	0	—	237	> 85
,, ,, ...			1928	7	2	1,955	2	0·10	280	34
,, ,, ...			1929	11	0	2,783	0	—	253	>306
Total				42	4	13,520	4	0·03	322	710
A × K K and E segregates	U.C.H. series	F_3 1928	dextral side	19	7	1,761	16	0·91	94	3·0
			sinistral side	11	7	1,564	22	1·41	144	1·1
		Total ...		30	14	3,325	38	1·13	112	1·9
		F_4 1928	dextral side	29	8	910	16	1·73	32	2·1
			sinistral side	46	16	2,346	62	2·58	52	1·1
		Total ...		75	24	3,256	78	2·34	44	1·8
	Catford series	F_3 1927 to 1929	dextral side	15	1	899+	4	0·44	60	34
			sinistral side	32	4	2,393+	8	0·33	75	24
		Total ...		47	5	3,292+	12	0·36	70	26

Summarising, we reach the conclusions—

(1) In A × E and E × K crosses, the E-ness which is put in does not systematically emerge as such in F_3, F_4 and F_5.

(2) In A × E crosses, less E-ness generally emerges than was put in, *i.e.*, high E-ness is reduced, and one K group has been obtained ; on the other hand, high E-ness sometimes emerges.

(3) In E × K crosses, high E-ness is reduced.

(4) In A × K crosses, more E-ness emerges than was put in and high E-ness may appear.

(*h*) *The nature of E broods and E-ness.*—E broods then are essentially sinistral broods: the dextral snails in them are only phenotypic dextrals and have no genetical dextrality. The mechanism by which they are produced seems fairly clear. The basis of E-ness is something which is pulling the snails in a brood towards dextrality, and most of them are somewhere near an equipoise between this influence and their genetical sinistrality. This is an impossible position, for even if the shell is coiled on the flat and is neither dextral nor sinistral the body cannot be neutral. Neutrality, therefore, is fatal, and the conflict of purpose kills the majority of the embryos and leads to the appearance of various monstrous snails. Some of these are viable, among them the dextrals, which are twisted to the right presumably because of a mistake in the first division of the eggs: this necessarily leads to a snail of dextral appearance (if it leads to an adult at all) without producing any change in the genetic constitution. As in flat, half-flat, and scalariform snails, the monstrosity itself is not heritable. The tendency to mal-development is, however, clearly a heritable quality: its genetic nature is by no means so plain.

In both of our line-bred families, sinistral broods have sooner or later given rise to E broods, and a number of these E broods when bred on have established ε strains which continue as such. Similarly, some of the original K broods carried on have given rise to stable κ strains. We have already (above, p. 74) discussed the difficulty of sharply distinguishing ε and κ lines from one another: if together they form a continuous series, the end terms are sufficiently distinct and they separate out from one another in such a way that it is at any rate necessary to consider the possibility of their being really different genetically. Similarly, we can distinguish strains with a large percentage of dextrals (high ε strains) from those with a small percentage (low ε strains), and each breeds true. Hence it is possible that there is more than one kind of E-ness. If there is, the phenotypic expressions which emerge from crosses made with ε snails are so confused that it is not possible to analyse the results in these terms, and we propose provisionally to look upon all E-ness as essentially the same thing. We may also note the possibility that the quality might be carried in α strains, though obviously it can obtain expression only in sinistral snails. We have no clear evidence that brood size is determined by factors which are independent of those controlling E-ness, though it is possible that such exist.

Broadly speaking, an explanation of E-ness may be sought along two lines:—

(1) We may suppose it to be an inherent "constitutional" character of sinistral snails, none of which are entirely free from it. Under our conditions of breeding, this "weakness" is liable to be exaggerated, errors of development are more frequent, and phenotypic dextrals become more abundant. It is not a transitory environmental effect: a strain, once it has received the impression, continues in the same way, though under the stimulus of crossing the tendency is, for a time at any rate, considerably diminished. Our method of selective breeding by self-fertilisation may without much difficulty be supposed to encourage this kind of defect and to effect the separation of

snails which show it as substrains with pretty constant characters. Whether the wild sinistral population in King Lane pond shows E-ness we do not know: HARGREAVES (1919) hatched out 18 isolated egg capsules laid by an indefinite number of wild sinistrals and got E broods from two, with 10 A, 3 K and 3 F broods. This kind of "explanation" of E-ness in effect appeals to the "germ-weakening" on which MACBRIDE (1924, p. 229) lays so much stress: it is vague and not very satisfying, and we have several κ lines which have gone on for a number of generations without showing any signs of E-ness, so that mere continuance of in-breeding will certainly not always produce it.

(2) Alternatively, we may suppose that E-ness depends on a definite genetic factor, and, reducing the possibilities to the simplest terms, that A, K and E are allelomorphs. A is proved to be dominant to K and E. E appears in κ lines and separates itself off, and κ gets rid of ε (see *e.g.*, Table II); with two exceptions (pp. 81, 112) we have never had κ arise from ε; hence we may suppose that ε is generally recessive to κ. Correspondingly, it seems quite possible that we have K E heterozygotes analogous to A K and A E. It is also suggestive that this separation occurs in the earlier generations—the third, fourth and fifth in our line-breeding and in F_4 and F_5 of our A × E and A × K crosses: after this the ε and κ lines continue as such and the latter show no tendency to throw off more E.

On the whole our results are compatible with this hypothesis, though we have no clear evidence in its support from segregation ratios in the line-breeding. When we test it directly by crossing K and E, the results are equivocal. F_2 has 24 K broods and 21 E broods, all of low E-ness, $k = 5 \cdot 5$, and as a whole it is κ rather than ε, though definitely more ε than the κ put into the cross. In F_3 the ratio between E and K broods (16 : 51) would pass for 1 : 3, but the E broods quite fail to reproduce the high E-ness of the original E parent, and they are in fact not certainly different *qua* percentage of dextrals from the E broods of F_2. We may evade these difficulties by assuming (1) that dominance is incomplete, (2) that the high E-ness put into the cross is masked by the vigour of heterosis. This brings us into the predicament that we cannot be sure whether a brood of, say, 150 sinistrals and 2 dextrals is a masked ε brood or a κ brood, and, if we assume that these alternatives are exclusive, makes the formal interpretation of K × E crosses impossible.

Or we may consider the possibility that E-ness is not of itself a type of sinistrality, but the product of an independent gene whose only phenotypic effect is the modification of sinistrality towards the production of odd dextrals and other monstrous forms, the allelomorph being simply the absence of E-ness. This interpretation involves the possibility that E-ness might be carried in α strains, though it could obtain expression only in sinistral snails. It is in a general way not inconsistent with most of our facts. Against it is (*a*) the impossibility of being sure that we ever have sinistrality completely free of E-ness, (*b*) the failure to get a definite separation of ε from κ among the recessive segregates of A × E crosses and in E × K crosses, and (*c*) the emergence of high E-ness in F_4 of an A × K cross in which the α and κ lines had been pure for four generations (the latter with 6 dextrals to 16,390 sinistrals) and have continued in the same way for three generations since. The occurrence is not altogether conclusive, for the α line came from a " dextral break-through," an abnormality which is associated with E-ness (below, p. 119), and it is possible that it carried E-ness which could not appear until it had sinistral snails to work on. This seems an unlikely interpretation, for similar dextrals were extensively used in the A × E crosses, and in F_3 and F_4, from these high E-ness is not so abundant as in similar crosses in which wild (Stelfox) dextrals were used : the other wild strains behaved as if they were, on this hypothesis, free of high E-ness.

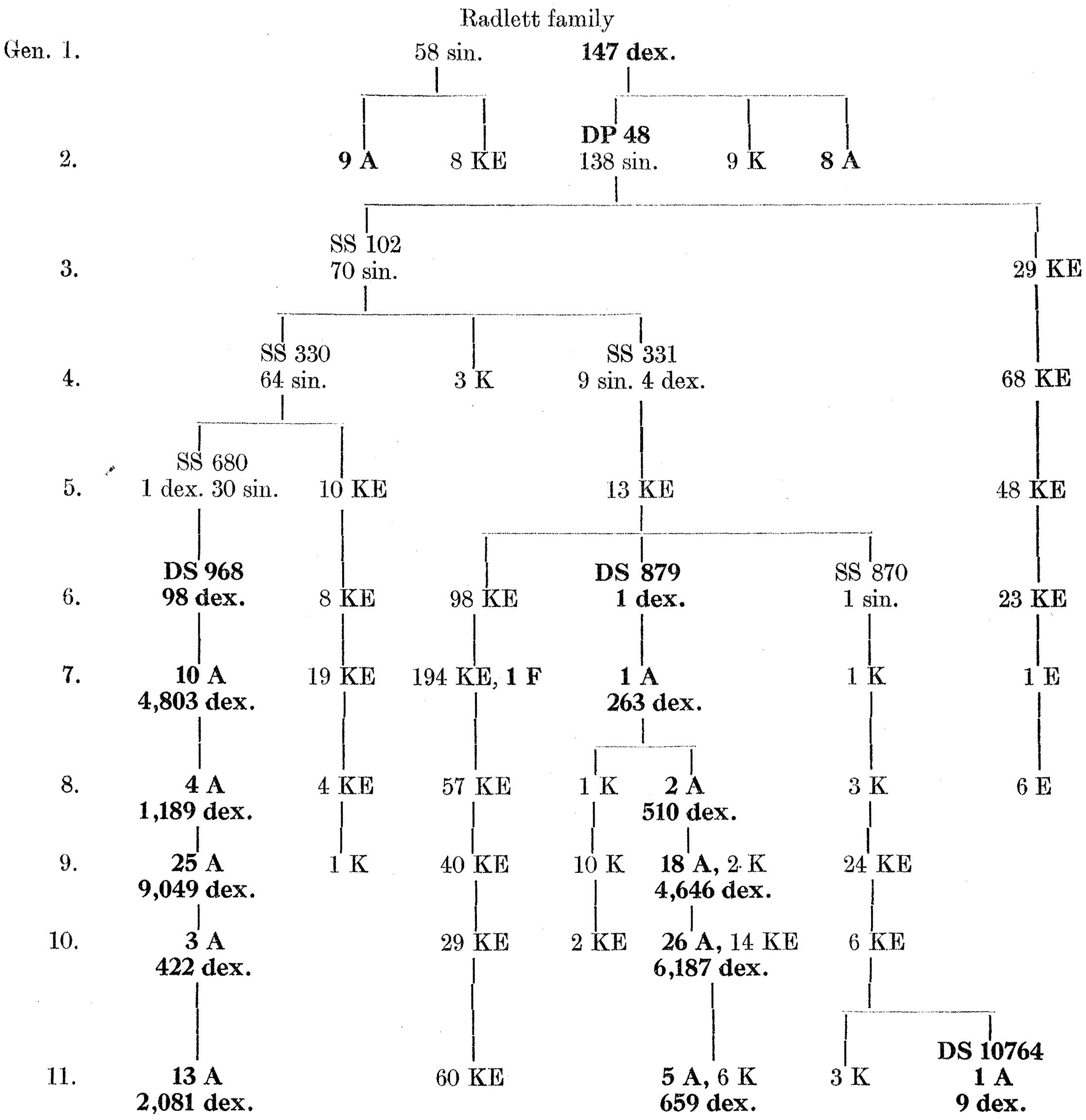
There are then substantial difficulties in the way of these explanations and of any others we have been able to think of, *e.g.*, that E-ness is a type of sinistrality not alternative to K-ness, but with its own dextral-determining allelomorph. It is certainly not " cytoplasmic " in the ordinary sense, since both sides of the crosses give the same results ; nor can it reasonably be supposed to be environmental. Taking one thing with another, there seem to be two interpretations available. (i) That high E-ness and K-ness are the ends of a graded series and that all sinistrals have a tendency to embryonic misdevelopment and the production of phenotypic dextrals, which varies in different strains and is heritable : this does little more than re-state the facts. (ii) That high E-ness is qualitatively different from the habit of κ strains to produce occasional dextrals, that it depends on a genetic factor, and that its manifestation is masked when it is associated with K-ness.

Our facts are very similar to those described by WRIGHT and EATON (1923) for otocephaly in in-bred strains of guinea-pigs. The monstrosity varies from a defect in Meckel's cartilage to cyclopia and on to an almost headless condition, and the different forms fall into a single graded series. Monsters appear suddenly in some substrains of animals, some of which afterwards produce more and more, so that by gen. 20 or thereabouts one strain may have 20 per cent. of monsters, others practically none. The tendency to produce them is distinctly heritable, though WRIGHT and EATON cannot fit their results on to any simple mendelian scheme any more than we can. They suggest that otocephaly depends on factors which control susceptibility to the environment and that there is segregation of different degrees of susceptibility in the earlier generations, followed by the relative fixation of a particular level in each substrain as some combination of factors becomes homozygous. This scheme would fit our data as well as another ; like other hypotheses invoking multiple factors, it is hardly susceptible to experimental verification.

2. *Dextral break-throughs* (*reverse dextral mutations*).

Our line breeding was from the first confused by the appearance of pure dextral A broods, breeding true, in places where sinistrals were to be expected. A typical example is shown (Table 30 : for details see Table V) in the Radlett family. DP 48 gave a brood of 138 sinistrals. These were bred on by self-fertilised singles and in gens. 3, 4

TABLE 30.—Occurrence of dextral break-throughs in related strains.



and 5 gave in all 122 K and 53 E broods. One of the latter (SS 680) was 30 sin. and 1 dex., and the odd dextral (DS 968) gave in gen. 6 a brood of 98 dextrals, which has been bred on extensively to gen. 11 with a total product of 55 A broods and 17,544 dextral snails, some of which have been used in A × K crosses and have given the same results as other dextral break-throughs and wild dextrals. The collateral broods in gen. 5 were also taken on and gave only K and E broods. The occurrence of this genotypic dextral A line in a wholly K E recessive strain cannot possibly be explained on the simple plan of dextral dominance and delayed inheritance. We can assume only a complete mutation to genotypic dextrality. The same assumption has to be made for the heterozygous AK strain that emerged in gen. 6 from a convulsed ε brood (DS 879 :

above, p. 81); presumably also for the A brood, which came in gen. 11 in a κ line of the same origin and for the F brood in gen. 7 in a related ε strain, though these two were not bred on.

The phenomenon is indeed not uncommon (Table 31). We have in our line-breeding ten examples which have been confirmed by further breeding, six proving homozygous, two heterozygous A K, and two heterozygous A E. Five others are probably of the same type, but they have not been carried on: one is an F brood and two are small A broods (eight and nine snails) which might possibly be ε broods. Particular interest attaches to 2819 (Table IV), where a sinistral single in a segregate E brood from another

TABLE 31.—Dextral break-throughs in line breeding.

Reference table.	Gen.	Parent.	Brood type.	Brood.		k for associated group.	Genetic constitution.	Remarks.
				Dex.	Sin.			
London family.								
I	2	SP 36	"C"	149	13	40	Het. AK	On one side of a pair of sibs from original K broods (below p. 124).
I	3	SS 4511	A	203	—	0·82	Homo. ...	From a K brood sib of SP 36.
I	3	SS 4020	A	96	—	0·05	Not bred	From a K brood sib of SP 36.
I	4	DS 4532	A	54	—	0·13	Homo. ...	From E-dex. in group ($k =$ 0·05) containing SS 4020.
I	5	DS 958	A	154	—	0·55	Homo. ...	From E-dex. in an $\varepsilon\kappa$ group of $k =$ 5·6.
II	7	DS 7364	A	190	—	54	Homo. ...	From E-dex. in κ group ($k =$ 64) from odd sin. in F brood.
Radlett family.								
V	6	DS 968	A	98	—	?	Homo. ...	From E-dex. in ε group ($k =$ 2·17).
VI	6	DS 879	A	263	—	?	Het. AK	From E-dex. in ε group (p. 81 above).
VI	11	DS 10764	A	9	—	7·0	Not bred	From E-dex. in κ group ($k =$ 4·9).
VI	7	SS 2689	F	241	3	0·97	Not bred	From E-sin. in ε group ($k =$ 0·136).
V	6	SS 2369	A	8	—	3·37	Not bred	From K brood in ε group ($k =$ 0·20).
IV	5	SS 2169	A	14	—	29	Het. AE	From K brood in segregating group from DP 75.
IV	7	SS 2819	A–E	24	48	4·0	Homo. ...	From sin. in segregating E brood from SS 2169: E brood following dextral brood: unique case.
IV	7	DP 2728	"C"	550	508	0·98	Not bred	From a pair of E-dextrals from segregate ε group ($k =$ 0·175).
IV	7	DS 2731	A	341	—	0·98	Het. AE	From E-dex. sib of DP 2728.

The two "C" broods are the product of unseparated pairs.

heterozygous break-through produced first a brood of 21 dextral mutants and then returned to normal and gave 48 sinistral and 3 dextral young.

There are two important features about their occurrence :—

(1) There is a tendency for them to be concentrated together. Table 30 shows two close together, and in the early history of the London family there were five nearly related (Table 34). Similarly, 2819 appeared in the progeny of 2169, and 2728 and 2731 in the same group.

(2) They have a distinct association with E-ness, especially with its initiation and when the parent itself is a phenotypic E-dextral. Eight arose from dextral parents in E broods : only two in κ groups, both from odd dextrals. In other five the groups of origin might well be called KE, or E-ness appears in the progeny.

TABLE 32.—Shows the occurrence of dextral break-throughs in relation to the total number of parallel K and E broods bred up to end of 1927.*

Generation of parent from start or separation of strain.	ε strains.		κ strains.		KE groups.	
	from sin.	from dex.	from sin.	from dex.	from sin.	from dex.
1	1 in 83	5 in 33	0 in 300	0 in 5	4 in 181	0 in 1
2	0 in 213	0 in 45	0 in 273	1 in 9	0 in 111	0 in 6
3	1 in 250	1 in 57	0 in 98	0 in 1	0 in 55	0 in 4
4	0 in 54	0 in 23	0 in 47	—	1 in 22	0 in 2
5	0 in 40	0 in 9	0 in 11	—	—	—
—	2 in 640	6 in 167	0 in 729	1 in 15	5 in 369	0 in 13

The occurrence of dextral break-throughs in our crossing experiments is in harmony with these principles. We had none till ε groups began to separate out in F_3 and F_4, and three out of the four came from dextrals in E broods, of which we planted out all that were available in 1929 :—

	Sinistral parents.	Dextral break-throughs.	Dextral parents.	Dextral break-throughs.
A × K : F_4	51	0	5	2 (A)
A × E : F_4 and F_5	138	1 (F)	37	1 (A)
E × K : F_3 and F_4	17	0	18	0

We conclude from these facts that dextral break-throughs are probably caused by the same influence that causes E-ness, just as X-rays may produce monsters and also

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* In all our further breeding of κ and ε strains in 1928 and 1929, only one occurred : 10764 from an odd dextral in gen. 5 of a κ line which broke out of a high ε strain (Table 30).

heritable mutations (MULLER, 1928). When the complete conversion to genotypic dextrality occurs, the excessive embryonic mortality disappears.

3. *F broods.*

F broods consist mainly of dextrals with one or two sinistrals. Phenotypically they are the reverse of E broods, but genetically they are quite different. A-ness has nothing associated with it, pulling towards sinistrality as the E-ness of K strains pulls towards dextrality. Nor should we expect F broods to arise as the culmination of E-ness: extreme E broods may occasionally contain more dextrals than sinistrals, but a great preponderance of dextrals (*e.g.*, 100 to 1) would mean 100 monsters to one normal snail, and if E-ness ever reached that degree it would presumably kill the whole brood. There is also this great difference, that (with one exception) the dextrals and sinistrals of F broods have proved to be genotypic as well as phenotypic wherever it has been possible to breed on from them.

F broods are not particularly small; the smallest proved brood is 17 dex., 1 sin., the largest 339 dex., 2 sin., the average about 155.

F broods arising in KE groups (of which we have had two) are regarded as dextral break-throughs and have been treated as such. In our line-breeding we have 17 F broods from selfed dextral singles (and two more presumable F broods from pairs), which as far as they have been tested (Tables II, III, IV) follow these rules:—

(1) They occur exclusively in heterozygous AE or AK strains, never in extracted α lines or in lines from dextral break-throughs;

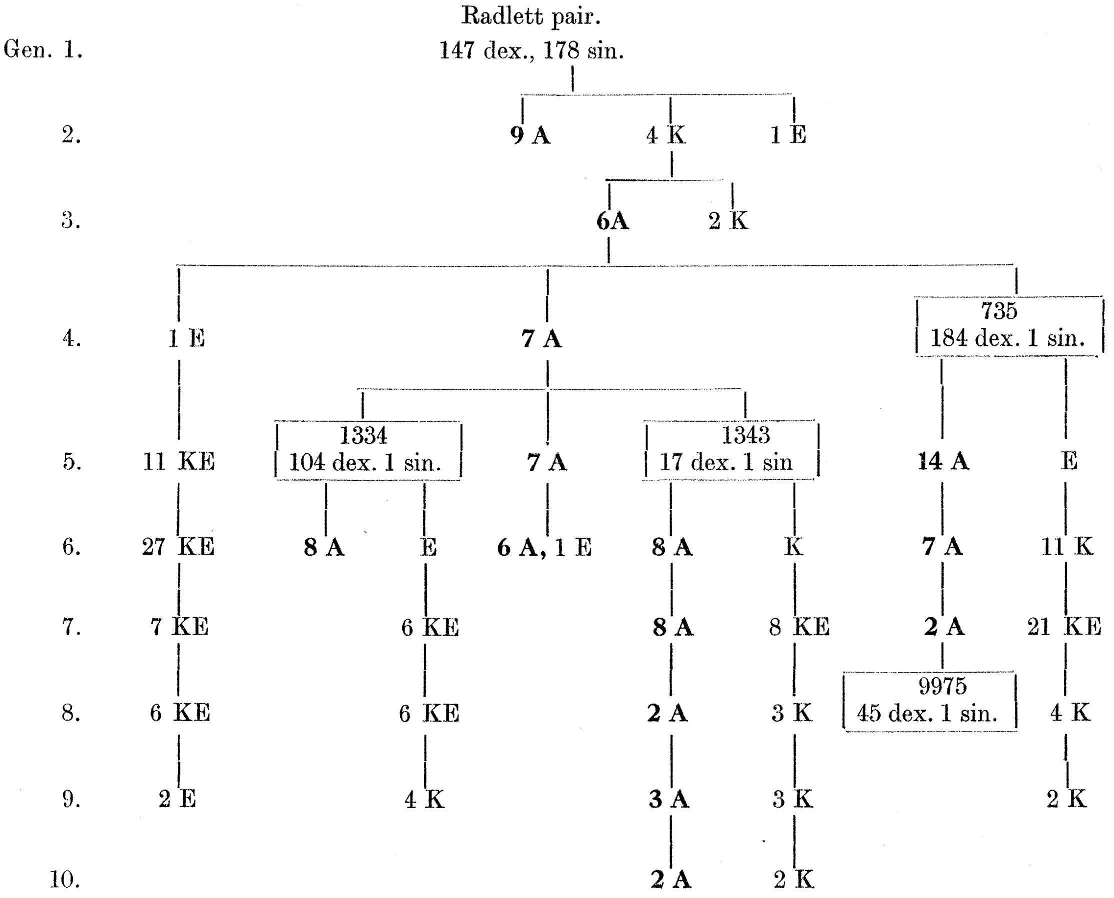
(2) They tend to cluster in certain lines (Table 33): in four instances two F broods are in the same group and one of these produced another in a subsequent generation: two more are related as parent to child;

(3) They are most frequent in generations 3, 4 and 5 (counting from the beginning of the line);

(4) Odd sinistrals (11 from 9 broods have been bred) give E or K lines, either small-brooded E, typical K or intermediate: where the odd sinistral lines can be compared with their related segregates they agree. Hence the odd sinistral is not a special phenomenon with one stereotyped behaviour, but gives rise to lines of just the types which arise in the ordinary course of segregation. In one instance (Table II: DS 1004: 152 dex., 5 sin.) two out of three sinistrals which were bred behaved like the dextrals and gave dextral broods, which afterwards segregated into A and K, *i.e.*, they were phenotypic sinistrals;

(5) The dextrals in F broods do not differ from the dextrals in other heterozygous groups: they may be heterozygous (*e.g.*, Table II) or homozygous (*e.g.*, Table III).

TABLE 33.—Showing the occurrence of four F broods, one of which is presumably a sinistral mutation.



We think, therefore, that the great majority of our F broods represent converted K or E broods, *i.e.*, they are incomplete dextral break-throughs and the odd sinistrals are snails which have escaped this conversion or slipped back. In the exceptional brood **1004** the conversion may be presumed to have taken place too late to affect the phenotype of all the sinistrals.

There are also 6 F broods in F_3 and F_4 of the A × K crosses (Table VII), 5 in F_3 and F_4 of the A × E crosses, and 3 in F_2 and F_3 of A × E back crosses (Tables VIII and IX), conforming in their place of occurrence to those in the line-breeding: none of the sinistrals have been bred on.

There are, however, difficulties—apparent and real. If F-ness and dextral break-throughs are forms of the same change it would be natural to expect that they would be associated together, whereas F-ness goes with segregating AK or AE groups and dextral break-throughs with E-ness, and though both clearly tend to cluster they do not cluster together. The difference, however, may be more apparent than real: dextral break-throughs cannot be identified in the segregating groups, and in them they may quite well occur along with F broods. But it is curious that the number of unconverted sinistrals is proportionately so small, generally 1 or 2 per brood, and never more than 5, in all only 45 sin. to 5167 dex. = 0·9 per cent. in 33 broods. The absence of broods with a substantial proportion of sinistrals certainly suggests fresh mutation to sinistrality as a better explanation, and there are 5 F broods which apparently must be of this type :—

(*a*) The dextrals of the F brood 735 (Table 33, Table III) were taken on through three generations of A broods and in the fourth gave an F. The odd sinistral of 735 gave a good K line.

(*b*) A dextral α line from DP 50 (Table IV) bred pure through five generations (in all 35 A broods) and in the sixth gave 13 A and 3 F (all from pairs) : not bred on.

(*c*) In two instances we had F broods from pairs in F_2 of the A side of A × E crosses where *ex hypothesi* only A broods could occur (Table VIII) : in one the crossing was shown to have occurred, in the other it was not proved. The product of the odd sinistral in both cases was E rather than K, and the grade of E-ness about the same as was put into the cross.

We suppose, therefore, that while the majority of F broods are partly converted K broods, a certain number (perhaps six) are A broods in which an odd snail has mutated to sinistrality. There are about 52 dextral mutations, taking dextral break-throughs and the common type of F brood together : our method of breeding has given them more chances to appear than the sinistral mutations, but scarcely in this proportion. Albino mutants have arisen three times.

VII. Analysis of the Line Breeding.

(*a*) *London family* (Tables I and II).

The London pair gave in generation 1 a brood of 350 sin. ; 34 of them were taken on as pairs and gave 13 K, 3 E and 1 " C " (SP 36) broods : 12 bred as singles produced 12 K broods : in all there are 25 K and 3 E (with 2118 sin. and 5 dex. snails) and one " C." Apart from the C brood, the London parents seem to be simple genotypical sinistrals, and we believe that the dextral-throwing component of SP 36 is a heterozygous " dextral break-through " (above, p. 116).

The original parents were not separated after pairing, and it is just possible that one of them was impure for A-ness (*i.e.*, the F_1 progeny of a K sinistral fertilised by an A dextral*), and (1) no cross-fertilisation occurred and the only progeny of

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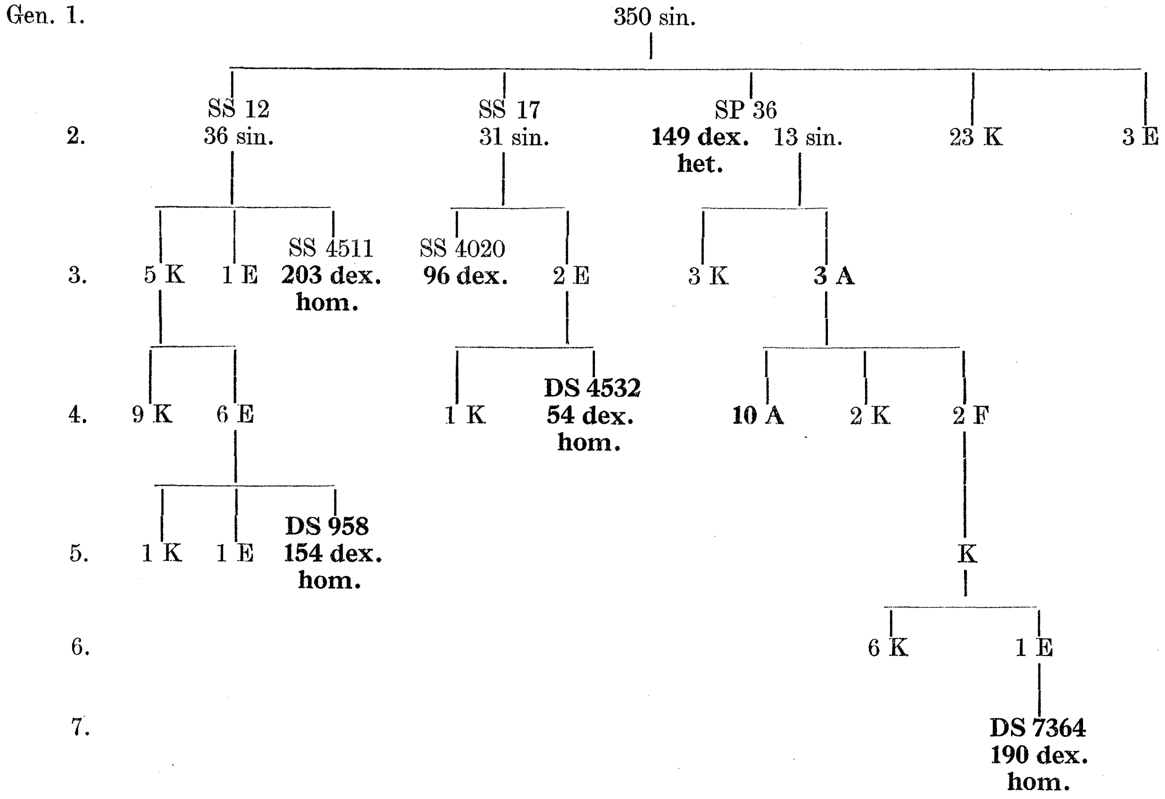
* As the population in the pond contains only some 3 per cent. of sinistrals this presumably happens not infrequently.

this AK parent carried on was the dextral-throwing snail in SP 36, or (2) that the AK parent laid no eggs itself and acted as male to the other, with a product of 1 dextral to at least 29 sinistral broods instead of a ratio of 1 to 1, or (3) various combinations of these possibilities, such as fertilisation followed by selfing. All of these hypotheses seem unlikely.

We should, therefore, interpret the London pair as giving a sinistral family with six dextral break-throughs, the incidence of which is summarised in Table 34. The genotypic dextrality is further increased by 8 F broods which appeared in the AK groups derived from SP 36. Apart from these, the whole family is E or K. Five lines were isolated and carried as far as gen. 6, three of which were taken further and are still living. On our classification, if the end products are considered, two are recognisable as ε lines (arising in gen. 4) and three as κ, and their history illustrates how these two forms tend to separate into pure lines. The ε line from 939 (Table I) is specially notable as our best example of large-brooded E. The albino K strain used in our crosses appeared in gen. 6 (Table II).

TABLE 34.—Incidence of dextral break-throughs in London family. Three arose from dextrals in E broods. Four are homozygous A, one heterozygous AK, one not bred.



The product of SP 36 (Table II) needs more detailed consideration. One parent was heterozygous (whatever its precise nature), the other K, the pairing being in the nature of a back-cross and giving 149 dextrals and 13 sinistrals, which no doubt represent the progeny of the AK and K parents respectively. Segregation of gametes having already occurred, phenotypic segregation appears in the next generation, which was :—

From sinistrals	3 K broods	3 A broods
From dextrals	7 (9)*	10 (13) A broods
Total	10 (12)	13 (16)

which is near enough to the 1 : 1 ratio expected.

Six of the K broods of gen. 3 were taken on in various degrees (Table II) and continued as K or KE as long as they were maintained (in three lines till gen. 10 in 1929). There is very little E-ness, the whole product being 273 K broods and 31 E broods and the best ε groups giving $k = 0 \cdot 87$ and $2 \cdot 8$: the only definite ε line started in gen. 4 (gen. 3 of the pairing : Table II).

Of the A broods in gen. 3, six were taken on. *Ex hypothesi*, all of them were the product of heterozygous snails, so that all the gen. 4 groups should be samples of the same population and should show a segregation ratio of 3 A : 1 KEF (F being regarded as before as perverted sinistral broods). They vary from 14 A, 1 KEF to 2 A, 4 K : neither of these is really incompatible with a 3 : 1 ratio, and adding them up we have :—

——	A.	KEF.	Total.
Observed	47	12	59
Calculated 3 : 1 ...	44	15	59

which agrees well with expectation.

In the further breeding the 40 available groups (Table 35) obtained up to 1928 tested for homogeneity and for compatibility with a 3 : 1 ratio, give $P = 0 \cdot 05$ and $0 \cdot 09$ respectively, and add up to 364 A and 129 KEF, against an expectation of 370 : 123.

> This coincidence might, of course, be due to the presence of compensating ratios. Some of the groups (*e.g.*, 2 A, 4 K or 10 A, 0 K) are not very near 3 : 1, and testing the six gen. 4 groups for homogeneity gives a P of only $0 \cdot 04$. A thorough analysis of all the data (summed in Table 35) does not, however, show any certain divergence from a 3 : 1 ratio, nor any clear differences between strains or generations, and taking them as a whole the facts fit pretty well with the theoretical segregation, though the possibility of there being some underlying diversity, possibly a cytoplasmic effect, must be borne in mind.

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* According as whether the broods from pairs are reckoned as one or two.

If we assume that our interpretation of F broods (of which there are eight) is wrong and reckon them with A rather than with KE, the fit with a 3 : 1 ratio is not so good (*e.g.*, in. gen. 3 we have 50 AF : 9 KE against 44 : 15), but it is still quite credible. Some, too, of the A broods may be dextral break-throughs, which naturally cannot be identified.

TABLE 35.—Heterozygous groups from S.P. 36 : 40 groups : 493 broods.

Gen. from cross.	Strain 4103.		Strain 192.		Strain 290.		Strain 300.		Strain 279.		Strain 289.		Total.	
	A.	KEF.	A.	KEF.	A.	KEF.	A.	KEF.	A.	KEF.	A.	KEF.	A.	KEF.
3	10	4	2	4	3	1	14	1	8	1	10	1	47	12
4	3	1	8	5	—	—	5	6	10	1	8	2	62	25
	7	1	9	6	—	—	8	2	1	1	—	—		
	3	0	—	—	—	—	—	—	—	—	—	—		
5	5	2	3	4	—	—	—	—	7	3	7	3	55	26
	—	—	10	0	—	—	—	—	7	1	4	5		
	—	—	0	2	—	—	—	—	—	—	6	2		
	—	—	6	4	—	—	—	—	—	—	—	—		
6	—	—	6	1	—	—	—	—	3	4	—	—	51	20
	—	—	7	1	—	—	—	—	5	2	—	—		
	—	—	5	4	—	—	—	—	6	1	—	—		
	—	—	—	—	—	—	—	—	5	3	—	—		
	—	—	—	—	—	—	—	—	6	2	—	—		
	—	—	—	—	—	—	—	—	8	2	—	—		
7	—	—	13	6	—	—	—	—	1	1	—	—	41	16
	—	—	14	6	—	—	—	—	—	—	—	—		
	—	—	13	3	—	—	—	—	—	—	—	—		
8	—	—	108	30	—	—	—	—	—	—	—	—	108	30
Total ...	28	8	204	76	3	1	27	9	67	22	35	13	364	129

In the progeny of SP 36, one ε strain ($k = 1 \cdot 6$) appeared, but as a whole the recessive component showed little E-ness (in all, 763 K broods and 87 E broods). From DS 706 in gen. 4 we obtained the clearest segregation and the most complete K-ness we have had (Table II), the total product to gen. 10 being 252 A broods and 114 K, without any F or E : this includes a pure line of 72 A broods comprising 18,704 dextrals from 1927–1929.

(*b*) *Radlett family* (Tables II–VI).

The original parents produced 150 dextrals and 178 sinistrals, which, in the light of all our experience, can confidently be regarded as an A brood and a K or E brood mixed together. From these we got :—

—	A.	K.	E.	"C."
From dextral pairs	2	3	—	2
„ „ singles	5	4	—	—
„ sinistral pairs	1	4	—	1
„ „ singles ...	6	2	1	—

the likeliest interpretation of which is :—

—	A.	KE.
From dextrals	11	12
„ sinistrals	9	12

or something near these figures. The pairing is evidently a back-cross analogous to that in SP 36 : one parent is heterozygous AK (an F_1 from a K sinistral fertilised by an A dextral), the other K.

The further breeding was unsystematic : five of the gen. 2 broods have been carried on more or less extensively.

DP 45, 288 *dextrals* (Table III) : heterozygous AK with 3 F broods from one of which an ε strain ($k = 1 \cdot 6$) came. After gen. 3 the evidence for heterozygosity is F broods only.

DP 50, 177 *dextrals* (Table IV) : heterozygous AK, from which were extracted pure α, κ and ε lines : there were 4 dextral break-throughs, including the unique case (SS 2819, Table IV), when a snail laid first an A brood and then an E brood. The pure α line contained 3 F broods in gen. 7, which are presumably A broods with odd sinistral mutants. An albino appeared in a low ε line in gen. 10 (Table IV).

DP 48, 137 *sinistrals* (Tables V and VI) which were bred abundantly into K and especially the high ε lines with which we have been so much concerned, and in which an albino strain arose in gen. 7. Of four dextral break-throughs, one (SS 2369, Table V) with a brood of 8 dextrals might be an E brood, another (Table VI) came from what we have called a convulsed ε group (above, p. 81) along with a κ strain, a third (Table VI) appeared as an F brood.

SS 5001, 200 *sinistrals* (Table III) gave a κ strain with a few E broods.

SP 67, 15 *sinistrals* (Table III): heterozygous AK or AE with two well-marked ε strains ($k = 0 \cdot 3$ and $0 \cdot 7$), one from the sinistral in an F brood.

The heterozygous groups in this family are not so suitable for numerical analysis as those in the London family, but we can collect in all 42 groups with 249 broods:—188A, 61KEF, the 3 : 1 expectation being 187 : 62. The worst agreements are such groups as 14A, 0KEF and 2A, 6KEF, but testing the whole series against a 3 : 1 expectation we get $P = 0 \cdot 23$, so that the aberrant groups are within the range of random sampling. Nor does more detailed analysis show any systematic or coherent departures from what the simple theory would expect.

(*c*) *General.*

These summaries and the pedigree tables show that our results are in the main concordant with the principles of dextral dominance and delayed inheritance. In actual practice, however, they are heavily coloured by the general tendency for dextrals to arise where sinistrals might be expected, *i.e.*, by what we call the "dextral pull." What exactly this means we do not know. We have detected no corresponding "sinistral pull": the few odd sinistrals unexpected on our hypothesis are presumably mutants and not more remarkable than the three albino strains which have arisen: we cannot, therefore, suppose that there is anything which might be called a balanced reaction. E broods, F broods and dextral break-throughs all tend to arise most frequently in the earlier generations: continued in-breeding leads to stable lines, α, κ or ε. This suggests that the dextral pull is due to something in the ancestry of the wild population (which contains a large excess of dextrals), which has impressed a tendency towards dextrality on the germinal structure which is enough, not infrequently, to overcome genic sinistrality, as was proposed in the 1925 paper. It is credible to imagine that this impression is made by the repeated and prolonged influence of genic dextrality such as might be imitated experimentally by continually back-crossing the progeny of A and E dextrals to A with the anticipation of producing dextral break-throughs.

VIII. SUMMARY.

1. The common fresh-water mollusc, *Limnœa peregra*, is normally dextral: a sinistral variety, in which the spiral twist of the body and shell is completely reversed, is very rare. The examples with which our work started came from a pond at Leeds.

2. Sinistrality behaves as a mendelian recessive character, but the appearance of any change of twist imposed by crossing is delayed by one generation and segregation occurs in F_3 by broods instead of in F_2 by individuals. Thus a sinistral fertilised by a dextral produces (F_1) sinistral young which (F_2) produce dextral broods: these dextrals

produce (F_3) dextral and sinistral broods in the proportion of 3 to 1. Similarly, a dextral fertilised by a sinistral produces dextrals in F_1 and F_2 and a 3 to 1 mixture of dextral and sinistral broods in F_3.

3. Albinism in this snail is also, as usual, a simple mendelian recessive, and is inherited directly; an albino fertilised by a pigmented produces pigmented young in F_1, and F_2 consists of broods each of which contain pigmented and albinos in the proportion of 3 to 1. The characteristic shell shape of an Irish lake form of the species also disappears in F_1 on crossing with a normal specimen.

4. It is suggested that the delay in the inheritance of sinistrality is due to the fact that the twist of the animal and its shell is determined at the first division of the egg. Pigmentation and shell shape, on the other hand, are not fixed till a later period in development, and the spermatozoon would have more time to bring its influence to bear.

5. This simple scheme of inheritance is a good deal interfered with by a general tendency for dextrals to appear where sinistrals would be expected.

(*a*) Genotypic dextrals, breeding true ("dextral break-throughs") arise not uncommonly in sinistral lines: dextral broods with a few sinistrals ("F broods") represent the same mutation in an incomplete form.

(*b*) Phenotypic dextrals often appear in sinistral broods ("E broods") and may constitute up to half the brood. The broods are small owing to maldevelopment and excessive embryonic mortality: the dextrals are "monsters" and are genetically equivalent to their sinistral sibs. The tendency to this aberration is heritable and probably depends on a factor whose manifestation can be obscured by more normal development.

6. Sinistral mutations are much less common. Three unrelated albino mutants have occurred.

The expenses have mostly been met by the Graham Research Fund of the University of London; help has also been received from the Government Grant Committee of the Royal Society. We are much indebted to many friends for help in different directions—to Mr. J. W. Taylor for the original material and to Mrs. Bateson, Dr. H. Chick, Mrs. Gibbs, Miss Rathbone, Messrs. L. E. Adams, T. H. Burlend, Greevz Fysher, the late W. H. Heathcote, H. F. Poole, T. H. Riches, H. G. Thornton and Capt. G. C. C. Damant, R.N. The main strains of interest are being kept alive, and we shall be glad to provide material for anyone who wants to pursue the matter further.

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APPENDIX.

(1) *Natural occurrences.*

In our previous list (1925, p. 117) we omitted the sinistral *peregra* recorded by J. E. COOPER ('Proc. Malac. Soc. Lond.,' 1925, vol. 16, p. 252), from Boveney, in Bucks. Specimens from the Tooting locality are in the Charles Oldham collection in the Manchester Museum and in the Ashford collection in the Leeds Museum; in the Alder collection in the Hancock Museum at Newcastle-upon-Tyne there are both dextral and sinistral examples of var. *lineatus* (actually ordinary malleate specimens) from Alderman Bean at Scarborough.

The record in the appendix to J. G. JEFFREYS' 'British Conchology' (1859, vol. 5, p. 153)—"found by Mr. WALLER in a pond at Balta"—is copied from a MS. note made by JEFFREYS in his own copy of vol. 1, now in the Radcliffe Library at Oxford. As the Rev. L. W. GRENSTED has pointed out to us, it is probably wrong to assume, as we did, that Balta in the Shetlands is intended. E. WALLER was an active collector in Ireland, especially in Tipperary, and evidently in frequent correspondence with JEFFREYS. There is no discoverable "Balta" in Ireland, but it seems likely Balla (Mayo), Balteagh (Derry), or one of the four Ballaghs (Roscommon, Tipperary, Cork) is the correct locality: "Walker" is misprinted for "Waller" on the same page. There is no mention of the specimen in WALLER's available writings on Irish snails ('Nat. Hist. Review,' 1854, vol. 1, p. 84; 'Journ. Roy. Dublin Soc.,' 1858, vol. 1, p. 386; vol. 2, p. 29).

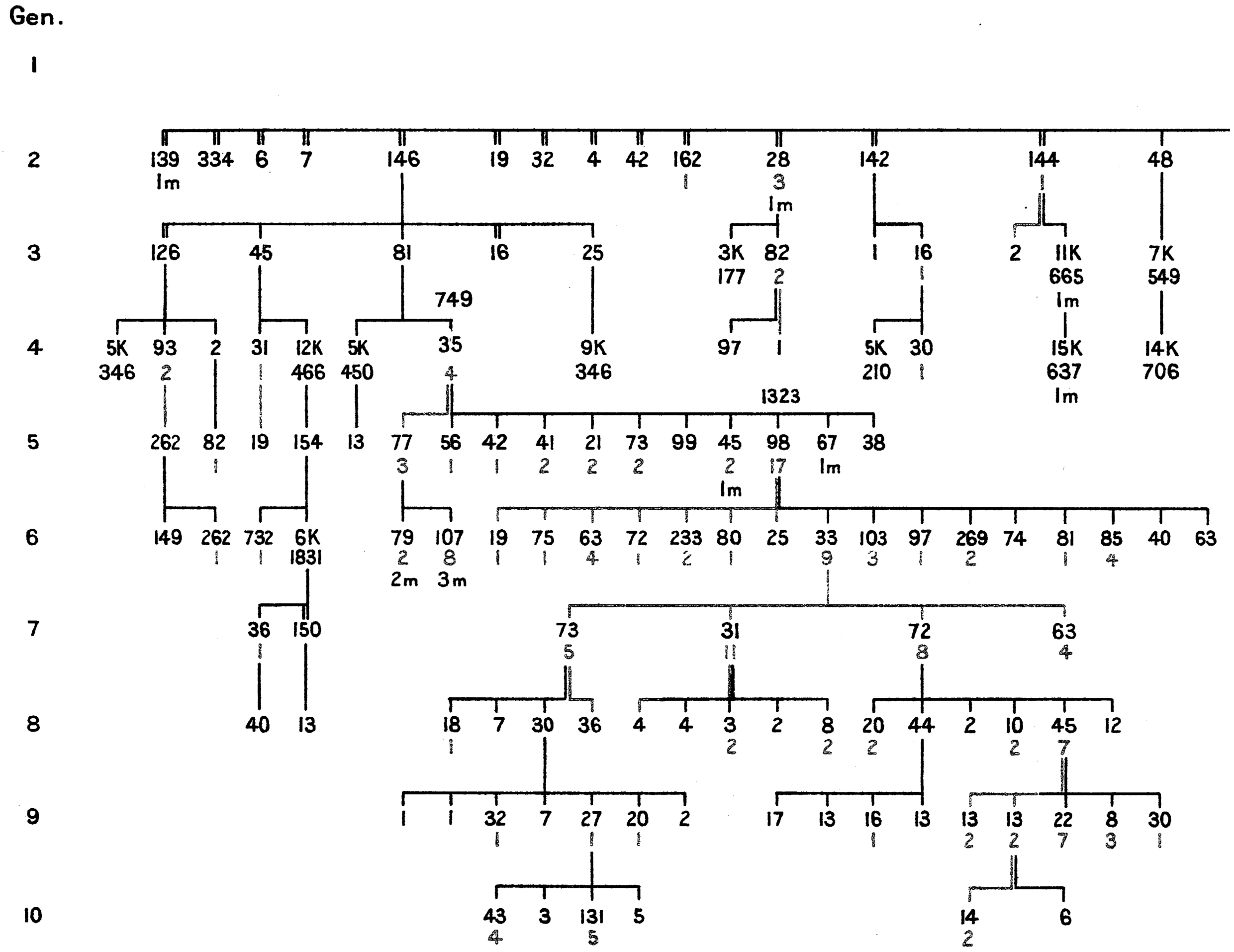
The King Lane pond at Leeds (Plate 10, fig. 10) became involved in a building scheme in 1924, but by the kind interest of Lord MOYNIHAN its destruction was averted, and it is now fenced off and preserved under the care of Mr. GREEVZ FYSHER, to whom we are indebted for the photograph taken before the alterations. The pond at Hesleden (referred to in "William Bateson, Naturalist," 1928, p. 68) has been visited several times since 1924 by Mr. FYSHER and ourselves, but its continued use as a duck pond seems to have destroyed all the snails, and no mollusca of any kind have been found; a few neighbouring ponds in better order have also been searched in vain. Water samples obtained in June, 1925, gave:—King Lane 43, Hesleden 58, and Leeds tap-water 12 mg. calcium per litre (S. S. RANDALL), so that the pond waters are not particularly soft.

In the pedigree table

means that a sinistral
four singles gave A br
E brood of 42 sinistra
E brood being of part
above.

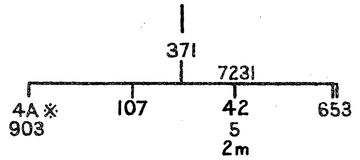
※ The total numbers
comparable with tho

TABLE I.



EXPLANATION OF PEDIGREE TABLES.

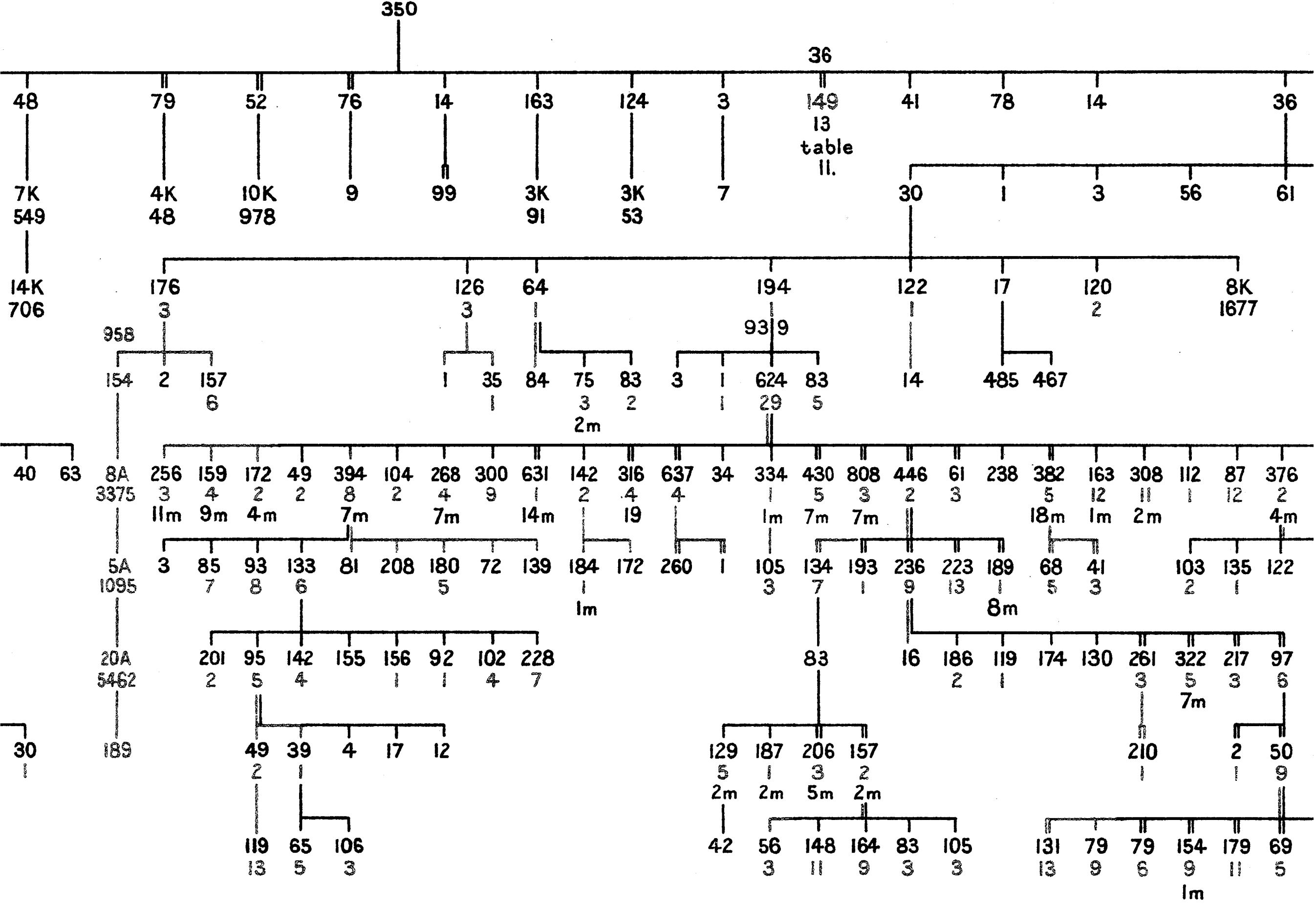
ee tables, red = dextral and black = sinistral. Such an entry as



sinistral single gave a brood of 371 dextrals: eight of these were taken on: ave A broods adding up to 903 snails, one gave a K brood of 107 sinistrals, one an 2 sinistrals, 5 dextrals and 2 monsters, and one pair gave an A brood of 653. The ; of particular interest and referred to in the text has its index number (7231) entered

umbers of snails are not entered, where for one reason or another the figures are not with those obtained in "standard" breeding.

London family



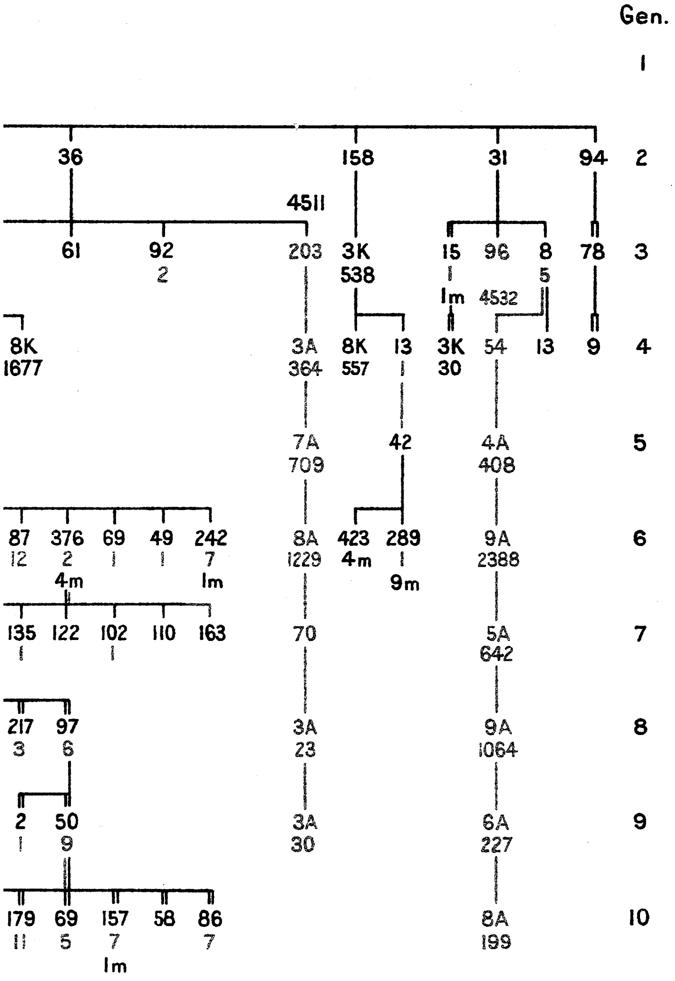
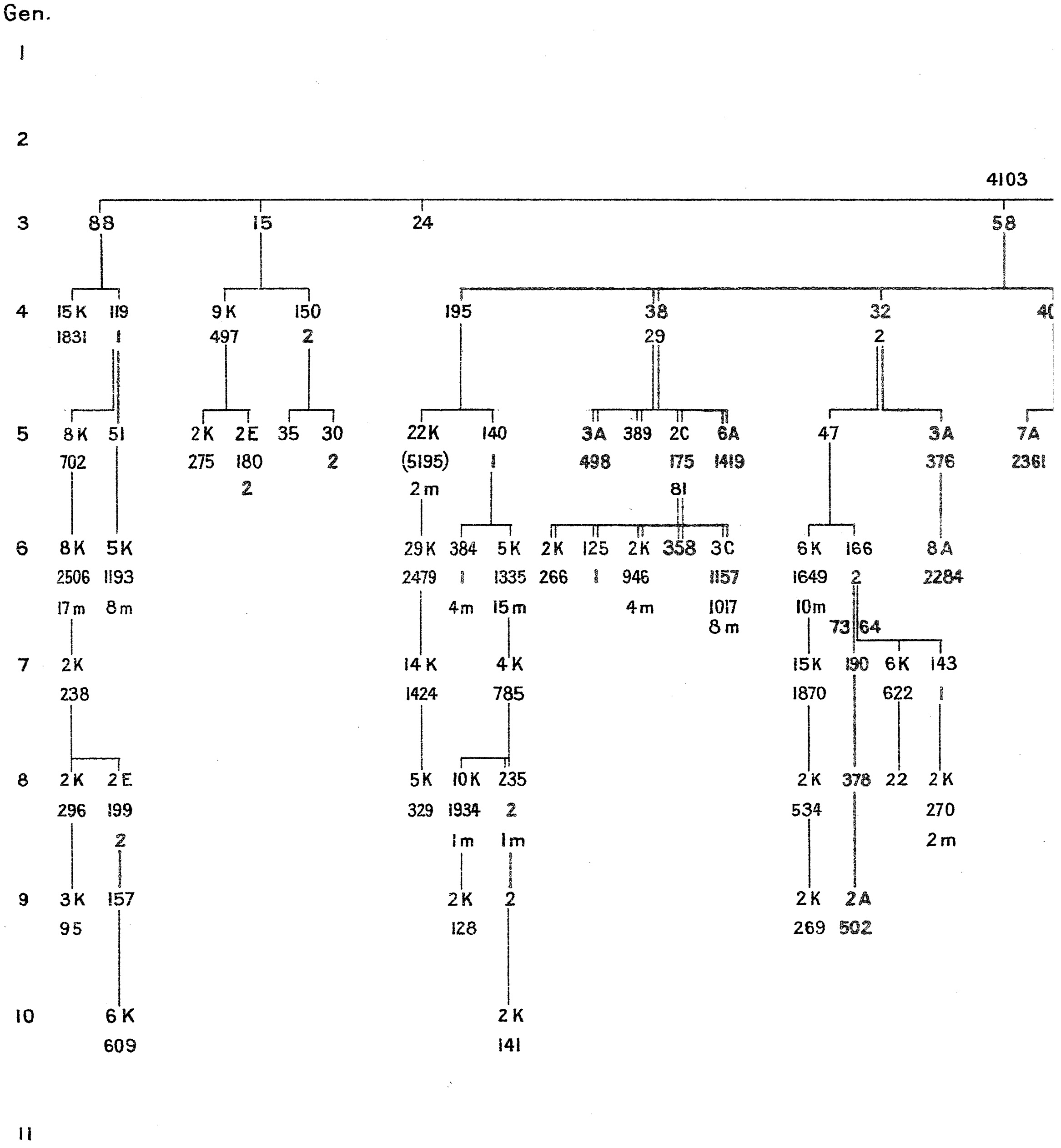
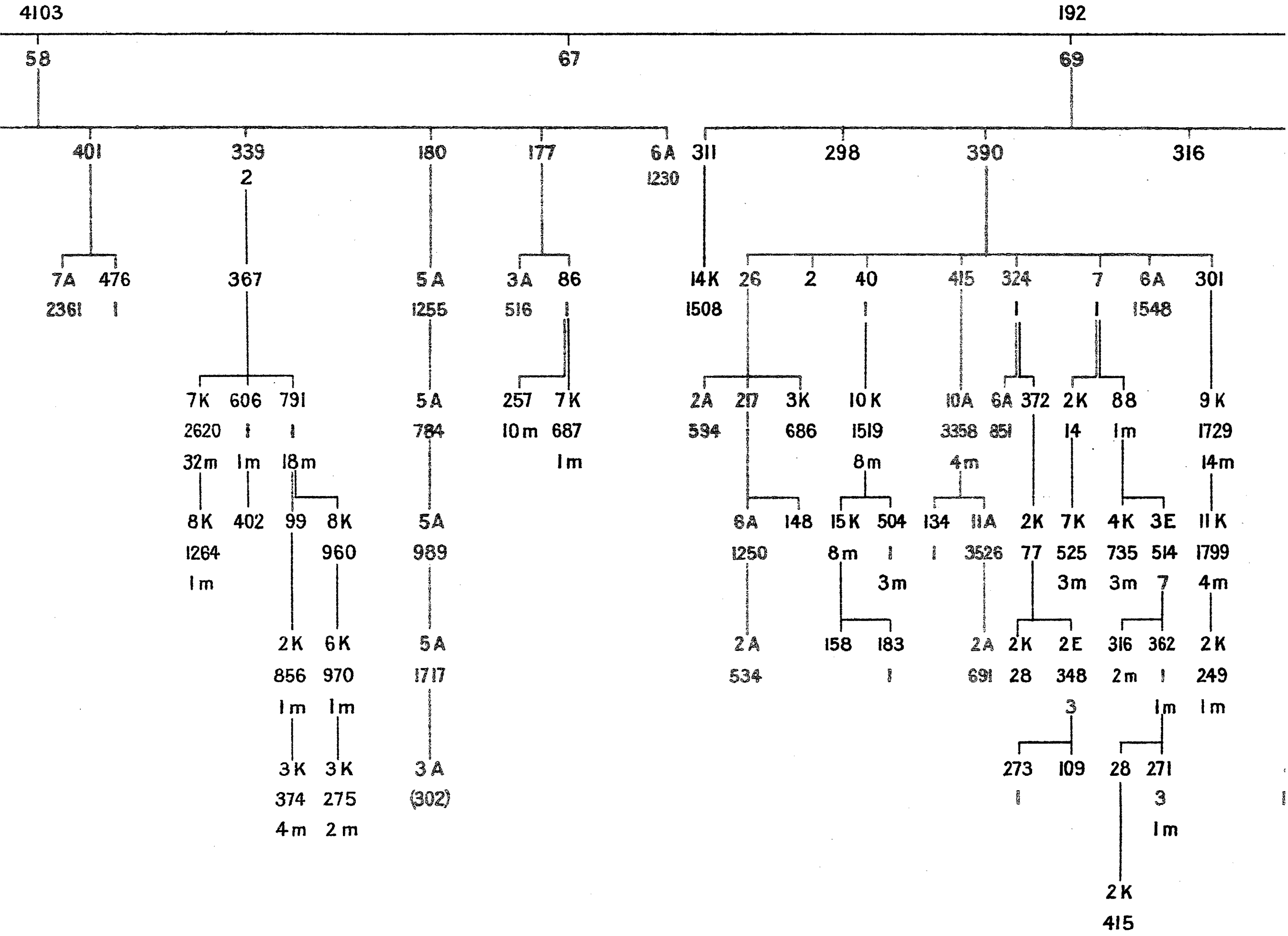
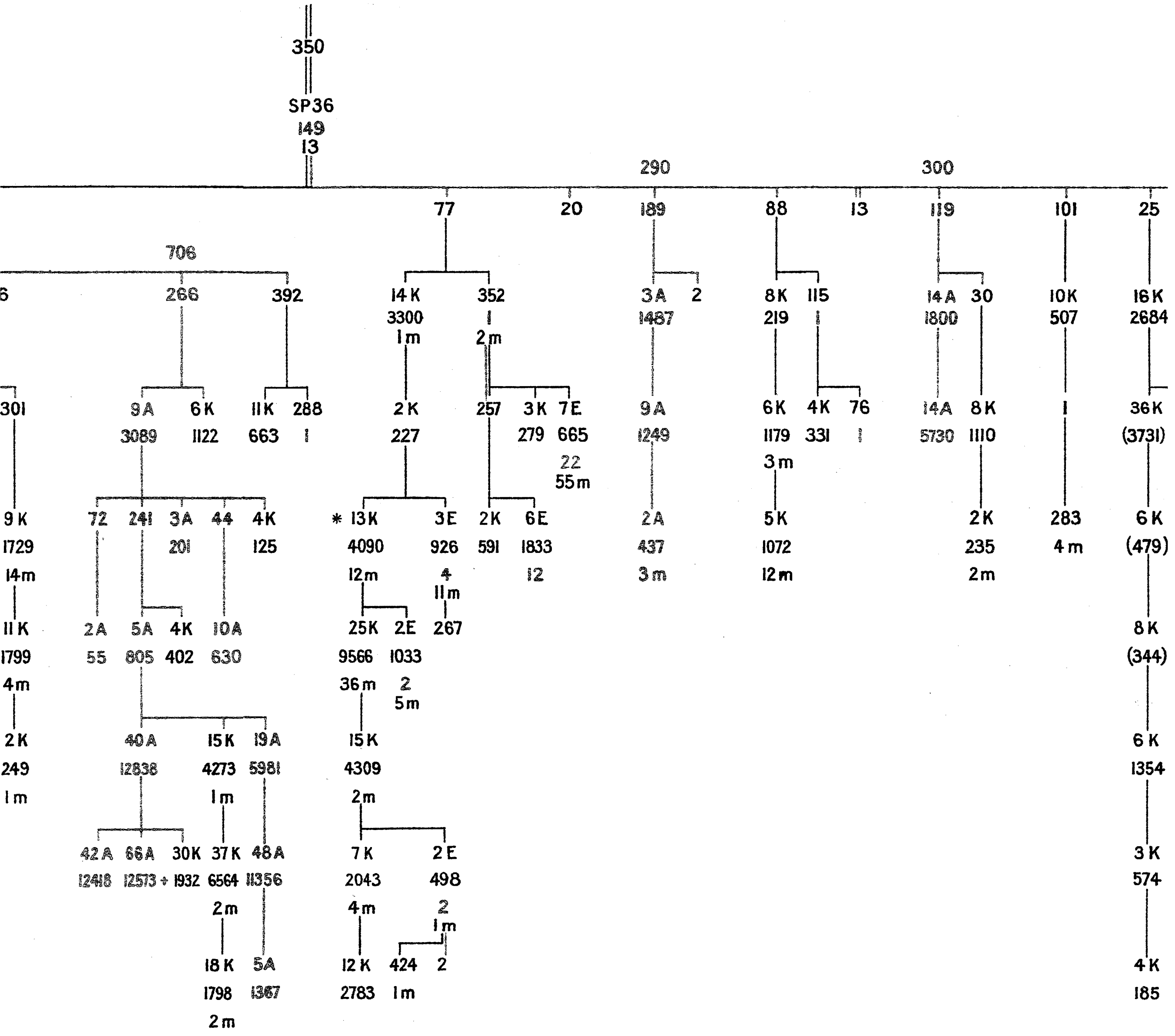
Gen.
1
2
3
4
5
6
7
8
9
10
36
158
31
94
4511
61
92
2
203
3K
538
15
1
1m
96
4532
8
5
78
8K
1677
3A
364
8K
557
13
1
3K
30
54
13
9
7A
709
42
4A
408
87
12
376
2
4m
69
1
49
1
242
7
1m
8A
1229
423
4m
289
1
9m
9A
2388
135
1
122
102
1
110
163
70
5A
642
217
3
97
6
3A
23
9A
1064
2
1
50
9
3A
30
6A
227
179
11
69
5
157
7
1m
58
86
7
8A
199

Table II. London family contd Descendants of S P 36.



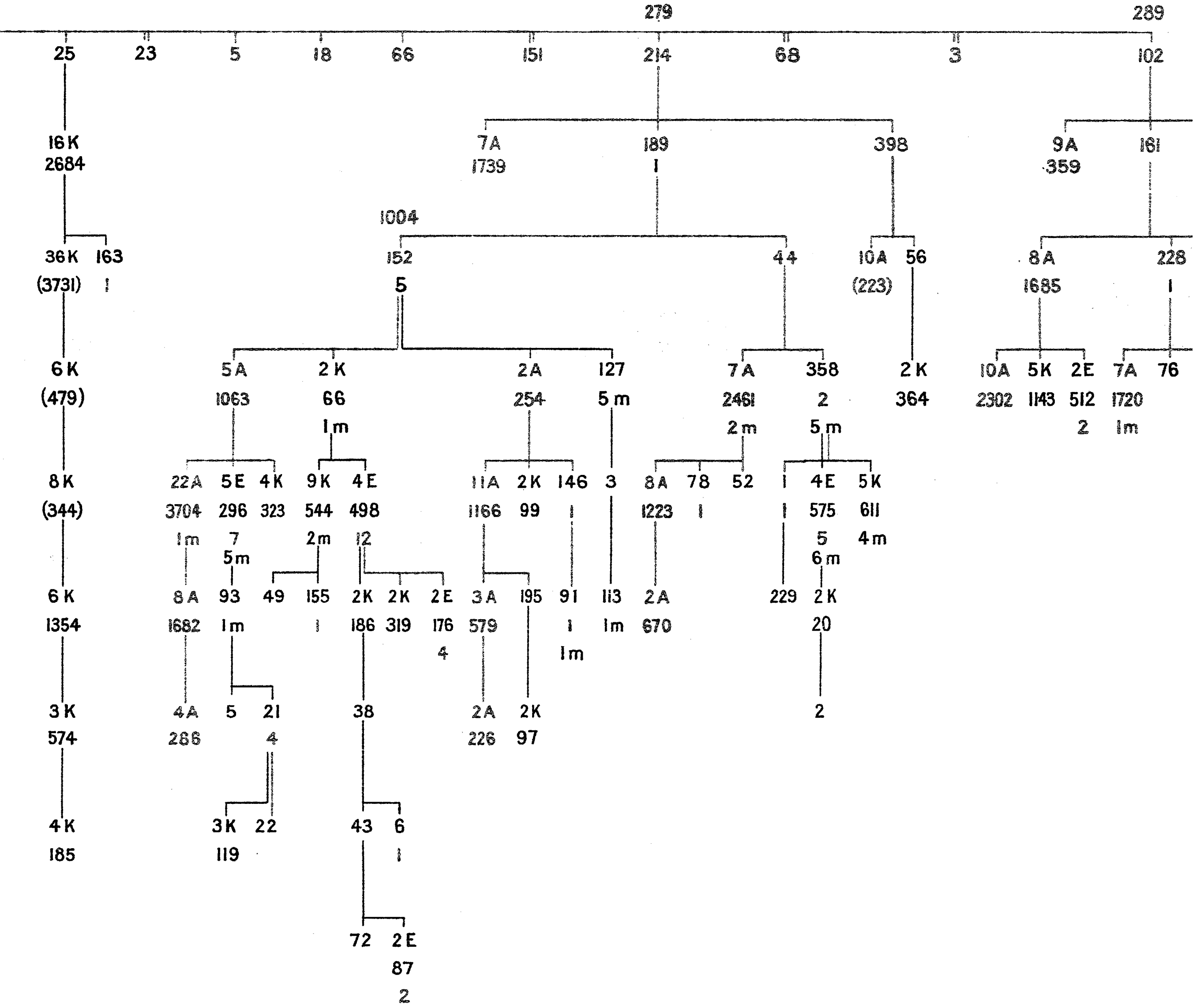

4103
192
58
67
69
401
339
2
180
177
6A
1230
311
298
390
316
7A
2361
476
1
367
5A
1255
3A
516
86
1
14K
1508
26
2
40
1
415
324
1
7
1
6A
1548
301
7K
2620
32m
606
1
1m
791
1
18m
5A
784
257
10m
7K
687
1m
2A
594
217
3K
686
10K
1519
8m
10A
3358
4m
6A
851
372
2K
14
88
1m
9K
1729
14m
8K
1264
1m
402
99
8K
960
5A
989
6A
1250
148
15K
8m
504
1
3m
134
1
11A
3526
2K
77
7K
525
3m
4K
735
3m
3E
514
7
11K
1799
4m
2K
856
1m
6K
970
1m
5A
1717
2A
534
158
183
1
2A
691
2K
28
2E
348
3
316
2m
362
1
1m
2K
249
1m
3K
374
4m
3K
275
2m
3A
(302)
273
1
109
28
271
3
1m
2K
415

Bra
owi



* albino 1629

Bracketed numbers are unreliable
owing to bad breeding conditions.


279
289
25
23
5
18
66
151
214
68
3
102
16K
2684
7A
1739
189
I
398
9A
359
161
1004
36K
(3731)
163
I
152
5
44
10A
(223)
56
8A
1685
228
I
6K
(479)
5A
1063
2K
66
Im
2A
254
127
5m
7A
2461
2m
358
2
5m
2K
364
10A
2302
5K
1143
2E
512
2
7A
1720
Im
76
8K
(344)
22A
3704
Im
5E
296
7
5m
4K
323
9K
544
2m
4E
498
12
11A
1166
2K
99
146
I
3
8A
1223
78
I
52
I
I
4E
575
5
6m
5K
611
4m
6K
1354
8A
1682
93
Im
49
155
I
2K
186
2K
319
2E
176
4
3A
579
195
91
I
Im
113
Im
2A
670
229
2K
20
3K
574
4A
286
5
21
4
38
2A
226
2K
97
2
4K
185
3K
119
22
43
6
I
72
2E
87
2

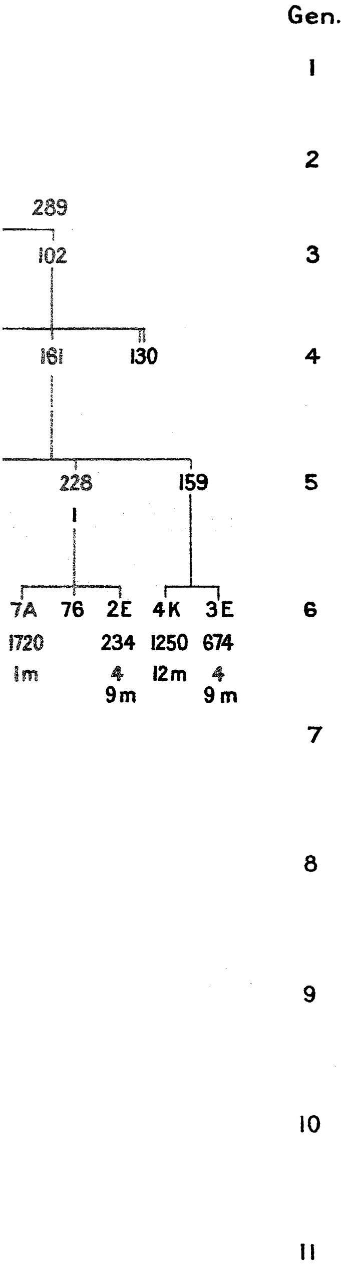
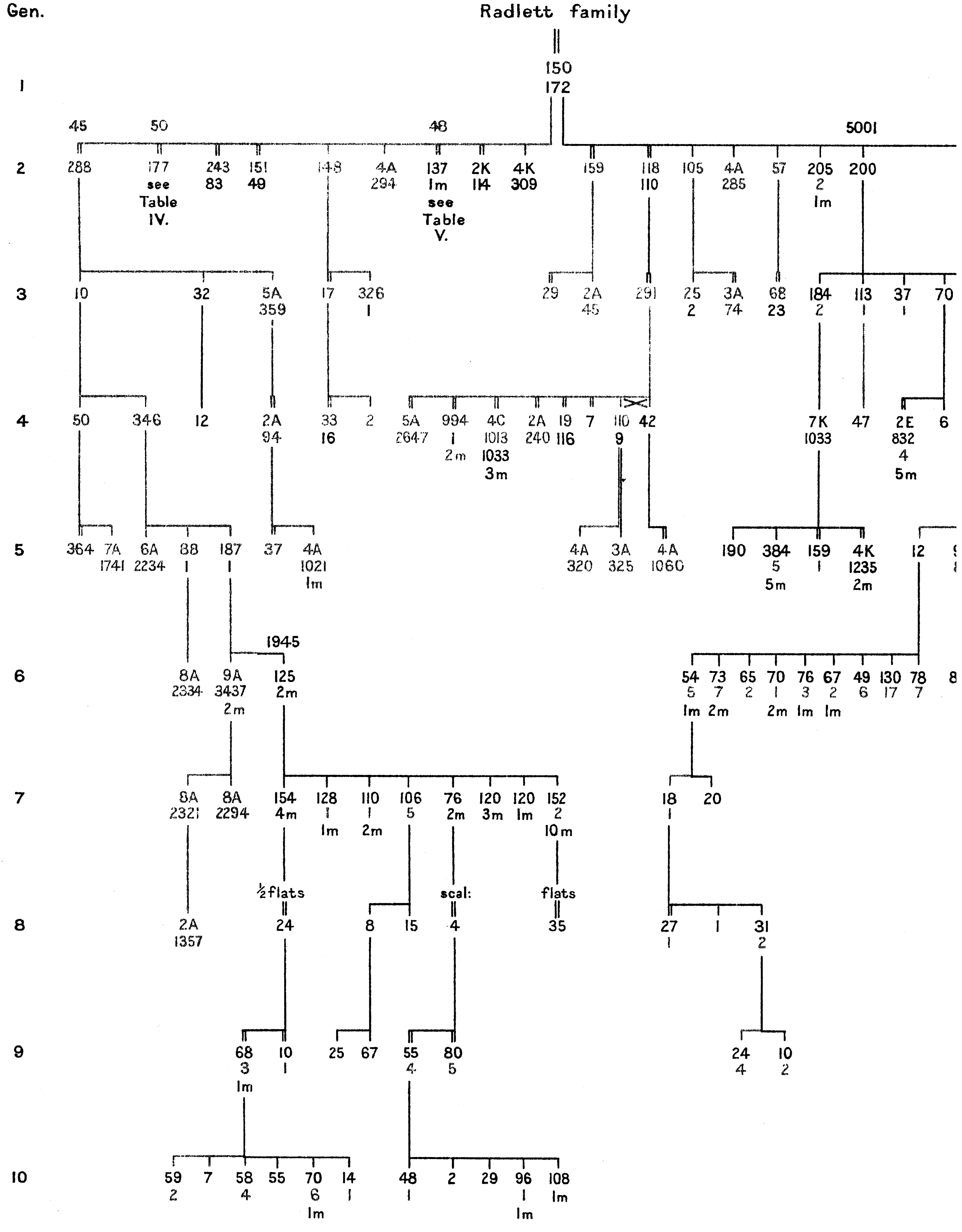
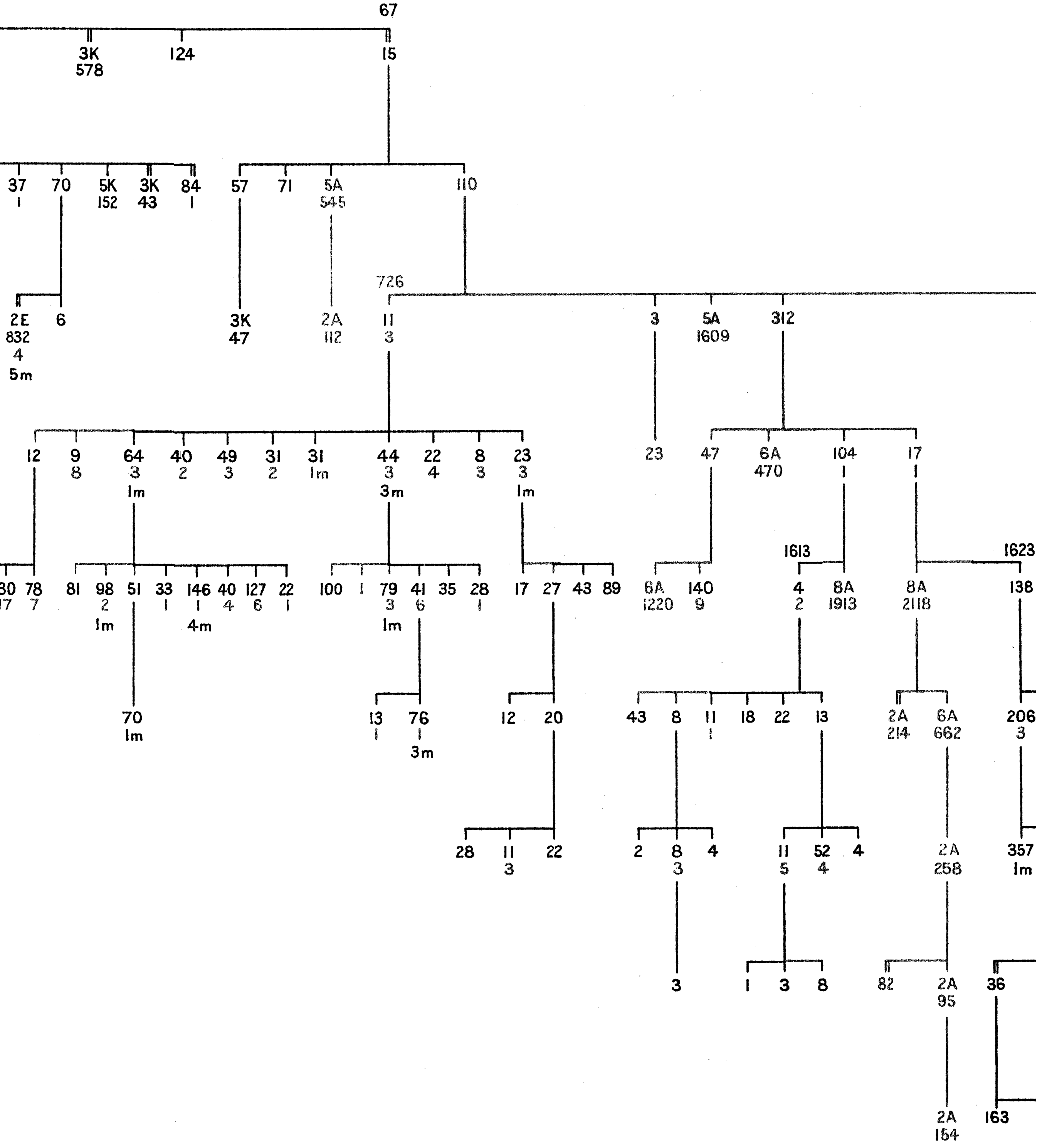
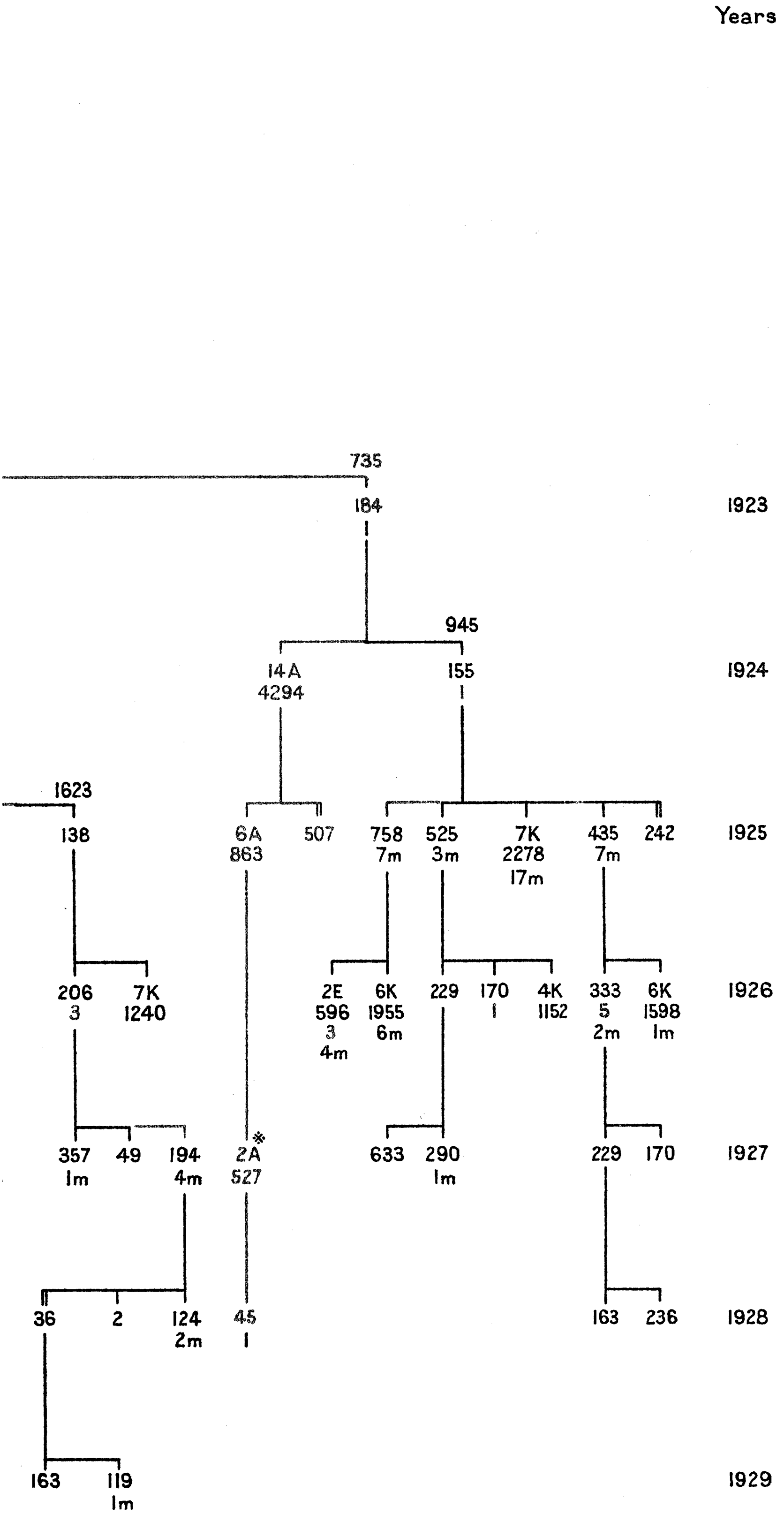

Gen.
1
2
289
102
3
161
130
4
228
159
5
7A
76
2E
4K
3E
6
1720
234
1250
674
1m
4
9m
12m
4
9m
7
8
9
10
11

TABLE III.

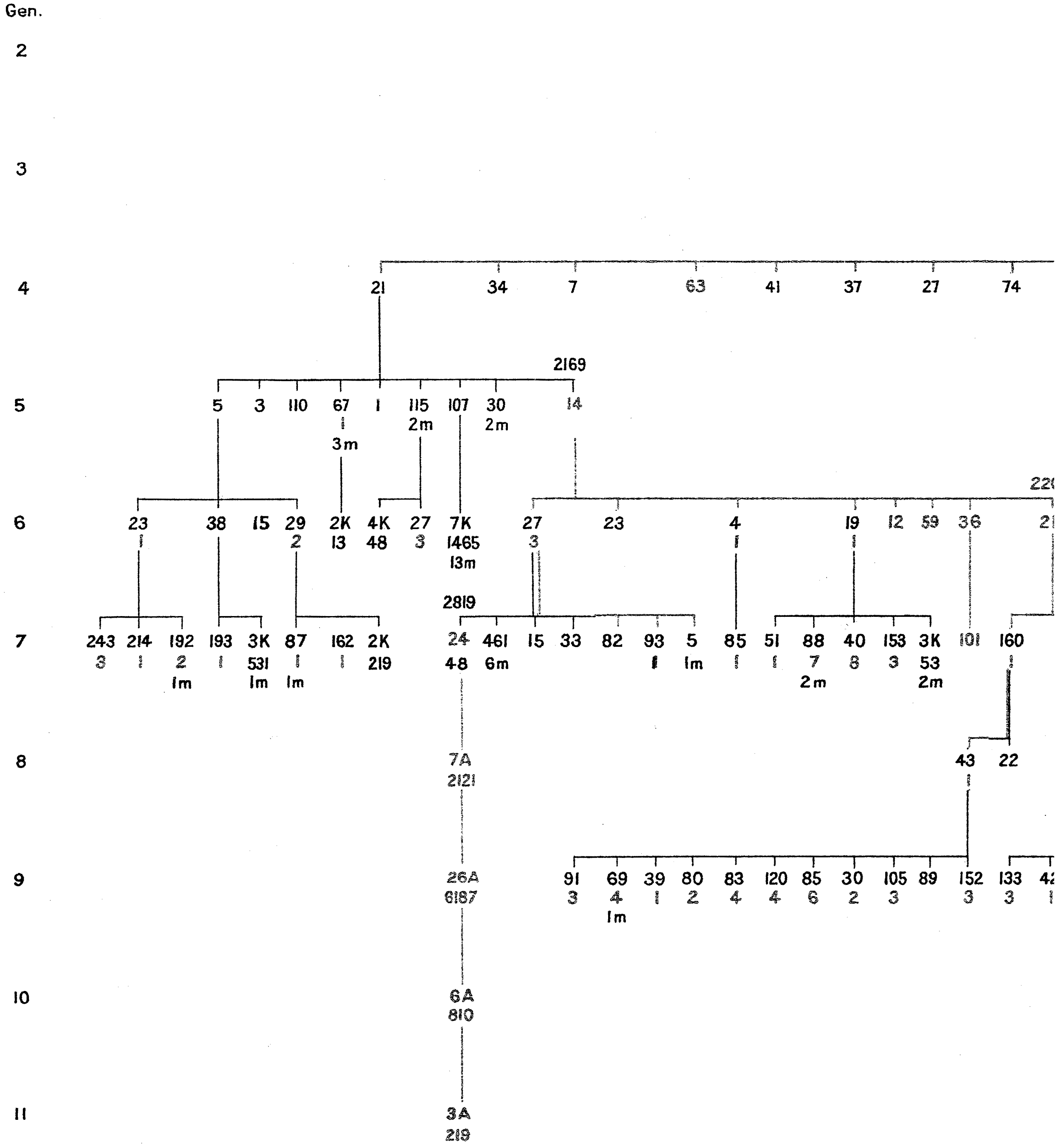

Gen.
Radlett family
1
150
172
2
45 50 48 5001
288
177 see Table IV.
243 83
151 49
148
4A 294
137 1m see Table V.
2K 114
4K 309
159
118 110
105
4A 285
57
205 2 1m
200
3
10
32
5A 359
17
326 1
29
2A 45
291
25 2
3A 74
68 23
184 2
113 1
37 1
70
4
50
346
12
2A 94
33 16
2
5A 2647
994 1 2m
4C 1013 1033 3m
2A 240
19 116
7
110 9
42
7K 1033
47
2E 832 4 5m
6
5
364
7A 1741
6A 2234
88 1
187 1
37
4A 1021 1m
4A 320
3A 325
4A 1060
190
384 5 5m
159 1
4K 1235 2m
12
6
1945
8A 2334
9A 3437 2m
125 2m
54 5 1m
73 7 2m
65 2
70 1 2m
76 3 1m
67 2 1m
49 6
130 17
78 7
7
8A 2321
8A 2294
154 4m
128 1 1m
110 1 2m
106 5
76 2m
120 3m
120 1m
152 2 10m
18 1
20
8
½ flats
scal:
flats
2A 1357
24
8
15
4
35
27 1
1
31 2
9
68 3 1m
10 1
25
67
55 4
80 5
24 4
10 2
10
59 2
7
58 4
55
70 6 1m
14 1
48 1
2
29
96 1 1m
108 1m

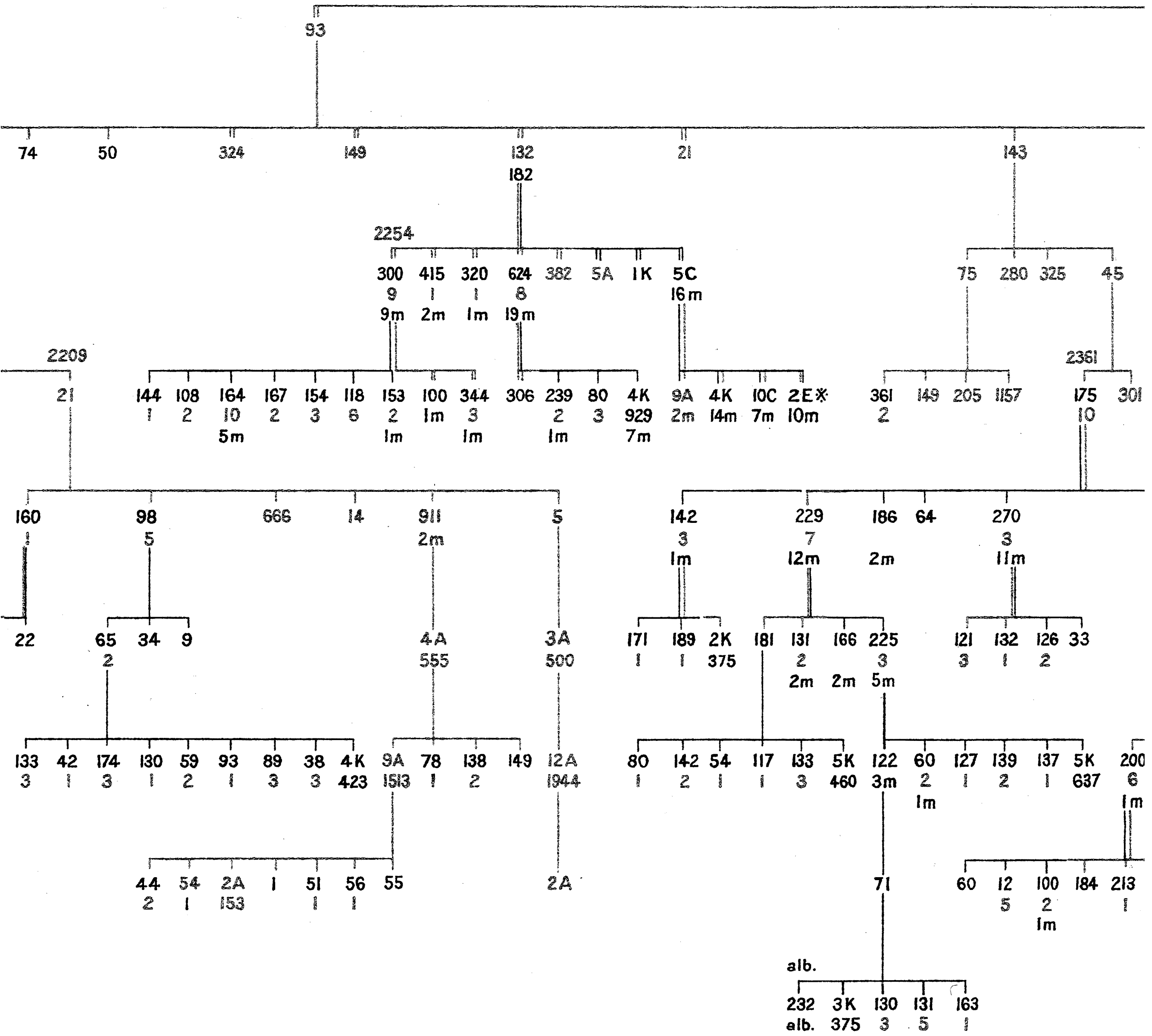

67
3K 578
124
15
37 1
70
5K 152
3K 43
84 1
57
71
5A 545
110
2E 832 4 5m
6
3K 47
2A 112
726
11 3
3
5A 1609
312
12
9 8
64 3 1m
40 2
49 3
31 2
31 1m
44 3 3m
22 4
8 3
23 3 1m
23
47
6A 470
104 1
17 1
30 17
78 7
81
98 2 1m
51
33 1
146 1
40 4
127 6
22 1
4m
100
1
79 3 1m
41 6
35
28 1
17
27
43
89
6A 1220
140 9
1613
4 2
8A 1913
8A 2118
1623
138
70 1m
13 1
76 1 3m
12
20
43
8
11 1
18
22
13
2A 214
6A 662
206 3
28
11 3
22
2
8 3
4
11 5
52 4
4
2A 258
357 1m
3
1
3
8
82
2A 95
36
2A 154
163



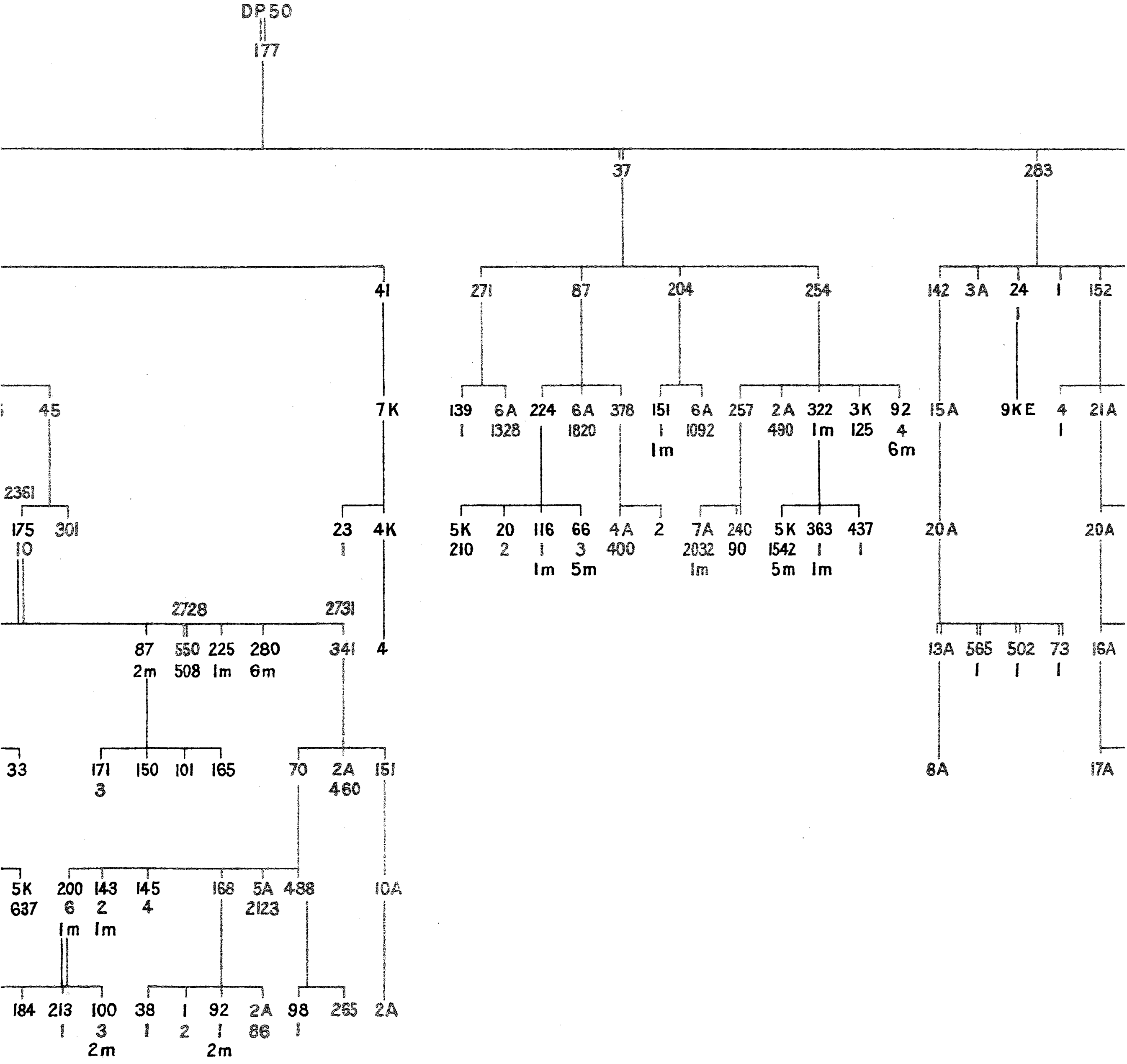
※ Delayed a year

Table IV. Radlett family cont^d Descendants of D P 50.





※ This indicates that the products of dextral pairs and sinistral pairs have been added together.



tral pairs
ether.

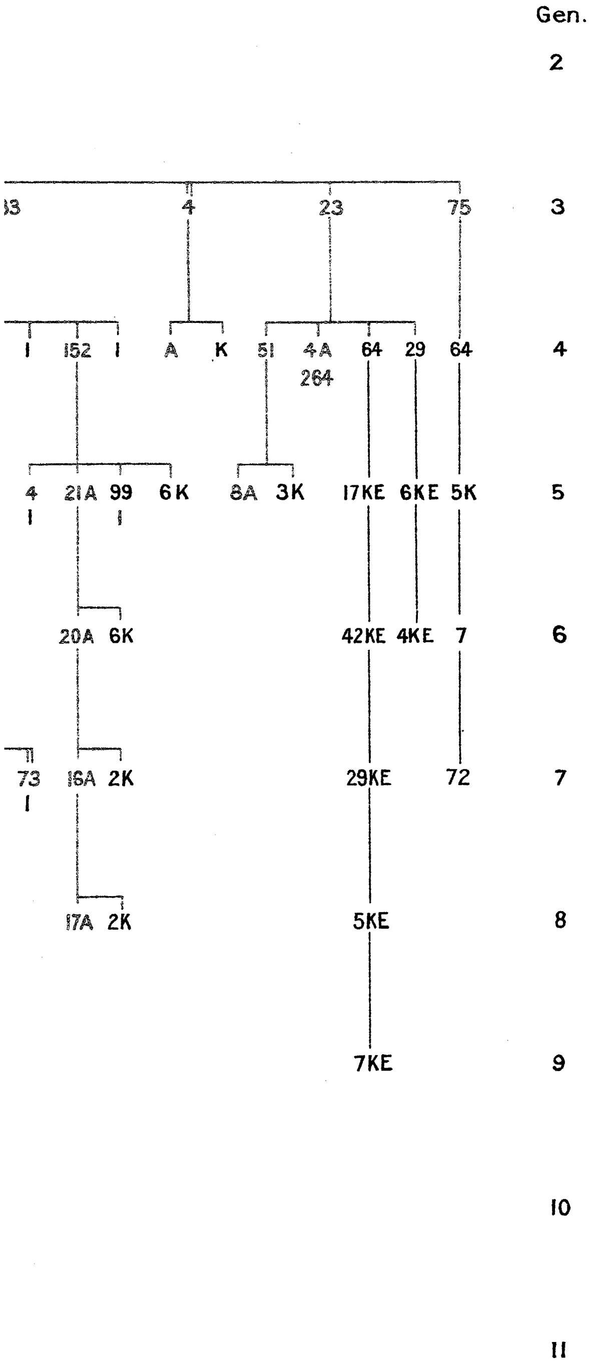
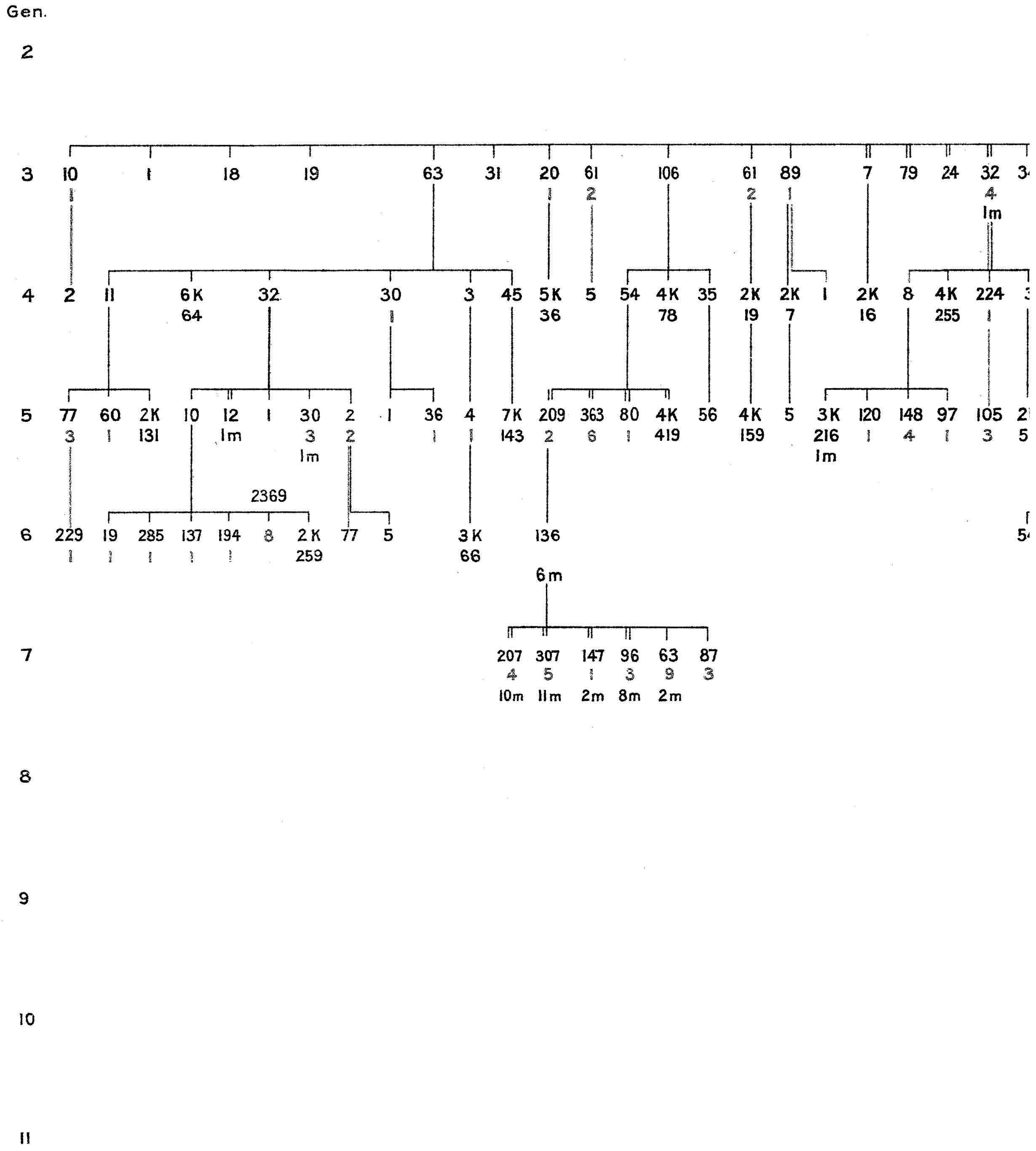
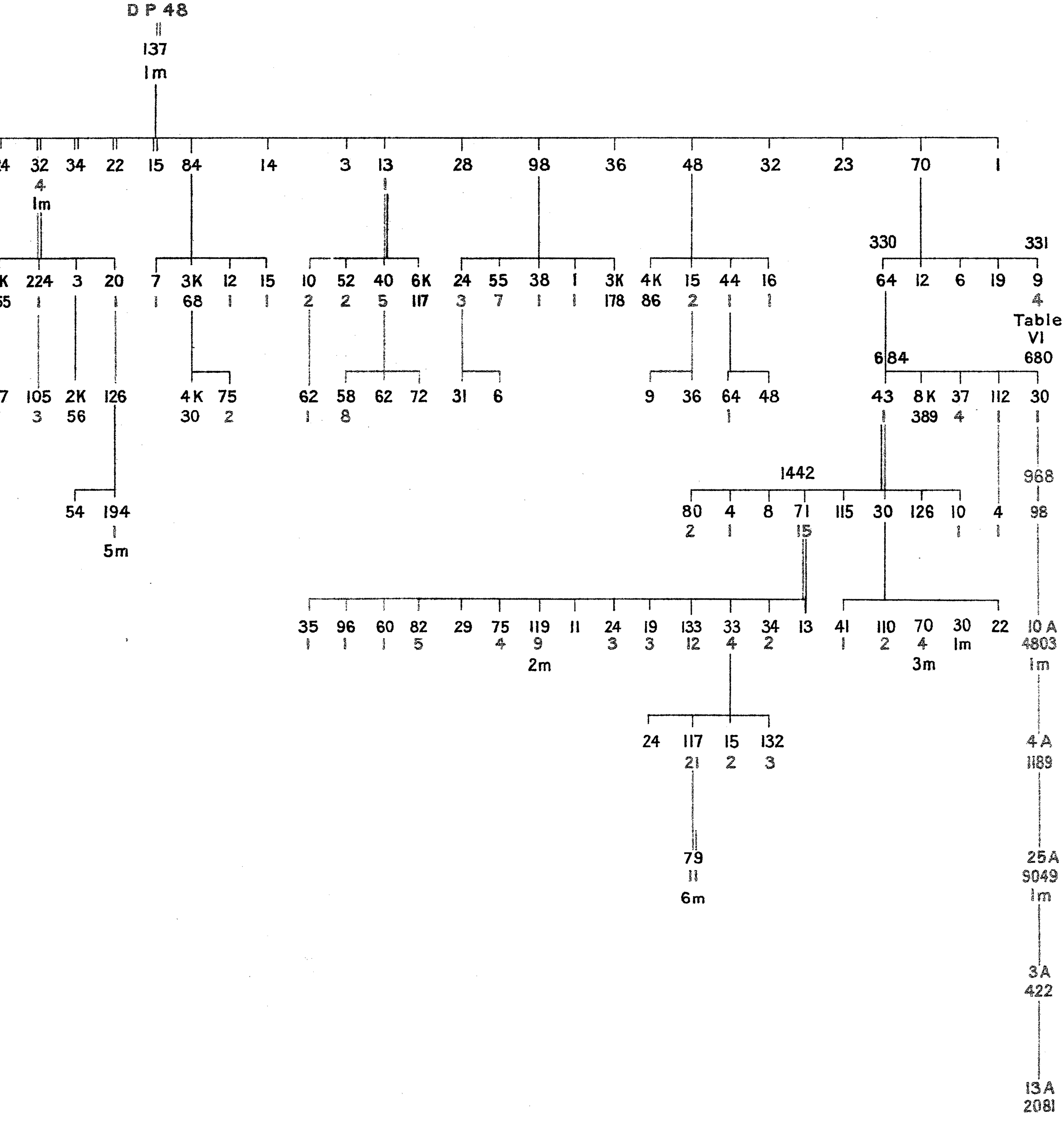

Gen.
2
33
4
23
75
3
I
152
I
A
K
51
4A
264
64
29
64
4
4
I
21A
99
I
6K
8A
3K
17KE
6KE
5K
5
20A
6K
42KE
4KE
7
6
73
I
16A
2K
29KE
72
7
17A
2K
5KE
8
7KE
9
10
11

TABLE V. Radlett family cont^{d}. Descendants of D P 48




D P 48
137
Im
24
32
4
Im
34
22
15
84
14
3
13
28
98
36
48
32
23
70
1
330
331
K
55
224
3
20
7
3K
68
12
15
10
2
52
2
40
5
6K
117
24
3
55
7
38
1
3K
178
4K
86
15
2
44
16
64
12
6
19
9
4
Table VI
684
680
7
105
3
2K
56
126
4K
30
75
2
62
1
58
8
62
72
31
6
9
36
64
48
43
8K
389
37
4
112
30
968
1442
54
194
5m
80
2
4
8
71
15
115
30
126
10
4
98
35
96
60
82
5
29
75
4
119
9
2m
11
24
3
19
3
133
12
33
4
34
2
13
41
110
2
70
4
3m
30
Im
22
10 A
4803
Im
24
117
21
15
2
132
3
4 A
1189
79
6m
25A
9049
Im
3A
422
13A
2081

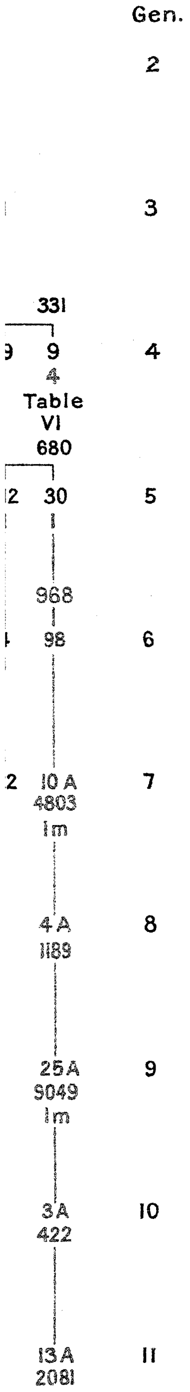
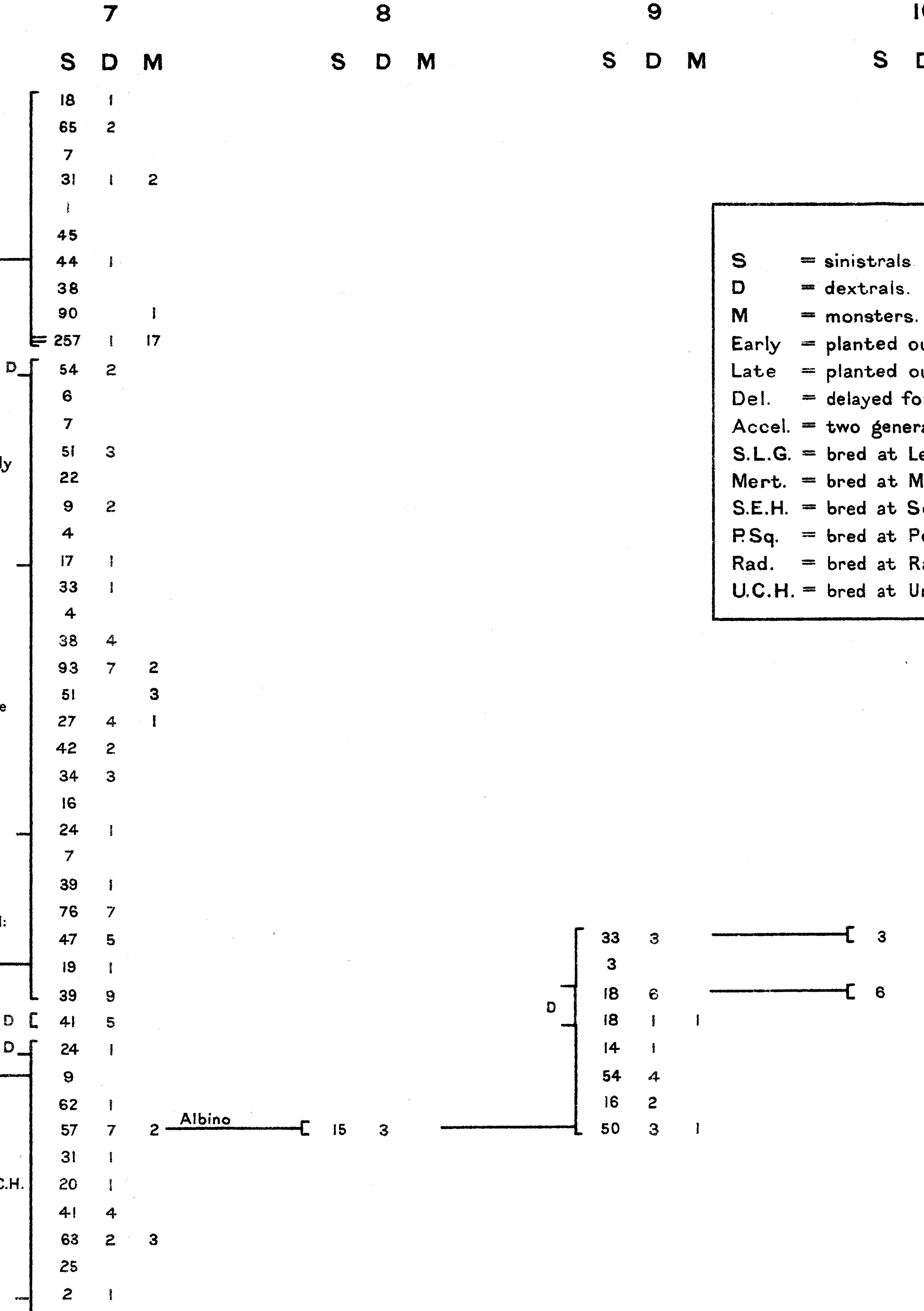

Gen.
2
3
331
9
9
4
4
Table
VI
680
12
30
5
968
98
6
2
10 A
4803
Im
7
4 A
1189
8
25 A
9049
Im
9
3 A
422
10
13 A
2081
11

TABLE VI. Radlett family. E strains from 331.

GENERATIONS 5 6

	S	D	M		S	D	M	
					14	1		
668	5				3			
					1			
					25	4		
				Early D	27	5		
					37	1		
					11	2		
					39	3		
					30	3		
					15	1		D
					47	4		
				Early	3	1		
					33	6		Early
					5			
					1			
						1		
					22	9		
677 D	54	3			11			
					15	3		
								Late
676 D	13	9						
								Del:
					47	1		
					35	4		
					166	5		D
				Late	68	1		D
					67	1		
					53	2		
					171	2		
					205			
								U.C.H.

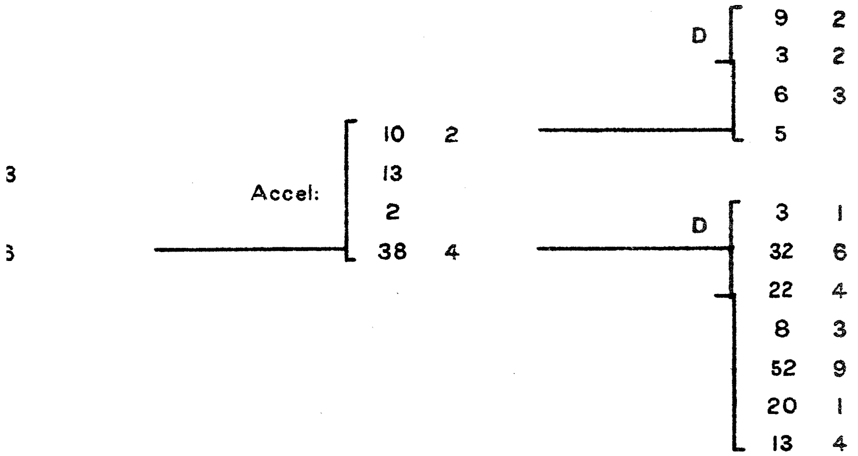


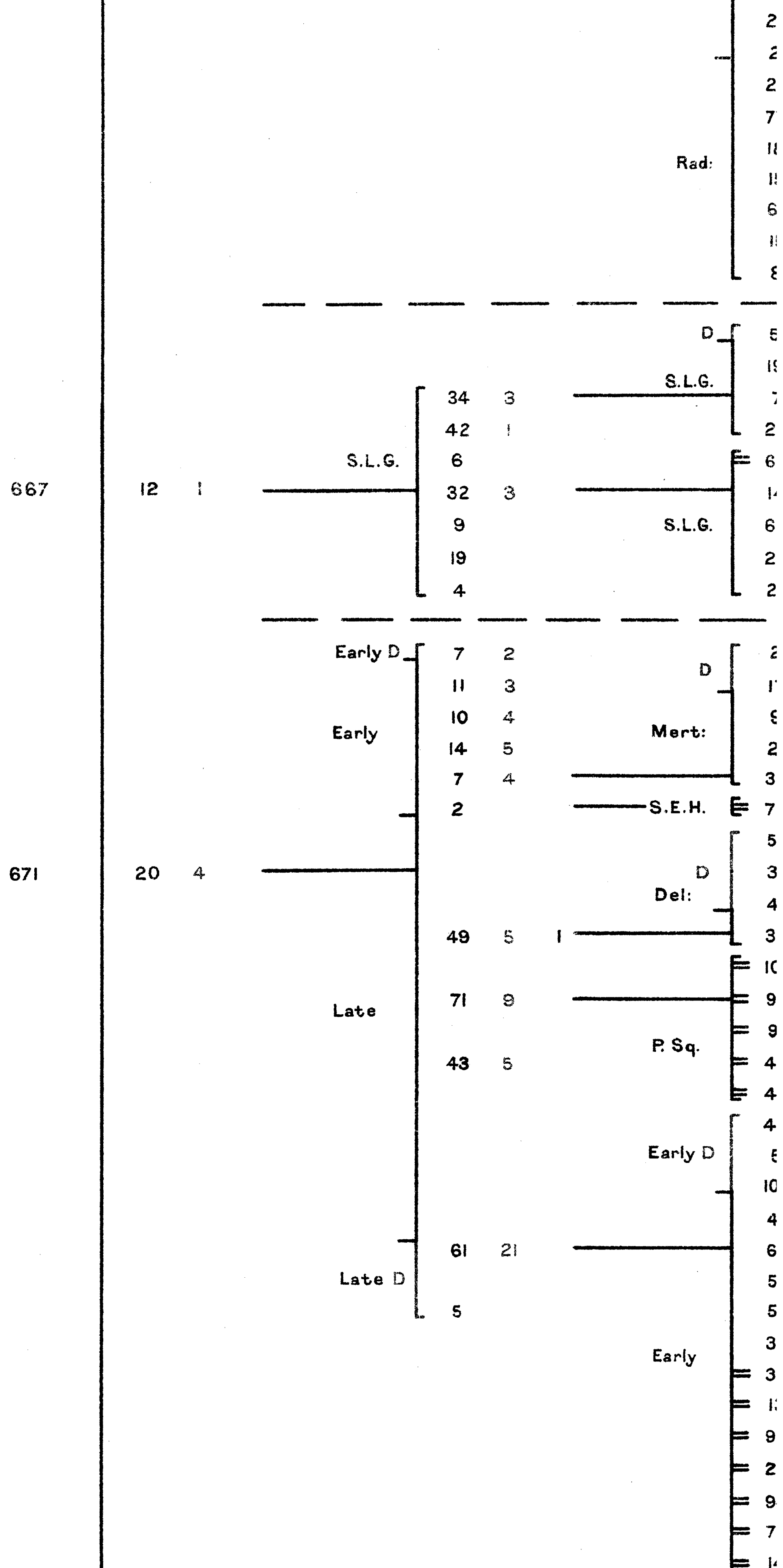
S = sinistrals.
D = dextrals.
M = monsters.
Early = planted out
Late = planted out
Del. = delayed for c
Accel. = two generatio
S.L.G. = bred at Leed
Mert. = bred at Mert
S.E.H. = bred at Sout
P.Sq. = bred at Pem
Rad. = bred at Radl
U.C.H. = bred at Univ

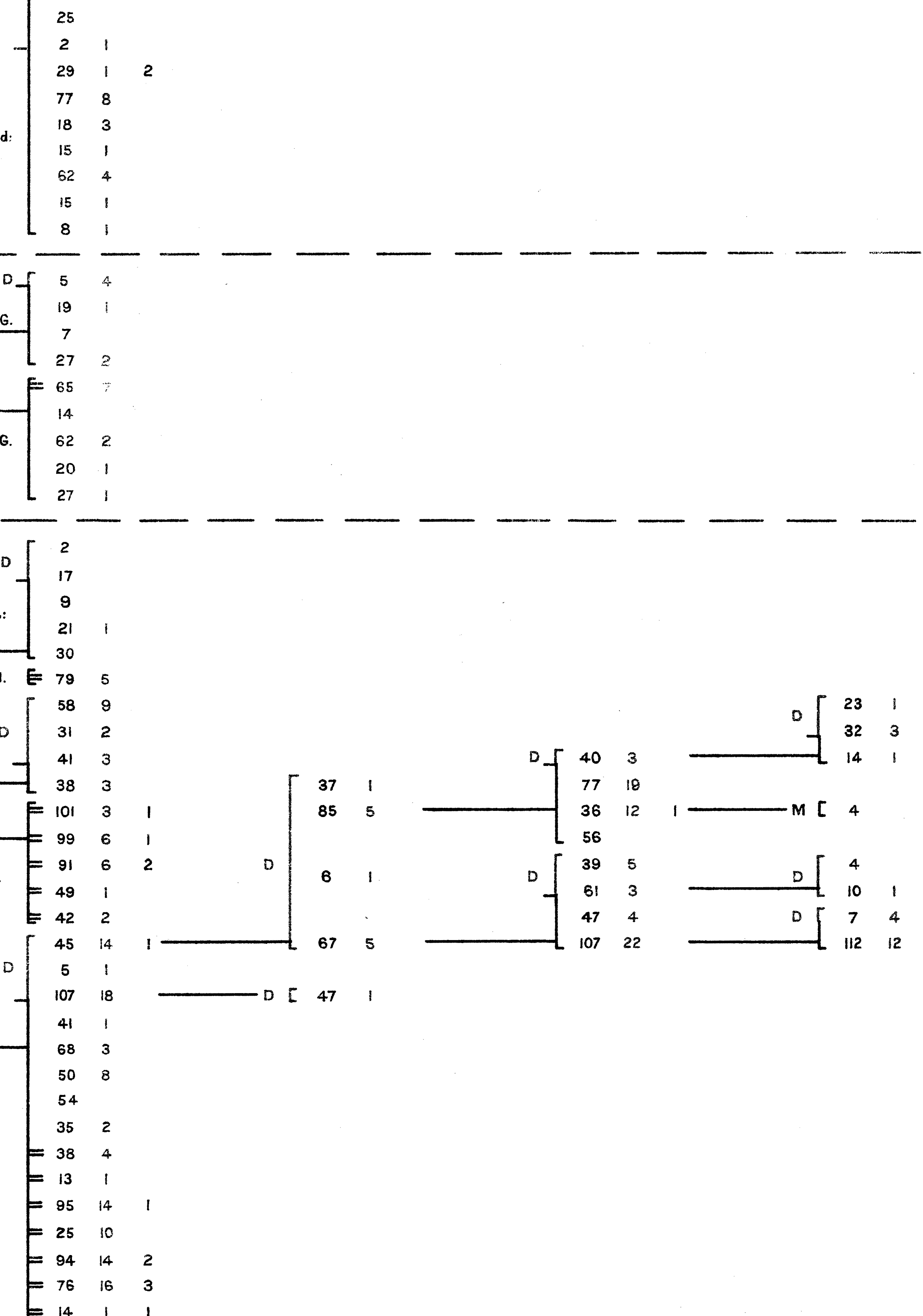
10	11	12
; D M	S D M	S D M

EXPLANATION

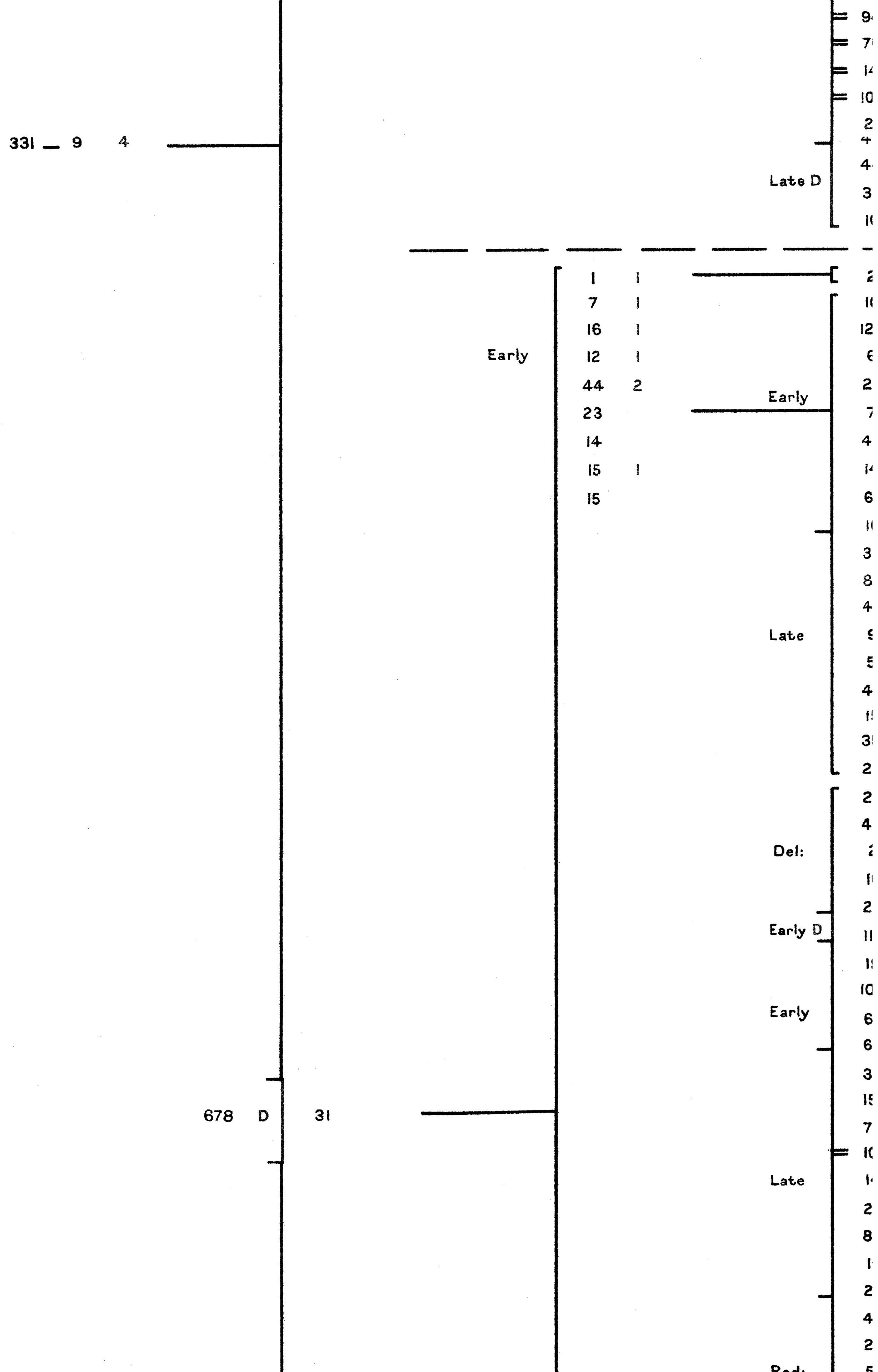
rals.
als.
;ers.
ed out early in the year.
ed out late in the year.
d for one year.
generations in oneyear.
at Leeds.
at Merton.
at South Eastern Hospital.
at Pembroke Square.
at Radlett.
at University College Hospital Medical School.




Rad:
D
S.L.G.
34 3
42 1
S.L.G.
6
667 12 1
32 3
S.L.G.
9
19
4
Early D
7 2
D
11 3
Early
10 4
Mert:
14 5
7 4
2
S.E.H.
671 20 4
D
Del:
49 5 1
71 9
Late
P. Sq.
43 5
Early D
61 21
Late D
5
Early

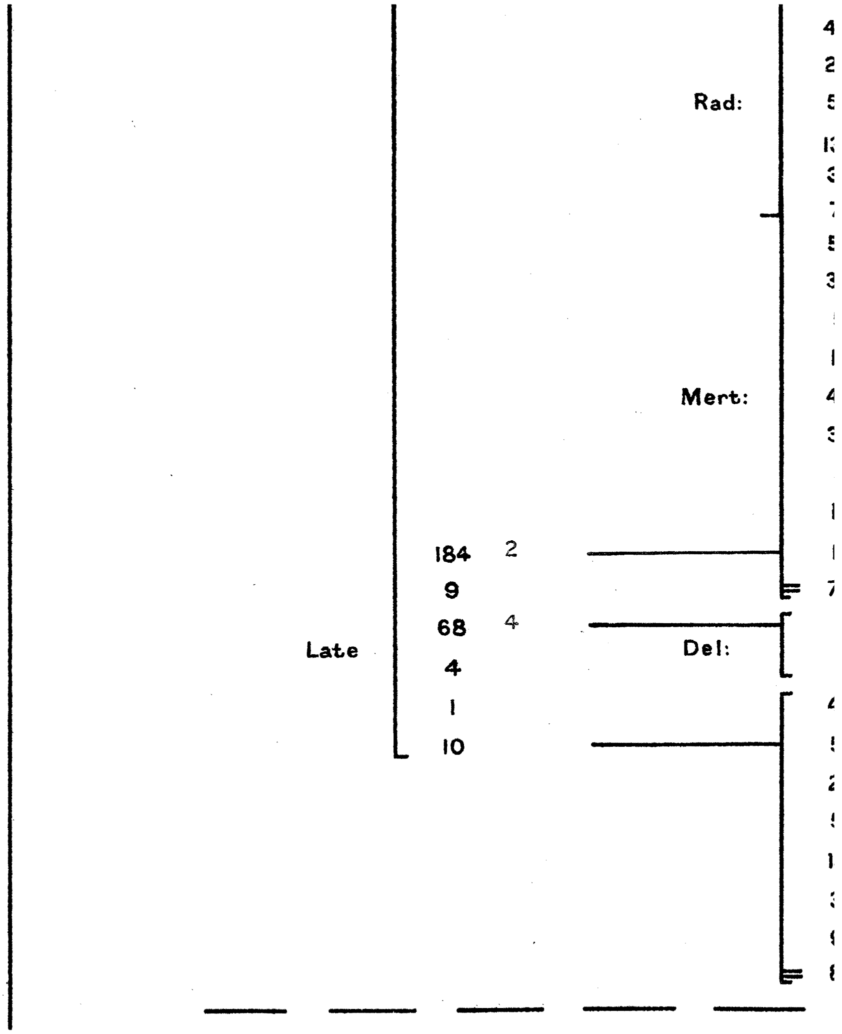

25
2 1
29 1 2
77 8
d:
18 3
15 1
62 4
15 1
8 1
D
5 4
19 1
G.
7
27 2
65 7
14
G.
62 2
20 1
27 1
D
2
17
9
:
21 1
30
I.
79 5
58 9
D
31 2
41 3
38 3
101 3 1
99 6 1
91 6 2
49 1
42 2
45 14 1
D
5 1
107 18
41 1
68 3
50 8
54
35 2
38 4
13 1
95 14 1
25 10
94 14 2
76 16 3
14 1 1
D
37 1
85 5
6 1
67 5
D
47 1
D
40 3
77 19
36 12 1
56
D
39 5
61 3
47 4
107 22
D
23 1
32 3
14 1
M
4
D
4
10 1
D
7 4
112 12

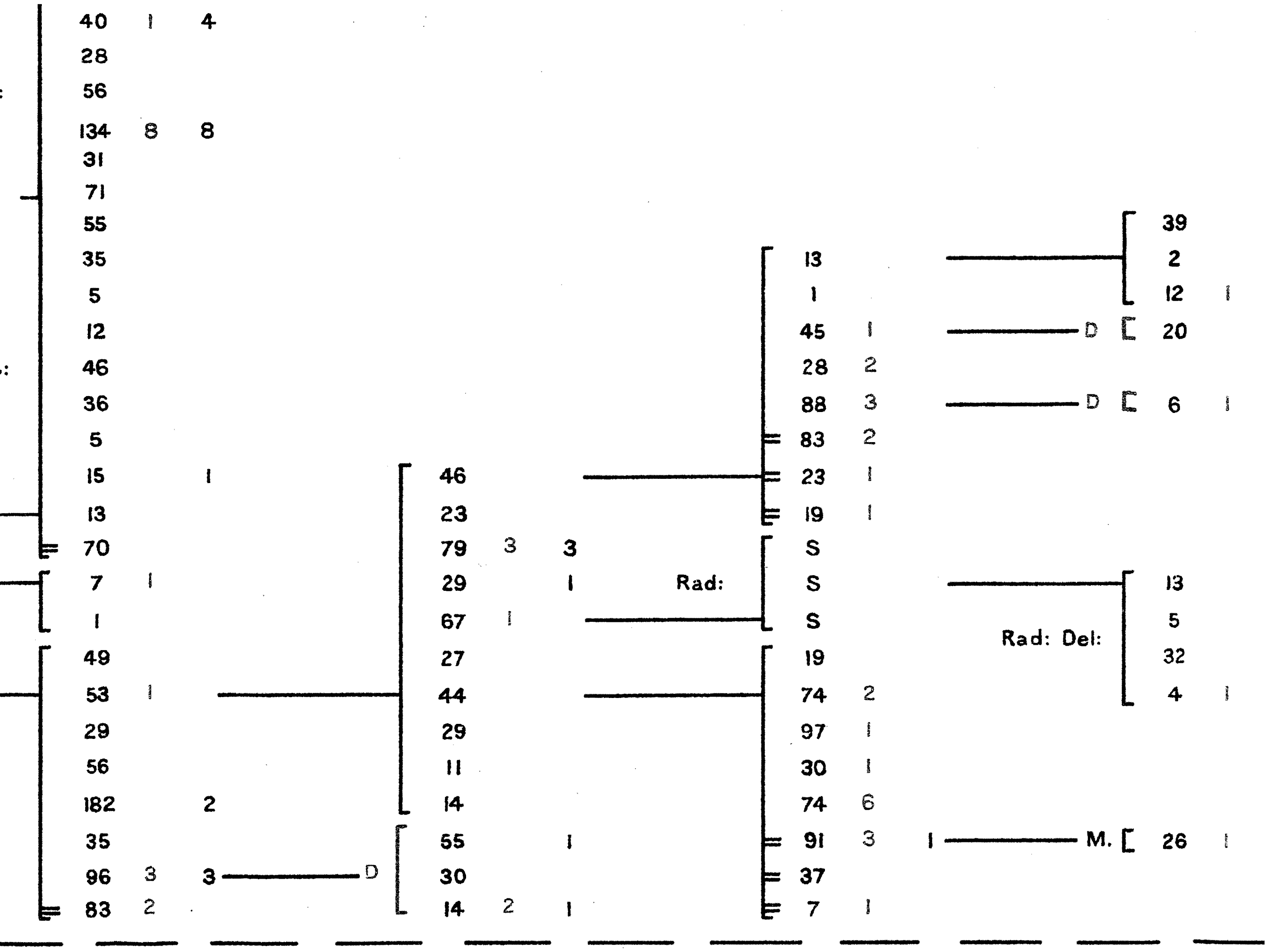
		D	32	7
			2	
			38	2
			97	2
			73	19
3	1		9	
2	3			
4	1			
4				
4				
0	1	D	109	17
7	4			
12	12			


331 — 9 4
Late D
Early
1 1
7 1
16 1
12 1
44 2
23
14
15 1
15
Early
Late
Del:
Early D
Early
Late
678 D 31

	94	14	2
	76	16	3
	14	1	1
	105		3
	21		
	45		1
	44	4	1
e D	36	1	1
	10	2	
	2		
	10	1	
	124	1	3
	6	1	
ly	29		
	7		
	48	5	
	14	1	1
	65		
	16	1	
	32	2	
	89	2	
	45	2	
e	9		
	5		
	44	2	
	15	2	
	35		
	27	3	1
	29	3	
	40	3	
:	2		
	16	1	
	28		
y D	118		3
	19		
	106	2	4
ly	69	6	
	68		1
	30		1
	151	3	
	70	1	
	101	2	2
e	14		
	20	1	
	80	1	
	10	1	
	29	1	
	40	1	4
	28		
l.	56		

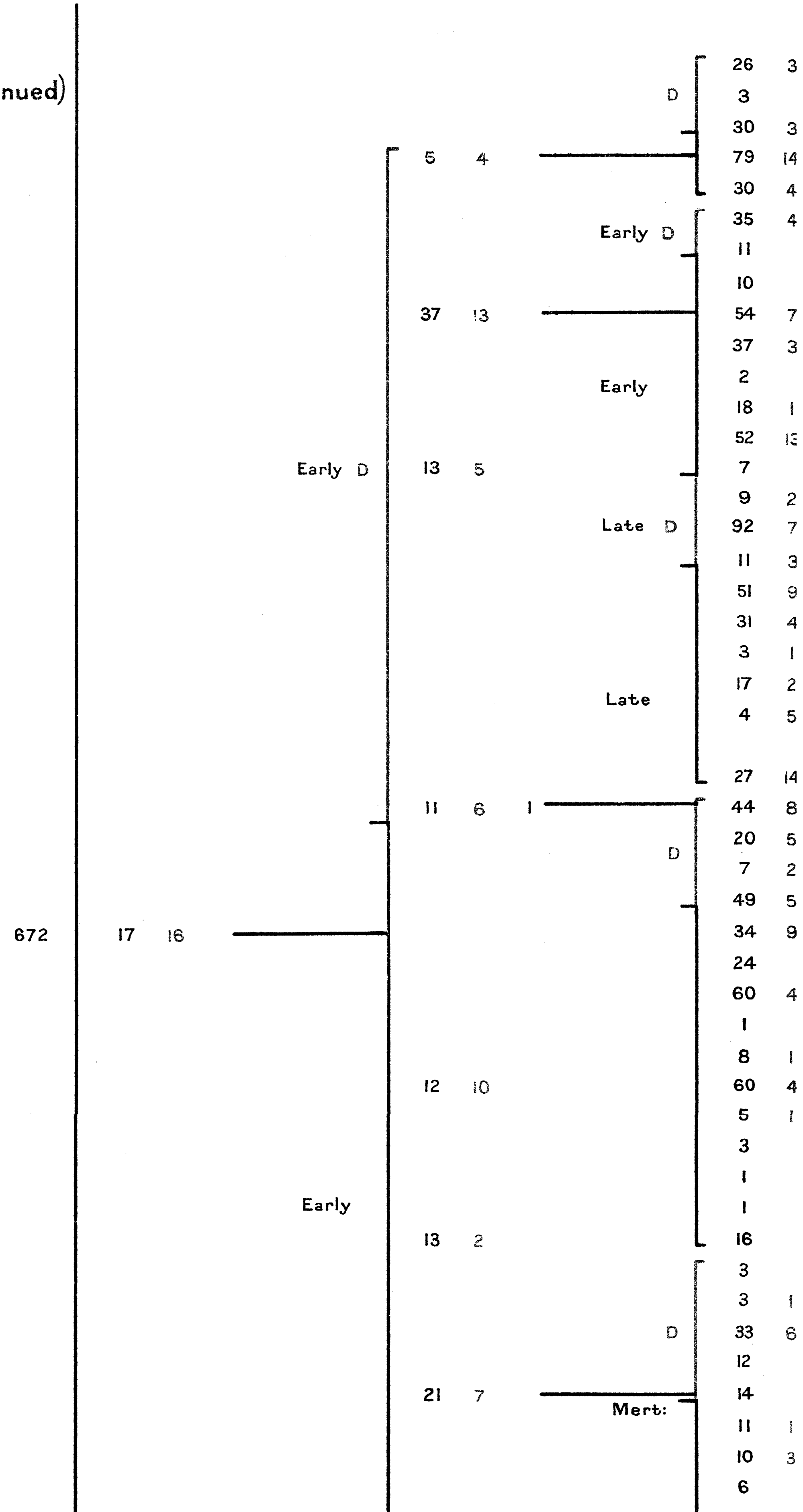

2
1
23
2
1


Rad:
Mert:
184
2
9
68
4
Late
Del:
4
1
10

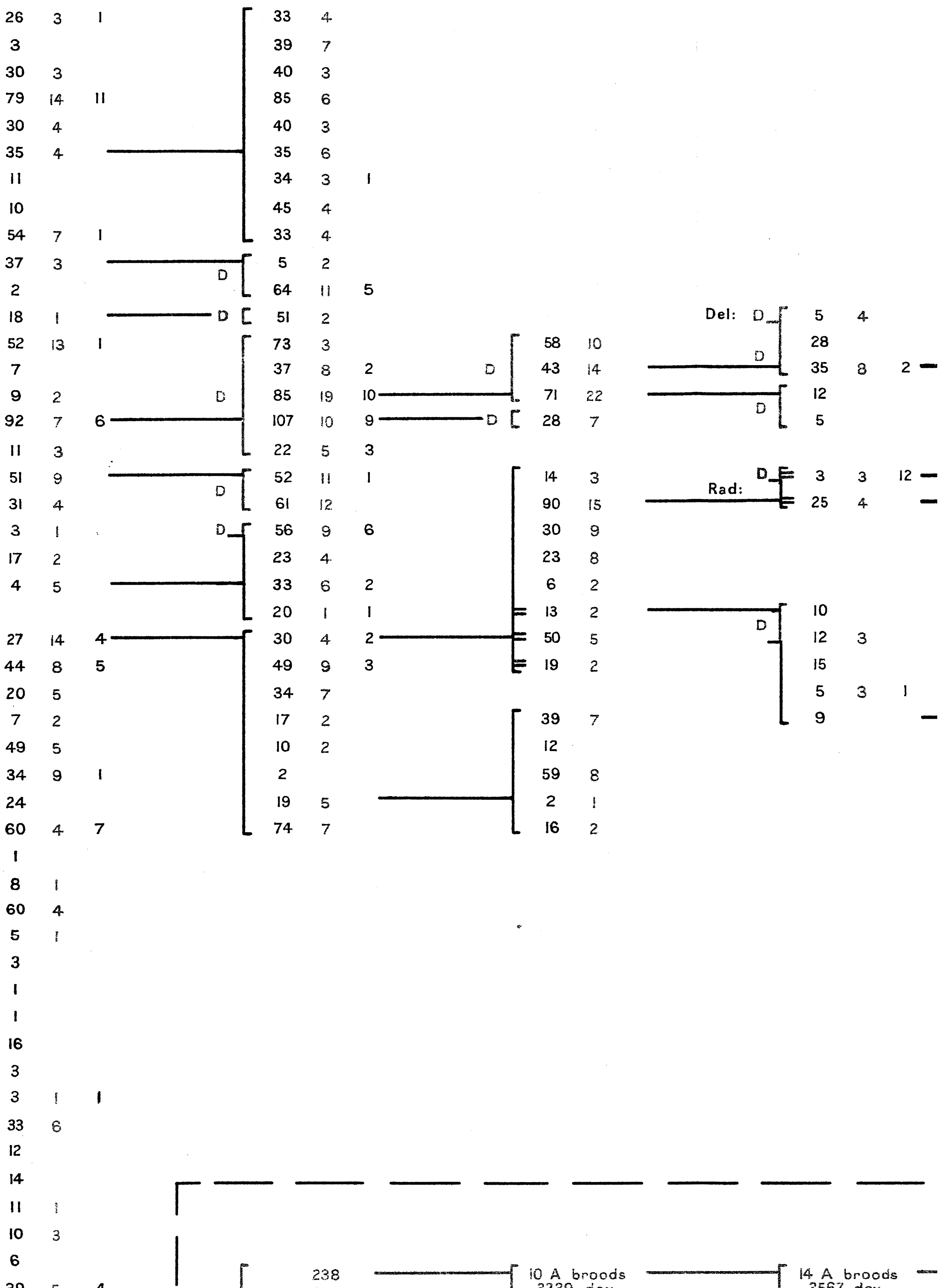

:
:
40 1 4
28
56
134 8 8
31
71
55
39
35
13
2
5
1
12 1
12
45 1
D 20
46
28 2
36
88 3
D 6 1
5
83 2
15 1
46
23 1
13
23
19 1
70
79 3 3
S
7 1
29 1
Rad:
S
13
1
67 1
S
5
49
27
19
Rad: Del:
32
53 1
44
74 2
4 1
29
29
97 1
56
11
30 1
182 2
14
74 6
35
55 1
91 3 1
M. 26 1
96 3 3
D
30
37
83 2
14 2 1
7 1

		1		
		23	2	
		1		
		17		
		73		2
		91		
9		12		
2		13		
12	1	1		
0				
6	1			
13				
5				
2		45	3	
4	1	27		
		11	1	
		5		
		42	2	
6	1	35		
		27		

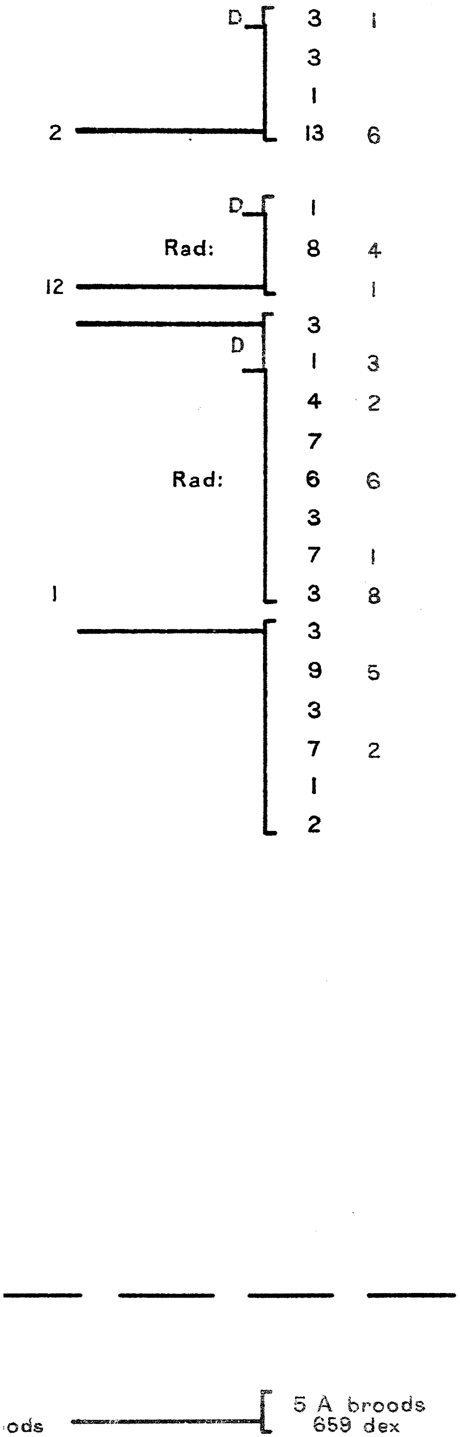
TABLE VI. (continued)

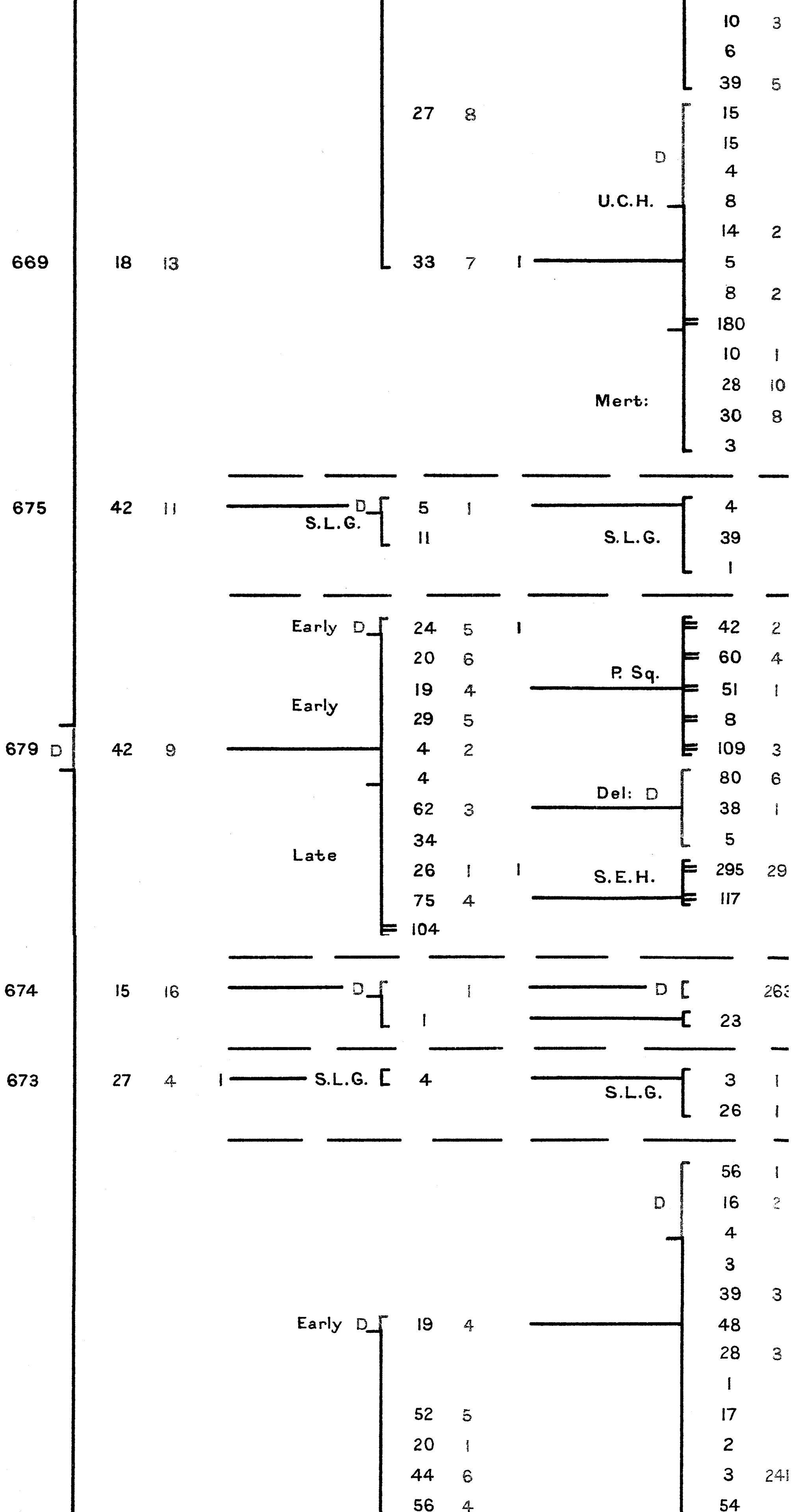


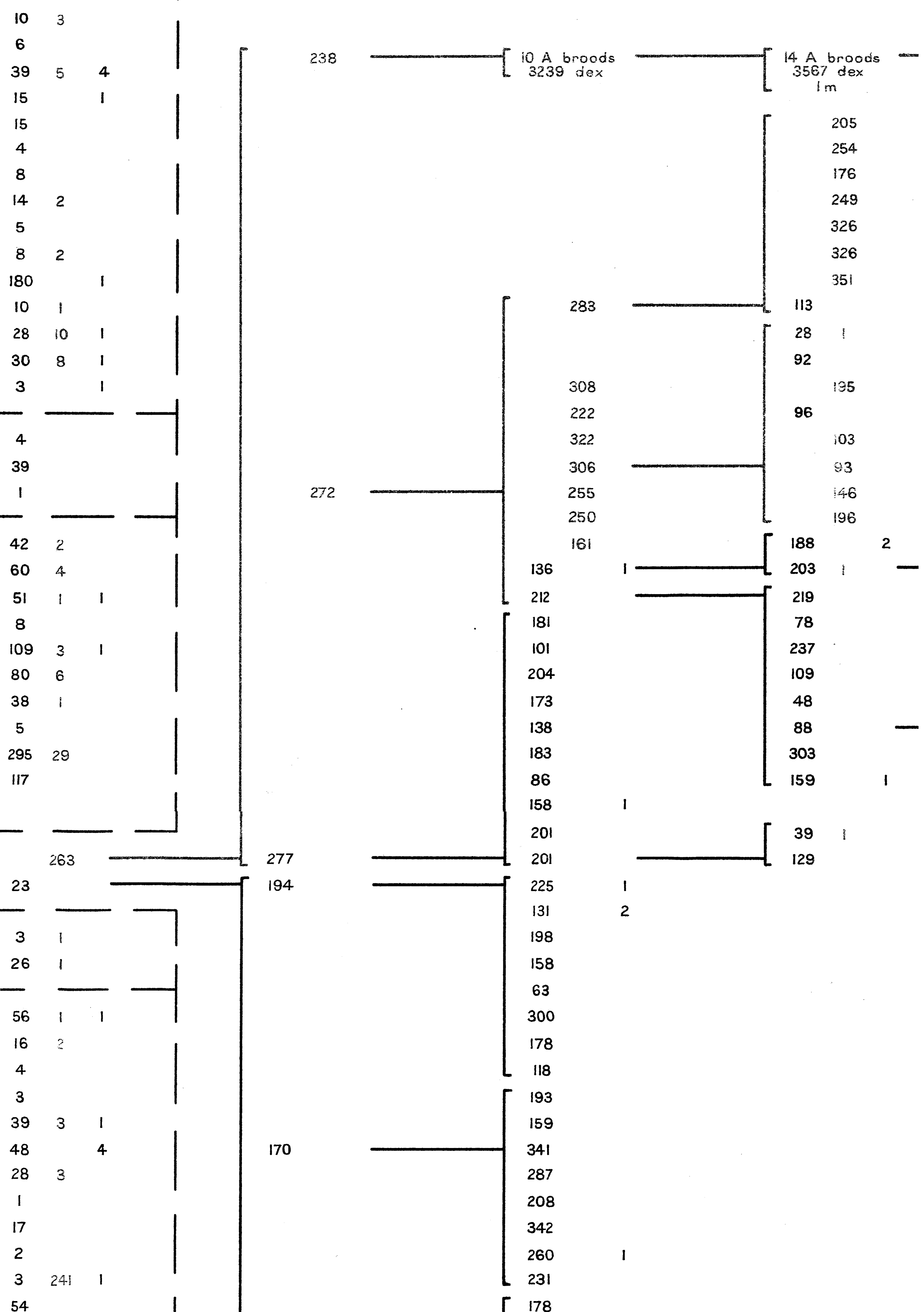
								26	3
							D	3	
								30	3
				5	4			79	14
								30	4
							Early D	35	4
								11	
								10	
				37	13			54	7
								37	3
							Early	2	
								18	1
								52	13
			Early D	13	5			7	
								9	2
							Late D	92	7
								11	3
								51	9
								31	4
								3	1
							Late	17	2
								4	5
								27	14
				11	6	1		44	8
								20	5
							D	7	2
								49	5
672	17	16						34	9
								24	
								60	4
								1	
								8	1
				12	10			60	4
								5	1
								3	
								1	
			Early					1	
				13	2			16	
								3	
								3	1
							D	33	6
								12	
				21	7			14	
							Mert:	11	1
								10	3
								6	

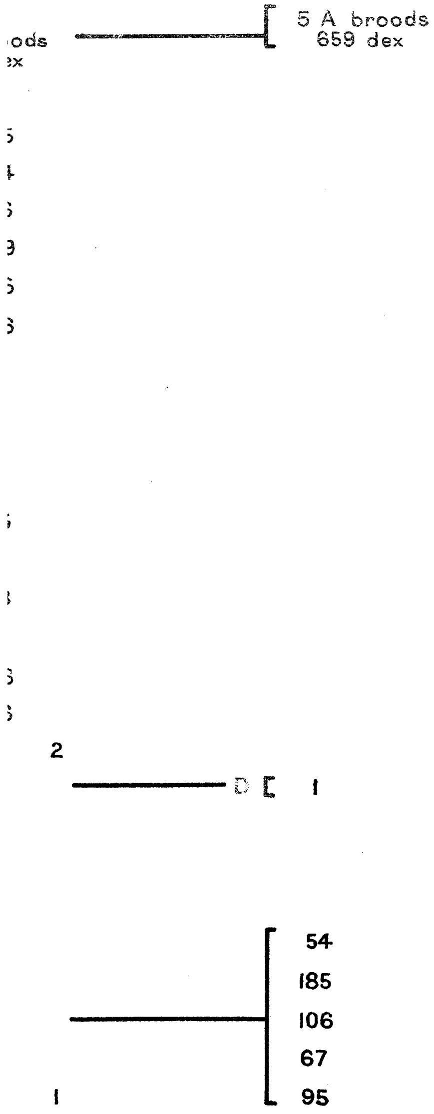


26 3 1
3
30 3
79 14 11
30 4
35 4
11
10
54 7 1
37 3
2
18 1
52 13 1
7
9 2
92 7 6
11 3
51 9
31 4
3 1
17 2
4 5
27 14 4
44 8 5
20 5
7 2
49 5
34 9 1
24
60 4 7
1
8 1
60 4
5 1
3
1
1
16
3
3 1 1
33 6
12
14
11 1
10 3
6
33 4
39 7
40 3
85 6
40 3
35 6
34 3 1
45 4
33 4
D
5 2
64 11 5
D
51 2
73 3
37 8 2
D
85 19 10
107 10 9
22 5 3
D
52 11 1
61 12
D
56 9 6
23 4
33 6 2
20 1 1
30 4 2
49 9 3
34 7
17 2
10 2
2
19 5
74 7
D
58 10
43 14
71 22
D
28 7
14 3
90 15
30 9
23 8
6 2
13 2
50 5
19 2
39 7
12
59 8
2 1
16 2
Del:
D
5 4
28
D
35 8 2
12
D
5
D
3 3 12
Rad:
25 4
10
D
12 3
15
5 3 1
9
238
10 A broods
14 A broods

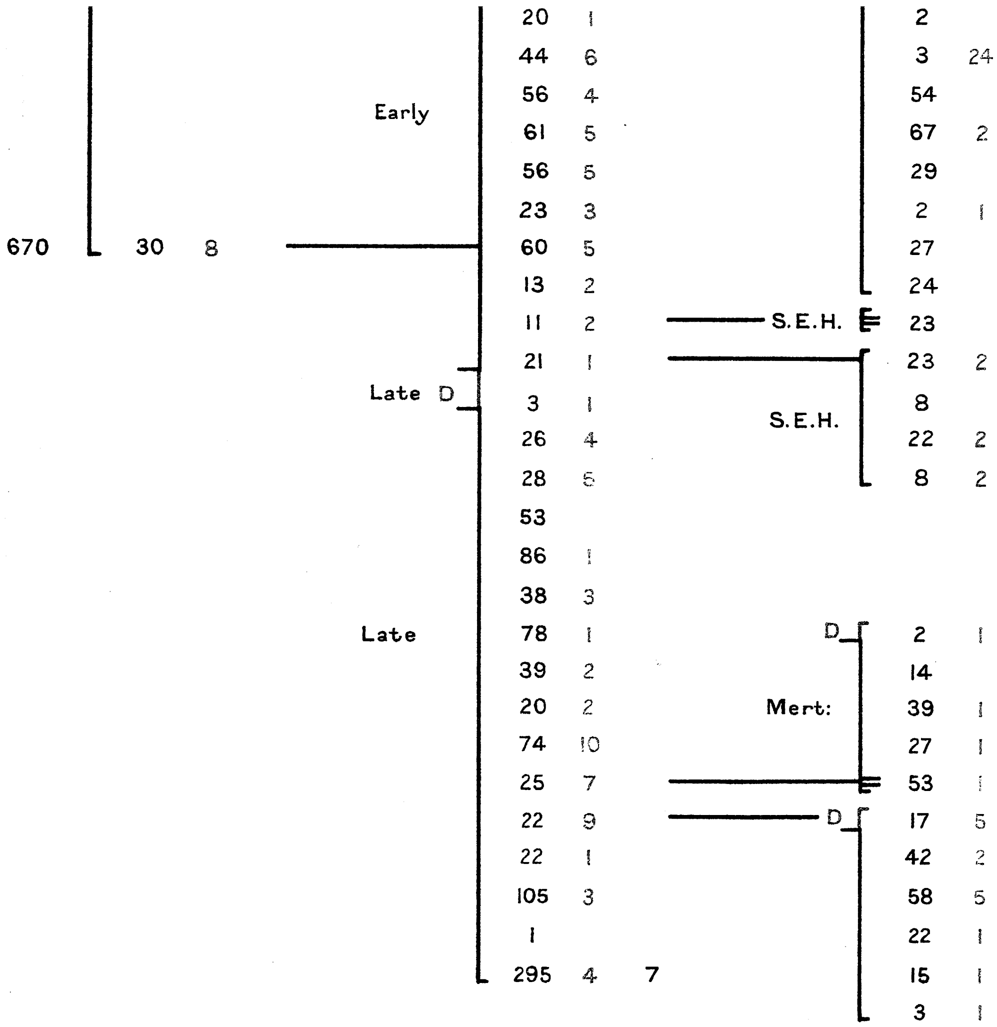

D
3 1
3
1
2 13 6
D
1
Rad: 8 4
12 1
3
D
1 3
4 2
7
Rad: 6 6
3
7 1
1 3 8
3
9 5
3
7 2
1
2
ods
5 A broods
659 dex


10 3
6
39 5
27 8
15
15
D
4
U.C.H.
8
14 2
669
18 13
33 7 1
5
8 2
180
10 1
28 10
Mert:
30 8
3
675
42 11
D
S.L.G.
5 1
11
4
S.L.G.
39
1
Early D
24 5 1
42 2
20 6
60 4
P. Sq.
Early
19 4
51 1
29 5
8
679 D
42 9
4 2
109 3
4
80 6
Del: D
62 3
38 1
34
5
Late
26 1 1
S.E.H.
295 29
75 4
117
104
674
15 16
D
1
D
263
1
23
673
27 4 1
S.L.G.
4
3 1
S.L.G.
26 1
56 1
D
16 2
4
3
39 3
Early D
19 4
48
28 3
1
52 5
17
20 1
2
44 6
3 241
56 4
54

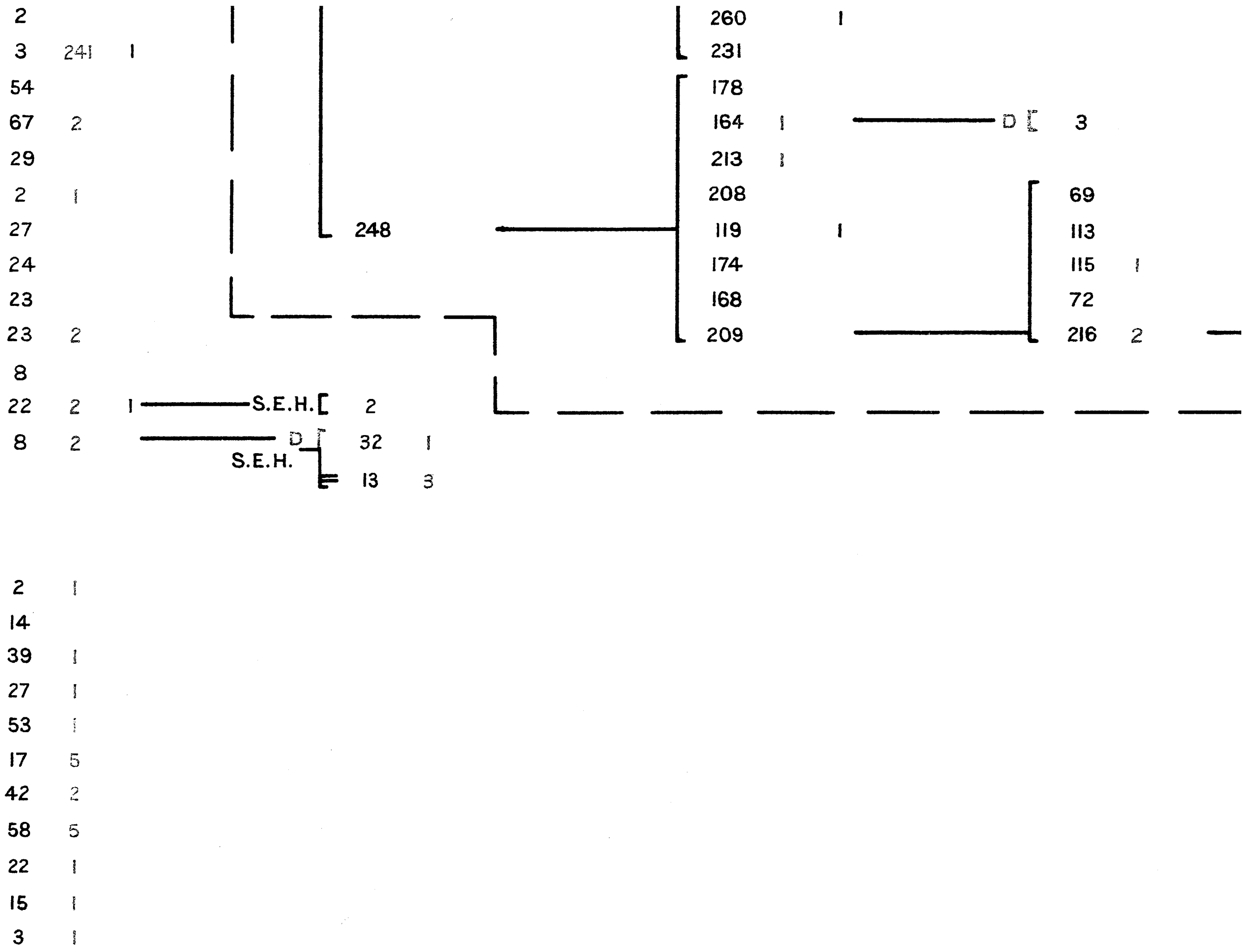

10 3
6
39 5 4
238
10 A broods
3239 dex
14 A broods
3567 dex
1 m
15 1
15
205
4
254
8
176
14 2
249
5
326
8 2
326
180 1
351
10 1
283
113
28 10 1
28 1
30 8 1
92
3 1
308
195
222
96
4
322
103
39
306
93
1
272
255
146
250
196
42 2
161
188
2
60 4
136
1
203
1
51 1 1
212
219
8
181
78
109 3 1
101
237
80 6
204
109
38 1
173
48
5
138
88
295 29
183
303
117
86
159
1
158
1
201
39
1
263
277
201
129
23
194
225
1
131
2
3 1
198
26 1
158
63
56 1 1
300
16 2
178
4
118
3
193
39 3 1
159
48 4
170
341
28 3
287
1
208
17
342
2
260
1
3 241 1
231
54
178



ods
ex
5 A broods
659 dex
2
D
1
54
185
106
67
95
1



Early
Late D
Late
670 30 8
20 1
44 6
56 4
61 5
56 5
23 3
60 5
13 2
11 2
21 1
3 1
26 4
28 5
53
86 1
38 3
78 1
39 2
20 2
74 10
25 7
22 9
22 1
105 3
1
295 4 7
S.E.H.
S.E.H.
D
Mert:
D
2
3 24
54
67 2
29
2 1
27
24
23
23 2
8
22 2
8 2
2 1
14
39 1
27 1
53 1
17 5
42 2
58 5
22 1
15 1
3 1


2
3 241 1
54
67 2
29
2 1
27
24
23
23 2
8
22 2 1
8 2
S.E.H.
2
D
32 1
S.E.H.
13 3
248
260 1
231
178
164 1
213 1
208
119 1
174
168
209
D
3
69
113
115 1
72
216 2
2 1
14
39 1
27 1
53 1
17 5
42 2
58 5
22 1
15 1
3 1

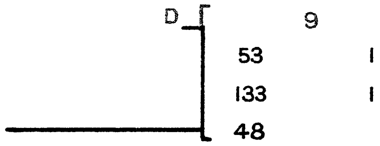
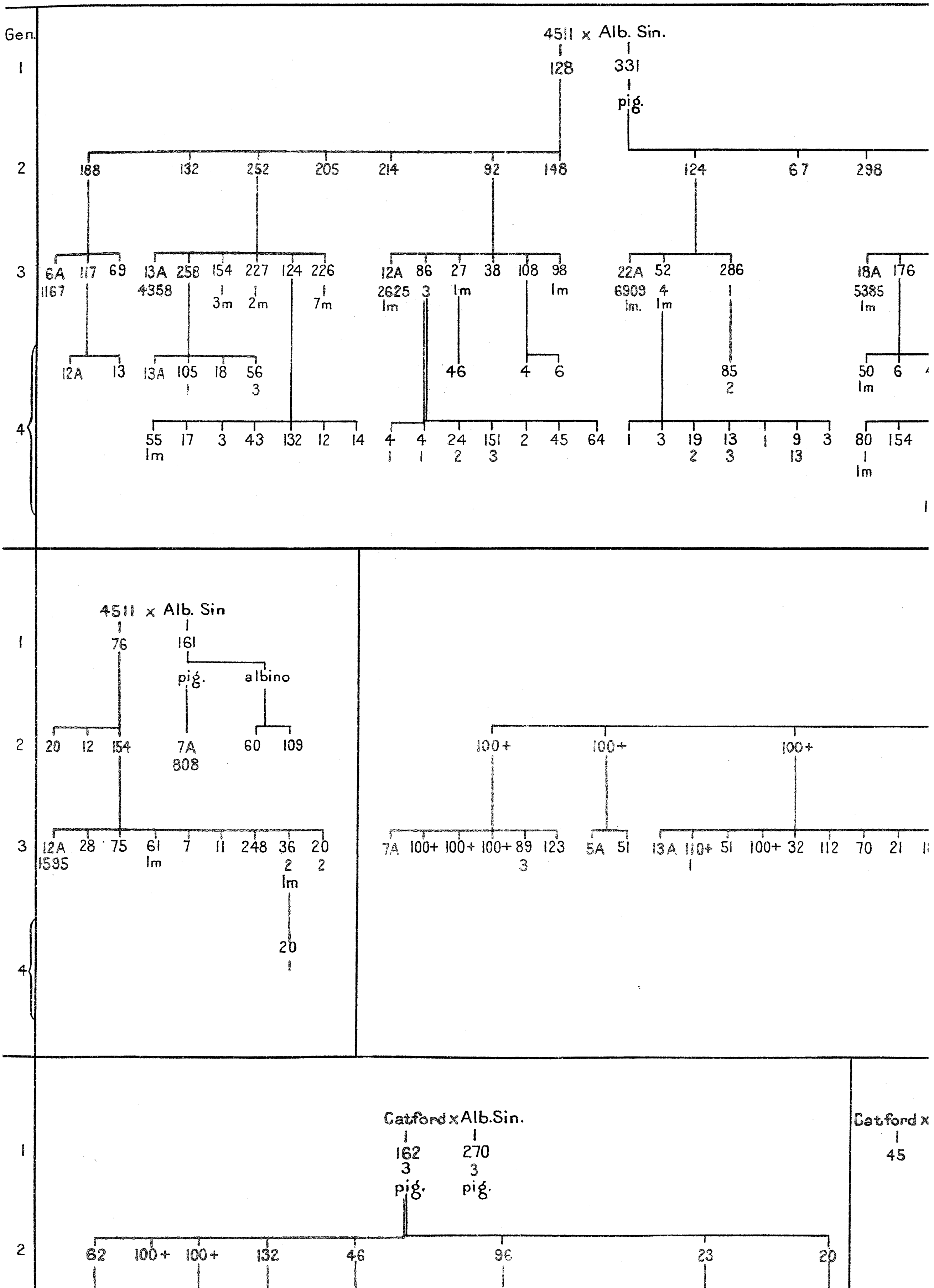
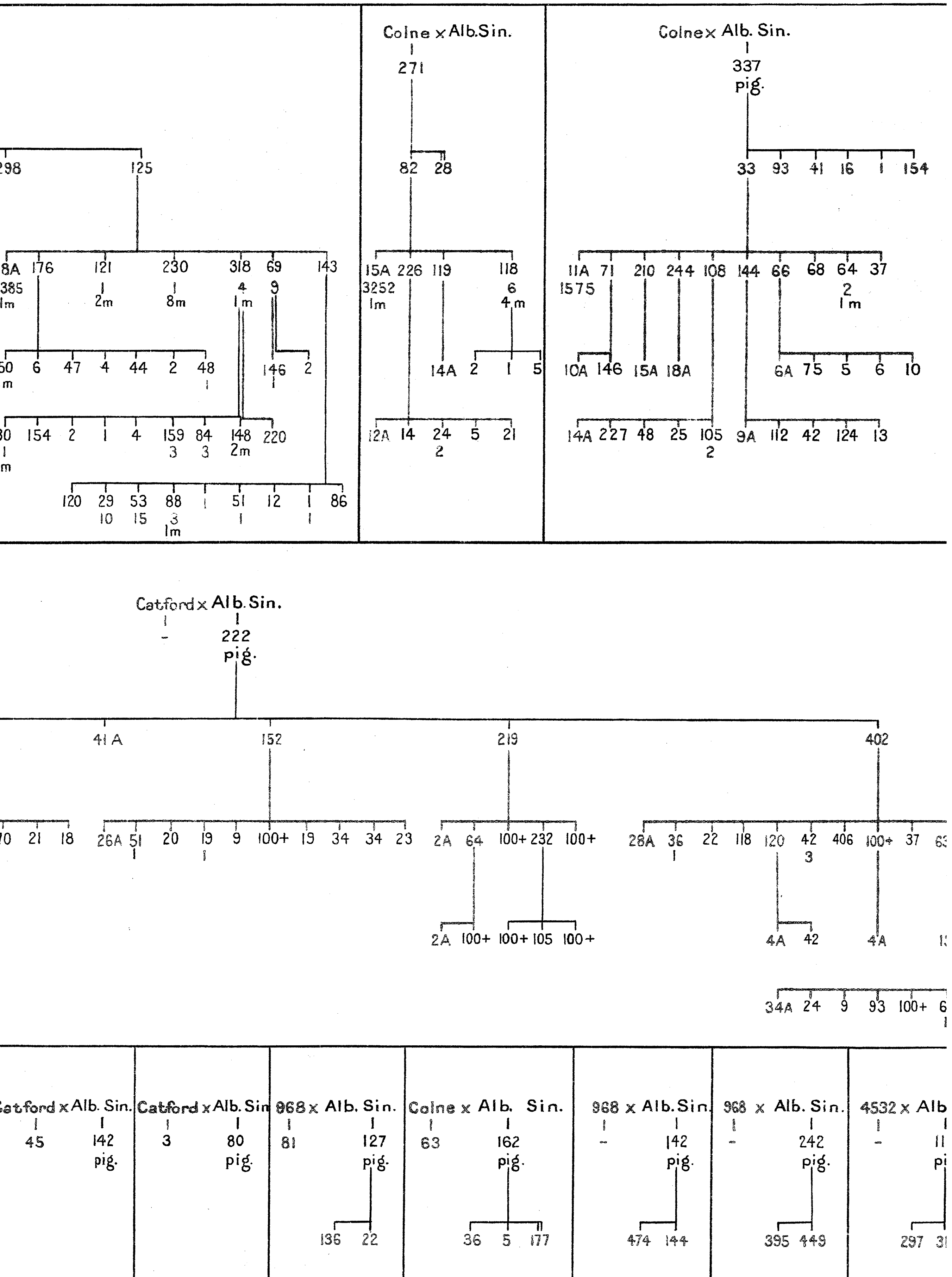
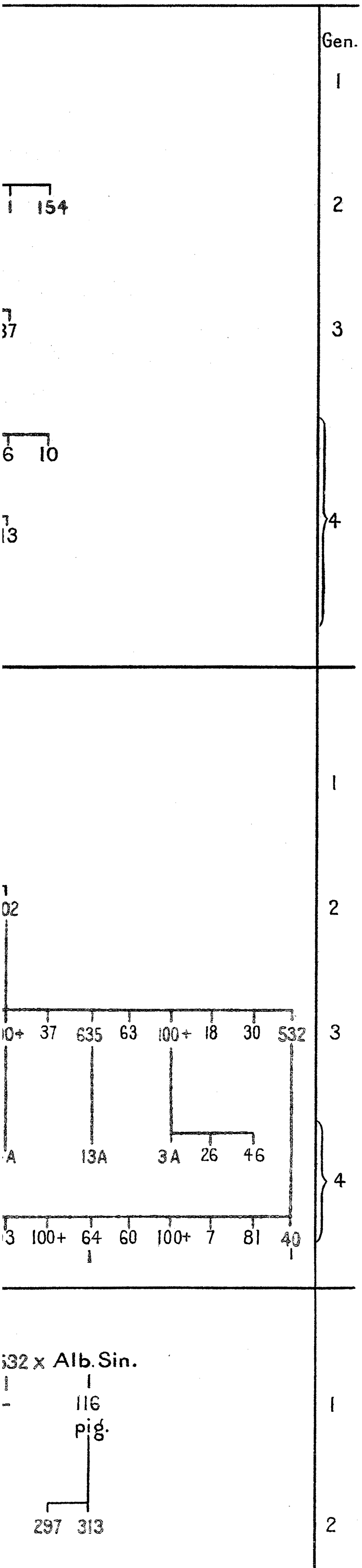
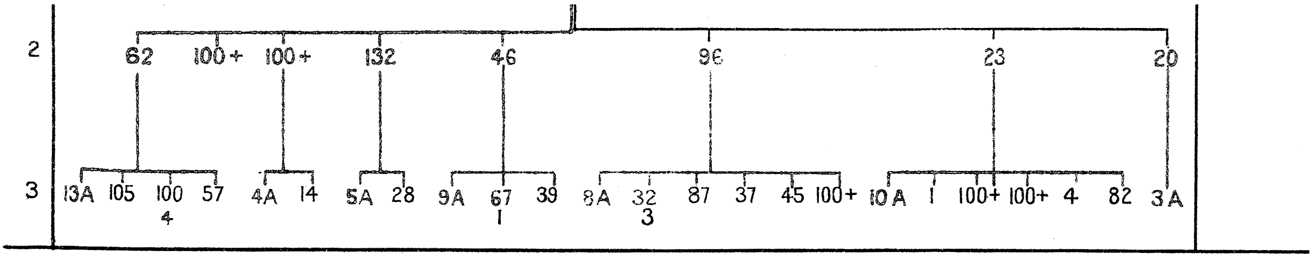

D
9
53
1
133
1
48

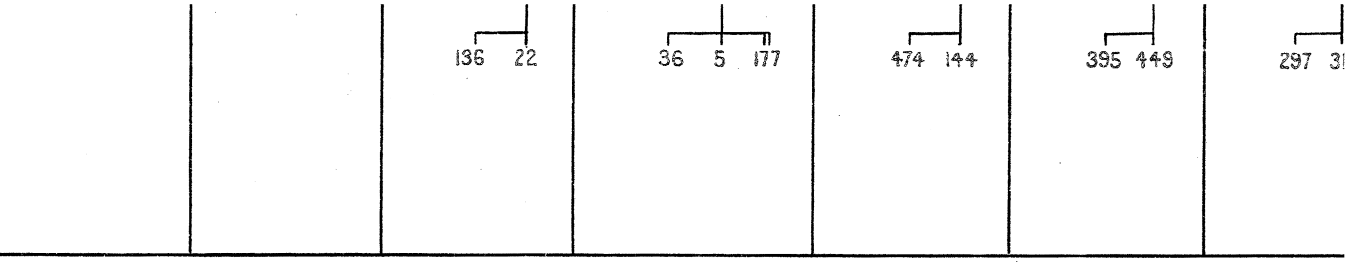
Table VII. A dextrals x K Sinistrals




298
125
8A 176 121 230 318 69 143
385 1 1 4 9
1m 2m 8m 1m
50 6 47 4 44 2 48
m 1
146 2
1
30 154 2 1 4 159 84 148 220
1 3 3 2m
m
120 29 53 88 1 51 12 1 86
10 15 3 1 1
1m
Colne x Alb.Sin.
271
82 28
15A 226 119 118
3252 6
1m 4m
14A 2 1 5
12A 14 24 5 21
2
Colne x Alb. Sin.
337
pig.
33 93 41 16 1 154
11A 71 210 244 108 144 66 68 64 37
1575 2
1m
10A 146 15A 18A
6A 75 5 6 10
14A 227 48 25 105
2
9A 112 42 124 13
Catford x Alb. Sin.
-
222
pig.
41 A
152
219
402
70 21 18
26A 51 20 19 9 100+ 19 34 34 23
1 1
2A 64 100+ 232 100+
2A 100+ 100+ 105 100+
28A 36 22 118 120 42 406 100+ 37 63
1 3
4A 42
4A
34A 24 9 93 100+ 6
Catford x Alb. Sin.
45
142
pig.
Catford x Alb. Sin
3
80
pig.
968 x Alb. Sin.
81
127
pig.
136 22
Colne x Alb. Sin.
63
162
pig.
36 5 177
968 x Alb. Sin.
-
142
pig.
474 144
968 x Alb. Sin.
-
242
pig.
395 449
4532 x Alb
-
11
pi
297 3


Gen.
1
2
3
4
1 154
37
6 10
13
1
2
3
4
02
0+ 37 635 63 100+ 18 30 532
A 13A 3A 26 46
3 100+ 64 60 100+ 7 81 40
532 x Alb. Sin.
1
116
pig.
2
297 313


2
3
62
100+
100+
132
46
96
23
20
13A
105
100
57
4
4A
14
5A
28
9A
67
39
1
8A
32
87
37
45
100+
3
10A
1
100+
100+
4
82
3A


136
22
36
5
177
474
144
395
449
297
3

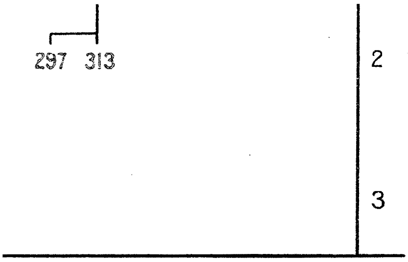
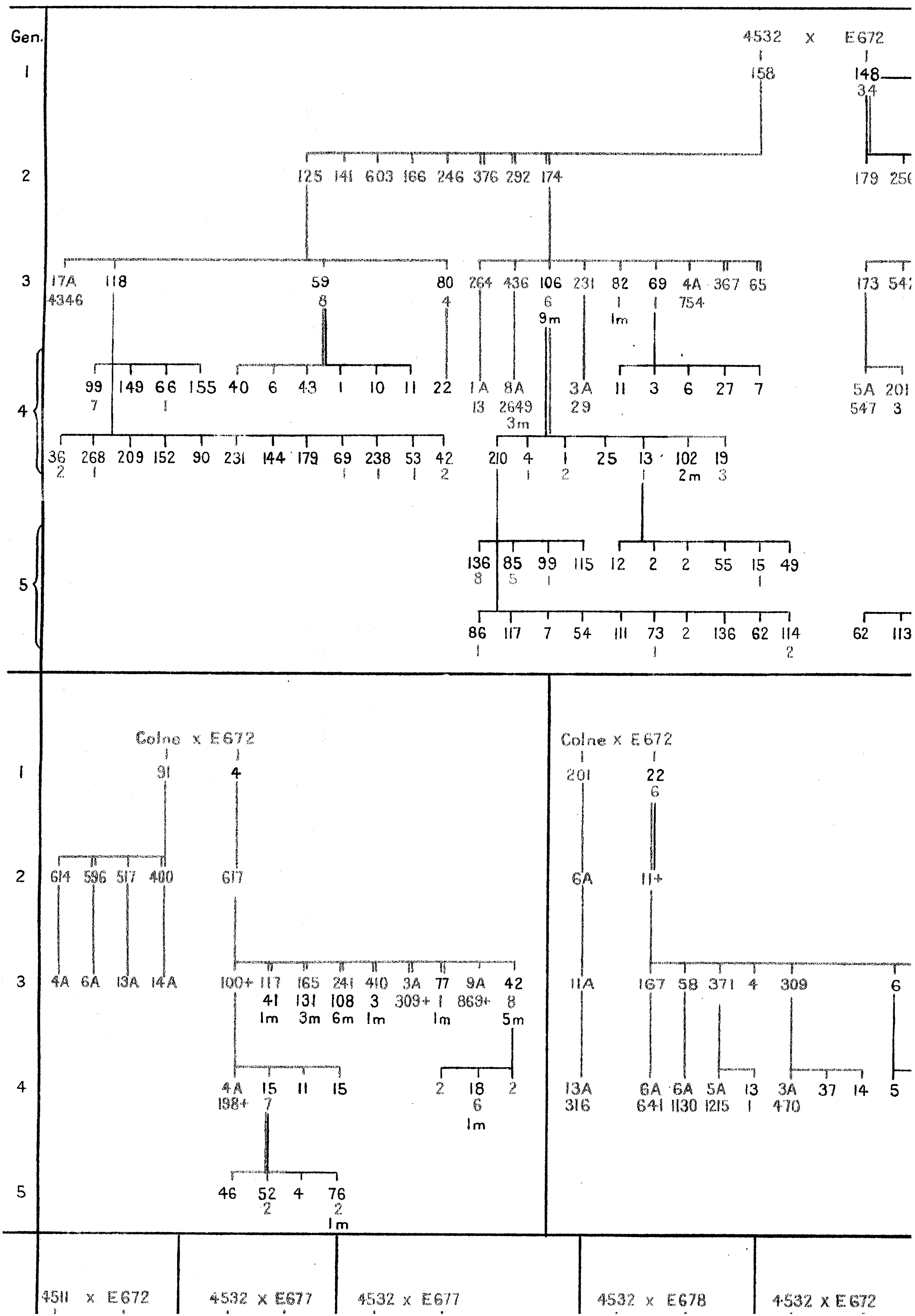
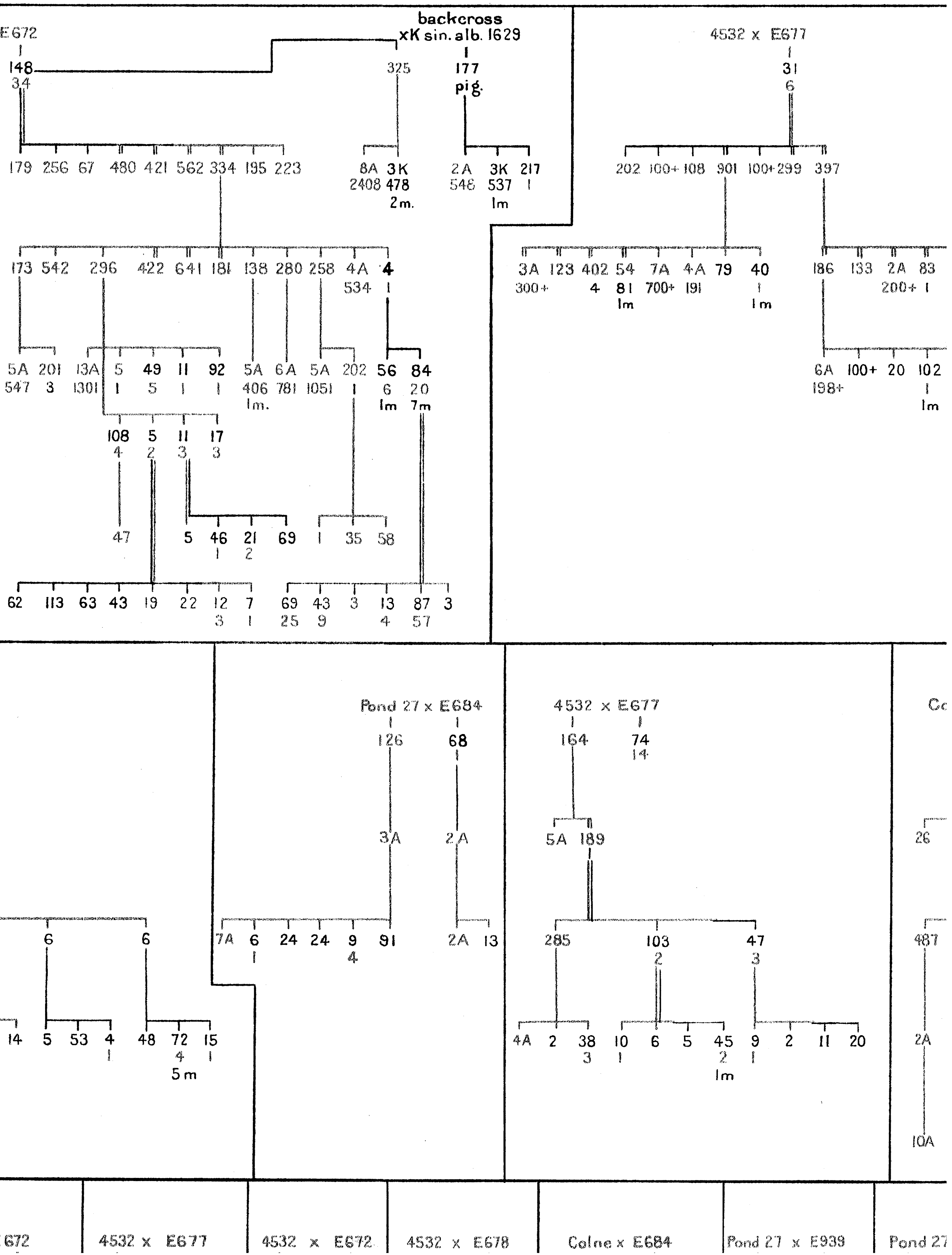
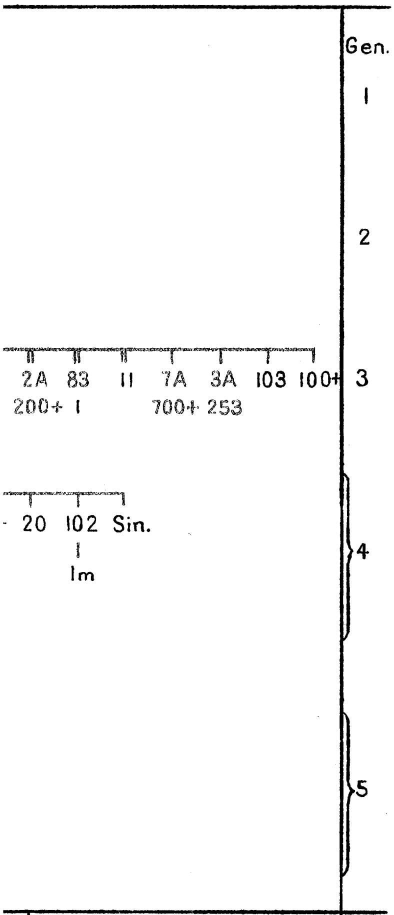
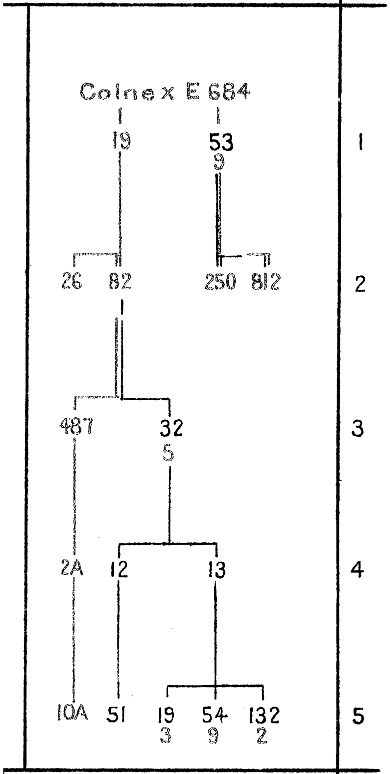

297
313
2
3

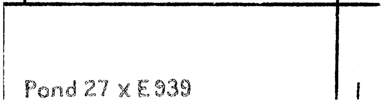
Table VIII. A dextrals x E dextrals

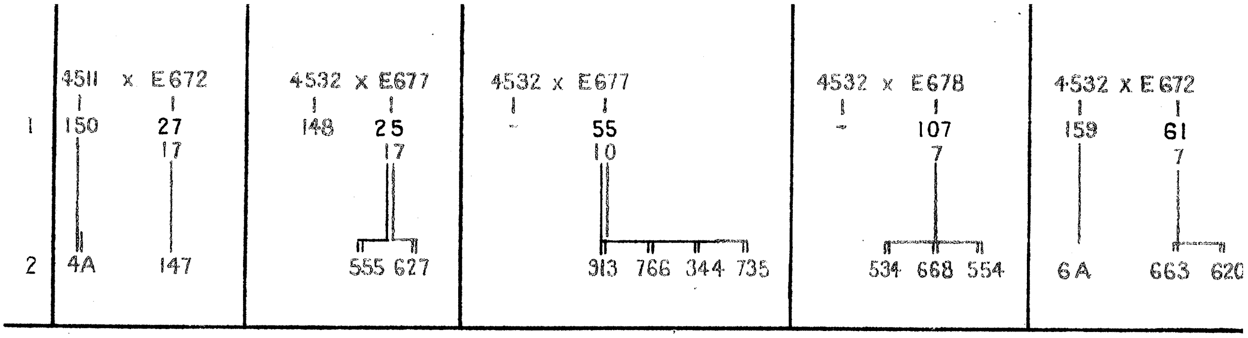


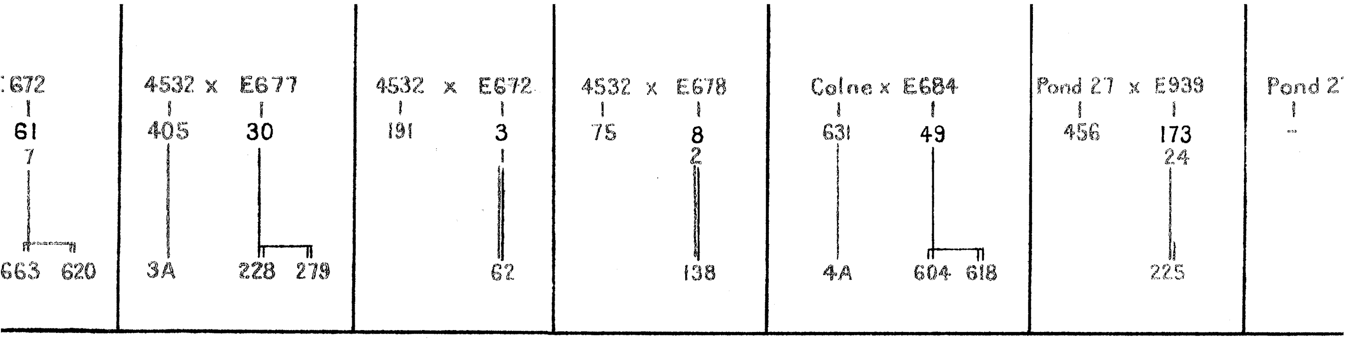

E672
148
34
backcross
xK sin. alb. 1629
325
177
pig.
179 256 67 480 421 562 334 195 223
8A 3K
2408 478
2m.
2A 3K 217
546 537 1
1m
173 542 296 422 641 181 138 280 258 4A 4
534 1
5A 201 13A 5 49 11 92 5A 6A 5A 202 56 84
547 3 1301 1 5 1 1 406 781 1051 1 6 20
1m. 1m 7m
108 5 11 17
4 2 3 3
47
5 46 21 69
1 2
1 35 58
62 113 63 43 19 22 12 7 69 43 3 13 87 3
3 1 25 9 4 57
4532 x E677
31
6
202 100+ 108 901 100+ 299 397
3A 123 402 54 7A 4A 79 40
300+ 4 81 700+ 191 1
1m 1m
186 133 2A 83
200+ 1
6A 100+ 20 102
198+ 1
1m
Pond 27 x E684
126 68
3A 2A
7A 6 24 24 9 91 2A 13
1 4
4532 x E677
164 74
14
5A 189
285 103 47
2 3
4A 2 38 10 6 5 45 9 2 11 20
3 1 2 1
1m
Co
26
487
2A
10A
6 6
14 5 53 4 48 72 15
1 4 1
5 m
672
4532 x E677
4532 x E672
4532 x E678
Colne x E684
Pond 27 x E939
Pond 27


Gen.
1
2
2A 83 11 7A 3A 103 100+ 3
200+ 1 700+ 253
- 20 102 Sin.
Im
4
5


Colne x E 684
19
53
9
1
26 82
250 812
2
487
32
5
3
2A 12 13
4
10A 51 19 54 132
3 9 2
5


Pond 27 x E 939
1


1
2
4511 x E672
150
27
17
4A
147
4532 x E677
148
25
17
555 627
4532 x E677
55
10
913 766 344 735
4532 x E678
107
7
534 668 554
4532 x E672
159
61
7
6A
663 620



672
61
7
663
620
4532 x E677
405
30
3A
228
279
4532 x E672
191
3
62
4532 x E678
75
8
2
138
Colne x E684
631
49
4A
604
618
Pond 27 x E939
456
173
24
225
Pond 2

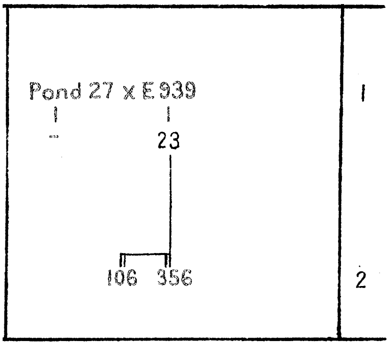
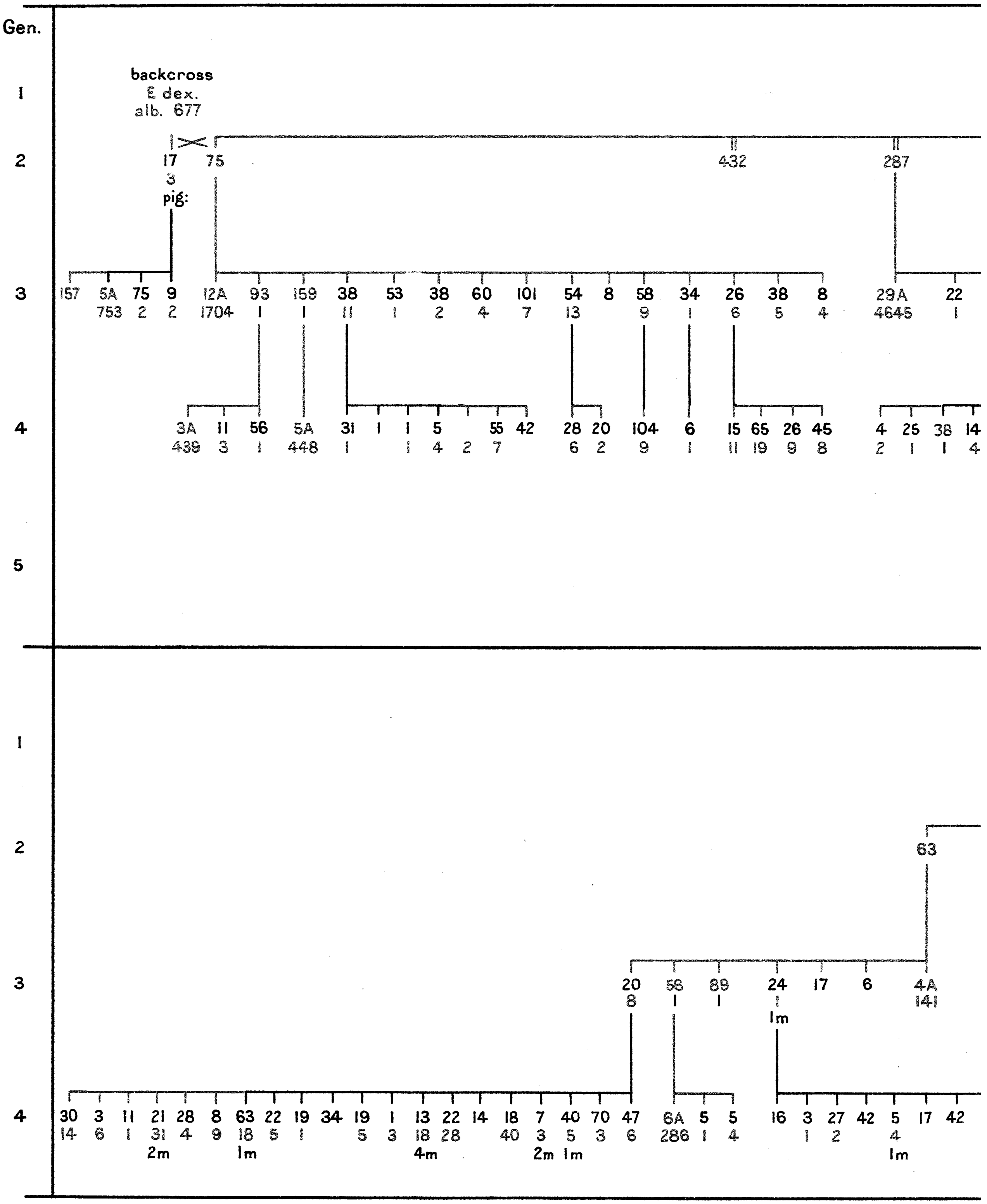
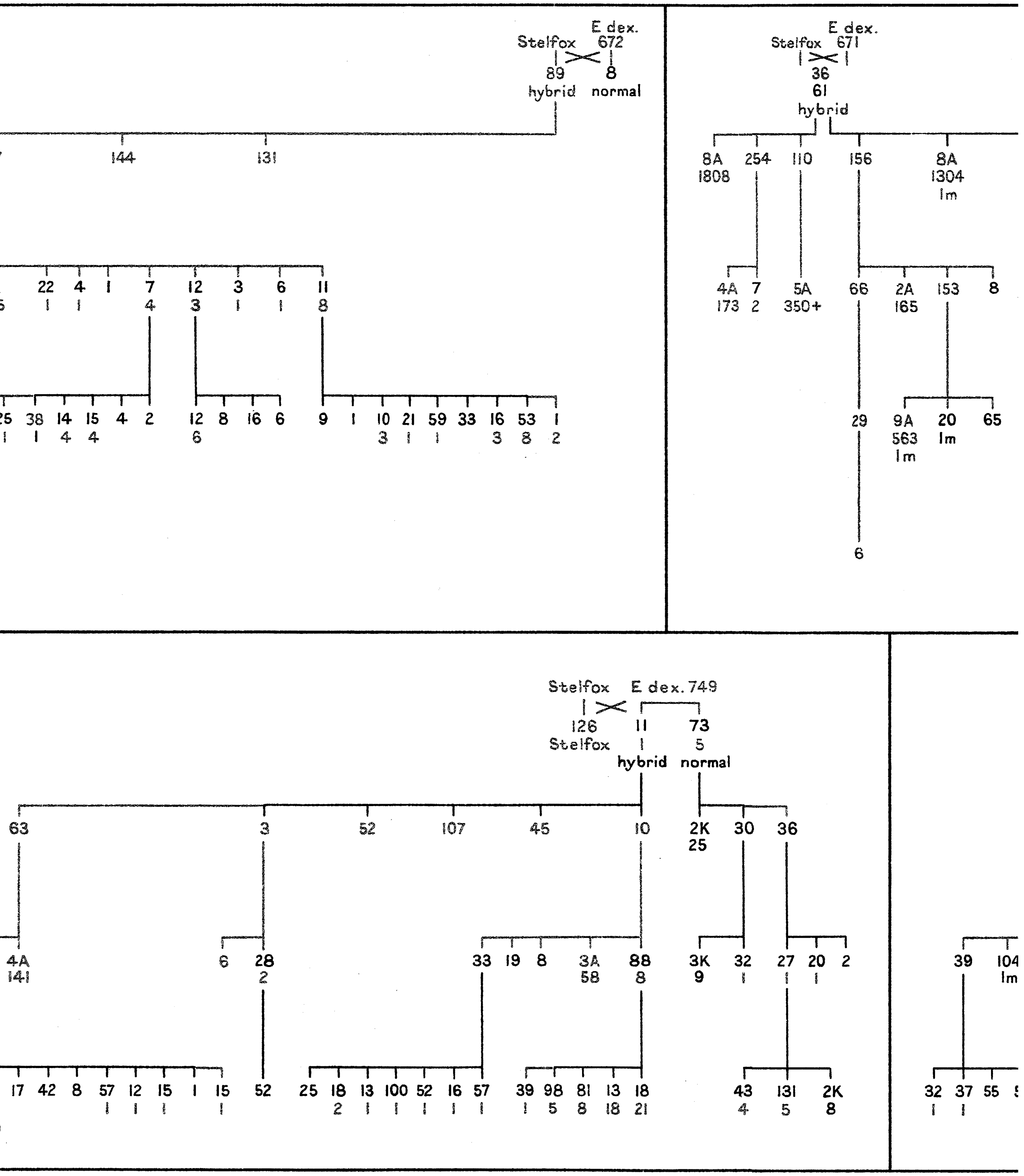
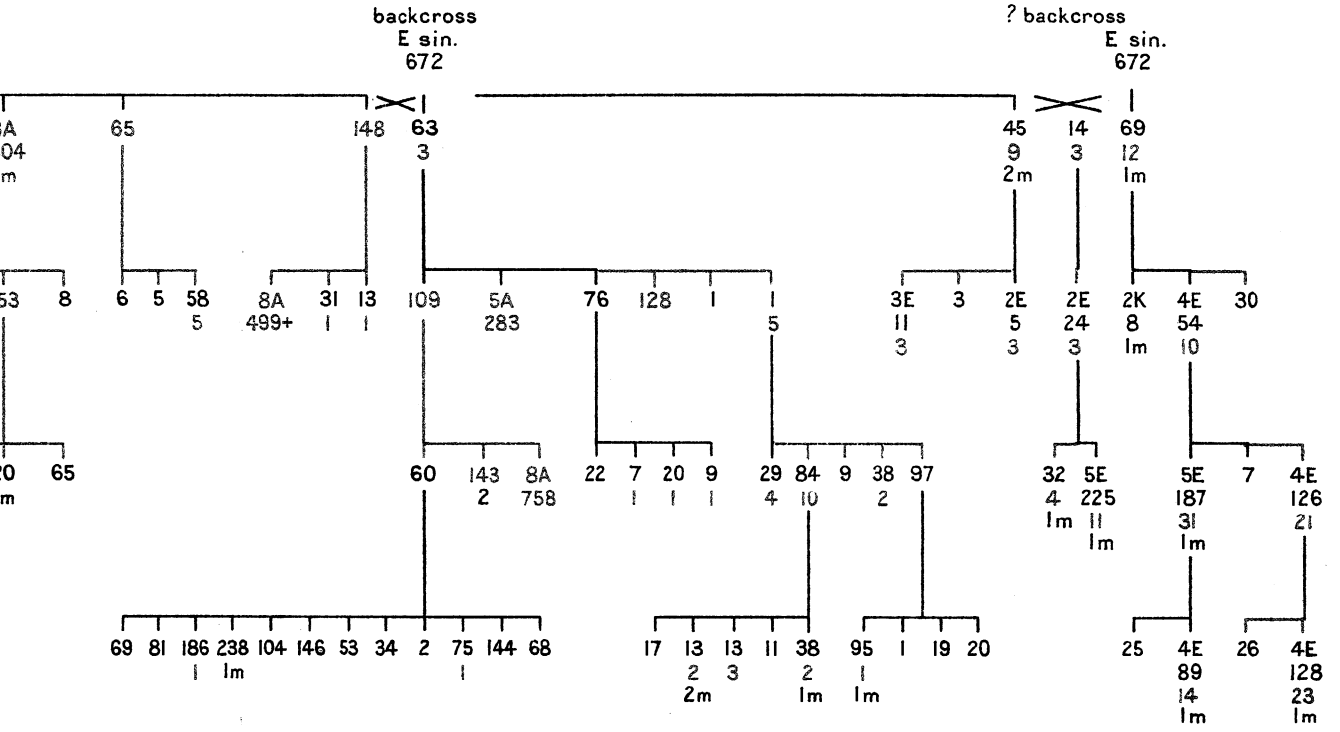

Pond 27 x E 939
23
106
356
1
2

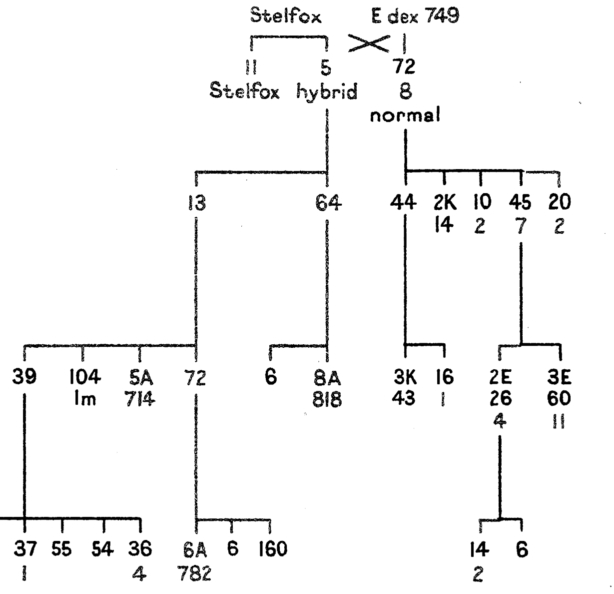
TABLE IX. Stelfox A dextrals X E dextrals



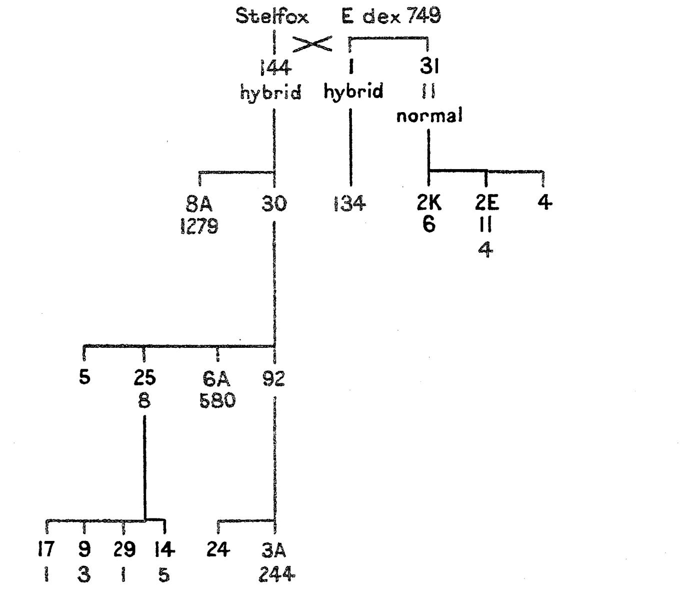

Stelfox
E dex. 672
89
8
hybrid
normal
144
131
Stelfox
E dex. 671
36
61
hybrid
8A 1808
254
110
156
8A 1304 lm
4A 173
7 2
5A 350+
66
2A 165
153
8
29
9A 563 lm
20 lm
65
6
Stelfox
E dex. 749
126 Stelfox
11
73 5
hybrid
normal
63
3
52
107
45
10
2K 25
30
36
4A 141
6
28 2
33
19
8
3A 58
88 8
3K 9
32
27
20
2
39
104 lm



backcross
E sin.
672
? backcross
E sin.
672
A
04
m
65
148
63
3
45
9
2m
14
3
69
12
1m
53
8
6
5
58
5
8A
499+
31
1
13
1
109
5A
283
76
128
1
1
5
3E
11
3
3
2E
5
3
2E
24
3
2K
8
1m
4E
54
10
30
20
m
65
60
143
2
8A
758
22
7
1
20
1
9
1
29
4
84
10
9
38
2
97
32
4
1m
5E
225
11
1m
5E
187
31
1m
7
4E
126
21
69
81
186
1
238
1m
104
146
53
34
2
75
1
144
68
17
13
2
2m
13
3
11
38
2
1m
95
1
1m
1
19
20
25
4E
89
14
1m
26
4E
128
23
1m



Stelfox
E dex 749
11
Stelfox
5
hybrid
72
8
normal
13
64
44
2K
14
10
2
45
7
20
2
39
104
1m
5A
714
72
6
8A
818
3K
43
16
1
2E
26
4
3E
60
11
37
1
55
54
36
4
6A
782
6
160
14
2
6



Stelfox
E dex 749
144
hybrid
1
hybrid
31
11
normal
8A
1279
30
134
2K
6
2E
11
4
4
5
25
8
6A
580
92
17
1
9
3
29
1
14
5
24
3A
244

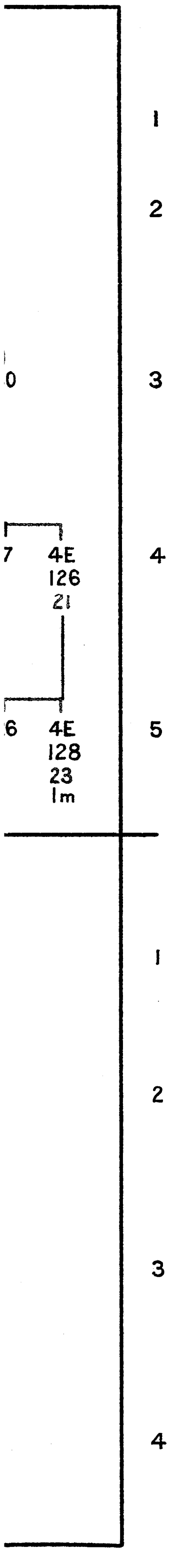
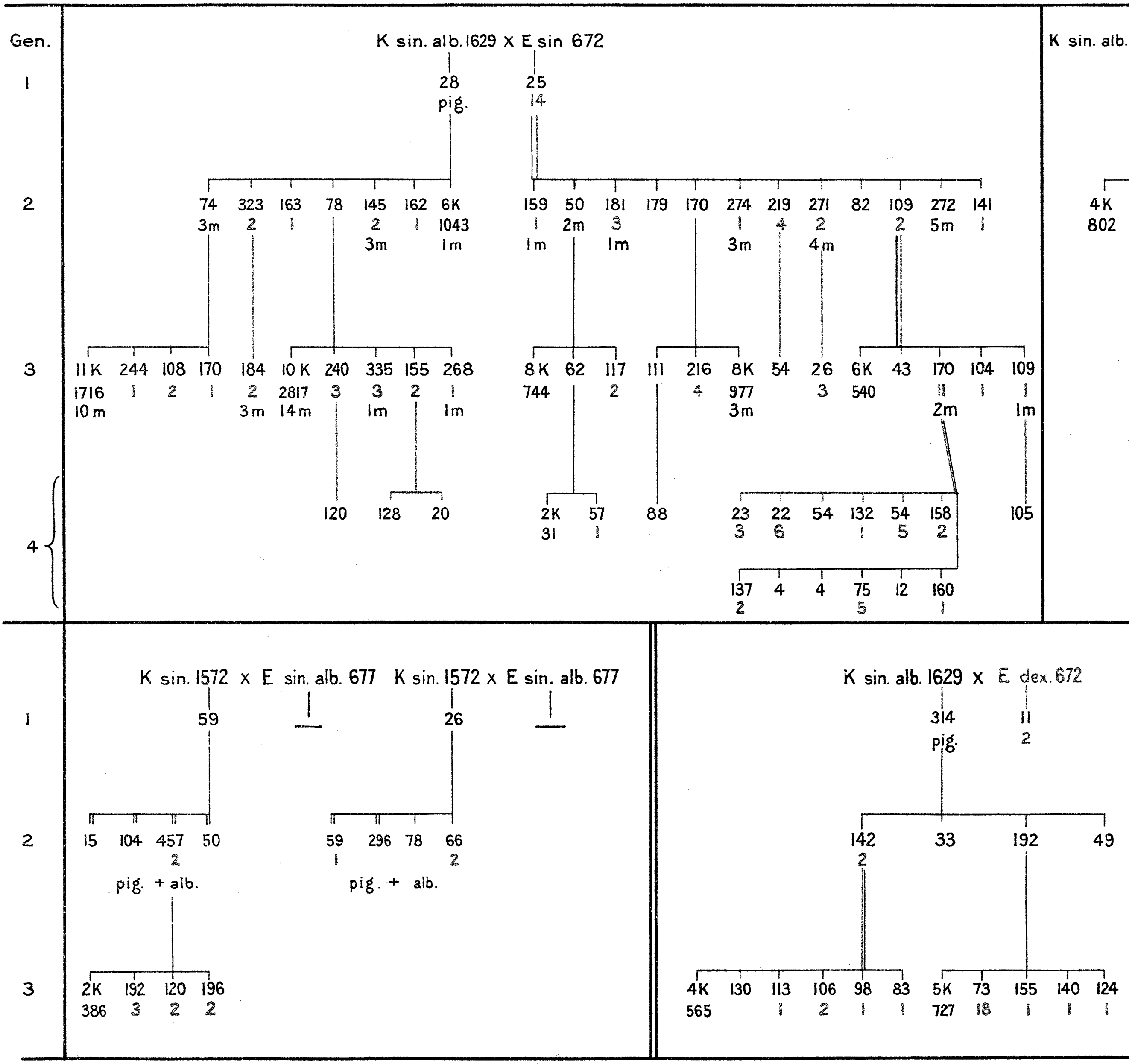
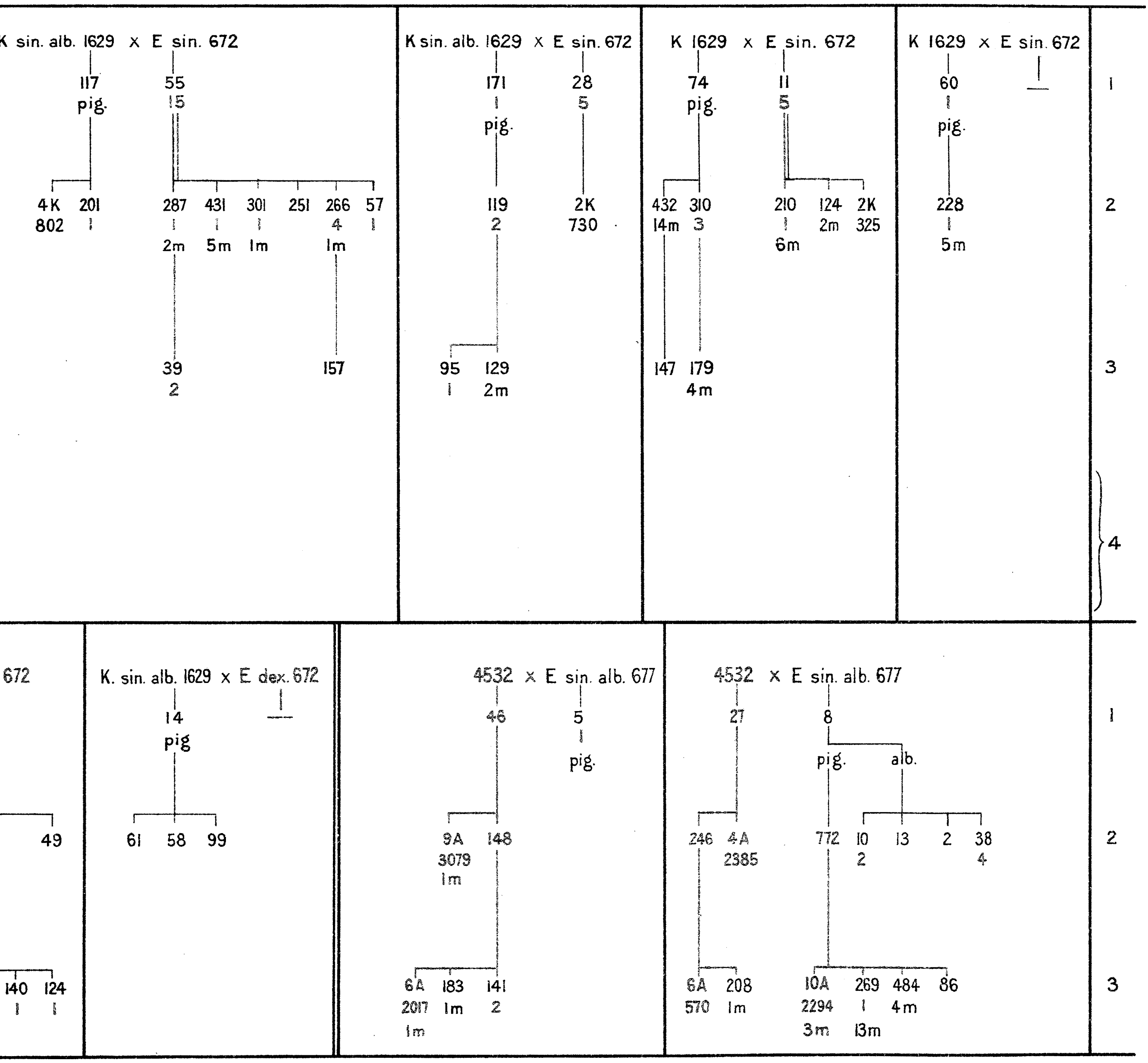

1
2
0
3
7
4E
126
21
4
6
4E
128
23
1m
5
1
2
3
4

TABLE X. K sinistrals x E sinistrals. K sinistrals x E dextrals. A dextrals x E



als x E. sinistrals.



In 1923–1925 waste sinistrals from our breeding were planted out in large numbers to 16 ponds in the Radlett neighbourhood, which seemed suitable for their reception and which were under regular examination ('Trans. Herts. Nat. Hist. Soc.,' 1919, vol. 17, p. 153; 1930, vol. 19, p. 1); nothing has been seen of them since. In March, 1925, about 300 K sinistrals were put into an artificial cement-lined pond in Dr. Price-Jones's garden, which contained a good many *Limnæa stagnalis* and some *Planorbis corneus*, together with sticklebacks and carp. They did well and bred freely and were abundant in 1926, when by some means unknown *Limnæa auricularia* got into the pond and flourished prodigiously. In 1927 sinistral *peregra* were few, and in 1928 and 1929 none have been found: it is obviously possible that competition with a closely-allied species is responsible for their disappearance.

(2) *Serological experiments.*

Rabbits were injected repeatedly with mashes of (1) A dextrals from dextral breakthroughs, (2) K sinistrals, (3) wild *L. peregra* from two different localities, (4) *Limnæa stagnalis*, and (5) *Planorbis corneus*. Their sera soon gave definite precipitation with the clear fluids obtained from live homologous snails by irritation and gentle squeezing. By these reactions *Planorbis corneus* could easily be distinguished from the rest, *L. stagnalis* was perceptibly different from *L. peregra*, but no difference could be made out between the four lots of *peregra*. The proteid constituents of dextrals and sinistrals are therefore probably not grossly different.

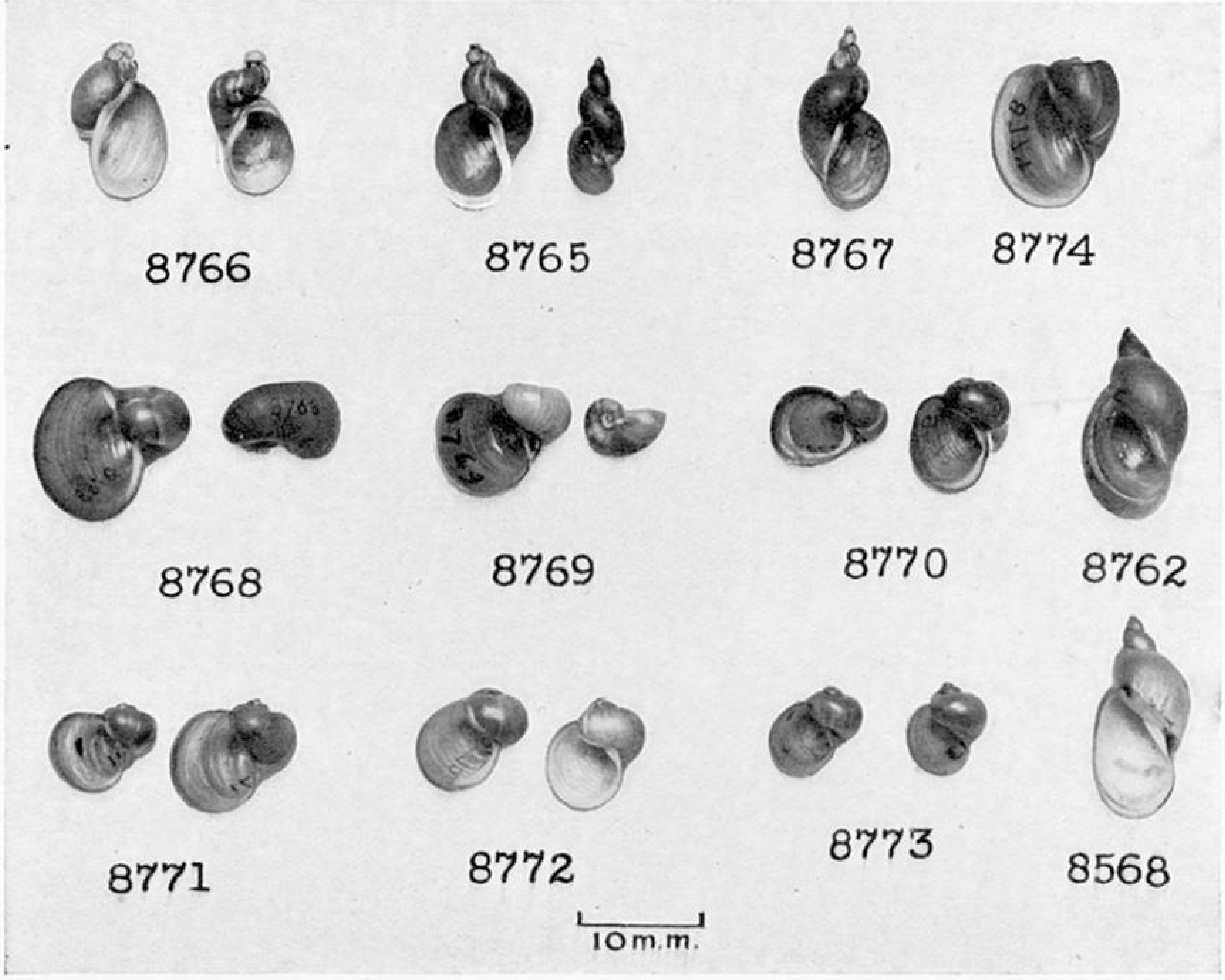


FIG. 8.

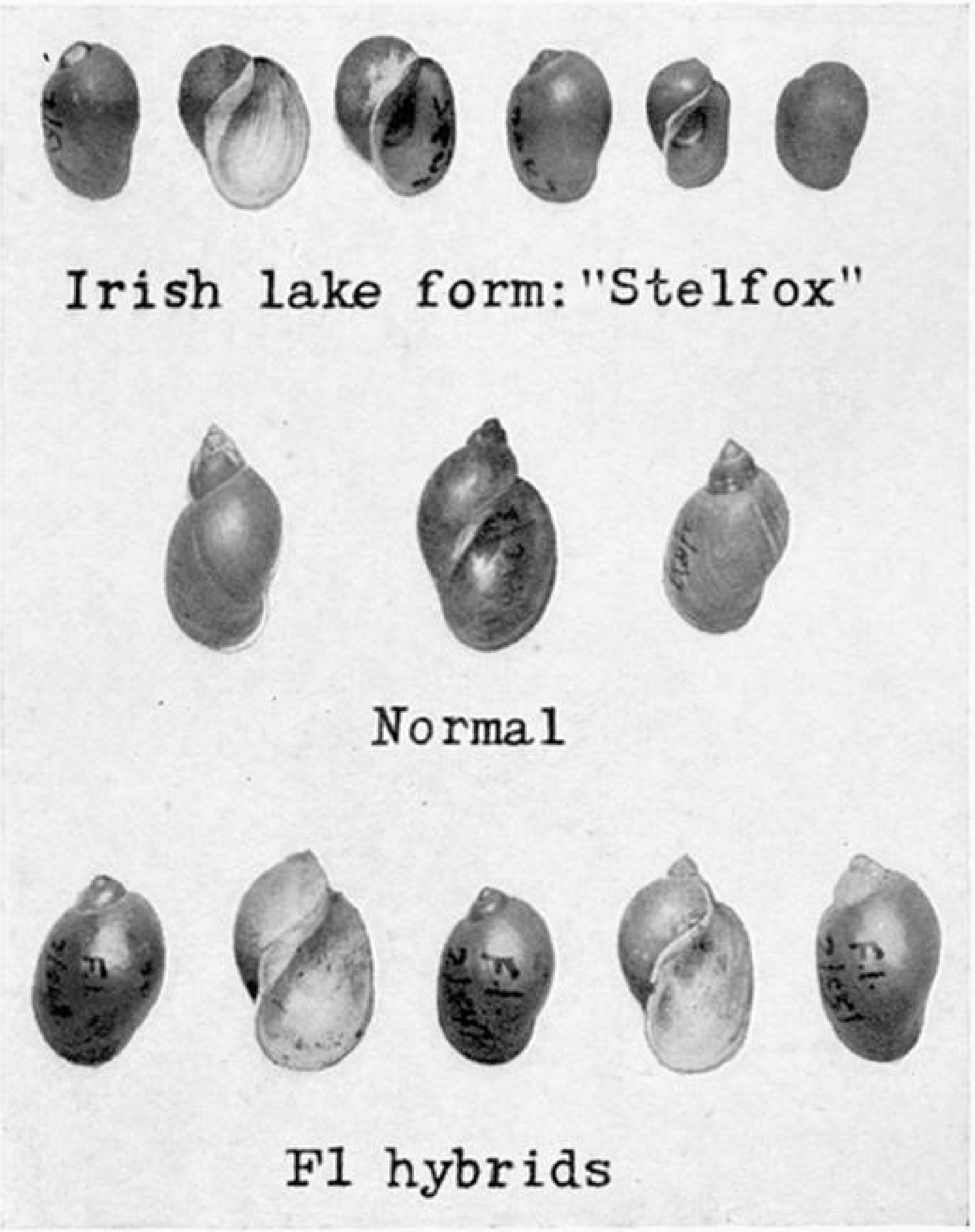


FIG. 9.

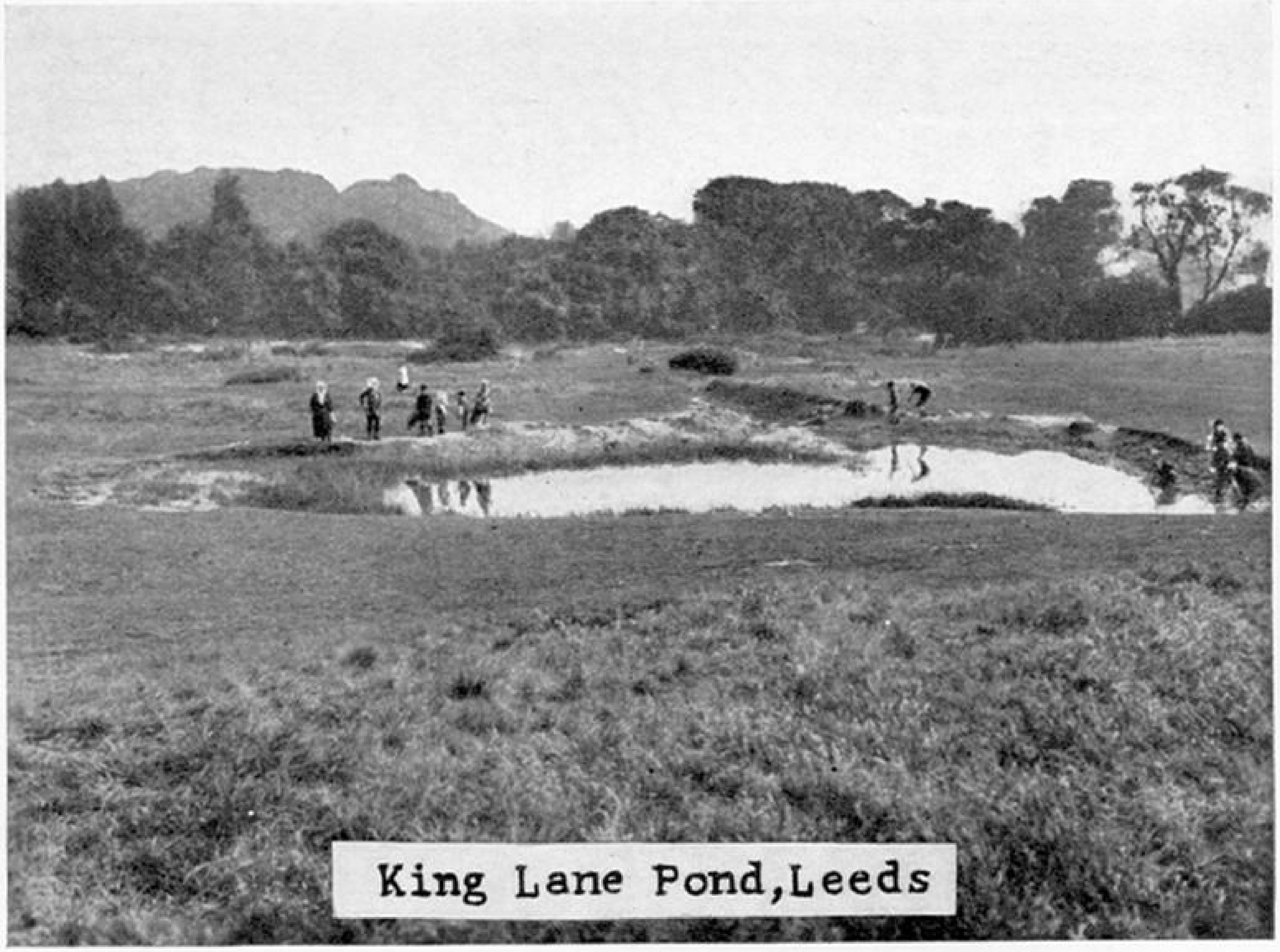


FIG. 10.

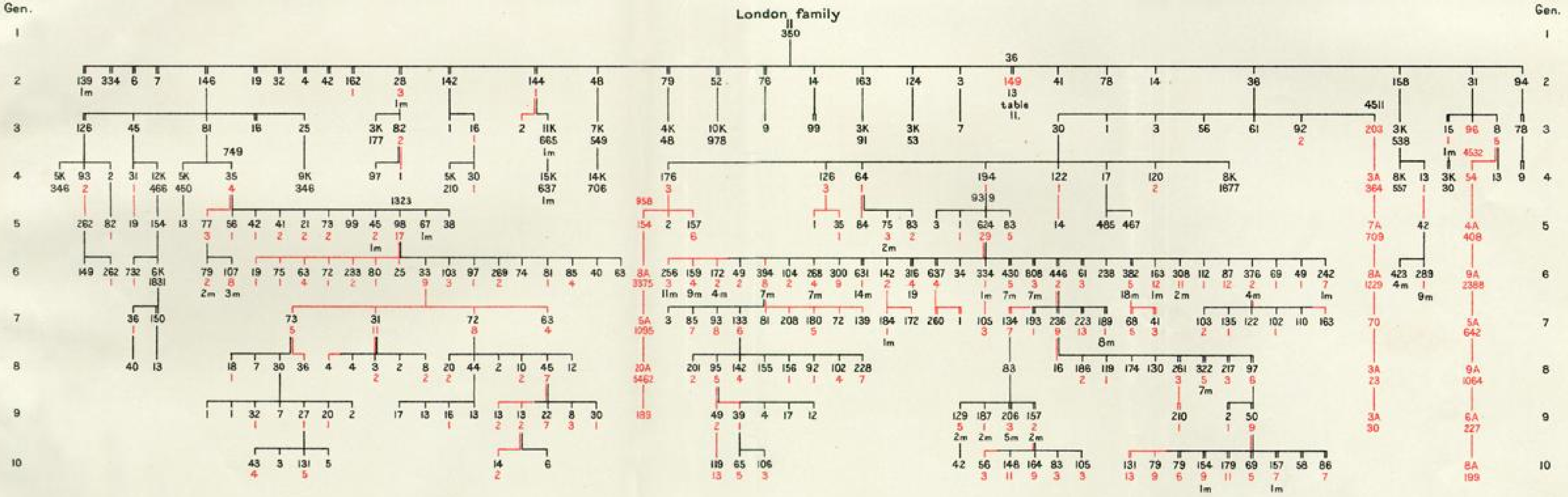
EXPLANATION OF PEDIGREE TABLES.

In the pedigree tables, red—dextral and black—sinistral. Such an entry as

means that a sinistral single gave a brood of 371 dextrals: eight of these were taken on: four singles gave A broods adding up to 903 snails, one gave a K brood of 107 sinistrals, one an E brood of 42 sinistrals, 5 dextrals and 2 monsters, and one pair gave an A brood of 653. The E brood being of particular interest and referred to in the text has its index number (7231) entered above.

※ The total numbers of snails are not entered, where for one reason or another the figures are not comparable with those obtained in "standard" breeding.

TABLE I.

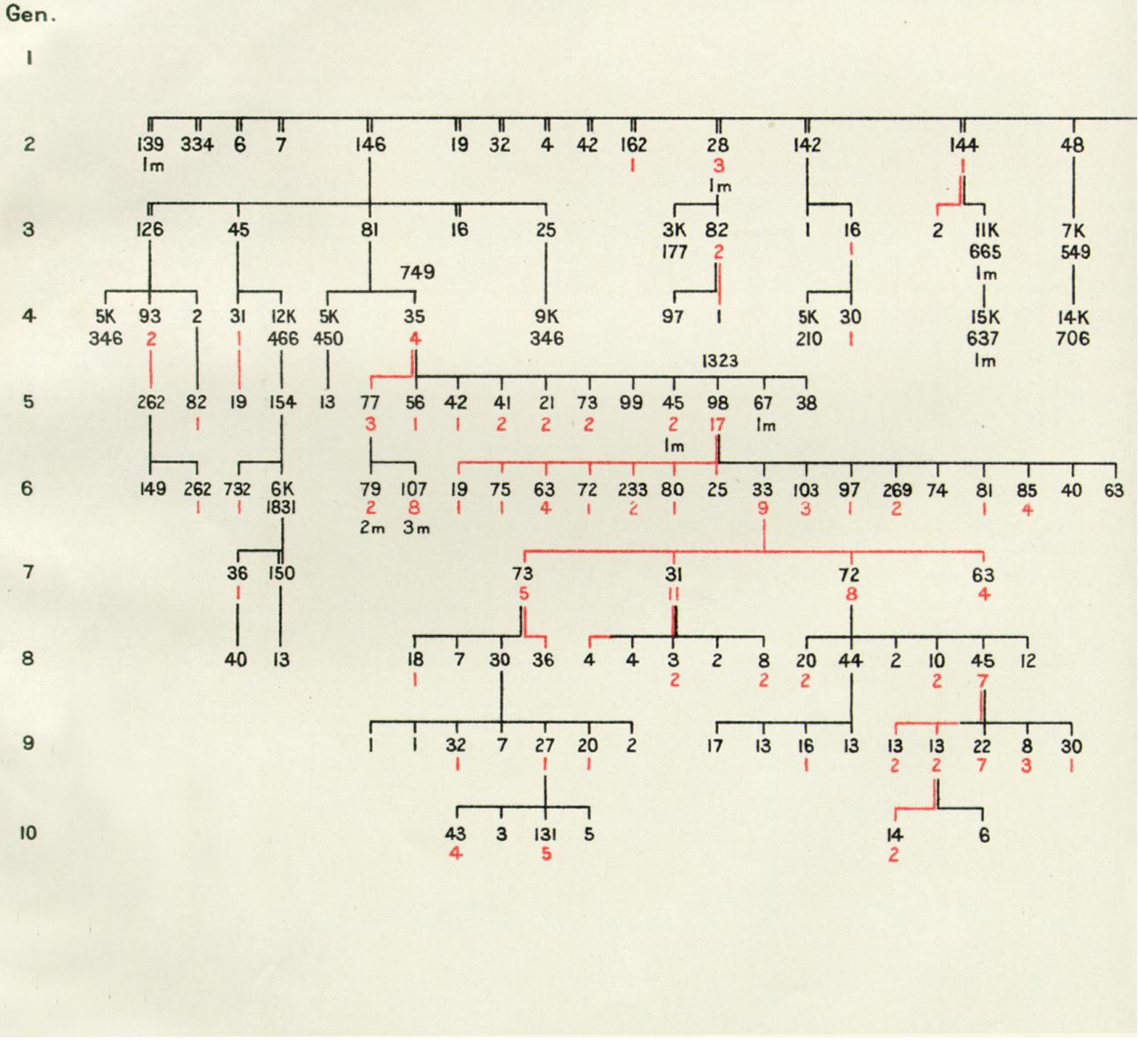


In the pedigree table

means that a sinistral
four singles gave A br
E brood of 42 sinistra
E brood being of part
above.

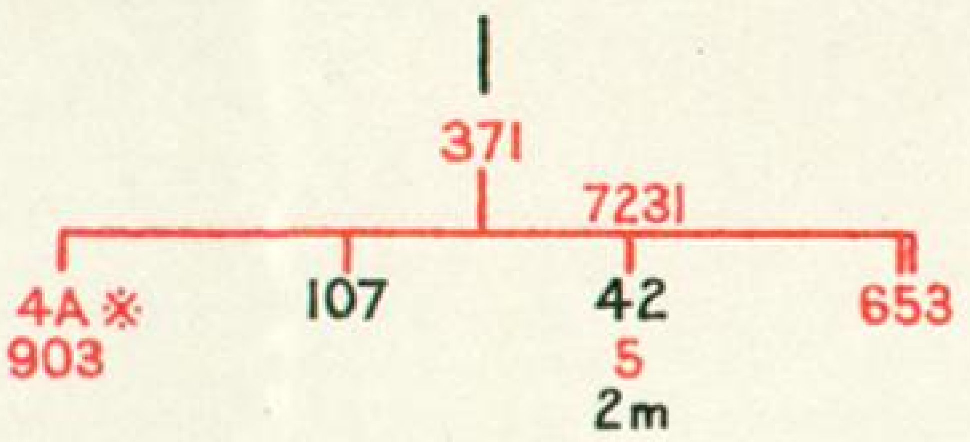
※ The total numbers
comparable with tho

TABLE I.



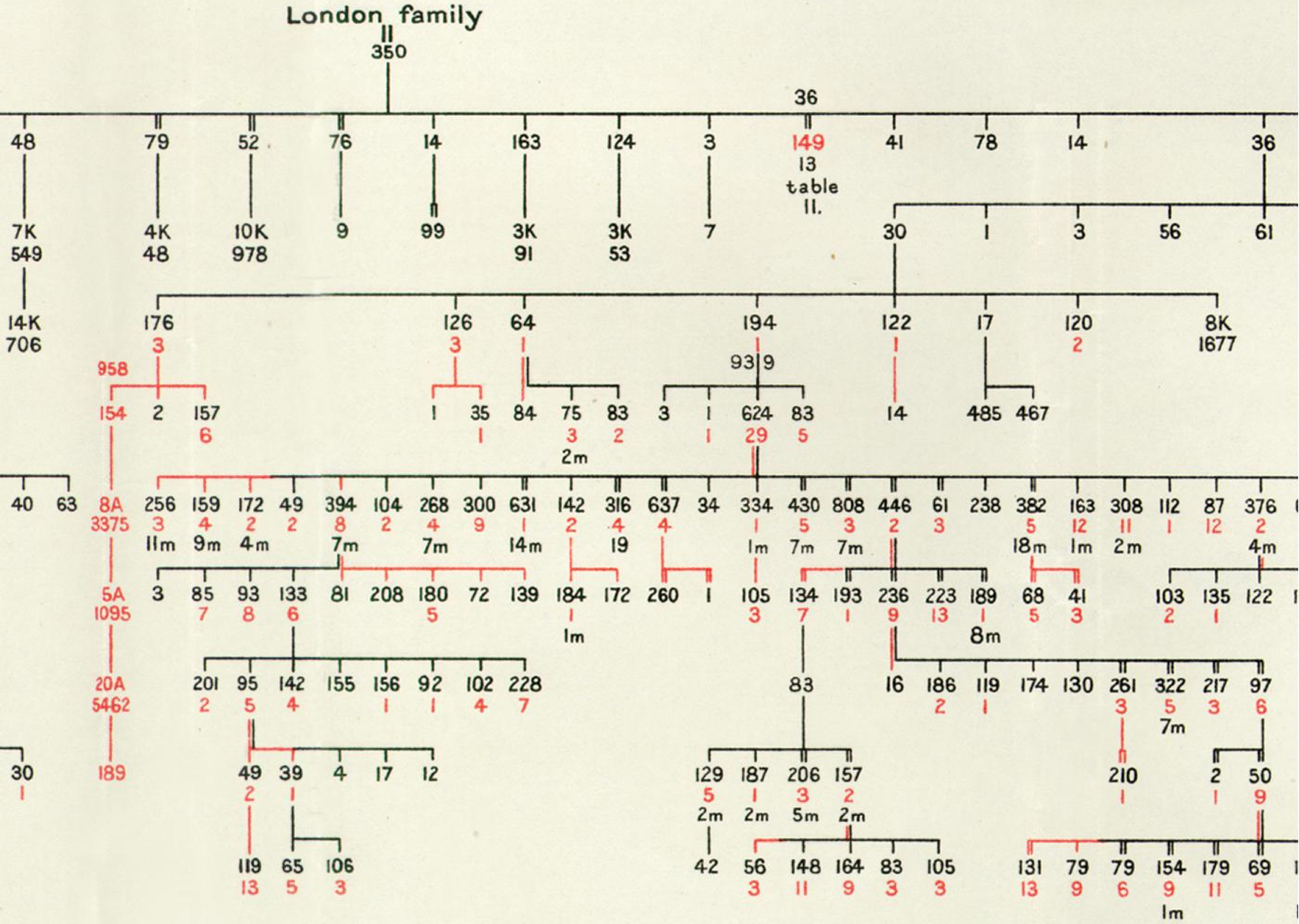
EXPLANATION OF PEDIGREE TABLES.

ee tables, red—dextral and black—sinistral. Such an entry as



sinistral single gave a brood of 371 dextrals: eight of these were taken on:
ave A broods adding up to 903 snails, one gave a K brood of 107 sinistrals, one an
2 sinistrals, 5 dextrals and 2 monsters, and one pair gave an A brood of 653. The
of particular interest and referred to in the text has its index number (7231) entered

umbers of snails are not entered, where for one reason or another the figures are not
with those obtained in "standard" breeding.



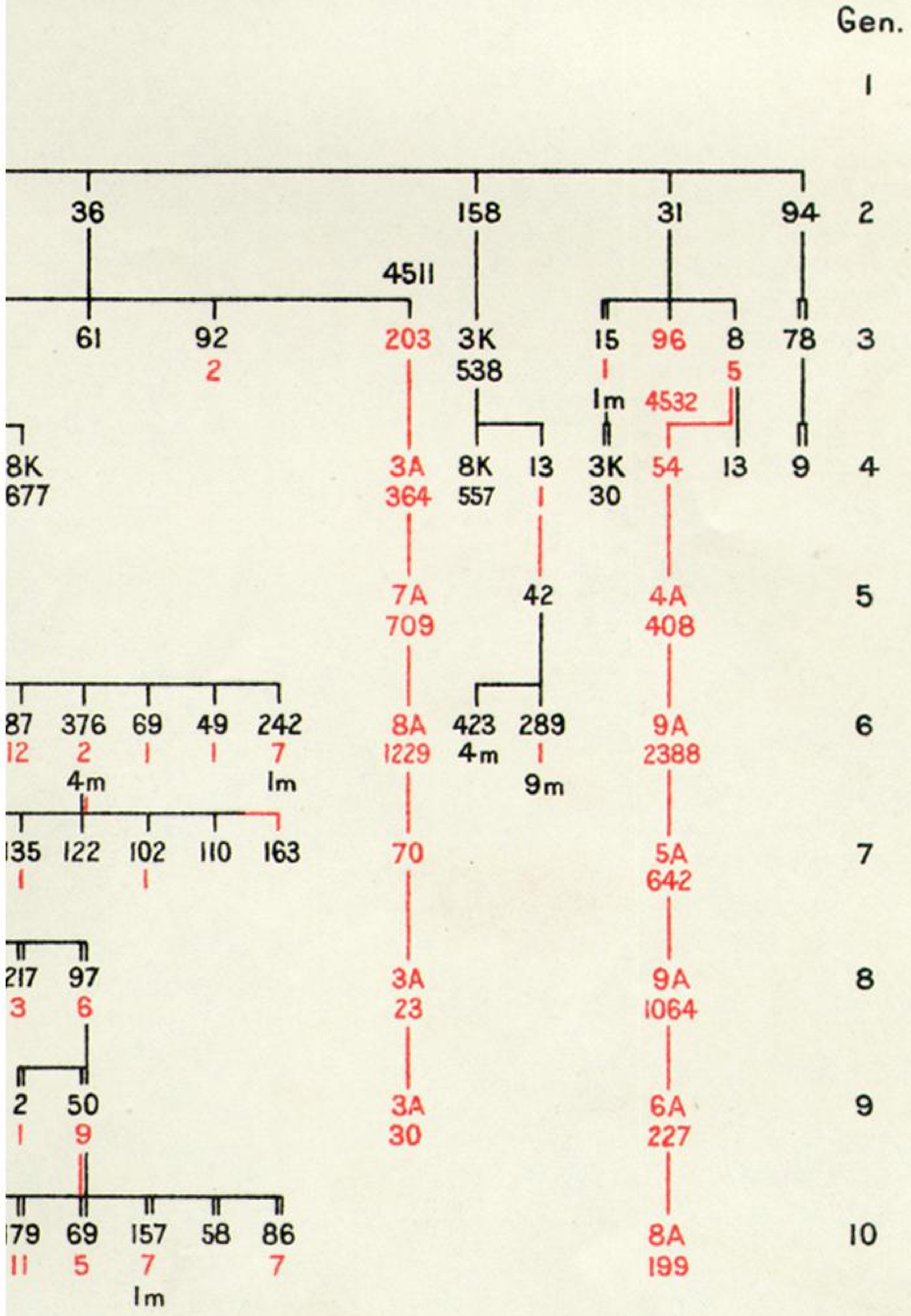
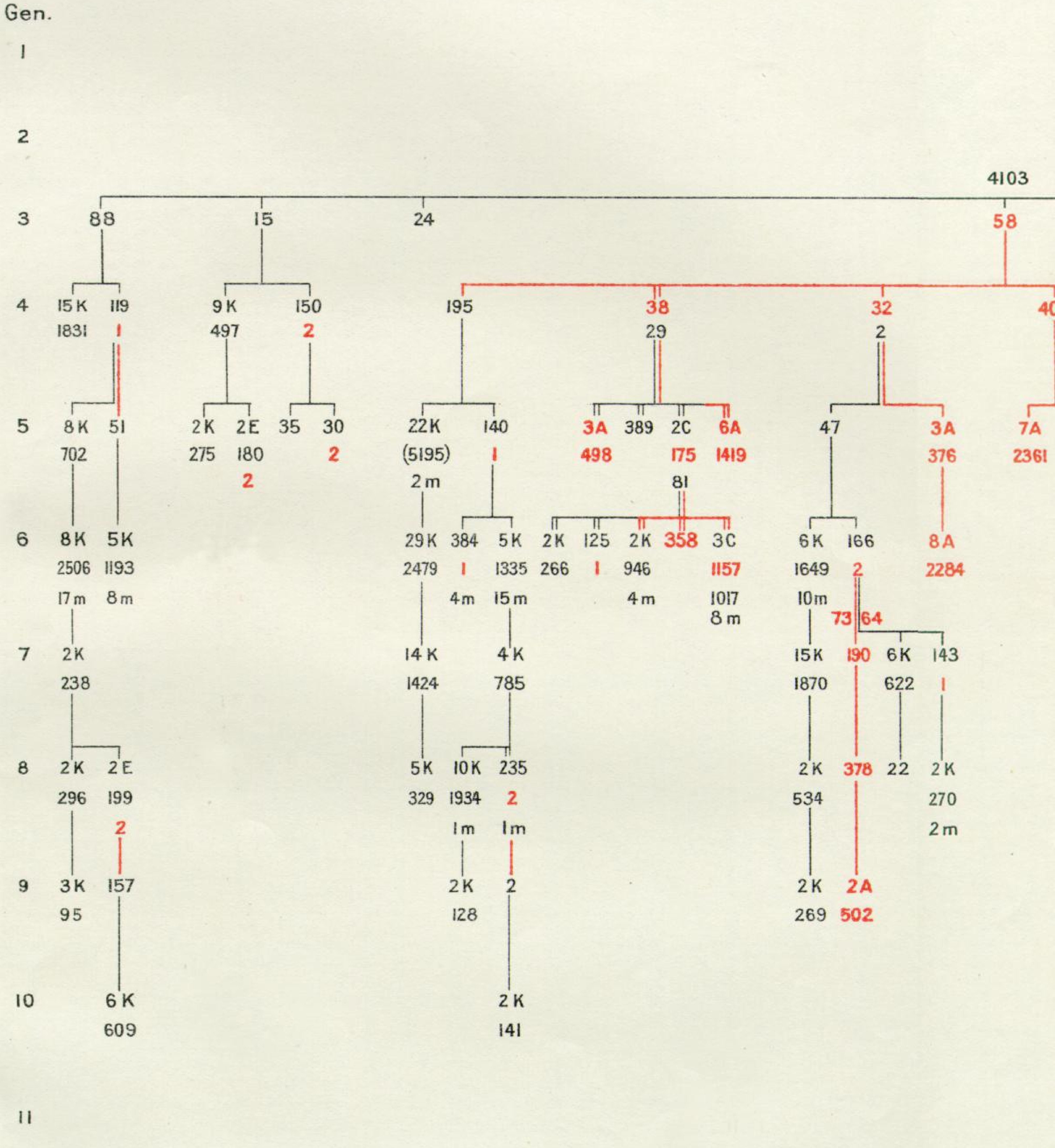

Gen.
1
36
158
31
94
2
4511
61
92
2
203
3K
538
15
96
8
78
3
1
5
Im
4532
8K
677
3A
364
8K
557
13
1
3K
30
54
13
9
4
7A
709
42
4A
408
5
87
12
376
2
4m
69
1
49
1
242
7
Im
8A
1229
423
4m
289
1
9m
9A
2388
6
135
1
122
102
1
110
163
70
5A
642
7
217
3
97
6
3A
23
9A
1064
8
2
1
50
9
3A
30
6A
227
9
179
11
69
5
157
7
Im
58
86
7
8A
199
10

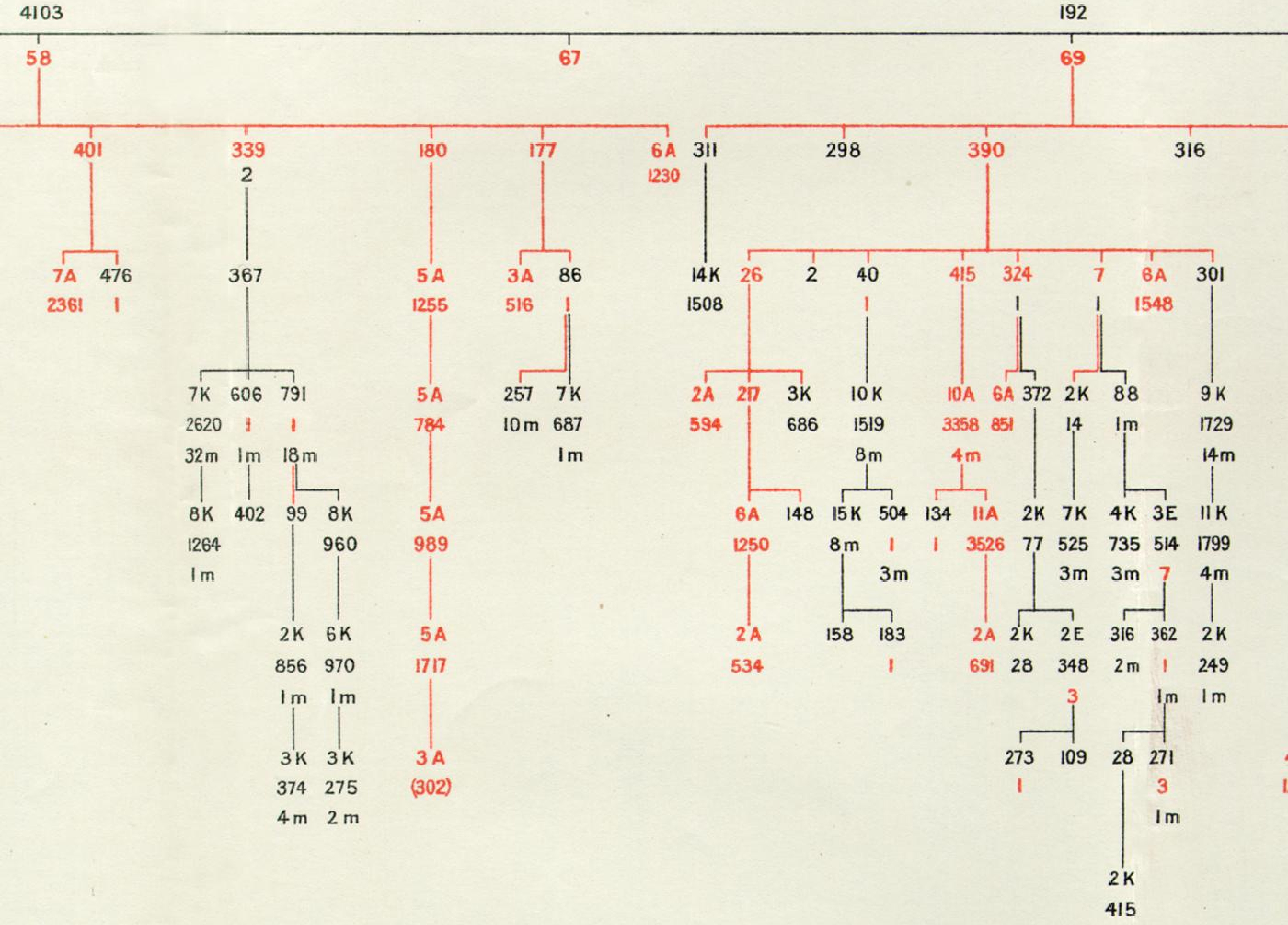
Table II. London family contd Descendants of SP 36.

* albino 1629

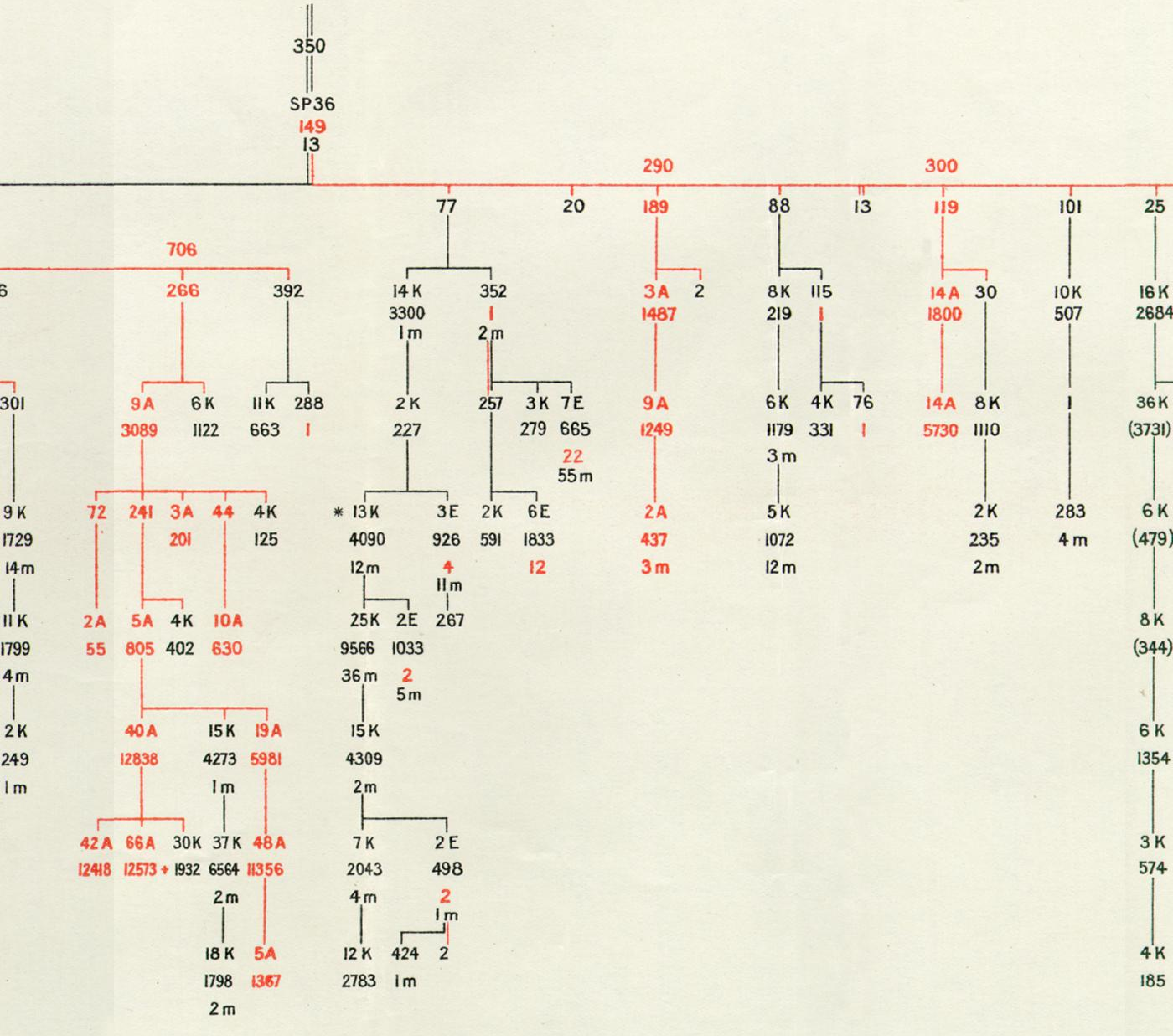
Bracketed numbers are unreliable owing to bad breeding conditions.

Table II. London family cont.^{d} Descendants of S P 36.



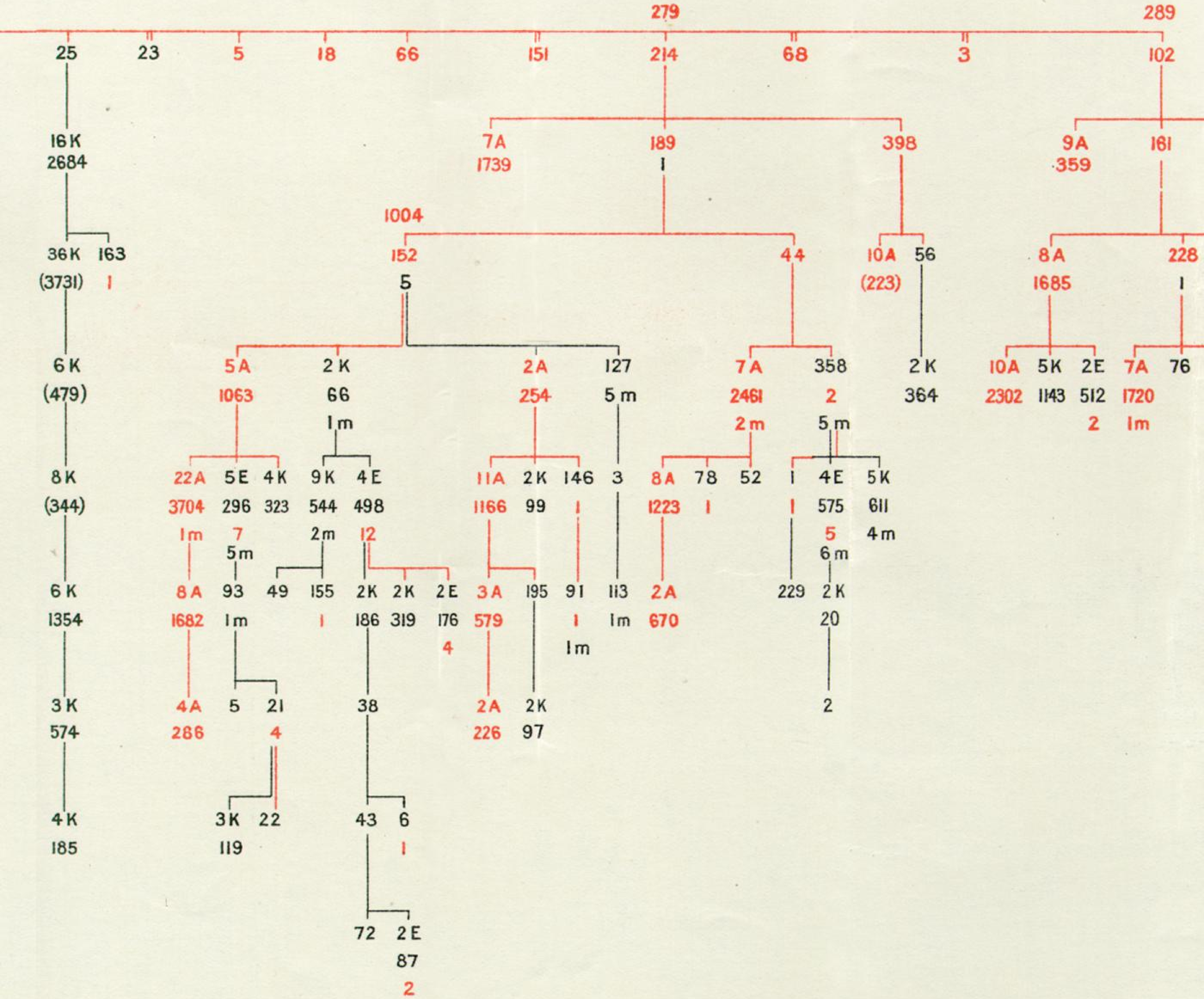

4103
192
58
67
69
401
339
2
180
177
6A
1230
311
298
390
316
7A
2361
476
1
367
5A
1255
3A
516
86
1
14K
1508
26
2
40
1
415
324
1
7
1
6A
1548
301
7K
2620
32m
606
1
1m
791
1
18m
5A
784
257
10m
7K
687
1m
2A
594
217
3K
686
10K
1519
8m
10A
3358
4m
6A
851
372
2K
14
88
1m
9K
1729
14m
8K
1264
1m
402
99
8K
960
5A
989
6A
1250
148
15K
8m
504
1
3m
134
1
11A
3526
2K
77
7K
525
3m
4K
735
3m
3E
514
7
11K
1799
4m
2K
856
1m
6K
970
1m
5A
1717
2A
534
158
183
1
2A
691
2K
28
2E
348
3
316
2m
362
1
1m
2K
249
1m
3K
374
4m
3K
275
2m
3A
(302)
273
1
109
28
271
3
1m
2K
415

Brac
owi



* albino 1629

Bracketed numbers are unreliable
owing to bad breeding conditions.


279
289
25
23
5
18
66
151
214
68
3
102
16K
2684
7A
1739
189
1
398
9A
359
161
1004
36K
(3731)
163
1
152
5
44
10A
(223)
56
8A
1685
228
1
6K
(479)
5A
1063
2K
66
1m
2A
254
127
5m
7A
2461
2m
358
2
5m
2K
364
10A
2302
5K
1143
2E
512
2
7A
1720
1m
76
8K
(344)
22A
3704
1m
5E
296
7
5m
4K
323
9K
544
2m
4E
498
12
11A
1166
2K
99
146
1
3
8A
1223
78
1
52
1
1
4E
575
5
6m
5K
611
4m
6K
1354
8A
1682
93
1m
49
155
1
2K
186
2K
319
2E
176
4
3A
579
195
91
1
1m
113
1m
2A
670
229
2K
20
3K
574
4A
286
5
21
4
38
2A
226
2K
97
2
4K
185
3K
119
22
43
6
1
72
2E
87
2

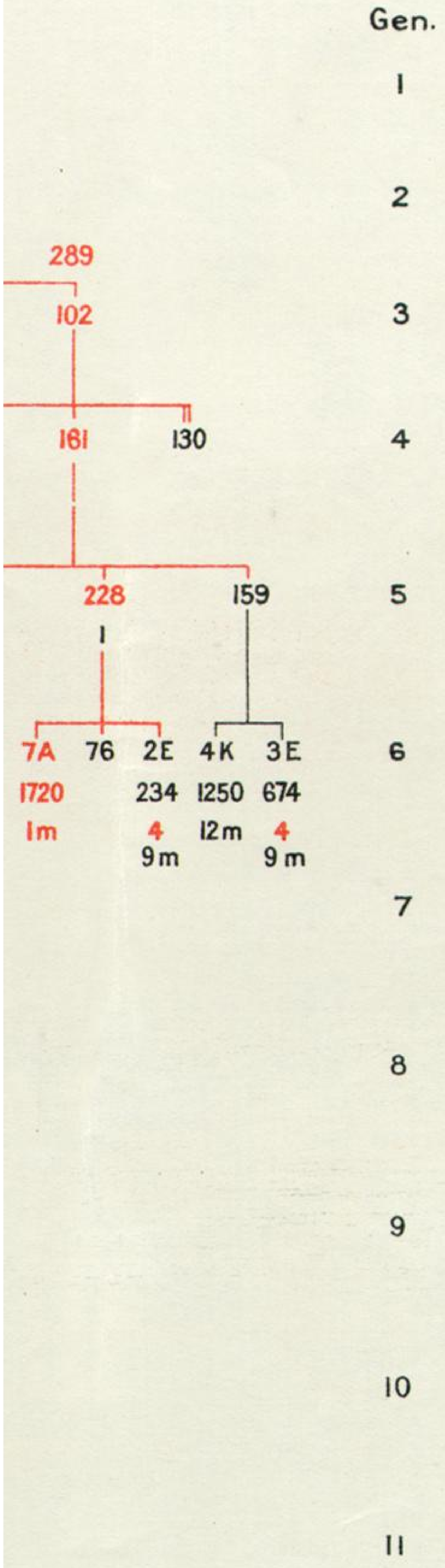
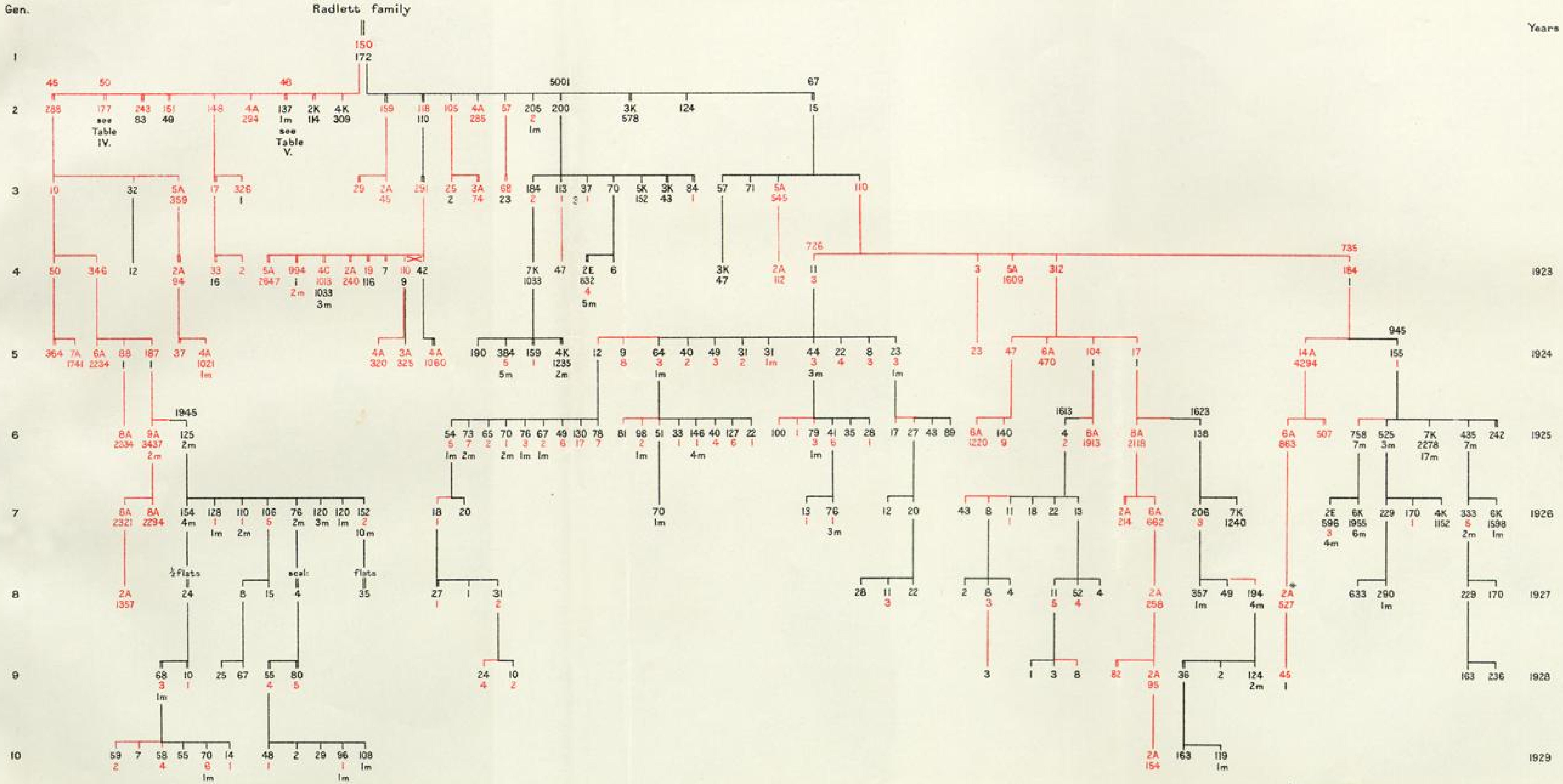
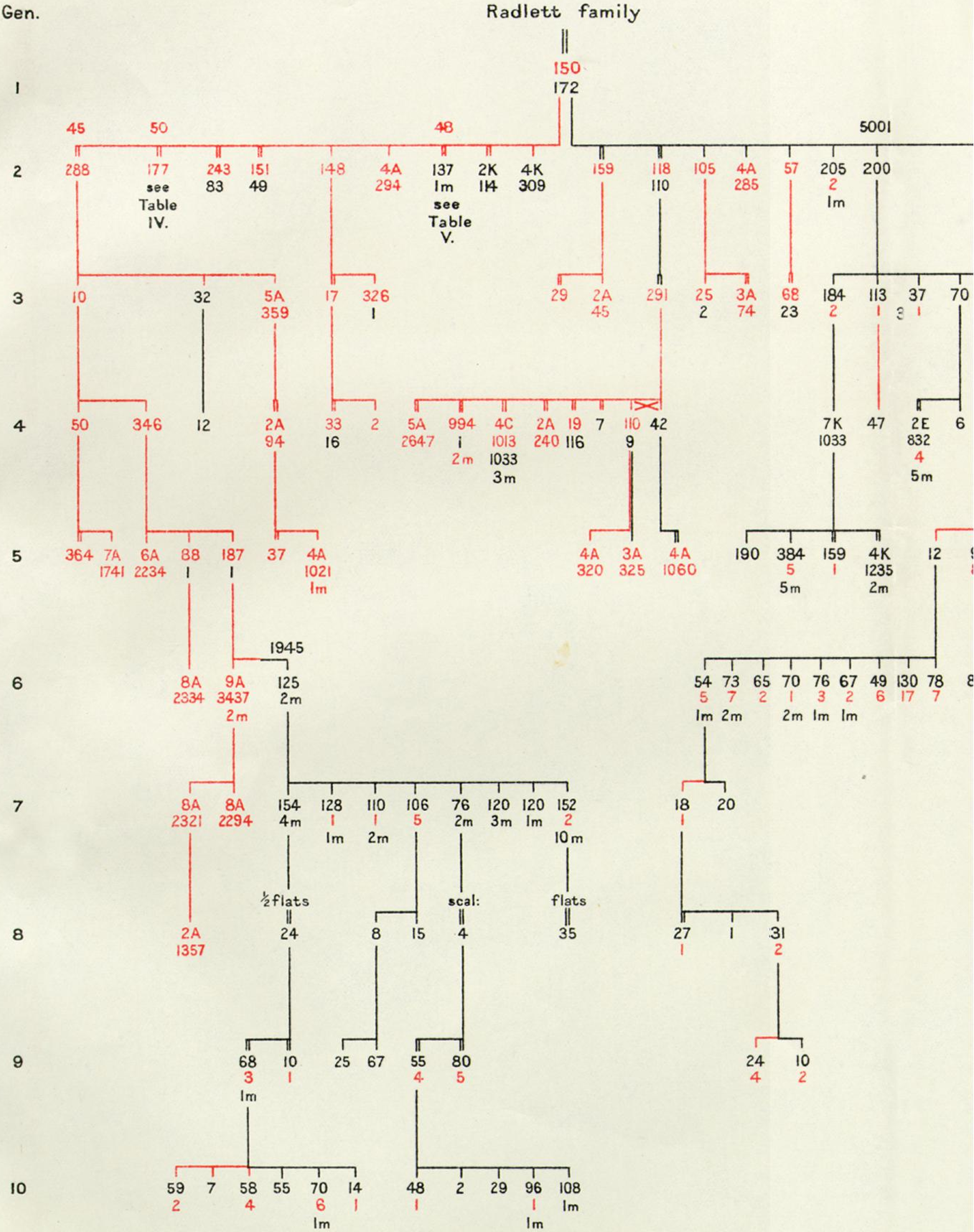

Gen.
1
2
289
3
102
161
130
4
228
159
5
1
7A
76
2E
4K
3E
6
1720
234
1250
674
1m
4
9m
12m
4
9m
7
8
9
10
11

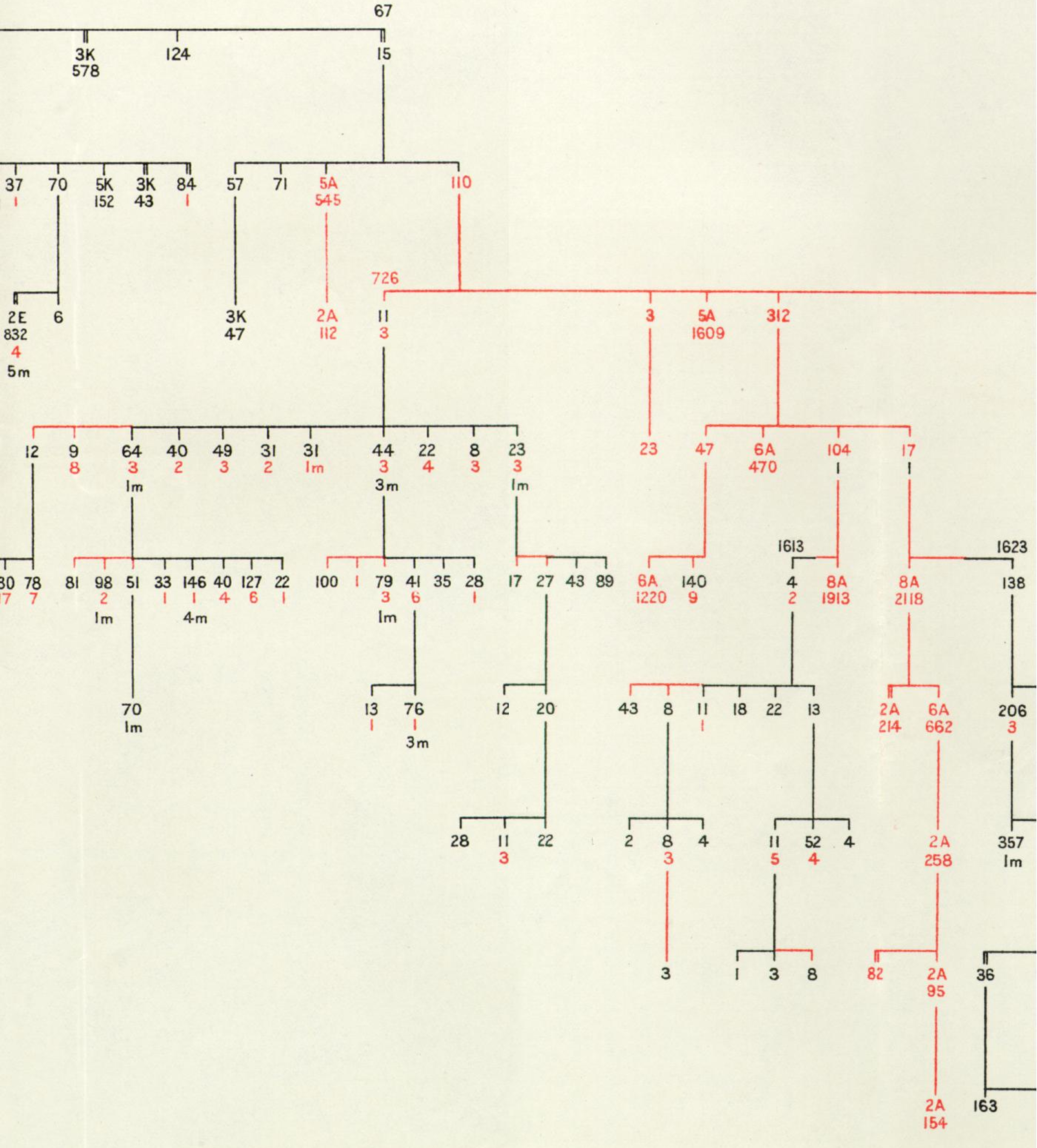
TABLE III.

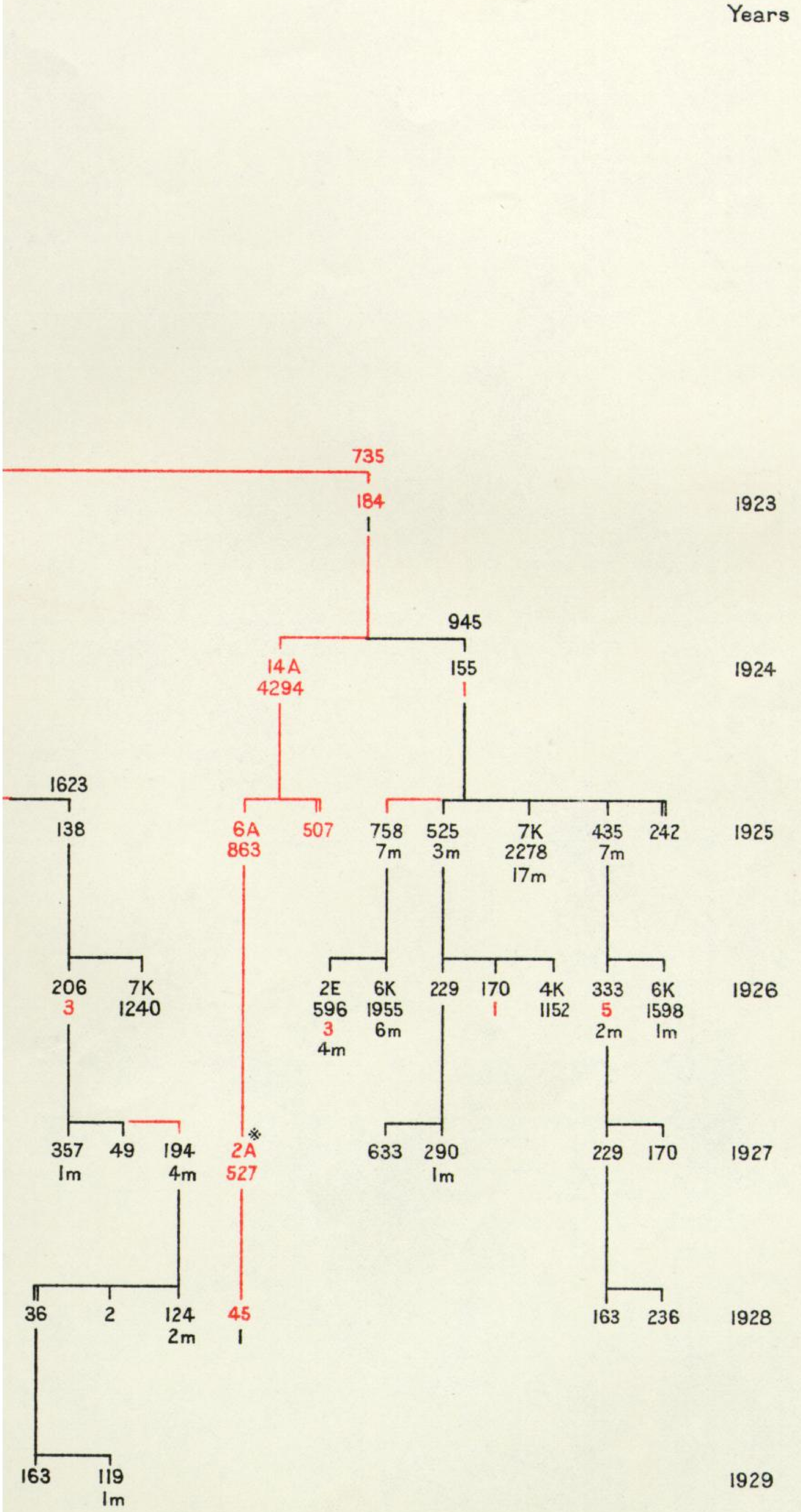


* Delayed a year

TABLE III.

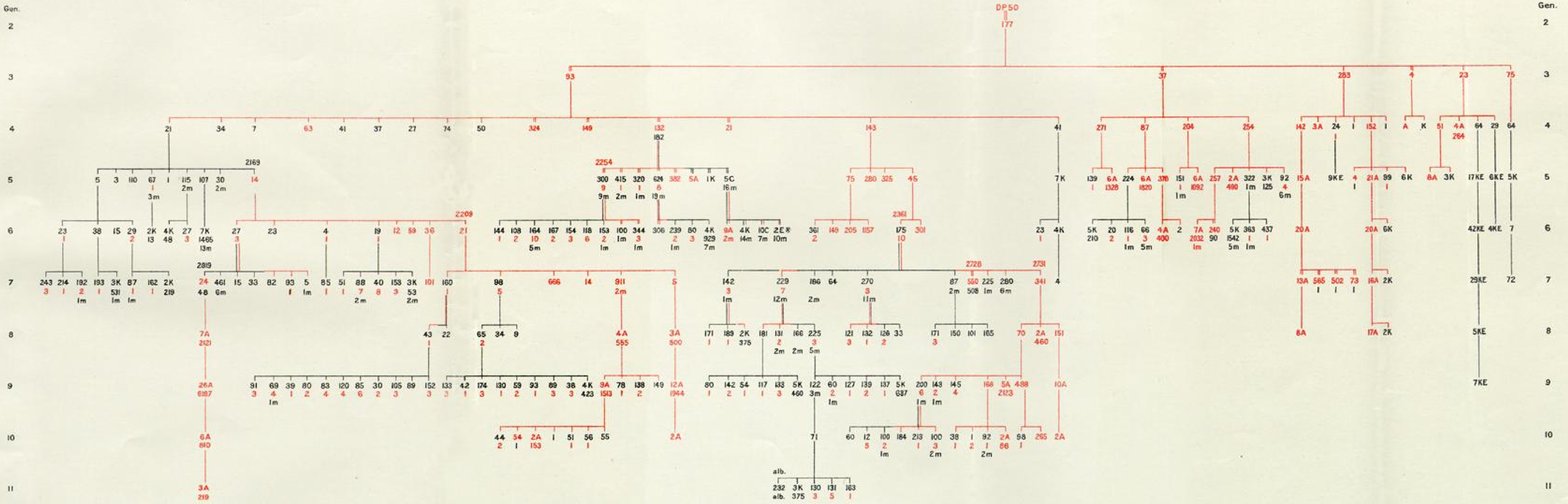

Gen.
Radlett family
1
150
172
45
50
48
5001
2
288
177 see Table IV.
243 83
151 49
148
4A 294
137 1m see Table V.
2K 114
4K 309
159
118 110
105
4A 285
57
205 2 1m
200
3
10
32
5A 359
17
326 1
29
2A 45
291
25 2
3A 74
68 23
184 2
113 1
37 1
70
4
50
346
12
2A 94
33 16
2
5A 2647
994 i 2m
4C 1013 1033 3m
2A 240
19 116
7
110
9
42
7K 1033
47
2E 832 4 5m
6
5
364
7A 1741
6A 2234
88 1
187 1
37
4A 1021 1m
4A 320
3A 325
4A 1060
190
384 5 5m
159 1
4K 1235 2m
12
6
1945
8A 2334
9A 3437 2m
125 2m
54 5 1m
73 7 2m
65 2
70 1 2m
76 3 1m
67 2 1m
49 6
130 17
78 7
7
8A 2321
8A 2294
154 4m
128 1 1m
110 1 2m
106 5
76 2m
120 3m
120 1m
152 2 10m
18 1
20
½ flats
scal:
flats
8
2A 1357
24
8
15
4
35
27 1
1
31 2
9
68 3 1m
10 1
25
67
55 4
80 5
24 4
10 2
10
59 2
7
58 4
55
70 6 1m
14 1
48 1
2
29
96 1 1m
108 1m


67
3K 578
124
15
37 1
70
5K 152
3K 43
84 1
57
71
5A 545
110
726
2E 832 4 5m
6
3K 47
2A 112
11 3
3
5A 1609
312
12
9 8
64 3 1m
40 2
49 3
31 2
31 1m
44 3 3m
22 4
8 3
23 3 1m
23
47
6A 470
104 1
17 1
1613
1623
30 17
78 7
81
98 2 1m
51
33 1
146 1
4m
40 4
127 6
22 1
100
1
79 3 1m
41 6
35
28 1
17
27
43
89
6A 1220
140 9
4 2
8A 1913
8A 2118
138
70 1m
13 1
76 1 3m
12
20
43
8
11 1
18
22
13
2A 214
6A 662
206 3
28
11 3
22
2
8 3
4
11 5
52 4
4
2A 258
357 1m
3
1
3
8
82
2A 95
36
2A 154
163



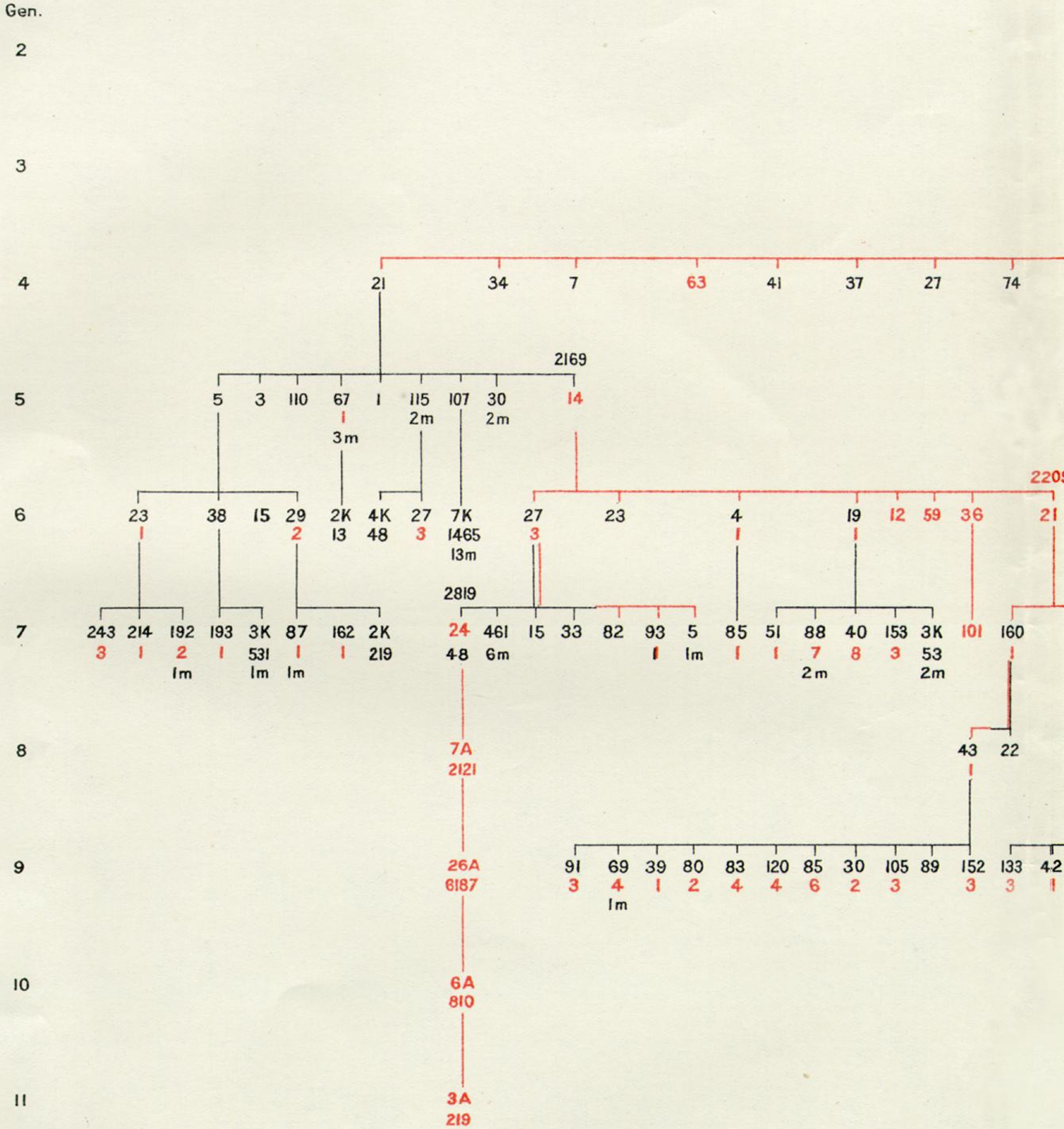
※ Delayed a year

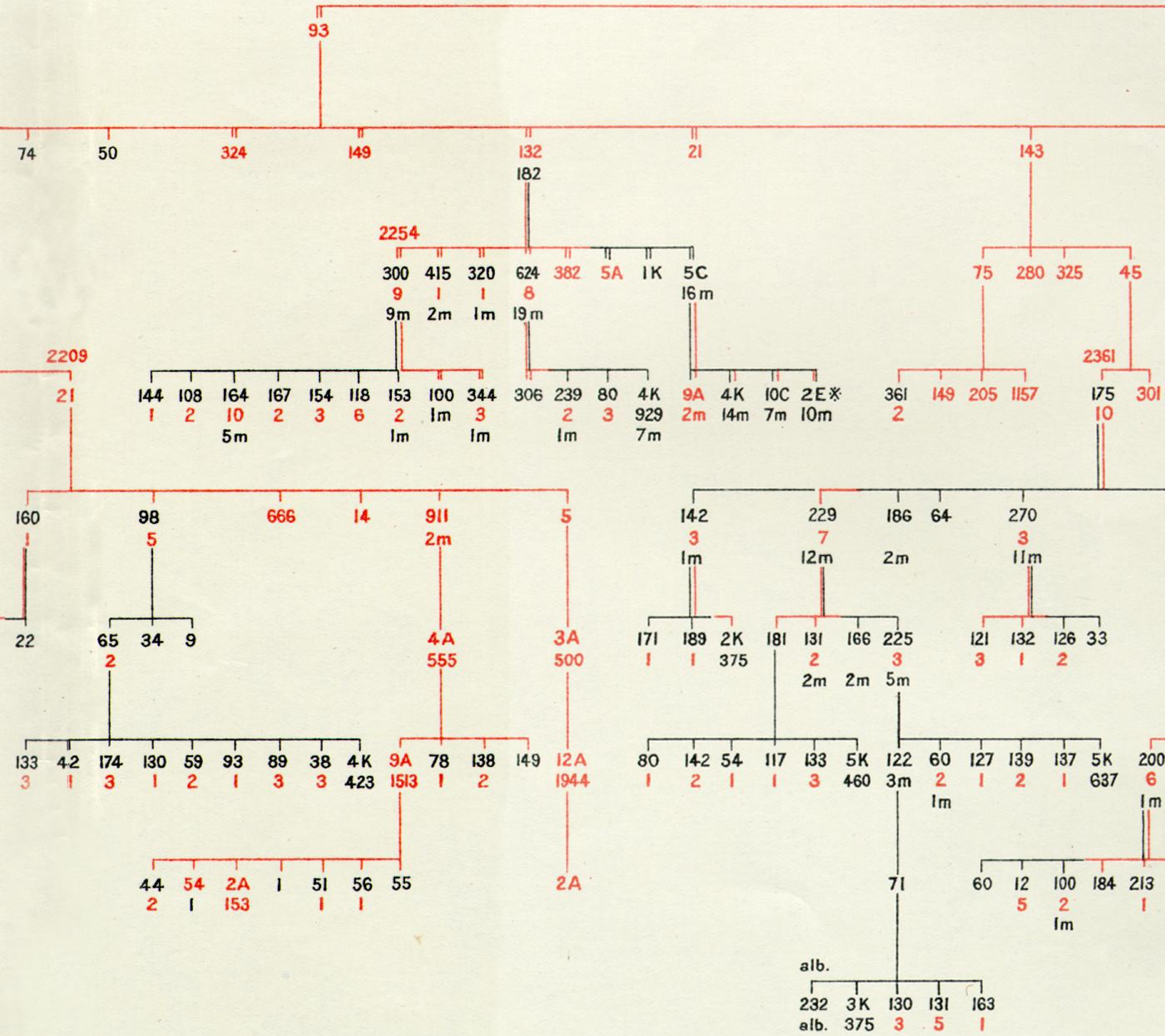
Table IV. Radlett family cont^d Descendants of D P 50.



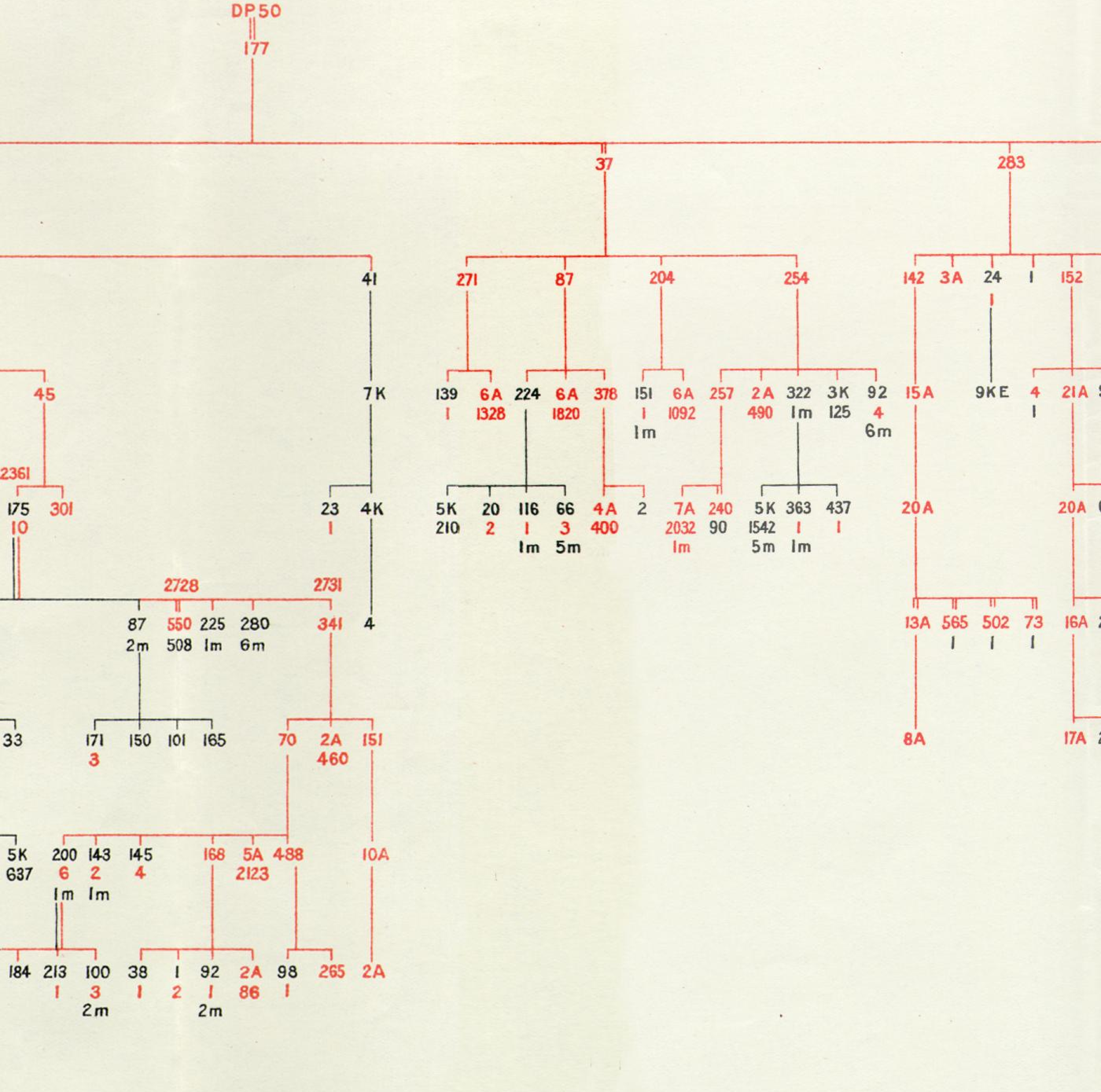
※ This indicates that the products of dextral pairs and sinistral pairs have been added together.

Table IV. Radlett family cont^{d} Descendants of D P 50.





※ This indicates that the products of dextral pairs and sinistral pairs have been added together.



tral pairs
ether.

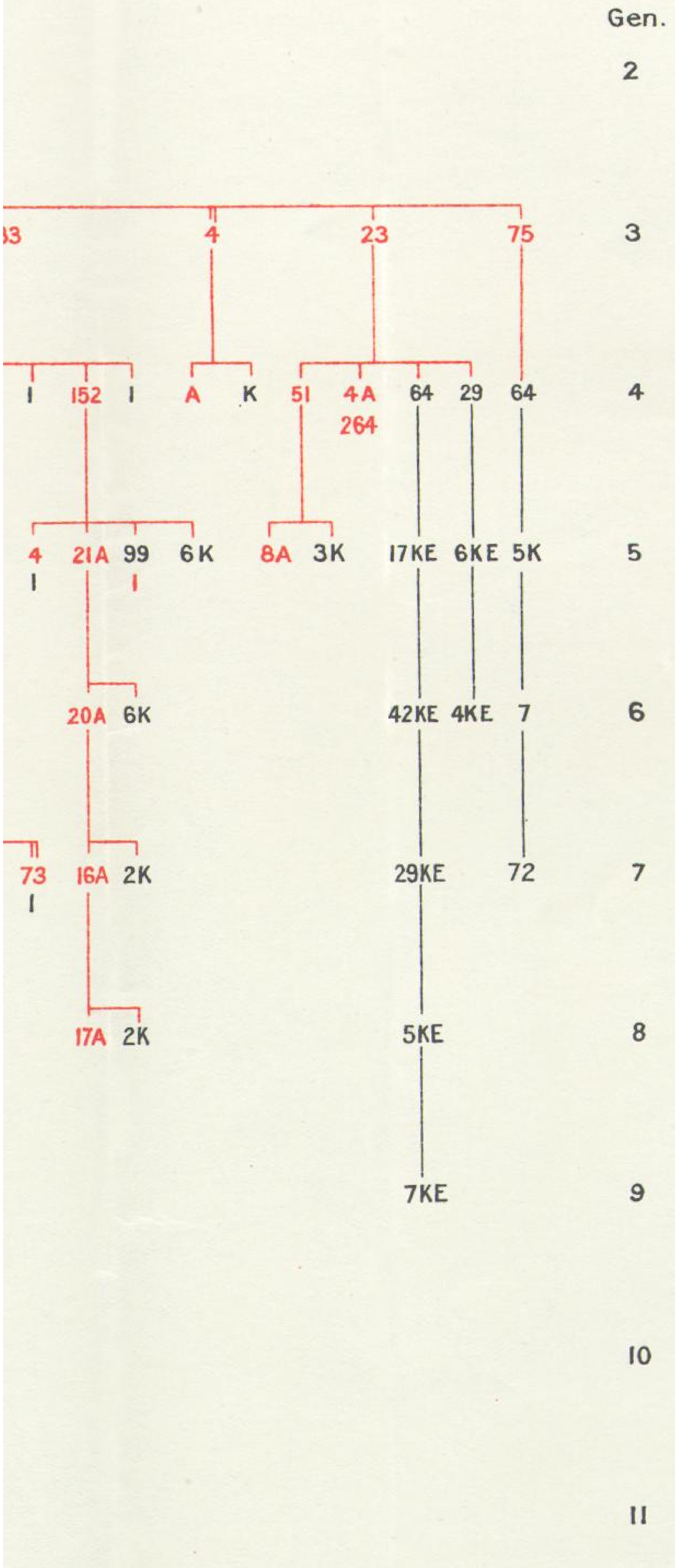

Gen.
2
33
4
23
75
3
I
152
I
A
K
51
4A
264
64
29
64
4
4
I
21A
99
I
6K
8A
3K
17KE
6KE
5K
5
20A
6K
42KE
4KE
7
6
73
I
16A
2K
29KE
72
7
17A
2K
5KE
8
7KE
9
10
11

TABLE V. Radlett family cont.d Descendants of D P 48

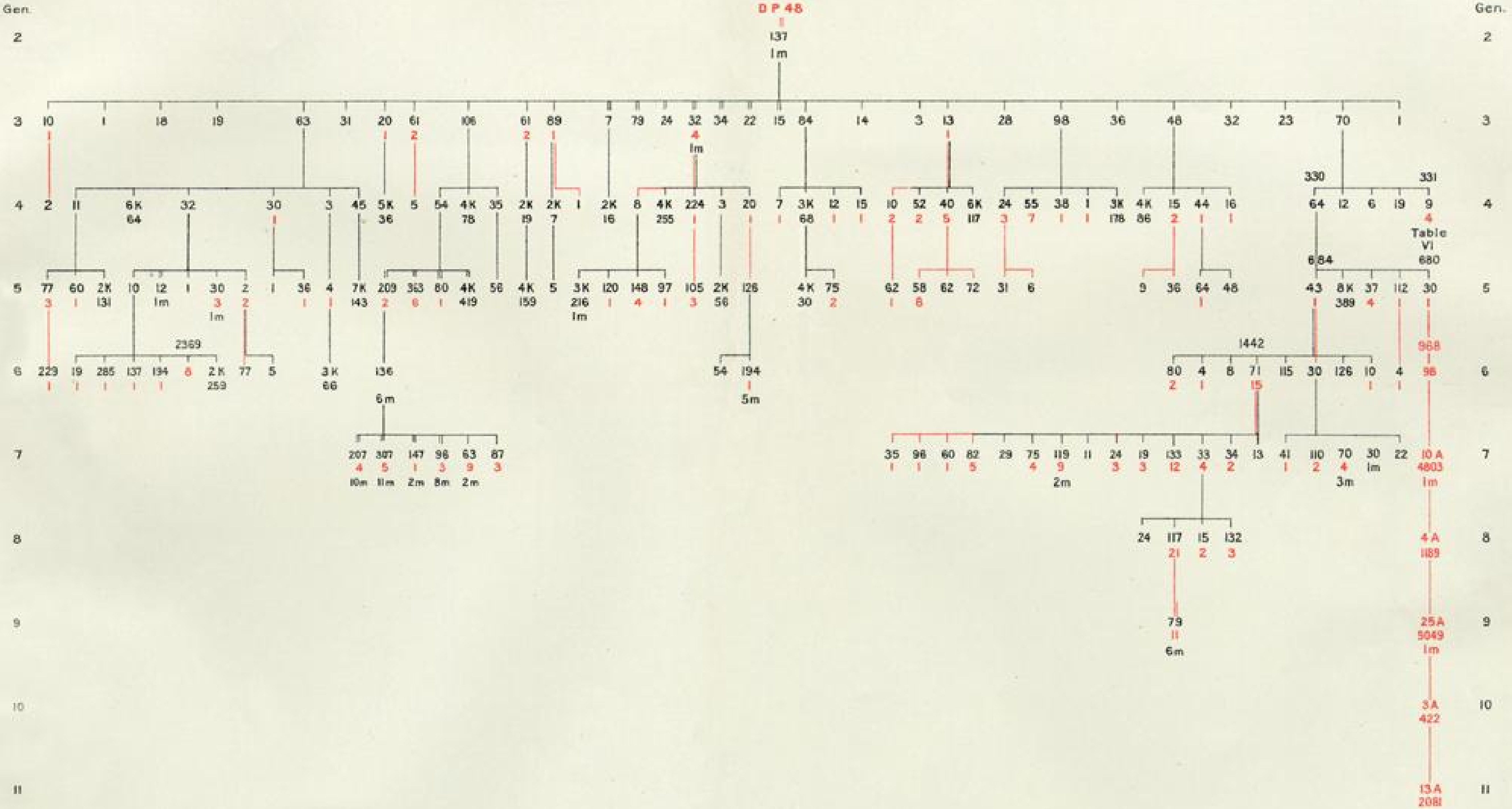
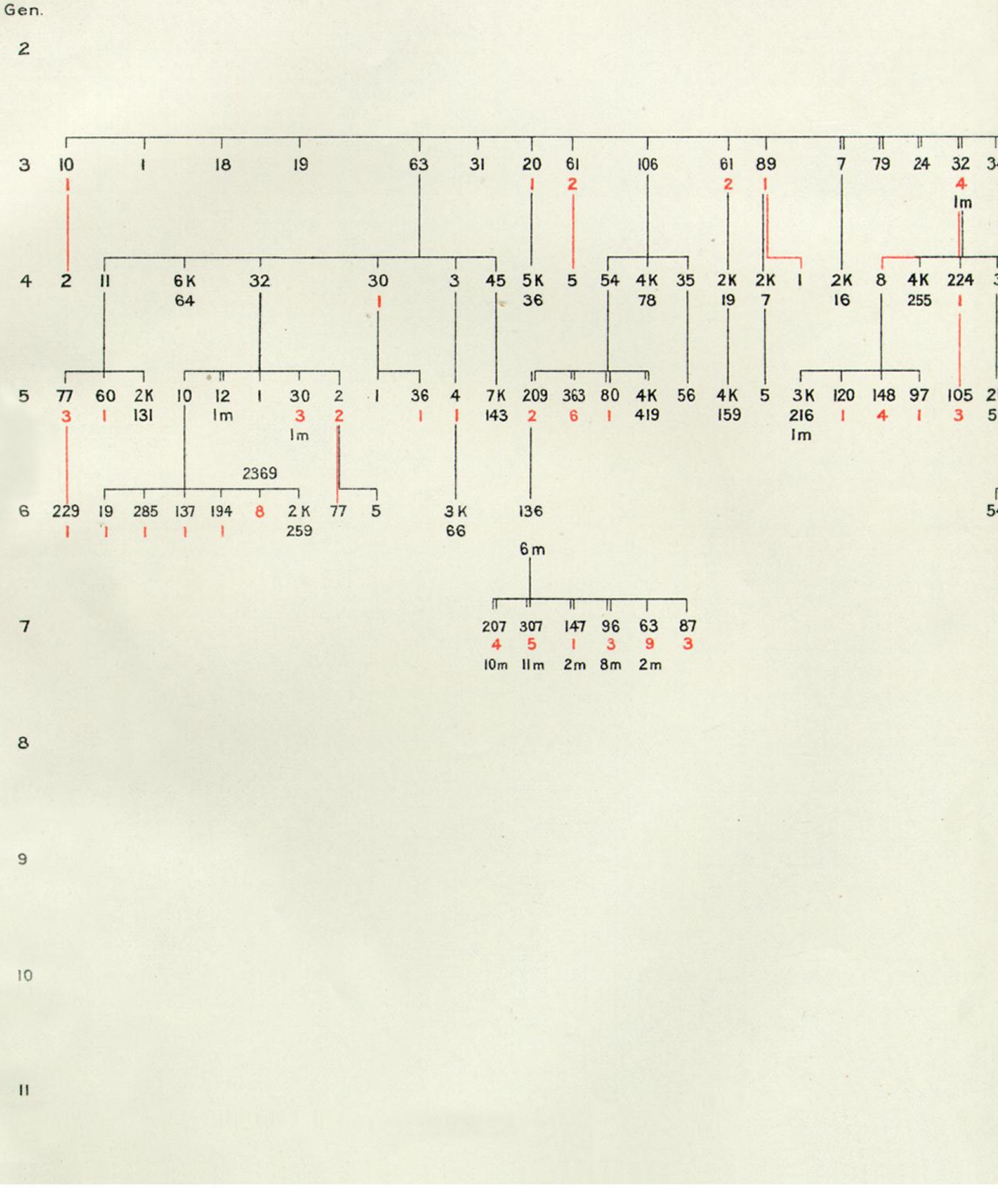
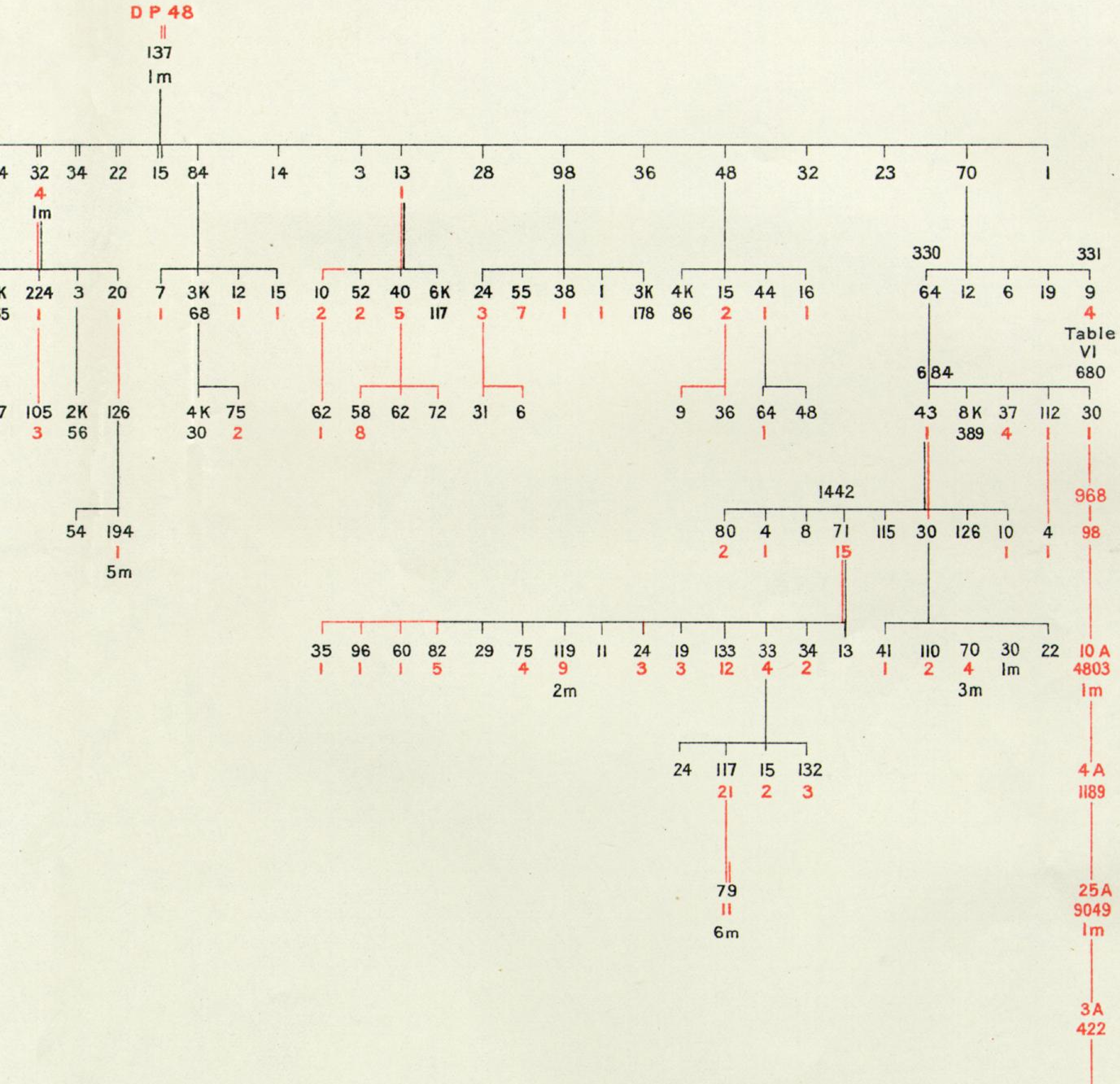


TABLE V. Radlett family contd. Descendants of D P 48





D P 48
11
137
1m
4 32 34 22 15 84 14 3 13 28 98 36 48 32 23 70 1
4
1m
1
330
331
K 224 3 20 7 3K 12 15 10 52 40 6K 24 55 38 1 3K 4K 15 44 16 64 12 6 19 9
35 1 1 1 68 1 1 2 2 5 117 3 7 1 1 178 86 2 1 1
4
Table
VI
684
680
7 105 2K 126 4K 75 62 58 62 72 31 6 9 36 64 48 43 8K 37 112 30
3 56 30 2 1 8 1 1 389 4 1 1
1442
968
54 194 80 4 8 71 115 30 126 10 4 98
1 2 1 15 1 1
5m
35 96 60 82 29 75 119 11 24 19 133 33 34 13 41 110 70 30 22 10 A
1 1 1 5 4 9 3 3 12 4 2 1 2 4 1m 4803
2m
3m
1m
24 117 15 132 4 A
21 2 3 1189
79
11
6m
25 A
9049
1m
3 A
422
13 A
2081

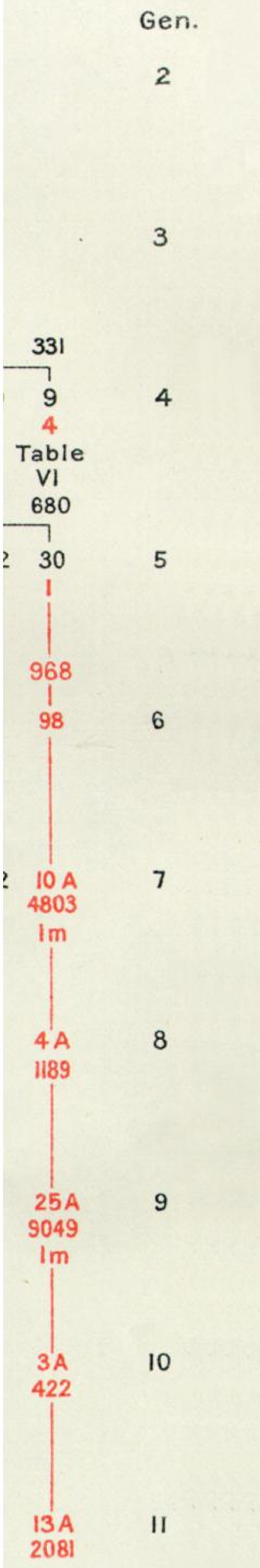

Gen.
2
3
331
9
4
4
Table
VI
680
30
5
1
968
98
6
10 A
4803
Im
7
4 A
1189
8
25A
9049
Im
9
3A
422
10
13A
2081
11

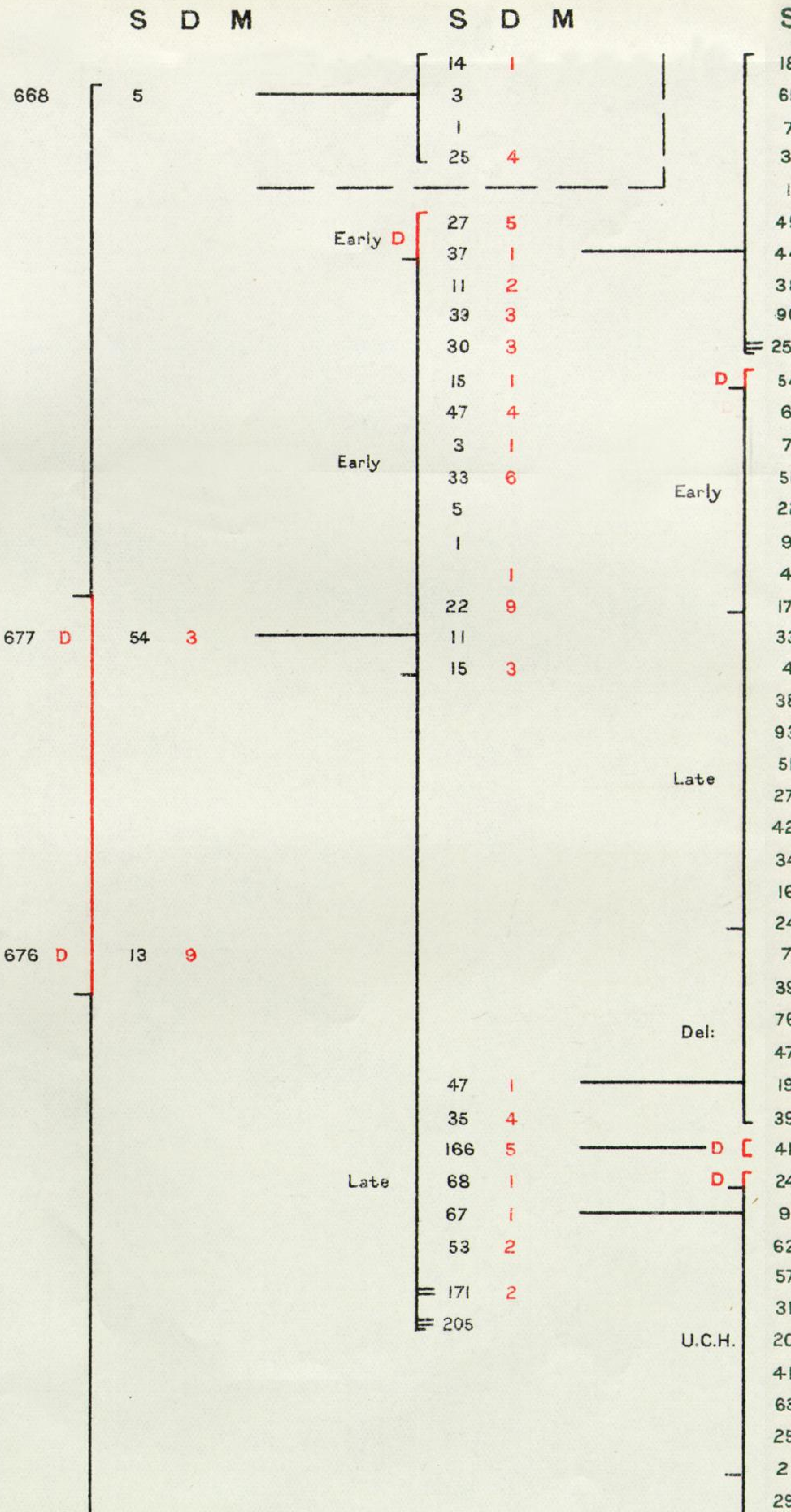
TABLE VI. Radlett family. E strains from 331.

EXPLANATION

S = sinistrals.
D = dextrals.
M = monsters.
Early = planted out early in the year.
Late = planted out late in the year.
Del. = delayed for one year.
Accel. = two generations in oneyear.
S.L.G. = bred at Leeds.
Mert. = bred at Merton.
S.E.H. = bred at South Eastern Hospital.
P.Sq. = bred at Pembroke Square.
Rad. = bred at Radlett.
U.C.H. = bred at University College Hospital Medical School.

TABLE VI. Radlett family. E strains from 331.

GENERATIONS 5 6



S = sinistrals
D = dextrals.
M = monsters.
Early = planted out e
Late = planted out l
Del. = delayed for o
Accel. = two generatio
S.L.G. = bred at Leeds
Mert. = bred at Mert
S.E.H. = bred at Sout
P. Sq. = bred at Pemb
Rad. = bred at Radle
U.C.H. = bred at Unive

10 11 12

D M S D M S D M

EXPLANATION

als

ls.

ers.

d out early in the year.

d out late in the year.

for one year.

nerations in oneyear.

t Leeds.

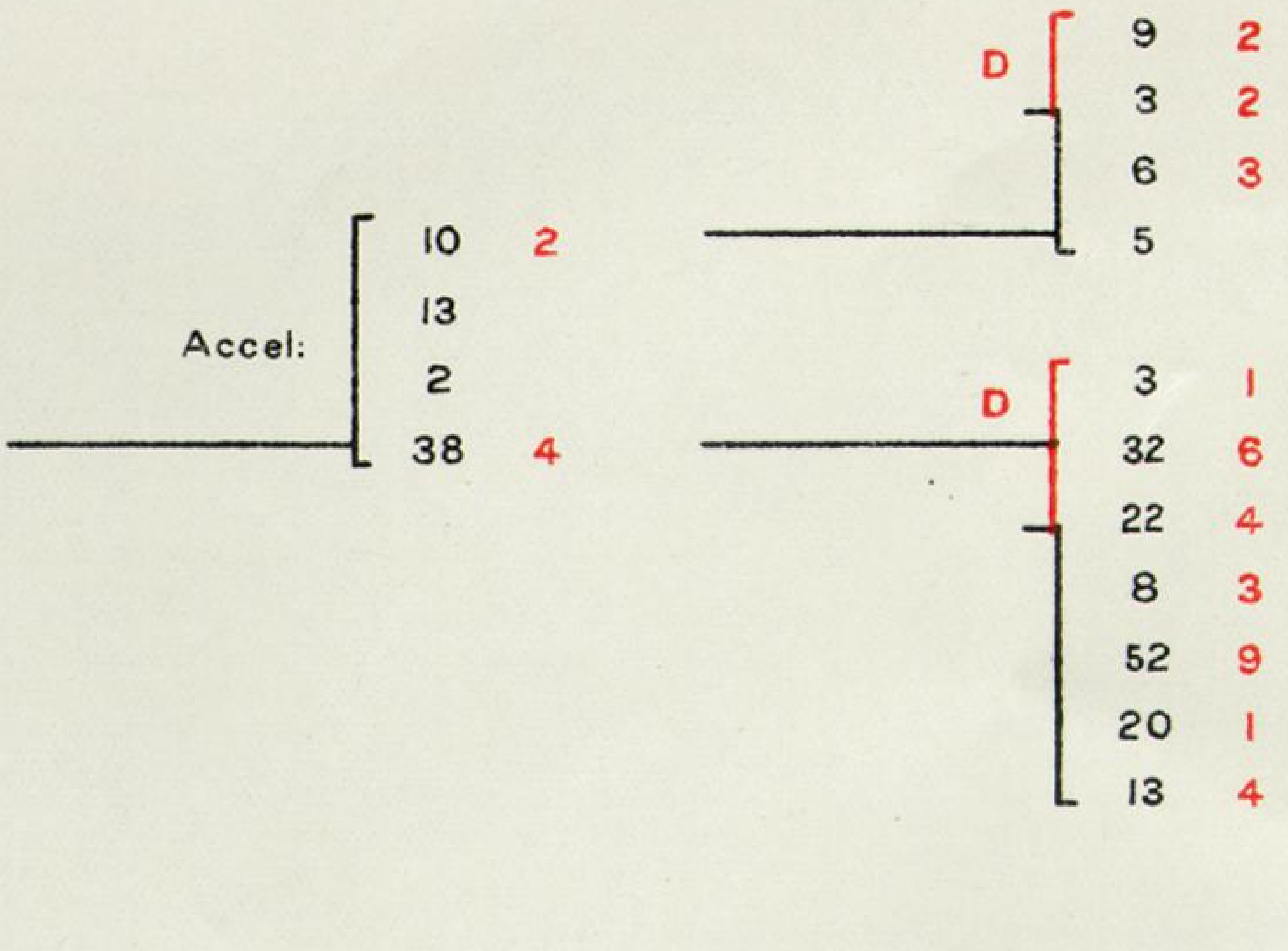
t Merton.

t South Eastern Hospital.

t Pembroke Square.

t Radlett.

t University College Hospital Medical School.




Rad:
D
S.L.G.
S.L.G.
34 3
42 1
6
32 3
9
19
4
667
12 1
S.L.G.
Early D
7 2
11 3
Early
10 4
14 5
7 4
2
D
Mert:
S.E.H.
671
20 4
D
Del:
49 5 1
Late
71 9
43 5
P. Sq.
Early D
61 21
Late D
5
Early


25
2 1
29 1 2
77 8
18 3
15 1
62 4
15 1
8 1
D 5 4
19 1
7
27 2
65 7
14
62 2
20 1
27 1
D 2
17
9
21 1
30
79 5
58 9
D 31 2
41 3
38 3
101 3 1
99 6 1
91 6 2
49 1
42 2
45 14 1
D 5 1
107 18
41 1
68 3
50 8
54
35 2
38 4
13 1
95 14 1
25 10
94 14 2
76 16 3
14 1 1
105 3
37 1
85 5
D 6 1
67 5
D 47 1
D 40 3
77 19
36 12
56
D 39 5
61 3
47 4
107 22
D 23 1
32 3
14 1
1 M 4
D 4
10 1
D 7 4
112 12

D [32 7
2
38 2
97 2
73 19
9

1
3
1

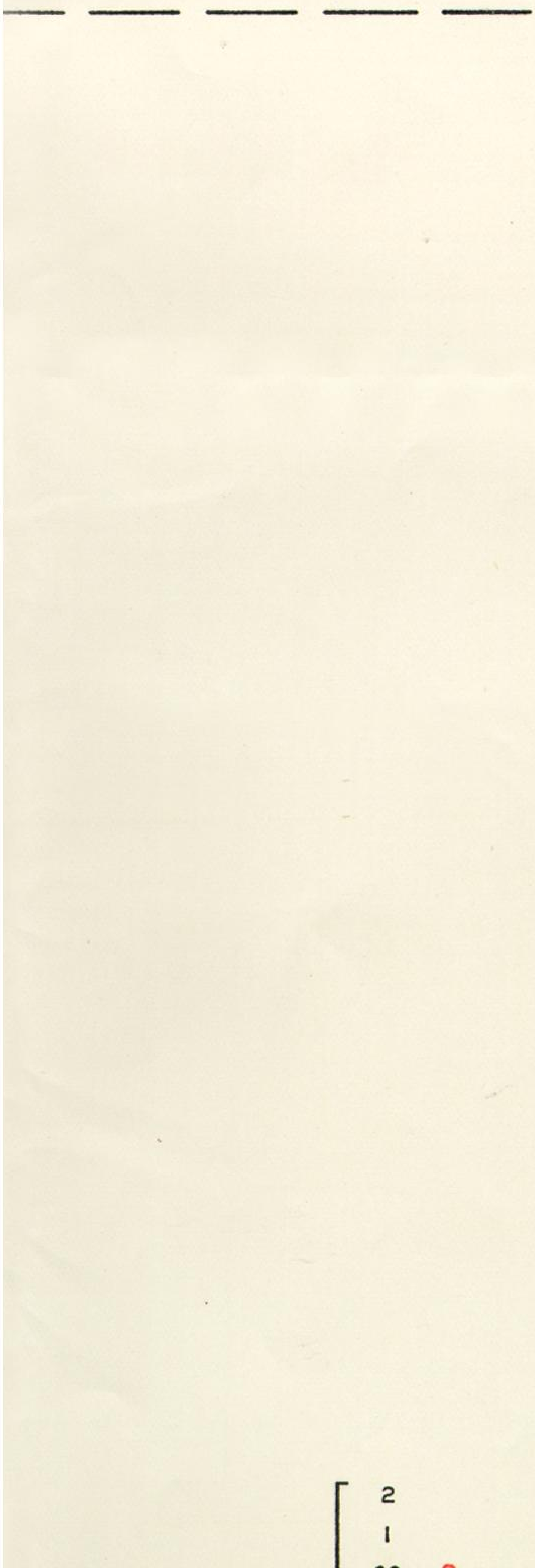
1
4
12

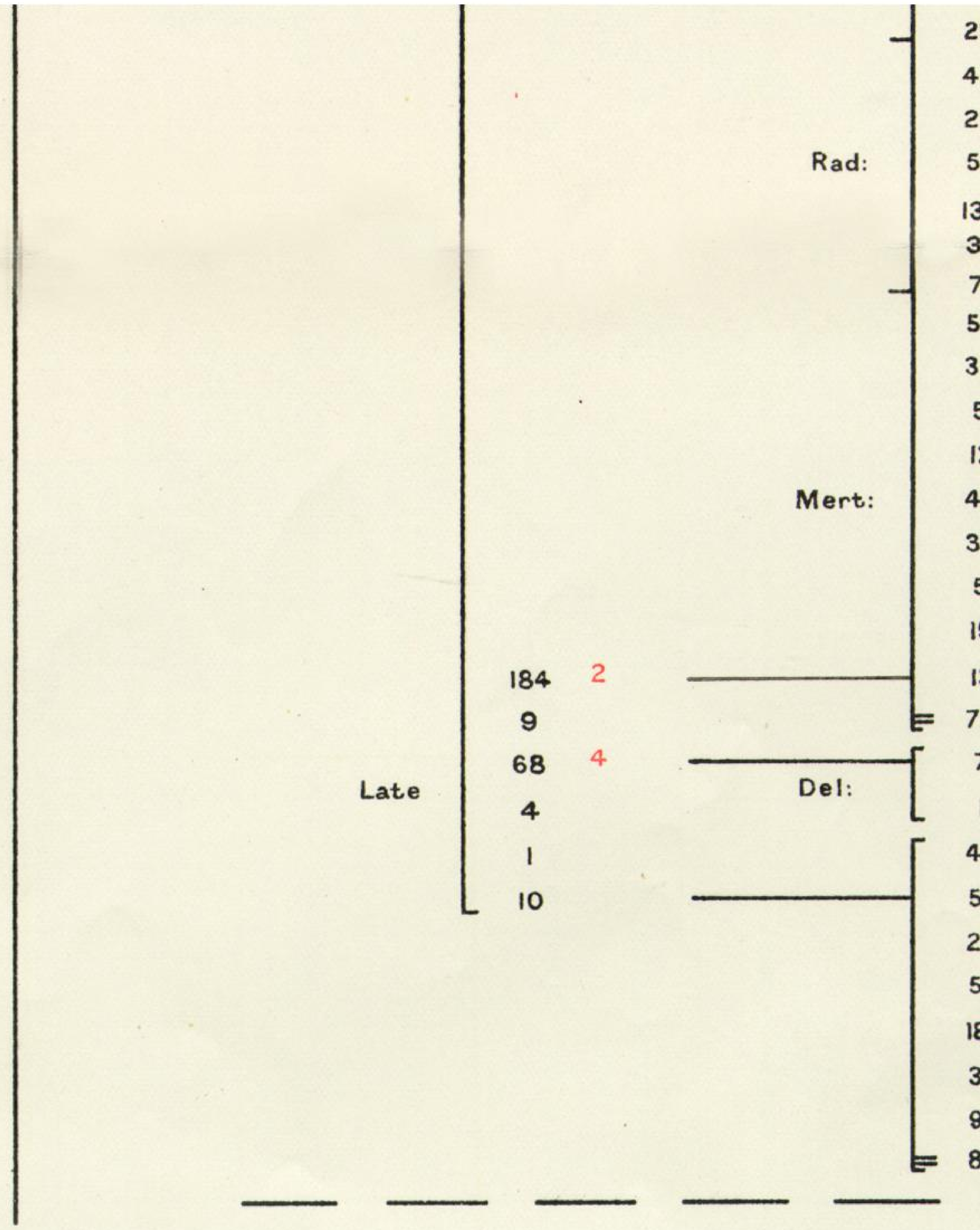
D [109 17

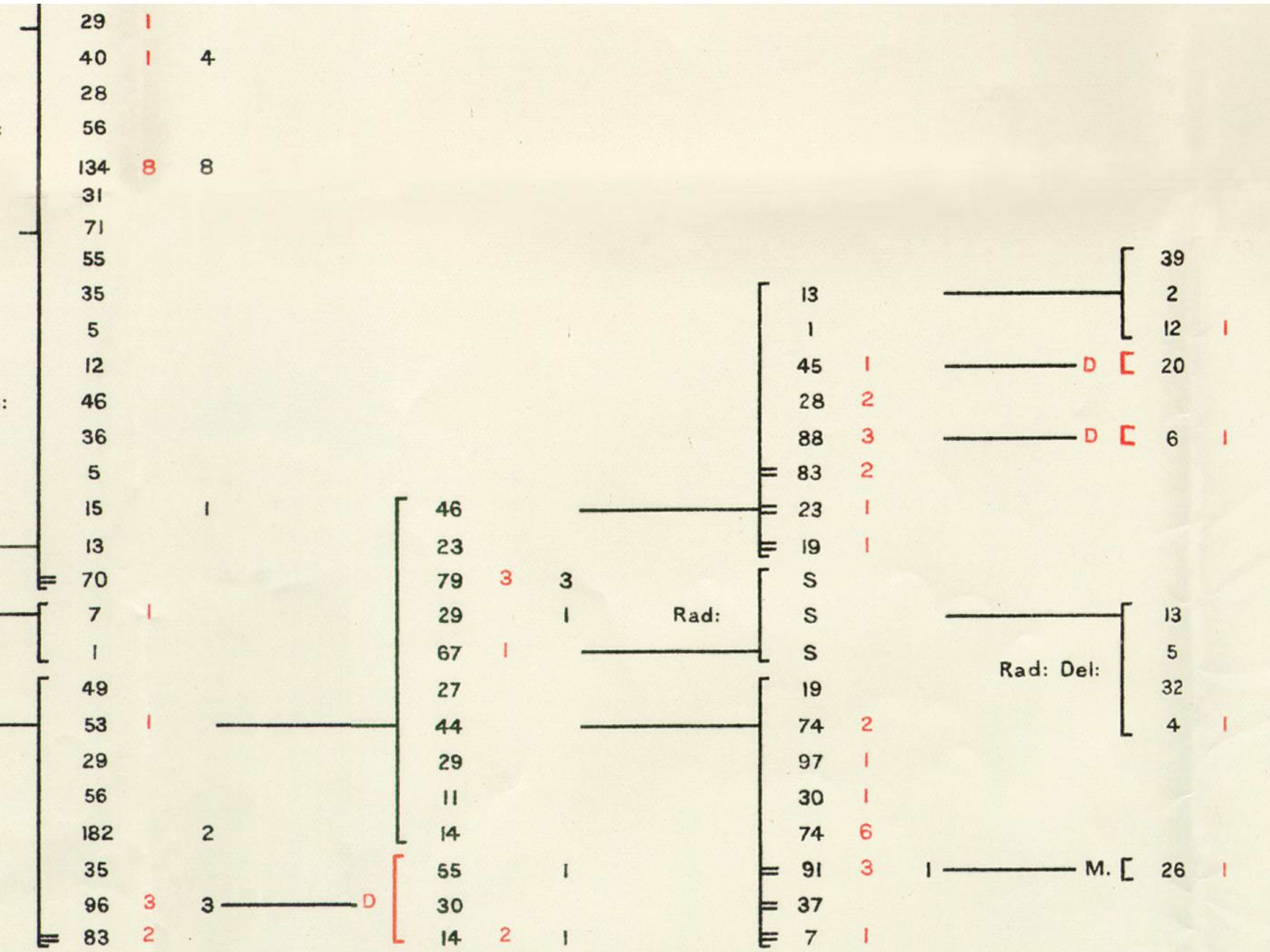

331
9
4
678
D
31
Early
1 1
7 1
16 1
12 1
44 2
23
14
15 1
15
Rad:
Late
Late D
Early
Late
Del:
Early D
Early
Late

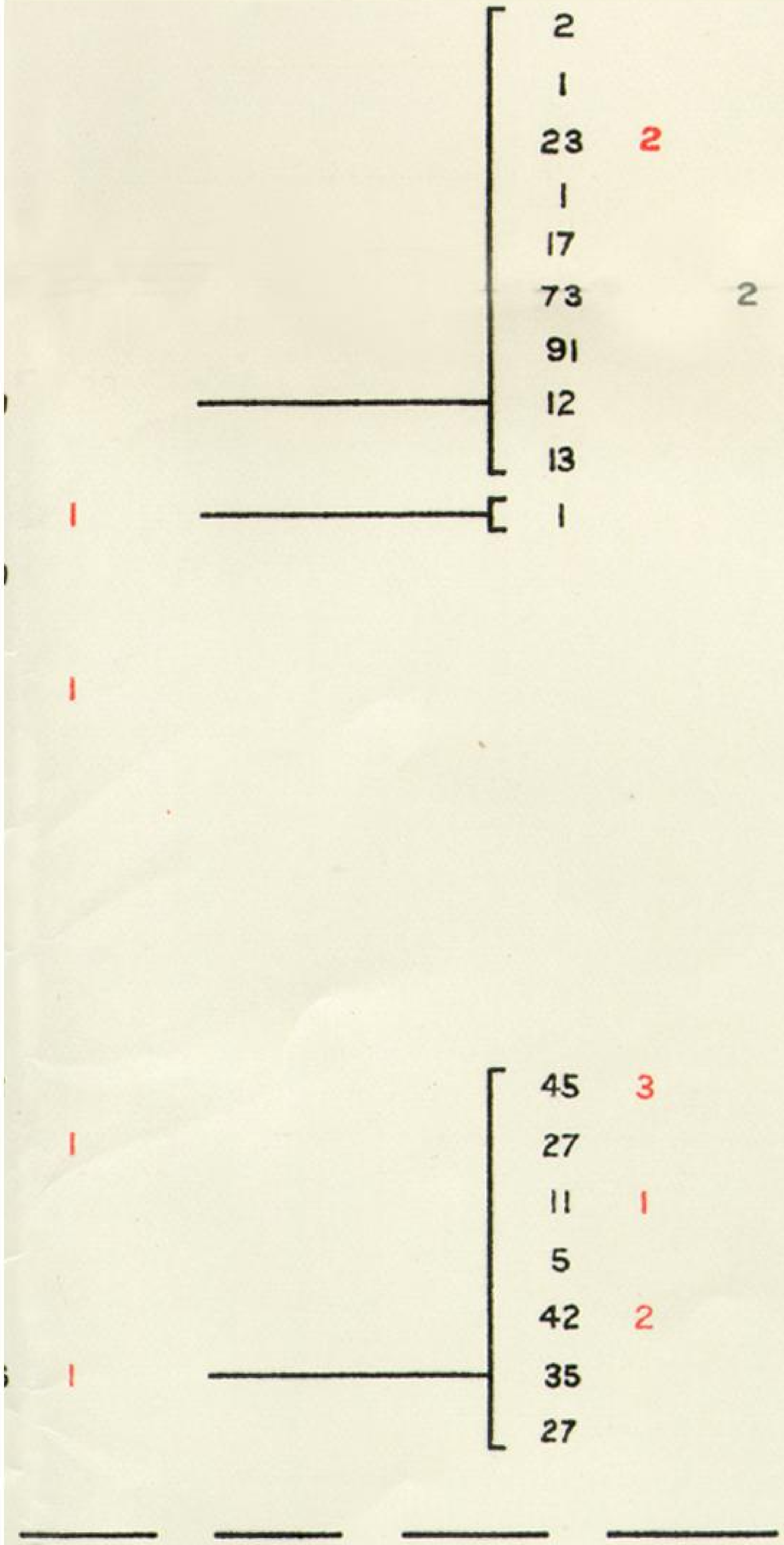
	76	16	3
	14	1	1
	105		3
	21		
	1		
	31	3	2
	21		1
	45		1
D	44	4	1
	36	1	1
	10	2	

	2		
	10	1	
	124	1	3
	6	1	
	29		
	7		
	48	5	
	14	1	
	65		
	16	1	
	32	2	
	89	2	
	45	2	
	9		
	5		
	44	2	
	15	2	
	35		
	27	3	1
	29	3	
	40	3	
	2		
	16	1	
	28		
D	118		3
	19		
	106	2	4
	69	6	
	68		1
	30		1
	151	3	
	70	1	
	101	2	2
	14		
	20	1	
	80	1	
	10	1	
	29	1	
	40	1	4


2
1


Rad:
Mert:
Late
184
2
9
68
4
Del:
4
1
10


29 1
40 1 4
28
56
134 8 8
31
71
55
35
5
12
46
36
5
15 1
13
70
7 1
1
49
53 1
29
56
182 2
35
96 3 3
83 2
46
23
79 3 3
29 1
67 1
27
44
29
11
14
D
55 1
30
14 2 1
13
1
45 1
28 2
88 3
83 2
23 1
19 1
Rad:
S
S
S
19
74 2
97 1
30 1
74 6
91 3
37
7 1
39
2
12 1
D 20
D 6 1
Rad: Del:
13
5
32
4 1
1 M. 26 1



2
1
23 2
1
17
73 2
91
12
13
1 1
1
45 3
1 27
11 1
5
42 2
1 35
27

TABLE VI. (continued)

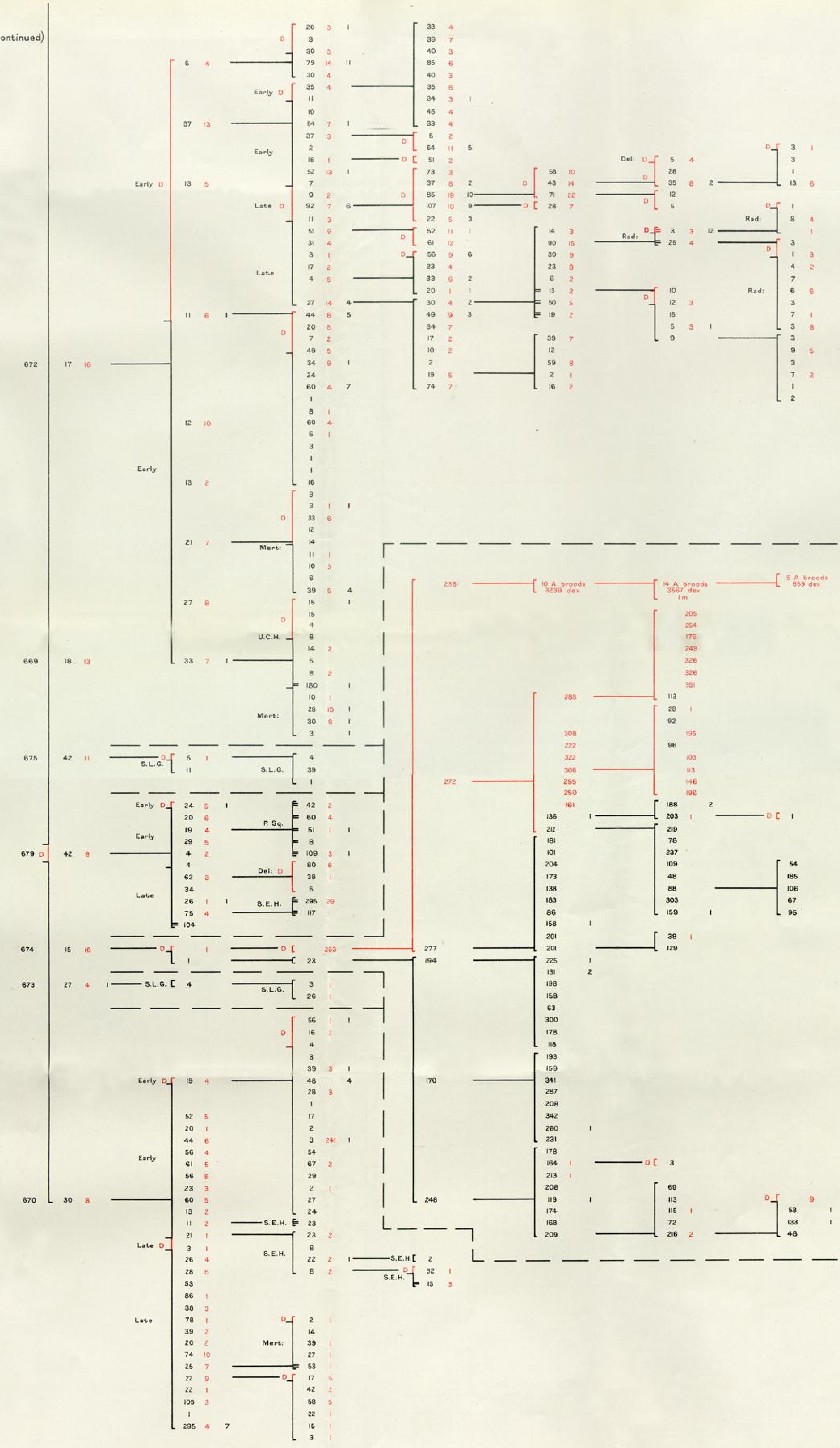
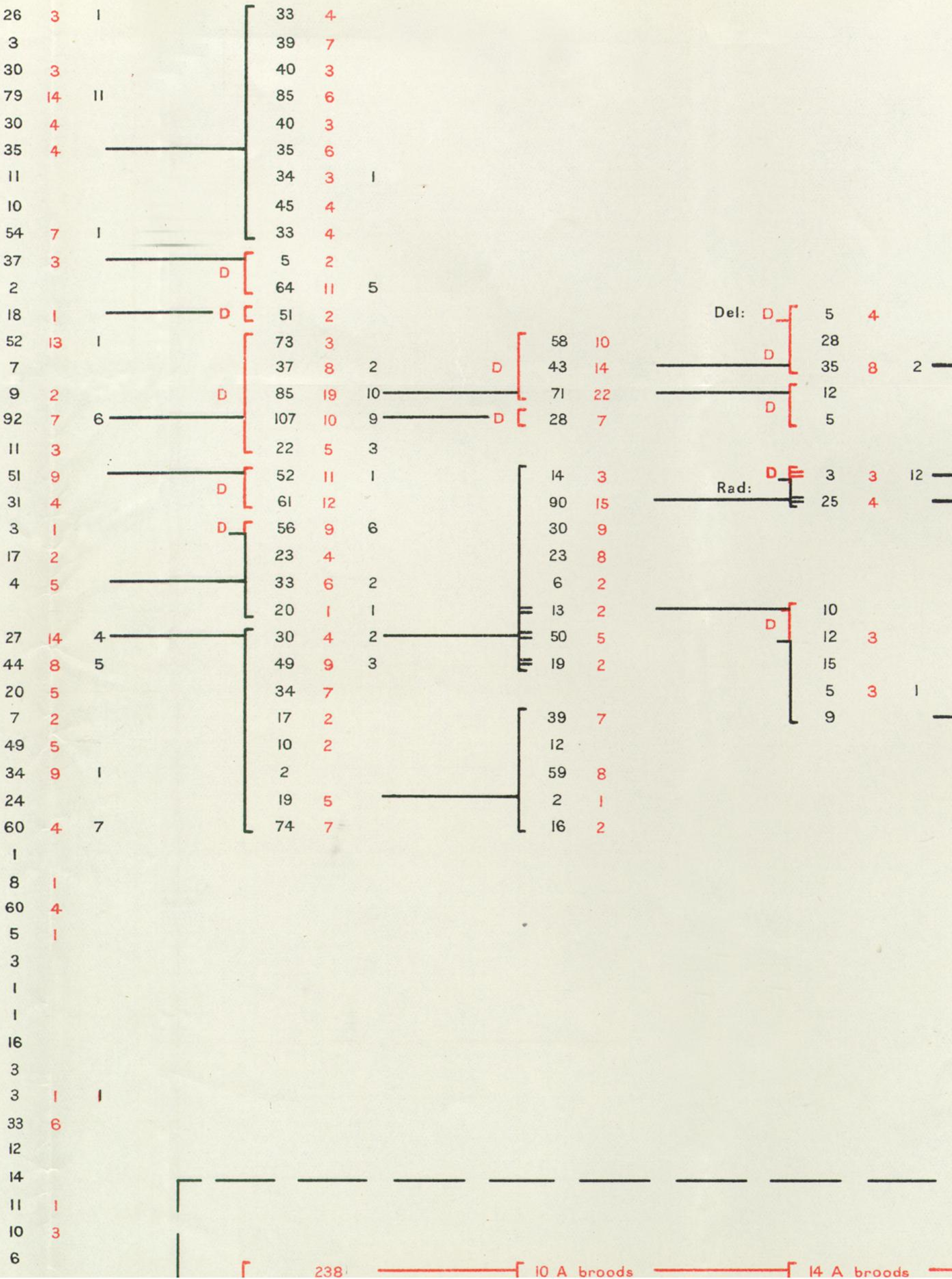
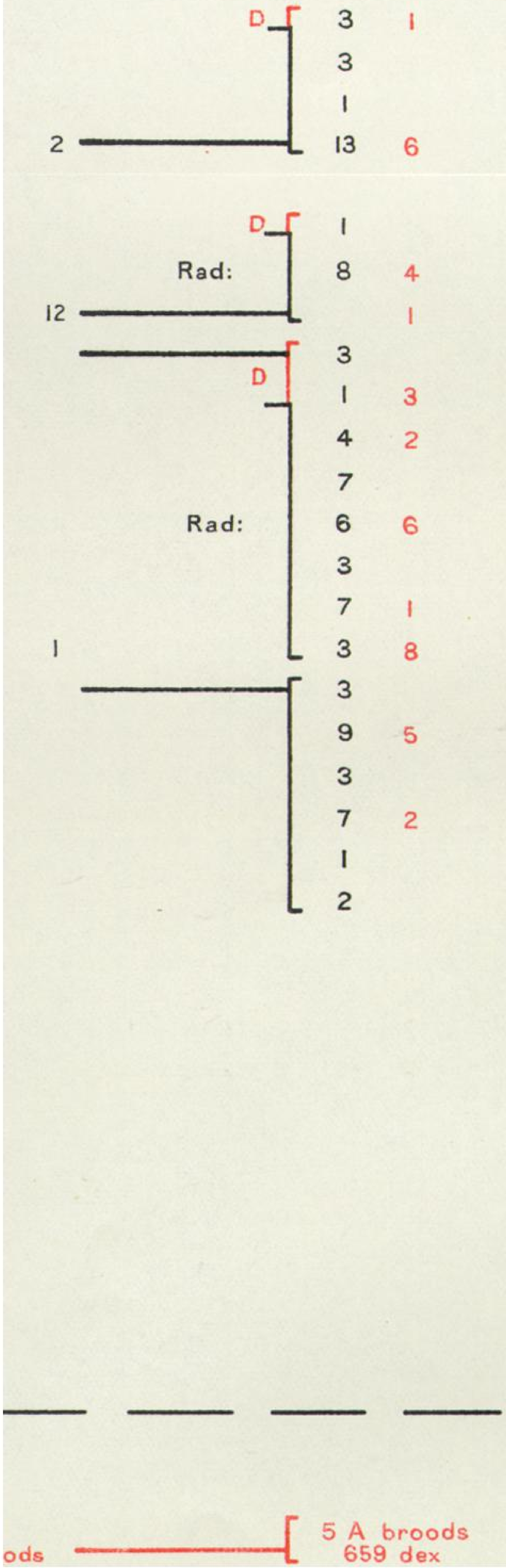


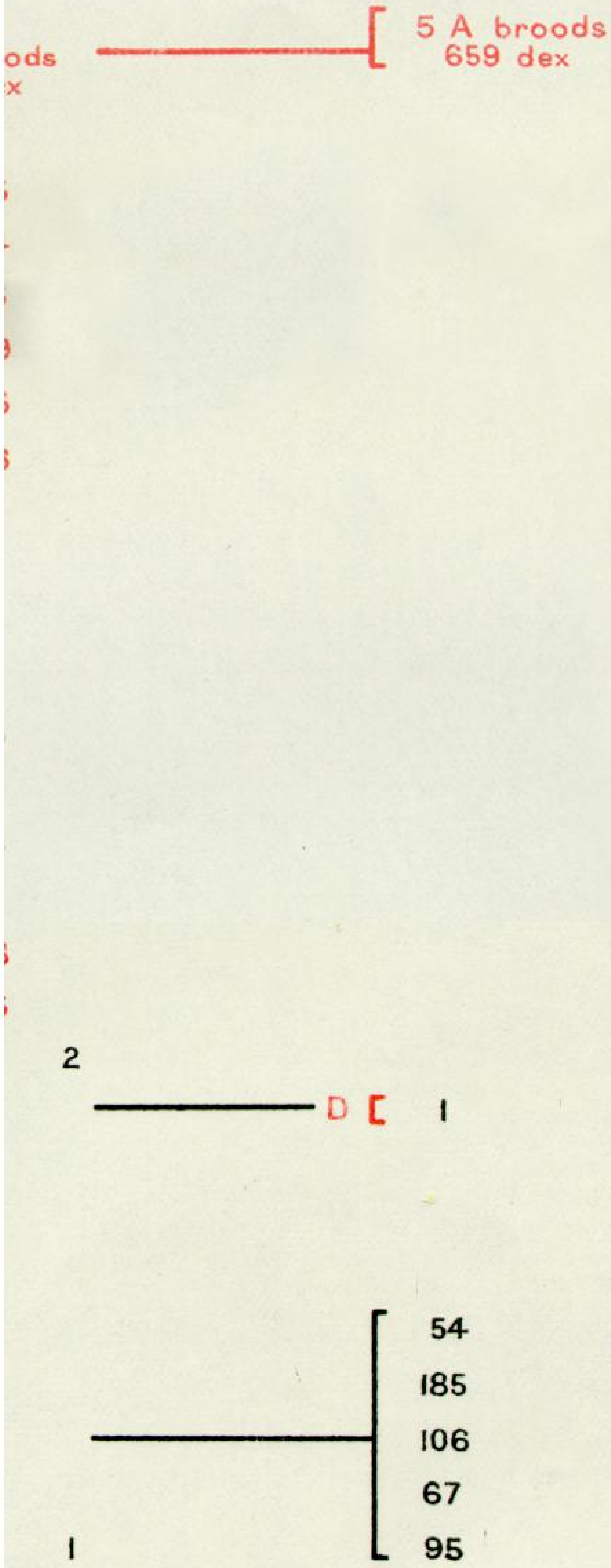
TABLE VI. (continued)

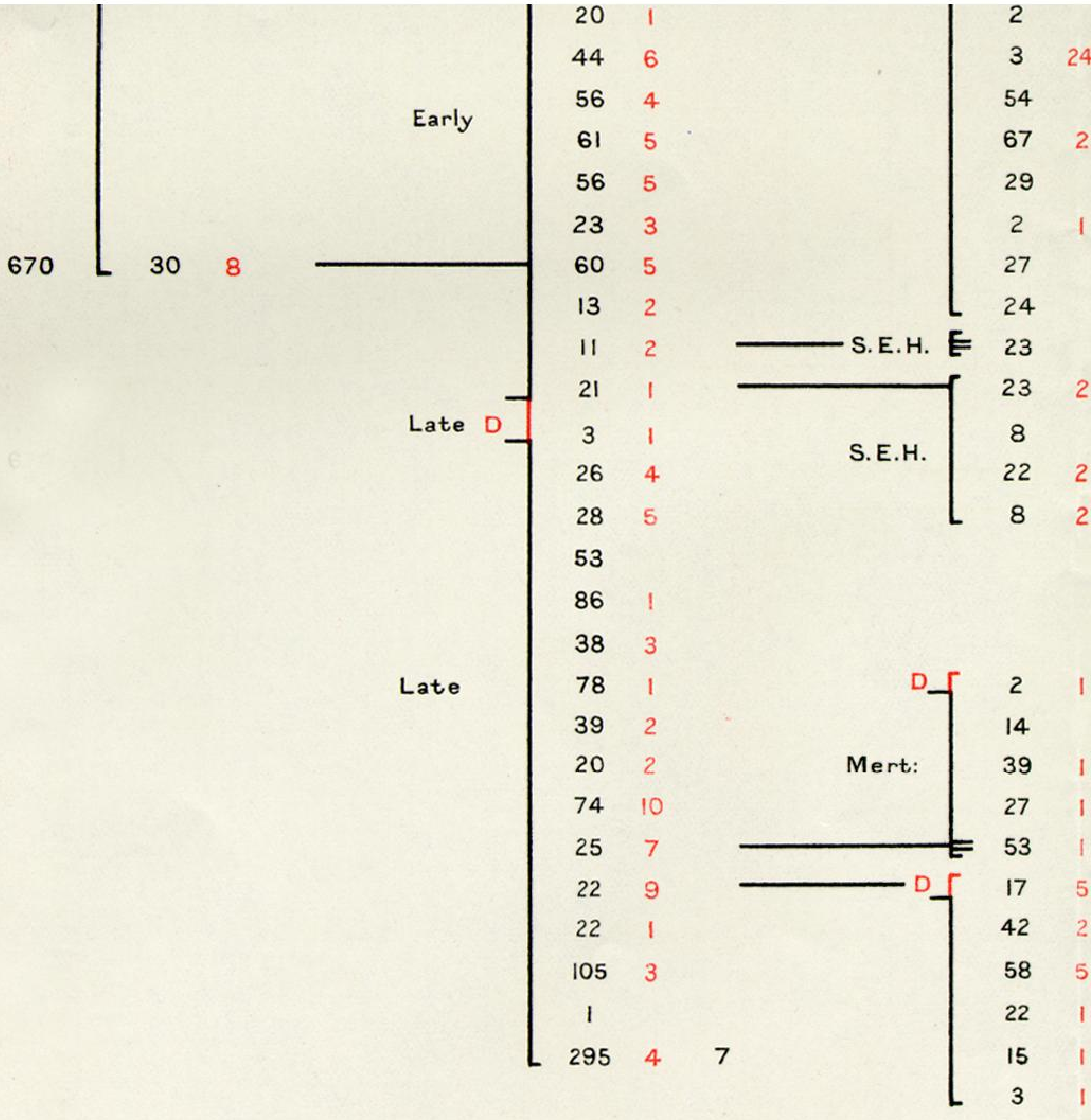

26 3 1
3
30 3
79 14 11
30 4
35 4
11
10
54 7 1
37 3
2
18 1
52 13 1
7
9 2
92 7 6
11 3
51 9
31 4
3 1
17 2
4 5
27 14 4
44 8 5
20 5
7 2
49 5
34 9 1
24
60 4 7
1
8 1
60 4
5 1
3
1
1
16
3
3 1 1
33 6
12
14
11 1
10 3
6
33 4
39 7
40 3
85 6
40 3
35 6
34 3 1
45 4
33 4
D
5 2
64 11 5
D
51 2
73 3
37 8 2
D
85 19 10
107 10 9
22 5 3
D
52 11 1
61 12
D
56 9 6
23 4
33 6 2
20 1 1
30 4 2
49 9 3
34 7
17 2
10 2
2
19 5
74 7
D
58 10
43 14
71 22
D
28 7
14 3
90 15
30 9
23 8
6 2
13 2
50 5
19 2
39 7
12
59 8
2 1
16 2
Del:
D
5 4
28
D
35 8 2
12
D
5
D
3 3 12
Rad:
25 4
10
D
12 3
15
5 3 1
9
238
10 A broods
14 A broods


D
3 1
3
1
2
13 6
D
1
Rad:
8 4
12
1
3
D
1 3
4 2
7
Rad:
6 6
3
7 1
1
3 8
3
9 5
3
7 2
1
2
ods
5 A broods
659 dex

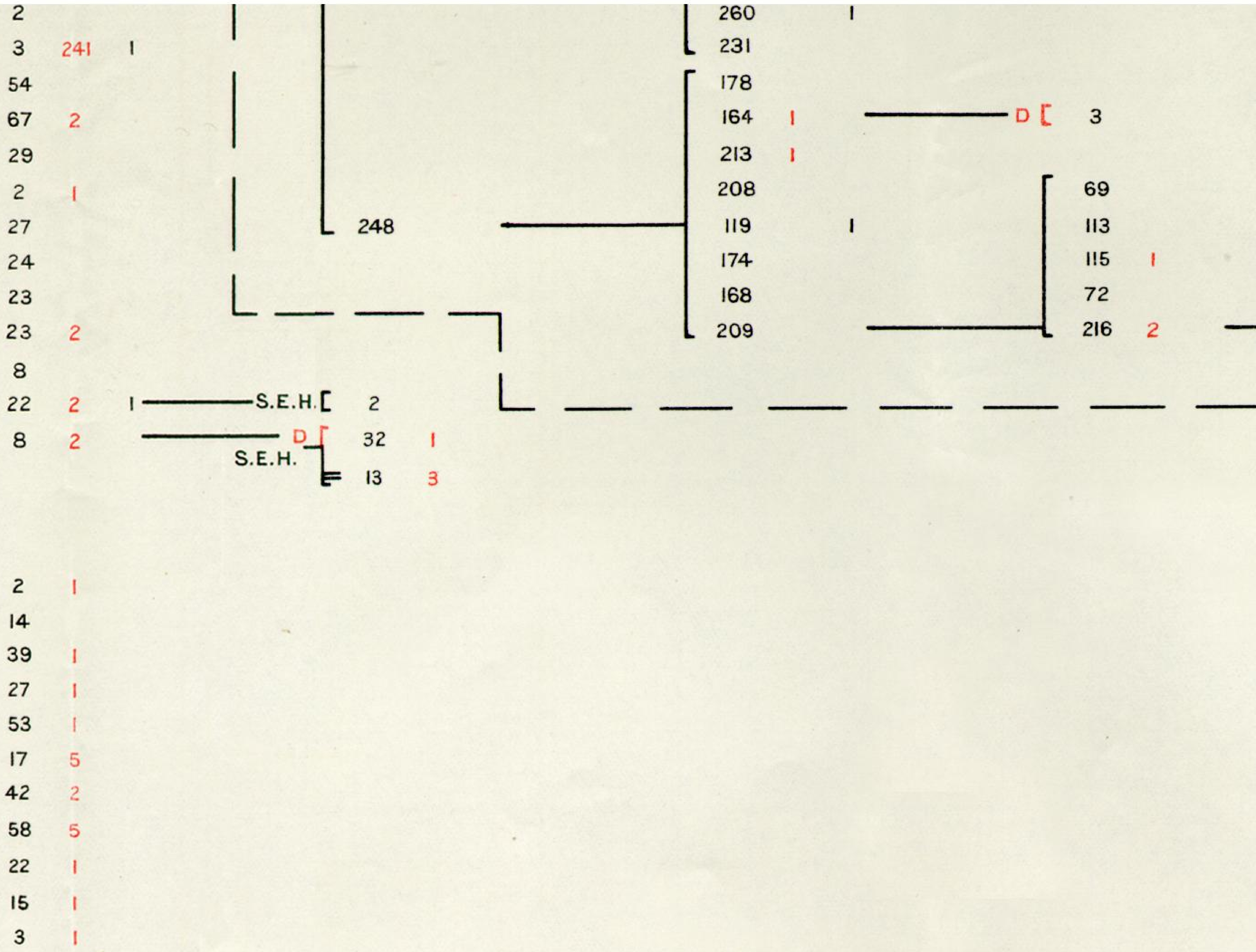

10 3
6
39 5
27 8
15
D
15
4
U.C.H.
8
14 2
669
18 13
33 7 1
5
8 2
180
10 1
28 10
Mert:
30 8
3
675
42 11
D
S.L.G.
5 1
11
S.L.G.
4
39
1
Early D
24 5 1
42 2
20 6
60 4
P. Sq.
Early
19 4
51 1
29 5
8
679 D
42 9
4 2
109 3
4
80 6
Del: D
62 3
38 1
34
5
Late
26 1 1
S.E.H.
295
75 4
117
104
674
15 16
D
1
D
1
23
673
27 4
1
S.L.G.
4
S.L.G.
3 1
26 1
56 1
D
16 2
4
3
39 3
Early D
19 4
48
28 3
1
52 5
17
20 1
2
44 6
3
56 4
54
Early


10 3
6
39 5 4
15 1
15
4
8
14 2
5
8 2
180 1
10 1
28 10 1
30 8 1
3 1
4
39
1
42 2
60 4
51 1 1
8
109 3 1
80 6
38 1
5
295 29
117
263
23
3 1
26 1
56 1 1
16 2
4
3
39 3 1
48 4
28 3
1
17
2
3 241 1
54
238
272
277
194
170
10 A broods
3239 dex
283
308
222
322
306
255
250
161
136 1
212
181
101
204
173
138
183
86
158 1
201
201
225 1
131 2
198
158
63
300
178
118
193
159
341
287
208
342
260 1
231
178
14 A broods
3567 dex
1 m
205
254
176
249
326
326
351
113
28 1
92
195
96
103
93
146
196
188 2
203 1
219
78
237
109
48
88
303
159 1
39 1
129


5 A broods
659 dex
2
D
1
54
185
106
67
95
1



670
30
8
Early
20 1
44 6
56 4
61 5
56 5
23 3
60 5
13 2
11 2
21 1
Late D
3 1
26 4
28 5
53
86 1
38 3
Late
78 1
39 2
20 2
74 10
25 7
22 9
22 1
105 3
1
295 4
7
2
3 24
54
67 2
29
2 1
27
24
S.E.H.
23
23 2
8
S.E.H.
22 2
8 2
D
2 1
14
Mert:
39 1
27 1
53 1
D
17 5
42 2
58 5
22 1
15 1
3 1


2
260
1
3
241
1
231
54
178
67
2
164
1
D
3
29
213
1
2
1
208
69
27
248
119
1
113
24
174
115
1
23
168
72
23
2
209
216
2
8
22
2
1
S.E.H.
2
8
2
D
32
1
S.E.H.
13
3
2
1
14
39
1
27
1
53
1
17
5
42
2
58
5
22
1
15
1
3
1

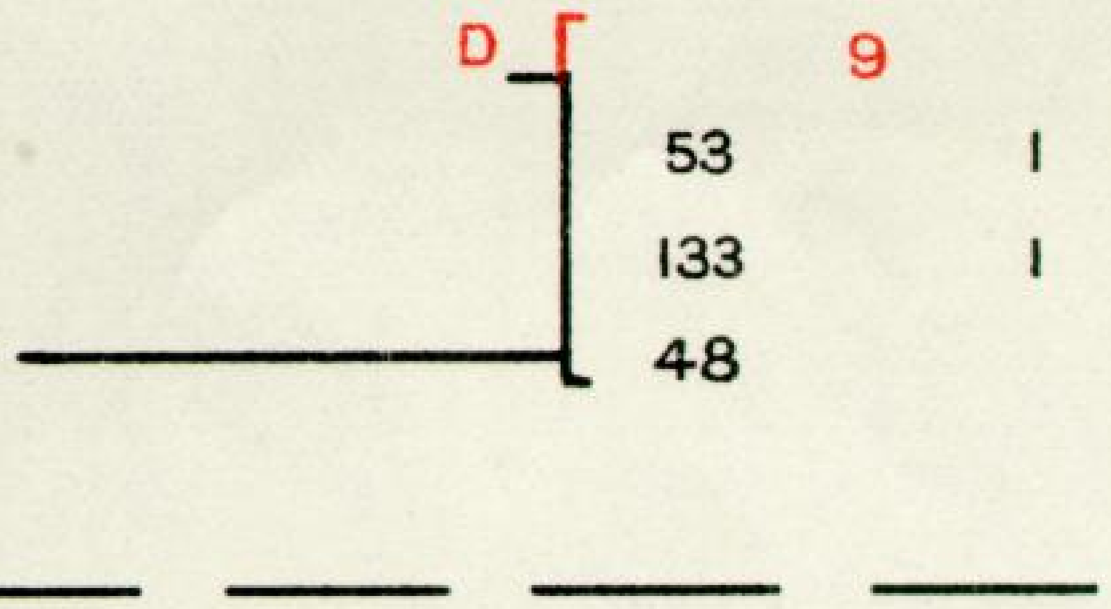

D
9
53
133
48

Table VII. A dextrals x K Sinistrals

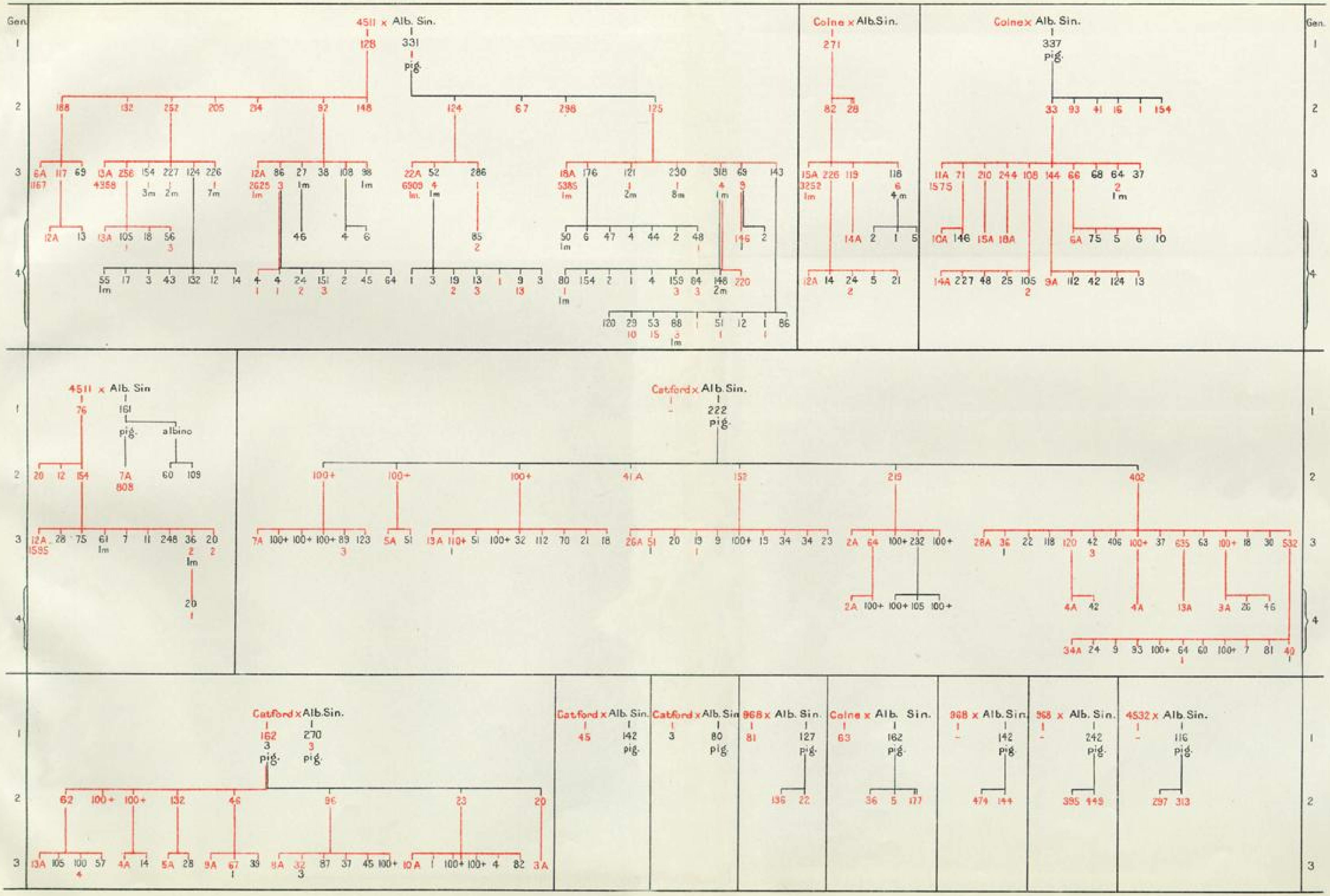
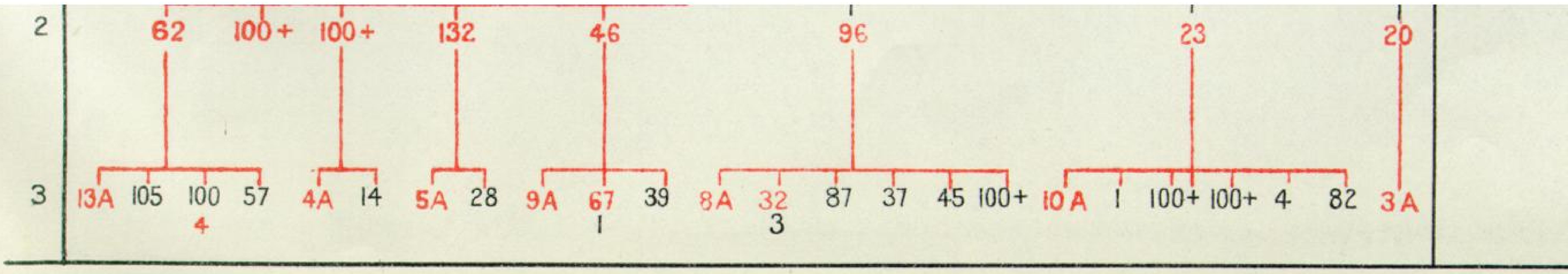
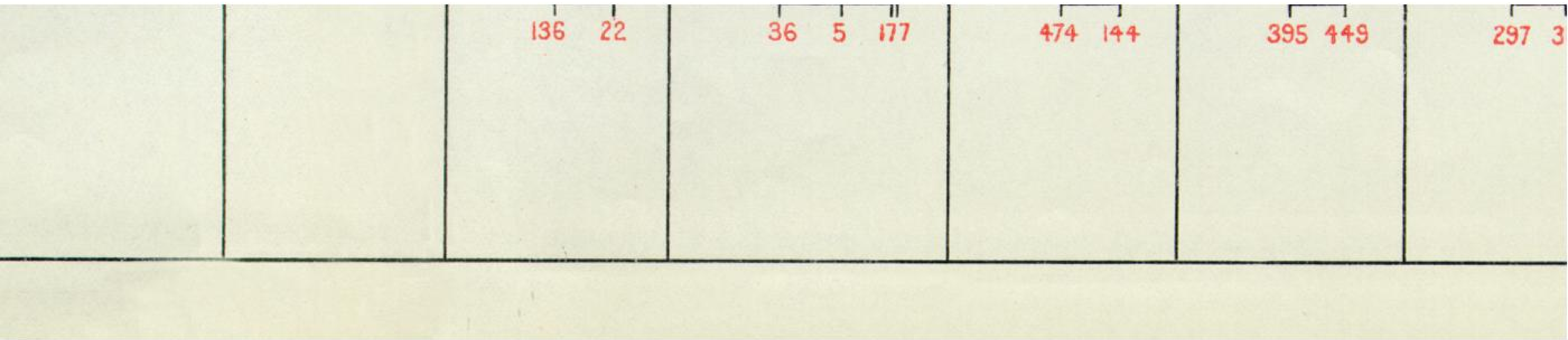


Table VII. A dextrals x K Sinistrals


Colne x Alb.Sin.
271
82 28
15A 3252 1m
226
119
118 6 4m
14A
2 1 5
12A 14 24 2 5 21
Colne x Alb. Sin.
337 pig.
33 93 41 16 1 154
11A 1575
71 210 244 108 144 66 68 64 2 1m 37
10A 146 15A 18A
6A 75 5 6 10
14A 227 48 25 105 2
9A 112 42 124 13
298 125
18A 5385 1m
176
121 1 2m
230 1 8m
318 4 1m
69 9
143
50 1m 6 47 4 44 2 48 1
146 1 2
30 1 m 154 2 1 4 159 3 84 3 148 2m 220
120 29 10 53 15 88 3 1m 1 51 1 12 1 1 86
Catford x Alb. Sin.
-
222 pig.
41 A 152 219 402
70 21 18
26A 51 1 20 19 1 9 100+ 19 34 34 23
2A 64 100+ 232 100+
2A 100+ 100+ 105 100+
28A 36 1 22 118 120 42 3 406 100+ 37 63
4A 42
4A
34A 24 9 93 100+ 6
Catford x Alb. Sin.
45
142 pig.
Catford x Alb. Sin
3
80 pig.
968 x Alb. Sin.
81
127 pig.
136 22
Colne x Alb. Sin.
63
162 pig.
36 5 177
968 x Alb. Sin.
-
142 pig.
474 144
968 x Alb. Sin.
-
242 pig.
395 449
4532 x Alb
-
297


Gen.
1
1 154
2
37
3
6 10
3
4
1
02
2
0+ 37 635 63 100+ 18 30 532
3
A 13A 3A 26 46
3 100+ 64 60 100+ 7 81 40
4
32 x Alb. Sin.
116
pig.
1
297 313
2


2
62
100 +
100 +
132
46
96
23
20
3
13A
105
100
57
4
4A
14
5A
28
9A
67
1
39
8A
32
3
87
37
45
100+
10 A
1
100+
100+
4
82
3 A


136
22
36
5
177
474
144
395
449
297

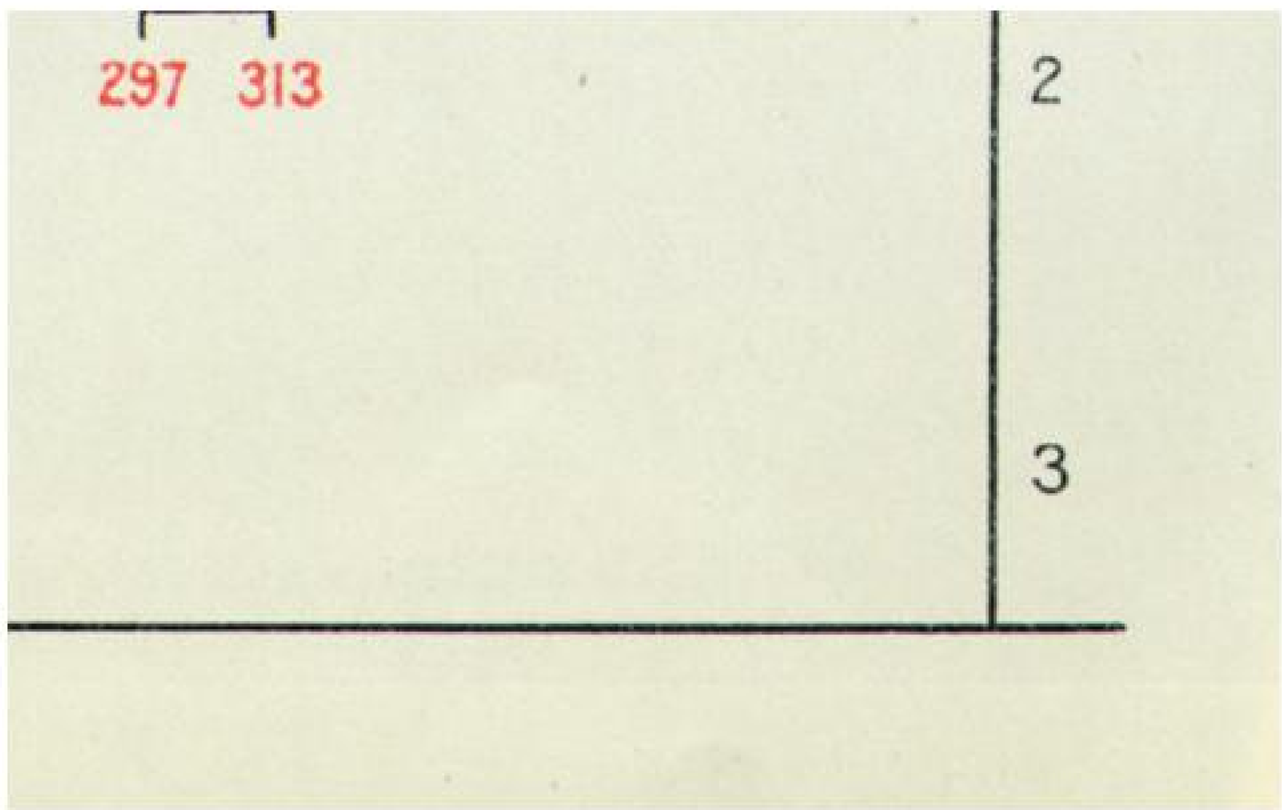

297
313
2
3

Table VIII. A dextrals x E dextrals

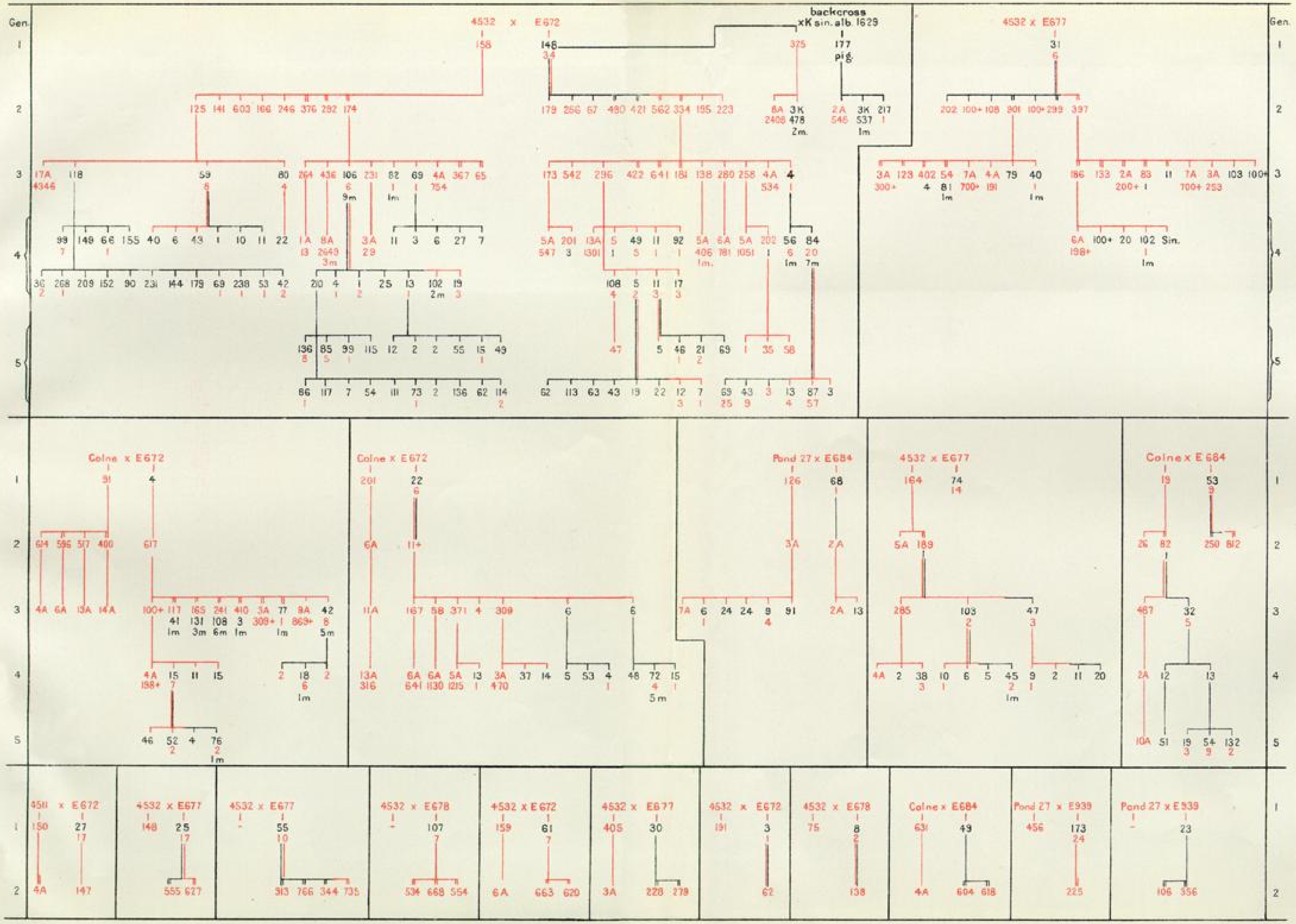
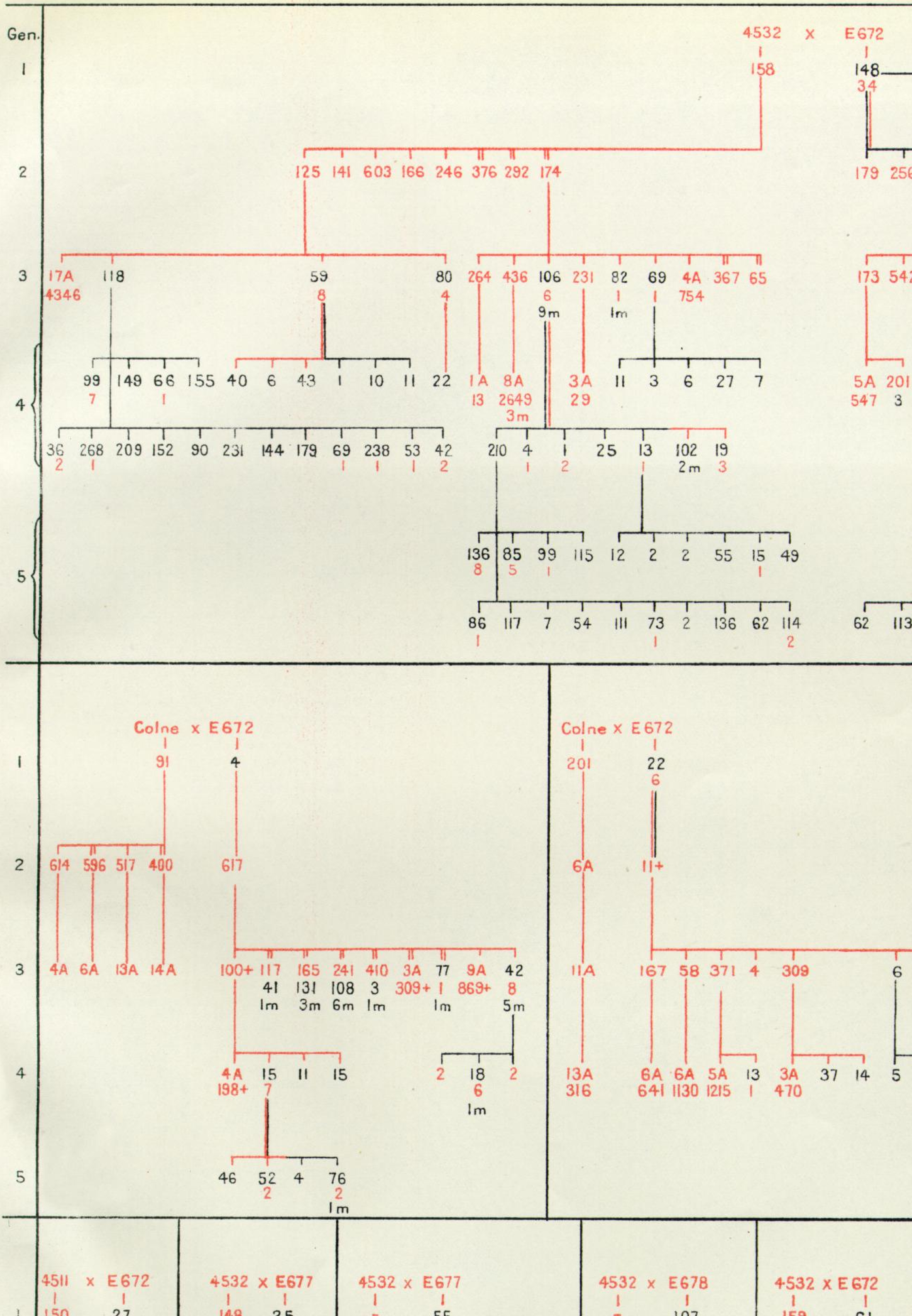
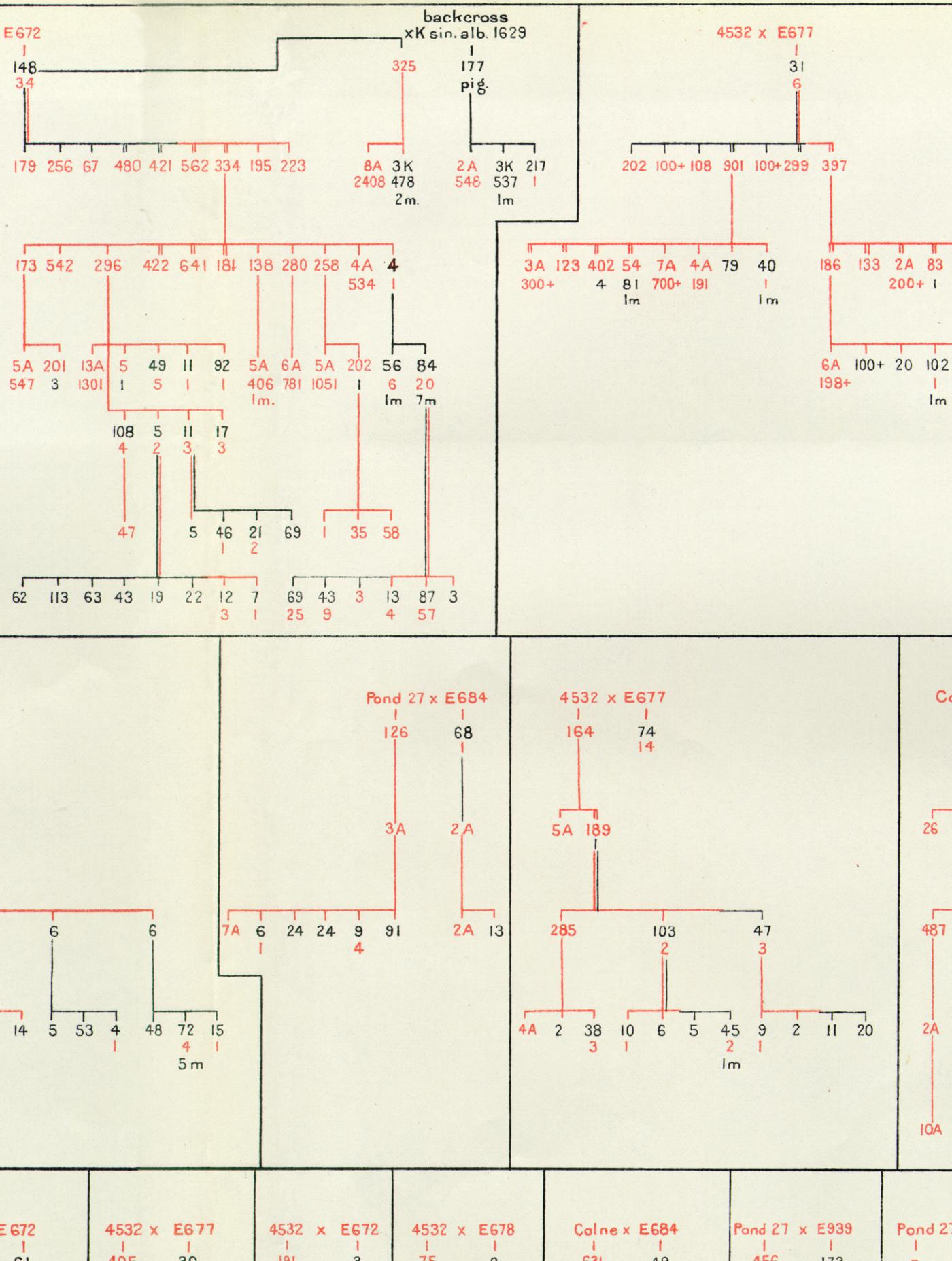
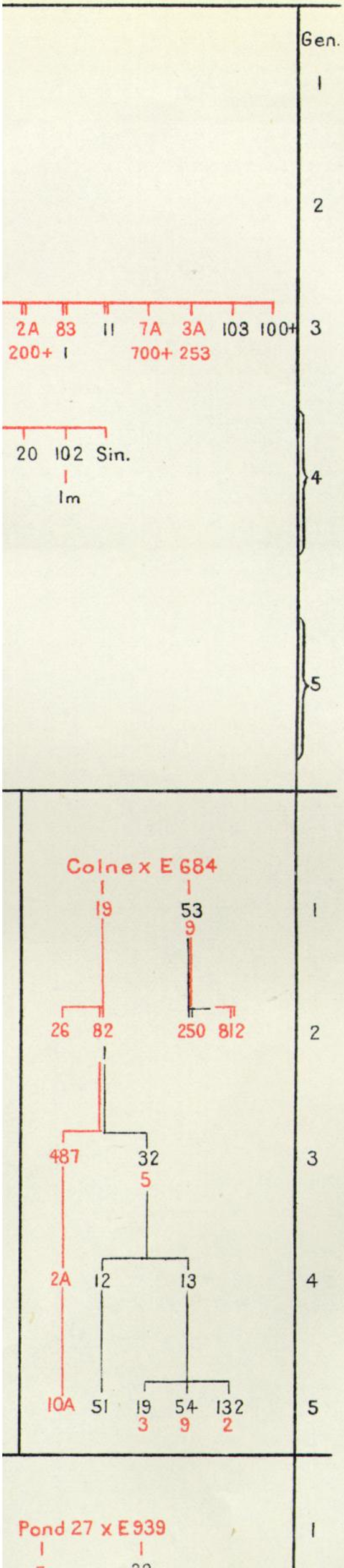
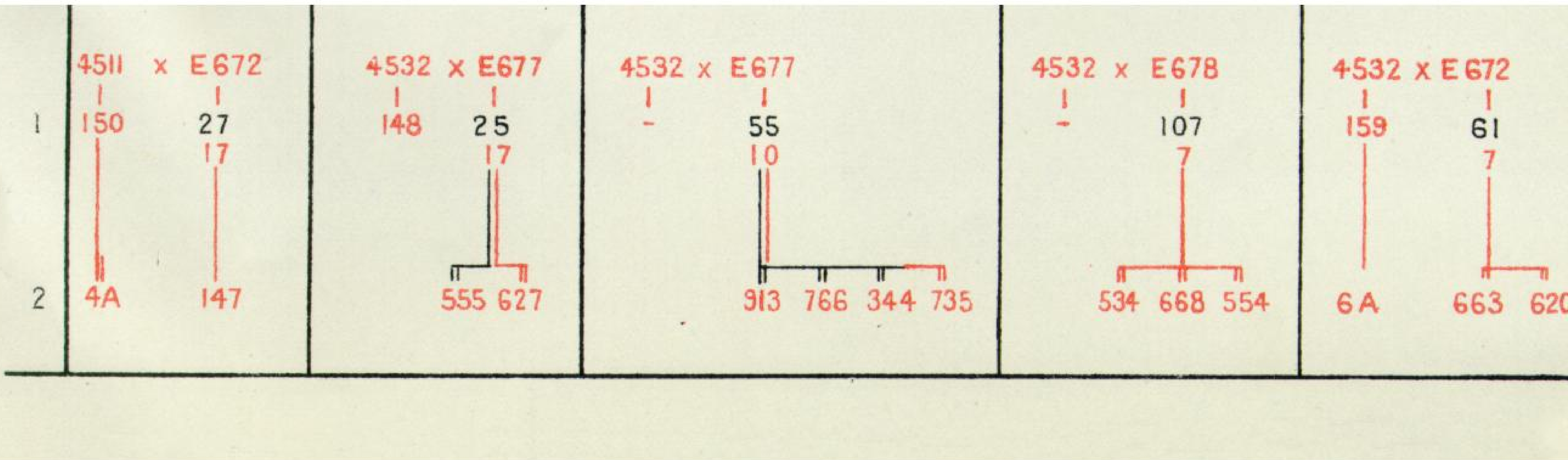


Table VIII. A dextrals x E dextrals

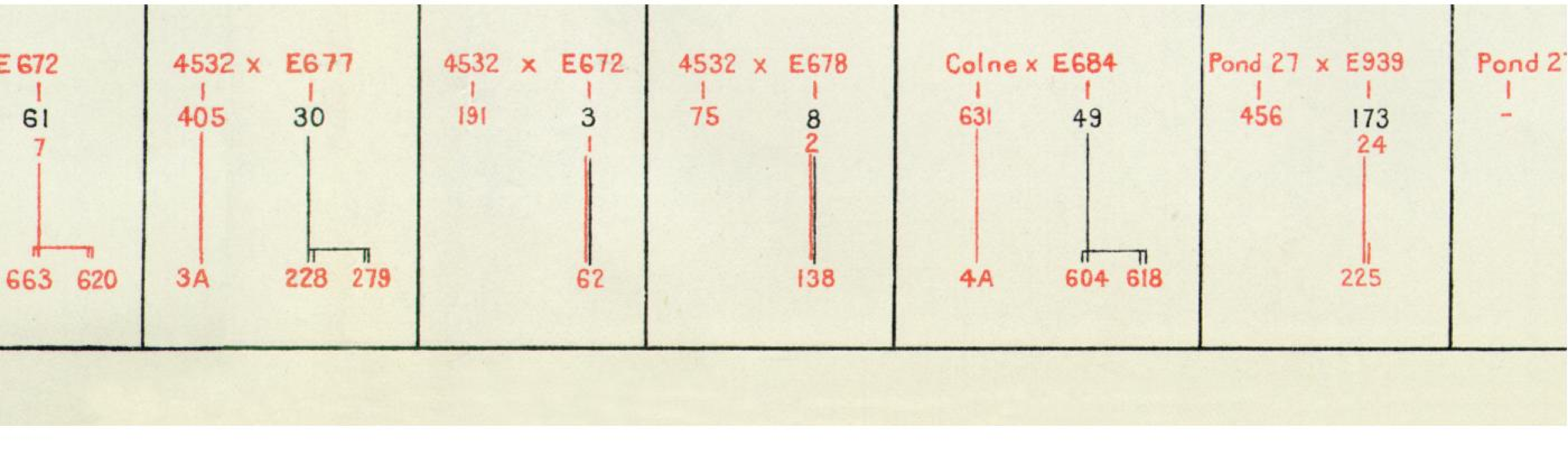


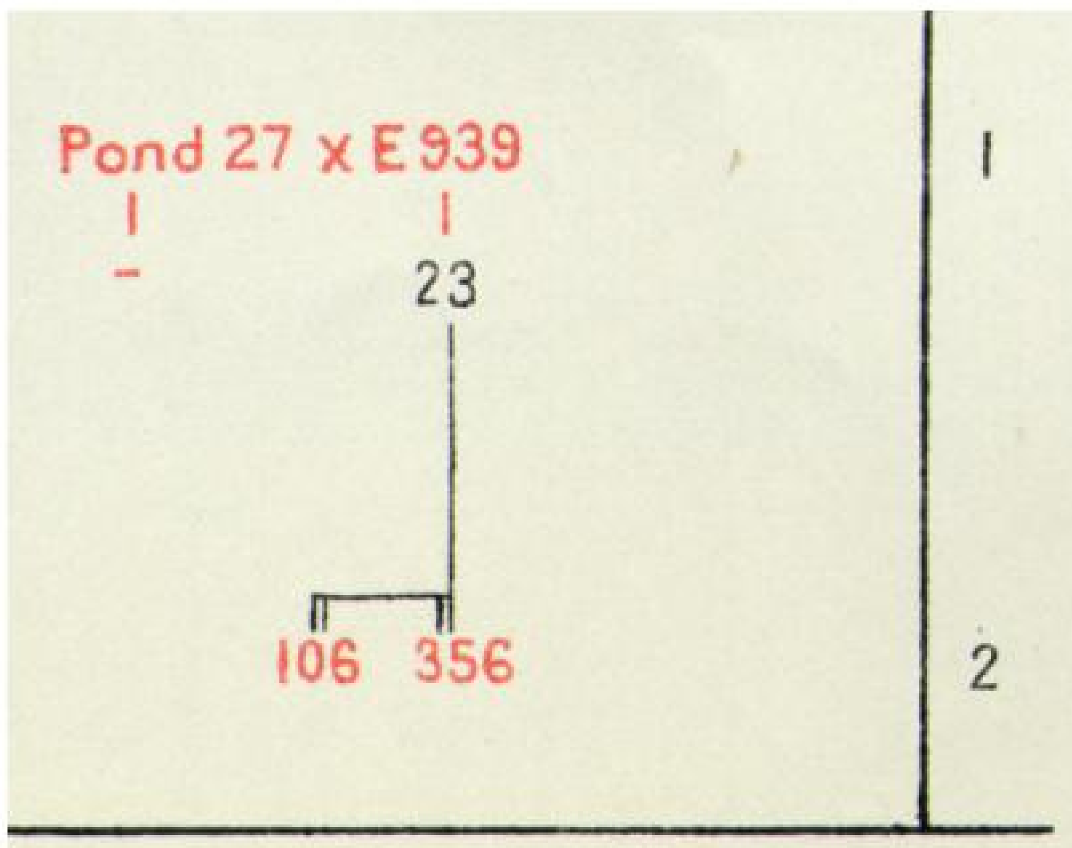

E672
148
34
backcross
xK sin. alb. 1629
325
177
pig.
179 256 67 480 421 562 334 195 223
8A 3K
2408 478
2m.
2A 3K 217
548 537 1
1m
173 542 296 422 641 181 138 280 258 4A 4
534 1
5A 201 13A 5 49 11 92 5A 6A 5A 202 56 84
547 3 1301 1 5 1 1 406 781 1051 1 6 20
1m. 1m 7m
108 5 11 17
4 2 3 3
47
5 46 21 69
1 2
1 35 58
62 113 63 43 19 22 12 7 69 43 3 13 87 3
3 1 25 9 4 57
4532 x E677
31
6
202 100+ 108 901 100+ 299 397
3A 123 402 54 7A 4A 79 40
300+ 4 81 700+ 191 1
1m 1m
186 133 2A 83
200+ 1
6A 100+ 20 102
198+ 1
1m
6 6
14 5 53 4 48 72 15
1 4 1
5m
Pond 27 x E684
126 68
1
3A 2A
7A 6 24 24 9 91 2A 13
1 4
4532 x E677
164 74
14
5A 189
285 103 47
2 3
4A 2 38 10 6 5 45 9 2 11 20
3 1 2 1
1m
Co
26
487
2A
10A
E672
4532 x E677
4532 x E672
4532 x E678
Colne x E684
Pond 27 x E939
Pond 27


Gen.
1
2
2A 83 11 7A 3A 103 100+ 3
200+ 1 700+ 253
20 102 Sin.
Im
4
5
Colne x E 684
19
53
9
1
26 82
250 812
2
487
32
5
3
2A 12 13
4
10A 51 19 54 132
3 9 2
5
Pond 27 x E939
1



1
2
4511 x E672
150
27
17
4A
147
4532 x E677
148
25
17
555 627
4532 x E677
-
55
10
913 766 344 735
4532 x E678
-
107
7
534 668 554
4532 x E672
159
61
7
6A
663 620


E672
61
7
663
620
4532 x E677
405
30
3A
228
279
4532 x E672
191
3
1
62
4532 x E678
75
8
2
138
Colne x E684
631
49
4A
604
618
Pond 27 x E939
456
173
24
225
Pond 27
-



Pond 27 x E939
1
-
1
23
106
356
1
2

TABLE IX. Stelfox A dextrals X E dextrals

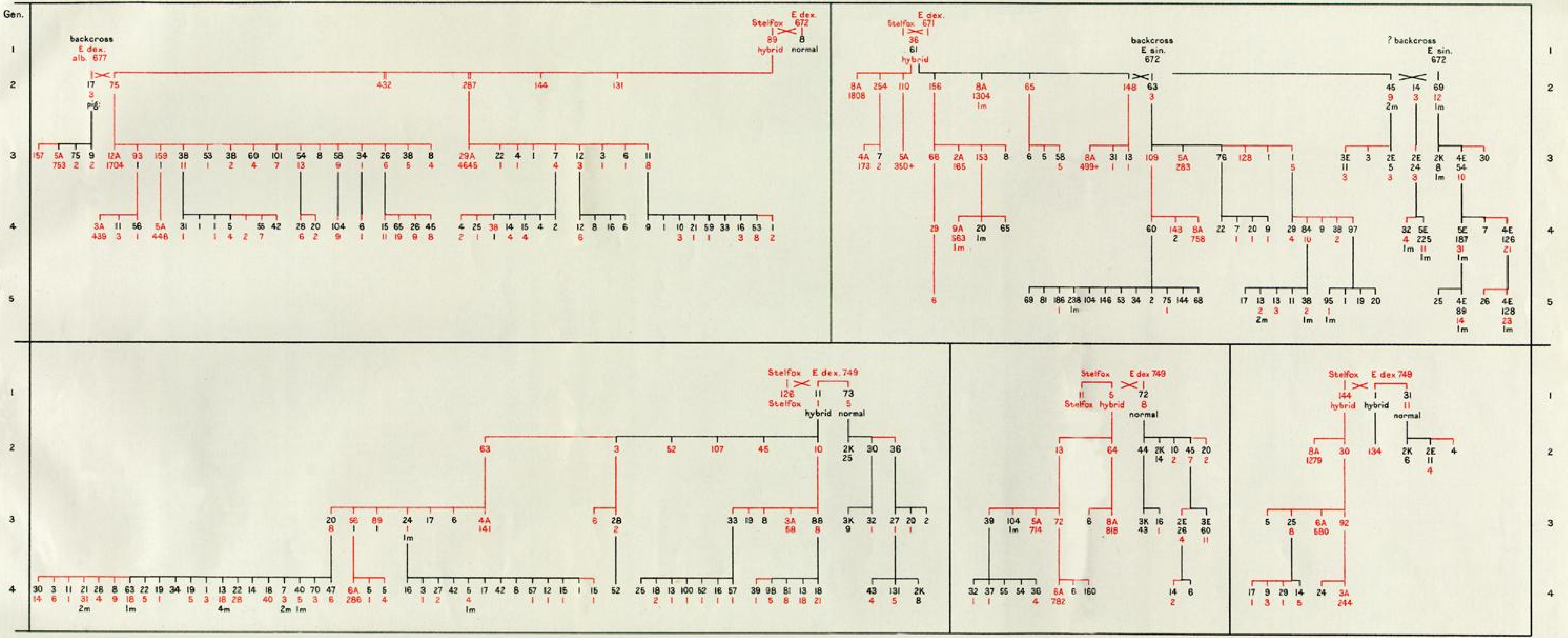
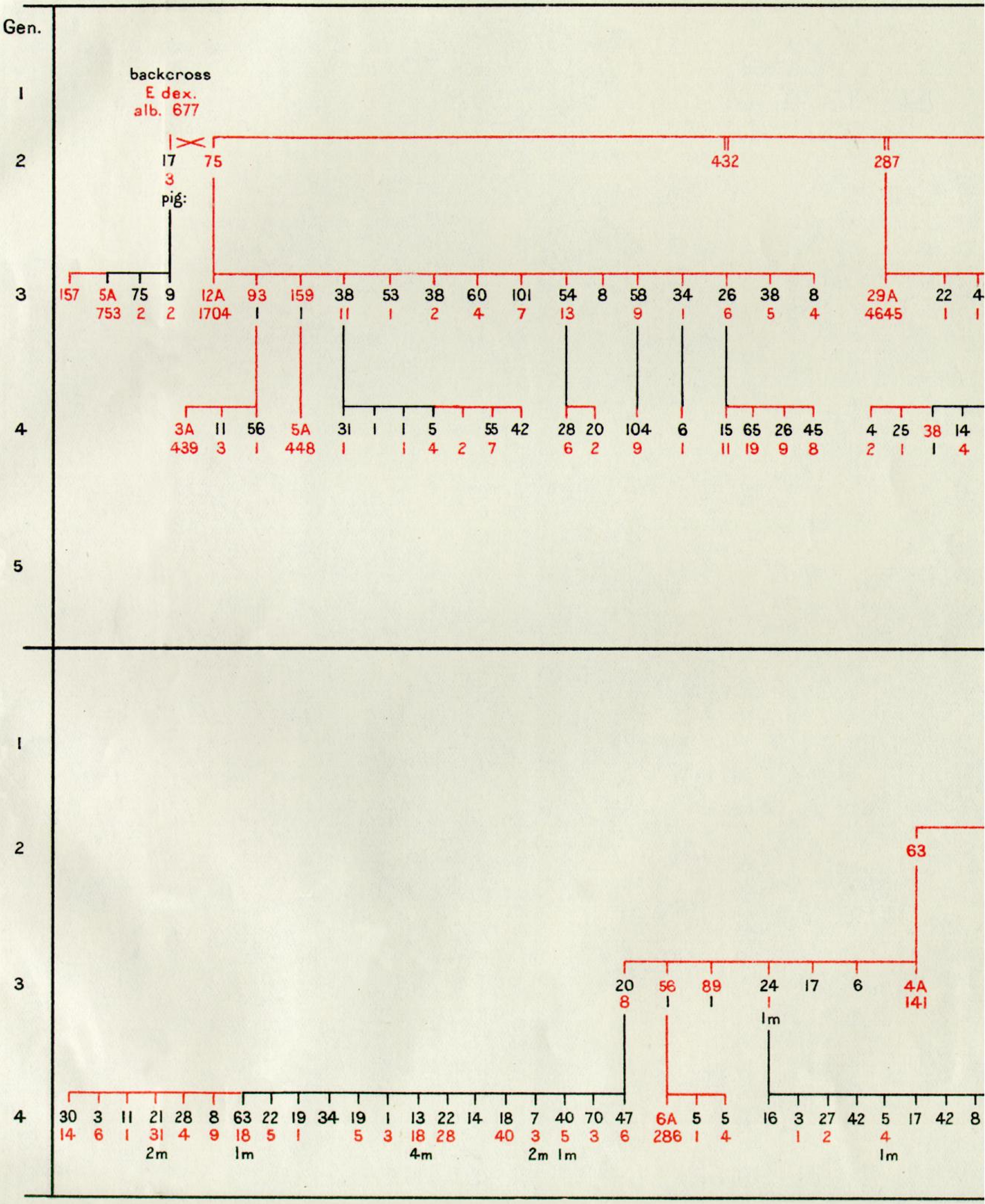
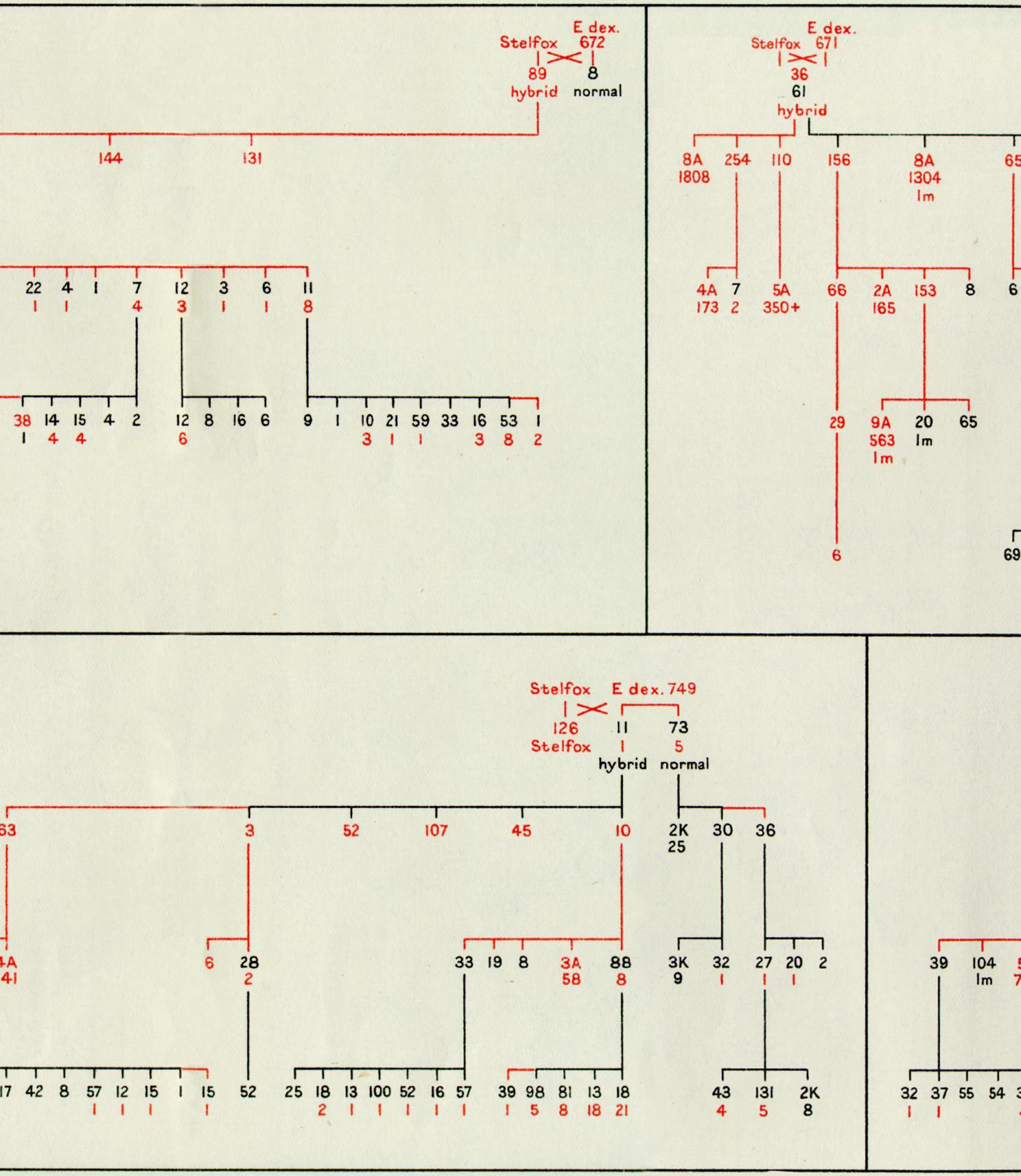
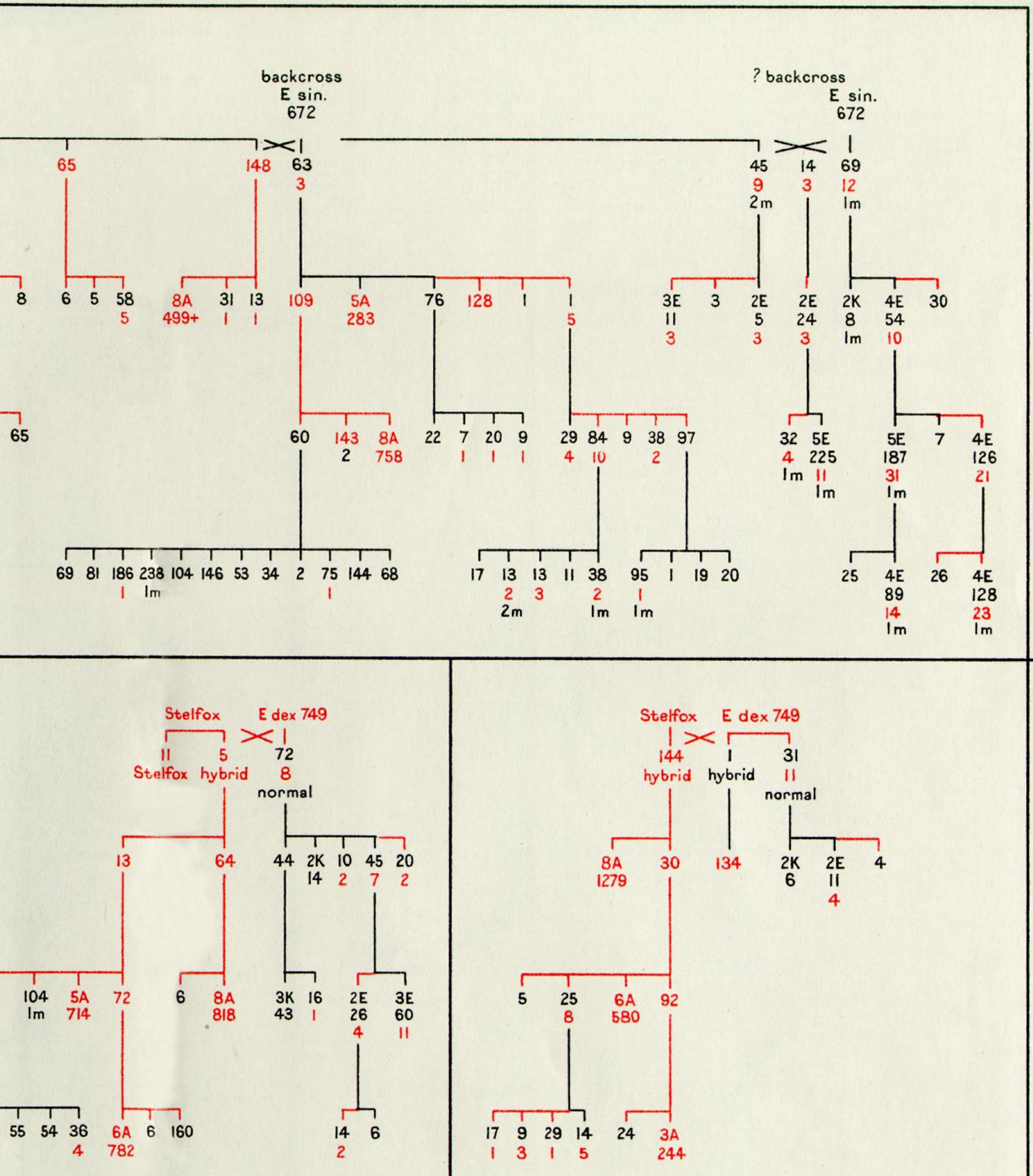


TABLE IX. Stelfox A dextrals X E dextrals




Stelfox
E dex. 672
89 hybrid
8 normal
144
131
22 1
4 1
1
7 4
12 3
3 1
6 1
11 8
38 1
14 4
15 4
4
2
12 6
8
16
6
9
1
10 3
21 1
59 1
33
16 3
53 8
1 2
Stelfox
E dex. 671
36
61 hybrid
8A 1808
254
110
156
8A 1304 1m
65
4A 173
7 2
5A 350+
66
2A 165
153
8
6
29
9A 563 1m
20 1m
65
6
69
Stelfox
E dex. 749
126 Stelfox
11 1 hybrid
73 5 normal
63
3
52
107
45
10
2K 25
30
36
4A 41
6
28 2
33
19
8
3A 58
88 8
3K 9
32 1
27 1
20 1
2
17
42
8
57 1
12 1
15 1
1
15 1
52
25
18 2
13 1
100 1
52 1
16 1
57 1
39 1
98 5
81 8
13 18
18 21
43 4
131 5
2K 8
39
104 1m
5 7
32 1
37 1
55
54


backcross
E sin.
672
? backcross
E sin.
672
Stelfox
E dex 749
Stelfox
hybrid
normal
Stelfox
E dex 749
hybrid
hybrid
normal

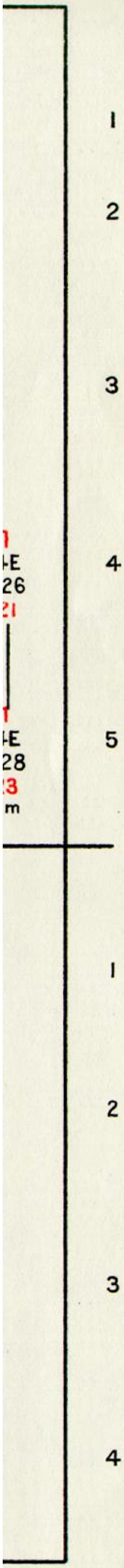

1
2
3
4
5
1
2
3
4
4E
26
21
4E
28
23
m

TABLE X. K sinistrals × E sinistrals. K sinistrals × E dextrals. A dextrals × E. sinistrals.

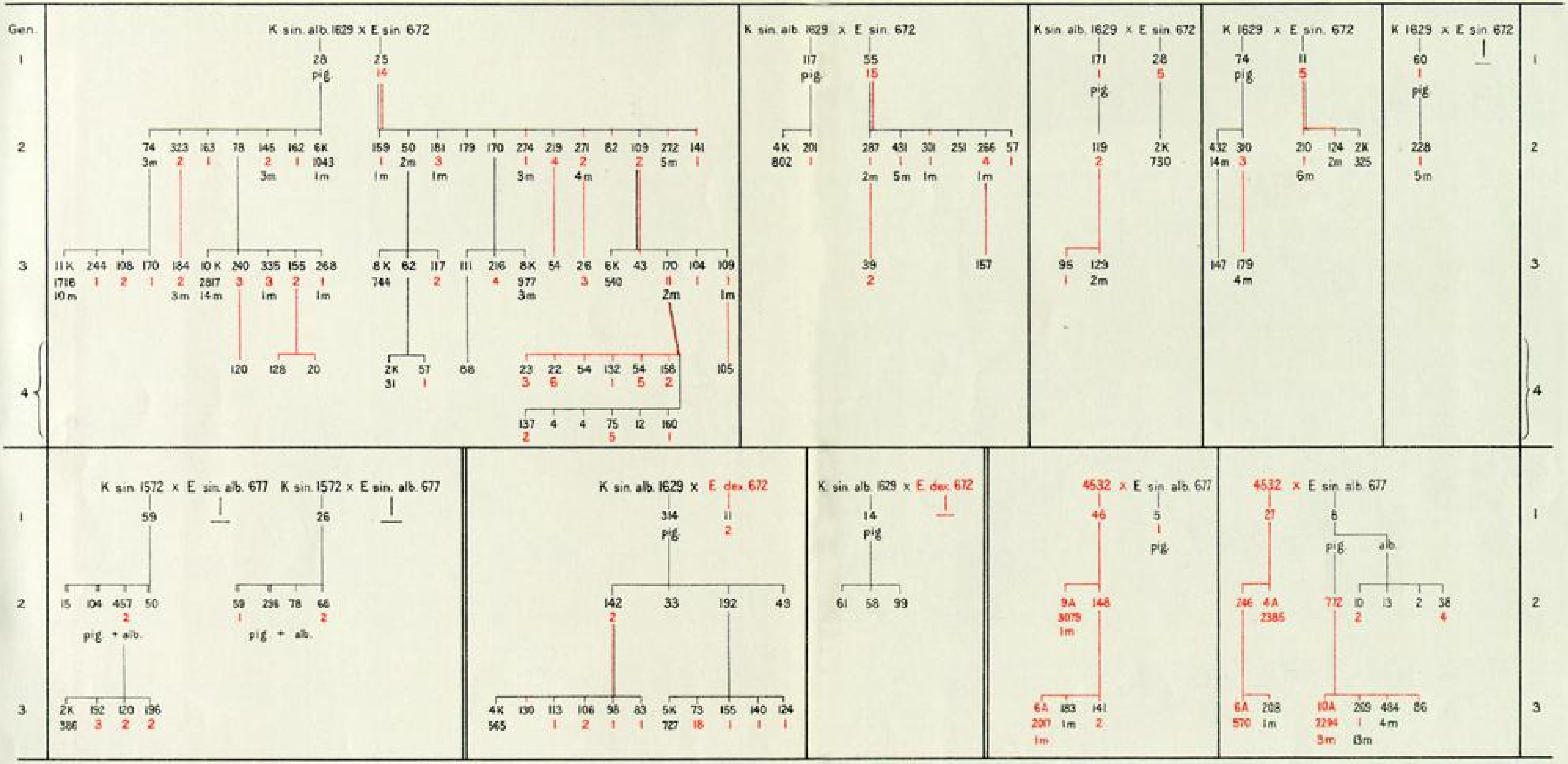
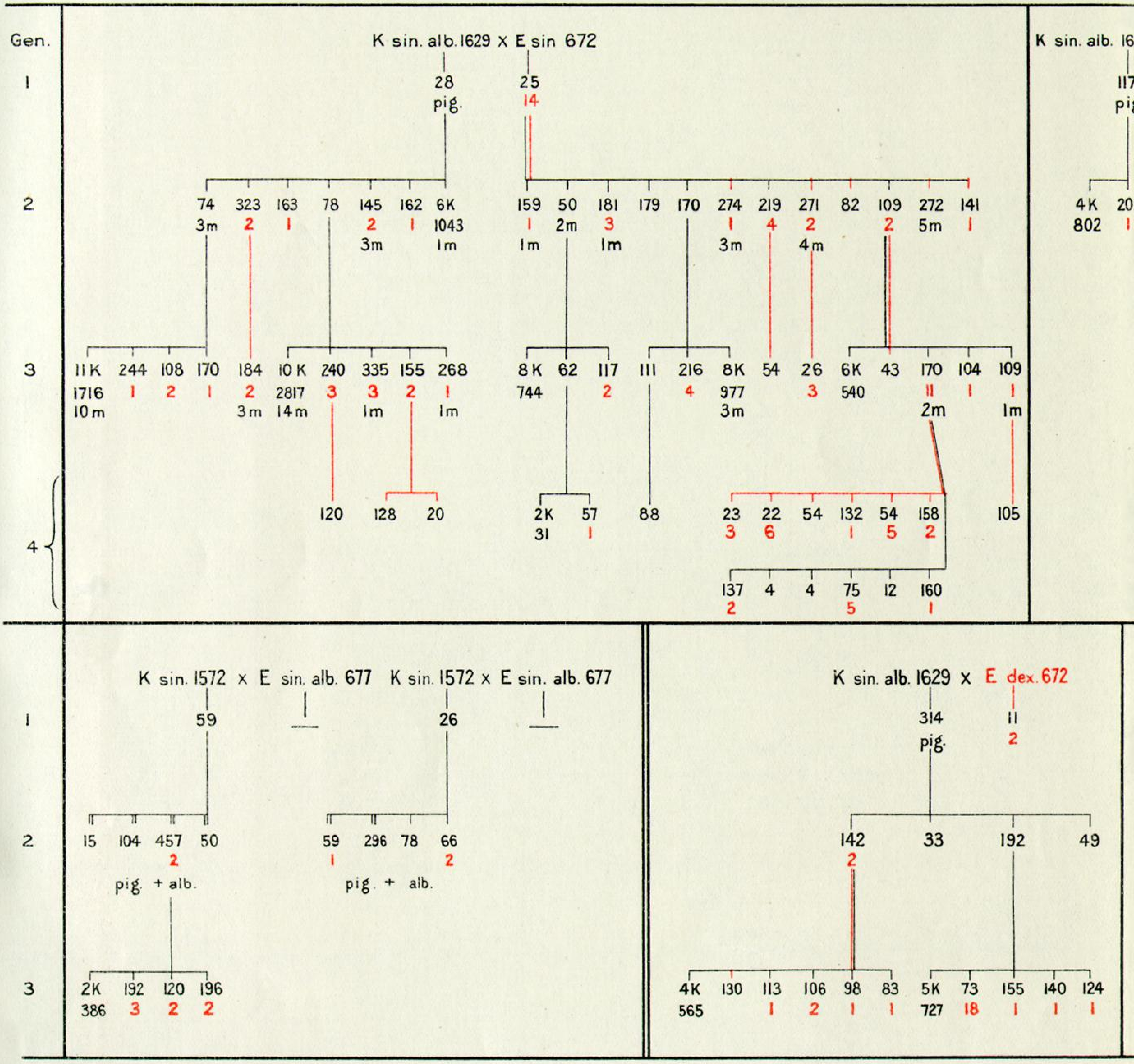


TABLE X. K sinistrals × E sinistrals. K sinistrals × E dextrals. A dextrals × E. s



ls x E. sinistrals.