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Nomenclature for the chromosomes of the common shrew (*Sorex araneus*)

BY

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(ISACC: International *Sorex araneus* Cytogenetics Committee)

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A G-band composite karyotype has been prepared for the common shrew (*Sorex araneus*). This includes multiple cut-outs of each chromosome arm (in different stages of contraction) derived from chromosome spreads prepared by a variety of methods by the different authors. The important features of each chromosome arm are described.

The nomenclature for the chromosome arms follows that of HALKKA *et al.* (1974) as clarified by FREDGA and NAWRIN (1977) and subsequent authors, *i.e.* italicised letters of the alphabet are used with *a* as the largest chromosome arm.

Different authors have used a variety of methods to describe the karyotype of (a) individuals and (b) the pattern of variation within populations. Also, definitions of chromosomal 'race' differ. We suggest a standardised scheme for the description of individuals, populations and chromosomal races.

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Un caryotype composite en bandes G a été préparé à partir de bras à différents niveaux de contraction, tirés de préparations que les présents auteurs ont obtenues par des méthodes variées.

La nomenclature des bras chromosomiques suit celle de HALKKA *et al.* (1974) modifiée par FREDGA et NAWRIN (1977) et généralement employée depuis. Les bras sont identifiés par des lettres en italique, *a* désignant le plus long d'entre eux.

La description (a) des caryotypes individuels et (b) du polymorphisme des populations obéit à des règles très variées suivant les auteurs. De plus, la définition des races chromosomiques diffère de l'un à l'autre. Nous suggérons un schéma standardisé pour ces descriptions, que ce soit au niveau des individus, des populations ou des races chromosomiques.

INTRODUCTION

The common shrew (*Sorex araneus*) has one of the most variable karyotypes of any mammal as a result of frequent Robertsonian (centric) fusion mutations (and probably other whole-arm rearrangements). Identification of regional forms or particular karyotypes within a population is near impossible with conventional staining techniques. Therefore, chromosome banding methods are an essential aid for the cytogeneticist working on *S. araneus*. The utility of such methods was realised as early as 1974, when HALKKA *et al.* prepared a nomenclature for the chromosomes of *S. araneus* based on Q-banding pattern. In this nomenclature, chromosome arms are described by letters of the alphabet with 'a' the largest and 'v' the smallest. FREDGA and NAWRIN (1977) used the same system for their G-band karyotypes, although by unfortunate circumstances they labelled the arm 'o' of HALKKA *et al.* by the letter 'm' and the arm 'm' of HALKKA *et al.* by the letter 'o'. Subsequent workers have generally used G-banding and all have followed the FREDGA and NAWRIN (1977) nomenclature system, except for Halkka and coworkers (HALKKA *et al.* 1987, HALKKA and SÖDERLUND 1987).

We recommend that in all future work the FREDGA and NAWRIN (1977) system is adopted, because of its widespread usage to date. This means that the recognised chromosome arm 'm' is smaller than 'o'; but there are also doubts as to whether 'g' is smaller than 'f' (SEARLE 1983) and whether 'i' is smaller than 'h' (V.T. Volobouev personal observation). We also recommend that

a.– italicised letters of the alphabet be used to identify chromosome arms or uniarmed chromosomes (*e.g. d*) where possible (*i.e.* in text and tables), to avoid confusion with words,

b.–the largest arm is given first in the description of biarmed chromosomes (*e.g. af*) without a numerical prefix, as a more logical and simplified system (closer to that adopted in the house mouse, *Mus musculus* which also displays considerable Robertsonian variation).

This paper refers only to the chromosomes of the common shrew, *Sorex araneus*. For a comparison between the karyotype of *S. araneus* and related species (*S. coronatus*, *S. granarius*) see VOLOBOUEV (1989).

THE G–BAND KARYOTYPE

Rather than present a simple diagrammatic idiogram, we decided to construct a composite karyotype from some of our better photomicrographs (Fig. 1 and 2). For each chromosome arm, three good quality pictures were selected, chosen for differences in chromosome contraction and staining pattern. Chromosome arms *g* - *r* are presented both in a dissociated state and as components of biarmed chromosomes. It should be noted that the chromosomes illustrated were prepared by a variety of techniques from different tissues after either direct preparation or culture *in vitro*. All chromosomes are reproduced at approximately the same magnification.

We hope that Figures 1 and 2 and accompanying text will be a valuable guide and reference. However, in order to help confirm identification of difficult chromosomes we urge new workers to make use of the many karyotypes and diagrammatic idiograms in the literature. Obviously, while a karyotype based on one chromosome spread may not illustrate such a wide range of possible staining patterns as we have presented here, one may be able to gauge more precisely the relative size of particular chromosome arms and the relative intensity of staining between arms under one particular staining regime. Further advice is freely available from any of the authors.

THE CHROMOSOMES
(Figures 1 and 2)

bc, *af*
These are the large invariant biarmed autosomes which are extremely easy to identify from their size and banding pattern.

de, *dv*
The 'X' chromosome (*de*), found in two copies in the female, is also an easily-identified, large biarmed chromosome. Males have one copy of the X and one copy of the Y_2 chromosome (and also one copy of the Y_1, see below). The long arm of the Y_2 chromosome is homologous to arm *d* of the X; there is also a distinct, but very small short arm (*v*) which is pale, like the centric region of the *e* arm of the X.

The variable chromosomes *g* – *r*
Chromosome arms *g* – *r* may occur as uniarmed chromosomes (with a centromere that appears terminal at the light microscope level) or as constituents of biarmed chromosomes. The chromosome arms *m* – *r*, while

being distinctly smaller than the other variable chromosome arms, are of rather similar size relative to each other (ranging from 2.4-3.4% of the haploid female genome: SEARLE 1983). These small chromosomes are sometimes rather difficult to distinguish from each other and from the Y_1 chromosome.

g

When the chromosomes are condensed, this arm has a very large dark block extending over most of the chromosome arm, but with a pale telomeric end. In longer chromosomes this large dark block resolves into two wide dark bands with a central narrow pale band. (Sometimes, in long chromosomes, the dark band furthest from the centromere stains more strongly, causing possible confusion with chromosome arm *i*). Also visible in long chromosomes is a narrow dark band within the pale telomeric region.

h

There is a narrow strong dark band at the centromere and, in longish chromosomes, other narrow and much less dark bands (normally four) are spaced evenly along the chromosome arm.

i

There are many dark bands along this arm. In long chromosomes, there are relatively strong dark bands near the telomere and the centromere.This arm is perhaps easiest identified from condensed chromosomes when interstitial dark bands coalesce to produce a very strong dark central band.

j

When a constituent of a biarmed chromosome, there are two narrow strong dark bands at the centromeric end and one or two less strong dark bands nearer the telomere. For certain chromosomal races, the centromere of *j* as a uniarmed chromosome appears terminal at the light microscope level and thus a similar pattern to that seen in biarmed chromosomes is observed (as illustrated in Fig. 2). However, in other chromosomal races the centromere in acrocentrics is located between the two major dark bands and a distinct short arm can be seen, which is particularly clear in conventionally-stained chromosome preparations.

k

This is an easily identified chromosome arm with a narrow strong dark band at the centromere and a wide strong dark band near the telomere.

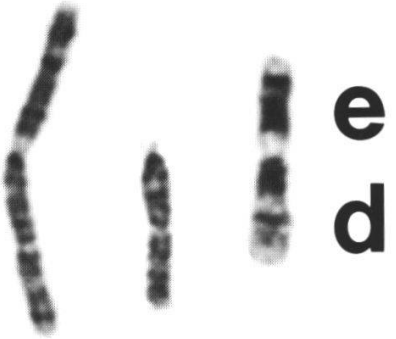
l

When the chromosomes are condensed, this arm has only a single wide dark band near the telomere. When the chromosomes are longer, a narrow pale band subdivides the wide dark block into two and a dark band is found near the centromere.

Figure 1.–Chromosome arms *a* - *i* (also, *v*, the short arm of Y_2). The unlabelled biarmed chromosomes are as follows (given left to right): *g* : *gm, gm* ; *h* : *hj, hi* ; *i* : *gi, hi.*

bc

af

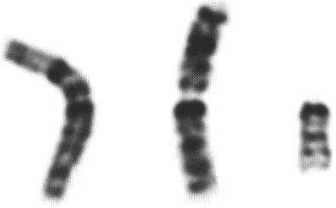


X Y_2 X

e

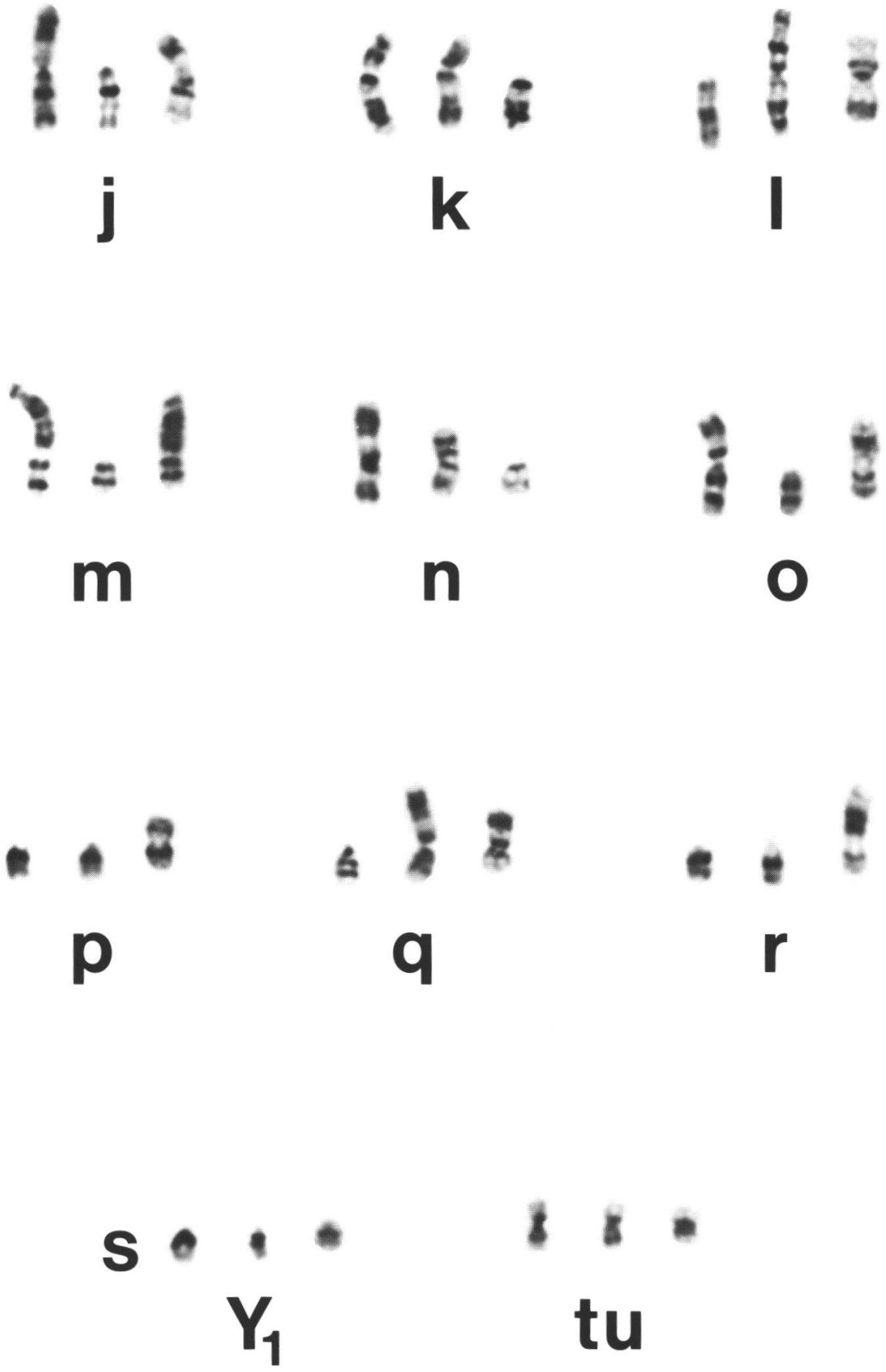
d

g



h

i


j
k
l
m
n
o
p
q
r
s
Y_1
tu

m, *o*

These chromosome arms are easily confused, as both are characterised by two narrow strong dark bands. However, in good preparations, several features should make identification unequivocal. Arm *m* is smaller, with narrower and more strongly-staining dark bands. There is a pale band at the telomere and a similarly sized interstitial pale band, but at most only a small pale band at the centromere. In chromosome arm *o* the centromeric, interstitial and telomeric pale bands generally appear to be of similar size. Studies in Germany, Finland and Britain suggest that chromosome arm *o* can have a telomeric nucleolus-organiser region (so that telomeric satellites may be seen: SEARLE 1983), not found on chromosome arm *m* (OLERT and SCHMID 1978, HALKKA and SÖDERLUND 1987, WALLACE and SEARLE 1990). In common shrews from near Aberdeen, U.K. ('Aberdeen' karyotypic race) C-banding revealed a telomeric band on chromosome arm *m* not found on *o* (SEARLE 1983).

n

This easily-identified arm has a narrow strong dark centromeric band and a wide, but less strong, dark band near the telomere.

p, *r* and *s*

These chromosome arms all have a main dark band close to the centromere and can be difficult to distinguish. Chromosome arm *s* is the Y_1 chromosome, one copy of which is present in males. A distinct short arm is often observed on the Y_1 chromosome (right-hand chromosome in Fig. 2) not seen on the uniarmed chromosomes *p* and *r*. Chromosome arm *p* is usually distinctly larger than chromosome arms *r* and *s*. The main dark band on *p* usually appears stronger and wider and closer to the centromere than that found on *r*, but not always. The dark band on *s* is also quite variable. A second, rather weaker dark band is almost always seen near the telomere on arm *r*, while such a band is not normal on *s* or on *p*, if the chromosomes are short. However, when the chromosomes are long, a faint telomeric dark band may also be present on *p*. In general, chromosome arms *p* and *r* are best distinguished when the chromosomes are short, in which case *p* can be seen to be slightly larger than *r* and the single dark band on *p* is distinctly darker and wider than either of the two dark bands on *r*. This is well-illustrated in Fig. 2 by chromosomes *pr* (given as an example of chromosome arm *p*) and *gr* (chromosome arm *r*). We also recommend that readers examine the karyotype in SEARLE and WILKINSON (1986). Other staining techniques may also help to distinguish chromosome arms *p*, *r* and *s*. As is usual for the Y chromosome in mammals, there is intense C-banding on chromosome arm *s* (SCHMID *et al.* 1982, SEARLE 1983); it is also late replicating and can be identified by RBG banding (SCHMID *et al.* 1982, VOLOBOUEV 1989). C-banding may also help to distinguish arms *p* and *r* (SEARLE 1983).

Figure 2. Chromosome arms *j* - *u*. The unlabelled biarmed chromosomes are as follows (given left to right): *j* : *jl, jl* ; *k* : *kr, kq*; *l* : *jl, jl* ; *m*: *gm, gm* ; *n* : *kn, mn* ; *o* : *no, io* ; *p* : *pr*; *q* : *kq, kq* ; *r* : *gr*.

q
As visualised down the light microscope this chromosome arm has a dark band actually on the centromere. In biarmed chromosomes at all stages of condensation, this centromeric staining is very distinctive. When the chromosomes are long, the arm has three clear dark bands and a pale band at the telomere.

tu
A distinctive small metacentric which is invariant in *S. araneus*. A large telomeric pale band constitutes about half of chromosome arm *u*.

Further Nomenclature Rules

In description of karyotypes and specific chromosomes of the common shrew, different workers often differ in the general cytogenetic terminology that they employ. We consider this to be understandable and admissible. Thus, uniarmed chromosomes may be described as 'acrocentrics' or 'telocentrics' according to the standpoint of individual workers. Similarly, biarmed chromosomes may be generalised as 'metacentrics' or else specified as 'metacentric', 'submetacentric' etc. Workers can describe the structural rearrangements that occur in the common shrew karyotype in the way that they think most appropriate. For example, the terms 'Robertsonian fusion', 'Robertsonian translocation' and 'centric fusion' all specify the same class of rearrangement and we believe that this is well-understood. Likewise, workers may choose how to describe the various forms of homozygous and heterozygous individuals that may occur, as long as they are careful with their definitions.

Thus, it is the nomenclature specific to the common shrew which we need to pursue further. We have already considered the nomenclature for individual chromosomes at some depth. With further regard to the sex chromosomes, the XX/XY_1Y_2 nomenclature will generally be clearer and more widely understood than the nomenclature of Halkka *et al.* (1974). However, on occasion it will be more appropriate to use *de* instead of 'X', *s* instead of 'Y_1' and *dv* instead of 'Y_2'.

Chromosomal Races

Different authors have different opinions as to what constitutes a 'chromosomal' (or 'karyotypic') race. Some may consider any homozygous form which has parapatric or allopatric distribution relative to other such forms, as a distinct 'race'. Others lump together a variety of such forms. While both strategies may be appropriate, we urge authors not to 'lump' or 'split' excessively and, when lumping, it is (a) desirable to lump forms likely to have common ancestry, (b) essential not to lump forms whose karyotypes include different metacentrics with monobrachial homology.

When a new chromosomal race is first described or when races are redefined, we recommend that a standardised description be presented, giving details of all the chromosomes and indicating any major within-race variation. An example of such standardised description is as follows:

'Oxford' race: XX/XY_1Y_2, *af*, *bc*, *hi*, *gm*, *jl*, *kq*, *no*, *pr*/*p*,*r*, *tu*.

Note that the chromosomes are given in approximate order of size. Within the Oxford race, two widespread forms are recognised: one characterised by the biarmed chromosome *pr* and the other characterised by the uniarmed chromosomes *p* and *r*.

As a further hypothetical possibility a karyotypic race described as:

XX/XY_1Y_2, *af*, *bc*, *hi*/*h*,*i*, *k*/*q*, *no*, *pr*, *g*, *j*, *l*, *m*, *tu* (note the general structure: sex chromosomes, biarmed chromosomes including variants, uniarmed chromosomes, *tu*).

This race is characterised by biarmed chromosomes *no* and *pr* and the uniarmed chromosomes *g*, *j*, *l* and *m* (the sex chromosomes and metacentrics *af*, *bc* and *tu* are invariant in the common shrew). Also, within the race there are two widespread forms (one characterised by the biarmed chromosome *hi* and the other characterised by the uniarmed chromosomes *h* and *i*) and a widespread polymorphism for arm combination *kq* such that both the biarmed chromosome *kq* and the uniarmed chromosomes *k* and *q* are found in the same population over a considerable proportion of the geographical area occupied by the race.

With the form of standardised description given above, we consider that only substantive variation within a chromosomal race should be recorded. The polymorphism found in the vicinity of hybrid zones with other races should not be included. (This polymorphism should be recorded when describing populations from the contact area, see below). Likewise, any widespread but low-level polymorphism (such as the polymorphism of arm combination *jl* in the Oxford race: SEARLE 1983) should not be included within the standardised description of a race.

The standardised description should be made when defining a new chromosomal race, but thereafter descriptions of karyotypes should be much shorter, including only those chromosome arms known to be variable in the complex of races under consideration. Thus, in Britain only chromosome arms *j*, *k*, *l*, *n*, *o*, *p*, *q* and *r* are known to be variable and therefore, in the context of Britain, the Oxford race may be described as having a karyotype *jl*, *kq*, *no*, *pr*/*p*,*r*.

Whenever a chromosomal race is newly described in the literature, we strongly recommend that a karyotype, constructed from cut-out chromosomes from one spread, be included in the publication.

POPULATIONS

If it should be desirable to provide a standardised description of a population (*i.e.* individuals from one particular collection site), the nomenclature is

similar to that for chromosomal races, except that all whole-arm variation (however low the frequency of certain forms), excluding aneuploids, should be recorded. However, the description should only include the variation that has actually been recorded and not that which has been predicted. Thus, the standardised description of an Oxford race population in East Anglia might be XX/XY_1Y_2, *af*, *bc*, *hi*, *gm*, *j/l*, *kq*, *no*, *p*, *r*, *tu*, meaning that individuals in this population are all homozygous for the biarmed chromosomes *hi*, *gm*, *kq* and *no* and for the uniarmed chromosomes *p* and *r*, while both the biarmed chromosome *jl* and the uniarmed chromosomes *j* and *l* occur within the population (*i.e.* there is a polymorphism for arm combination *jl*). Such a full description is usually unnecessary; thus, a maximally-polymorphic Oxford race population near to the 'Hermitage' race may adequately be described as *j/l*, *k/q*, *n/o*, *p/r*. Additional nomenclature is required to describe populations from within an inter-racial hybrid zone if the races are characterised by different biarmed chromosomes with monobrachial homology. Within the Oxford-Hermitage hybrid zone, in a population where all variable chromosome arms are known to be found in all possible biarmed and uniarmed states, the population would be described as *j/l*, *ko/kq/no/k/n/o/q*, *p/r*. However, if certain of the possible biarmed chromosomes have not been found at the site (*kq*, *pr*), the population should be described as *j/l*, *ko/no/k/n/o*, *p*, *q*, *r*. Note that biarmed chromosomes with monobrachial homology and any homologous uniarmed chromosomes are grouped in approximate order of size but with the biarmed chromosomes always given first.

INDIVIDUALS

Basically the same nomenclature as used for races and populations can be adapted for individuals. So, the standardised description of a homozygous male common shrew of the predominant geographic form of the Oxford race is 21, XY_1Y_2, *af*, *bc*, *hi*, *gm*, *jl*, *kq*, *no*, *pr*, *tu*. Two individuals which are heterozygous for arm combination *kq* and homozygous for the uniarmed chromosomes *k* and *q* would be described as *jl*, *k/q*, *no*, *pr* and *jl*, *no*, *pr*, *k*, *q*, respectively. Two types of Oxford-Hermitage hybrid could be *jl*, *ko/kq/no/n/q*, *pr* and *jl*, *ko/no/k/n*, *pr*, *q*, with the second hybrid having the uniarmed chromosomes *k* and *q* rather than the biarmed chromosome *kq*. As an alternative nomenclature for individuals whose karyotype includes metacentrics with monobrachial homology, the chromosomes may be ordered to show better the meiotic configuration that will be formed. For example, in terms of those chromosomes with monobrachial homology, the two hybrids above may be described as having karyotypes *q/qk/ko/on/n* and *k/ko/on/n*, respectively.

The nomenclature outlined for individuals is appropriate for variation that has arisen by Robertsonian (centric) fission or fusion or whole-arm reciprocal translocation. However, other chromosome variants may be found and we include a provisional nomenclature to cover these. This will be illustrated by ten examples:

1. 27, XY_1Y_2, $+Y_1$, + *p*, + 2 add, *af*, *bc*, *hi*, *gm*, *jl*, *kq*, *no*, *p*, *r*, *tu*
   Additional Y_1 and *p* (double trisomy) plus two additional chromosomes of unknown origin.

2. 21, XY_1Y_2, *af*, *bc*, *hi*, *gm*, *jl*, *kq*, *no*, *pr*, *tu* / 20, XY_1Y_2, - *no*, *af*, *bc*, *hi*, *gm*, *jl*, *kq*, *no*, *pr*, *tu* / 32, $XY_1Y_1Y_2Y_2$, 3 *af*, 3 *bc*, 3 *hi*, 3 *gm*, 3 *jl*, 3 *kq*, 3 *no*, 3 *pr*, 3 *tu*
   Mosaic with one cell clone of normal karyotype, another with monosomy for *no* and a third triploid.

3. 21, XY_1Y_2, *af*, *bc*, *hi*, *gm*, *kq*/cms (*kq*), *no*, *pr*, *tu* or as a shortened description: *kq*/cms(*kq*)
   Individual homozygous for biarmed chromosome *kq*, one copy of which has had a centromeric shift ('cms' only used for within-chromosome rearrangements).

4. inv(*kq*)
   Individual homozygous for biarmed chromosome *kq*, both copies of which carry an inversion.

5. *k*/dup,ins(*k*)
   Individual homozygous for the uniarmed chromosome *k*, on one copy of which a chromosomal segment has been duplicated and inserted elsewhere within the chromosome ('ins' it not used for movement of a centromere within a chromosome).

6. *kq*/del(*k*)/*q*
   Individual heterozygous for arm combination *kq* with a deletion on the uniarmed chromosome *k*.

7. 21, XY_1Y_2, *af*, *bc*, *hi*, *gm*, *kq*/rcp(*kq*,*tu*)/*tu*, *no*, *pr* or as a shortened description: *kq*/rcp(*kq*,*tu*)/*tu*
   Individual homozygous for the biarmed chromosome *kq* with one copy involved in a reciprocal translocation with *tu*.

8. *kq*/tan(*k*,*tu*)/*q*/*tu*
   Individual heterozygous for arm combination *kq* with one copy of *k* involved in a tandem fusion with *tu*.

9. ins(*k*,*k*)
   Individual homozygous for uniarmed chromosome *k* with material inserted from one chromosome to the other.

10. *kq*/*no*/dup,ins(*n*,*k*)/*o*/*q*
    Individual heterozygous for arm combinations *kq* and *no* with a duplication of part of chromosome *k* and insertion of that material into chromosome *n*.

CONCLUSION

In this paper we have attempted to be as comprehensive as possible in our description of chromosome arms, our nomenclature for chromosomes, and our nomenclature for the cytogenetic characteristics of chromosomal races, populations and individuals. Clearly, the success of our nomenclature will depend on whether it can be used simply and reliably and whether workers choose to use it. We hope to learn of any problem with the scheme and any suggested additions. As a committee we will continue our task of standardisation of descriptions of karyotypic variation in the common shrew, *Sorex araneus*.

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REFERENCES

FREDGA K. and NAWRIN J., 1977. Karyotype variability in *Sorex araneus* L. (Insectivora, Mammalia). *Chromosomes Today 6*: 153-161.

HALKKA L. and SÖDERLUND V., 1987. Random NOR-activation in polymorphic and stable chromosomes of *Sorex araneus* L. *Hereditas 106*: 293-294.

HALKKA L., HALKKA O., SKARÉN U. and SÖDERLUND V., 1974. Chromosome banding pattern in a polymorphic population of *Sorex araneus* from northeastern Finland. *Hereditas 76*: 305-314.

HALKKA L., SÖDERLUND V., SKARÉN U. and HEIKKILÄ J., 1987. Chromosomal polymorphism and racial evolution of *Sorex araneus* L. in Finland. *Hereditas 106:* 257-275.

OLERT J. and SCHMID M., 1978. Comparative analysis of karyotypes in European shrew species. I. The sibling species *Sorex araneus* and *S. gemellus*: Q-bands, G-bands, and position of NORs. *Cytogenet. Cell Genet. 20*: 308-322

SCHMID M., SCHEMPP W. and OLERT J., 1982. Comparative analysis of karyotypes in European shrew species. II. Constitutive heterochromatin, replication patterns, and sister chromatid exchanges in *Sorex araneus* and *S. gemellus*. *Cytogenet. Cell Genet. 34*: 124-135.

SEARLE J.B., 1983. Robertsonian chromosomal variation in the common shrew *Sorex araneus* L. *Ph. D. Thesis, University of Aberdeen.*

SEARLE J.B. and WILKINSON P.J., 1986. The XYY condition in a wild mammal: an XY/XYY mosaic common shrew (*Sorex araneus*). *Cytogenet. Cell Genet. 41*: 225-233.

WALLACE B.M.N. and SEARLE J.B., 1991. Synaptonemal complex studies of the common shrew (*Sorex araneus*). Comparison of Robertsonian heterozygotes and homozygotes by light microscopy. *Heredity 65*: 359-367.

VOLOBOUEV V.T., 1989. Phylogenetic relationships of the *Sorex araneus-arcticus* species complex (Insectivora, Soricidae) based on high-resolution chromosome analysis. *J. Heredity 80*: 284-290.