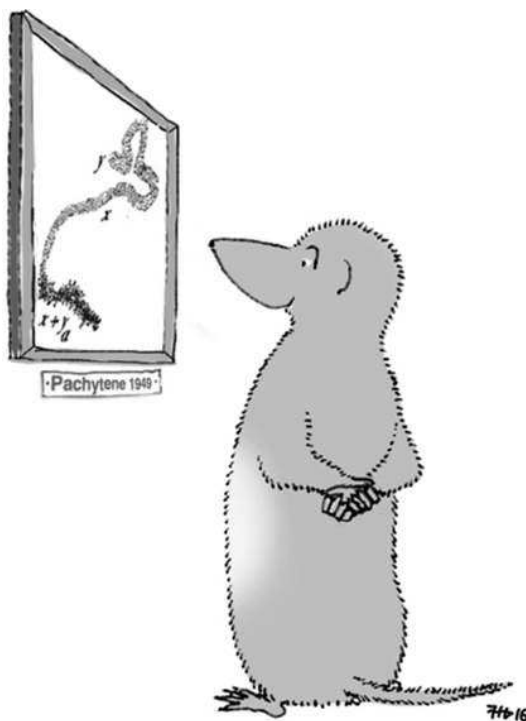


1

Milestones in Common Shrew Chromosomal Research

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Mr Robertson is fascinated by the first drawings of his amazing sex chromosomes.

This chapter reviews the history of chromosomal and related studies of the common shrew, which have been formative in the scientific discovery of karyotypic variation in mammals and its potential role in speciation.

Chromosomal research in the common shrew and related species has a history now almost 70 years long, beginning with the studies of R. Bovey, a pupil of the distinguished cytogeneticist R. Matthey, who worked at the University of Lausanne. Bovey (1948, 1949) examined specimens collected in Switzerland

and described for the first time the sex chromosome trivalent in male meiosis of common shrews. Paradoxically, the animals studied (two males only) in this pioneer work did not belong to the common shrew *Sorex araneus* itself but to a sibling species that is now recognised as *Sorex coronatus*.

The next research efforts took place in Britain. The Australian cytogeneticist G. B. Sharman came to Britain in the mid 1950s to work in the laboratory of C. E. Ford, with the aim of studying the unusual sex chromosomes that Bovey reported in *Sorex*. Sharman had a particular interest in multiple sex chromosome systems and described one such in the long-nosed potoroo, *Potorous tridactylus*, in Tasmania (Sharman *et al.*, 1950; Sharman, 1991). Sharman's (1956) studies on shrews in Britain involved true *S. araneus*, and he was able to confirm the occurrence of the XY_1Y_2 sex chromosome trivalent in males of this species. Thus, the 'X' chromosome was actually a compound of the true X chromosome and an autosome, the 'Y₁' the true Y chromosome and the 'Y₂' the unattached autosome (Sharman, 1991). Other investigations of British *S. araneus* revealed chromosome polymorphism within and between populations, representing one of the first examples of intraspecific variation of the karyotype in mammals (Ford *et al.*, 1957; Ford and Hamerton, 1958). These early studies on shrews were at the beginning of the 'modern era' of cytogenetics, contemporary with the discovery of the correct number of human chromosomes, which became possible by the simple expedient of hypotonic treatment of cells before fixation, meaning that the chromosomes became well separated from one another (Hsu, 1979).

Another zoologist from Lausanne, A. Meylan, continued investigations in common shrews in Switzerland and other European countries. He found a fascinating pattern of chromosomal variation in common shrews from various parts of western and central Europe (Meylan, 1960, 1964, 1965; Matthey and Meylan, 1961), and two distinct karyotypes were clearly differentiated, designated as Types A and B (Meylan, 1964). Karyotypes of these two types had previously been made (Type A by Bovey in Switzerland and Type B by Sharman in Britain). J. L. Hamerton and C. E. Ford noted that the shrews of Jersey had a karyotype similar to Bovey's Swiss shrews and very different from shrews in Britain, and would have had precedence for the discovery of the two distinct 'common shrew' karyotypes had they published earlier, but their account came out well after Meylan's (Ford and Hamerton, 1970; see also Meylan, 1960; Sharman, 1991). The monomorphic Type A and the polymorphic Type B karyotypes were very distinctive, and it is not surprising that they should be considered separate species; thus Ott (1968) described Type A as a new species, *Sorex gemellus*. The intraspecific variation described by Ford *et al.* (1957) and the interspecific variation described by Meylan (1964) spurred on new research efforts over a wide geographic area.

Chromosomal investigations continued in Britain by Ford, colleagues and family (P. J. Ford was the son of C. E. Ford and made a camping trip to the Scottish islands to collect shrews for karyotyping) (Ford and Graham, 1964; Ford and Hamerton, 1970; Ford, 1971). Studies also started in the eastern parts of the distribution range, in European Russia and Siberia (Orlov and Alenin, 1968; Kozlovsky, 1969, 1970, 1972; Orlov and Kozlovsky, 1969; Král and Radjabli, 1974; Orlov, 1974). New findings were reported from Scandinavia (Fredga, 1973; Halkka *et al.*, 1974; Fredga and Nawrin, 1977) and central and south-eastern Europe (Olert, 1973a; Dulić, 1977; Olert and Schmid, 1978; Král *et al.*, 1979). Extensive and intensive research began in Poland (Fedyk, 1980; Wójcik and Fedyk, 1985; Wójcik, 1986), and the first data were obtained from the former Czechoslovakia (Zima and Král, 1985) and Bulgaria (Belcheva and Kolevska, 1986).

Chromosomal banding was used early in common shrew cytogenetic research, applied to amenable karyotypes with low chromosome numbers (Halkka *et al.*, 1974; Král and Radjabli, 1974, 1976; Fredga and Nawrin, 1977; Olert and Schmid, 1978; Schmid *et al.*, 1982). Halkka *et al.* (1974) introduced a nomenclature for the chromosomes of *S. araneus* based on Q-banding pattern, and Fredga and Nawrin (1977) used the same system for G-band karyotypes. A slightly revised system was subsequently applied in other studies. The findings from Britain were enriched and synthesised in the PhD thesis by Searle (1983) and those from Siberia in the thesis of Volobouev (1983). These important achievements were published in a series of papers (Aniskin and Volobouev, 1980a, b, 1981; Searle, 1984a, b, 1988b; Searle and Wilkinson, 1987).

Another important PhD thesis originated in Switzerland, from Hausser (1976), demonstrating that Type A was a separate, morphologically distinct species, and this was followed by a series of papers in which support for the idea was elaborated. Although externally very similar, mandible morphometric differences allowed Meylan's Type A and B shrews to be distinguished (Hausser and Jammot, 1974; Hausser, 1978). Their taxonomy was also modified, with Type B remaining as *S. araneus* but with *S. coronatus* (the oldest species name available within the range of Type A) taking precedence over the short-lived designation of *S. gemellus* (Meylan and Hausser, 1978). This weird new Latin name for Type A common shrews (*S. coronatus* definitely does not bear a crown!) was due to the spring moulting pattern of the lost type specimen from which the species was first described. The mandibular differentiation of *S. araneus* and *S. coronatus* allowed their distribution to be mapped more widely (Olert, 1973b; Loch, 1977; Homolka, 1981; Mys *et al.*, 1985; Turni and Müller, 1996), and notable studies, enabled by the development of biochemical identification of living individuals, documented their ecological differentiation (Neet, 1989; Neet and Hausser, 1990).

In this period, it became clear that the unusual XX/XY_1Y_2 sex chromosome constitution demonstrated in *S. araneus* and *S. coronatus* occurs also in other related shrew species. This conspicuous feature is assumed to be inherited from the common ancestor as an apomorphy, and the species sharing the composite sex chromosomes represent a monophyletic lineage, called originally the *araneus-arcticus* group (Meylan and Hausser, 1973; Hausser, 1984), later recognised as the *S. araneus* group (Hausser, 1991; Zima *et al.*, 1998). Besides the west European *S. coronatus*, the *S. araneus* group includes the North American species *S. arcticus* and *S. maritimensis* (Meylan, 1968; Meylan and Hausser, 1973; Ivanitskaya and Kozlovsky, 1983; van Zyll de Jong, 1983; Volobouev and van Zyll de Jong, 1988), *S. tundrensis* with a Holarctic distribution (Kozlovsky, 1971; Král and Radjabli, 1976; Ivanitskaya and Kozlovsky, 1983; Okhotina, 1983; Meylan and Hausser, 1991), the eastern Palaearctic *S. daphaenodon* (Fedyk and Ivanitskaya, 1972), the Iberian *S. granarius* (Hausser *et al.*, 1975, 1985), the Caucasian *S. satunini* (Kozlovsky, 1973) and *S. asper* from Tien-Shan in central Asia (Ivanitskaya *et al.*, 1986). Chromosomal evolution and the phylogenetic relationships among the species of the *S. araneus* group were investigated by Volobouev (1989) and Volobouev and Dutrillaux (1991).

Other *Sorex* species, such as *S. isodon* and *S. samniticus*, were shown to have different karyotypes lacking the sex chromosome trivalent in males, even though they are phenotypically quite similar to the common shrew. This karyotypic difference demonstrates that they are not members of the *S. araneus* group (Kozlovsky and Orlov, 1971; Graf *et al.*, 1979), although *S. samniticus*, sharing up to seven chromosome arms with *S. araneus*, could be considered a sister species to the *S. araneus* group as a whole (Dannelid, 1994). Lapini and Testone (1998) described a new shrew species (*S. arunchi*) from north-eastern Italy, which they claimed to be distinct from but related to *S. araneus* (Lapini *et al.*, 2001). A year later, an erstwhile chromosomal race of *S. araneus* distributed in the central and southern Alps and in the Apennine peninsula was elevated to the species rank based on evidence for genetic isolation, and named *S. antinorii* (Brünner *et al.*, 2002a). The taxon described from north-eastern Italy probably belongs to this species, and molecular data call the validity of *S. arunchi* into question (Yannic *et al.*, 2012).

By the 1980s, the studies of chromosomal variation over the wide geographic range of *S. araneus*, discovering new chromosomally distinct forms ('chromosomal races') (e.g. Searle, 1984a; Wójcik and Fedyk, 1985; Chapter 5), went in tandem with studies examining the contacts allowing hybridisation of these forms (i.e. chromosomal hybrid zones). Almost without exception the chromosomal variation in *S. araneus* could be attributed to Robertsonian fusions and fissions and whole-arm reciprocal translocations, which greatly simplified the

interpretation of the phylogeny of the races and the chromosomal hybrid zones (see Chapters 3, 6 and 8). The first thorough documentation of intraspecific variation in *S. araneus* (Ford *et al.*, 1957), of a polymorphism within one population in southern England, was based on studies, it turned out, carried out in the middle of a hybrid zone between the later-named Oxford and Hermitage chromosomal races (Searle, 1986a). The shrews were captured in the vicinity of the government research laboratory of C. E. Ford, which itself was also located within the hybrid zone. As well as Britain (Searle, 1986a; Hatfield *et al.*, 1992), hybrid zone studies were also carried out in Sweden, Poland and Siberia (Frykman and Bengtsson, 1984; Fedyk, 1986; Aniskin and Lukianova, 1989; Fedyk *et al.*, 1991), and chromosomal heterozygotes characterised by complex meiotic configurations were documented in some zones, while other zones were dominated by novel chromosomal forms whose presence minimised the occurrence of complex heterozygotes. These findings were influential in wider considerations of hybridisation and speciation (Barton and Hewitt, 1985; Barton *et al.*, 2007). One of the surprising findings that emanated from these early hybrid zone (and also laboratory hybridisation) studies was that the fertility cost associated with chromosomal heterozygosity was not necessarily large (Searle, 1984c, 1986b; Garagna *et al.*, 1989; Mercer *et al.*, 1992; Wallace and Searle, 1994). Indeed, the overall picture from the early studies of hybridisation in *S. araneus* was that chromosomal rearrangements need not necessarily be viewed as agents for reproductive isolation.

Given these vibrant studies on various aspects of the cytogenetics of the common shrew and related species, it was natural for a forum to arise to promote discussion about shrew chromosomes. Appropriately the first international meeting on common shrew cytogenetics was held in Oxford, close to the place of the first discovery of chromosomal variation in the common shrew. It took place in 1987, and consisted of 23 participants from seven countries (Fig. 1.1). This successful conference, organised by J. B. Searle and P. J. Wilkinson, resulted in the founding of the International *Sorex araneus* Cytogenetics Committee (ISACC), with the aim to enhance and support research collaboration in this area, and to hold similar meetings on a regular basis. Through these meetings the community of researchers working on chromosomes and related topics in the common shrew has been remarkably interactive and collaborative. The work promoted and fostered by the ISACC has helped to make the common shrew one of the foremost mammalian models for the study of chromosome variation and evolution. After the promising start in Oxford, another seven meetings were organised successively at three-year intervals (Lausanne 1990, organised by J. Hausser; Brno 1993, organised by J. Zima; Uppsala 1996, organised by K. Fredga; Białowieża 1999, organised by J. M. Wójcik; Paris



Figure 1.1 Participants of the meeting 'Population and Evolutionary Cytogenetics of *Sorex araneus*' held in Oxford, 30–31 August, 1987. Upper row (standing), from right to left: Stanisław Fedyk, Karl Fredga, Vitaly Volobouev, Cornelis Neet, Walter Mills, Charles E. Ford, Peter King, Frédérique Bosshard, Bengt O. Bengtsson, Nick Barton, Ingrid Frykman, Simon Mercer, Erland Dannelid, Jan Zima. Lower row (squatting), from right to left: Pernille Wilkinson, Silvia Garagna, Jacques Hausser, Peter Vogel, Jacek Szymura, Carlo A. Redi, Mats Malmquist, Jan M. Wójcik. (Photo by Jeremy B. Searle).

2002, organised by V. Volobouev; Saint Petersburg 2005, organised by N. S. Bulatova and M. V. Zaitsev; and York 2008, organised by J. B. Searle). The proceedings of these meetings were published promptly in international journals (Hausser, 1991; Zima *et al.*, 1994; Fredga and Searle, 1996; Searle and Wójcik, 2000; Volobouev, 2003; Searle and Bulatova, 2007). The abstracts of other contributions, not included in the proceedings, were synoptically published in an article summarising the ISACC heritage by Searle *et al.* (2007).

The friendly and collaborative atmosphere of the community of cytogeneticists, molecular biologists, population geneticists, ecologists, ethologists and others produced significant achievements. One of the reasons for this success is that the ISACC had a very stable membership and all participating members contributed considerably through their commitment and hard work. Several international projects focused on the topic were supported by the European Union (EU: Marie

Curie Actions, INTAS) and by national resources that enabled investigations to extend to new geographic areas, involve new laboratories and employ advanced methodical approaches. The ISACC coordinated several joint efforts aimed at standardisation of various research aspects. A standardised nomenclature for the chromosomes of *S. araneus* was accepted (Searle *et al.*, 1991), rules of definition and nomenclature of chromosomal race were proposed and applied (Hausser *et al.*, 1994), and lists of the currently recognised races were compiled (Zima *et al.*, 1996; Wójcik *et al.*, 2003). The important paper on the standard chromosome nomenclature of the common shrew was republished nearly 20 years later (Searle *et al.*, 2010), to enable better accessibility to interested readers.

The collaborative research projects spawned and encouraged by the ISACC followed many different routes. The chromosomes of the common shrew were further characterised using various banding techniques and fluorescence *in situ* hybridisation (FISH) (Zhdanova *et al.*, 2005; Belonogova *et al.*, 2006; Minina *et al.*, 2007; Biltueva *et al.*, 2011). The intensive mapping of the geographic distribution of chromosomal races and their hybridisation continued in Britain, France, Switzerland, Germany, the Czech Republic, Poland, the Baltic states, Scandinavia, the Balkans, Ukraine, Belarus, European Russia and Siberia (White *et al.*, 2010; see Chapters 5 and 8 for detailed references). Fertility and meiotic studies reached new peaks, including the production of a recombination map (Borodin *et al.*, 2008) (see Chapter 7). Molecular and morphometric studies took great strides with studies of allozymes, mitochondrial sequences, microsatellites and geometric morphometric analyses of skulls, characterising colonisation history and gene flow across hybrid zones (Taberlet *et al.*, 1994; Wyttenbach *et al.*, 1999; Brünner *et al.*, 2002b; Ratkiewicz *et al.*, 2002; Anderson *et al.*, 2004, 2005; Jadwiszczak *et al.*, 2006; Polly, 2007; White and Searle, 2008; Yannic *et al.*, 2009; Horn *et al.*, 2012; Polly *et al.*, 2013) (see Chapters 4, 9 and 10). The studies performed on common shrews provided some important insights that led to the concept of ‘northern glacial refugia’ in phylogeography (Bilton *et al.*, 1998). As described in Chapter 11, a series of excellent molecular papers have convincingly shown a role for chromosomes in speciation (Basset *et al.*, 2006a, b, 2008), the ‘holy grail’ of shrew studies. Following a dedicated series of studies on gene mapping (Dixkens *et al.*, 1998; Serov *et al.*, 1998; Zhdanova *et al.*, 2003), the common shrew was selected as one of the first 17 species of mammals with a genome sequence (J. B. Searle, pers. comm.; Lindblad-Toh *et al.*, 2011). The particular female shrew used for that genome was collected by J. B. Searle from an island off the Lake District of England; the shrew showed particularly low heterozygosity and therefore was well-suited for the study. The island concerned, Piel Island, is famous as a place from where a pretender king tried to conquer the rest of the country in 1487 (and failed); the

‘Shrew of Piel’ had a more significant legacy than the ‘King of Piel!’ The shrew genome (further refined: see Chapter 3) offers tremendous opportunities for future research on *S. araneus*.

One of the strengths of the ISACC was that it brought together researchers ranging from Britain to Siberia, throughout the whole distribution of the common shrew. Since the last meeting the centre of gravity of shrew research has moved eastwards to Russia, which has become the new bastion of shrew cytogenetics, with much exciting new work (e.g. Bulatova *et al.*, 2011; Polyakov *et al.*, 2011; Matveevsky *et al.*, 2012; Shchipanov and Pavlova, 2013, 2017; Borisov *et al.*, 2014), but there has been less research from other countries (although see e.g. Mackiewicz *et al.*, 2017).

The overall knowledge on chromosomal variation in *S. araneus* and its evolutionary significance has been summarised in a number of review articles (Searle, 1988a, b, 1993; Wójcik and Zima, 1987; Bengtsson and Frykman, 1990; Wójcik, 1993; Fedyk, 1995; Searle and Wójcik, 1998; Wójcik *et al.*, 2002; Orlov *et al.*, 2004; Shchipanov and Pavlova, 2016a, b). The importance of the common shrew in the study of speciation has been evaluated and compared with another outstanding model, the house mouse (*Mus musculus*), which also displays remarkable chromosomal variation involving Robertsonian fusions and whole-arm reciprocal translocations (Capanna, 1991; Searle, 1993; White *et al.*, 2010; Macholán *et al.*, 2012; Lavrenchenko and Bulatova, 2016). Crowcroft (1957), Churchfield (1990), Hausser *et al.* (1990) and Churchfield and Searle (2008) have summarised general aspects of the biology of the common shrew, and a comprehensive review of the evolution of shrews is provided by a book edited by Wójcik and Wolsan (1998). The research into chromosomal variation of the common shrew and related topics is thus an exceptional example of fruitful international cooperation with significant achievements.

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