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History of discovery and recognition of XY_1Y_2 systems and chromosome polymorphism in mammals

BY

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Summary.—SHARMAN, G. B., 1991. History of discovery and recognition of XY_1Y_2 systems and chromosome polymorphism in mammals. *In*: J. HAUSSER, ed. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat.* 19.1: 7-12.

AGAR (1923) reported chromosome numbers 10 female, 11 male in the kangaroo *Macropus ualabatus* (= *Wallabia bicolor*). During meiosis the XY bivalent was “possibly sometimes independent but more often attached to one of the autosomes”. DARLINGTON (1937) included *M. ualabatus* amongst species with multiple sex chromosome systems and proposed that meiotic segregation was as in the XY_1Y_2 dioecious plant *Rumex*.

BOVEY (1948, 1949) reported a sex chromosome trivalent at meiosis in male *Sorex*. He did not have chromosome material from female animals but considered that the trivalent was composed of XY_1Y_2 chromosomes as in *M. ualabatus*. The published works of BOVEY and MATTHEY (1949) prompted new research on marsupial chromosomes and an XY_1Y_2 system was found in *Potorous tridactylus* (SHARMAN *et al.* 1950, SHARMAN and BARBER 1952). WAHRMAN and ZAHAVI (1955) described an XY_1Y_2 system in *Gerbillus*. The description of the XY_1Y_2 system of *Sorex araneus* was accompanied by the discovery of intrapopulation autosome polymorphism in the same species (SHARMAN 1956).

Résumé.—SHARMAN, G. B., 1991. Histoire de la découverte et de l'identification des systèmes XY_1Y_2 et du polymorphisme chromosomique chez les mammifères. *In*: J. HAUSSER, dir. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat.* 19.1: 7-12.

AGAR (1923) décrit des nombres chromosomiques de 10 (femelle) et 11 (male) chez le kangourou *Macropus ualabatus* (= *Wallabia bicolor*). Il reporte que durant la méiose le

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bivalent XY est “peut-être parfois indépendant mais le plus souvent attaché à un des autosomes”. DARLINGTON (1937) inclut *M. ualabatus* parmi les espèces à chromosomes sexuels multiples et suggère que la ségrégation méiotique fonctionne comme chez la plante dioïque *Rumex*, qui présente un complexe XY_1Y_2 .

BOVEY (1948, 1949) rapporte que le mâle de *Sorex* présente un trivalent sexuel à la méiose. Bien qu’il ne dispose pas de données concernant la femelle, il considère qu’il s’agit d’un complexe XY_1Y_2 comme chez *M. ualabatus*. La publication des travaux de BOVEY et MATTHEY (1949) stimula de nouvelles recherches sur les chromosomes des marsupiaux et un système XY_1Y_2 fut découvert chez *Potorous tridactylus* (SHARMAN *et al.* 1950, SHARMAN et BARBER, 1952). WAHRMAN et ZAHAVI (1955) ont décrit un système analogue chez *Gerbillus*. La description du système XY_1Y_2 de *Sorex araneus* s’accompagna de la découverte d’un polymorphisme autosomique dans les populations de la même espèce (SHARMAN 1956).

The first known mammalian multiple sex chromosome system was found in a marsupial of the kangaroo family Macropodidae. AGAR (1923) found ten mitotic chromosomes in female and eleven or twelve mitotic chromosomes in male *Macropus ualabatus* (= *Wallabia bicolor*, the swamp wallaby). Agar also discovered, without realizing its identity, the marsupial nucleolus organizing region (NOR) which, some 45 years later, was shown to be on the X chromosomes of kangaroos (HAYMAN and MARTIN 1969). The NOR appears as a non-staining gap and when close to the centromere region, as in the compound X chromosome of *W. bicolor* (Fig. 1.1: X-2-7a), it makes the chromosome appear to be composed of two distinct elements. In female *W. bicolor* the NOR is much less evident (SHARMAN 1973, Fig. 13).

Due to presence of the NOR the ancestral X and Y chromosome portions of the XY_1Y_2 trivalent may appear to form a separate bivalent at meiosis (Fig. 1.1) thus leading AGAR (1923) to conclude that the XY bivalent was ‘possibly sometimes independent’.

The chromosomes of *W. bicolor* were again examined in 1961 and the presence of an XY_1Y_2 male: XX female system was confirmed (SHARMAN 1961). Meanwhile DARLINGTON (1937) had included the species amongst plants and animals with multiple sex chromosome systems and proposed that meiotic segregation was as in XY_1Y_2 *Rumex*.

BOVEY (1948, 1949) found 23 mitotic chromosomes and ten bivalents and a trivalent at first division of meiosis in two male *Sorex* from Switzerland but he did not examine the chromosomes of female animals. Bovey’s first hypothesis assumed the occurrence of reciprocal translocation between an ancestral X chromosome and an autosome with loss of the ancestral Y and formation of a neo Y, the homologue of the translocated autosome. That hypothesis was rejected in favour of a second which assumed tandem fusion between long arm of a submetacentric X chromosome and an autosome to give, using BOVEY’S (1949) notation, an $XYYa$ system functionally equivalent to the XY_1Y_2 system of ‘*Macropus ualabatus*’.

Publications from the University of Lausanne (BOVEY 1948, MATTHEY 1949) stimulated Australian cytogeneticists to undertake new work on kangaroo chromosomes. In 1950 an XY_1Y_2 male: XX female system was found in the Tasmanian race of the rat-kangaroo, *Potorous tridactylus* (*P. t.*

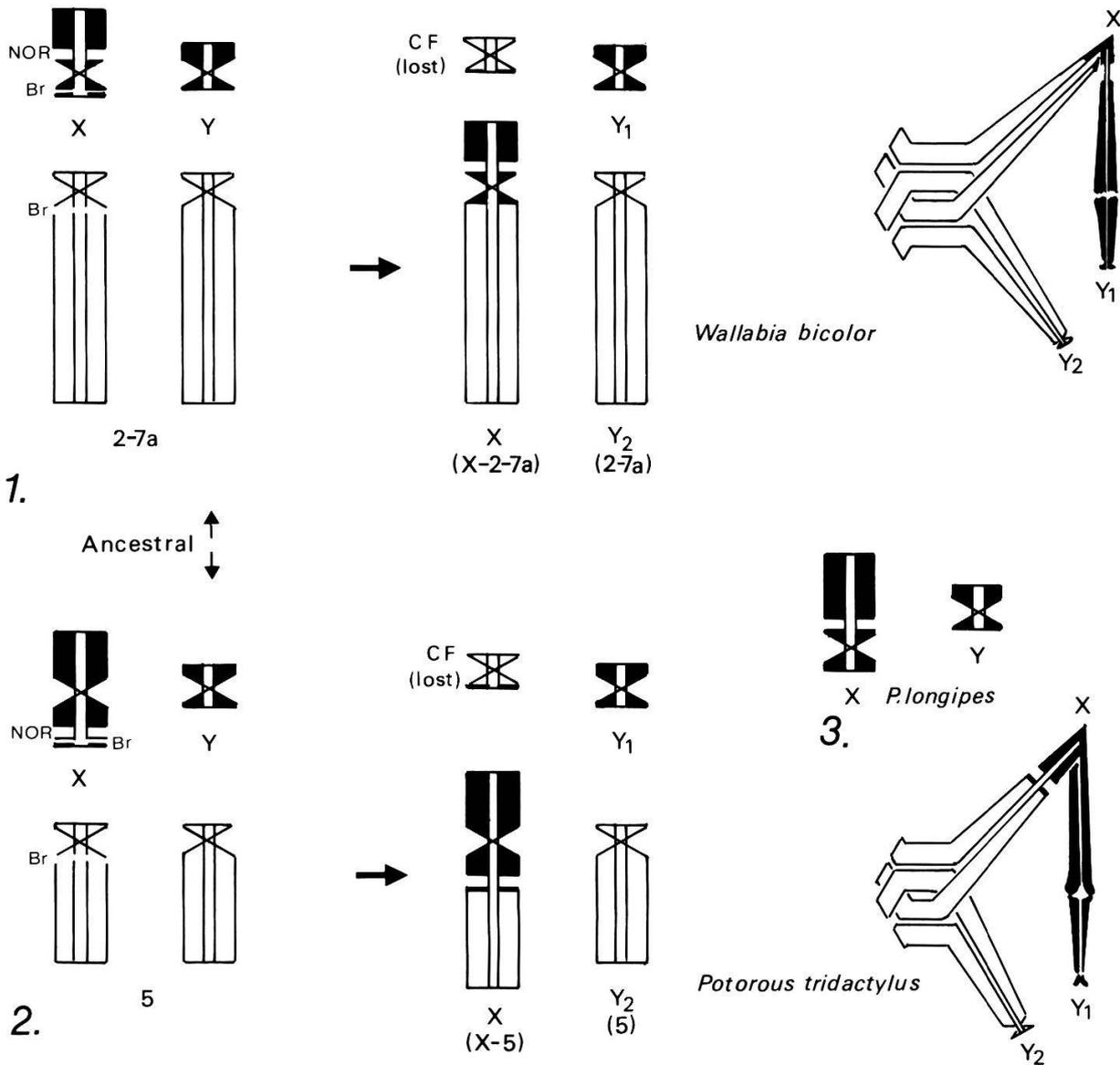


Figure 1.1.—Origin of the XY₁Y₂ multiple sex chromosome system of *Wallabia bicolor* (Marsupialia: Macropodidae) — «centric» fusion between ancestral X chromosome and autosome 2–7a to produce a compound X chromosome (X–2–7a) and Y₂ chromosome (2–7a). Orientation of trivalent at first metaphase shown at right. Br, point of chromosome breakage and reunion; CF, centric fragment; NOR, nucleolus organizing region.

2.—Origin of the XY₁Y₂ multiple sex chromosome system of *Potorous tridactylus* (Marsupialia: Potoroidae) — tandem fusion between ancestral X chromosome and autosome 5 to produce a compound X chromosome (X–5) and Y₂ Chromosome (5). Orientation of trivalent at first metaphase shown at right. Other lettering as in legend to Fig. 1.1.

3.—Sex chromosomes of *Potorous longipes* (Marsupialia: Potoroidae).

apicalis). The compound X chromosome (Fig. 1.2, X-5) was assumed to have arisen by tandem fusion between the short arm of an ancestral X and the long arm of an acrocentric (no. 5) autosome (SHARMAN *et al.* 1950, SHARMAN and BARBER 1952). A similar sex chromosome system was later found in the nominate subspecies, *P. t. tridactylus* (JOHNSTON and SHARMAN 1977). A search for the two further then described forms of *Potorous* proved fruitless and both are now presumed to be extinct.

Tandem fusions may induce a state of near or total sterility in their heterozygous carriers so WHITE (1954) argued that the compound X chromosomes of *Sorex* and *Potorous* must have arisen, initially, as 'centric' fusions. SEEBECK and JOHNSTON (1980) described, in *Potorous longipes* which had hitherto escaped detection as a separate species, eleven pairs of autosomes from which the five pairs and autosomal portion of the compound X of *P. tridactylus* may be derived. In *P. longipes* the NOR is in the long arm of the X chromosome proximal to the centromere (Fig. 1.3) so it is possible that the compound X of *P. tridactylus* did arise by 'centric' fusion followed by a further, within chromosome, rearrangement which mimics a tandem fusion (JOHNSTON *et al.* 1984).

Gerbillus gerbillus became the second eutherian mammal known to have XY_1Y_2 sex chromosomes (MATTHEY 1954, 1955, WAHRMAN and ZAHAVI 1955) but the mode of origin of the trivalent of that species remained conjectural. The occurrence of an XY_1Y_2 system in the *Sorex araneus* group (BOVEY 1948, 1949) was confirmed in *S. araneus* from Britain in 1956 and it was shown that the compound X was obviously the result of a near centric fusion (SHARMAN 1956). More importantly, however, *S. araneus* was shown to have intrapopulation chromosome polymorphism, more fully reported in the following year (FORD *et al.* 1957).

No attempt will be made to summarise the extensive and valuable series of papers on various aspects of the cytogenetics of *S. araneus* since the discovery of intrapopulation chromosome polymorphism in that species. Other studies on *Sorex* chromosomes have contributed to two important aspects of evolutionary biology. When C.E. Ford and J.L. Hamerton examined shrews from Jersey they did not find intrapopulation chromosome polymorphism but they did find karyotypes which, except for X chromosome morphology could be reconciled with those BOVEY (1949) had reported for shrews from Switzerland (see MATTHEY 1959 p. 205). MEYLAN (1965) later showed that the two "chromosome races", as they were then called, were sympatric without detected hybridization and suggested that two biological species might be included in what was currently named *Sorex araneus*. The chromosome differences between the two races heralded their recognition as distinct species. Twenty years ago it became evident that sex in mankind was not a matter of X and Y chromosomes but was determined purely by the presence or absence of a Y chromosome (FORD *et al.* 1959, JACOBS and STRONG 1959). SEARLE (1984) has added *S. araneus* to the growing list of eutherian and marsupial mammals in which a single Y chromosome determines basic gonadal sex and male reproductive anatomy, irrespective of the number of X chromosomes present.

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