

Zeitschrift:	Mémoires de la Société Vaudoise des Sciences Naturelles
Herausgeber:	Société Vaudoise des Sciences Naturelles
Band:	19 (1991-1999)
Heft:	1: The cytogenetics of the <i>Sorex araneus</i> group and related topics
 Artikel:	 History of discovery and recognition of XY1Y2 systems and chromosome polymorphism in mammals
Autor:	Sharman, G.B.
DOI:	https://doi.org/10.5169/seals-260072

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 05.08.2025

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

History of discovery and recognition of XY₁Y₂ systems and chromosome polymorphism in mammals

BY

G.B. SHARMAN¹

Summary.—SHARMAN, G. B., 1991. History of discovery and recognition of XY₁Y₂ 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 XY₁Y₂ 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 XY₁Y₂ chromosomes as in *M. ualabatus*. The published works of BOVEY and MATTHEY (1949) prompted new research on marsupial chromosomes and an XY₁Y₂ system was found in *Potorous tridactylus* (SHARMAN *et al.* 1950, SHARMAN and BARBER 1952). WAHRMAN and ZAHAVI (1955) described an XY₁Y₂ system in *Gerbillus*. The description of the XY₁Y₂ 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 XY₁Y₂ 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 rapporte que durant la méiose le

¹Logan Road 1, Evandale, Tasmania 7212, Australia.

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 XY₁Y₂.

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 XY₁Y₂ 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 XY₁Y₂ 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 XY₁Y₂ 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 XY₁Y₂ 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 XY₁Y₂ 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 XY₁Y₂ *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 XY₁Y₂ 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 XY₁Y₂ male: XX female system was found in the Tasmanian race of the rat-kangaroo, *Potorous tridactylus* (*P. t.*

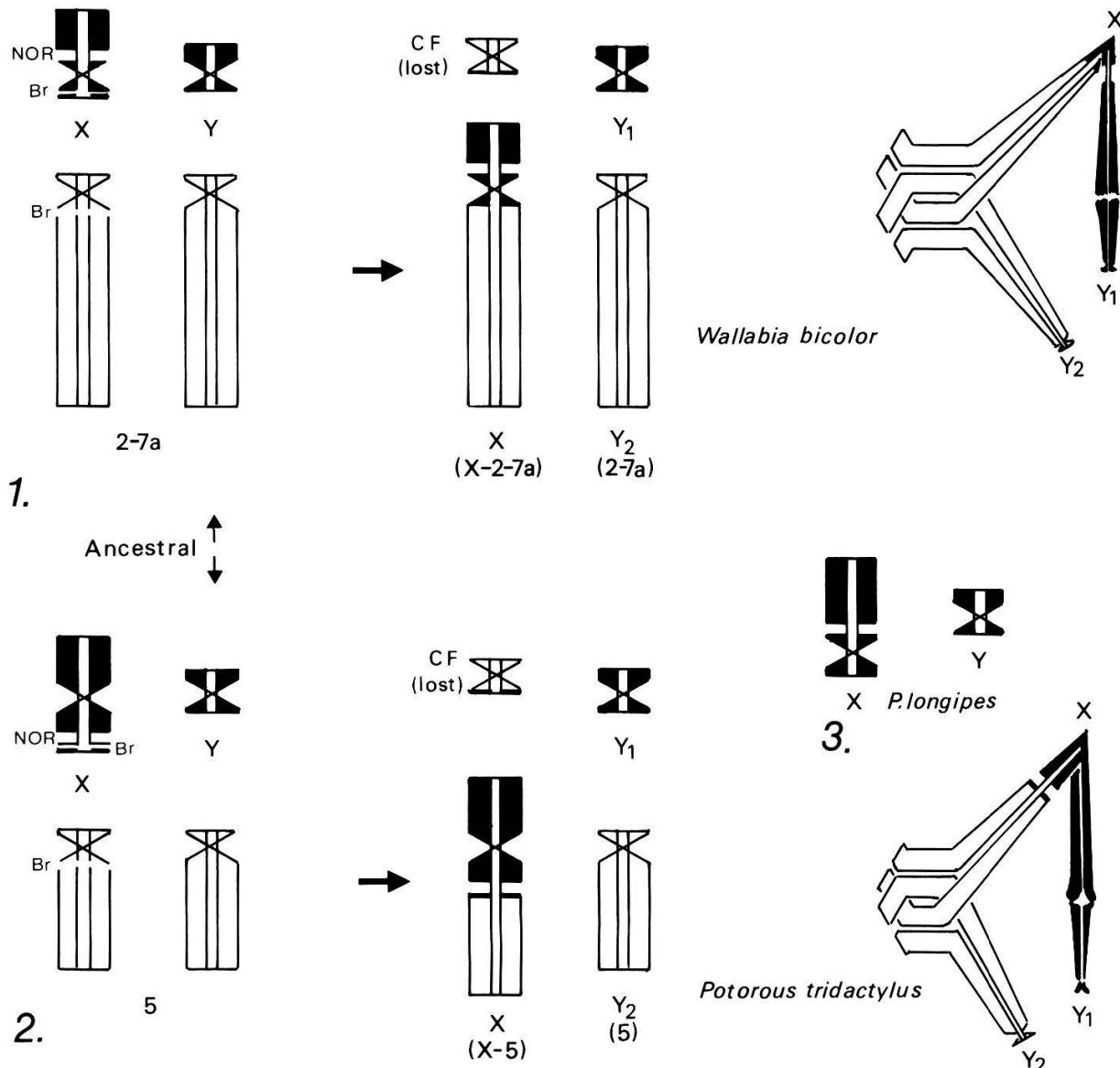


Figure 1.1.—Origin of the XY₁Y₂ multiple sex chromosome system of *Wallaby bicolor* (Marsupialia: Macropodidae) – «centric» fusion between ancestral X chromosome and autosome 2–7a to produce a compound X chromosome (X-2–7a) and Y₂ chromosome (2–7a). Orientation of trivalent at first metaphase shown at 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 *Protorous 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 XY₁Y₂ 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 XY₁Y₂ 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.

REFERENCES

- AGAR W.E., 1923. The male meiotic phase in two genera of marsupials (*Macropus* and *Petauroides*). *Quart. J. Micr. Sci.* 67: 183-202.
- BOVEY R., 1948. Un type nouveau d'hétérochromosomes chez un Mammifère: le trivalent sexuel de *Sorex araneus* L. *Arch. J. Klaus Stift. Vererbungs forsch.* 23: 507-510.
- BOVEY R., 1949. Les chromosomes des Chiroptères et des Insectivores. *Rev. Suisse Zool.* 56: 371-460.
- DARLINGTON C.D., 1937. Recent Advances in Cytology (2nd ed.). *Churchill, London.*
- FORD C.E., HAMERTON J.L. and SHARMAN G.B., 1952. Chromosome polymorphism in the common shrew. *Nature* 180: 392-393.
- FORD C.E., JONES K.W., POLANI P.E., DE ALMEIDA J.C.C. and BRIGGS J.H., 1959. A sex-chromosome anomaly in a case of gonadal dysgenesis (Turner's syndrome). *Lancet*, 1959 (i): 711-713.
- HAYMAN D.L. and MARTIN P.G., 1969. Cytogenetics of marsupials. In: K BENIRSCHKE, ed. Comparative Mammalian Cytogenetics, p. 191-217. *Springer Verlag, New York.*
- JACOBS P.A. and STRONG J.A., 1959. A case of human intersexuality having a possible XXY sex-determining mechanism. *Nature* 183: 302-303.
- JOHNSTON P.G., DAVEY R.J. and SEEBECK J.H., 1984. Chromosome homologies in *Potorous tridactylus* and *P. longipes* (Marsupialia: Macropodidae) based on G-banding pattern. *Aust. J. Zool.* 32: 319-324.
- JOHNSTON P.G. and SHARMAN G.B., 1977. Studies on Populations of *Potorous* Desmarest (Marsupialia) II. Electrophoretic, chromosomal and breeding studies. *Aust. J. Zool.* 25: 733-747.
- MATTHEY R., 1949. Les Chromosomes des Vertébrés. *Rouge, Lausanne.*
- MATTHEY R., 1954. Un cas nouveau de chromosomes sexuels multiples dans le genre *Gerbillus* (Rodentia-Muridae-Gerbillinae). *Experientia* 10: 464-465.
- MATTHEY R., 1955. Nouveaux documents sur les chromosomes des *Muridae*. Problèmes de cytologie comparée et de taxonomie chez les *Microtinae*. *Rev. Suisse Zool.* 62: 163-206.
- MATTHEY R., 1959. Formules chromosomiques de *Muridae* et de *Spalacidae*. La question du polymorphisme chromosomique chez les Mammifères. *Rev. Suisse Zool.* 66: 175-209.
- MEYLAN A., 1965. Répartition géographique des races chromosomiques de *Sorex araneus* L. en Europe (Mamm.-Insectivora). *Rev. Suisse Zool.* 72: 636-646.
- SEARLE J.B., 1984. A wild common shrew (*Sorex araneus*) with an XXY sex chromosome constitution. *J. Reprod. Fert.* 70: 353-356.
- SEEBECK J.H. and JOHNSTON P.G., 1980. *Potorous longipes* (Marsupialia: Macropodidae); a new species from Eastern Victoria. *Aust. J. Zool.* 28: 119-134.
- SHARMAN G.B., 1956. Chromosomes of the common shrew. *Nature* 177: 941-942.
- SHARMAN G.B., 1961. The mitotic chromosomes of marsupials and their bearing on taxonomy and phylogeny. *Aust. J. Zool.* 9: 38-60.
- SHARMAN G.B., 1973. The chromosomes of non-eutherian mammals. In: A.B. CHIARELLI and E. CAPANNA, ed. Cytotaxonomy and Vertebrate Evolution, p. 485-530. *Academic Press, London.*
- SHARMAN G.B. and BARBER, H.N., 1952. Multiple sex chromosomes in the marsupial *Protorous*. *Heredity* 6: 345-355.

- SHARMAN G.B., MC INTOSH A.J. and BARBER H.N., 1950. Multiple sex chromosomes in the marsupials. *Nature* 166: 996.
- WAHRMAN J. and ZAHAVI A., 1955. Cytological contributions to the phylogeny and classification of the rodent genus *Gerbillus*. *Nature* 175: 600.
- WHITE M.J.D., 1954. Animal Cytology and Evolution (2nd ed.). Univ. Press, Cambridge.