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REVIEW ARTICLE

# New species with B chromosomes discovered since 1980

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**Abstract** A survey of new species with B chromosomes (Bs), based on a collection of 900 publications, gives an estimate of 406 +B species discovered since they were last surveyed in 1980. There are 13 species of fungi, 136 plants and 257 animals with newly discovered Bs. The fungi, the single bird and the 100 species of fish are all new entries which were unknown in 1980. New species with B chromosomes continued to be found on a regular basis, and there is opportunity for trying to further our knowledge of the genomic properties and evolutionary significance of these enigmatic chromosomes.

**Keywords** B chromosomes · New species with Bs · Fungi · Plants · Animals

## Introduction

B chromosomes have been a subject of interest since they were first discovered in the plant bug insect *Metapodius*, by Wilson in 1906, 1907 [214, 215]. Wilson referred to them as supernumerary chromosomes, and listed their essential properties which we still recognise today as being their main diagnostic features: namely, may be present or absent, do not pair with the standard A chromosome set, no obvious effect on the phenotype, no relationship with environmental factors, and non-essential to their host organism. Their significance increased once they were discovered in maize, and named as B chromosomes (Bs) by Randolph in 1928 [163]. Their presence in rye [75] also stimulated fascination in their enigmatic properties in plants, and research in their properties grew steadily in both plants and animals as new cases were discovered. The significance of their role in the genome has been tracked through a number of reviews up to the present time, and a selection of the most recent significant publications are listed in Table 1, although it has to be said that in most cases we only know of their occurrence, and there is a blank canvas about their properties and biological significance. We have now reached the point where examples are coming to notice of a few species where Bs have functional genes (Table 1), although it still remains to be discovered what these B-genes actually do to account for the manifold effects on the phenotype of their hosts.

The present manuscript does not attempt to review the history of B chromosomes. The purpose is to update the number of species known to have Bs since the last such list was published in 1982 [93], and to add some comments on the diversity of newly discovered species since 1980. The *B Chromosome Atlas* in the B-book of 1982 [93] listed 1007 angiosperms, 9 gymnosperms and 263 animals known to carry Bs, a total of 1279 species. To compile this data a hard copy (reprints and photocopies) collection was made of 1373 papers of the world literature that could be traced over a period of ten years. Clearly it was not possible to trace every publication citing Bs during this time, and number of 1279 is therefore an underestimate.

The purpose of the current exercise is to augment this 1982 list based on a collection of publications produced since 1980, and to identify all new species with Bs recorded up to the present time (2017). This list is of necessity also an

In Honour of Prof AK Sharma, the Founder and Editor-in-Chief of the *Nucleus*

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**Table 1** Selected reviews on B chromosomes since 1980

| | |
|---|---|
| 1982 | Jones RN, Rees H. B *chromosomes*. 1982 Academic Press [93] |
| 2000 | Camacho JPM, Sharbel TF, Beukeboom LW. B chromosome evolution. Philos.Trans. R. Soc. Lond B 2000;355:163–178. [31] |
| 2005 | Camacho JPM. B chromosomes, in Gregory TR (ed): The Evolution of the Genome. 2005; pp. 223-286. (Elsevier, San Diego 2005). [32] |
| 2006 | Burt A, Trivers R. B chromosomes. In: Genes in Conflict: the Biology of Selfish Genetic Elements. 2006; Chapter 9: 325-380. University Press. [25] |
| 2009 | Carlson WR. The B chromosome of maize, in: J.L. Bennetzen, S. Hake (Eds.), Maize Handbook - Volume II: Genetics and Genomics, Springer, 2009; pp. 459–480. [35] |
| 2013 | Houben, Banaei-Moghaddam AM, Klemme S. Biology and Evolution of B Chromosomes. Springer, 2013; Chapter 10, in: Plant Genome Diversity Volume 2 (ed. IJ Leitch), pp 149-165. [85] |
| 2014 | Houben A, Banaei-Moghaddam AM, Klemme S, Timmis JN. Evolution and biology of supernumerary B chromosomes, Cell. Mol. Life Sci. 2014;71: 467–478. [86] |
| 2015 | Banaei-Moghaddam AM, Martis MM, Macas J, Gundlach H, Himmelbach A, Altschmied L, Mayer FX, Houben A. Genes on B chromosomes: old questions revisited with new tools. Biochimica et Biophysica Acta 2015;1849: 64-70. [8] |
| 2017 | Valente GT, Nakajima RT, Fantinatti BEA, Marques DF, Almeida RO, Simões RP, Martins C. B chromosomes: from cytogenetics to systems biology. Chromosoma. 2017; 126:73-81. [196] |
| 2017 | Houben A. B Chromosomes – A Matter of Chromosome Drive. Front. Plant Sci. 2017; 8210. doi:10.3389/fpls.2017.00210. p1-8. [87] |

underestimate, since some papers are not available, and certain journals do not give open access, and cannot be used.

## Materials and methods

The materials consist of the collection of the 900 publications used the compile the data in Table 2, and the method is the process of reading this extensive literature and extracting the names of the new species with B chromosomes from these papers.

## Results

The data are recorded in detail in Table 2 which shows 13 species of fungi, 136 plants and 257 animals, giving a total of 406 new species with Bs. Together with the 1980 data we reach a total of 1685 +B species known at the present time. A summary of the data in Table 2 is given in Table 3, and is discussed here in comparison with the 1982 lists.

## Discussion

The first noticeable feature for the species listed in Table 2 is the presence of the 13 species of fungi with Bs, whereas none were listed in 1982. The fungi are listed separately from the plants since they are taxonomically distinct and their chromosomes are not studied in the same way using light microscopy. It is also a controversial matter as to whether we can truly call them Bs, as discussed in details by Covert [47]. Their tiny chromosomes are studied by separating them using gel electrophoresis. The studies are mostly done on pathogenic species affecting crop plants, and a basic set can be identified as well as a number of additional small dispensable chromosomes which are the Bs (sometimes called minichromosomes). It is also a feature that some of the extra chromosomes in fungi have genes that encoding detectable phenotypes, as recently noted in the wheat pathogen *Mycosphaerella graminicola* which has 8 dispensable chromosomes carrying 17 genes, compared to the 770 genes on the essential ones [184].

The 27 species in four families of gymnosperms with Bs are reviewed by Muratova [135], while there were 9 cases in five families in 1980. Muratova described the Bs in mitotic tissues, on the basis of their smaller size and distinctive structural properties, although aspects of their behaviour at meiosis are known from other works. It is noteworthy that most species have only one or two Bs, and higher numbers are rare. Tashev [187] considers that the distribution the Bs in *Picea abies* is related with the geographic factors, and has a possible adaptive role. Precisely how this adaptation works is conjectural.

In the flowering plants, a modest 18 new species with Bs are recorded for the dicotyledons, compared with 510 in 1980. Two new families appear in the data, namely Malpighiaceae, with two species, and the Stylidiaceae with just one. In general, most of the papers in this section deal mainly with the occurrence of Bs, their size variation, chromatic status and meiotic behaviour. Sharma et al. [178] describe the transmission of the additional chromosome in a triplo-4 individual of *Plantago lagopus,* which is significant since it later led to a novel hypothesis on the origin of the Bs in this species. *Butea monosperma* (Leguminosae) is one of those rare cases of B chromosomes in tree species

**Table 2** Full list of new species found with Bs since 1980

| | | |
|---|---|---|
| **Fungi** (13) dispensable fragments from gel electrophoresis | | |
| *Alternaria alternata* | +Bs | Johnson et al. 2001 [92] |
| *Alternaria arborescens* | +Bs | Hu et al. 2012 [89] |
| *Cochliobolus carbonum* | +Bs | Covert 1998 [47] |
| *Cochliobolus heterostrophus* | +Bs | Tzeng et al. 1992 [194] |
| *Colletotrichum gloeosporioides* | +mini chrs. | Masel et al. 1993 [123] |
| *Fusarium oxysporum* | +Bs | Ma et al. 2010. [116] |
| *Fusarium poae* | +Bs | Vanheule et al. 2016 [198] |
| *Gibberella fujikuroi* | +Bs | Covert 1998 [47] |
| *Leptosphaeria maculans* | +mini Bs | Leclair et al. 1996 [106] |
| *Magaporthe grisea* | +Bs | Mills and McCluskey 1990 [132] |
| *Magnaporthe oryzae* | +mini chrs. | Chuma et al. 2003 [39] |
| *Mycosphaerella graminicola* | +dispensable chrs. | Stukenbrock et al. 2010 [184] |
| *Nectria haematococca* | +Bs | Mills and McCluskey 1990 [132] |
| **Plants (136)** | | |
| Gymnosperms (27) | | |
| *Cunninghamia lanceolate* | 2n = 22 + 1–2B | Muratova 2000 (Russian) [135] |
| *Cupressus glabra* | 2n = 22 + 1B | Muratova 2000 (Russian) [135] |
| *Cupressus arizonica* | 2n = 22 + 1–2B | Muratova 2000 (Russian) [135] |
| *Ephedra foliata* | 2n = 14 + fragment | Muratova 2000 (Russian) [135] |
| *Ephedra major* | 2n = 14 + 2B | Muratova 2000 (Russian) [135] |
| *Larix gmelinii* | 2n = 24 + 1B | Muratova 2000 (Russian) [135] |
| *Larix sukaczewii* | 2n = 24 + 1B | Muratova 2000 (Russian) [135] |
| *Metasequoia glyptostroboides* | 2n = 22 + 1B | Muratova 2000 (Russian) [135] |
| *Picea abies* | 2n = 24 + 0–4B | Tashev et al. 2014 [187] |
| *Picea ajanensis* | 2n = 24 + 1–3B | Muratova 2000 (Russian) [135] |
| *Picea albertiana* | 2n = 24 + 1–6B | Muratova 2000 (Russian) [135] |
| *Picea brachytyla* | 2n = 24 + 1B | Muratova 2000 (Russian) [135] |
| *Picea engelmannii* | 2n = 24 + 1–2B | Muratova 2000 (Russian) [135] |
| *Picea* x *fennica* | 2n = 24 + 1B | Muratova 2000 (iRussian) 135] |
| *Picea glauca* | 2n = 24 + 1–6B | Muratova 2000 (Russian) [135] |
| *Picea glehnii* | 2n = 24 + Bs | Hizume et al. 1988 [83] |
| *Picea jezoensis* | 2n = 24 + 1B | Muratova 2000 (Russian) [135] |
| *Picea meyeri* | 2n = 24 + 1–2B | Muratova 2000 (Russian) [135] |
| *Picea obovata* | 2n = 24 + 1–4B | Muratova 2000 (Russian) [135] |
| *Picea sitchensis* | 2n = 24 + 1–5B | Muratova 2000 (Russian) [135] |
| *Picea wilsonii* | 2n = 24 + 1–5B | Muratova 2000 (Russian) [135] |
| *Pinus sylvestris* | 2n = 24 + 1B | Muratova 2000 (Russian) [135] |
| *Podocarpus macrophyllus* | 2n = 38 + Bs | Hizume et al. 1988 [83] |
| *Pseudosuga mensieii* | 2n = 22 + 1B | Muratova 2000 (Russian) [135] |
| *Sequoia sempervirens* | 2n = 66 + 1,3B | Muratova 2000 (Russian) [135] |
| *Taxodium ascendens* | 2n = 22 + 2B | Muratova 2000 (Russian) [135] |
| *Taxus canadensis* | 2n = 24 + fragment | Muratova 2000 (Russian) [135] |
| Dicotyledons (18) | | |
| Caryophyllaceae | | |
| *Acanthophyllum laxiusculum* | 2n = 30 + 0–3B | Ghaffari and Bidmeshkipoor 2002 [72] |
| Compositae | | |
| *Guizotia scabra* | 2n = 30 + 1B | Hiremath and Murthy 1986 [82] |
| *Brachycome dichromosomatica* | 2n = 4 + 0–3B | John et al. 1991 [91] |
| *Centaurea kandavanensis* | 2n = 20 + 0–3B | Ghaffari 1998 [71] |

**Table 2** continued

| | | |
|---|---|---|
| Cruciferae | | |
| *Boechera holboellii* | 2n = 14,21 + Bs | Sharbel et al. 2005 [177] |
| *Boechera drummondii* | 2n = 14,21 + Bs | Sharbel et al. 2005 [177] |
| Leguminosae | | |
| *Butea monosperma* | 2n = 18 + 0–1B | Raghuvanshi and Pande 1985 [160] |
| Malpighiaceae | | |
| *Banisteria laevifolia* | 2n = 20 + Bs | Singhal et al. 1985 [182] |
| *Hiptage benghalensis* | 2n = 56 + B | Singhal et al. 1985 [182] |
| Plantaginaceae | | |
| *Plantago lagopus* | 2n = 12 + B | Sharma et al. 1985 [178] |
| Polygonaceae | | |
| *Rheum tanguticum* | 2n = 22 + 0–7B | Yanping et al. 2011 [218] |
| Solanaceae | | |
| *Nicotiana sylvestris* | 2n = 24 + Bs | Lespinasse et al. 1987 [107] |
| *Nierembergia aristata* | 2n = 16 + 0–5B | Acosta and Moscone 2011 [3] |
| *Solanum viarum* | 2n = 24 + Bs | Dnyansagar and Pingle 1979 [52] |
| Stylidiaceae | | |
| *Stylidium crossocephalum* | 2n = 14 (multiple genomes) + Bs | Coates 1980 [42] |
| Violaceae | | |
| *Hybanthus atropurpureus* | 2n = 16 + 0–4B | Seo et al. 2010 [176] |
| *Hybanthus communis* | 2n = 32 + 0–1B | Seo et al. 2010 [176] |
| *Hybanthus hasslerianus* | 2n = 32 + 0–1B | Seo et al. 2010 [176] |
| Monocotyledons (91) | | |
| Araceae | | |
| *Schismatoglottis irrorate* | 2n = 52 + 0–12B | Okada 1992 [141] |
| Colchicaeae | | |
| *Androcymbium gramineum* | 2n = 18 + 0–1B | Margeli et al. 1999 [121] |
| *Androcymbium rechingeri* | 2n = 18 + 2B | Margeli et al. 1999 [121] |
| *Androcymbium wyssianum* | 2n = 18 + 0–1B | Margeli et al. 1999 [121] |
| Compositae | | |
| *Ajania fruticulosa* | 2n = 36 + 0–2,4B | Garcia et al. 2006 [69] |
| *Artemisia ferganensis* | 2n = 36 + 1B | Valles et al. 2001 [197] |
| *Artemisia barrelieri* | 2n = 36 + Bs | Torrell et al. 2003 [190] |
| *Artemisia fragrans* | 2n = 18 + Bs | Torrell et al. 2003 [190] |
| *Artemisia pygmaea* | 2n = 18 + 1–4B | Garcia et al. 2007 [70] |
| *Artemisia rigida* | 2n = 18 + 1–4B | Garcia et al. 2007 [70] |
| *Artemisia tridentate* | 2n = 18 + Bs | Torrell et al. 2003 [190] |
| *Artemisia tripartite* | 2n = 18 + 1–4B | Garcia et al. 2007 [70] |
| *Artemisia herba-alba* | 2n = 18 + Bs | Torrell et al. 2003 [190] |
| *Leucanthemum ircutianum* | 2n = 36 + 3B | Love 1978 [114] |
| Commelinacae | | |
| *Tradescantia canaliculate* | 2n = 24 + 4B | Love 1978 [114] |
| *Tradescantia ohiensis* | 2n = 24 + Bs | Hauber 1987 [81] |
| Gramineae | | |
| *Aegilops crassa* | 2n = 28 + Bs | Sheidai et al. 2002 [179] |
| *Aegilops tripsacoides* | 2n = 14 + 2B | Friebe et al. 1995 [65] |
| *Aegilops triuncialis* | 2n = 14 + Bs | Sheidai et al. 2002 [179] |
| *Aegilops umbellulata* | 2n = 14 + Bs | Sheidai et al. 2002 [179] |
| *Agropyron cristatum* | 2n = 14 + 0–6B | Chen et al. 1993 [37] |
| *Agropyron mongolicum* | 2n = 14 + 0–6B | Chen et al. 1993 [37] |

**Table 2** continued

| | | |
|---|---|---|
| *Agropyron striatum* | 2n = 14 + 1B | Love 1978 [114] |
| *Briza humilis* | 2n = 14 + Bs | Murray 1984 [136] |
| *Oryza sativa indica* | 2n = 24 + 0–2B | Cheng et al. 2000 [38] |
| *Phalaris minor* | 2n = 14 + 0–1B | Love 1978 [114] |
| *Phleum himalaicum* | 2n = 14 + 0–1B. | Love 1978 [114] |
| *Sorghum stipoideum* | 2n = 10 + 2B | Wu 1992 [217] |
| *Polypogon fugax* | 2n = 21 + 1B. | Love 1978 [114] |
| Liliaceae | | |
| *Allium arvense* | 2n = 16 + Bs | Marcucci and Tornadore 1997 [120] |
| *Allium barthianum* | 2n = 16 + Bs | Hamoud et al. 1990 [80] |
| *Allium barsczewskii* | 2n = 32 + 1B | De Sarker et al. 1997 [50] |
| *Allium cardiostemon* | 2n = 16 + 1B | Hosseini and Go 2010 [88] |
| *Allium carrinatum* | 2n = 16 + 0–3B | Blagojević et al. 2007 [17] |
| *Allium cappadocicum* | 2n = 16 + 1B | De Sarker et al. 1997 [50] |
| *Allium consanguineum* | 2n = 16 + 0–1B | Love 1978 [114] |
| *Allium curtum* | 2n = 16 + 4B | Ozhatay and Johnson 1996 [147] |
| *Allium dictyoscordum* | 2n = 16 + 1B | Hosseini and Go 2010 [88] |
| *Allium dictyoprasum* | 2n = 16 + 1B | Ozhatay and Johnson 1996 [147] |
| *Allium ericetorum* | 2n = 16 + 1B | Wetschnig 1995 [212] |
| *Allium flavum* | 2n = 16 + 2B | Krahulcova 2003 [99] |
| *Allium fuscoviolaceum* | 2n = 16 + 1B | Ozhatay and Johnson 1996 [147] |
| *Allium griffithianum* | 2n = 16 + 0–1B | Dutta and Bandyopadhyay 2014 [53] |
| *Allium kuramense* | 2n = 16 + Bs | Fritsch et al. 1998 [67] |
| *Allium montanum* | 2n = 32 + 3B | Wetschnig 1992 [211] |
| *Allium przewalskianum* | 2n = 16 + 0–2B | Ao 2008 [5] |
| *Allium iranicum* | 2n = 32 + Bs | Ghaffari 2006 [73] |
| *Allium stamineum* | 2n = 16 + Bs | Loidl 1982 [111] |
| *Allium taeniopetalum* | 2n = 16 + 1B | Fritsch and Astanova 1998 [66] |
| *Allium tardans* | 2n = 16 + 0–1B | Tzanoudakis 1986 [193] |
| *Allium ursinum* | 2n = 14 + 0–1B | Vujosević and Blagojević 2002 [208] |
| *Bellevalia gracilis* | 2n = 8 + 0–3B | Ozhatay and Johnson 1996 [147] |
| *Bellevalia sarmatica* | 2n = 8 + 2–3B | Ozhatay and Johnson 1996 [147] |
| *Muscari armeniacum* | 2n = 18 + 0–3B | Ozhatay and Johnson 1996 [147] |
| *Muscari latifolium* | 2n = 18 + 1–2B | Ozhatay and Johnson 1996 [147] |
| *Muscari neglectum* | 2n = 36 + 1B | Ozhatay and Johnson 1996 [147] |
| *Ornithogalum montanum* | 2n = 18 + 1–2B | Ozhatay and Johnson 1996 [147] |
| *Ornithogalum balansae* | 2n = 24 + 1B | Ozhatay and Johnson 1996 [147] |
| *Ornithogalum ulophyllum* | 2n = 16 + 0–2B | Ozhatay and Johnson 1996 [147] |
| *Ornithogalum wiedemanni* | 2n = 14 + 0–2B | Ozhatay and Johnson 1996 [147] |
| *Allium przewalskianum* | 2n = 16 + 0–2B | Ao 2008 [5] |
| Orchidaceae | | |
| *Anoectochilus roxburghi* | 2n = 30 + Bs | Vij and Shekhar 1985 [202] |
| *Bulbophylum reptans* | 2n = 38 + Bs | Mehra and Sehgal 1974 [128] |
| *Calanthe puberula* | 2n = 40 + 1B | Mehra and Kashyap 1984 [129] |
| *Calanthe rubens* | 2n = 40 + 2B | Teoh 1980 [188] |
| *Calanthe veratrifolia* | 2n = 40 + 0–2B | Teoh 1980 [188] |
| *Cirrhopetalum viridiflorum* | 2n = 38 + 0–3B | Mehra and Kashyap 1978 [126] |
| *Coelogyne punctulata* | 2n = 38 + 0–2B | Mehra and Sehgal 1974 [128] |
| *Cypripedium cordigerurn* | 2n = 20 + 0–2B | Vij et al. 1986 [203] |
| *Dendrobium bicameratum* | 2n = 38 + 0–4B | Mehra and Kashyap 1984 [129] |

**Table 2** continued

| | | |
|---|---|---|
| *Dendrobium coelogvne* | 2n = 40 + 4B | Vatsala 1981 [199] |
| *Eria dalzellii* | 2n = 24 + 5–7B | Jorapur and Kulkarni 1979 [94] |
| *Eria microchilos* | 2n = 24 + 5–11B | Jorapur and Kulkarni 1979 [94] |
| *Eria paniculata* | 2n = 38 + 0–2B | Vij et al. 1986 [203] |
| *Eria spicata* | 2n = 40 + 2B | Vij and Shekhar 1985 [202] |
| *Gastrochilus pseudodistichum* | 2n = 38 + 2–7B | Vij et al. 1986 [203] |
| *Goodyera biflora* | 2n = 32 + 2B | Mehra and Kashyap 1979 [127] |
| *Goodyera fusca* | 2n = 32 + 2B | Mehra and Kashyap 1979 [127] |
| *Goodyera schlechtendaliana* | 2n = 30 + 1B | Mehra and Sehgal 1980 [130] |
| *Habenaria acuifera* | 2n = 42 + 0–2B | Mehra and Sehgal 1974 [128] |
| *Habenaria clavigera* | 2n = 46 + 0–2B | Vij et al. 1986 [203] |
| *Habenaria ensifolia* | 2n = 42 + 1–2B | Kashyap and Mehra 1983 [97] |
| *Habenaria stenostachya* | 2n = 42 + 2B | Mehra and Sehgal 1974 [128] |
| *Liparis langipes* | 2n = 22 + 6B | Vij et al. 1986 [203] |
| *Malaxis cylindrostachya* | 2n = 30 + 0–2B | Mehra and Kashyap 1984 [129] |
| *Peristylus fallax* | 2n = 30 + 0–3B | Mehra and Kashyap 1978 [126] |
| *Peristylus* goodyeroides | 2n = 46 + 1–3B | Mehra and Sehgal 1980 [130] |
| *Peristylus stanostachyus* | 2n = 42 + 1–2B | Mehra and Sehgal 1974 [128] |
| *Phaius mishmensis* | 2n = 44 + 2B | Vij and Shekhar 1985 [202] |
| *Pholidota articulata* | 2n = 40 + 0–3B | Mehra and Kashyap 1984 [129] |
| Polemoniaceae | | |
| *Lnanthus pachyphyllus* | 2n = 36 + 0–3B | Patterson 1980 [148] |
| **Animals (257)** | | |
| Platyhelminthes (1) | | |
| *Polycelis nigra* | n = 8 + Bs | Beukeboom et al.1996 [14] |
| Arthropods crustacea (8) | | |
| *Branchipus schaeffer* | n = 10 + 0–3 B | Beladjal et al. 2002 [11] |
| *Echinogammaru berilloni* | n = 26 + 1–9B | Lop 1989 [112] |
| *Homarus gammarus* | 2n = 95.5 modal no. + Bs | Hughes 1982 [90] |
| *Hyperiella dilatate* | 2n = 58 + 0–2B | Libertini and Lazzaretto 1993 [108] |
| *Nephrops norvegicus* | 2n = 131–140 + Bs | Deiana et al. 1996 [49] |
| *Palinurus elephas* | 2n = 138–150 + Bs | Salvadori et al. 2012 [169] |
| *Palinurus gilchristi* | 2n = 120–132 + 3–7B | Coluccia et al. 2005 [45] |
| *Palinurus mauritanicus* | 2n = 138–150 + Bs | Coluccia et al. 2004 [44] |
| Arthropods-Insecta (53) | | |
| Arachnida | | |
| *Metagagrella tenuipes* | 2n = 18 + 0–19B | Tsurusaki 1993 [191] |
| Coleoptera | | |
| *Dichotomius geminatus* | 2n = 18, Xy + 1B | Cabral-de-Mello et al. 2010 [26] |
| *Dichotomius sericeus* | 2n = 18, Xy + 0–2B | Amorim et al. 2016 [4] |
| Diptera | | |
| *Drosophila nasuta albomicana* | 2n = 6 + 0–3B | Ramachandra and Ranganath 1985 [161] |
| *Drosophila subsilvestris* | 2n = 6 + 0–5B | Gutknecht et al. 1995 [79] |
| *Megaselia scalaris* | 2n = 6 + Bs | Wolf et al. 1991 [216] |
| *Simulium vernum* | 2n = 6 + Bs | Brockhouse et al. 1989 [22] |
| *Simulum juxtacrenobium* | 2n = 6 + Bs | Brockhouse et al. 1989 [22] |
| *Simulium costatum* | 2n = 6 + Bs | Brockhouse et al. 1989 [22] |
| Hemiptera | | |
| *Alebra albostriella* | 2n = 22 + XO♂ + 0–2B | Kuznetsova et al. 2013 [102] |
| *Alebra wahlberg* | 2n = 22 + XO♂ + 0–2B | Kuznetsova et al. 2013 [102] |

**Table 2** continued

| | | |
|---|---|---|
| Homoptera | | |
| *Cacopsylla peregrine* | 2n = 24 + X + B | Nokkala et al. 2003 [139] |
| *Psylla foersteri* | 2n = 14 + X | Nokkala et al. 2000 [138] |
| *Rhinocola aceris* | 2n = 10 + X + 0–3B | Kuznetsova et al. 1997 [101] |
| Hymenoptera | | |
| *Partamona cupira* | 2n = 34♀, n = 17♂ + 0–1B | Brito et al. 2010 [21] |
| *Partamona criptica* | 2n = 34♀, n = 17♂ + Bs | Tosta et al. 2014 [192] |
| *Partamona helleri* | 2n = 34♀, n = 17♂ + 0–4B | Tosta et al. 2014 [192] |
| *Partamona rustica* | 2n = 34♀, n = 17♂ + Bs | Tosta et al. 2014 [192] |
| *Nasonia vitripennis* | 2n = 10♀, n = 5♂ + Bs | Werren and Assem 1986 [213] |
| *Tetragonisca fiebrigi* | 2n = 34♀, n = 17♂ + 2B | Barth et al. 2011 [10] |
| *Trichogramma kaykai* | 2n = 10♀, n = 5♂ + 1B | Stouthamer et al. 2001 [183] |
| *Trypoxylon albitarse* | 2n = 32♀, n = 16♂ + 2B | Araujo et al. 2001 [6] |
| Neuroptera | | |
| *Hemerobius marginatus* | 2n = 12 + 0–2Bs | Nokkala 1986 [137] |
| Lepidoptera | | |
| *Euphydryas colon* | n (♂/♀) = 31 + 1–6B | Pearse and Ehrlich 1979 [152] |
| Orthoptera | | |
| *Abracris flavolineata* | 2n = 23 XO♂, 24XX♀ + 0–2B | Bueno et al. 2013 [23] |
| *Anacridium aegyptium* | 2n = 23 XO♂, 24XX♀ + Bs | Abdel-Haleem et al. 2009 [1] |
| *Aiolopus strepens* | 2n = 23 XO♂, 24XX♀ + Bs | Suja et al. 1987 [186] |
| *Arcyptera fusca* | 2n = 21XO♂, 22XX♀ + 0–4B | Lopez-Fernandez and Gosalvez 1983 [113] |
| *Aretza* sp. 1 | 2n = 21XO♂, 22XX♀ + Bs | King and John 1980 [98] |
| *Chorthippus vagans* | 2n = 15XO♂, 16XX♀ + Bs | Cabrero and Camacho 1987 [27] |
| *Ctenodecticus granatensis* | 2n = 25XO♂, 26XX♀ + Bs | Camacho et al. 1981a [29] |
| *Cylindrotettix santarosae* | 2n = 21XO♂ + B | Confalonieri and Bidau 1986 [46] |
| *Cylindrotettix obscurus* | 2n = 21XO♂ +Bs | Confalonieri and Bidau 1986 [46] |
| *Dasymys rufulus* | 2n = 36 + 0–3B | Volobujev et al. 2000 [207] |
| *Dichroplus elongatus* | 2n = 21XO♂, 22XX♀ + Bs | Remis and Vilardi 1986 [165] |
| *Dichroplus pratensis* | 2n = 19XO♂, 20XX♀ + Bs | Bidau 1987 [16] |
| *Eumigus monticola* | 2n = 19XO♂, 20XX♀ + 0–1B | Ruiz-Ruano et al. 2016 [167] |
| *Euthystira brachyptera* | 2n = 17XO♂, 18XX♀ + Bs | Fletcher and Hewitt 1980 [62] |
| *Eyprepocnemis plorans* | 2n = 23XO♂, 24XX♀ + Bs | Camacho et al. 1980 [28] |
| *Hemideina crassidens crussicruris* | 2n = 15XO♂, 22XX♀ + 2B | Morgan-Richards 2000 [134] |
| *Heteracris littoralis* | 2n = 21XO♂, 22XX♀ + Bs | Cano and Santos 1988 [33] |
| *Leptysma* sp. | 2n = 14neo X, neo Y + 1B | Colombo and Remis 1997 [43] |
| *Leptysma argentina* | 2n = 19XO♂, 20XX♀ + 1B | Colombo and Remis 1997 [43] |
| *Metuleptea brevicornis adspersa* | 2n = 21XO♂, 22XX♀ + 1B | Grieco and Bidau 1999 [78] |
| *Omocestus bolivari* | 2n = 17XO♂, 18XX♀ + Bs | Camacho et al. 1981b [30] |
| *Omocestus burri* | 2n = 17XO♂, 18XX♀ + 0–3B | Santos et al. 1993 [171] |
| *Podisma kanoi* | 2n = 23XO♂, 24XX♀ + 1B | Bugrov et al. 2007 [24] |
| *Psophus stridulus* | 2n = 21XO♂, 22XX♀ + Bs | Suja et al. 1986 [185] |
| *Pycnogaster cucullate* | 2n = 27XO♂, 28XX♀ + Bs | Sentis and Fernandez-Piqueras 1985 [175] |
| *Rhammatocerus brasiliensis* | 2n = 23XO♂, 24XX♀ + 0–1B | Oliveira et al. 2011 [142] |
| *Sinipta dalmani* | 2n = 21XO♂, 22XX♀ + 1B | Colombo and Remis 1997 [43] |
| *Sphingonotus coerulans* | 2n = 23XO♂, 24XX♀ + 0–4B | Gosalvez et al. 1985 [74] |
| *Zoniopoda tarsata* | 2n = 23XO♂, 24XX♀ + Bs | Vilardi 1986 [204] |
| Chordates amphibia (29) | | |
| *Ambystoma jeffersonianum* | 2n = 28 + 0–1B | Green 2004 [77] |
| *Amolops liangshanensis* | 2n = 26 + 0–1B | Green 2004 [77] |

**Table 2** continued

| | | |
|---|---|---|
| *Chiropterotriton arboreus* | 2n = 26 + 0–2B | Green 2004 [77[ |
| *Chiropterotriton chiropterus* | 2n = 26 + 0–7B | Green 2004 [77] |
| *Chiropterotriton dimidiatus* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Chiropterotriton lavae* | 2n = 26 + Bs | Green 2004 [77] |
| *Chiropterotriton* sp. | 2n = 26 + Bs | Green 2004 [77] |
| *Dendropsophus nanus* | 2n = 30 + 1B | Medeiros et al. 2006 [125] |
| *Dendrotriton rabbi* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Dicamptodon tenebrosus* | 2n = 28 + 0–10B | Brinkman et al. 2000 [20] |
| *Discoglossus pictus* | 2n = 28 + 0–2B | Green 2004 [77] |
| *Gastrotheca espeletia* | 2n = 26 + 1–9B | Schmid et al. 2002 [173] |
| *Hyla sp. aff. circundata* | 2n = 24 + 1B | Baldissera et al. 1993 [7] |
| *Hypsiboas albopunctatus* | 2n = 22 + 0–3B | Ferro et al. 2012 [60] |
| *Lineatriton lineola* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Megaelosia massarti* | 2n = 28 + 1B | Rosa et al. 2003 [166] |
| *Nototriton picadoi* | 2n = 26 + 0–4B | Green 2004 [77] |
| *Oedipina poelzi* | 2n = 26 + 0–2B | Green 2004 [77] |
| *Oreobates barituensis* | 2n = 22 + 1–2B | Ferro et al. 2016 [61] |
| *Oreobates berdemenos* | 2n = 22 + Bs | Ferro et al. 2016 [61] |
| *Oreobates discoidalis* | 2n = 22 + Bs | Ferro et al. 2016 [61] |
| *Physalaemus olfersii* | 2n = 22 + 0–1B | Milani et al. 2011 [131] |
| *Pseudoeurycea rex* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Pseudoeurycea smithi* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Rana temporaria* | 2n = 26 + 0–4B | Green 2004 [77] |
| *Scaphiopus hammondi* | 2n = 28 + 0–1B | Green 2004 [77] |
| *Thorius dubitus* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Thorius narisovalis* | 2n = 26 + 0–1B | Green 2004 [77] |
| *Thorius pennatulus* | 2n = 26 + 0–1B | Green 2004 [77] |
| Chordates reptilia (12) | | |
| *Anniella pulchra* | 2n = 20 + 0–4B | Bertolotto et al. 2004 [13] |
| *Enyalius bilineatus* | 2n = 36 + 0–2B | Bertolotto et al. 2002 [12] |
| *Gymnodactylus amarali* | 2n = 38–40 + 0–1B | Pellegrino et al. 2009 [154] |
| *Lacerta parva* | 2n = 24 + 0–2B | Kupriyanova 1980 [100] |
| *Lacerta lepida* | 2n = 30 + 0–1B | Bertolotto et al. 2004 [13] |
| *Micrablepharus atticolus* | 2n = 50 + 0–3B | Yonenaga-Yassuda and Rodrigues 1999 [222] |
| *Mabuya mabouya* | 2n = 30 + 0–1B | Bertolotto et al. 2004 [13] |
| *Micrablepharus atticolus* | 2n = 50 + 0,1B | Bertolotto et al. 2004 [13] |
| *Micrablepharus maximiliani* | 2n = 50 + 0–1B | Yonenaga-Yassuda and Rodrigues 1999 [222] |
| *Nothobachia ablephara* | 2n = 62 + 0–2B | Pellegrino et al. 1999 [153] |
| *Scelopurus graciosus* | 2n = 30 + 0,1B | Bertolotto et al. 2004 [13] |
| *Takydromus sexlineatus* | 2n = 40 + 0,2B | Bertolotto et al. 2004 [13] |
| Chordates pisces (100) | | |
| *Alburnus alburnus* | 2n = 50 + 0–2B | Schmid et al. 2006 [174] |
| *Apareiodon piracicabae* | 2n = 54 + 0–1B | Falcao et al.1984 [55] |
| *Apareidon piracicabae* | 2n = 54 + 0–1B | Carvalho et al. 2008 [36] |
| *Apteronotus albifrons* | 2n = 24 + 0–4B | Carvalho et al. 2008 [36] |
| *Astatotilapia latifasciata* | 2n = 44 + 0–2B | Ramos et al. 2016 [162] |
| *Astyanax altiparae* | 2n = 50 + 1B | Carvalho et al. 2008 [36] |
| *Astyanax bockmanni* | 2n = 50 + 0–2B | Daniel et al. 2012 [48] |
| *Astyanax eigenmanniorum* | 2n = 50 + 0–1B | Torres-Mariano 2008 [189] |
| *Astyanax fasciatus* | 2n = 46 + 1B | Moreira-Filho 2001 [133] |

**Table 2** continued

| | | |
|---|---|---|
| *Astyanax aff. Mexicanus* | 2n = 50 + 0–2B | Carvalho et al. 2008 [36] |
| *Astyanax paranae* | 2n = 50 + 0–1B | Silva et al. 2014 [181] |
| *Astyanax scabripinnis* | 2n = 50 + 1–2B | Salvador and Moreira-Filho 1992 [168] |
| *Astyanax schubarti* | 2n = 36 + 1B | Moreira-Filho 2001 [133] |
| *Astyanax* sp. | 2n = 50 + 1–2B | Carvalho et al. 2008 [36] |
| *Bergiaria westermani* | 2n = 56 + 0–5B | Salvador and Moreira-Filho 1992 [168] |
| *Callichthys callichthys* | 2n = 58 + Bs | Oliveira et al. 1993 [144] |
| *Characidium cf. fasciatum* | 2n = 50 + 0–4B | Maistro et al. 1998 [118] |
| *Characidium gomesi* | 2n = 50 + Bs | Maistro et al. 2004 [119] |
| *Characidium oiticicai* | 2n = 50 + 0–3B | Carvalho et al. 2008 [36] |
| *Characidium* sp. | 2n = 50 + 0–2B | Carvalho et al. 2008 [36] |
| *Characidium zebra* | 2n = 50 + 0–1B | Venere et al.1999 [200] |
| *Cichla monoculus* | 2n = 48 + 0–3B | Feldberg et al. 2004 [57] |
| *Cichla* sp. | 2n = 48 + 0–3B | Feldberg et al. 2004 [57] |
| *Corydoras aeneus* | 2n = 60 + 0–3B | Oliveira et al.1988 [143] |
| *Crenicichla lepidota* | 2n = 48 + 0–3B | Pires et al. 2015 [156] |
| *Crenicichla reticulata* | 2n = 48 + 0–3B | Feldberg et al. 2004 [57] |
| *Cyphocharax modestus* | 2n = 54 + 0–2B | Gravena et al. 2007 [76] |
| *Cyphocharax nageli* | 2n = 54 + 1B | Carvalho et al. 2008 [36] |
| *Cyphocharax saladensis* | 2n = 54 + Bs | Sampaio et al. 2016 [170] |
| *Cyphocharax spilotus* | 2n = 54 + 1B | Carvalho et al. 2008 [36] |
| *Cyphocharax voga* | 2n = 54 + Bs | Sampaio et al. 2016 [170] |
| *Electrophorus electricus* | 2n = 52 + 0–1B | Cardoso et al. 2015 [34] |
| *Erythrinus Erythrinus* | 2n = 54/53 + 0–3B | Oliveira et al. 2008 [146] |
| *Gymnogeophagus balzanii* | 2n = 48 + Bs | Feldberg and Bertollo 1984 [56] |
| *Haplochromis fisheri* | 2n = 44 + 1B | Yoshida et al. 2001 [225] |
| *Haplochromis obliquidens* | 2n = 44 + 0–2B | Poletto et al. 2010 [158] |
| *Haplochromis plagiodon* | 2n = 44 + 1–3B | Yoshida et al. 2001 [225] |
| *Haplochromis pyrrhocephalus* | 2n = 44 + 0–3B | Yoshida et al. 2001 [225] |
| *Haplochromis tanaos* | 2n = 44 + 0–1B | Yoshida et al. 2001 [225] |
| *Hisonatus leucofrenatus* | *2n* = 54 + 0–2B | Carvalho et al. 2008 [36] |
| *Hyla* sp. *aff. circumdata* | 2n = 24 + 1B | Baldissera et al. 1993 [7] |
| *Hyphessobrycon eques* | 2n = 50 + 0–1B | Piscor and Parise-Maltempi 2015 [157] |
| *Hypostomus* sp. | 2n = 67 + 1B | Carvalho et al. 2008 [36] |
| *Hypostomus* sp.3 | 2n = 82 + 0–2B | Carvalho et al. 2008 [36] |
| *Iheringichthys labrosus* | 2n = 56 + 0–1B | Vissotto et al. 1999 [205] |
| *Labeotropheus trewavasae* | 2n = ?? + Bs | Clark et al. 2017 [41] |
| *Laetacara cf. dorsigera* | 2n = 43–46 + Bs | Martins-Santos et al. 2005 [122] |
| *Leporinus friderici* | 2n = 54 + Bs | Venere et al. 1999 [200] |
| *Leporinus* sp. | 2n = 54 + 0–1B | Carvalho et al. 2008 [36] |
| *Lithochromis rufus* | 2n = 44 + 1B | Yoshida et al. 2001 [225] |
| *Loricaria prolixa* | 2n = 62 + 0–5B | Carvalho et al. 2008 [36] |
| *Loricaria* sp. | 2n = 62 + 1–3B | Carvalho et al. 2008 [36] |
| *Megalonema platinum* | 2n = 54 + 0–1B | Carvalho et al. 2008 [36] |
| *Melanochromis auratus* | 2n = 44 + Bs | Clark et al. 2017 [41] |
| *Metriaclima greshakei* | 2n = 44 + Bs | Clark et al. 2017 [41] |
| *Metriaclima lombardoi* | 2n = 44 + 0–1B | Poletto et al. 2010 [158] |
| *Metriaclima mbenji* | 2n = 44 + Bs | Clark et al. 2017 [41] |
| *Metynnis lippincottianus* | 2n = 62 + 2B | Carvalho et al. 2008 [36] |
| *Metriaclima zebra* | 2n = 44 + Bs | Clark et al. 2017 [41] |

**Table 2** continued

| | | |
|---|---|---|
| *Metynnis maculatus* | 2n = 62 + 0–1B | Baroni et al. 2009 [9] |
| *Microlepidogaster leucofrenatus* | 2n = 54 + 0–2B | Salvador and Moreira-Filho 1992 [168] |
| *Moenkhausia intermedia* | 2n = 50 + 0–1B | Portela et al. 1988 [159] |
| *Moenkhausia sanctaefilomenae* | 2n = 50 + 1–8B | Foresti et al. 1989 [64] |
| *Neochromis greenwoodi* | 2n = 44 + 0–2B | Yoshida et al. 2001 [225] |
| *Neoplecostomus paranensis* | 2n = 54 + 0–2B | Carvalho et al. 2008 [36] |
| *Neochromis rufocaudalis* | 2n = 44 + 1–2B | Yoshida et al. 2001 [225] |
| *Oligosarcus pintoi* | 2n = 50 + 0–1B | Falcao et al. 1984 [55] |
| *Orestias chungarensis* | 2n = 52 + 0–3B | Carvalho et al. 2008 [36] |
| *Parauchenipterus galeatus* | 2n = 58 + 0–2B | Lui et al. 2009 [115] |
| *Piabina argentea* | 2n = 52 + 0–1B | Carvalho et al. 2008 [36] |
| *Pimelodella kronei* | 2n = 58 + 0–1B | Foresti et al. 1992 [63] |
| *Pimelodus ortmanni* | 2n = 56 + 0–4B | Borin and Martins-Santos 2004 [18] |
| *Pimelodus* sp. | 2n = 56 + 0–4B | Borin and Martins-Santos 2004 [18] |
| *Piabina argentea* | 2n = 52 + 0–1B | Salvador and Moreira-Filho 1992 [168] |
| *Poecilia formosa* | 2n = 46 + micro Bs | Lamatsch et al. 2011 [104] |
| *Prochilodus brevis* | 2n = 54 + 0–2B | Oliveira et al. 2008 [146] |
| *Prochilodus cearenis* | 2n = 54 + Bs | Pauls and Bertollo 1990 [151] |
| *Prochilodus lineatus* | 2n = 54 + 0–7B | Oliveira et al. 1997 [145] |
| *Prochilodus mariae* | 2n = 54 + 0–3B | Carvalho et al. 2008 [36] |
| *Prochilodus nigricans* | 2n = 50 + Bs | Venere et al. 1999 [200] |
| *Prochilodus scrofa* | 2n = 54 + 0–5B | Pauls and Bertollo 1983 [150] |
| *Pundamilia pundamilia* | 2n = 44 + 1–3B | Yoshida et al. 2001 [225] |
| *Rhamdia branneri* | 2n = 58 + 0–4B | Carvalho et al. 2008 [36] |
| *Rhamdia hilarii* | 2n = 58 + 0–5B | Fenocchio and Bertollo 1990 [58] |
| *Rhadia quelen* | 2n = 58 + 0–2B | Hochberg and Erdtmann 1988 [84] |
| *Rhamdia branneri* | 2n = 58 + Bs | Abucarma and Martins-Santos 2001 [2] |
| *Rhamdia hilarii* | 2n = 58 + Bs | Fenocchio and Bertollo 1990 [58] |
| *Rhamdia quelen* | 2n = 58 + 0–1B | Fenocchio et al. 2000 [59] |
| *Rhamdia sapo* | 2n = 58 + Bs | Valcarcel et al. 1993 [195] |
| *Rhamdia* sp. | 2n = 58 + Bs | Abucarma and Martins-Santos 2001 [2] |
| *Rhamdia voulezi* | 2n = 58 + 0–2B | Lui et al. 2009 [115] |
| *Satanoperca jurupari* | 2n = 48 + 0–3B | Oliveira et al. 2008 [146] |
| *Schizodon nasutus* | 2n = 54 + 0–1B | Carvalho et al. 2008 [36] |
| *Steindachnerina biornata* | 2n = 54 + Bs | Sampaio et al. 2016 [170] |
| *Steindachnerina insculpta* | 2n = 54 + 0–2B | Gravena et al. 2007 [76] |
| *Strongylura hubbsi* | 2n = 50 + 0–2B | Carvalho et al. 2008 [36] |
| *Symbranchus marmoratus* | 2n = 44 + 0–2B | Carvalho et al. 2008 [36] |
| *Rhamdia voulezi* | 2n = 58 + Bs | Abucarma and Martins-Santos 2001 [2] |
| *Trichomycterus davisi* | 2n = 54 + 0–2B | Oliveira et al. 2008 [146] |
| *Trichomycterus* sp. | 2n = 54 + 0–2B | Carvalho et al. 2008 [36] |
| Chordates birds (1) | | |
| *Taeniopygia guttata* | 2n = 80 + 1B | Pigozzi and Solari 1998 [155] |
| Chordates mammals (53) | | |
| *Akodon aff. aroiculoides* | 2n = 24 + 1B | Yonenaga-Yassuda et al. 1992 [220] |
| *Akodon mollis* | 2n = 22 + Bs | Lobato et al. 1982 [110] |
| *Akodon montensis* | 2n = 24 + 0–2B | Silva and Yonenaga-Yassuda 2004 [180] |
| *Alouatta seniculus* | 2n = 46 + 1–3B | Vujošević and Blagojević 2004 [209] |
| *Apodemus argenteus hokkaidi* | 2n = 44 + XX/XY + 1B | Obara and Sasaki 1997 [140] |
| *Apodemus agrarius* | 2n = 48 + Bs | Kartavtseva, 1994 [96] |

**Table 2** continued

| | | |
|---|---|---|
| *Apodemus flavicollis* | 2n = 48 + 0–4 + B | Vujošević and Zivkovic 1987 [210] |
| *Apodemus mystacinus* | 2n = 48 + 2B | Vujošević and Blagojević 2004 [209] |
| *Apodemus speciosus* | 2n = 48 + 0–3B | Volobujev 1981 [206] |
| *Apodemus sylvaticus* | 2n = 24 + 0–3B | Gadi et al. 1982 [68] |
| *Bandicota indica nemorivaga* | 2n = 44/45 XX/X0 mosaic | Gadi et al. 1982 [68] |
| *Capreolus pygargus* | 2n = 70 + 1–14B | Vujošević and Blagojević 2004 [209] |
| *Cricetulus triton* | 2n = 48 + 1–2B | Vujošević and Blagojević 2004 [209] |
| *Crocidura suaveolens* | 2n = 40 + 1B | Vujošević and Blagojević 2004 [209] |
| *Dasymys rufulus* | 2n = 36 + 1–3B | Vujošević and Blagojević 2004 [209] |
| *Dicrostonyx groenlandicus* | 2n = 46XY♂, XX♀ + 2B | Borowik and Engstrom 1993 [19] |
| *Dicrostonyx kilangmiutak* | 2n = 47–50 + 1–8B | Vujošević and Blagojević 2004 [209] |
| *Golunda ellioti* | 2n = 54 + 0–4B | Rao et al. 1979 [164] |
| *Holochilus brasiliensis* | 2n = 56 + 0–2B | Yonenaga-Yassuda et al. 1987 [221] |
| *Holochilus vulpinus* | 2n = 36 + 1–3B | Vujošević and Blagojević 2004 [209] |
| *Homo sapiens* | 2n = 46 + Bs? | Liehr et al. 2008 [109] |
| *Mazama americana* | 2n = 52 + 5B | Vujošević and Blagojević 2004 [209] |
| *Mazama gouazoubira* | 2n = 70 + 1–2B | Vujošević and Blagojević 2004 [209] |
| *Melomys littoralis* | 2n = 48 + 0–4B | Volobujev 1981 [206] |
| *Metaleptea brevicornis adspersa* | 2n = 22XO♂ +B | Bidau 1986 [15] |
| *Moschus sibiricus* | 2n = 58 + 1–2B | Vujošević and Blagojević 2004 [209] |
| *Microtus longicaudus* | 2n = 66 + 0–10B | Judd and Cross 1980 [95] |
| *Nectomys rattus* | 2n = 52 + 0–3B | Silva and Yonenaga-Yassuda 2004 [180] |
| *Nectomys squamipes* | 2n = 52 + 0–3B | Maia et al. 1984 [117] |
| *Nyctalus leisleri* | 2n = 44 + 1–3B | Vujošević and Blagojević 2004 [209] |
| *Nyctereutes p. procyonides* | 2n = 36 + XY + 2B | Yosida et al. 1983 [224] |
| *Nyctereutes p. viverinus* | 2n = 38 + 1–8B | Vujošević and Blagojević 2004 [209] |
| *Oecomys cf. concolor* | 2n = 60 + 1–2B | Vujošević and Blagojević 2004 [209] |
| *Oligoryzomys flavescens* | 2n = 64 + 0–2B | Silva and Yonenaga-Yassuda 2004 [180] |
| *Oryzomys angouya* | 2n = 58 + 0–2B | Silva and Yonenaga-Yassuda 2004 [180] |
| *Oryzomys flavescens* | 2n = 64 + 1–2 B | Sbalqueiro et al. 1991 [172] |
| *Oryzomys fornesy* | 2n = 64 + 1–2B | Vujošević and Blagojević 2004 [209] |
| *Otomys irroratus* | 2n = 24–26 + 1–9B | Vujošević and Blagojević 2004 [209] |
| *Petauroides volans* | 2n = 28 + 0–4Bs | McQuade et al. 1994 [124] |
| *Proechimys iheringi* | 2n = 60 + 0–5B | Yonenaga-Yassuda et al. 1985 [219] |
| *Proechimys* sp. 2 | 2n = 26 + 0–1B | Silva and Yonenaga-Yassuda 2004 [180] |
| *Rattus rattus kandianus* | 2n = 40 + 0–1B | Yosida 1976 [223] |
| *Rattus rattus frugivorus* | 2n = 38 + 0–3B | Ladron de Guevara et al. 1981 [103] |
| *Rattus rattus thai* | 2n = 42 = 1–6B | Vujošević and Blagojević 2004 [209] |
| *Rattus rattus tanezumi* | 2n = 42 + 0–1B | Yosida 1976 [223] |
| *Sooretamys angouya* | 2n = 58 + 2B | Ventura et al. 2015 [201] |
| *Thomomys bottae* | 2n = 76 + 0–12B | Patton and Sherwood 1982 [149] |
| *Thamnomys dolichurus* | 2n = 52,54 + 4–7B | Civitelli et al. 1989 [40] |
| *Thamnomys gazellae* | 2n = 52 + Bs | Civitelli et al. 1989 [40] |
| *Thomomys umbrinus* | 2n = 76 + 0–30B | Patton & Sherwood 1982 [149] |
| *Trinomys iheringi* | 2n = 60 + Bs | Fagundes et al. 2004 [54] |
| *Tscherskia triton* | 2n = 28 + 0–2B | Volobujev 1981 [206] |

**Table 3** Summary of new species with Bs since 1980

| | |
|---|---|
| Fungi = 13 | |
| Plants = 136 | |
| Gymnosperms = 27 | |
| Dicotyledons = 18 | |
| Monocotyledons = 91 | |
| Animals = 257 | |
| Platyhelminthes = 1 | |
| Arthropods | |
| Crustacea = 8 | |
| Insects = 53 | |
| Chordates | |
| Amphibians = 29 | |
| Reptiles = 12 | |
| Fishes = 100 | |
| Birds = 1 | |
| Mammals = 53 | |
| Total species = 406 | |

[160], where the small euchromatic B was found in five out of 29 trees in a park in Lucknow in India. The presence of Bs in *Acanthophyllum laxiusculum* increases the chiasma frequency of the A chromosomes, but with an effect which is higher for plants with odd compared with even numbers of Bs [72]. This so-called *odd–even* effect is known in several plant and animal species and the mechanism of its action remains a mystery. The Australian daisy *Brachycome dichromosomatica*, 2n = 4, has only two As and from 0–3 Bs of two types [51, 105]. It is one the few plant species where detailed sequence analysis of plant B chromosomes has been undertaken, and a family of 176-bp tandem repeats specific to the B have been isolated and described [91].

The monocotyledons, in contrast with the 18 dicots have a larger number of 91 new species, but fewer than the 497 in listed in 1982. One reason for this difference could be that there are many species, such as those in the Liliaceae and Orchidaceae, which have large genomes that are attractive to cytologists, and which are therefore more intensively studied. It is also a truism that many species are investigated cytogenetically because they have not been previously studied, and there is opportunity to add to the chromosome knowledge base. Blagojević et al. [17] make the interesting point that B chromosomes should be regarded as a significant component of the eukaryote genetic system in organisms which carry them, since they are found in so many species at the population level. Chen et al. [37] noted no relationship between the presence of Bs and the ecological and climatic conditions in 21 natural populations of *Agropyron cristatum* and *A. mongolicum*. In *Sorghum stipoideum* the Bs are totally eliminated from stems and leaves [217].

In the animal kingdom, we are dealing with 257 new species with Bs, which is close to the 263 listed in 1982. In addition to that we have a large number of new entries (100) for fishes as well as one new entry for birds. There are also many new species of amphibia, reptiles and mammals. It is notable too how many orthoptera have been studied, no doubt on account of their large and amenable karyotypes.

The flat worm *Polycelis nigra* is a new species additional to the previous three [14]. This species is of interest since it can reproduce sexually or asexually, and has a complex mode of transmission. In the beetle *Dichotomius geminatus* the mapping of repetitive DNAs provided evidence of an association of 5S rRNA and histone H3 genes in insects, and there was also a similarity in repetitive DNA between the B and A chromosomes [26]. The arachnid *Metagagrella tenuipes* (2n = 18) was studied in 8 populations in Japan, and has up to 19 Bs [191]. All 19 Bs appear all be univalent at meiosis, and no correlation was found between the number of Bs and external morphologies or habitat type. In *Drosophila subsilvestris* a species-specific satellite DNA family (pSsP216) was found mainly on the Bs and at in the centromeric heterochromatin of the A chromosomes, and the authors suggest that the Bs may have been derived from the A chromosomes [79]. A SCAR marker was developed to show the presence of Bs in the stingless bee *Partamona cupira* [21]. Araujo et al. [6] have identified a mechanism in the haplodiploid wasp *Trypoxylon albitarse* whereby meiosis is regularised for limiting the number of Bs to one, thereby integrating the B as a regular member of the chromosome complement. In the acridid *Aiolopus strepens* there is an odd–even effect of the number of Bs on B pairing, and also on the number of macrospermatids, which are increased with odd numbers. Ruiz-Ruano et al. [167] investigated the origin of the B by analysing 27 families of satellite DNA, of which two of the families were found only on the B and many others on the A chromosomes as well. Detailed studies indicated a possible intraspecific origin of the B from the proximal third of the S8 autosome. The discovery of two types of Bs in five natural populations of *Eyprepocnemis plorans* opened up a whole new field of evolutionary studies in this species, as well as discovering effects on A chromosome chiasma frequency and distribution [28]. In contrast, there were no effects of Bs on chiasma frequency variation in *Heteracris littoralis*, although there was an increase in macrospermatids production [33].

Twenty-nine new species of amphibia are recorded since 1980, when there were only ten species known. A review by Green [77] summarised the main features of the structure and evolution of the B chromosomes of 26 species of amphibians, including the earlier known cases. There is detailed information on the variation in structure, size and chromatic status, as well as the distribution pattern of their occurrence within and between species. They are generally large in size and amenable to study. The Pacific giant salamander, *Dicamptodon tenebrosus* has up to 10 Bs, but the number varies over different regions of the Pacific Northwest of North America [20]. The Bs in this species have been isolated by microdissection and their DNA hybridised to genomic DNA of a number of related species, and demonstrating that they originate from the standard A complement.

Only three species of reptiles with Bs were known by 1980, and this number has now increased up to 12. Bertolotto et al. [13] reviewed the system of Bs in lizards and described their structural variation, chromatic status and influence over the A chromosomes.

There were no fishes represented in the 1980 data. They made their first appearance in the 1980s/1990s, and then their numbers increased rapidly until they now account for more than 100 species, with many coming from studies in Brazil. The cyprinid fish *Alburnus alburnus* has some of the largest B chromosomes known in vertebrates. There are two morphological types, and only one or two Bs may be present with variable frequency in different populations. The Bs are completely heterochromatic, replicate their DNA late, and are composed of specific retrotransposable elements [174]. The large B represents 10% of the size of the genome size. Carvalho et al. [36] reviewed the occurrence of Bs neotropical fishes and pointed out that the greatest number occurred in the order Characiformes, with a lot of variation within as well as between species in their number, morphology and size, and tabulated the data for thirty-one species. In *Astatotilapia latifasciata* an investigation into the transcriptionally active repeated non-coding DNA (BncDNA) of the heterochromatic Bs found transcripts that are processed differentially in different tissues. This BncDNA potentially has actions which influence the maintenance of Bs in mitotic cells as well as meiotic drive in gametic cells [162]. Yosida et al. [225] sequenced a BAC clone from cichlid fishes in Lake Victoria and found several protein coding genes, suggesting that the Bs have a functional role, contrary to the widespread belief that they are simply selfish genetic elements. In this sense, the Bs in fishes have made highly significant contribution to the knowledge of Bs in the genetic system.

The first observation of B chromosomes in birds, in the zebra finch *Taeniopygia guttate* was recently described, in 1998 [155]. A single B was found in the germ cells of male and female, and described as being euchromatic in oocytes and strongly heterochromatic in spermatocyte.

An additional 53 mammals have now been described compared with the 19-species known in 1980, giving a total of 72. Silva and Yonenaga-Yassuda [180] reviewed the eight then known Brazilian rodents and found them to be heterogeneous in size, generally heterochromatic and late replicating.

Many of the publications simply deal with the discovery of Bs in particular species and a description of the Bs in term of their size variation (some are minute) and chromatic status. More detail is given in the review of Bs in mammals by Volobujev [206]. An analysis the DNA sequences in the marsupial *Petauroides volans* found the B to be composed of a heterogenous mixture of sequences, some unique to the B and others to the centromeric regions of the A chromosomes. [124].

## Conclusions

The main findings of the current survey on new species discovered with Bs since 1980 are that organisms with these enigmatic chromosomes continue to be discovered on a regular basis, and they augment our knowledge base on this topic of growing interest. It should also be pointed out that certain species which are currently contributing much of the recent knowledge on the molecular organisation, origin and active genes in Bs were known before the discovery of the Bs listed in Table 2, and these will doubtless be reviewed in future publications.

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