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RESEARCH ARTICLE

Variation in chromosome numbers and the sex determination system in the Gerromorpha with special reference to the family Gerridae

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We assess karotypic variation in the heteropteran infraorder Gerromorpha. Counts of autosomes, m-chromosomes and sex chromosomes are obtained from literature reports for 51 species, including 35 in the family Gerridae. Placing these data on recently derived phylogenies reveals that XX/X0 sex determination is ancestral to the clade containing the Gerridae and Veliidae, but that XX/XY sex determination has been secondarily derived several times. Our results confirm the absence of m-chromosomes in the Gerromorpha, but contrary to previous reviews, we find intermediate levels of variation in chromosome counts and sex-determining systems when compared to other Heteropteran clades. A new karological analysis reveals that the X chromosome of *Aquarius remigis* (Say, 1832) is the largest chromosome, which contrasts with *A. najas* (De Geer, 1773) in which it the X chromosome is the smallest. This karyotypic difference supports molecular evidence that the *A. remigis* group of species is not closely related to other species in the genus *Aquarius* Schellenburg, 1800.

**Keywords:** Hemiptera; Gerromorpha; Gerridae; karyotype; sex determination

### Introduction

We report the chromosome number and mechanism of sex determination for 51 species within the heteropteran infraorder Gerromorpha. This report updates previous reviews of karyotypic variation in the Gerromorpha which included only 21 (Ueshima 1979; Andersen 1982) or 34 (Papeschi and Bressa 2006) species. We place the karyotypic information in a phylogenetic context and re-evaluate conclusions derived from the earlier reviews.

Gerromorphan karyotypes have previously been characterized as varying little in autosomal chromosome number, having predominantly XX/X0 sex determination and lacking m-chromosomes (*op. cit.)*. The latter are atypical chromosomes that are usually

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(but not always) minute compared to autosomes and are distinguished by meiotic behavior that differs from both autosomes and sex-chromosomes. Among other peculiarities, they are achiasmatic, as are sex-chromosomes in the Heteroptera, but unlike sex-chromosomes, they undergo reductional separation at the first division and equational separation at the second (for more detailed descriptions of the meiotic behaviors of autosomes, sex-chromosomes and m-chromosomes, see Ueshima (1979) and Papeschi and Bressa (2006)). M-chromosomes are found in a number of other heteropteran clades but have not been found in the Gerromorpha (Ueshima 1979; Papeschi and Bressa 2006; Castanhole et al. 2008; Kuznetsova, Grozeva, Nokkala, and Nokkala 2011; Souza et al. 2014; Pereira et al. 2015).

The predominance of XX/X0 sex determination in the Gerromorpha is unusual among heteropteran clades. In the majority of heteropteran species (71%), sex is determined via the familiar XX/XY chromosomal system in which females inherit an X chromosome from each parent whereas males inherit an X chromosome from their mother and a Y chromosome from their father (Ueshima 1979; Papeschi and Bressa 2006). However, several variations on this mechanism are also quite common and often co-exist with XX/XY systems within the same taxonomic family (op. cit.). The second most common system of sex determination is XX/X0, which occurs in 15% of species. In these species Y chromosomes are absent and the male karyotype is designated as X0, signifying one X chromosome and no Y. The great majority of heteropteran species have either XX/XY or XX/X0 sex determination, but multiple X chromosomes have been found in approximately 13% of species, with some having as many as five X chromosomes. These systems are designated X_n/X_{n-1} Y or X_n/X_{n-1}0, with n designating the number of X-chromosomes in females. Multiple Y chromosomes are rare but have been described in two families in the infraorder Pentatomorpha (Papeschi and Bressa 2006).
Some authors distinguish an additional category of sex-chromosomal variation: the presence of neo-X or neo-Y chromosomes. Neo-sex chromosomes are derived by fusion of ancestral X or Y chromosomes with one chromosome of an autosomal pair. They are rare in the Heteroptera, having been described in only 0.5% of species distributed across in five families (Papeschi and Bressa 2006), including one gerromorphan species in the family Hebridae, *Hebrus pusillus* (Fallén, 1807) (Nokkala and Nokkala 1999).

In contrast to the majority of heteropterans, the two early reviews of gerromorphan karyotypes indicated that XX/X0 sex determination (hereafter denoted simply as X0) was almost universal in the Gerromorpha (Ueshima 1979; Andersen 1982). The more recent review by Papeschi and Bressa (2006) shows Y chromosomes present in every gerromorphan family but does not provide data at the species level and does not give the prevalence of XY versus X0 sex determination in the Gerromorpha. Ueshima (1979) surmised that X0 is the ancestral sex determination system not only for the Gerromorpha but also for Heteroptera as a whole. If X0 is the ancestral condition for the Gerromorpha, the few occurrences of XY systems or systems with multiple X chromosomes (X<sub>n-1</sub>Y or X<sub>n-1</sub>0) within the infraorder represent secondary derivations. Subsequent discoveries of Y chromosomes in other gerromorphan species have prompted several authors to question this hypothesis (Calabrese and Tallerico 1984, 1987; Nokkala and Nokkala 1999). Similarly, documentation of Y chromosomes in basal heteropteran clades has cast doubt on the hypothesis that X0 is the ancestral state for the Heteroptera as a whole (Nokkala and Nokkala 1984; Grozeva and Nokkala 1996). We use our expanded data set to re-evaluate the prevalence of X0 sex determination in the Gerromorpha and to determine the ancestral state for the most well represented family, the Gerridae.
We also present a new karyologic analysis for the gerrid species *Aquarius remigis* (Say, 1832) and estimate of the size of its X chromosome. This species is of particular interest because it is the signature species in the *Aquarius remigis* species group, comprising *A. remigis, A. amplus* (Drake and Harris, 1938) and *A. remigoides* (Gallant and Fairbairn, 1996). The taxonomic structure and phylogenetic position of this group have been difficult to discern and its classification remains uncertain (e.g., Michel 1961; Andersen 1990, 1993, 1995; Damgaard, Andersen, and Sperling 2000; Damgaard 2006; Damgaard, Moriera, Weir, and Zettel 2014). Although still classified in the genus *Aquarius* Schellenburg, 1800, molecular phylogenetic analyses now place these species as more closely related to *Gerris* species than to other *Aquarius* species (Damgaard and Cognato 2006; Damgaard and Christiansen 2007; Damgaard 2012; Damgaard et al. 2014). Based on its phenotypic and genetic distance from other *Aquarius* species and from *Gerris* species, Damgaard has recommended that the *remigis* group should be classified as a separate genus, but this taxonomic change has not yet been implemented (Damgaard and Christiansen 2007; Damgaard et al. 2014). The signature species, *A. remigis*, is itself problematic from a taxonomic perspective. It is one of the most widely distributed and phenotypically variable of the temperate gerrids (Michel 1961; Calabrese 1974; Andersen 1990; Brennan and Fairbairn 1995; Fairbairn 2005; Damgaard and Christiansen 2007; Fairbairn and King 2009), and populations show marked genetic differentiation both within and among regions (Zera 1981; Preziosi and Fairbairn 1992; Gallant, Preziosi, and Fairbairn 1993). Populations from California and Oregon are particularly distinct with respect to genital morphology, body color, life history and flight propensity (Michel 1961; Calabrese 1974; Fairbairn and King 2009; Fairbairn, personal observations). Michel (1961) considered these western populations a separate species and Calabrese (1974) gave them subspecific status.
However more recent comparisons of allozyme frequencies and of the shape of the internal genital components among populations from across North America have not supported separate taxonomic classification of western *A. remigis* (Presziosi and Fairbairn 1992; Gallant et al. 1993; Damgaard and Christiansen 2007), and all *A. remigis* are still considered a single species (Polhemus and Chapman 1979; Andersen 1990; Damgaard and Christiansen 2007; Damgaard et al. 2014). The phylogenetic position and taxonomic status of the *Aquarius remigis* group and of its signature species therefore remain a key issue in fully resolving the phylogeny of the Gerridae.

In addition to this significance for gerromorphan systematics, *Aquarius remigis* is a model species for studying dispersal polymorphisms (e.g., Fairbairn 1988; Fairbairn and King 2009; Kaitala and Dingle 1992, 1993), multilevel selection (Eldakar, Wilson, Dlugos, and Pepper 2010; Chang and Sih 2013), and sexual selection and sexual dimorphism (e.g., Fairbairn 1992, 2005, 2007; Sih and Krupa 1995; Fairbairn and Preziosi 1994, 1996; Watson, Arnqvist, and Stallmann 1998; Preziosi and Fairbairn 2000; Sih, Lauer, and Krupa 2002; Bertin and Fairbairn 2005). In the latter context, a recent study quantifying the effect of sex-linked genes on body size and sexual dimorphism has underlined the need to verify the sex-determination mechanism in this species and to estimate the relative size of the X chromosome (Wolak 2013).

Calabrese and Tallerico (1982) published a karyotype for *A. remigis* from Aguirre Springs, New Mexico but they did not assess the relative size of the X chromosome. Our intent is to measure the relative size of the X chromosome and also to determine if the chromosome count and sex determination system for *A. remigis* from California match those of the New Mexican population. Differences between the karyotypes of Californian *A. remigis* and those from New Mexico would suggest a reassessment of the taxonomic status for populations from the western region.
Material and methods

*Aquarius remigis* are surface-dwelling, semi-aquatic predators found on streams and small rivers throughout much of temperate and subtropical North America and Mesoamerica (Calabrese 1974; Andersen 1990; Preziosi and Fairbairn 1992; Gallant et al. 1993; Damgaard and Christiansen 2007). They are among the largest of the temperate gerrids, ranging in length from about 11–17 mm (Brennan and Fairbairn 1995). As is typical of water striders, they subsist primarily by capturing insects and other small arthropods that fall on the water surface and become trapped in the surface film. Female *A. remigis* oviposit on submerged, solid surfaces, but the newly hatched nymphs swim to the surface and all five nymphal stages live on the water surface. Most populations have one or two generations per year and overwinter as adults in reproductive diapause (Fairbairn 1985; Blanckenhorn 1991; Blanckenhorn and Fairbairn 1995). However, low altitude populations in Southern California have a more flexible reproductive pattern and laboratory cultures kept under long day conditions (14L:10D) maintain continuous reproduction.

For our karyologic analysis of *A. remigis* we used the testes of reproductively mature, adult males from a laboratory culture maintained under 14L:10D at the University of California, Riverside. The males sampled were first or second generation, lab-reared descendants of adults captured from natural populations in western San Bernardino County, California. Each male was anesthetised with chloroform prior to dissection. The four testes were then removed and immediately placed in modified Carnoy fixative (3:1 absolute ethanol : glacial acetic acid) for minimum 48 hours and kept at 4°C. After being fixed, the testes were stained with 2% solution of aceto-orcein for 3–4 days (Kiseliova, Toderas, and Derjanschii 1998) and then squashed in a drop of
45% acetic acid. Squashed preparations were scanned immediately under oil immersion using an Olympus™ BX51 (DIC) microscope. Microphotographs of mitotic and meiotic metaphase plates were taken with a Sony HDR-HC1K camera. Our karyotypic interpretations are based on 90 metaphase plates prepared from 38 males.

As is typical of Hemipteran insects (e.g., Thomas 1987; Papeschi and Bressa 2006; Melters, Paliulis, Korf, and Chan 2012; Bardela, Gil-Santana, Panzera, and Vanzela 2014; Souza et al. 2014; Pereira et al. 2015), all species in the Gerromorpha have holocentric chromosomes that are globular in shape and lack a localized centromere (Ueshima 1979; Andersen 1982; Calabrese and Tallerico 1982, 1984, 1987; Newman and Cheng 1983; Spence and Maddison 1986; Grozeva, Nokkala, and Simov 2009; Castanhole 2009). This makes it difficult to discern distinct characteristics of individual chromosomes other than size. However, the sex chromosomes can be distinguished from autosomes because they undergo equational rather than reductional division during meiotic metaphase I and hence do not form a bivalent during this phase (Ueshima 1979; Spence and Maddison 1986; Papeschi and Bressa 2006). We estimated the relative size of the X chromosome for 10 male A. remigis from meiotic metaphase I plates in which all of the chromosomes were separated clearly enough for accurate measuring. Using ImageJ software (Rasband 2015), we measured the area of all 21 chromosomes and summed these areas to get a total chromosome area. The relative size of the X chromosome was then estimated as the area of the X chromosome divided by the total chromosome area. We also ranked the 21 chromosomes from largest to smallest by area and determined the rank of the X chromosome for each male.

To assess the phylogenetic history of sex determining systems within the Gerridae and to place the karyotype of A. remigis in its phylogenetic context, we mapped species’ chromosome counts and sex-chromosome systems onto a phylogeny of...
the subfamily Gerrinae derived from Damgaard et al. (2014). We trimmed the original
tree to include only species with known karyotypes, and with two exceptions, we
included only the species used by Damgaard et al. (2014). The two exceptions are
species used as outgroups for the subfamily Gerrinae. Damgaard et al. (2014) used
_Cylindrostethus costalis_ (Schmidt, 1915) to represent the subfamily Cylindrostethinae
and _Brachymetra unca_ (Shaw, 1933) to represent the subfamily Charmatometrinae, but
we could not include these species because their karyotypes have not been determined.
We, therefore, substituted their congeners, _Brachymetra albinerva_ (Amyot and Serville,
1843) and _Cylindrostethus palmaris_ (Drake and Harris, 1934) to represent these
subfamilies. To assess the history of sex determining systems more broadly in the
Gerromorpha, we mapped the frequency of sex determining systems (X0, XY and X–
Y) on a phylogeny of gerromorphan families and subfamilies derived from Damgaard
(2008, 2012). As above, we trimmed the tree to include only families containing
species with known karyotypes.

**Results**

Our karyologic study of _Aquarius remigis_ verifies the earlier conclusions of Calabrese
and Tallerico (1982). Photomicrographs of mitotic metaphase in spermatogonia and of
meiotic metaphase I in primary spermatocytes consistently revealed a karyotype
consisting of 21 chromosomes: ten pairs of autosomes plus a single X chromosome
(Figure 1a, 1b). Thus, the diploid karyotype of male _A. remigis_ is 2n = 20A + X0. Also
in agreement with Calabrese and Tallerico (1982), we found no evidence of any m-
chromosomes.

{FIGURE 1a AND 1b NEAR HERE}
The X chromosome of *A. remigis* was consistently the largest chromosome. It ranked first by area in each of the 10 males measured and averaged 12.9% (SD 5.8%) larger than the largest autosome. The difference in size between the X chromosome and the largest of the autosomes was highly statistically significant ($t_{2\text{-tailed}} = 6.300$, df 9, P < 0.001). By area, the X chromosome comprised an average of 7.4% (SD 0.4%) of the diploid chromosome complement of males; by extension, two X chromosomes would comprise 13.8% of the diploid chromosome complement in females. These values compare to expected values based on chromosome counts of 1/21 = 4.8% in males and 2/22 = 9.1% in females.

To assess the distribution of chromosome counts and sex determination systems in the Gerromorpha, we assembled literature reports for 51 species, including 30 species not listed in Ueshima (1979) or Andersen (1982). We also found reports of seven new analyses for previously reported species. Most of the duplicate analyses confirmed previous reports, but we found conflicts for three species. For *Gerris marginatus* (Say, 1832), Ueshima (1979) reported a male chromosome count of $2n = 20A + X0$, citing Montgomery (1901), and Andersen (1982) repeated this, citing Ueshima. However, Calabrese and Tallerico (1982) reported a chromosome count of $2n = 18A + XY$ for the same species. They argued that Montgomery may have been studying a different species because in 1901 at least three currently recognized species were included under the name *G. marginatus*. Given this taxonomic uncertainty, we use the karyotype reported by Calabrese and Tallerico for *G. marginatus*. Unfortunately, conflicting reports for two other species could not be similarly resolved. Ueshima (1979), followed by Andersen (1982), reported a chromosome count of $2n = 22A + X0$ for *Aquarius paludum* (Fabricius, 1794), citing a series of papers by Wilke (1907, 1912, 1913). This karyotype is for the subspecies *Aquarius paludum paludum* (Fabricius, 1794) which
occurs throughout the Palearctic region. Ueshima (but not Andersen) also listed the karyotype $2n = 22A + XY$ reported by Takenouchi and Muramoto (1968) for *A. paludum*. This karyotype may be for the subspecies *A. p. amamiensis* (Miyamoto, 1958) which occurs only in Japan. Although an early comparison based on the mitochondrial gene cytochrome oxidase subunit I (COI) could not distinguish *A. p. amamiensis* from *A. p. paludum* (Damgaard and Zettel 2003), more recent consensus analyses based on both genetic and morphological characters (Damgaard and Cognato 2006) or additional genetic sequences alone (Damgaard et al. 2014) do clearly separate the two subspecies. Because both subspecies occur in Japan (Damgaard et al. 2014) and the subspecific status of the sample used by Miyamoto (1958) is not certain, we include both karyotypes under the species name *A. paludum*. We were similarly unable to resolve the conflicting reports for *Hebrus ruficeps* (Thomson, 1871). Ueshima (1979) and Andersen (1982) report a chromosome count of $2n = 18A + X0$ for males of this species, citing Cobben (1968). However, Nokkala and Nokkala (1999) report a karyotype of $22A + XY$ for the same species. The latter authors note that their observations differ from those of Cobben, but provide no explanation for the disparity. We, therefore, report both karyotypes. Because the karyotypic status remains uncertain for both *H. ruficeps* and *Aquarius paludum*, we do not include either species in our estimates of the prevalence of sex determining systems and we exclude *Hebrus ruficeps* from the summary of autosomal chromosome numbers.

Our compilation of karyotypes reveals diploid autosome counts ranging from 18 to 38 in the Gerromorpha (Figure 2). Counts of 18 and 20 are most prevalent and equally common, with 13 species each, and the second most common category is 22, with 12 species. Together these categories comprise more than three quarters (76%) of the known gerromorphan karyotypes. Among the Gerridae, the modal diploid
autosomal count is 20 with a range of 18 to 30, and 80% of species have counts of 18,
20 or 22.

The majority of species have X0 sex determination but this mechanism is far
from universal (Table 1, Figures 3, 4). Eleven species have XY sex determination,
including seven within the Gerridae, and one species in the family Mesovelliidae has
five X chromosomes and X,Y sex determination (Ekholm 1941; Grozeva et al. 2009).
As noted above, there are also conflicting reports of both XY and X0 for Aquarius
paludum in the Gerridae and for Hebrus ruficeps in the Hebridae. Thus, Y
chromosomes occur in at least 12 and possibly 14 species representing about a quarter
(23.5%–27.5%) of the reported gerromoran karyotypes. Within the Gerridae, the
prevalence of XY sex determination is between 20% (7/35) and 22.9% (8/35). By
comparison, the prevalence of Y chromosomes among species from other gerromoran families is between 31.3% (5/16) and 37.5% (6/16). This suggests a slightly lower
prevalence of Y chromosomes in the Gerridae, but the difference is far from statistically
significant ($X^2 = 0.887$, df 2, $P > 0.25$).

Figure 3 places the sex determining systems on a phylogeny of the most well-
represented subfamily, the Gerrinae, with species from two other subfamilies within
Gerridae and its sister family, Veliidae, as outgroups. This phylogenetic representation
indicates that the ancestral condition for the Gerrinae is X0 and that there have been at
least two transitions to XY. One transition occurred on the branch leading to the clade
containing Gerris comatus (Drake and Hottes, 1925a), G. marginatus, G. insperatus
(Drake and Hottes, 1925b) and G. alacris (Hussey, 1921), and another occurred on the
branch leading to Limnoporus canaliculatus (Say, 1832). If Aquarius paludum is XY as
reported by Takenouchi and Muramoto (1968), a third transition must also have occurred on the branch leading to this species.

In Figure 4, the frequencies of X0, XY and X_{n-1}Y sex determination are shown on a phylogeny of subfamilies within the Gerridae - Veliidae clade and within three other gerromorphan families: Hydrometridae, Hebridae and Mesoveliidae (Damgaard 2008, 2012). The analysis within the Gerrinae (above) established that XY systems are derived within this subfamily, and this combined with the absence of XY in the five species of Halobatinae (the sister group of all other Gerridae), suggests that X0 sex determination is the ancestral state in the Gerridae as a whole. If this is correct, the species with XY sex determination in the subfamilies Trepobatinae and the Rhagadotarsinae represent independent derivations. Although sampling is sparse outside of the Gerridae, X0 systems predominate in the three veliid subfamilies as well as in the clade containing the families Hydrometridae and Hebridae. These observations further support the hypothesis that X0 sex determination is the ancestral state for the family Gerridae.

Discussion

The chromosome complement of 2n = 20A + X0 that we observed for male Aquarius remigis is typical of species in the family Gerridae with respect to both the number of autosomes and the sex-determination system. It also agrees with the previously published karyotype for this species from New Mexico (Calabrese and Tallerico 1982) and so does not provide evidence supporting separate subspecific or specific status for Californian A. remigis. Because the chromosome counts and the sex-determination system are so conserved in the Gerrinae, the A. remigis karyotype is not informative
with respect to its phylogenetic position as a sister clade of *Gerris* (Figure 3; Damgaard et al. 2014). Nor does our new information contribute meaningfully to consideration of new generic status for *A. remigis* and its sister species, *A. remigoides* and *A. amplus* (Damgaard et al. 2014).

Few authors have reported the relative size of the X chromosome in gerromorphan species and published photographs are often not of sufficient resolution for this to be assessed. Nevertheless, the available examples suggest considerable interspecific variation (Andersen 1982). The X chromosome is the largest or one of the largest chromosomes in *Gerris costae* (Herrich-Schäffer, 1950) (Grozeva et al. 2009) and *G. gibbifer* (Schummel, 1982) (Poisson 1936); of average or intermediate size in *G. asper* (Fieber, 1860), *G. lateralis* (Schummel, 1832), *Limnoporus notabilis* (Drake and Hottes, 1925a) and *Tachygerris opacus* (Champion, 1898) (Ekblom 1939; Spence and Maddison 1986; Callebrese and Tallerico 1987); one of the smallest chromosomes in *Limnogonus aduncus* (Drake and Harris, 1933) (Castanhole et al. 2008); and the smallest in *Aquarius najas* (Poisson, 1936). Within the genus *Gerris* Fabricius, 1794, the two species with large X chromosomes are closely related and in a different clade than the two with intermediate X chromosomes, and the latter are sister species (Figure 3; Damgaard et al. 2014). This clustering suggests that the relative size of the X chromosome may show phylogenetic patterning. If so, the stark contrast between *Aquarius najas*, where the X chromosome is the smallest, and *A. remigis*, where it is the largest by a significant margin, supports Damgaard’s evidence that *A. remigis* and *A. najas* are not closely related, and that *A. remigis* should be assigned to a new genus.

As discerned in previous reviews, the X0 sex-determination system clearly predominates in the Gerromorpha. Of the 51 species for which we have data, at least 37 (72.5%) and possibly as many as 39 (76.5%) have X0 sex determination. All other
species have XY sex determination with the exception of *Mesovelia furcata* (Mulsant and Rey, 1852) in which males are X_{0}Y (Grozeva et al. 2009). The prevalence of X_{0} sex determination may be slightly higher in the Gerridae than in the other families sampled, but previous observations of universal X_{0} in the Gerridae (Ueshima 1979, p. 92; Andersen 1982, p. 56) are not supported by the new data.

The high prevalence of X_{0} sex determination in the Gerromorpha is unusual in the Heteroptera. In a review of chromosomal sex determination across 1145 heteropteran species in 42 families, Ueshima (1979, pp. 91–99) found X_{0} sex determination in only 15.1% of species whereas 73.9% were XY. The remainder had multiple X chromosomes with (8.3%) or without (2.7%) a Y, or multiple Y chromosomes (one species). A more recent survey of 1600 heteropteran species in 46 families found similar proportions: 14.7% X_{0}, 71.4% XY, and 13.5% with multiple X’s or multiple Y’s (one species) (Papeschi and Bressa 2006). The remaining 0.5% were categorized as neo-sex chromosome systems and the authors did not specify either the numbers or the types of sex chromosomes for these species. Y-chromosomal systems also predominate at the family level: Y chromosomes are universal in 24 families (53.3%), occur in a portion of species in 16 families (35.6%), and are entirely absent from only five families (11.1%) (Papeschi and Bressa 2006).

In spite of the prevalence of Y-chromosomal systems in the Heteroptera, Ueshima (1979) argued that X_{0} sex determination is the ancestral state for the entire suborder, as well as for the infraorder Gerromorpha. Several authors have subsequently questioned this hypothesis, based on findings of XY systems in additional gerromorphan species (Calabrese and Tallerico 1984, 1987; Nokkala and Nokkala 1999) as well as in more basal heteropteran families (Nokkala and Nokkala 1984; Grozeva and Nokkala 1996). Our phylogenetic reconstructions cannot address the
question of the ancestral state for the Heteroptera or even for the Gerromorpha. However, our data do clearly support the hypothesis that X0 is the ancestral state for the subfamily Gerrinae, the family Gerridae, and most likely also for the clade containing the Gerridae plus Veliidae. The eight (or nine) XY systems found within this clade appear to have evolved through five (or six) independent evolutionary transitions from the ancestral X0 state.

Andersen (1982) characterized the variation in chromosome number in the Gerromorpha as ‘quite insignificant’. While this may be an exaggeration (see below), our more extensive compilation of species does reveal relatively little variation not only in the sex-determining system, but also in the numbers of autosomes. Our observation that 76% of reported diploid autosomal counts are between 18 and 22 supports this characterization for the infraorder as a whole, and variation is particularly low in the most well-characterized family, the Gerridae, where 80% of species have between 18 and 22 autosomes. Nevertheless, our compilation has considerably broadened the range of diploid autosomal chromosome counts reported for this infraorder. Ueshima (1979), Andersen (1982) and Papeschi and Bressa (2006) reported a range of between 18 and 30. In our compilation, the lower limit remains 18, but a recent report of the karyotype of *Rhagovelia whitei* (Breddin, 1898) extended the upper limit to 38 (Castanhole, Pereira, Souza, and Itoyama 2012). The modal autosome count for the species listed in Ueshima (1979) and Andersen (1982) was 20, but our expanded sampling has extended this to include both 18 and 20. Within the Gerridae, however, the mode remains at 20.

Our compilation also supports the conclusion of previous reviewers (Ueshima 1979; Andersen 1982; Papeschi and Bressa 2006) that m-chromosomes are absent from the Gerromorpha. These enigmatic chromosomes have been found in at least 14 families in the Heteroptera, including two of the most speciose (Coriedae and
Lygaeidae) and several aquatic families (Corixidae, Naucoridae, Notonectidae and Pleidae) (Ueshima 1979; Papeschi and Bressa 2006). It is premature to conclude that m-chromosomes will not be found in more broadly across the Heteroptera as more karyotypes are resolved. However, their absence from the species included in our survey is strong evidence that they are absent from the Gerridae and supports the prediction that they are also absent throughout the Gerromorpha.

Relative to other families in the Heteroptera, the variation in chromosome counts and sex-determination systems that we found in the Gerridae and in our limited samples of other gerromorphan families is neither unusually low nor unusually high. Many families have much lower karyotypic variation than apparent in Gerromorphan families. Examples include the Rhopalidae which consistently have 2n = 13 or 15 with two m-chromosomes and X0 sex determination; the Scutelleridae with 2n = 12–14, no m-chromosomes, and XY sex determination; and the Corixidae with 2n = 24–26, one pair of m-chromosomes and XY sex determination (Ueshima 1979; Papeschi and Bressa 2006; Souza et al. 2014). At the other extreme, many families show much more variation in both the numbers of chromosomes and their distribution among categories (i.e., autosomes, sex chromosomes and m-chromosomes) than we found in the Gerromorpha (Ueshima 1979; Thomas 1987; Papeschi and Bressa 2006; Castanhole et al. 2008; Kuznetsova et al. 2011; Souza et al. 2014; Kaur and Gaba 2015). For example, species in the Lygaeidae have diploid chromosome counts varying from 2n = 10–30, may or may not have m-chromosomes, and have many different sex-determining systems including X0, XY, Xn-1Y and XYn (Ueshima 1979; Papeschi and Bressa 2006). Several subfamilies of Lygaeids show almost this full range of karyotypic variation (Ueshima 1979). Similarly, in the Coreidae, the diploid karyotype varies from 2n = 13 to 28, and the sex-determining system can be X0, Xn-1O or XY with almost the full
range of variation occurring within a single subfamily, the Corinae (Papeschi and
Bressa 2006; Souza et al. 2014). Among aquatic Heteroptera, the most variable families
are: the Belostomatidae with chromosome counts varying from 2n = 4–30 and XY, X_n-
Y and neo-XY sex-determination systems; and the Nepidae with 2n varying from 22–
46 and X0, XY or X_n-1Y sex determination (Papeschi and Bressa 2006). Clearly, the
rate of karyotypic evolution has been highly labile both within and among heteropteran
families. Discerning the evolutionary causes and functional significance of the
variation in heteropteran karyotypes and their rate of evolution remains a challenge for
future research.

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Table 1: Diploid autosomal chromosome counts and sex chromosomes for males of 27 species from five families in the infraorder Gerromorpha.

Data for an additional 24 species in the family Gerridae, subfamily Gerrinae are shown in Figure 3.

| FAMILY, subfamily | Species                        | Number of autosomes | Male sex chromosomes | Source                          |
|-------------------|--------------------------------|----------------------|-----------------------|---------------------------------|
| GERRIDAE          |                                |                      |                       |                                 |
| Charmatometrinae  | *Brachymetra albinerva* (Amyot and Serville, 1943) | 24                   | XO                    | Castanhole et al. (2010)        |
| Cylindrostethinae| *Cylindrostethus palmaris* (Drake and Harris, 1934) | 28                   | XO                    | Castanhole et al. (2010)        |
| Halobatinae       | *Asclepios shiranui* (Esaki, 1924) | 22                   | XO                    | Newman and Cheng (1983)         |
|                   | *Halobates flaviventris* Eschscholtz, 1822              | 30                   | XO                    | Newman and Cheng (1983)         |
|                   | *H. germanus* White, 1883                                   | 30                   | XO                    | Newman and Cheng (1983)         |
|                   | *H. micans* Eschscholtz, 1822                               | 30                   | XO                    | Newman and Cheng (1983)         |
|                   | *H. robustus* Barber, 1925                                  | 30                   | XO                    | Newman and Cheng (1983)         |
| Rhagadotarsinae   | *Rheumatobates rileyi* Bergroth, 1892                      | 18                   | XY                    | Calabrese and Tallerico (1984)  |
|                   | *R. crassifemur* Esaki, 1926                                | 20                   | XO                    | Pereira et al. (2015)           |
| Trepobatinae      | *Halobatopsis platensis* Berg, 1879                         | 24                   | XO                    | Castanhole et al. (2010)        |
|                   | *Metrobates hesperius* Uhler, 1871                          | 18                   | XY                    | Calabrese and Tallerico (1984)  |
| VELIIDAE          |                                |                      |                       |                                 |
| Microveliinae     | *Hebrovelia* sp.                                             | 20                   | XO                    | Ueshima (1979)                  |
|                   | *Microvelia douglasi* Scott, 1874                            | 20                   | XY                    | Ueshima (1979)                  |
|                   | *M. reticulata* (Burmeister, 1835)                          | 20                   | XO                    | Ueshima (1979); Grozeva et al. (2009) |
| Rhagoveliinae     | *Rhogovelia beckii* Drake and Harris, 1936                  | 18                   | XY                    | Onopa (1981)                    |
|                   | *R. tenuipes* Champion, 1898                                | 22                   | XO                    | Pereira et al. (2015)           |
|                   | *R. whitei* Breddin, 1898                                   | 38                   | XO                    | Castanhole et al. (2012)        |
|                   | *R. zela* Drake, 1959                                       | 22                   | XO                    | Pereira et al. (2015)           |
| Veliinae          | *Velia caprai* Tamanini, 1947                               | 24                   | XO                    | Ueshima (1979)                  |
|                   | *V. pelagonensis* Hoberlandt, 1941                           | 24                   | XO                    | Grozeva et al. (2009)           |
| Family       | Genus              | Species                  | Chromosomes | Sex Chromosomes | Reference(s)             |
|--------------|--------------------|--------------------------|-------------|-----------------|--------------------------|
| HYDROMETRIDAE| Merragata          | hebroides White, 1877    | 26          | XO              | Ueshima (1979)           |
|             | Hydrometrinae      |                          |             |                 |                          |
|             | Hydrometra         | gracilenta Horváth, 1899 | 18          | XO              | Grozeva et al. (2009)    |
|             | H. lineata Eschscholtz, 1822 | 18 | XO | Ueshima (1979) |
|             | H. procera Horváth, 1905 | 18 | XY | Ueshima (1979) |
| MESOVELIIDAE| Mesovelia          | furcate Mulsant and Rey, 1852 | 30 | X₄Y | Ueshima (1979); Grozeva et al. (2009) |
Figure Captions

Figure 1: Chromosomes from metaphase plates of spermatogonial cells and primary spermatocytes of males of *Aquarius remigis* (Say, 1832): (A) mitotic metaphase in spermatogonia showing the male diploid chromosome number 2n = 21; (B) meiotic metaphase I in primary spermatocytes showing 10 pairs of autosomes and a single X chromosome (indicated by the arrow). Scale bar 10 µm.

Figure 2: The distribution of autosomal chromosome counts for 50 species in the infraorder Gerromorpha. Counts for species in the family Gerridae are indicated by black bars. *Hebrus ruficeps ruficeps* Thomson, 1871 (family Hebridae) is excluded because of conflicting reports of autosomal chromosome counts (see Table 1).

Figure 3. Diploid autosomal chromosome numbers and sex chromosomes for males from 24 species and six genera in the family Gerridae, subfamily Gerrinae. Species from two other subfamilies within the Gerridae (Charmatometrinae and Cylindrostethinae) and from the family Veliidae (sister clade to the Gerridae) are included as outgroups. The cladogram is adapted from Damgaard et al. (2014) and is a consensus phylogeny based on parsimony analysis of 2268 bp of DNA sequence data from genes encoding COI+II, 16S rRNA and 28S rRNA. Only species with known karyotypes are shown. Arrowheads denote transitions (black) or possible transitions (grey) from XX/X0 to XX/XY sex determination. Karyotype descriptions follow Ueshima (1979) and Andersen (1982), except where noted by superscripts. Additional sources are: aGrozeva et al. (2009), bCalabrese and Tallerico (1982), cpresent study, dTakenouchi and Muramoto (1968; as noted in Ueshima 1979 and Calabrese and Tallerico 1982), eSpence and Maddison (1986), fCalabrese and Tallerico (1984),
Calabrese & Tallerico (1987), Castanhole et al. (2008), Castanhole, Pereira, Souza, and Itoyama (2010).

Figure 4: Numbers of species with XX/X0, XX/XY and other sex determination systems by subfamily and family within the infraorder Gerromorpha. The cladogram is adapted from Damgaard (2008, 2012) and is based on a parsimony analysis of 64 morphological characters and 2.5 kb of DNA sequence data from the mitochondrial genes cytochrome c oxidase subunit I + II (COI + II) and large mitochondrial ribosomal subunit (16S rRNA) and the nuclear gene large nuclear ribosomal subunit (28S rRNA). Only subfamilies containing species with known karyotypes are shown.
Figure 1a

Figure 1b

Figure 2

![Bar chart showing the number of species against diploid autosome count. The bars are colored black for Gerridae and gray for Others.](chart.png)
