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Forum

The Ant Chromosome database – ACdb: an online resource for ant (Hymenoptera: Formicidae) chromosome researchers

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Abstract: Ants are an important and diverse natural insect group exhibiting astonishing variation in chromosome number and structure. Their haploid chromosome numbers range from n = 1 to n = 60 and include diverse karyotypes comprising various different types of chromosome. This marked variation first attracted attention over 40 years ago, and has led to several theories concerning the evolution of chromosome change and the manner in which it may have promoted and contributed to ant species diversification. Despite the significance of ants, their chromosome numbers have been only sporadically documented and assembled. We present here the Ant Chromosome database – ACdb (www.ants.ufop.br), which was conceived as a regularly updated online tool for rapid access to data regarding ant karyology. ACdb is an easy-to-use database which will advance the accession and dissemination of cytogenetic knowledge of the Formicidae. At present, it contains 1080 entries of chromosome and karyotype data for 520 named species from 134 genera in 11 subfamilies. Basic information on karvotypes and chromosome numbers is provided, along with relevant karyotype formulae, which summarize chromosomal structure. ACdb highlights the challenge to ant cytogeneticists to improve the available chromosome knowledge of the Formicidae. Chromosome counts are still lacking in several subfamilies and many genera, while banding data are unavailable for most ant species. We trust that the database will inspire efforts to improve cytogenetic knowledge of these significant insects.

Key words: Genome, chromosome, nucleus, ant, evolution, karyotype.

Introduction

Chromosomes as the carriers of genes are the units of inheritance, which are duplicated and transmitted between cells during cell division. This was understood before the discovery of the DNA molecule, in light of the chromosome theory of heredity by Walter S. Sutton, and acknowledgement of the link between genes and chromosomes (GANETZKY & HAWLEY 2016). Further, the recognition of linear chromosomes and understanding that they are found in all eukaryotes was an important evolutionary transition, which allowed the partitioning of the genome (SCHUBERT 2007). The basic chromosome mitotic structure appears to be preserved across all plants and animals. It encodes the fundamental information of an organisms' genome. Chromosome numbers have been used extensively in systematics and are important in species delimitation (BAI & al. 2018) and lineage diversification (CRISTIANO & al. 2013).

Ants are an important insect group which exhibits considerable diversity in chromosome numbers, varying from n = 1 in the Australian bulldog ant Myrmecia croslandi (see CROSLAND & CROZIER 1986, IMAI & TAYLOR 1989, TAYLOR 2015) to n = 60 in the giant neotropical ant Dinoponera lucida (see MARIANO & al. 2008). The marked variation in chromosome number across species attracted the attention of the first ant cytogeneticists, and several mechanisms regarding the manner in which this diversity has evolved have been proposed. These include the "Minimum Interaction Theory" proposed by IMAI & al. (1994), in which rearrangements that involve Robertsonian fissions are important. Karyological evolution in ants generally tends towards an increase in chromosome number apparently serving to reduce the risk of deleterious rearrangements resulting from interactions between chromosomes in the nucleus (IMAI & al. 1988, IMAI & al. 1994). Nevertheless, this general trend in chromosome increase is probably subject to certain limits and other chromosomal rearrangements also induce changes in ant karyotypes. They include inversions and fusions (CARDOSO & al. 2014). Cytogenetic knowledge about ants, as well as other organisms, has been regularly summarized in previously published compendiums and reviews. LORITE & PALOMEQUE (2010) contributed the most recent comprehensive summary of ant chromosome numbers and karyotypes, including a supplement which provides at least 750 records. It is easy to find different online database sites for ants, including Ant Web (www.antweb.org) and Antwiki (www.antwiki.org), but these databases are mainly concerned with literature, species distribution, and systematics. Indeed, none of them specifically include cytogenetic data. Bolton's Catalogue, which has been published electronically (BOLTON & al. 2007), reports cytogenetic information for some taxa. Recently, many online databases for cytogenetic information have become available (PERUZZI & BEDINI 2014), mainly for plants. Some of them are specific for a taxonomic group or ecosystem (Roa & al. 2017). A comprehensive database of all plants was published by RICE & al. (2015).

The work reported here aims to compile the current cytogenetic knowledge of ants for presentation in a digital



Fig. 1: Phylogenetic relationship between Formicidae subfamilies redrawn from MOREAU & BELL (2013) and the haploid chromosome count distribution. The figure shows subfamilies for which a considerable number of studies are available. On the right, representative ant species with a remarkably low or high chromosome count. Ant images from AntWeb (www.antweb.org), top to bottom: *Strumigenys louisianae* (ANTWEB1038234), *Typhlomyrmex meire* (CASENT0915350), *Oecophylla smaragdina* (CASENT0070232), *Myrmecia pilosula* (CASENT0217500), *Tapinoma melanocephalum* (CASENT0173215), and *Dinoponera lucida* (CASENT0104920).

and straightforward online database. We here present the Ant Chromosome database – ACdb (www.ants.ufop.br) (Fig. 1) in recognition that knowledge of ant karyotypes provides important information which will advance our understanding of ant evolutionary biology and systematics.

Cytogenetic data assembly

Several compilations and reviews of ant chromosome counts and karyotypes have been published over recent decades (CROZIER 1975, LORITE & PALOMEQUE 2010). Our starting point was the comprehensive publication of LORITE & PALOMEQUE. We have retrieved all ant chromosome counts assembled by these authors by checking all of the publications involved. Additionally, we carried out structured searches in the following scientific databases: ISI Web of Knowledge, SCOPUS, and Google Scholar, using the following search terms: "ant", "chromosome", "cytogenetic", and "karyotype". Manuscripts mentioning or describing ant chromosome counts and karyotypes were accessed and the information was recorded.

The parameters recorded include the species name, diploid chromosome set (2n), haploid chromosome set (n), and karyotype. Karyotype information that provides the number of each type of chromosome (e.g., whether a chromosome was metacentric – M, submetacentric – SM, telocentric - T, subtelocentric - ST, or acrocentric - A) was accessed when it was reported by the original study. Similarly, the number of haploid or diploid chromosomes, or both if applicable, was recorded. Each distinct chromosome count was considered, so that, where counts vary among specimens each is recorded as an individual record (entry) in the database. In addition, varying conspecific chromosome counts from different localities or populations are registered individually. To make ACdb functional, taxonomic names were standardized using only recognized valid names provided by Bolton's catalog version 2.5.4 (www.antcat.org).

Dolichoderinae Dolichoderus

Cytogenetic data

Species	haploid(<i>n</i>)	diploid(2 <i>n</i>)	country(ies)	karyotype	notes	references
Dolichoderus quadripunctatus		28	Japan			<u>Imai 1969</u>
Dolichoderus scabridus	14	28	Australia		in Crozier 1966 as Diceratoclinea scrabida	Crozier 1966 Imai et al. 1977
Dolichoderus thoracicus		33	Malaysia		as D. bituberculatus	<u>Imai et al. 1983</u>
Dolichoderus thoracicus		30	Malaysia, Indonesia		as D. bituberculatus	<u>Imai et al. 1983</u> <u>Imai et al.</u> <u>1985</u>
Dolichoderus sp.		18	Malaysia			<u>Goni et al. 1982</u>
Dolichoderus lutosus		10	Brazil	4M+6SM		<u>Santos et al. 2016</u>
Dolichoderus bidens		18	Brazil	6M+12SM		<u>Santos et al. 2016</u>
Dolichoderus voraginosus		20	Brazil	14M+6SM		Santos et al. 2016
Dolichoderus diversus		22	Brazil	10M+12SM		<u>Santos et al. 2016</u>
Dolichoderus imitator		38	Brazil	6M+28SM+4A		<u>Santos et al. 2016</u>
Dolichoderus decollatus		38	Brazil	6M+32SM		Santos et al. 2016
Dolichoderus attelaboides		38	Brazil	2M+50SM+6A		Santos et al. 2016

http://ants.ufop.br/dolichoderinaedolichoderus.html

Fig. 2: Table of cytogenetic data generated by the Ant Chromosome database – ACdb. In this example, data were browsed for the genus *Dolichoderus*.



Fig. 3: Frequency histogram of the haploid chromosome count generated by the Ant Chromosome database – ACdb. In this example, data were browsed for the genus *Dolicho-derus*, haploid counts are shown; diploid (2n) values are converted for (n).

Ant Chromosome database – ACdb conception and data access

ACdb is available at the address http://www.ants.ufop.br hosted at the Universidade Federal de Ouro Preto – UFOP. Chromosome counts, haploid or diploid, locality and country of individual report, karyotype and the reference are presented in tabular form. All information can be searched or browsed by Subfamily and Genus, and data output can be presented as a table (Fig. 2) or a frequency histogram of the haploid chromosome counts (Fig. 3). When the dip-



Fig. 4: Frequency distribution of haploid chromosome ant entries in the Ant Chromosome database – ACdb in May 2018.

loid number alone is known, the histogram automatically represents its haploid conversion. Each entry is referenced by the study or studies which described or reported appropriate details. Further information is provided in the "notes" column. For example, it can include former names of species as used when their chromosome number was published. The query results, by subfamily or genus, can be downloaded by clicking the bottom link generating a csv file. In the "Statistics menu" a general histogram for all species can be generated and the total number of entries reported. Browsing by subfamily locates a histogram at subfamily level. The database will be progressively kept Tab. 1: Number of chromosome counts for species and morphospecies by subfamily of Formicidae actually in the Ant Chromosome database.

Subfamilies	Species and morphospecies
Amblyoponinae	4
Dolichoderinae	70
Dorylinae	11
Ectatomminae	66
Formicinae	214
Heteroponerinae	2
Myrmeciinae	94
Myrmicinae	460
Ponerinae	144
Proceratiinae	4
Pseudomyrmecinae	11
Total entries	1080

up to date by the correction of potential errors or flaws and by the addition of new records. Cytogenetic information can be submitted to the database using the link under the menu "submit" by filling-up the form.

The ACdb data: retrospect and prospect

As of May 2018, a total of 1080 entries in 134 genera and 11 subfamilies have been made available. From these entries, 520 named species have at least one chromosome report (some species show more than one chromosome count) and more than 200 were records from morphospecies. The most frequent haploid chromosome number is n = 10, followed by n = 9 and n = 11 (Fig. 4). The 520 named species represent $\sim 3\%$ of the ant species currently known (with ~ 16,000 taxa in all according to AntWeb as of January, 2018). There is information from 11 of the 20 subfamilies of Formicidae. The coverage of available cytogenetic data varies widely across subfamilies. The larger subfamilies comprise the majority of entries: Myrmicinae accounts for 42.60% (460), Formicinae for 19.81% (214), and Ponerinae for 13.33% (144) of all entries (Tab. 1). With respect to the country from which the records were taken, the majority come from Australia, Malaysia, India, and Indonesia (249, 166, 97, and 62 entries, respectively) mainly because most of the studies were effected by Imai and Crozier and associates (e.g., CROZIER 1975, IMAI & al. 1977, 1988). Other records included 119 from Brazil and 80 from the United States of America.

Details on the karyotypes of ants, such as chromosome morphology according to centromere position, has been incorporated for 234 entries. This information was added to the database when the authors provided the karyotype formula or when it could be determined by evaluating published data. Two different chromosome nomenclatures have been used previously to describe the chromosome morphology of ants. The most frequent was that proposed by LEVAN & al. (1964), which was based on the centromeric index. Some authors however, described karyotypes following the nomenclature proposed by IMAI & al. (1991) which considers heterochromatin patterns.

Conclusions and perspectives

Ants show an astonishing variety of karyotypes that may be related to their huge species diversity, forms, and functions. Changes in chromosomes may play an important role in speciation by promoting reproductive isolation (KING 1993). However, the importance of mechanisms that underlie chromosome changes and speciation remains poorly understood. Indeed, a growing number of cytogenetic studies in ants have emphasized that chromosome evolution has accompanied genus and species diversification (LORITE & PALOMEQUE 2010). The application of fluorescence in situ hybridization (FISH) and comparative analyses of chromosome-based phylogenetic trees has been made possible by the advances in the study of ant chromosomes (CRISTIANO & al. 2013, CARDOSO & al. 2014).

Reviews and compilations of ant chromosome counts are generally published periodically. As noted by LORITE & PALOMEQUE (2010), the previous substantial and unique global compilation of ant karyotypes was published by CROZIER in 1975. The speed with which the data are currently generated and published demands a new approach to the gathering and dissemination of ant karyotype data. Acdb is a public, straightforward and easily used resource about ant cytogenetics designed for use by interested researchers.

Based on the study of chromosomes in the species complexes of the Australian genus *Myrmecia*, IMAI & al. (1994) proposed the "Minimum Interaction Theory". This proposes a mechanism which prevents deleterious rearrangements produced by the interaction of chromosomes in the nucleus. The result is that overall chromosome evolution in eukaryotes proceeds towards increase in the number of chromosomes, and reduction of their average size (IMAI & al. 2002). Advances in the cytogenetic knowledge of Formicidae will allow for the identification of patterns and processes underlying chromosome variations, resulting in an improved understanding of ant systematics, evolution, and chromosome biology.

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