

Parallel pathways of karyotype evolution in the superfamily Chalcidoidea (Hymenoptera)

Параллельные направления эволюции кариотипа в надсемействе Chalcidoidea (Hymenoptera)

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KEY WORDS: Hymenoptera, Chalcidoidea, chromosomes, karyotypes, parallel evolution.

КЛЮЧЕВЫЕ СЛОВА: Hymenoptera, Chalcidoidea, хромосомы, кариотипы, параллельная эволюция.

ABSTRACT. Main pathways of karyotype evolution in the superfamily Chalcidoidea are reviewed in the light of the recent phylogenetic reconstruction [Heraty et al., 2013]. A chromosome set with $n = 11$ and all subtelocentric and/or acrocentric chromosomes could represent an ancestral character state for the Chalcidoidea. The most frequent haploid karyotypes in the superfamily, i.e. these having five metacentrics and/or submetacentrics of similar size ($n = 5$) and analogous chromosome sets with $n = 6$ and an additional small subtelocentric or acrocentric chromosome are supposed to have arisen independently within several major clades of the superfamily Chalcidoidea.

РЕЗЮМЕ. Основные направления эволюции кариотипа надсемейства Chalcidoidea рассмотрены в свете последней филогенетической реконструкции [Heraty et al., 2013]. Хромосомный набор с $n = 11$ и всеми акроцентрическими и/или субтелоцентрическими хромосомами, вероятно, представляет собой предковое состояние для Chalcidoidea. Очевидно, наиболее часто встречающиеся в надсемействе гаплоидные кариотипы, т.е. имеющие в своем составе пять метацентриков и/или субметацентриков сходного размера ($n = 5$) и аналогичные хромосомные наборы с $n = 6$ и дополнительной небольшой субтелоцентрической или акроцентрической хромосомой, независимо возникли в нескольких крупных филогенетических ветвях надсемейства Chalcidoidea.

The superfamily Chalcidoidea is an extremely diverse, taxonomically complicated and economically important group of parasitic wasps with an estimated species number of about 500000 [Munro et al., 2011; Heraty et al., 2013]. However, chromosomes of only about 170 chalcid species (i.e. far less than 0.1%) are studied up to now. Nevertheless, these species belong to 14 families (about 2/3 of more than twenty currently recognized ones [Heraty et al., 2013]), therefore allow-

ing for certain general conclusions. This paper is dedicated to the famous Russian chalcidologist, Dr. Vladimir A. Trjapitzin, who celebrates his 85th birthday in July 2013.

Chromosome number in the superfamily varies from $n = 3$ to $n = 12$ (see [Gokhman, 2009] for review). For a certain period in the past, all chalcid families were subdivided into the so-called “low-numbered” and “high-numbered” ones having $n = 3–7$ and $n = 8–12$ respectively (except for the family Aphelinidae with $n = 3–11$ [Gokhman & Gumovsky, 2009]). However, subsequent research demonstrated a substantially more complex pattern. Specifically, lower chromosome numbers ($n = 5–7$) were found in the families Eurytomidae and Encyrtidae that were initially regarded as “high-numbered” [Gokhman & Mikhailenko, 2008; Gokhman, 2010]. Moreover, karyotypes of “low-numbered” species tend to contain metacentric and/or submetacentric chromosomes (M/SM), whereas subtelocentrics and/or acrocentrics (ST/A) usually predominate in chromosome sets of “high-numbered” groups.

Certain (mostly indirect) evidence suggests that a chromosome set with $n = 11$ and all ST/A could represent an ancestral character state for the superfamily Chalcidoidea. Specifically, $n = 11$ can be found in more basal Microhymenoptera, i.e. in the superfamilies Cynipoidea (Figitidae) and Diaprioidea (Diapriidae) [Gokhman, 2009, 2011]. Among Chalcidoidea, $n = 11$ with all ST/A was found only in the family Encyrtidae; a minimally derived condition ($n = 10$ with all but one ST/A that could represent a single centric fusion) was also detected in the Encyrtidae and Eurytomidae [Gokhman & Gumovsky, 2009]. The latter character state can also be found in the Cynipoidea (Cynipidae) and Platygastroidea (Scelionidae) [Gokhman, 2009; Fusu et al., 2013]. However, karyotypes with $n = 10$ in the genus *Podagrion* Spinola, 1811 can again reflect a condition minimally derived from the preceding one (contrary to Fusu [2008]).

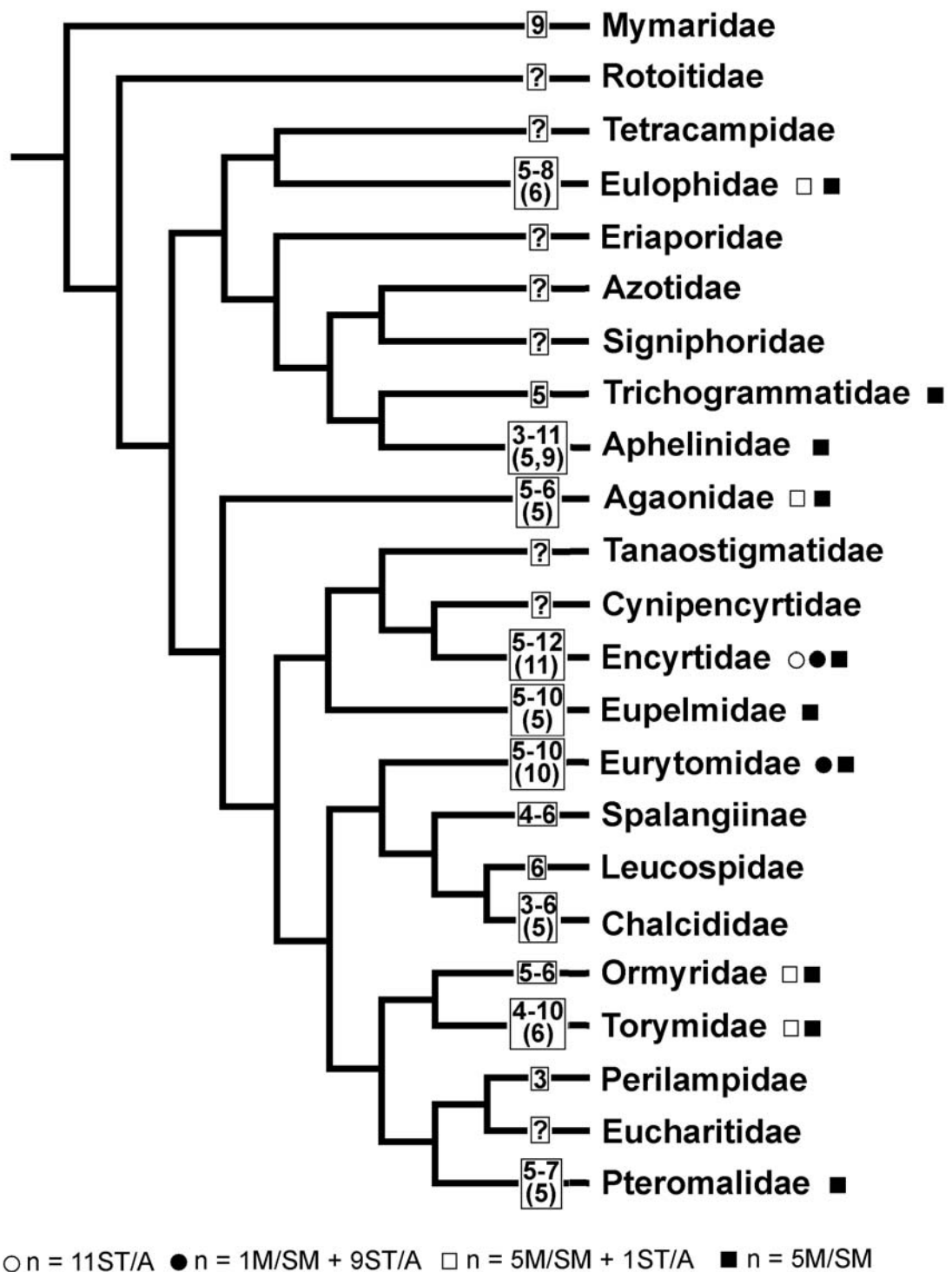


Fig. 1. Phylogenetic tree of karyotypically studied families/subfamilies of the superfamily Chalcidoidea (simplified from Heraty et al. [2013] with variation ranges of haploid chromosome numbers and some ancestral/derived character states of chromosomal sets superimposed onto it. Modal chromosome numbers are given in parentheses.

Рис. 1. Филогенетическое древо кариотипически изученных семейств/подсемейств надсемейства Chalcidoidea (по [Heraty et al., 2013], упрощено) с указанием пределов изменчивости гаплоидных хромосомных чисел и некоторых базальных/продвинутых состояний признаков хромосомных наборов. Модальные хромосомные числа приведены в скобках.

As far as haploid karyotypes with lower chromosome numbers are concerned, these having five M/SM of similar size are the most widespread among different groups of the superfamily Chalcidoidea. Specifically, they can be found in 10 out of 14 studied families, i.e. in the Eulophidae, Trichogrammatidae, Aphelinidae, Agaonidae, Encyrtidae, Eupelmidae, Eurytomidae, Ormyridae, Torymidae and Pteromalidae (Fig. 1). In addition, similar karyotypes with $n = 6$ and an additional small ST/A that are likely to represent the preceding stage of the process of consecutive centric fusions, were found in the Eulophidae, Agaonidae, Ormyridae and Torymidae.

In the family Eulophidae alone, where the latter character state should be considered as ancestral, transitions to the above mentioned one with $n = 5$ took place at least three times (see [Gokhman, 2009] for review). Analogous transitions also occurred in the families Ormyridae and Torymidae (at least once and twice respectively) that are only distantly related to the Eulophidae. These data confirm that the karyotype with five large M/SM and an additional small ST/A could be ancestral for many “low-numbered” families.

Recent phylogenetic analysis [Heraty et al., 2013] indicates that multiple parallel chromosomal fusions took place in a number of lineages of the superfamily Chalcidoidea, i.e. in the Spalanginae + Leucospidae + Chalcididae as well as in the Eulophidae, Trichogrammatidae, Agaonidae, Ormyridae and within the Aphelinidae, Encyrtidae and Eupelmidae, and possibly also in the Perilampidae + Eucharitidae + Pteromalidae and within the family Torymidae (Fig. 1; see also [Gokhman & Gumovsky, 2009]). Karyotype evolution in the Chalcidoidea therefore represents an excellent example of parallel evolution and karyotypic orthoselection [White, 1973] in particular.

The analysis by Heraty et al. [2013] also defined a few chalcid families as non-monophyletic. It may appear tempting to speculate that this feature can account for relatively high variation in the chromosome number within at least some of these distantly related groups (e.g. Eupelmidae with $n = 5-10$ and Aphelinidae with $n = 3-11$). However, this conclusion seems incorrect at least in respect to certain apparently monophyletic genera, such as *Eurytoma* Illiger, 1807 and *Metaphycus* Mercet, 1917 (both have $n = 5-10$) that belong to the families Eurytomidae and Encyrtidae respectively [Gokhman & Mikhailenko, 2008; Gokhman, 2010].

Recent cytogenetic data could also provide new insights into the phylogenetic analysis of the superfamily Chalcidoidea. For example, number of nucleolus organizing regions (NORs) can vary within this group (see [Gokhman, 2009] for review, as well as [Van Vugt et al., 2005, 2009; Bolsheva et al., 2012]). Specifically, members of the families Eulophidae, Aphelinidae and Pteromalidae carry only one paired NOR, whereas two out of the five A chromosomes in the haploid karyotype of *Trichogramma kaykai* Pinto et Stouthamer, 1997 (Trichogrammatidae) bear NORs, not to mention

an additional NOR on the B chromosome [Van Vugt et al., 2005, 2009]. Nevertheless, these data do not provide phylogenetically important information, since all studied families (except for the Pteromalidae) belong to the same major clade of Chalcidoidea [Heraty et al., 2013].

Authors of the recent phylogenetic analysis [Heraty et al., 2013] also suggest that certain clades of soft-bodied Chalcidoidea that come out at the base of the resulting phylogenetic tree, are in fact more distantly related than it was shown in the cited paper. Given this information, chromosomal study could shed more light on relationships of these groups. However, karyotype structure is unknown for many families and their subordinate taxa that belong to this clade.

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