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Karyosystematics of parasitic Hymenoptera: taxonomic decisions at the species level

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Abstract. A review of karyological approaches in parasitic Hymenoptera taxonomy at the species level is given. Closely related forms of parasitic Hymenoptera, differing in karyotype structure are subdivided into the following categories: (1) morphologically distinct species; (2) species with weak differences in external morphology (= sibling species s. str.); (3) morphologically identical populations; (4) chromosomal morphs (as a part of population polymorphism); (5) individuals carrying spontaneous chromosomal mutations. This classification is illustrated by the examples from different taxa of parasitic Hymenoptera.

Key words: karyosystematics, taxonomy, parasitic Hymenoptera.

Parasitic Hymenoptera are one of the largest and most taxonomically complicated groups of insects (Quicke, 1997). Despite the great practical significance of parasitic wasps which control various pests in forestry and agriculture (Gauld, Bolton, 1988), many aspects of parasitic Hymenoptera systematics and karyosystematics in particular, are insufficiently studied. Opinions on the use of chromosomal characters for solving taxonomic problems at the species level in parasitic wasps have changed substantially during the last 30-35 years. At the beginning of this period, R.H. Crozier, a leading expert in the field of Hymenoptera karyology, wrote in his well-known review (Crozier, 1975): “The stability of chromosome number within Chalcidoidea, Ichneumonoidea and Cynipoidea [superfamilies of parasitic wasps karyologically studied at that time – V. G.] suggests that cytotaxonomy might be most useful at the family level or higher, unlike the situation elsewhere in the order”. However, some papers describing differences in chromosome number between closely related species of the chalcid family Torymidae appeared at the same time as Crozier’s work (Goodpasture, 1975; Goodpasture, Grissell, 1975). Nevertheless, most specialists considered these data as exceptions till the end of the 1980s.

The next period of karyotaxonomic studies of parasitic Hymenoptera started in the beginning of the 1990s (Gokhman, 1991, 1993; Gokhman, Quicke, 1995). The authors of the cited papers were first who discovered that chromosomal differences between closely related species of parasitic wasps were fairly common, especially in certain groups with wide variation of karyotypic features. Now, karyological data are widely used for solving taxonomic problems at the species level in parasitic Hymenoptera (Gokhman et al., 1998; Baldanza et al., 1999; Giorgini, Baldanza, 2004; Gokhman, 2005; Pedata et al., 2005), including morphometric analysis of karyotypes and differential chromosome staining (Gokhman, 1997, 2005; Baldanza et al., 1999; Gokhman, Westendorff, 2000, 2003; Giorgini, Baldanza, 2004).

It is well known nowadays that chromosomal analysis allows and facilitates the detection and identification of closely related species and forms of parasitic wasps. It also provides additional information on the differentiation of species and populations. The above mentioned forms, which differ in details of karyotype structure, can be subdivided into the following categories according to their taxonomic rank and morphological isolation: (1) morphologically distinct species; (2) species with weak differences in external morphology (= sibling species sensu stricto); (3) morphologically identical populations; (4) chromosomal morphs (as a part of population polymorphism); (5) individuals carrying spontaneous chromosomal mutations. The first case is fairly trivial, because there are many examples of chromosomal differences between morphologically distinct species of the same genus (Gokhman, 2005). These species differ in chromosome numbers or in other characters (relative length of chromosomes, their centromere index, size and localisation of heterochromatic segments etc.). Parasitic wasps of the genus *Dirophanes* Foerster, 1869 (Ichneumonidae) display a good example of this situation (Gokhman, 1997). For instance, *D. callopus* (Wesmael, 1845) has 2n = 18, differing from *D. fulvitarsis* (Wesmael, 1845) and *D. invisor* (Thunberg, 1824) which have 2n = 20. However, two latter species notably differ from each other in relative lengths and centromeric indices of chromosomes as well as in the distribution of heterochromatic segments.

On the other hand, the detection of chromosomal morphs and spontaneous chromosomal mutations within certain species of parasitic wasps is probably more important for population genetics than for taxonomy. So, two different chromosomal forms with 2n = 21 were detected in ichneumonid wasp, *Tycherus bellicornis* (Wesmael, 1845) normally having 2n = 20 (Gokhman, 1989); the two forms with 2n = 21 arose from translocations and subsequent meiotic non-disjunction and aneuploidy. In another member of the family Ichneumonidae, *Ichneumon gracilentus* Wesmael, 1845, the only specimen having 2n = 25 (a trisomic for a small chromosome) was detected among several dozens of individuals with 2n = 24 (Gokhman, 1993).

More than 15 similar situations are now known for parasitic wasps of the families Ichneumonidae, Braconidae, Cynipidae, Aphelinidae, Encyrtidae, Pteromalidae and Torymidae (Giorgini, Baldanza, 2004; Gokhman, 2005; Pedata et al., 2005). Species with weak differences in external morphology as well as morphologically identical populations, i.e. forms belonging to the above mentioned categories (2) and (3), or sibling species s. l., are therefore of special interest for taxonomists. For example, I (Gokhman, 1991) have described two new species of the family Ichneumonidae, *Aethecerus ranini* Gokhman, 1991 and *Tycherus australogeminus* Gokhman, 1991 (both have 2n = 22), differing in chromosomal and morphological characters from closely related *Ae. dispar* Wesmael, 1845 (2n = 24) and *T. ischiomelinus* (Gravenhorst, 1829) (2n = 18), respectively.

Perhaps the most interesting data have been obtained in chromosomal research of populations of *Anisopteromalus calandrae* (Howard, 1881) (the family Pteromalidae), a cosmopolitan parasite of various stored-product pests, mainly Coleoptera. Many aspects of the ecology and behaviour of this species were thoroughly studied in connection with its wide use in biological control. Under these circumstances, discovery of two chromosomal forms with n = 5 and 7 in *A. calandrae* was quite unexpected. Then, we started a detailed study of morphology, behaviour, life-history strategies and preferred hosts of *A. calandrae* in laboratory populations of various origin (Gokhman et al., 1998, 1999; Gokhman, Timokhov, 2002; Timokhov, Gokhman, 2003). Preliminary studies demonstrated that strains of *A. calandrae* with different chromosome numbers differed from each other in certain morphological characters. We have found a few constant characters delimiting two well-separated population groups (Gokhman et al., 1998; Gokhman, Timokhov, 2002). Further studies revealed two groups of strains differing in their sexual behaviour, including sound signals emitted by males during courtship. These groups were reproductively isolated, although populations within the same group were fully compatible. We revealed that strains of *A. calandrae* had two different life-history strategies. Most of the differences between the two laboratory strains of *A. calandrae* distinctly point to their divergence within the well-known r/K continuum; the MSU and ICSP strains should therefore be respectively considered as K and r strategists (Gokhman et al., 1999). The individuals with n = 5 prefer to attack Anobiidae, whereas the individuals with n = 7 usually parasitize Curculionidae and Bruchidae. It is obvious that the differences between the two host groups can be interpreted in terms of the r/K continuum; Anobiidae and Curculionidae are considered as K and r strategists, respectively. If it is true, a lot of biological features of the *A. calandrae* complex can be explained adequately. Specifically, strains of parasitic wasps with n = 7 (probable r strategists) are better adapted to r-strategic hosts, whereas those having n = 5 and possessing many features of K strategists prefer K-strategic hosts (Timokhov, Gokhman, 2003).

Our studies therefore showed that the *A. calandrae* complex harboured two sibling species. Although the type specimen of *A. calandrae* is lost, morphological features of the species with n = 7 better fit the original description, and this species should be therefore considered as *A. calandrae* s. str. Since the *A. calandrae* complex actually includes two closely related species, all accumulated data on its biological features need reconsideration. It shows again the necessity of chromosomal analysis for studying of parasitic wasp species, including those which have a practical importance (Gokhman, Timokhov, 2002).

Significant differences concerning relative lengths and centromere indices of chromosomes were found in sibling species of the genus *Nasonia* Ashmead, 1904 (Pteromalidae): *N. vitripennis* (Walker, 1836), *N. longicornis* Darling, 1990, *N. giraulti* Darling, 1990 with n = 5 and in *Aphelinus varipes* (Foerster, 1841) s.l. (Aphelinidae) with n = 4 (Gokhman, Westendorff, 2000; Gokhman, 2005).

We also revealed morphologically identical sympatric populations with different chromosome numbers in the families Braconidae and Ichneumonidae. Specifically, a form with 2n = 12 was found in *Charmon cruentatus* Haliday, 1833 (Braconidae) together with specimens having 2n = 10; individuals with the intermediate chromosome number (2n = 11) were not detected (Gokhman, 2005). Similarly, specimens with 2n = 24 and 26 were found in *Ichneumon extensorius* L., 1758 and *I. suspiciosus* Wesmael, 1845 (Gokhman, 1993). However, formal description of new species of parasitic wasps seems inappropriate for all listed cases. Firstly, a few specimens with deviating chromosome numbers were studied in all mentioned situations, and therefore size and lifetime of those populations cannot be estimated even approximately. Secondly, the examined forms cannot be differentiated morphologically.

A more interesting case is an existence of populations with different chromosome numbers in *Aphidius ervi* Haliday, 1834 from the family Braconidae (Gokhman, Westendorff, 2003). In addition to 2n = 10 that is typical for this species, females with 2n = 12 were found in a certain population. A chromosomal study of these females showed that they differed from those having 2n = 10 in existence of an additional pair of small acrocentric chromosomes. These acrocentrics consist almost entirely of heterochromatin and have a specific mitotic behaviour, usually occupying a peripheral position on the metaphase plate. We suppose that these chromosomes may carry a special factor which doubles chromosomes in meiosis and thus leads to thelytoky. If it is true, we have therefore detected a new type of factor affecting sex ratio in the offspring of parasitic wasps.

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