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# Recent advances in biosystematics of *Trichogramma* and *Trichogrammatoidea* (Hymenoptera, Trichogrammatidae)

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**Abstract.** Among the egg parasites used extensively for biological control of various lepidopterous pests all over the world the species of *Trichogramma* and *Trichogrammatoidea* (Hymenoptera, Trichogrammatidae) are the most important. The mode of reproduction of most of these is arrhenotoky while a few in *Trichogramma* is thelytoky, the later could be facultative with change in temperature, from one mode to the other. Since 1977, a large number of new species were described and studies on different aspects made world over. The studies made include crossing experiments which proved existence in nature of sibling species and other categories of incipient speciation which otherwise are difficult to discern. Studies on isozyme and enzyme analyses showed important differences among species and populations of *Trichogramma*, so also response by these to different chemical insecticides. Scanning electron microscopy is yet another important tool to supplement other differentiating factors. Other biological characters aiding systematics include sex ratio, life and fertility table studies showing breeding potential, host preferences, temperature tolerance, etc.

**Keywords.** Arrhenotoky; thilytoky; sibling species; isozyme; enzyme.

## 1. Introduction

Species of *Trichogramma* and *Trichogrammatoidea* (Hymenoptera, Trichogrammatidae) are amongst the most important egg parasites of mostly Lepidoptera, the latter mostly being noxious pests of agricultural and horticultural crops. Because of the comparative ease with which most of these egg parasites could be mass produced on laboratory factitious host insects, these are being released against target pests for biological control all over the world, especially in the People's Republic of China, USSR and USA.

Most species are arrhenotokous while a few in *Trichogramma*, e.g. *T. embryophagum* Htg. are thelytokous. However, there are instances of change in mode of reproduction with change in temperature.

This article contains information on the biosystematic studies made on these parasites after 1977 when a comprehensive article on this subject was published (Nagarkatti and Nagaraja 1977). As per our present understanding on the trend of organic evolution, the modern systematics should be as comprehensive as possible. The present emphasis on the subject takes into consideration not only the taxonomy based until recently on external morphology, but also genetics, ecology and other biological parameters. An attempt in this direction is made in this paper on the two genera of the family Trichogrammatidae.

Since 1977 (Nagarkatti and Nagaraja 1977), quite a number of papers on the complex components of biosystematics of these genera have appeared. These include crossing experiments, bioecology, biochemistry, effect of chemical pesticides and temperature tolerance in addition to descriptions of new species based mainly on morphological characters. The recent literature on these is too complex and voluminous to condense in a short article like this. However, an attempt is made here to project some salient points on the subject.

Voegele and Pintureau (1982) based on available literature listed known 64 species of *Trichogramma* and divided them into 14 groups with description of two new species. They also included a key to differentiate these groups based on male genitalia and, in addition, made a detailed study on 10 species amongst them. Nagaraja (1978a) made a detailed biosystematic study on 10 species and a subspecies of *Trichogrammatoidea* using numerical taxonomy with 45 characters. Further to this, a detailed experimental hybridisation work was made (Nagaraja 1978b) and life and fertility tables on 6 species and a hybrid were worked out (Nagaraja 1986).

A large number of taxonomic papers describing new species all over the world have appeared in recent years. Existence in nature of sibling species, semispecies and other intraspecific categories are being recognised. This has enhanced the complexity of modern systematics and restricted the role of museum taxonomist specially of groups like Trichogrammatidae to identify a given taxa without understanding the supplementary information on biology, etc.

## 2. Crossing experiments

### 2.1 *Trichogramma*

This section deals with the discovery of 4 new species on the basis of morphology and results of crossing experiments made between these and other known related species. The new species are named tentatively as follows:

*Trichogramma* sp. A. — Ex *Agrius convolvuli* (L.) (Lep., Sphingidae) on *Colocasia antiquorum*, Vijayapura, 25 km away from Bangalore.

*Trichogramma* sp. B. — Ex *Danaus chrysippus* (L.) (Lep., Danaidae) on *Calotropis gigantea*, Saligrama (Dakshina Kannada Dist.), Bangalore.

*Trichogramma* sp. C. — Ex *Scirpophaga incertulas* (Walker) (Lep., Pyralidae) on *Oryza sativa*, Hebbal.

*Trichogramma* sp. D. — Ex *A. convolvuli* on *C. antiquorum*, Mandya.

The species A and C are closely related to each other and *T. hesperidis* Nagaraja and *T. flandersi* Nagaraja and Nagarkatti. Reciprocal crosses were arranged as shown below:

| | | |
|---|---|---|
| TA × TC | TB × TD | TD × *T. chilotraeae* |
| TA × *T. hesperidis* | TC × *T. hesperidis* | TD × *T. achaeae* |
| TA × *T. flandersi* | TC × *T. flandersi* | |

*Trichogramma* sp. D (TD) resembles partly *T. chilotraeae* Nag. and Nagar. and *T. achaeae* Nag. and Nagar. The number of parental females used was 9–50 in one to 6 replicates. The $F_1$ progeny produced were from 7–956 with the female progeny produced from 0–21·24%. In normal breeding, each species produced 60–75% females. The total progeny produced by each parental female allowed with alien males was 0·5–31·22 per female while the average progeny from the homogamic matings was above 60 per female. The males in these crosses usually were aggressive and less discriminatory with alien females but the females mostly were discriminatory against these males.

## 2.2 *Trichogrammatoidea*

Nagarkatti and Nagaraja (1977) mentioned the series of crossing experiments made on *Trichogramma* and *Trichogrammatoidea*. In the latter, 5 populations of *T. bactrae bactrae* Nag. when crossed between them showed considerable degree of reproductive isolation in some of them suggesting possibilities of incipient genetic divergence towards speciation.

Additional interesting experiments were made by the author in the Philippines on 3 populations of *T. cojuangcoi* Nag., the egg parasite of the cocoa moth, *Conopomorpha cramerella* (Snell.) (Lep., Gracillariidae) in Southeast Asia. These populations were collected from Mindanao (Philippines), Sabah (Eastern Malaysia) and Halmahera (Indonesia) islands attacking the same host (table 1).

*T. robusta* is a distinct species, differing morphologically from *T. cojuangcoi*. There is extremely restricted gene exchange with *T. cojuangcoi*. The hybrids from all these crosses did not survive for raising hybrid cultures. The stocks from the islands of Mindanao, Negros and Luzon (all Philippines) were interfertile. However, the ones from Mindanao and Negros produced lesser $F_1$ progeny.

**Table 1.** Crossing experiments between 3 populations of *Trichogrammatoidea cojuangcoi* from Mindanao (Philippines), Sabah (E. Malaysia) and Halmahera (Indonesia), *T. robusta* and two of the above populations and 3 stocks (including Mindanao's) of *T. cojuangcoi* within the Philippines.

| Pairs-crossed ♂♂ ♀♀ | Parental ♀♀ used | No. Repl. | $F_1$ Progeny ♂♂ | ♀♀ | ♀♀(%) | Per parental ♀ |
|---|---|---|---|---|---|---|
| Phil × Halm | 125 | 5 | 2,601 | 245 | 8·61 | 22·77 |
| Halm × Phil | 90 | 4 | 1,591 | 86 | 5·13 | 18·63 |
| Sabah × Halm | 100 | 4 | 1,328 | 19 | 1·41 | 13·47 |
| Halm × Sabah | 75 | 3 | 1,127 | 33 | 2·85 | 15·47 |
| Phil × Sabah | 105 | 5 | 2,030 | 157 | 7·18 | 20·83 |
| Sabah × Phil | 105 | 5 | 1,758 | 233 | 11·70 | 18·96 |
| Cavt × Mind | 21 | 1 | 336 | 339 | 50·22 | 32·14 |
| Mind × Cavt | 25 | 1 | 374 | 485 | 56·46 | 34·36 |
| Mind × Bacd | 50 | 2 | 383 | 177 | 31·61 | 11·20 |
| Bacd × Mind | 50 | 2 | 413 | 321 | 34·86 | 12·68 |
| T.rb × Mind | 75 | 3 | 1,198 | 12 | 1·07 | 16·13 |
| Mind × T.rb | 75 | 3 | 2,120 | 12 | 0·56 | 28·43 |
| T.rb × Sabah | 50 | 2 | 1,037 | 31 | 2·90 | 21·36 |
| Sabah × T.rb | 75 | 3 | 2,300 | 30 | 1·29 | 31·07 |

Phil, Philippines; Halm, Halmahera; Sabah, Sabah populations of *T. cojuangcoi*; Cavt, Cavite; Mind, Mindanao; Bacd, Bacolod stocks of *T. cojuangcoi*; *T. rb*, *T. robusta*.

## 3. Biological observations

### 3.1 *Scanning electron microscopy*

The earliest study of *Trichogramma* using scanning electron microscopy was made by Voegele *et al* (1975) who studied female antennae and found differences in the number of sensillae on ventral part of the club in 3 species studied, *T. maltbyi* Nag. and Nagar., *T. evanescens* Westwood and *T. brasiliensis* (Ashm.). Preliminary attempts made by Dr S Nagarkatti in USA (Anon 1972) on male genitalia *in situ* and male antennae of *Trichogramma* sp. confirmed the relative position of different genitalic parts and sensillae respectively, that were observed earlier under microscope. Pointel (1977) also made a similar study in France. Hung (1982) reported existence of petal like structures on distal end of tibia of both sexes of 6 species of *Trichogramma*. These were thin and transparent, used probably for transferring secretion from abdomen to the wings to increase aerodynamic function (Hung 1982) and possibly diagnostic. Wang *et al* (1986) observed two ring segments in antennae in both sexes of *T. dendrolimi* Mats., and in other species as well, one free and another firmly attached to the base of funicle. Both these were observed earlier by the author under microscope, but since one is indistinct, it has been shown in all drawings in a dotted line.

### 3.2 *Behaviour in parasitism*

Thorpe and Dively (1985) observed in the laboratory the parasitism of *Heliothis virescens* (F.) (Lep., Noctuidae) eggs in 1·8 l (13 × 13 cm), 43 l (23 × 23 × 62 cm) and 400 l (2 × 2 × 1 m) arenas with soyabean foliage as the substrate, by *Trichogramma minutum* Riley, *T. pretiosum* Riley and *T. exiguum* Pinto and Platner. The trend of parasitism by each species, especially *T. minutum* and *T. pretiosum*, differed.

Intraspecific differences towards certain hosts have been observed in France by Ferreira and Pintureau (1983) in *T. minutum*. A strain of this species was reported to be the best in controlling *Mythimna unipuncta* (How.) (Lep., Noctuidae). Glas *et al* (1981) found that *T. cacoeciae* Marchall laid slightly more eggs in *Mamestra brassicae* (L.) (Lep., Noctuidae) and rejected *Pieris brassicae* (L.) (Lep., Pieridae) from a distance even without antennating them while *T. evanescens* laid more eggs in *P. brassicae*.

The biological differences between two sibling species, *Trichogrammatoidea lutea* Gir. and *T. prabhakeri* Nag. were shown (Nagaraja 1986). These differences include (i) sex ratio, 1♂ : 1·131 ♀♀, and 1♂ : 4·324 ♀♀; (ii) the finite rate of natural increase ($\lambda$), 1·4677 ♀♀/♀/day and 1·4223 ♀♀/♀/day; (iii) generation time (T) 10·0309 and 9·7608 days and (iv) net female production ($R_0$) 46·910 and 31·147 ♀♀/♀/generation, respectively.

### 3.3 *Role of temperature*

The role of temperature in biological differences between populations and species of *Trichogramma* has to be emphasised. Voegele and Russo (1981) observed in France that in *T. rhenana* Voegele and Russo, parasite of *Ostrinia nubilalis* (Hub.) (Lep., Pyralidae) the threshold temperature for development was 15°C and the species was able to develop at the maximum of 34°C while *T. schuberti* Voegele and Russo was found to develop at temperature as low as 11°C but did not survive above 33°C. Russo and Voegele (1982) working on 4 species, the above two and *T. nubilale* Ertle and Davis and *T. maidis* Pintureau and Voegele at temperatures ranging from 11°C to 34°C observed that there were two groups each having distinct temperature requirement.

Cabello and Vargas (1985) found that *T. cardubensis* Vargas and Cabello being thelytokous at 20°C for 41 generations changed to arrhenotoky above 28°C and reverted to thelytoky at 20°C. Whether this is also a case of thelytoky to amphitoky and vice versa has to be further investigated.

### 3.4 *Studies on isozymes and enzymes*

A large number of papers have been published in recent years on this subject on *Trichogramma.* Hung (1982) compared electrophoretically collected samples of *T. pretiosum* from Maryland, Arkansas, Georgia and Texas (USA) and found differences in the isozyme analyses of different enzymes and discovered a sibling species on the basis of these studies. Enzymatic study of 10 strains from 9 species of *Trichogramma* were made by Pintureau and Babault (1982). The esterases, malate-dehydrogenases and tetrazolium-oxidases allowed distinguishing of related species, supplementary information on them and distant species. The groupings based on this study conformed to the ones made on the basis of external morphology. As a result of work on *T. evanescens*, *T. chilonis* Ishii, *T. pretiosum*, *T. cacoeciae*, *T. pieris* and *T. dendrolimi*, Cao *et al* (1986) suggested use of esterase isozyme analyses that could aid taxonomy of the genus. Hung and Huo (1985) studied the electrophoretic banding patterns for the malic enzyme, phosphoglucomutase and phosphoglucose isomerase in 20 laboratory cultures of 14 species of *Trichogramma.* Variations in PGM in *T. exiguum*, *T. marylandense* Thorpe and *T. pretiosum*, in PGI in *T. exiguum*, *T. marylandense*, *T. minutum* and *T. perkinsi* Gir., while in ME only in *T. pretiosum* were observed by these authors.

Hung (1982) reported that the studies made on caryotypes of *T. chilonis*, *T. evanescens*, *T. nubilale* Ertle and Davis and *T. pretiosum* did not show significant differences and all had n = 2 sm + 2T + 1 A. However the species could readily be distinguished by zymograms of superoxide dimutase and esterase.

### 3.5 *Response to insecticides*

Chemical insecticides have been tested on *Trichogramma* in several countries. Kapustina (1977) found that Trichlorphon and Phosalone at 0·01% would not affect different races of *T. evanescens* and *T. cacoeciae pallida* Meir of Orshan race, *T. embryophagum* Hertig from Byelorussia but suggested releases not earlier than 3 to 4 days after sprayings. In India Paul (1986) mentioned that toxicity level of a particular insecticide possibly differed on different species of *Trichogramma* while synthetic pyrethroids, fenvalerate and flucythrinate, monocrotophos, endrin, phosalone and endosulfan were relatively safer to *Trichogramma.* The species studied were *T. chilonis*, *T. brasiliensis*, *T. japonicum* (Asm.) and *T. perkinsi.* The nomenclature of the last species needs confirmation.

## 4. Discussion

The importance of biosystematics has been stressed in dealing especially with sibling species, semispecies and biological races which are abound in *Trichogramma* and *Trichogrammatoidea*. It is the realistic approach to understand the complex ramifications of the process of evolution. The taxonomists of the above mentioned genera till fifties of this century were attempting to classify them on the basis of colour, length of antennal hairs, wing fringe, etc. Attempts were made to study male genitalia in *Trichogramma evanescens* by Hintzelman (1925) and other species by Ishii (1941) and Tseng (1965). It was in 1968 that Nagarkatti and Nagaraja made a detailed study of male genitalia of *Trichogramma* by interpreting and naming various parts of the genitalia. Subsequently the authors discovered a large number of new species from India and elsewhere. Taking cue from this work which laid down certain criteria as diagnostic to the taxonomy of the above two genera, entomologists working on them world over discovered numerous new species. According to the latest list compiled by Voegele and Pintureau (1982), Pang (unpublished results) and some more new species yet to be described by the author, there are over 85 species of *Trichogramma* and 25 of *Trichogrammatoidea* known to date as compared with 19 and 8 species, respectively, prior to 1968 (*Trichogramma*) and 1978 (*Trichogrammatoidea*).

Apart from the taxonomic studies based on male genitalia and other external characters, a large series of crossing experiments conducted during the past two decades brought to light existence of sibling species, semi-species, etc and those of disputed status requiring further investigations. Thus, two stocks of *T. minutum*, one on either side of Rocky Mountains (USA), did not interbreed, showing reproductive isolation (Nagarkatti and Fazaluddin 1973). Such species need to be considered as sibling species. The other examples include *Trichogramma* sp. A, *T.* sp. B and *T. hesperidis* Nag., mentioned in the text. Few more examples are *T. japonicum* and *T. pallidiventris* Nag. in *Trichogramma* and *T. lutea* Gir. and *T. prabhakeri* Nag. and the 3 distinct populations of *T. cojuangcoi* in *Trichogrammatoidea*. In addition, there are numerous morphologically indistinguishable species, but spatially widely separated whose status has to be determined by using biological methods. To quote an example *Trichogrammatoidea guamensis* Nag. is described from material collected in Guam on eggs of *Lampides boeticus* (L.) (Lep., Lycaenidae) and *T. cojuangcoi* in Southeast Asia. These two parasites are almost indistinguishable morphologically from each other. But owing to nonavailability of live material from Guam, the crossing trials could not be made. However, none of the several hundreds of eggs on *L. boeticus* on *Crotolaria* sp. and *Cajanus cajan* collected in India and the Philippines and Papua New Guinea, was parasitised by *T. guamensis*. The only parasites reared from these eggs were an unidentified species of *Telenomus* (Hym., Scelionidae) and *Trichogrammatoidea armigera* Nag., *T. guamensis* and *T. cojuangcoi* could possibly be sibling species. However, until results of crossing experiments on these parasites are available, their taxonomic status remains provisional.

In the section on crossing experiments, one could see that *T.* sp. A, *T.* sp. C and *T. hesperidis* produced extremely few progenies per parental female (0·50–4·00/parental female). This happened possibly due to the mechanical injury in the female reproductive system during mating by alien males (heterogamic matings) or antigenic reaction in the female to the alien sperms, indicating mechanical or chemical isolation, common in heterogamic matings. This being apart, there are instances like restricted progeny production even with a substantial number of female production as observed in the cross between Bacolod (Negros) and Mindanao populations of *T. cojuangcoi*. This could be the positive instance of incipient divergence on way to speciation.

The problem with sibling species where the reproductive isolation has not resulted in external manifestation has to be fully understood. This phenomenon is very frequent in these parasites. This factor therefore has to be borne in mind by the taxonomist when identifying such species from spatially isolated areas. Another factor worth mentioning is that the sympatric diverging populations of a species show greater reproductive isolation than the allopatric ones, thus perpetuating the evolutionary process and preventing wastage of sperms. This is possibly the instance of character displacement (Brown and Wilson 1956) observed in ants. An almost similar instance was observed in *Trichogramma* (Nagaraja 1973).

The data on biological parameters should also be taken into consideration like the ones occurring in *T. lutea* and *T. prabhakeri* (Nagaraja 1978b). These should include host and habitat preferences in the intraspecific populations, within the ambit of species. *T. lutea* and *T. prabhakeri* and Halmaheran, Sabah and Philippine populations of *T. cojuangcoi* could be considered as semispecies with respect to each other although there appeared to be greater reproductive isolation between the former two species which ultimately may develop into full species. There are hence innumerable intraspecific forms allover the world, each having attained different levels of distinctiveness in the process. The other examples in parasitic Hymenoptera include *Aphytis* spp. (Hym., Aphelinidae) (Rao and DeBach 1969a,b).

The study on isozymes of enzymes is very important step in the modern approach to systematics. Where the morphological distinctiveness is lacking, these analyses and the reaction of each parasite species or population to a given chemical pesticide add to the systematics on the group of the said parasite. The numerical taxonomy as explained by Sokal and Sneath (1963) is the most logical expression of biosystematics with respect to the groups like *Trichogramma* and *Trichogrammatoidea* with all their cryptic species and other incomplete evolutionary stages.

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