

Reassessment of *Trichogramma euproctidis* (Girault, 1911) (Hymenoptera: Trichogrammatidae)

Пересмотр статуса *Trichogramma euproctidis* (Girault, 1911) (Hymenoptera: Trichogrammatidae)

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КЛЮЧЕВЫЕ СЛОВА: скрещивания, яйцевой паразитоид, Hymenoptera, морфометрия, синонимия, систематика.

ABSTRACT: The *nomen dubium* status is applied to *Trichogramma turkestanicum* Meyer, 1940, leading to the restoration of the status of *T. meyeri* Sorokina, 1981. Two Moroccan strains, identified as *T. voegelei* Pintureau, 1990, and one Portuguese strain, identified as *T. meyeri*, were compared by means of their morphometric characteristics and crossings. Among the 10 morphometric characters measured and the six ratios calculated, 15 showed significant differences but only 20% of these differences were in accordance with the specific separations. Crossings indicated higher levels of reproductive incompatibility between the strains of *T. voegelei* than between the two species. Concerning esterase markers, literature data are consistent with the present results showing that *T. voegelei* and *T. meyeri* are closely related. Therefore, we suggest that these species are synonymous. A comparison of the *T. euproctidis* types with *T. meyeri* suggested another synonymy. Consequently, the valid name for the species studied is *T. euproctidis* (Girault, 1911).

РЕЗЮМЕ: Применение статуса *nomen dubium* к *Trichogramma turkestanicum* Meyer, 1940 ведет к восстановлению статуса *T. meyeri* Sorokina, 1981. Две марокканские линии, определенные как *T. voegelei* Pintureau, 1990, и одна португальская линия, определенная как *T. meyeri*, были сравнены по морфометрическим характеристикам и с помощью скрещиваний. Среди 10 морфометрических признаков и шести их отношений, 15 показали достоверные различия, однако лишь 20% этих отличий совпадало с границами видов. Скрещивания показали более высокий уровень репродуктивной несовместимости между линиями *T. voegelei*, нежели между двумя видами. Результаты исследования эстеразных маркеров соответствуют литературным данным, что демонстрирует близкое родство между *T. voegelei* и *T. meyeri*. Таким

образом, мы предполагаем, что эти виды являются синонимами. Сравнение типов *T. euproctidis* и *T. meyeri* также позволяет предполагать их синонимию. Следовательно, валидным названием для изученного вида является *T. euproctidis* (Girault, 1911).

1. Introduction

The genus *Trichogramma* Westwood, 1833, worldwide in its distribution, includes numerous species parasitizing insect eggs, mainly Lepidoptera eggs. Its systematics is still raising a lot of difficulties due to the minute size of the species and to the large number of closely related species. The characters used in systematics include the reproductive compatibility as well as the morphological, biochemical and genetic similarity (DNA analysis) [Pinto *et al.*, 1991; Pintureau, 1991, 1993a, b; Pinto, 1998; Silva *et al.*, 1999].

The aim of the present work was to reconsider the validity of some related species from Eurasia and north Africa: *T. turkestanicum* Meyer, 1940 found in Uzbekistan and Portugal [Neto, Pintureau, 1995], synonymized to *T. meyeri* Sorokina, 1981 by Pintureau [1990], *T. voegelei* Pintureau, 1990 from France and Morocco [Pintureau, 1991], and *T. euproctidis* (Girault, 1911) collected in Europe, without any indication of the precise regions [Pintureau, 1990]. After reconsideration of the synonymy between *T. turkestanicum* and *T. meyeri*, the latter species was compared with *T. voegelei* by means of morphometric characteristics and crossings. The literature data on enzymes (esterases) were reviewed. Finally, the available information on the lectotype of *T. euproctidis*, kept in the United States National Museum of Natural History (Smithsonian Institution) in Washington (USNM) [Pinto *et al.*, 1978], and on other individuals of the same series was compared with the data recorded for the other species.

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Table 1. *Trichogramma* strains studied.
Таблица 1. Изученные линии рода *Trichogramma*.

Species	Strain	Origin	Host	Host plant	Date of collection
<i>T. voegelei</i>	MK	Tadla (Morocco)	<i>Vanessa cardui</i> (Lep.: Nymphalidae)	<i>Malva sylvestris</i> (Malvaceae)	October 1990
	T27		<i>V. cardui</i>	<i>M. sylvestris</i>	November 1998
<i>T. meyeri</i> (ex- <i>T. turkestanica</i>)	PB	Faro (Algarve, Portugal)	Lep.: Noctuidae	<i>Lycopersicon esculentum</i> (Solanaceae)	September 1991

2. Materials and methods

The morphometric study and the crossings were carried out on the strains listed in table 1. The two strains MK and T27 were identified as *T. voegelei* based on their morphology, which is in agreement with that of the type [Pintureau, 1990], and also on their geographic origin which is consistent with the species distribution [Bourarach, El Ghanmi, 1990]. The strain PB was identified as *T. turkestanicum* (synonymized to *T. meyeri*) because of the basal notch of the dorsal lamina of the male genital capsule [Neto, Pintureau, 1995]. The depth of this notch, which appears to be larger in *T. voegelei*, was used as the diagnostic character to separate the two species [Pintureau, Keita, 1989; Pintureau, 1994].

The morphometric study concerned 10 male characters, three of the antennae and seven of the genitalia:

length of flagellum (FL), width of flagellum (FW), length of the longest flagelliform seta (FSL), length of the dorsal lamina (DLL), width of the dorsal lamina (DLW), length of the genital capsule (GL), apical distance defined by the paramere length (AD), length of the ventral ridge (VRL), length of the volsellae (VSL) and length of the intervolsellar process (IPL). These morphological characters have been illustrated by Pinto (1998). In addition, six ratios between the measured characters were calculated (Table 2). Measurements were taken from 15 or 16 males of each strain (MK, T27 and PB). These individuals were reared on *Ephestia kuehniella* Zeller (Lep.: Pyralidae) eggs, irradiated with UV and stored for less than one week at 3°C. They were then dorsoventrally mounted under coverslips in Faure liquid after clarifying in 10% KOH. Each individual was photographed with a camera connected to a binocular

Table 2. Means \pm standard errors of the measured characters (in 1/100 mm) and the character ratios in the males of two strains of *T. voegelei* (MK and T27) and one strain of *T. meyeri* (PB).

Таблица 2. Средние значения \pm стандартные ошибки изученных признаков (в единицах 1/100 mm) и их отношений у самцов двух линий *T. voegelei* (МК и Т27) и одной линии *T. meyeri* (PB).

Characters	MK (N=15)	T27 (N=15)	PB (N=16)	p ^{ANOVA}
FL	16.53 \pm 0.18(a)	18.89 \pm 0.14(b)	16.46 \pm 0.18(a)	<0.0001
FW	2.39 \pm 0.11(a)	2.75 \pm 0.07(b)	2.64 \pm 0.07(b)	0.0253
FSL	8.82 \pm 0.07	9.00 \pm 0.07	9.07 \pm 0.18	0.1638
DLL	2.43 \pm 0.02(b)	2.54 \pm 0.03(c)	2.29 \pm 0.06(a)	0.0001
DLW	2.06 \pm 0.03(b)	2.18 \pm 0.03(c)	1.76 \pm 0.06(a)	<0.0001
GL	7.74 \pm 0.06(b)	7.88 \pm 0.06(b)	7.45 \pm 0.09(a)	0.0004
AD	1.91 \pm 0.03(a)	2.13 \pm 0.03(b)	1.96 \pm 0.04(a)	<0.0001
VRL	1.63 \pm 0.05(a)	1.93 \pm 0.03(b)	1.95 \pm 0.06(b)	<0.0001
VSL	1.05 \pm 0.03(b)	0.96 \pm 0.03(a)	0.94 \pm 0.03(a)	0.0133
IPL	0.70 \pm 0.02(b)	0.82 \pm 0.02(c)	0.63 \pm 0.02(a)	<0.0001
FSL/FW	3.80 \pm 0.20(b)	3.31 \pm 0.07(a)	3.45 \pm 0.11(a)	0.0442
IPL/AD	0.37 \pm 0.01(b)	0.39 \pm 0.01(b)	0.32 \pm 0.01(a)	<0.0001
VSL/AD	0.55 \pm 0.02(b)	0.45 \pm 0.01(a)	0.48 \pm 0.01(a)	<0.0001
DLL/DLW	1.19 \pm 0.02(a)	1.17 \pm 0.02(a)	1.34 \pm 0.07(b)	0.0255
VRL/GL	0.21 \pm 0.01(a)	0.25 \pm 0.004(b)	0.26 \pm 0.01(b)	<0.0001
AD/GL	0.25 \pm 0.004(a)	0.27 \pm 0.002(b)	0.26 \pm 0.005(b)	0.0003

If the ANOVA is significant, different letters in a line indicate significant differences (p<0.05) according to the Fisher PLSD test.

microscope, at two magnifications, i.e. $\times 280$ (antennae) and $\times 1170$ (genitalia). Measurements were then taken on the photos, using a ruler calibrated in mm and then converted into true lengths (in 1/100 mm). To compare the strains, each character and ratio was analyzed by an ANOVA followed by Fisher PLSD tests. Moreover, a discriminant factorial analysis (DFA) was performed to discriminate between the three strains based on the 16 characters and ratios.

Reciprocal crossings between the strains were performed in order to analyse a F1 generation and, when this crossing was fertile, a F2 generation as well. The offspring of intra-strain crossings and of virgin females were used as the control. Eggs of *E. kuehniella*, parasitized by each strain, were isolated before the parasitoid emergence, each in an individual glass tube, in order to obtain virgin females. After emergence, inter or intra-strain pairs were established and each, as well as virgin females, was offered about 500 *E. kuehniella* eggs and a droplet of diluted honey. Some F1 females were inseminated by their male siblings, then isolated, and subjected to the same treatment as their mothers in order to obtain a F2 generation. The experiment was conducted at 23°C and L:D 16:8. Percentage of female mortality after 7 days, fecundity during the first 7 days of egg-laying (i.e. number of parasitized eggs identified by their dark colour), percentage of emergence (i.e. ratio of the number of emerged adults to the number of parasitized eggs $\times 100$), and sex ratio of the offspring (i.e. percentage of females) were recorded at each generation.

Since only females are diploid and can be hybrid in F1, the sex ratio of this generation indicates the compatibility level of a crossing. The few F2 crossings performed were used to confirm the conclusions drawn from F1 crossings. Because of haplo-diploidy, these F2 crossings were in fact backcrosses (males can only be hybrid from the F2 offspring, and only then in a very variable manner). Fecundity, proportion of emergence and sex ratio in each crossing were compared using ANOVAs followed by Fischer PLSD tests. Results of crossings were synthesized with the help of a reproductive isolation index quantifying the compatibility level between two forms. The selected index (Ir), adapted to the haplo-diploid species, is based on the sex ratio of F1 offspring [Pintureau, 1991].

3. Designation of *nomina dubia* and restoration of the status of *T. meyeri*

Trichogramma turkestanicum, described from Uzbekistan by Meyer [1940], was designated as a senior synonym to *T. meyeri* (a species also described from Uzbekistan) by Pintureau [1990] and Neto & Pintureau [1995]. Nevertheless, Meyer's description of *T. turkestanicum* ("Forewing longer than body. Forewing length two times its width. Abdomen longer than head+thorax. Colour dark brown. Length 0.32 mm. Host *H. armigera*") is inadequate and no type is available (the neotype proposed by Pintureau, 1990, is inappropriate and its

designation is invalid because it does not originate from the same region in Uzbekistan). Such a situation now encourages, in accordance with a decision taken at the XX international congress of entomology [Pintureau, Pinto, 1998], a re-consideration of *T. turkestanicum* as a *nomen dubium*, i.e. a name of unknown or doubtful application, and the restoration of the status of *T. meyeri*. This nomenclatural change avoids any controversy due to the absence of type material [Pintureau, Pinto, 1996].

In the same paper Meyer has also briefly described two other species. *Trichogramma pallida* Meyer, 1940 was designated as a junior synonym of *T. dendrolimi* Matsumura, 1926 by Pintureau [1990], and *T. pini* Meyer, 1940 was designated as a junior synonym of *T. piniperda* Wolff, 1915 by Pintureau [1990, 1998]. Like *T. turkestanicum*, *T. pallida* and *T. pini* have an inadequate description and no available type, and must therefore be considered as *nomina dubia*.

4. Comparison of *T. meyeri* and *T. voegelei*

Morphometric study

Means and standard errors of the different characters and ratios in the three strains MK, T27 and PB appear in table 2. Only one character, the length of the longest flagelliform seta (FSL), does not show a significant difference. Among the other three characters of the antennae, one (FW) is smaller in the strain MK (i.e. one of the *T. voegelei* strains), another (FSL/FW) is larger in the same strain, and the last (FL) is larger in the strain T27 (i.e. the other *T. voegelei* strain). These characters are, thus, of no value in establishing the species identity.

Only three characters of male genitalia out of 12 are of value in determining the species: GL and IPL/AD are larger in *T. voegelei*, and DLL/DLW is larger in *T. meyeri*. Three variables (DLL, DLW and IPL) are different in the three strains, and the other 6 variables are different in only one *T. voegelei* strain: AD is larger in the strain T27, VSL and VSL/AD are larger in the strain MK, and VRL, VRL/GL and AD/GL are smaller in the same strain.

Among the 15 antennal and genital variables showing significant differences, only three (i.e. 20%) are, thus, of value in discriminating between *T. voegelei* and *T. meyeri*. On the contrary, the two strains MK and T27 of *T. voegelei* differ by 80% of the characters (12 out of 15). Consequently, these data do not confirm the separation of *T. voegelei* and *T. meyeri*, which may be synonymous.

The DFA supported this result (Fig. 1): the strain MK of *T. voegelei* is closer to the strain PB belonging to *T. meyeri* than to the strain T27 also belonging to *T. voegelei*. In this analysis, the first axis and the second axis bear 78.8% and 21.2% of the information, respectively. The eigenvectors indicate that the strain T27 is mainly separated from the other two strains according to the first axis by FL, VRL, FSL/FW and VSL/AD, and that the strains MK and PB are mainly separated according to the second axis by the same characters, except for one (FSL instead of VSL/AD).

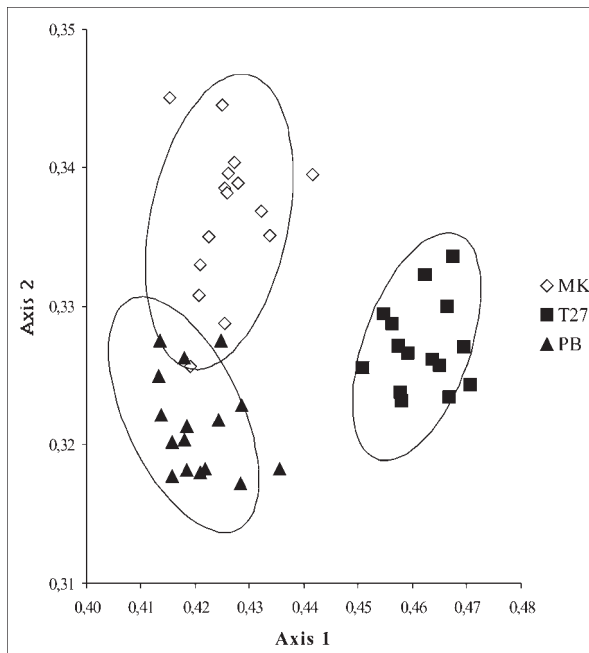


Fig. 1. Scatter diagram of male individuals belonging to two strains of *T. voegelei* (MK and T27) and one strain of *T. meyeri* (PB), following a discriminant factorial analysis (axes 1–2) performed with 10 morphometric characters and 6 ratios. Ellipses include 95 % individuals.

Рис. 1. Скаттер-диаграмма самцов, принадлежащих к двум линиям *T. voegelei* (МК и Т27) и одной линии *T. meyeri* (PB), построенная по результатам дискриминантного факторного анализа (оси 1–2) 10 морфометрических признаков и 6 их отношений. Эллипсы включают 95 % особей.

Crossing analysis

In the haplo-diploid species showing arrhenotokous parthenogenesis, such as the *Trichogramma* species studied, the compatibility of a crossing is indicated by the presence of females in the offspring originating from this crossing. Results of the crossings performed between the three strains MK, T27 and PB appear in table 3. Virgin females produced only male progeny demonstrating an arrhenotokous parthenogenesis.

Contrary to the intra-strain crossings, the F1 crossings between the strains T27 and PB or T27 and MK produce few or no females in the progeny. The absence of females, and thus of hybrids, is recorded in the crossing direction “female PB or MK × male T27”. In the other crossing direction, the female percentage is clearly smaller than this percentage observed in the parental strains (Table 3). This phenomenon is recorded not only in crossings between two strains of *T. voegelei* but also in crossings between one strain of *T. voegelei* and one strain of *T. meyeri*, and thus does not define the two species. Among the two feasible F2 crossings, that involving two strains of the same species (T27 and MK) did not result in progeny, whereas the crossing involving two strains of different species (T27 and PB) led to a normal sex ratio. These crossings thus confirm that the observed barriers do not correspond to the current specific divisions.

Numbers of parasitized eggs are lower in the inter-strain crossings than in the intra-strain ones, the differences being even further marked with virgin females (Table 3). Moreover, the two types of F1 females pro-

Table 3. Characteristics of females of three *Trichogramma* strains, virgin or mated to a male belonging to the same or another strain, and of their progeny.

Таблица 3. Характеристики самок трех линий рода *Trichogramma* (девственных и скрещиваемых с самцами той же или другой линии) и их потомства.

	Crossing		Mortality (1)		Parasitized eggs	Emergence (2)		Sex ratio (3)	
	Female	Male	N	%		N ₁	%	N ₂	%
Virgin	T27	–	20	5.0	50.3±2.6 (f)	1006	97.1(bcd)	977	0(a)
Females	PB	–	20	15.0	37.4±3.6(de)	747	94.8 (bc)	708	0 (a)
Intra-strain crossings	T27	T27	20	10.0	45.2±2.4(ef)	903	97.1 (bcd)	877	75.1 (d)
	PB	PB	20	60.0	32.2±3.5(cd)	644	93.2 (b)	600	72.3 (d)
Inter-strain crossings	T27	PB	27	44.4	23.1±2.6 (bc)	598	96.3 (cd)	576	36.5 (c)
	PB	T27	33	63.6	18.5±2.5 (b)	582	95.9 (cd)	558	0 (a)
F1	T27	MK	35	8.6	21.1±2.1 (b)	720	92.6 (b)	667	10.8 (b)
	MK	T27	32	84.4	4.6±1.1 (a)	83	97.6 (d)	81	0 (a)
F2	T27.PB	T27	20	85.0	71.6±10.1 (g)	1433	59.1 (a)	847	77.8(d)
	T27.MK	T27	25	80.0	0	0	–	0	–
p ^{ANOVA}					<0.0001	<0.0001		<0.0001	

(1) Percentage of female mortality 7 days after emergence.

(2) Percentage of the number of adults to the number of parasitized eggs. In N₁, progenies distributed in less than 10 parasitized eggs were excluded. ANOVA performed on the proportion of emergence after arcsine[√] transformation.

(3) Percentage of female progeny. In N₂, progenies including less than 10 imagoes were excluded. ANOVA performed on the proportion of females after arcsine[√] transformation.

Different letters in a column indicate significant differences (p<0.05) according to the Fisher PLSD test.

Table 4. Morphometric data recorded in *T. euproctidis* and *T. meyeri*, including the types, by different authors.
Таблица 4. Морфометрические данные по *T. euproctidis* и *T. meyeri* (включая типы), полученные разными авторами.

Source(s)	GW/GL	AD/GL	VRL/GL	AL/HTL	FSL/FW	OL/HTL
<i>T. euproctidis</i>						
Pinto et al. (1978) (1)	0.41					
J.D. Pinto, in litt. 1983; or B. Pintureau, unpubl. results (2)	0.38	0.26	0.38		2.24 or 2.35	
J.D. Pinto, in litt. 1997 (2)	0.42	0.27	0.28	0.68	2.70	1.02
<i>T. meyeri</i>						
Sorokina (1981) (3)	0.43	0.31	0.19		3.20	
Pintureau (1987) (4)	0.38			0.89	3.22	
Neto and Pintureau (1995); or J.D. Pinto, in litt. 2000 (5)	0.32	0.27			2.90–3.50	0.82
J.D. Pinto, in litt. 1997 (6)	0.39	0.29		0.67	3.10	
Present study		0.25–0.27	0.21–0.26		3.31–3.80	

(1): lectotype; (2): series of the lectotype; (3): individuals from Uzbekistan; (4): individuals from France; (5): individuals from Portugal; (6): type.

AD — apical distance; AL — aedeagus length; FSL — length of the longest flagelliform seta; FW — width of flagellum; GL — length of the genital capsule; GW — width of the genital capsule; HTL — hind tibia length; OL — ovipositor length; VRL — length of the ventral ridge.

duced substantially different numbers of parasitized eggs. Females resulting from a crossing between the two strains of *T. voegelei* were sterile, while those originating from the interspecies crossing “female T27 x male PB” produced more parasitized eggs than the parental strains. Such an increase in the parasitization efficiency can be explained by a heterosis effect which appears to confirm the co-specificity of *T. voegelei* and *T. meyeri*.

The percentage of emergence does not substantially differ in the F1 individuals and in the controls. On the contrary, an important preimaginal mortality was recorded in the feasible F2 generation from inter-strain crossings. It is important to remember that this mortality is associated with notable parasitization efficiency. The percentage of female mortality after 7 days seems to be higher in the mated females than in the virgin ones, and sometimes still higher when the male and the female of the pair belong to different strains (female T27 x male PB). In addition, the F1 females showed a clear increase in their mortality (Table 3).

The reproductive isolation index (Ir) between the two strains T27 and MK of *T. voegelei* is 0.928, and is only 0.757 between the strain T27 of *T. voegelei* and the strain PB of *T. meyeri*. Therefore, the two species *T. voegelei* and *T. meyeri* cross better than the two populations belonging to the same species of *T. voegelei*. Such ambiguous results together with those of the morphometric study support the view that the two species are synonymous.

Comparison of esterases

Esterases of *T. voegelei* and *T. meyeri* were analysed by Pintureau [1990, 1993b, c] and by Neto & Pintureau [1995], respectively. In spite of their variability, the enzymes encoded by two loci are very similar in the two species: *T. voegelei* from France shows the allele 0.07 at

the locus Est 1, *T. voegelei* from Morocco the allele 0.13, while *T. meyeri* from Portugal has the alleles 0.07 and 0.08; *T. voegelei* from France shows the allele 0.22 at the locus Est 2, *T. voegelei* from Morocco the allele 0.24, while *T. meyeri* has both alleles. On the contrary, Est 5' shows the allele 0.50–0.53 in *T. voegelei* and alleles 0.45–0.48 and/or 0.48–0.51 in *T. meyeri*.

Nei's genetic distance between the two species was calculated by Neto & Pintureau [1995]. Although the value calculated is high (0.54), it is less than the maximum found between the closely related species *T. voegelei* and *T. evanescens* Westwood, 1833 or *T. brassicae* Bezdenko, 1968 and *T. evanescens* [Pintureau, 1993b].

5. Comparison of *T. meyeri* and *T. euproctidis*

The species *T. euproctidis* was described by Girault [1911], who indicated that two males and one female deposited in the USNM are considered types. A lectotype was chosen in this series by Pinto *et al.* [1978]. Another male and another female from the same series as the lectotype were deposited in the Illinois Natural History Survey (J.D. Pinto, in litt. 1997). Several inaccurate drawings of male genitalia and antennae of these types have been made [Pang, 1985, 1988; Pintureau, 1987]. However, poorly mounted individuals or unrelated specimens could explain these errors. For instance, according to Pinto [1998], the record of *T. alpha* Pinto “is based on two old uncleared slides in the National Museum of Natural History identified by A. Girault as *T. euproctidis*”.

Several morphometric data recorded on the types seem also to be erroneous. For example, the values calculated for GW/GL, VRL/GL and FSL/FW by J.D. Pinto (in litt. 1983) or B. Pintureau (unpublished results) appear underestimated or overestimated (Table 4). More

recently, other measurements were taken on remounted individuals, especially specimens deposited in Illinois, by J.D. Pinto [in litt. 1997]. These data were compared to those recorded on the *T. meyeri* type [J.D. Pinto, in litt. 1997], to those taken on illustrations of *T. meyeri* from Uzbekistan [Sorokina, 1981], to those taken on individuals of *T. meyeri* from Portugal [Neto, Pintureau, 1995; J.D. Pinto, in litt. 2000] or France [Pintureau, 1987], and to those from the present study (Table 4).

There appear to be very few differences between *T. euproctidis* and *T. meyeri*. Only OL/HTL and VRL/GL show a clear gap and VRL is often difficult to measure. A third difference, with regard to FSL/FW, is slight and probably insignificant. Such results lead us to consider *T. meyeri* as a junior synonym of *T. euproctidis*.

6. Discussion and conclusion

Systematics of the genus *Trichogramma* is difficult because of the large numbers of closely related species and diagnostic characters. Morphology alone is often insufficient and the combination of several methods is thus necessary. However, these methods sometimes provide contradictory data, and any reliable conclusions can be made only after their critical analysis. For instance, the use of only trivial morphological characters to describe *T. turkestanicum* led us to select the *nomen dubium* status for this species and consequently to restore the status of *T. meyeri*.

Study of several groups of characters led us to the conclusion that *T. meyeri* and *T. voegelei* are not only extremely similar but even synonymous, with *T. voegelei* as a junior synonym. Morphometric characters, for example, showed a greater difference between two strains of *T. voegelei* (80% of the characters are different) than between the two supposedly different species (20% of the characters are different).

The absence of hybrids between two strains (i.e. the absence of females among the progeny resulting from the crossing of two strains in haplo-diploid insects like *Trichogramma* species) is supposed to indicate a genetic isolation and thus the existence of two different species. Nevertheless, some exceptions to this rule are known. For instance, Pinto *et al.* [1991] showed that numerous incompatibilities exist between populations in *T. minutum* Riley, and that the phenomenon is less pronounced in *T. deion* Pinto and Oatman, 1986 and inconspicuous in *T. pretiosum* Riley, 1879. Pinto and Stouthamer [1994] confirmed that reproductive incompatibility does not always lead to the correct species definition in the genus *Trichogramma*. Those nonreciprocal or reciprocal incompatibilities could originate from the infection of one of the studied strains by *Wolbachia*, an endosymbiotic bacterium, or from the infection of both strains by two different forms of *Wolbachia* [Hoffmann, Turelli, 1997]. Nevertheless, the incompatibilities described in *T. deion* are not induced by *Wolbachia* [Stouthamer *et al.*, 1996] and, moreover, *Wolbachia*-induced cytoplasmic incompatibility are unknown in the genus *Trichogramma*.

We recorded reproductive incompatibilities between the studied strains of *T. voegelei* and *T. meyeri*. Among these strains, PB is devoid of *Wolbachia* [Jager *et al.*, 1997], while T27 and MK have an unknown status of infection. These data are, however, sufficient to rule out the involvement of *Wolbachia* in the observed incompatibilities since a crossing of any female with a male PB must be normal and the crossing "female T27 × male PB" is partially incompatible.

Nevertheless, recorded incompatibilities have no value in separating the species because they are stronger between the two studied strains of *T. voegelei* (Index of reproductive isolation $I_r=0.93$) than between one strain of *T. voegelei* and one strain of *T. meyeri* ($I_r=0.76$). The present results appear in accordance with other I_r values which were unable to discriminate between the two species: $I_r=0.14$ or 0.50 between *T. voegelei* from France and Morocco (two crossings performed by Pintureau, 1991, with two different French strains), and $I_r=0.51$ between *T. voegelei* from Morocco and *T. meyeri* from Portugal [Neto, Pintureau, 1995]. Together with the heterosis phenomena observed for the number of eggs parasitized by certain hybrids (present work, and Neto & Pintureau, 1995), all these I_r values tend to confirm the synonymy between the two species.

These complications in the interpretation of the crossing experiments led Neto & Pintureau [1995] to misunderstand the relationships between *T. voegelei*, *T. meyeri* and *T. brassicae*: the three species were correctly supposed to be closely related, but *T. voegelei* and *T. brassicae* were considered as being the closest ones. Indeed, the compatibility between *T. voegelei* and *T. meyeri* appeared lower than that between *T. voegelei* and *T. brassicae*, two species which can produce hybrids presenting a thelytokous mode of reproduction [Pintureau, Babault, 1981].

Comparison of esterase in *T. voegelei* and *T. meyeri* does not allow for the confirmation or the rejection of their synonymy. However, the differences recorded mainly affect the only locus Est 5', and can be explained by an insufficient sampling. Finally, the morphological comparison of this species, *T. meyeri*, with the different types of *T. euproctidis* led us to conclude that these two names were also synonymous and therefore to retain only *T. euproctidis* (Girault).

Trichogramma euproctidis was considered as a species of the *pretiosum* group by Pintureau [1990, 1994, 1998], *T. voegelei* as a member of the *evanescens* group [Pintureau, 1990, 1994], and *T. turkestanicum* (= *T. meyeri*) as a species either of the *pretiosum* group [Pintureau, 1990, 1993c] or of the *evanescens* group [Pintureau, 1994; Neto & Pintureau, 1995]. Although this problem of classification does not exist for Pinto who merged in 1998 the *evanescens* and *pretiosum* groups into the same section *exiguum*, we believe that the species studied belongs to the *evanescens* group. The geographic distribution of *T. euproctidis* includes Egypt, France, Morocco, Portugal and Uzbekistan [Sorokina, 1981; Pintureau, 1990; Neto, Pintureau, 1995;

Hansen, 2000], Turkey [D. Kostadinov, in litt. 1996; material sent by T. Koçlu in 1996 and 1998, and by F. Bin in 2002], and possibly Germany [S.A. Hassan, in litt. 1996] and Japan [Girault, 1911].

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