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Detecting intraspecific hybrids in *Testudo hermanni* (Gmelin 1789)

Introduction

Crosses among various species and subspecies of genus *Testudo* have been documented. Literature citations of interspecific *Testudo* cross-breeding or unintentional hybridization compiled by the authors include those listed by Fritz & Cheylan 2001 or Vinke & Vinke 2004. Citations of intraspecific crosses between *Testudo hermanni hermanni* and *Testudo hermanni boettgeri* are less well described (Mayer 1992a, Mayer 1992b, Bruekers 1995, Veidt & Fritz 2001).

In this paper, the terms “crosses” and “hybrids” will be used interchangeably, even though the word “hybrid” has the positive connotation of a selectively chosen, intended crossing between related subspecies or species.

Within the much larger and geographically contiguous eastern part of the range of *Testudo hermanni*, there is considerable regional variation. As a result, *Testudo hermanni hercegovinensis* (Werner 1899) has been described from the northwesternmost tip of the Balkan Peninsula. Widespread speculation that other undescribed regional subspecies occur elsewhere is highlighted by Vetter (2006). Nonetheless, the conclusions based on genetic analysis carried out by Fritz *et al.* (2006) have concluded that only 2 geographically separated subspecies of *T. hermanni* are valid, namely those defined by Bour (1987): *Testudo hermanni hermanni* and *Testudo hermanni boettgeri*. These are abbreviated henceforth as *Thh* and *Thb*.

Awareness and the prevention of intraspecific cross-breeding in Mediterranean tortoises is vital for the management of wild populations of Hermann’s Tortoise. The genetic pollution of natural populations of *Testudo hermanni hermanni* in Italy has been recorded by Frisenda & Ballasina (1990) for tortoises in Tuscany which resulted from cross-breeding with Balkan tortoises. At the same time they indicate the existence of non-autochthonous tortoise populations on the Adriatic coast near Venice and the Abruzzi, while Campi (in 2002) mentions the release of confiscated *Thb* near Bari in south-eastern Italy. In the Bosco della Mesola in north-eastern Italy tortoises with hybrid characters have been found (Bertorelle 2007). Perez *et al.* (2009) carried out genetic analysis according to the methods of Forlani *et al.* (2005), and concluded that cross-bred tortoises occur within this population. However, their genetic investigation cannot prove whether the hybridisation has occurred naturally, as intergradation at the interface between both subspecies, or whether it is the result of the liberation of non-native, Balkan tortoises by man (Bertolero *et al.* 2011).

In southern France, in the Var region, *Thb* specimens as well as intergrades have turned up (Guyot & Pritchard 1999). The origin of such tortoises has been attributed to the release or escape of tortoises once kept as pets, as well as tortoises once held, then released, by the original SOPTOM rehabilitation centre in the area.

The danger of cross-breeding of the last remaining native *Thh* in the Massif de Albera in Spain with *Thb* was reported by Soler *et al.* 2010. That various specimens of *Thb* have turned up in the Albera and adjacent areas containing released *Thh* tortoises from legitimate head-starting programmes show the real peril of genetic pollution in future.

Consequently it is essential to have easily accessible parameters for distinguishing cross-bred tortoises and *Thb* in all areas in which there are individuals or institutions committed to conservation. Such information is equally vital for private individuals who raise Hermann's Tortoises in captivity, and whose efforts may someday be incorporated into reintroduction programmes.

This article aims to furnish data which will facilitate the morphometric differentiation of cross-bred Hermann's Tortoises. Nonetheless we believe that our morphologic description should be complemented with a genetic analysis, and also with an analysis of pholidosis (morphometric parameters), to achieve an absolute identification of crossbreeds.

Material and Methods

Morphometric data were obtained from 10 first-generation cross-bred specimens *Thb* ♂ (male) × *Thh* ♀ (female, see photo 1, breeders) which had grown according to normal growth rates in captivity (see Willemsen & Hailey 2001, Costa *et al.* 2005) as well as from 12 F_1 crosses produced of *Thh* male × *Thb* female (photo 2, breeders) showing certain abnormal morphological parameters consistent with rapid growth in captivity. Three of these crosses exhibited pyramiding of carapace scutes. One female as well, classified as a juvenile, has shown faster than normal growth. This 2 year-old specimen appears to be twice that age, based on the relation between age and maximum carapace length (Cheylan 1981, Soler Massana & Martínez Silvestre 2005). The plastron seams of all specimens appear normal.

We photo-documented and analysed 15 parameters (Bender 2001) of the tortoises studied: Length (according to the method of Bertolero *et al.* 2008 see fig. 1), black plastral bands, pattern of the fourth vertebral scute, pattern of the fifth vertebral scute,

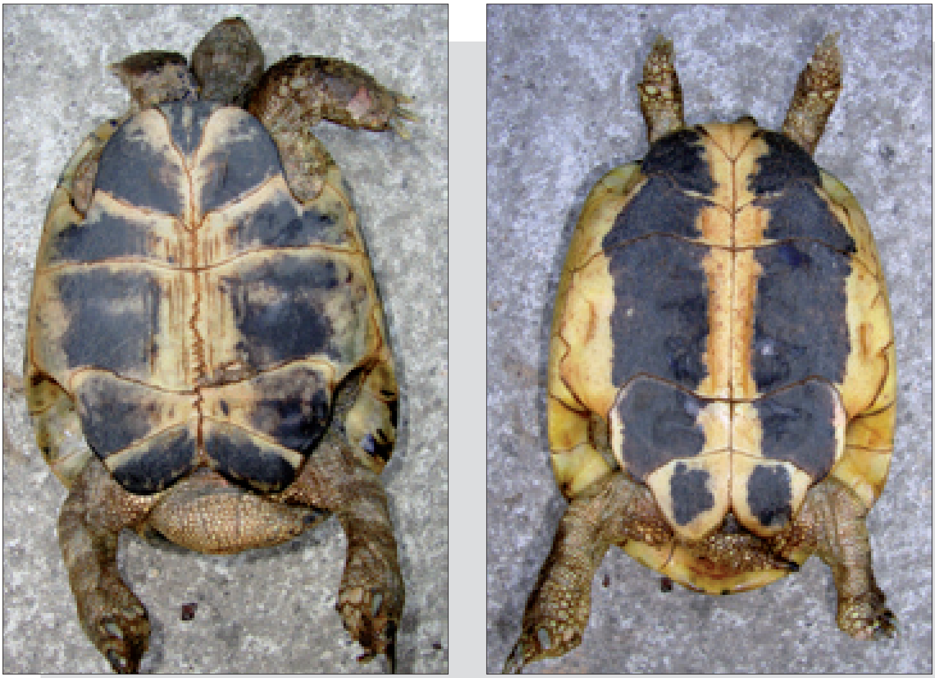


Photo 1: Parents of the crosses *Thb* ♂ × *Thh* ♀. Photos: J. Soler

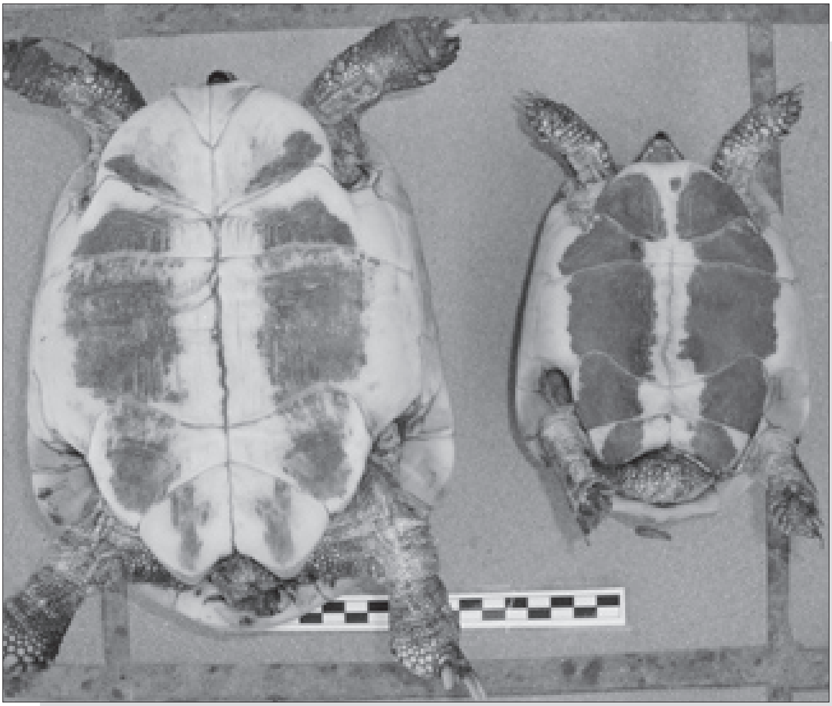


Photo 2: Parents of the crosses *Thh* ♂ × *Thb* ♀ (Scale: cm). Photo: J. Soler

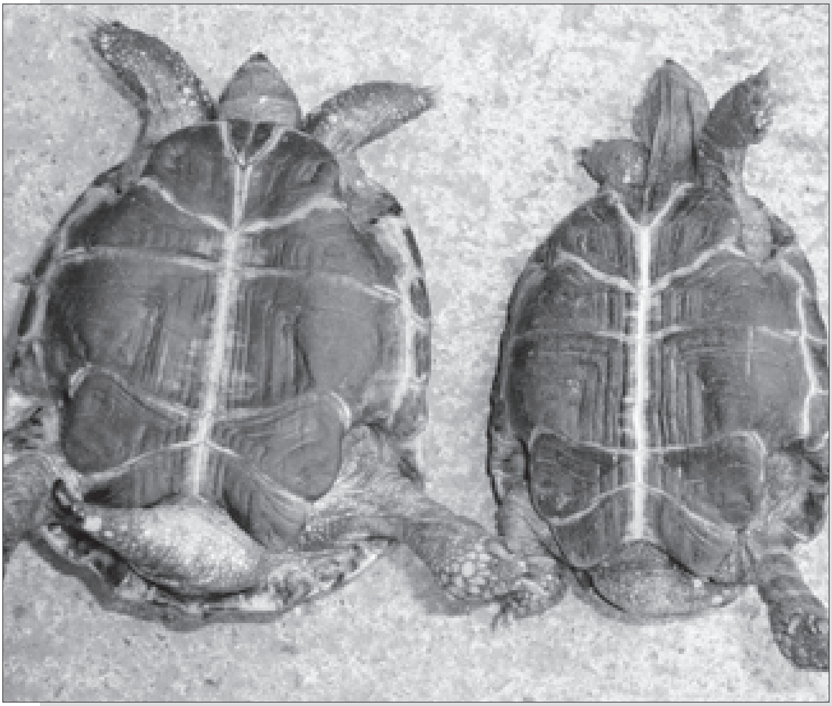


Photo 3: Crosses *Thh* ♂ × *Thb* ♀ with black hyperpigmentation oft he plastra Photo: J. Soler

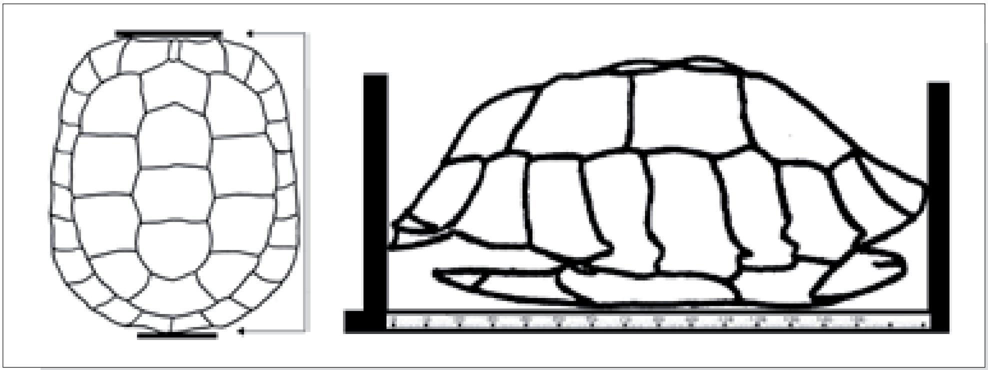


Fig. 1 Graph showing method used to measure maximum length of tortoises

(see figs. 2, 3, 4 – see VETTER [2006] for the nomenclature of the scutes), supracaudal scute divided/undivided, presence/absence of inguinal scutes, degree of plastral concavity in males, presence/absence of yellow spotting of subocular scales, scale coloration of the top of the head, overall coloration, ratio of pectoral and femoral seams (FS ÷ PS) as well as the ratio between humeral and femoral seams (HS ÷ FS), (see fig. 5), pigmentation of gular scutes, and pattern of the pectoral scutes, particularly in males (see fig. 6).

All these parameters were carefully compared with specimens of both subspecies having clearly documented geographical origins (see fig. 7). In addition, these parameters were compared to data furnished in the literature (STEMMLER 1968, CHEYLAN 1981, BOUR 1987, STUGREN & KAVVADIAS 1989, ARTNER & ARTNER 1997, GUYOT & DEVAUX 1997, WILLEMSEN & HAILEY 1999a, WILLEMSEN & HAILEY 1999b, CHEYLAN 2001, SOLER *et al.* 2001, VETTER 2006, WEGEHAUPT 2008, SCHWEIGER 2009, MASCORT 2010).

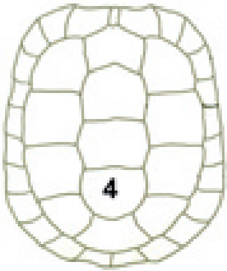
Results

Crosses between *Testudo hermanni boettgeri* ♂ × *Testudo hermanni hermanni* ♀

	Breeders		Crosses adult and subadult	
	Thb ♂	*Thh* ♀	♂	♀
n:	1	1	3	7
Length (mm)	172	199	max./min.	
			151/131.5	211/131
Weight (g)	1,102	1,410	593/400	1837/395
Humeral-femoral ratio	2.25	1.29	Mean value	
			1.89	1.95
Femoral-pectoral ratio	0.68	1.25	Mean value	
			0.84	0.74

Tab. 1. Biometry of the breeder animals and of their progeny, as well as photographic record of the most characteristic parameters (Photographic plates 1).

Pattern of fourth vertebral scute



Testudo hermanni hermanni
Always with a central dark spot.

Testudo hermanni boettgeri
Usually a small dark spot[1], often completely lacking[2], but some specimens from Bosnia and Herzegovina[4] and from around Thessaloniki may bear a large dark spot.


1

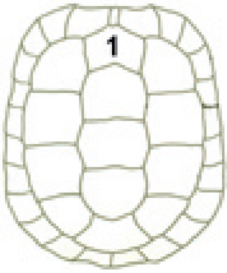

2


3


4

Fig. 2

Pattern of first vertebral scute



Testudo hermanni hermanni
Generally, a large dark central blotch is present (more than 50% of the scute area). Preponderantly black (70-80%) in certain Mallorca populations and in that of the Albera Mountains [2] (Spain).

Testudo hermanni boettgeri
Highly variable according to population. Very dark in specimens from northeastern Peloponnesus[1] (nearly 80% of the surface area), and unmarked in specimens from southwestern Peloponnesus[2] (a dark outline present, occupying 20% of the scute area).


1


2


1


2

Fig. 3

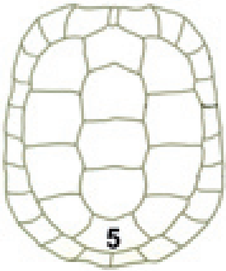
Pattern of fifth vertebral scute  	
Testudo hermanni hermanni Generally with a yellow figure shaped like a keyhole.	***Testudo hermanni boettgeri*** A keyhole-shaped yellow figure is nearly always lacking.
	

Fig. 4

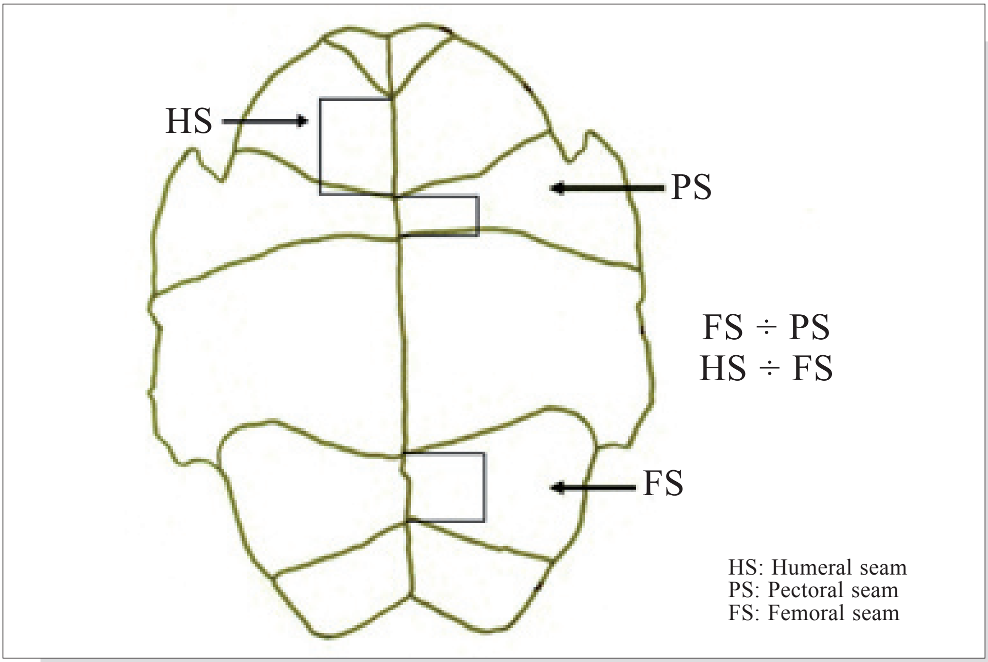


Fig. 5 (Parameters measured on the plastral shields)

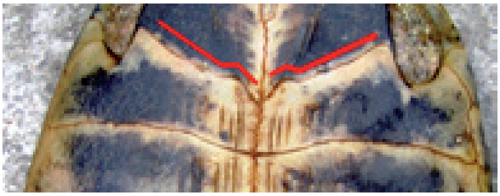
Pattern of the pectoral scute, especially in males	
Testudo hermanni hermanni	*Testudo hermanni boettgeri*
	

Fig. 6.

Geographical location	Numbers of samples
Testudo hermanni hermanni	
1. Albera mountains (Northern Spain)	**6**
2. Mallorca (Balearic Islands, Spain)	**101**
3. Menorca (Balearic Islands, Spain)	**14**
4. Lake Baratz (Northeastern Sardinia)	**2**
5. Massif des Maures (France)	**3**
6. Tuscany region (Western Italy)	**9**
Testudo hermanni boettgeri	
7. Karvelas (Peninsula Mani, Southwestern Peloponnese, Greece)	**3**
8. Kyllini Mountains (Northeastern Peloponnese, Greece)	**1**
9. Manolas (Northwestern Peloponnese, Greece)	**1**
10. Igoumenitsa (Epirus region, Wesern coast of Greece, near the Albanian border)	**1**
11. Thessaloniki (Central Macedonia, Greece)	**14**
12. Mostar (Southwestern Bosnia and Herzegovina)	**1**

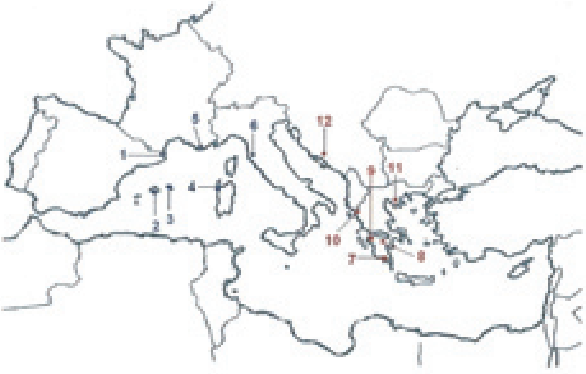


Fig. 7

Parameters of crosses *Thb* ♂ × *Thh* ♀		Agreement / Non-conformity	
		Thb	*Thh*
1. Black plastral bands		✓	✓
2. Pattern of fourth vertebral		✓	✓
3. Pattern of first vertebral		✓	✓
4. Pattern of fifth vertebral		✓	✓
5. Supracaudal scute	divided	✓	
	undivided		✓
6. Inguinal scutes	present	✓	✓
	absent		
7. Plastral concavity in male	visible		
	lacking	×	×
8. Yellow colour of subocular scales	present		✓
	absent	✓	
9. Colouration on top of head	yellow	✓	✓
	greenish	✓	
	greyish	✓	✓
10. Overall carapace colouration		✓	
11. FS / PS	males	✓	
	females	✓	
12. HS / FS	males	✓	
	females	✓	✓
13. Pigmentation of gular scute	lacking		✓
	slight		
	heavy	✓	
14. Pectoral scute, especially in males		✓	
15. Maximum carapace length		✓	
Total agreement with:		14	10

Tab. 2. The resulting data have allowed the construction of a table showing the convergence and divergence of crosses between *Thb* ♂ and *Thh* ♀, with both subspecies of Hermann's Tortoise, see table 2. Agreement: ✓. Non-conformity with either subspecies: ×

Photographic table 1

Photographic record of principal hybrid traits of
Thb **♂ ×** ***Thh*** **♀**

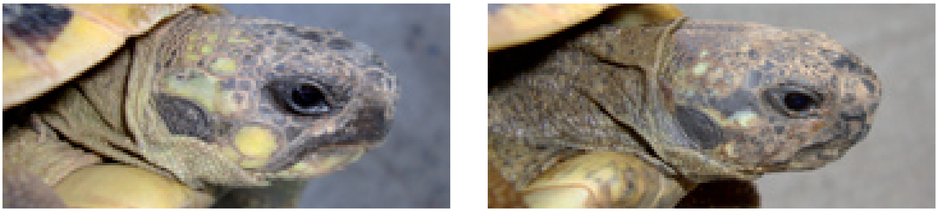
Plaston pattern

Carapace coloration and pattern, overall coloration very close to *Thb*

Supracaudal scute undivided or divided

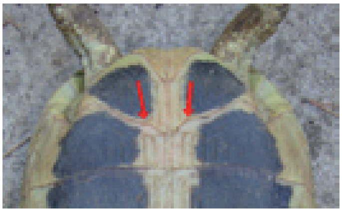
Inguinal scutes present

Subocular yellow blotches on scales, present or not present



Photographic record of principal hybrid traits of
***Thb* ♂ × *Thh* ♀**

Pectoral scute pattern



First vertebral scute pattern, 40 to 60% covered with a dark blotch

Fourth vertebral scute pattern, without or with a central dark spot

Fifth vertebral scute pattern, with or without keyhole-shaped yellow blotch

Gular scute pattern, often heavily grayish-black

Photo: J. SOLER

Photo: J. SOLER

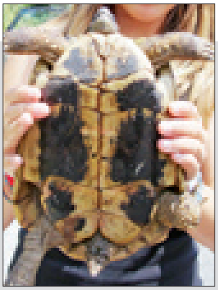


Photo: M. ARESTÉ

It is now obvious which of the parameters agree with those of the breeders, *Thb* ♂ and *Thh* ♀.

1. The black plastron bands show traits compatible with both subspecies. Some individuals (5 individuals) have fully continuous black bands, except on the humeral scutes, whereas in others (also 5 individuals) the discontinuity is obvious, there is no dark pigment on the anal scutes, and there is significant yellow pigmentation on the rim peripheral to the dark bands.

2.-4. Patterns of the first, fourth, and fifth vertebral scute indicate similarity to both, *Thb* and *Thh*.

5. Some specimens have an undivided supracaudal scute (2 ♂♂ and 5 ♀♀), and in some it is divided (1 ♂ and 2 ♀♀), that is, 30% of the sample. In this case, the affinity with *Thb* is obvious.

6. The presence of inguinal scutes on all specimens is in close agreement with *Thh*.

7. There is also a morphometrical trait present among the crosses, which is not found in wild specimens of either subspecies, namely, the lack of plastral concavity in the (sexually mature) males.

8. The yellow colour of the subocular scales may be present or absent. The group contains specimens with the yellow scales (6 individuals) and others (4 individuals) lacking them, or having only tiny, pale or whitish spotting.

9. The top of the head on some specimens has greyish-colored scales, while other specimens bear yellow scales.

10. The overall coloration of the carapace is very close to that of *Thb*, that is of the father, according to the colour spectrum offered by GUYOT & DEVAUX (1997) their carapace background colour is pale yellowish or light ochre, with dark, not very black or greyish blotches on the scutes.

11. The relative size of the pectoral and femoral sutures (FS ÷ PS) has a mean value of 0.84 in males and 0.74 in females. These ratios are unequivocally very close to *Thb*. STEMMLER (1968) and BOUR (1987) both calculate this ratio to be between 0.81-0.87 in *Thb*. Among Macedonian tortoises, CHEYLAN (2001) provide values of 0.83 for ♂♂ and 0.72 for ♀♀ an.

12. The relative size of humeral and femoral seams (HS ÷ FS), has a mean value of 1.89 in males and 1.95 in females. These results are very close to the number 2, characteristic of *Thb* (2.14 and 2.60 for tortoises form Greece or former Yugoslavia according to STEMMLER 1968). However, the same author gives this ratio as 1.93 among *Thh* from Sardinia. These results are nearly identical to those we obtained among our cross-bred specimens.

13. The gular scutes bear a black to greyish hyperpigmentation in 2 tortoises and 3 tortoises show moderate pigmentation, while 5 others totally lack black pigmentation on the gulars.

14. The pattern on the pectoral scutes, especially in males, clearly agrees with that of both males and females of *Thb*.

15. In size, the cross-bred specimens are

Photo: C. PFAU

Photo: J. SOLER

Photo 4:
Plastral views of *Thb* (from left to right): 1 & 2 Southern Peloponnese, near Karvelas, 3 Northern Peloponnese near the Kyllini Mountains, 4 Nordwest Peloponnese, near Manolas, 5 Bosnia and Herzegovina, near Mostar.

very similar to eastern Hermann's Tortoises. In the group of hybrids, 2 females exceed 210 mm in length, and another measures 197 mm.

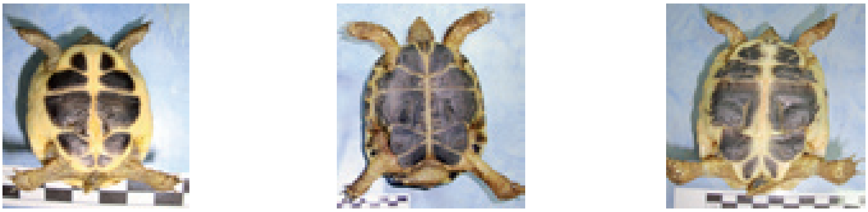
In these cases of cross-breeding a *Thb* male with a female of *Thh* ♀ we may declare that of the 15 analysed parameters, 14 belong to the eastern Hermann's Tortoise and 10 to the western. With the exception of the lack of plastral concavity in males, it seems therefore, that the dominant genes belong to the male *Thb* line.

Crosses between *Testudo hermanni hermanni* ♂ × *Testudo hermanni boettgeri* ♀

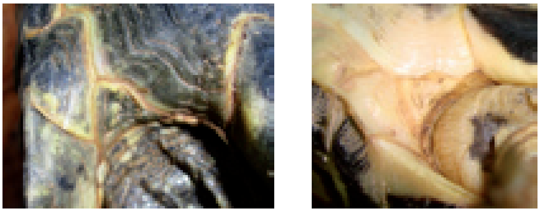
	Breeders		Crosses Adult, young and neonate		
	Thh ♂	*Thb* ♀	♂	♀ young	neonates
n:	1	1	2	1	9
Length (mm)	147	198	max. / min.		
			146 / 136	89.20	44.78 / 38.39
Weight (g)	576	1609	649 / 426	122	20 / 13
Humeral-femoral ratio	1.71	2.1	Mean value		
			2.39	1.60	2.04
Femoral-pectoral ratio	1.56	0.81	Mean value		
			0.72	0.91	0.89

Tab. 3. Biometry of breeding animals and their progeny as well as photographic record of the principal characteristics (photo plates 2).

Photographic table 2

Photographic record of principal hybrid traits of *Thh* ♂ × *Thb* ♀
Plastron pattern

Carapace coloration and pattern, overall coloration very close to *Thb*

Supracaudal scute undivided or divided

Inguinal scutes present

Subocular yellow blotches on scales, present or not present


Photographic record of principal hybrid traits of
***Thb* ♂ × *Thh* ♀**

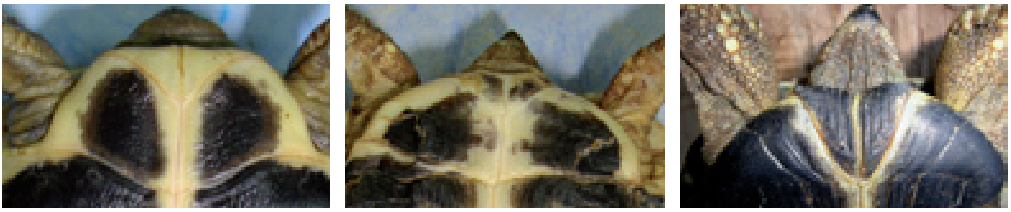
Pectoral scute pattern

First vertebral scute pattern, 40 to 60% covered with a dark blotch

Fourth vertebral scute pattern, without or with a central dark spot

Fifth vertebral scute pattern, with or without keyhole-shaped yellow blotch

Gular scute pattern, often heavily grayish-black



Parameters of crosses *Thh* ♂ ×*Thb* ♀		Agreement / Non-conformity	
		Thh	*Thb*
1. Black plastral bands		✓	✓
2. Pattern of fourth vertebral		✓	✓
3. Pattern of first vertebral		✓	✓
4. Pattern of fifth vertebral		✓	✓
5. Supracaudal scute	divided	✓	
	undivided		✓
6. Inguinal scutes	present	✓	
	absent		
7. Plastral concavity in male	visible		
	lacking	×	×
8. Yellow colour of subocular scales	present	✓	
	absent		✓
9. Colouration on top of head	yellow	✓	✓
	greenish	✓	
	greyish		
10. Overall carapace colouration		✓	✓
11. FS / PS	male		✓
	female	✓	
12. HS / FS	male	✓	✓
	female	✓	✓
13. Pigmentation of gular scute	lacking	✓	
	slight	✓	
	heavy		✓
14. Pectoral scute pattern especially in males			✓
15. Maximum carapace length			✓
Total agreement with:		12	13

Tab. 4. In this case as well, the data have allowed a tabular demonstration of the morphometric convergence and divergence between cross-bred specimens of both subspecies, compared with those of each subspecies of *Testudo hermanni*. Agreement: ✓. Non-conformity with either subspecies: ×

1. The black plastral bands provide compatible characteristics with both subspecies. Most specimens bear a greater likeness to *Thh*. However, both adult males examined show an extreme hyperpigmentation of the plastron (see photo 3). These specimens are reminiscent of *Thb* from the Sparta region in Greece (Willemsen & Hailey 1999a). This trait was also described by Bruekers (1995), who refers to a thin midline yellow stripe dividing both sides of the plastron.

2.-4. The vertebral scute patterns suggest both *Thb* and *Thh*. Two specimens have very light-coloured vertebral scutes, lacking dark spotting on the first and fifth scute. However, these are both neonates, and their patters may evolve over time until sexual maturity is reached, as described by Wagner (2006) for *Thb*.

5. Cross-breeding yielded but a single specimen with an undivided supracaudal scute, that is, 8.3% of the hybrid sample.

6. All of these crosses possessed inguinal scutes. Thus it would seem that there is a genetic predominance of *Thh*, but it should be noted that the female *Thb* also had inguinal scutes on both sides.

7. The absence of plastral concavity in the cross-bred males remains unexplained, as this morphological trait has not been observed in wild specimens of either subspecies. However, as all the cross-bred specimens are not yet fully grown, possibly the concavity will develop over time.

8. The subocular scales bear yellow coloration in 10 specimens, whereas in 2 the colour is whitish or greyish.

9. The top of the head has yellow and greenish scales.

10. The overall carapace coloration of most specimens (8) is very close to that of *Thh*, that is, of the male. However, 4 of the crosses are very light in colour, thus objectively speaking, more similar to *Thb*.

11. The ratio of the pectoral to femoral seams has a mean value of 0.89 in neonates, 0.91 for the immature female, and 0.72 for adult males. These are all close to *Thb*.

12. The mean value of the humeral to femoral seam is in all specimens close to 2.01. This result is close to the data attributable to *Thb*, but not far from the values for certain populations of *Thh* (see also in the discussion below).

13. The gular scutes bear greyish-black hyperpigmentation in 2 tortoises; in the others the gulars are totally unpigmented.

14. The pattern of the pectoral scute, particularly in males, clearly agrees with that of both male and female specimens of *Thb*.

15. We have but 2 male cross-bred specimens to compare in size to *Thh*. These do not differ in size from males of *Thh* of the same age, but as both of these are still young (8 years old), they may grow further.

Thus, in cases of cross-breeding between a *Thh* ♂ and *Thb* ♀, it appears that 12 of the 15 analysed parameters occur in the western, and 13 in the eastern race of Hermann’s Tortoise. Apparently, the dominant genes in these crosses belong to the female lineage of *Thb* even as the differences are not so obvious.

Discussion

From the data obtained, and without having to analyse morphological anomalies of a genetic origin, such as albinism, scute duplication, teratological malformations (Wermuth 1971, Martínez Silvestre *et al.* 1988, Martínez Silvestre & Soler 2000, Martínez Silvestre & Soler 2001) and from abnormal growth in captivity (Weser 1988, Krüger 2008) parameters of reasonable certainty exist for one to be able to distinguish crosses between *Thh* and *Thb*.

1. Morphometric parameters without or with only slight variation within the subspecies
Plastral concavity in male
Femoral-pectoral ratio FS / PS
Pectoral scute pattern especially in males

2. Morphometric parameters with medium to large variation within the subspecies
Black plastral bands
Pattern of first vertebral
Pattern of fourth vertebral
Pattern of fifth vertebral
Pigmentation of gular scute
Overall carapace coloration
Maximum carapace length
Yellow colour of subocular scales
Humeral-pectoral ratio HS / FS
Colouration on top of head
Inguinal scute presence
Supracaudal scute division

Tab. 5. The 15 parameters we consider appropriate for detecting possible cross-breeding are divided into two groups.

The first group includes traits which are practically without variation in each parental subspecies, and therefore can be used as determinants of possible cross-breeding.

It should be taken into account regarding the concavity of the plastron, that in many captive-bred male specimens of either subspecies which grow rapidly, this depression may fail to develop, thus resulting in a totally flat or even convex plastron. The cross-bred males which we have studied all have a flat plastron, and all had been raised in near-natural, outdoor conditions. Plastral concavity is a secondary sexual characteristic in some chelonians and is influenced by testosterone (Evans 1952, Guix *et al.* 2001). It may be speculated that the cross-bred males have a lower level of testosterone than males of either parental subspecies. Whereas climate may influence the testosterone level (Kuchling *et al.* 1981, Guix *et al.* 2001), in the case of our study group, climatic factors may be excluded, as the hybrids were raised under natural conditions in a Mediterranean climate. To date in this study, none of the cross-bred animals has bred with another nor with any of the specimens in the parental breeding group, thus nothing can be deduced concerning their sexual behaviour nor fertility. But given the genetic influence of one of the tortoise subspecies may be demonstrated in certain wild populations (see above), we conclude that cross-bred tortoises of at least one sexes are certainly fertile.

The data obtained from the pectoral-femoral scute ratios are very reliable. Bibliographic data supplied by a number of authors permit a precise differentiation between subspecies. Among *Thb* the determinant values for specimens originating in Macedonia, Greece, and "Yugoslavia" are 0.83, 0.93 and 1.17 in males, 0.72, 0.71 and 0.68 in females (see table 5 in Cheylan 2001). For *Thh* the accepted values are 2, 1.78, 1.58, and 1.57 in males, and 1.47, 1.41, 0.92, and 1.38 for female specimens originating in the Massif des Maures, Corsica, Tuscany, and Sardinia (Stemmler 1968, Cheylan 2001). The ratios obtained in our study of crosses show 0.84 in males and 0.74 in females produced by *Thb* ♂ × *Thh* ♀. In the case of hybrids between *Thh* ♂ × *Thb* ♀ we have data only on three small juveniles (2.1), which are 0.89, 0.91, and 0.72 respectively. There is thus an obvious agreement with the preponderant genetic influence of *Thb* in the resulting genetic pollution. Equally obvious is the sexual dimorphism expressed by the ratios, the higher ones belonging to the males, much lower values to the females (Stemmler 1968).

In the case of the humeral-femoral ratios, the results are highly variable, in accordance with disparate data published on different populations of *Thh*. Stemmler (1968) gives a ratio of 2.74 for Corsican tortoises, and for those from southern France, 1.56. We point out that this study consisted of but a tiny sample (2 and 6 tortoises respectively). On the other hand, the same author provides a value of 1.94 for 60 Sardinian tortoises. While the input from this author is significant as a reference, the contributions from more recent and more extensive sampling need to be taken into account. From our study, we have concluded that this parameter does not help to distinguish a cross-bred tortoise.

The pattern of the pectoral scute is a trait which exhibits little variability in either subspecies of Hermann's Tortoises. The shape of these scutes is particularly notable in the males of both races (see figure 6). Male hybrids clearly showed the pectoral scute shape of a *Thb*. This was constant finding no matter the parental combination, in all male crosses.

All of the traits described in this first group of morphometric parameters may be said to be indicative of a possible intraspecific cross. But these must be complemented by examining the traits in the second group, which are more variable within the parental subspecies.

Whereas the black plastral bands in *Thh* are nearly always continuous, in *Thb* this trait is highly variable (Willemsen & Hailey 1999a). We present photographic documentation (see photo 4) of tortoises from Greece and Bosnia and Hercegovina, showing that confusion with hybrids is a possibility.

Likewise, the pattern of the first, fourth, and fifth vertebral scute is highly variable among *Thb* specimens, as is pigmentation of the gular scute, but these traits are relatively well-defined in *Thh*. Thus the chance of mistaking a cross-bred tortoise for *Thb* is considerable, based on these criteria.

The overall coloration of the crosses tends to be that of the male parent, meaning that chromatic dominance is carried in the male genes. Nonetheless within the same clutch or the same generation, we have noted considerable variation in individual coloration. Some specimens are very dark, while others lack dark markings on some of the carapace scutes.

The presence or absence of central dark markings on some scutes is generally hereditary. The male *Thb* parent lacked a dark blotch in the centre of the fourth and fifth vertebral scutes, and passed this on to the next generation.

The plastron may be hyperpigmented as well, or lack dark pigment on the anal scutes, for example. With such high variability in overall coloration among hybrid progeny, this adds to the challenge of identifying a possible hybrid.

One trait which helps to classify a cross-bred tortoise is the adult size of a specimen raised under natural conditions. When the father of a cross-bred tortoise is *Thb*, the young will achieve a greater size than adults of either sex of *Thh*. In our study, the 4 adult female hybrids had a mean size of 199.5 mm, while the 3 not fully mature adult males had a mean carapace length of 138.5 mm. If we include the mean maximum size of Corsican specimens, the largest in the western subspecies at 179 mm for females and 149 mm for males (Cheylan 2001). There is some speculation on the large size of *Testudo hermanni* in Corsica, which could be the result of hybridisation with *Thb*, which had been brought to the island by former time sailors. However, future genetic studies based upon nuclear DNA and microsatellites, similar to the study by Fong & Chen (2010) on Taiwan turtles, may vindicate or invalidate this hypothesis, see also below in the discussion.

The yellow coloration of subocular scales is a variable trait, present in the majority of specimens of the western race. Most *Thh* exhibit this characteristic, but it is absent in some specimens, particularly those from southern France. Its absence has also been noted in some *Thh* specimens on Mallorca. Among *Thb*, the presence or absence of yellow scales is highly variable. Among the hybrids of which the mother was *Thb*, ten of twelve specimens have yellow scales below the eye, whereas two have whitish or greyish scales. In crosses in which the mother was *Thh*, the variation is also present (four specimens with and six without), the dominance of the eastern subspecies seems the greater. This parameter may be very significant in detecting crosses arising from a *Thh* ♀ × and *Thb* ♂, especially in specimens from the same clutch or generation.

The scale coloration on the top of the head is also highly variable among all the hybrids, some having very yellow scales and others mostly greyish (particularly when the mother was *Thb*), but also when the mother was *Thh*. Yellow, greyish, or greenish scales may cover the top of the head in such crosses. A predominance of the male genes would seem to predominate in determining the head coloration of the progeny.

Inguinal scutes seem to be an important trait within *Thb* populations, though they are absent in certain ecotypes from the Balkans (Wegehaupt 2008, Wegehaupt 2009, Mascort 2010). It seems that in the nominal western race, the inguinals most often are absent, but they may be present at times. All hybrids in the study possessed inguinal scutes. Thus we believe this trait to be inconclusive with regard to detecting a cross-bred tortoise.

The supracaudal scute is of some importance in detecting hybrids, but the presence of an undivided supracaudal should not be taken as evidence of intraspecific crossing, as a divided or undivided supracaudal scute may commonly be present within the same *Thb* population. Specimens from Bulgarian, Greek, and Dalmatian populations may have as many as 18, 16.6, and 12% undivided supracaudals (Stemmler 1968, Meek & Inskeep 1981, Nöllert & Nöllert 1981). An undivided supracaudal among *Thh* is rare, but does occur. For example, on Sardinia, this trait appears in 1.7% of the population (Stemmler 1968) This trait is much more common among the crosses produced by *Thb* ♂ × *Thh* ♀ (n = 3), but also occurs in the opposite parental combination (n = 1). It seems that this trait is transmitted by the *Thb* parent, regardless of gender. Indeed, the presence of an undivided supracaudal in a tortoise otherwise appearing to be *Thh* may be indicative that it is a cross.

It is challenging to explain the absence of plastral concavity in male hybrid tortoises. That this trait appears in animals raised under natural conditions and otherwise exhibiting normal growth is all the more strange. It may be that in any cross-bred or intergrade chelonians, no matter the parental subspecies, that secondary sexual characteristics are more weakly expressed. Thus, mature animals whose secondary sexual characteristics seem inchoate may be cross-bred tortoises.

Cross-breeding in zones of contact is natural, just as phenotypical variability within the same genotype is common among reptiles (Gómez-Mestre, 2010, see also Parham *et al.* 2006 and Fritz *et al.* 2007 regarding *Testudo graeca*). Thus, the identification of a putative hybrid should be made not only on the basis of external characteristics but also of genetic data. Needless to say, such analyses must include both the maternal and paternal lineage.

Often research of the relationship of different populations is done by analysing the mitochondrial DNA, but these analyses are only valid for the maternal line of inheritance, since the mitochondria are passed to the offspring with the oocyte. This means in our case, that a hybrid of a *Thh* ♀ and a *Thb* ♂ would be classified as a *Thh* by using only this method, and the influence of the *Thb* ♂ would remain undetected (see above, for example this could be the case in *Testudo hermanni* from Corsica). Therefore it seems wise, that in cases when the influence of alien species or subspecies cannot be ruled out, the genetic analysis should be carried out using nuclear DNA sufficiently differentiating microsatellites to elucidate the lineage of a certain animal. It would be beyond the scope of this paper to discuss this topic here at length, so please refer to Bertorelle *et al.* (2002), for an explanation of this set of problems by example of the Galapagos tortoises.

Regarding research at the population level, and especially when contemplating conservation and/or reintroduction projects, we recommend using different methods in combination: Morphological (e.g. pholidosis and carapace characteristics), ecological (e.g. patterns of dispersal, microclimate, vegetation characteristics, and also influences of incubation and husbandry conditions on the fitness of the animals to be released) as well as genetic methods (clarification of the descent of every animal to be released, regarding maternal and paternal lineage).

Summary

Reliably distinguishing between hybrids of both races of *Testudo hermanni* is not easy. Nonetheless, in many cases there are criteria which help in detecting such crosses.

Heredity transmission	Heredity of ♂ parameter independent of the subspecies	*Thb* independent of the sex of the parent	*Thh* independent of the sex of the parent	New trait occurring in neither parental subspecies
Parameter Nr.	8, 10, et 1	8, 11, 15, 14, 13, 12, 5, 2, 3, 9 et 4	6, 2, 3, 4, 12 et 13	7

Tab. 6. To summarize, we have prepared a chart listing those traits appearing in the crosses which are linked to the sex of one of the parent animals, or to the general configuration of the subspecies.

Characters:

1. Black plastral bands
2. Pattern of fourth vertebral
3. Pattern of first vertebral
4. Pattern of fifth vertebral
5. Supracaudal scute division
6. Inguinal scute presence
7. Lacking Plastral concavity in male
8. Yellow colour of subocular scales
9. Colouration on top of head
10. Overall carapace coloration
11. Femoral-pectoral ratio FS / PS
12. Humeral-pectoral ratio HS / FS
13. Pigmentation of gular scute
14. Pectoral scute pattern especially in males
15. Maximum carapace length

The analysis of these parameters in combination ought to permit the detection of intraspecific hybrids of Hermann's Tortoises in many cases, but only in the first generation (F_1). Furthermore our data suggest that the *Thb* genotype is more dominant than that of *Thh*.

To distinguish beyond the F_1 generation, whether both parents were hybrids or only one of them (the other belonging clearly to either subspecies) is of course more difficult. To do so in such cases would require nuclear DNA analysis.

We may conclude that the possibility of intraspecific intergrades is higher among populations of the nominal subspecies. This may be explained by the development of the pet trade in *Testudo hermanni*, consisting mostly of specimens from south-eastern Europe, of which hundreds of thousands were collected and shipped out, from the 1960s through the 1980s (BLATT & MÜLLER 1974, LAMBERT 1979, DUMONT 1979). The chances of an uprooted Balkan tortoise escaping or being liberated in the preferred holiday countries, into an area in which *Thh* occurs, was and remains very high. At present this trade continues at a reduced volume (TÜRKOZAN *et al.* 2008, VINKE & VINKE 2009). There is large-scale production of tortoises to supply the legal pet trade in such countries as Slovenia, in which several farms produce a total of 4,000 tortoises annually (PHILIPPEN 2007). All of these tortoises are destined for sale in western countries such as Germany, France, and Spain. Not all of the tortoises sold wind up in responsible hands.

The private breeding of Mediterranean tortoises in western Europe offers other challenges, as *Testudo hermanni* is one of the most widely bred taxa. The breeding roster of the *Nederlands-Belgische Schildpadden Vereniging* specifies 783 hatchlings of *Thb* (including "*hercegovinensis*") and 22 of *Thh* between 2008-2010 (see www.trionyx.nl, last accessed on 23.12.10). The 2006 breeding figures of the *German Chelonia Group* indicated 2913 *Thb* hatchlings and 165 *Thh* hatchlings. We realize that these statistics are not all-inclusive, and urge all potential breeders to record their hatchings of these subspecies respectively on the appropriate official rosters of each institution. From such data, particularly when the geographical origin of the breeding adults is known, the management of natural areas inhabited by tortoises is potentially helped should re-introduction become a possibility. The fertility of captives under varying geographical and other conditions may also shed light on the relative fertility of natural populations not yet studied in situ. The goal is to prevent any further intraspecific cross-breeding among captive Hermann's Tortoises, and to sow the conservation ethic among tortoise keepers in these countries. It behoves the leaders of the chelonian societies to discuss these matters persuasively with their membership! The likelihood of halting further releases or escapes of cross-bred tortoises into remaining natural populations, as described by Campi (2002) is of top priority.

In Catalonia, the husbandry and breeding of captive Mediterranean tortoises is more strictly regulated than CITES, and the subspecies designation is avoided to minimize confusion and deliberate masking of the geographical origin of the captives; *Thh* is an indigenous species to the region. All captive breeders of native wildlife must be registered, and are urged to commit themselves to being of service vis a vis species reintroduction programmes insofar as is feasible. The *Centre de Recuperació d´Amfibis i Rèptils de Catalunya* (CRARC) supervises the activities of these authorized breeders so as to prevent any possibility of genetic pollution among the offspring. The forty authorized *Thh* breeders produced 3424 neonate tortoises between 1998 and 2010, all of which are suitable for repatriation in natural habitat according to established protocols.

The possibility of genetic pollution of either tortoise subspecies throughout the ranges of both are more significant, and may lead to the irreparable loss of unique identifying traits in either subspecies (Cappio 2010). We must underscore the urgency of being very strict in breeding tortoises in captivity, and must do everything possible to prevent cross-breeding, which in no way contributes to wildlife conservation in the Mediterranean basin. We hope that this article paves the way for future, all-encompassing studies of hybridization within and among Mediterranean tortoise species.

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