

Notes on *Maniola telmessia* (Zeller, 1847) from the Eastern Aegean islands, with new insights about its populations on the Greek islands of Kárpáthos and Kássos (Lepidoptera : Nymphalidae Satyrinae)

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Samenvatting. Beschouwingen over *Maniola telmessia* (Zeller, 1847) op de oostelijke Egeïsche eilanden, met nieuwe inzichten in verband met de populaties op de Griekse eilanden Kárpáthos en Kássos (Lepidoptera : Nymphalidae Satyrinae)
De verspreiding van *Maniola telmessia* (Zeller, 1847) op de Egeïsche eilanden wordt geschetst : de soort wordt voor de eerste maal vermeld van het Griekse eiland Kássos. Dan volgt een kort verslag over de fenologie van de soort op de Zuidoost-Egeïsche eilanden in 1992 en 1993. De geografische variatie van *M. telmessia* op de Egeïsche eilanden wordt besproken in het licht van nieuwe gegevens. De populaties van de eilanden Kárpáthos en Kássos blijken sterk te verschillen van de overige, zowel morfologisch (vleugeltekening, spotting) als genetisch (electroforese). Toch worden ze hier niet als nieuwe ondersoort beschreven, daar de verschillen niet absoluut konstant zijn. Het subspecies-concept wordt besproken en recente kritiek (Collins 1991) wordt aangehaald. Biogeografische consequenties van deze nieuwe inzichten worden besproken.

Résumé. Considérations sur *Maniola telmessia* (Zeller, 1847) dans les îles égéennes orientales, avec de nouvelles notions à propos des populations des îles grecques de Kárpáthos et de Kássos (Lepidoptera : Nymphalidae Satyrinae)
La répartition de *Maniola telmessia* (Zeller, 1847) dans les îles égéennes est esquissée : l'espèce est mentionnée pour la première fois de l'île grecque de Kássos. Suit un bref aperçu de la phénologie de l'espèce dans les îles du sud-est égéen en 1992 et 1993. La variation géographique de *M. telmessia* dans les îles grecques est discutée à la lumière de nouvelles données. Les populations des îles de Kárpáthos et de Kássos apparaissent très différenciées par rapport aux autres populations, tant au point de vue morphologique (dessins alaires, spotting) que génétique (électrophorèse). Néanmoins, elles ne sont pas décrites comme sous-espèce nouvelle, les différences n'étant pas absolument constantes. Le concept sous-espèce est discuté et la critique récente (Collins 1991) est citée. Les conséquences biogéographiques sont tirées de ces nouvelles notions.

Key words : *Maniola telmessia* - Kárpáthos - Kássos - Greece - geographical variation - spotting - subspecies concept - biogeography

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Introduction

Recently, the geographical variation of *Maniola telmessia* (Zeller, 1847) both in Turkey and on the Eastern Aegean islands has been studied in much detail and all hitherto described subspecies from both areas have been sunk in synonymy (van Oorschoot & van den Brink 1992; Olivier 1990, 1993). Olivier (1993: 168-171) designated a lectotype for *Maniola telmessia*, thus restricting its type-locality to Marmaris, in the present-day Turkish province of Muğla. In the same publication, the author also noted the distinctive features in wing markings and spotting characters of the Kárpáthos population as compared to the remaining *telmessia* populations, thereby suggesting that it represents a so far undescribed subspecies. The Eastern Aegean islands were revisited in late May and June of both 1992 and 1993, after completion of last study.

On that occasion, additional material was collected on the islands of Kárpáthos, Ródos, Sími and Kós, while material was also collected on Káossos, Tílos, Kálímnos and Léros, islands from where no material was available at the time of writing last-mentioned study - although *M. telmessia* was known to occur on three out of these four islands (see Olivier 1993: 199, table 12). Its presence on Káossos is recorded here for the first time.

In the present contribution, we will illustrate the western limit of the distribution range of *M. telmessia* in the Aegean Sea, which differs substantially from that presented by Tauber & Tauber (1968: 83) and new data will be reported on its phenology on the Aegean islands. After that, the new data we now have on its geographical variation on the Eastern Aegean islands will be analyzed and the resulting new insights will be considered in deciding whether or not the Kárpáthos (and Káossos) material belongs to a distinct subspecies. Finally, some considerations about the applicability of the subspecies concept will be discussed and biogeographical consequences of these findings will be dealt with.

Distribution range of *Maniola telmessia* (Zeller, 1847) on the Aegean islands

During the last decennium, the Eastern Aegean islands have been well-investigated lepidopterologically and the geographical distribution of the genus *Maniola* in this area may now be considered as almost completely known. Only on one of these islands (Lésvos), sympatry of two taxa of this genus - *M. telmessia* and *M. megala* (Oberthür, 1909) - has been positively identified. Tauber & Tauber (1968: 83) include the islands of Psará, Híos, Inoússes, Astipálea, Anáfi, Amorgós and Níssiros within the general distribution range of *M. telmessia*, though they have not seen any material from these islands. On Psará and Amorgós, one finds *M. jurtina janira* (Linnaeus, 1758), while on Híos and Inoússes only *M. chia* Thomson, 1987 is known, and on Níssiros only *M. halicarnassus* Thomson, 1990 seems to occur (Thomson 1987a, 1992; Olivier 1993). No *Maniola* at all seems to be present on Astipálea (Olivier 1992) and there is no information at all for the island of Anáfi (its geographic position, however, almost certainly precludes the possibility of *M. telmessia* occurring there).

M. telmessia is now known to occur on Kastellórizo, Káossos, Kárpáthos, Ródos, Sími, Tílos, Kós, Psérimos, Kálímnos, Télendos, Léros, Pátmos, Sámos, Fourni, Ikaría and Lésvos (Olivier 1993 and present study). The distribution of *M. telmessia* on the Aegean islands is illustrated on fig. 1.

Phenology

1992 was a late season and at the time of the first author's visit to the Eastern Aegean islands, *M. telmessia* was still fresh on Tílos on 25/27.V (the males still outnumbering the females). By mid-June males were worn and becoming rare, while females were common and starting to aestivate (Olivier, pers. obs. on Kós, Kálímnos and Léros).

1993 was again a very late season, and on 21.V males were relatively common and very fresh on Ródos, while the females were just emerging and

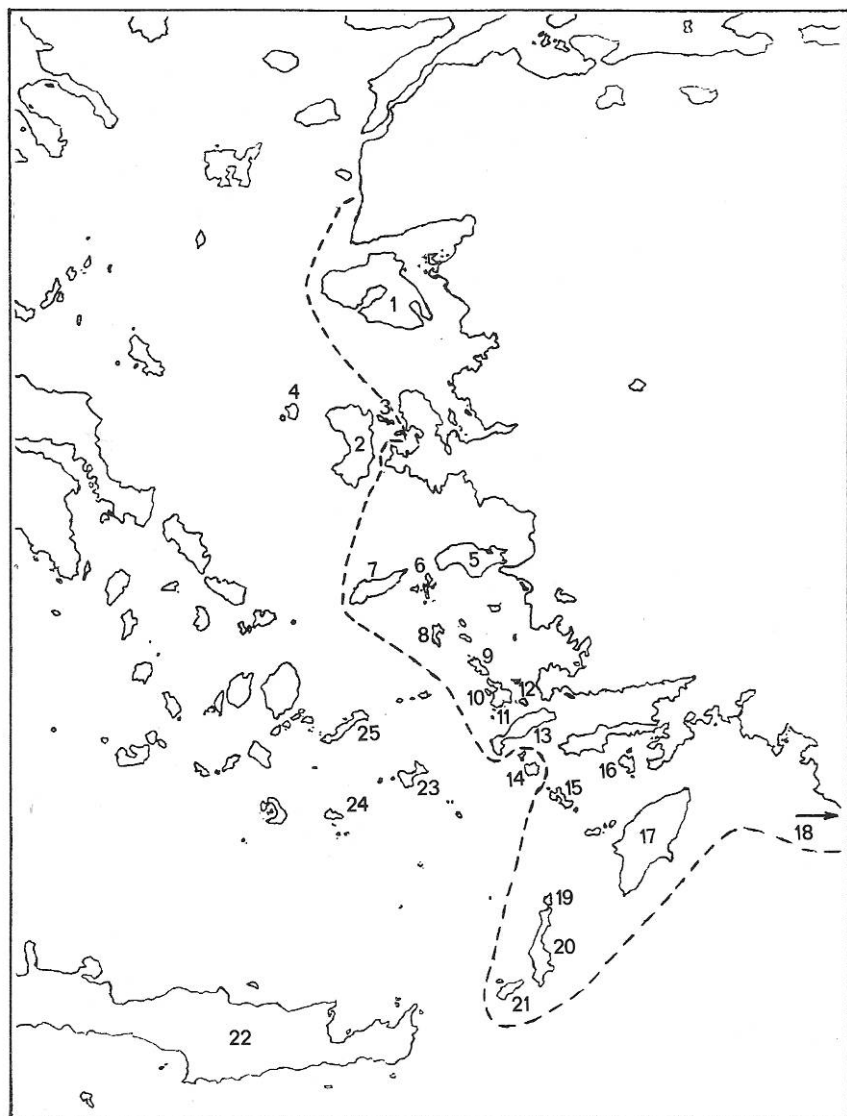


Fig. 1 : Geographical distribution of *Maniola telmessia* (Zeller, 1847) on the Aegean islands (----- western limit of the distribution range of *M. telmessia* in the Aegean Sea)

- | | | | | |
|-------------|---------------|--------------|------------------|---------------|
| 1. Lésvos | 6. Foúrni | 11. Kálimnos | 16. Sími | 21. Káossos |
| 2. Híos | 7. Ikaría | 12. Psérimos | 17. Ródos | 22. Kríti |
| 3. Inoússes | 8. Pátmos | 13. Kós | 18. Kastellórizo | 23. Astipálea |
| 4. Psará | 9. Léros | 14. Níssiros | 19. Sariá | 24. Anáfi |
| 5. Sámos | 10. Téliendos | 15. Tílos | 20. Kárpáthos | 25. Amorgós |

quite rare. The same was the case on Kássos on 22/24.V. On Kárpathos, both sexes were also fresh, the males outnumbering the females although the latter were already well out in the south of the island (Pilé) on 25 & 28.V. In the north of the island (vic. Diáfáni), however, on 26.V only one single female was observed while the males were common. A few days later, however, on Sími (1/3.VI), males were mostly worn and clearly outnumbered by fresh females, that were common and quite active, mainly feeding on *Origenum*.

Geographical variation

Size

The smallest-sized specimens appear to be those from Kássos, Kárpathos and Tílos, while those from Ródos and Lésvos are only slightly larger. Material from Sími is larger (especially when comparison is made with samples from different islands collected in the same year). Material from Kós and Léros appears to comprise, on average, the largest-sized specimens known from any island, those from Kálimnos and Sámos being slightly smaller-sized, while males become a little larger again on Fourni and Ikaría (Olivier 1993: 146, 148-151: tables 6 and 7; present study: tables 1 and 2).

Size appears to vary substantially between years on the same island, between samples from different localities on the same island in the same year, as well as between islands. Relative differences in size between these tend to be maintained over different years. Hence, variation in size may be subject to environmental factors (climate, host-plant quality, etc.), but within genetically determined limits. Size does not appear to be a taxonomically significant character supporting a subspecific distinction of the Kárpathos and Kássos populations.

Wing markings

In males, the orange-red patch situated in the submarginal and postdiscal area on the upperside forewing is nearly always well-expressed in samples collected during 1992 and 1993 on Ródos, Sími, Tílos, Kálimnos and Léros.

Olivier (1993: 146) noted that the Kárpathos population is remarkable in that the orange patch on upperside forewing is usually much more extended than in any other examined population, stretching downwards well beyond v2 and often reaching v1, extending basad well into the cell; the veins in the orange patch not or only very slightly marked in brown (see Plate 1 of the present study). Again this appears to be the case when Kárpathos material from 1993 is compared to other material, including that collected in 1992 and 1993, except that from Kássos that agrees with the Kárpathos specimens. Comparison with material from - for instance - Ródos, Tílos and Bozburun (Prov. Muğla) revealed, however, that the orange patch in about 10% of the Kárpathos/Kássos samples from 1993 was not more extended than that of the most extremely marked specimens of first-mentioned populations. The veins are (relatively) well-marked in brown in about 15% of the 1993 Kárpathos and 30% of the Kássos sample, as in material from other populations. In material from some other populations, the orange patch is lacking the brown marking of the veins in about 5-10% of the specimens. There is thus a relatively

small but significant overlap in the range of variation of the Kárpáthos/Káossos material with that of (some) other populations.

When series are compared, females from Kárpáthos and Káossos also differ at a first glance from those from other populations, but single specimens from these and most specimens from Ikaría appear (nearly) indistinguishable from Kárpáthos/Káossos specimens (Olivier 1993: 147 and Plate 2 of the present study).

Spotting

Spotting in *Maniola telmessia* has been treated extensively by Olivier (1993) and for an account of scoring techniques, the naming of the various spots etc., one is referred to that publication.

The material collected in 1992 and 1993 has been analyzed and the various data are presented on tables 1 to 4 of the present study (compare with Olivier 1993: 148-151: tables 6 and 7, 156-159: tables 8 and 9). Spotting will be discussed in the present contribution only insomuch as it is relevant to an evaluation of the taxonomic status of the Kárpáthos and Káossos populations.

When all the 1992 and 1993 samples from the various islands are considered, it still remains obvious that the hindwing underside spot-number is distinctly lower in Kárpáthos material of both sexes than in that of any other population examined. The Káossos sample has a significantly higher average spot-number than that of any of the Kárpáthos samples in both sexes, but values are distinctly lower than those in any of the remaining populations examined, especially in the females. For both the Kárpáthos and Ródos material, comparison between 1984, 1989 and 1993 samples of moderate size ($n \geq 13$) revealed the same steady tendency towards a higher average spot-number in both sexes (only in females from Ródos the average spot-number drops significantly between 1984 and 1989 but is higher than in any of the previous years in 1993). On both islands, 1993 samples were collected on two different localities in order to estimate interdemetic differentiation within single islands. On Ródos, spot-number was a little higher in males from Psínthos than in males from Soroní, but this difference was spectacular between females of both samples. The value of the latter comparison is, however, much diminished as only 6 females could be collected at Soroní. On Kárpáthos, only males could be compared. Those from vic. Diafáni (north of the island) had a higher spot-number than those from Pilés (south of the island), the difference being small, however.

Insomuch as these could be compared, there appear to be similar trends in interseasonal change in spot-number among populations from different islands, but these changes remain much smaller than are the relative differences in spot-number between these populations in the same year. Differences between samples from different localities on single islands may be significant in some cases, but these appear far less than differences between (global) samples from different islands. In general, the present data give further support to the genetic nature of the observed differences in spot-

number between populations from different localities and islands. Another aspect of spotting, beside spot-number is the **expression** of single spots. Using the present method, some spots below a narrow threshold of spot-size will not be scored. Various techniques for analyzing expression of spotting and consequences of these approaches are discussed elsewhere (e.g. Brakefield 1984, Brakefield & Dowdeswell 1985, Windig 1991, Goulson 1993): these are beyond our technical possibilities. It is worth stressing, however, that when present, the spots are - in the very most cases - very small and barely contrasting with the hindwing background in material from both Kássos and especially Kápathos of both sexes, as opposed to most specimens from the remaining populations on the Eastern Aegean islands.

Other characters

Examination of both the male and female genitalia of Kápathos specimens did not reveal any differentiating features when compared to these structures in material from other populations. Thomson (in litt., 6.X.1989) found no differences in the immature stages of Kápathos specimens as compared to those from other *telmessia* populations.

Thomson (1987b) carried out an electrophoretic study of six island populations of *telmessia*. Interestingly, the Kápathos material appeared to be much more differentiated from the remaining populations than these were among each other, with distinct allele frequencies at a few loci. An extension of this analysis to 14 localities (10 island populations and 4 populations from the adjacent Turkish mainland) confirmed the distinct nature of the Kápathos sample, although a sample from one other island (Foúrnei) diverged as much as the Kápathos material from the other populations (Thomson in litt., 30.IX.1990).

Discussion

Both morphology (wing markings and spotting) and electrophoresis reveal the distinct character of the *M. telmessia* population from Kápathos as compared to other populations. While electrophoresis has not been performed on Kássos material, morphological features reveal a close resemblance of that island's population with that of the nearby island of Kápathos.

Unfortunately, the small islet of Sariá was not inspected. The width of the sea between that island and Kápathos is only 50 m, hence one may expect that *telmessia* also occurs here and in a form quite similar to that on Kápathos.

The present situation poses a problem as how to interpret taxonomically the pattern observed. When whole samples are compared, the Kápathos/Kássos populations emerge as a distinct entity (vide supra). When single specimens, however, are considered, it appears that a small proportion of these among material from both islands cannot be distinguished from more extreme specimens among material from other populations, as far as wing markings are concerned. A similar situation applies to spotting: for instance,

two-spotted males (splay 2) and nought females are commonly found both among Kárpáthos/Káossos specimens and specimens from other areas. We therefore somewhat reluctantly abandon our initial intention to describe a new subspecies of *M. telmessia* from Kárpáthos (and Káossos).

The present case brings forth the opportunity to discuss to some extent the applicability of the subspecies concept. In an extremely interesting paper reviewing concepts and studies concerned with speciation, especially among Lepidoptera, Collins (1991) includes a discussion on this subject and largely invalidates the relevance of the subspecies category in the context of the speciation process, stating (p. 50): «The adaptive value of much morphological variation - including that used to characterize subspecies - is often unclear, and while such characters may at first appear taxonomically useful, they may not be well correlated with overall genetic differentiation among populations within a species». We will quote Collins (l.c.: 55-56) further and at length, as we feel his conclusions appear very important, having the potential to generate many future discussions on the subject matter : «Subspecies are recognizably different geographic populations or sets of populations assigned formal taxonomic rank (...). Many evolutionary biologists feel the naming of morphological subspecies is largely an arbitrary decision, which on the one hand may help catalog variation within a species, but on the other hand may actually mislead further study by implying a specific genetic status and by ignoring other significant patterns of divergence.

Four specific objections can be raised against the subspecies concept. First, there is no testable criterion to assign the subspecies rank, such as reproductive isolation as a test for species status. How different must a population be to be called a subspecies? Second, a subspecies may be a

Plate 1 : *Maniola telmessia* (Zeller, 1847) : Males

- 1-3, 5-6. Pilés (Kárpáthos, Greece) (300 m), 12.VI.1989, leg. et coll. A. Olivier.
4. Óros Kalí Limní (Kárpáthos, Greece) (800-1000 m), 9.VI.1989, leg. et coll. A. Olivier.
7. 2 km E. Ágios Isídoros (Ródos, Greece) (600-800 m), 29.V.1989, leg. et coll. A. Olivier.
8. 1 km SE. Livádia (Tílos, Greece) (0-50 m), 25.V.1992, leg. et coll. A. Olivier.
9. Bozburun (Daraçya Yarımadası, prov. Muğla, Turkey) (0-50 m), 22.IV.1990, leg. et coll. A. Olivier.
10. 2 km N. Asfendioú (Kós, Greece) (100 m), 25.V.1988, leg. et coll. A. Olivier.
11. 1 km E. Évdilos (Ikaría, Greece) (50 m), 14.V.1987, leg. et coll. A. Olivier.
12. Míthimna (Lésvos, Greece) (0-50 m), 28.V.1987, leg. et coll. A. Olivier.

Plate 2 : *Maniola telmessia* (Zeller, 1847) : Females

- 1-4. Pilés (Kárpáthos, Greece) (300 m), 7-12.VI.1989, leg. et coll. A. Olivier.
5. Láerma (Ródos, Greece) (250 m), 30.V.1989, leg. et coll. A. Olivier.
6. 1 km SE. Livádia (Tílos, Greece) (0-50 m), 25.V.1992, leg. et coll. A. Olivier.
7. Bozburun (Daraçya Yarımadası, prov. Muğla, Turkey) (0-50 m), 21.IV.1990, leg. et coll. A. Olivier.
8. 2 km N. Asfendioú (Kós, Greece) (100 m), 25.V.1988, leg. et coll. A. Olivier.
9. Stavrinfides (Sámos, Greece) (400-700 m), 31.V.1988, leg. et coll. A. Olivier.
10. Évdilos (Ikaría, Greece) (0-50 m), 6.VI.1988, leg. et coll. A. Olivier.

Plate 1

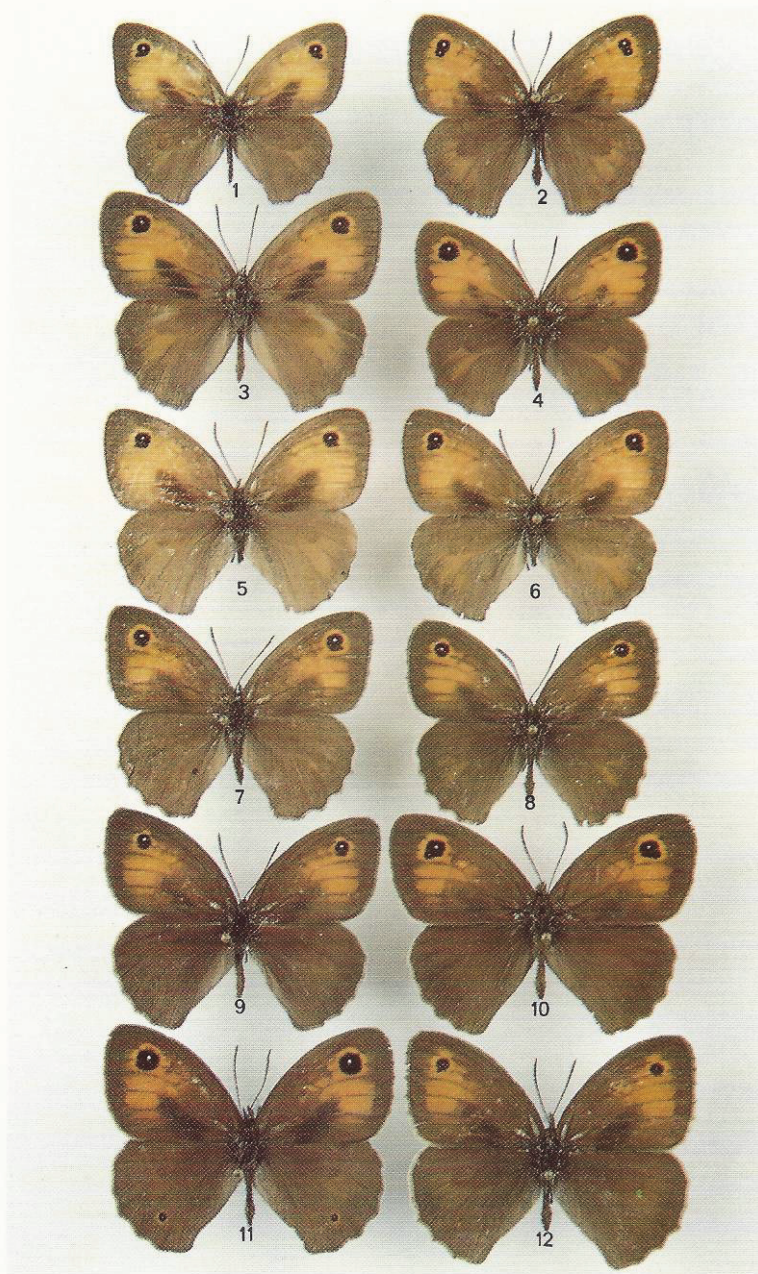


Plate 2



TABLE 1: *Maniola telmessia* (Zeller, 1847), MALES: right forewing size (from base to apex) and spotting characters (forewing underside and hindwing upperside) (see also Olivier 1993: 148 – 149, Table 6)

Area of origin	Number of specimens examined	Forewing size in mm			Forewing underside apical spot			Hindwing upperside postdiscal spot in s3		
		Min.	Max.	Mean	1 white pupil n	%	2 white pupils n	%	absent n	present n
Kássos (late May 1993)	111	17.3	21.4	19.30	28	24.78	85	75.22	111	98.23
Kárpáthos (June 1984)	14	17.2	21.2	19.85	4	28.57	10	71.43	14	100
Kárpáthos (June 1989)	42	17.5	22.8	19.91	28	65.12	15	34.88	41	95.35
Kárpáthos (April 1990)	6	17.2	20.5	19.05	5	83.33	1	16.67	6	100
Kárpáthos: Píles (late May 1993)	50	17.2	21.9	19.48	21	42.00	29	58.00	48	96.00
Kárpáthos: vic. Diafáni (late May 1993)	39	17.3	21.8	19.30	11	28.21	28	71.79	37	94.87
Kárpáthos: both localities (late May 1993)	89	17.2	21.9	19.40	32	35.96	57	64.04	85	95.51
Kárpáthos (all specimens)	151	17.2	22.8	19.57	69	45.39	83	54.61	146	96.05
Ródos (May 1972)	9	18.8	21.0	19.43	4	44.44	5	55.56	4	44.44
Ródos (June 1984)	20	18.6	20.5	19.59	13	65.00	7	35.00	12	60.00
Ródos (April 1986)	14	19.2	22.3	20.90	5	35.71	9	64.29	5	35.71
Ródos (late May 1989)	19	17.6	21.3	19.80	10	52.63	9	47.37	11	57.89
Ródos (April 1990)	14	17.3	22.2	20.09	9	64.29	5	35.71	14	100
Ródos: Soroní (late May 1993)	34	18.4	21.1	19.66	16	45.71	19	54.29	23	65.71
Ródos: Psíñthos (late May 1993)	39	17.8	20.6	19.53	20	50.00	20	50.00	21	52.50
Ródos: both localities (late May 1993)	73	17.8	21.1	19.59	36	48.00	39	52.00	44	58.67
Ródos (all specimens)	149	17.3	22.3	19.78	77	50.99	74	49.01	90	59.60
										61
										40.40

TABLE 1 : continued

Area of origin	Number of specimens examined	Forewing size in mm			Forewing underside apical spot				Hindwing upperside postdiscal spot in s3			
		Min.	Max.	Mean	1 white pupil n	%	2 white pupils n	%	absent n	%	present n	%
Sími (April 1990)	5	20.0	22.0	20.56	5	100	0	0	4	80.00	1	20.00
Sími (June 1993)	28	18.4	22.4	19.80	15	50.00	15	50.00	23	76.67	7	23.33
Sími (all specimens)	33	18.4	22.4	19.92	20	57.14	15	42.86	27	77.14	8	22.86
Tilos (late May 1992)	106	16.8	21.6	19.34	41	37.61	68	62.39	66	60.55	43	39.45
Kós (late May 1988)	49	18.7	23.3	21.41	36	73.47	13	26.53	37	75.51	12	24.49
Kós (June 1992)	6	19.8	21.7	20.98	3	50.00	3	50.00	4	66.67	2	33.33
Kós (all specimens)	55	18.7	23.3	21.36	39	70.91	16	29.09	41	74.55	14	25.45
Kálimnos (June 1992)	13	18.7	22.4	20.61	9	64.29	5	35.71	6	42.86	8	57.14
Léros (June 1992)	4	19.7	23.0	21.18	3	60.00	2	40.00	2	66.67	1	33.33

TABLE 2 : *Maniöta telmessia* (Zeller, 1847), FEMALES : right forewing size (from base to apex) and spotting characters (forewing underside and hindwing upperside) (see also Olivier 1993 : 150 – 151, Table 7)

Area of origin	Number of specimens examined	Forewing size in mm			Forewing underside apical spot				Hindwing upperside postdiscal spot in s3			
		Min.	Max.	Mean	1 white pupil	2 white pupils	absent	present	n	%	n	%
Kássos (late May 1993)	13	19.6	22.2	21.14	1	7.69	12	92.31	13	100	0	0
Kárápathos (June 1984)	14	20.1	25.1	22.65	0	0	14	100	14	100	0	0
Kárápathos (June 1989)	88	19.7	24.7	22.64	10	11.36	78	88.64	88	100	0	0
Kárápathos (late May 1993)	51	20.1	25.0	22.60	1	1.96	50	98.04	51	100	0	0
Kárápathos (all specimens)	153	19.7	25.1	22.63	11	7.19	142	92.81	153	100	0	0
Ródos (May 1972)	7	23.5	25.6	24.17	0	0	7	100	6	85.71	1	14.29
Ródos (June 1984)	19	20.8	24.8	22.96	0	0	19	100	19	100	0	0
Ródos (April 1986)	8	24.3	26.8	25.38	1	12.50	7	87.50	7	87.50	1	12.50
Ródos (late May & June 1989)	33	19.2	25.2	22.86	1	3.03	32	96.97	33	100	0	0
Ródos : Soroní (late May 1993)	6	20.7	24.6	22.42	0	0	6	100	6	100	0	0
Ródos : Psínthos (late May 1993)	21	20.9	24.6	22.88	0	0	21	100	21	100	0	0
Ródos : both localities (late May 1993)	27	19.2	24.6	22.77	0	0	27	100	27	100	0	0
Ródos (all specimens)	94	19.7	26.8	23.17	2	2.13	92	97.87	92	97.87	2	2.13
Sími (June 1993)	50	19.7	25.7	22.99	6	12.00	44	88.00	49	98.00	1	2.00
Tíros (late May 1992)	56	20.0	24.7	22.49	0	0	56	100	55	98.21	1	1.79
Kós (late May 1988)	42	22.8	26.6	25.18	6	14.29	36	85.71	41	97.62	1	2.38
Kós (June 1992)	27	22.1	26.9	24.67	1	3.70	26	96.30	27	100	0	0
Kós (all specimens)	69	22.1	26.9	24.98	7	10.14	62	89.86	68	98.55	1	1.45
Kálimnos (June 1992)	44	20.3	26.0	23.71	3	6.67	42	93.33	44	97.78	1	2.22
Léros (June 1992)	23	21.0	26.7	25.10	0	0	23	100	23	100	0	0

TABLE 3 : *Maniota telmessia* (Zeller, 1847), MALES : hindwing underside spot-pattern (spot number and spot position)
(see also Olivier 1993 : 156 – 157, Table 8)

Area of origin	Number of specimens examined	Number of hindwing spots			Spot frequency						Total spot number	
		Min.	Max.	Mean	anal		median		costal			
					1	2	3	4	5	6		
Kássos (late May 1993)	112	1	6	3.03	48	111	39	1	108	32	339	
	Kárpáthos (June 1984)	13	0	3	1.00	1	7	0	0	5	0	13
	Kárpáthos (June 1989)	43	0	5	1.93	9	37	2	0	34	1	83
	Kárpáthos (April 1990)	6	0	3	1.83	1	5	0	0	5	0	11
	Kárpáthos : Píléis (late May 1993)	50	1	4	2.42	13	50	6	0	44	8	121
	Kárpáthos : vic. Diáfáni (late May 1993)	39	0	5	2.64	11	36	11	0	35	10	103
	Kárpáthos : both localities (late May 1993)	89	1	5	2.52	24	86	17	0	79	18	224
	Kárpáthos (all specimens)	151	0	5	2.19	35	135	19	0	123	19	331
Ródos (May 1972)	9	2	6	3.78	6	9	5	3	9	2	34	
	Ródos (June 1984)	20	0	6	3.40	13	19	8	1	19	8	68
	Ródos (April 1986)	14	2	6	4.43	12	14	12	1	14	9	62
	Ródos (late May 1989)	19	2	6	4.26	18	19	8	1	19	16	81
	Ródos (April 1990)	14	3	5	4.00	9	14	8	1	14	10	56
	Ródos : Soroní (late May 1993)	35	2	6	4.31	25	35	23	8	35	25	151
	Ródos : Psínthos (late May 1993)	40	2	6	4.55	35	40	33	4	40	30	182
	Ródos : both localities (late May 1993)	75	2	6	4.44	60	75	56	12	75	55	333
Ródos (all specimens)	151	0	6	4.20	118	150	97	19	150	100	634	

TABLE 3 : continued

Area of origin	Number of specimens examined	Number of hindwing spots			Spot frequency						Total spot number
		Min.	Max.	Mean	anal		median		costal		
Sími (April 1990)	5	1	6	4.00	3	4	3	1	5	4	20
Sími (June 1993)	30	2	5	3.87	20	30	21	1	30	14	116
Sími (all specimens)	35	1	6	3.89	23	34	24	2	35	18	136
Tilos (late May 1992)	109	1	6	4.07	78	108	70	9	109	70	444
Kós (late May 1988)	49	2	6	3.80	28	49	30	4	49	26	186
Kós (June 1992)	6	2	6	4.33	4	6	4	1	6	5	26
Kós (all specimens)	55	2	6	3.85	32	55	34	5	55	31	212
Kálimnos (June 1992)	14	2	6	4.14	8	14	8	3	14	11	58
Léros (June 1992)	3	2	5	3.00	1	3	1	0	3	1	9

TABLE 4 : *Maniola telmessia* (Zeller, 1847), FEMALES : hindwing underside spot pattern (spot number and spot position)
(see also Olivier 1993:158 – 159, Table 9)

Area of origin	Number of specimens examined	Number of hindwing spots			Spot frequency							Total spot number
		Min.	Max.	Mean	anal		median		costal			
					1	2	3	4	5	6		
Kássos (late May 1993)	13	0	2	0.69	0	1	0	1	6	1	9	
Kárpáthos (June 1984)	14	0	1	0.07	0	0	0	0	1	0	1	
Kárpáthos (June 1989)	88	0	2	0.09	0	3	0	0	5	0	8	
Kárpáthos (late May 1993)	51	0	2	0.18	0	1	0	0	8	0	9	
Kárpáthos (all specimens)	153	0	2	0.12	0	4	0	0	14	0	18	
Ródos (May 1972)	7	0	4	2.00	3	3	0	0	6	2	14	
Ródos (June 1984)	19	0	4	2.00	5	10	0	0	14	9	38	
Ródos (April 1986)	8	0	5	2.25	1	6	1	0	7	3	18	
Ródos (late May & June 1989)	33	0	5	1.36	4	11	1	0	22	7	45	
Ródos : Soroní (late May 1993)	6	0	3	1.33	0	2	0	0	4	2	8	
Ródos : Psínthos (late May 1993)	21	0	5	2.62	7	14	3	0	20	11	55	
Ródos : both localities (late May 1993)	27	0	5	2.33	7	16	3	0	24	13	63	
Ródos (all specimens)	94	0	5	1.89	20	46	5	0	73	34	178	
Sími (June 1993)	50	0	5	1.70	7	21	3	0	36	18	85	
Tílos (late May 1992)	56	0	5	2.16	14	30	4	0	45	28	121	
Kós (late May 1988)	42	0	5	1.95	9	19	3	0	33	18	82	
Kós (June 1992)	27	0	4	1.85	3	14	0	0	21	12	50	
Kós (all specimens)	69	0	5	1.91	12	33	3	0	54	30	132	
Kálimnos (June 1992)	45	0	5	2.27	9	23	8	0	37	25	102	
Léros (June 1992)	22	0	4	2.00	4	11	1	0	17	11	44	

TABLE 5 : Butterfly species number and relative level of endemism (specific and subspecific) on Kríti, Kápathos and Ródos, related to some geographic variables (area, altitude, distance from the mainland).

Island	Area (km ²)	Altitude (highest point) (m)	Distance from the mainland (km)	Species number n	Endemics	
					n	%
Kríti	8259	2456	96 (from the Pelopónnisos) 71 (from Kápathos)	41	4	9.76 (1)
Kápathos	277	1215	93 (44.5 km from Ródos)	23	1	4.35 (2)
Ródos	1403	1215	17.5	47	2	4.26 (3)

- (1) With the addition of *Gegenes nostradamus* (Fabricius, 1793) (Coutsis & Olivier 1993), there are now 41 butterfly species known from Kríti.
- (2) *Polyommatus agestis agestis* ([Denis & Schiffermüller], 1775) should be added to the butterfly species list from Kápathos (H. Pieper in litt. 25.VIII.1993). If *Maniola telmessia* from Kápathos is also considered as an endemic entity, the value would rise to 8.70 %.
- (3) If the Ródos population of *Zerynthia cerisy* is added as a third endemic, the value would rise to 6.38 %.

member of a clinal or mosaic array of variable populations. Geographic variation in several characters may not be congruent, making geographical limits for a subspecies quite arbitrary. Third, other populations undistinguished by phenotype may actually have diverged in more significant ways, such as adaptations to new hostplants, shifts in mating time, etc. Fourth, traditional morphological subspecies are not necessarily undergoing incipient speciation, even when isolated in unique environments (...) the origin of reproductive isolation is conservative and may require special circumstances of population genetics».

We feel strongly sympathetic with these views in several respects, although we believe that responsibly defined subspecies usefully reflect plausible historical and biogeographical developments (cf. Olivier 1993). We are aware, however, that the subspecies (defined on morphological criteria) covers only part of significant variation within species (vide supra, Collins 1991: 56).

While studying the taxonomy and biogeography of the butterflies of Ródos and other Aegean islands, problems were experienced concerning an appropriate evaluation of the taxonomic status of some differentiated butterfly populations (e.g. *Zerynthia cerisy* (Godart, [1824]) and *Glaucopsyche alexis* (Poda, 1761) on Ródos). In such instances, it becomes somewhat ambiguous to assess the level of endemism among the butterfly fauna of different islands (cf. the chapter «Biogeography» in Olivier 1993 for further discussion and implications). In the latter study, it was noted that the relatively high level of endemism, as well as relative impoverishment of the fauna of Ródos, Kápathos and Kríti, seems to be positively correlated with the current geographic distance of these islands from the mainland but also with the relative age of their present isolation. These findings still seem

to hold in face of the present new data and evidence (see table 5 of the present study and Olivier op. cit. for further discussion).

Maniola telmessia from Kárpáthos (and Káossos), that we cannot consider as a subspecies on morphological grounds - the differentiating characters not being entirely constant, as stated before - could, perhaps, be an incipient or even a full species, considering the results of Thomson's electrophoretic study. We ourselves do not feel qualified to decide on this matter. The problem, however, is certainly worth the attention and future investigations, including cross-breeding experiments, would be very welcome.

Acknowledgments

We wish to thank Mr A. Riemis (Turnhout, Belgium) and Mr D. van der Poorten (Antwerpen) for putting at our disposal significant comparative material of *M. telmessia* collected in 1984 on resp. Kárpáthos and Ródos; Dr G. Thomson (Lockerbie, Scotland) for interesting and stimulating correspondence over the years; Dr H. Pieper (Zoologisches Museum, Kiel, Germany) for the communication of some interesting distribution records; Mr H. Henderickx (Mol, Belgium) for preparing the colour Plates 1 and 2.

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Boekbespreking

Thomas, J. & Lewington, R. : *The Butterflies of Britain & Ireland.*

25 x 25 cm, 224 p., 68 kleurenplaten, 35 tekstfiguren, 70 verspreidingskaarten, Dorling Kindersley Ltd., 9 Henrietta Street, London WC2E 8PS, gebonden, 1991, £ 16.99 (ISBN 0-86318-591-6).

Waarschijnlijk is in geen enkel land ter wereld de dagvlinderfauna in al zijn aspecten zo goed bekend als in Groot-Brittannië. De studies, gedaan door de Britten, op gebied van de ecologie, populatiedynamica, biologie, gedrag, verspreiding en bescherming van alle 60 op de Britse Eilanden als resident voorkomende soorten zijn ongeëvenaard.

Dit werk is geschreven door Dr Jeremy Thomas, een vooraanstaand wetenschapper verbonden aan het Institute of Terrestrial Ecology's Furzebrook Research Station te Dorset, en auteur van enkele baanbrekende boeken en artikels op gebied van de ecologie en bescherming van dagvlinders (o.a. *Maculinea!*). In dit boek wordt elke van de 60 indigeen voorkomende soorten, alsook enkele uitgestorven soorten en zeldzame dwaalgasten, uitvoerig besproken. Hierbij worden diverse aspecten als het gedrag, de vliegtijd, de ecologie, de voedselplanten, de geografische variabiliteit, de ontwikkelingsstadia (ei, rups, pop) en de graad van zeldzaamheid, belicht. Een groot extra pluspunt is dat al deze thema's op een inhoudelijk wetenschappelijk hoogstaande en tegelijk vlot leesbare, tot een breder publiek gerichte leesstijl worden aangesneden.

De co-auteur, Richard Lewington, is verantwoordelijk voor alle kleurenplaten en tekstfiguren. De kwaliteit hiervan is echt van een uitzonderlijk niveau, zelden benaderd in andere werken. Naast de tekst is er zo voor elke soort een kleurenplaat, waarop naast een diagram met de fenologie van de diverse ontwikkelingsstadia, ook de boven- en onderzijde (deze laatste in natuurlijke rusthouding!) van beide geslachten voortreffelijk wordt geïllustreerd, samen met markante geografische vormen en aberraties. Tevens worden van elke soort verder nog het ei, de rups en de pop zeer aanschouwelijk afgebeeld. Voor elke soort is er tenslotte een verspreidingskaartje in de Britse Eilanden.

Het boek werd, naar mijn bescheiden mening, volledig terecht bekroond met een «Natural World Book of the Year Award» en hoort thuis in de bibliotheek van elke Europese lepidopteroloog, natuurliefhebber of zelfs simpelweg amateur van mooie boeken. Prima werk!

A. Olivier