The butterflies of the Greek island of Níssiros (Lepidoptera: Hesperioidea & Papilionoidea)

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Samenvatting. De dagvlinders van het Griekse eiland Níssiros (Lepidoptera: Hesperioidea & Papilionoidea)
Na een korte inleiding over het Griekse eiland Níssiros en een bespreking van de beperkte bestaande literatuur, worden de 28 met zekerheid van het eiland bekende dagvlindersoorten behandeld. Een biogeografische analyse suggereert kolonisatie voornamelijk vanuit het noorden (Kós en Bodrum schiereiland), door middel van dispersie, daar Níssiros sinds haar bovendrijven in het Pleistoceen altijd een eiland is geweest.

Résumé. Les papillons diurnes de l'île grecque de Níssiros (Lepidoptera: Hesperioidea & Papilionoidea)
Après un bref aperçu des généralités de l'île grecque de Níssiros et une revue de la littérature existante restreinte, les 28 espèces de papillons diurnes connues actuellement avec certitude de l'île sont traitées. Une analyse biogéographique suggère une colonisation principalement à partir du nord (Kós et péninsule de Bodrum) par dispersion, vu que, depuis son émersion dans le courant du Pléistocène, Níssiros a toujours été une île.

Key words: butterflies – Níssiros – Kós – Tílos – Bodrum peninsula – islands – Mediterranean – Greece.

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Introduction

The Greek island of Níssiros lies in the SE Aegean Sea, between the island of Kós to the north and the island of Tílos to the south-east, at distances of about resp. 15.5 km and 13 km. To the east, it is separated by a distance of about 16 km from the Reşadiye Yarımadası Peninsula (Prov. Muğla, Turkey). Only 3.5 km to the north of Níssiros lies the islet of Gialí. The geographic position of Níssiros is shown on Fig. 1.

Níssiros is a round island with an area of 43 km^2 and a diameter of about 7 km and is composed of young igneous rocks. The highest point, Profítis Ilías, has an altitude of 698 m and is situated in about the middle of the island. The general geomorphology of Níssiros is totally determined by the large volcano with five craters — also in the middle of the island — that makes the soil fertile and the vegetation lush, in sharp contrast with that of some neighbouring islands like Tílos and Símí.

From 1912 till 1945, the island was under Italian administration and the only published lepidopterological records available until the 1990's (Turati 1929; Ghigi 1929; Hartig 1940; Bernardi 1961, 1971; Bretherton 1966) resulted from limited collecting activities by Prof. Alessandro Ghigi in August 1926. He collected only eight butterfly taxa during his brief visit, i.e. *Iphiclides podalirius podalirius* (Linnaeus, 1758), *Pieris brassicae brassicae* (Linnaeus, 1758), *Lampides boeticus* (Linnaeus, 1767), *Danaus chrysippus chrysippus* (Linnaeus, 1758), *Limenitis reducta herculeana* Stichel, [1908], *Polygonia egea* (Cramer, [1775]), *Hipparchia fatua fatua* Freyer, 1843 and, finally, *Maniola halicarnassus* Thomson, 1990 (listed as "*Epinephele jurtina telmessia* L." by Turati, 1929: 181, cf. Olivier & Coutsis 1995: 4). In March 1970 and September 1981, Dr. Harald Pieper visited Níssiros, while Dr. George Thomson did so in July 1990. Through their courtesy, the so far unpublished resulting records are listed here. Pamperis (1997) visited it as well, as his photographs of *M. halicarnassus*, taken on 27.V.1991 (pp. 396–397), prove. I personally visited this lovely island twice, in late May 1992 and in April 1995. The results of this collecting, along with the literature records, are dealt with in the systematic section below. 28 species are retained here as being reliably recorded from the island, three of these for the first time (marked with an asterisk).

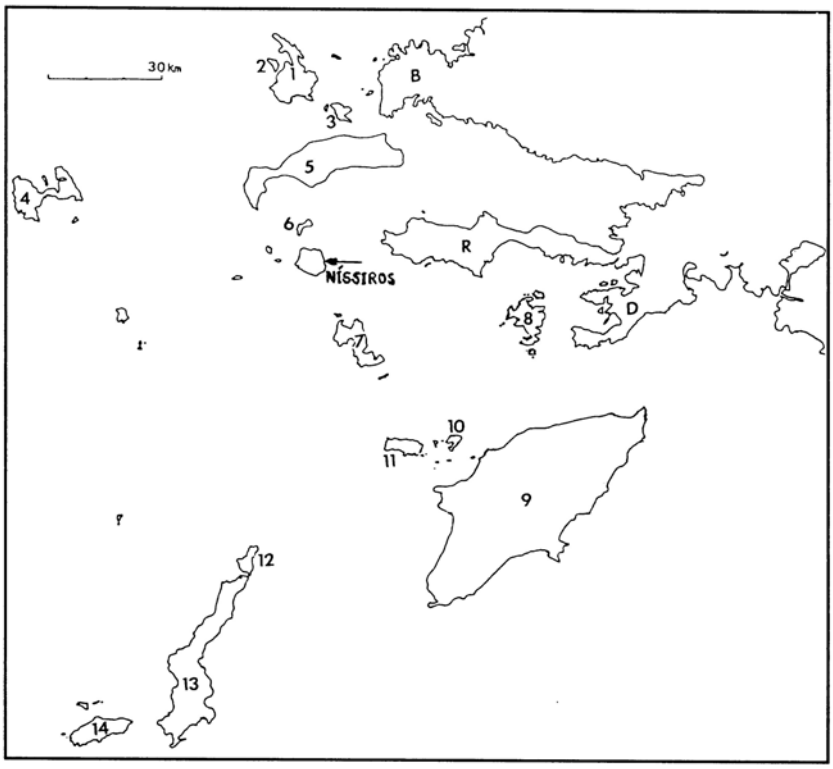

Fig. 1. Geographic situation of the island of Níssiros in the SE Aegean.

R	Reşadiye Yarımadası	5	Kós	11	Hálki
D	Daraçya Yarımadası	6	Gialí	12	Sariá
1	Kálimnos	7	Tílos	13	Kárpathos
2	Télendos	8	Símí	14	Kássos
3	Psérimos	9	Ródos		
4	Astipálea	10	Alimniá		

Systematic Part

The localities on Níssiros where collecting took place are plotted on Fig. 2; they are as follows:

1 — Mandráki (0–50 m). Lush orchards and olive groves on the outskirts of the village.

2 — Mandráki (50–150 m). Along the walls leading up to the medieval Venetian fortress and along the "Cyclopean Wall".

3 — Profítis Ilías (200–450 m). On the plateau at the foot of the hill and on its lower slopes: mostly maquis, only locally more degraded (garrigue).

4 — 3 km NW Emborió (100 m). Flower-rich (April 1995) orchards, mainly with olive trees.

5 — Emborió (200 m). Only one sighting.

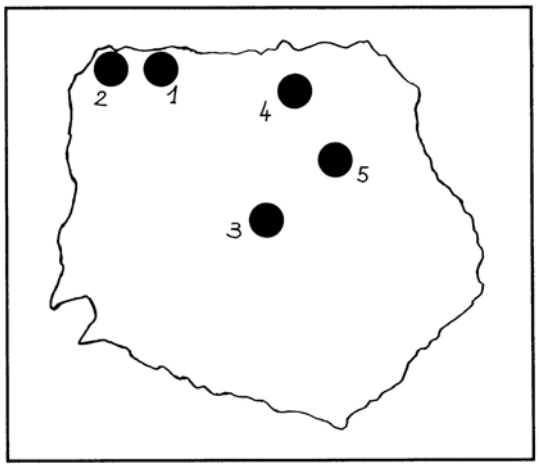

Fig. 2. Map of Níssiros, with localities listed in the Systematic Part

1. Mandráki (0–50 m)
2. Mandráki (50–150 m)
3. Profítis Ilías (200–450 m)
4. 3 km NW Emborió (100 m)
5. Emborió (200 m)

***Carcharodus alceae alceae* (Esper, [1780])**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
– Mandráki (50–150 m), 31.V.1992
– Profítis Ilías (200–450 m), 30.V.1992
Previously plotted from Níssiros on a distribution map in Pamperis (1997: 462).

***Carcharodus orientalis* Reverdin, 1913**
– Profítis Ilías (200–450 m), 29.V.1992
Previously reported by Olivier (1993b: 21). Identity confirmed by examination of the (male) genitalia.

***Carcharodus stauderi ambiguus* (Verity, 1925)**
– Mandráki (50–150 m), 31.V.1992
– Profítis Ilías (200–450 m), 29.V.1992, 30.V.1992
Previously reported by Olivier (1994: 87), further plotted from Níssiros on a distribution map in Pamperis (1997: 470). Identity confirmed by examination of the (male) genitalia.

***Zerynthia cerisy* (Godart, [1824])**
– Mandráki (0–50 m), 5.IV.1995
– 3 km NW Emborió (100 m), 6.IV.1995
Pieper (in litt. 25.VIII.1993) observed the species on Níssiros on 12–20.III.1970.

***Iphiclides podalirius podalirius* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
Previously reported by Turati (1929: 178), Bernardi (1971: 25), Olivier (1993a: 198 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1110 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 28). Pieper (in litt.

25.VIII.1993) observed the species on Níssiros on 8–21.IX.1981, while Thomson (in litt. 19.VIII.1990) did so in Mandráki on 17.VII.1990.

***Papilio machaon syriacus* Eller, 1936**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
– Mandráki (50–100 m), 31.V.1992, 7.IV.1995
Pieper (in litt. 25.VIII.1993) observed the species on Níssiros on two occasions, resp. on 12–20.III.1970 and on 8–21.IX.1981.

***Colias crocea* (Fourcroy, 1785)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
Previously plotted from Níssiros on a distribution map in Pamperis (1997: 70).

***Euchloe* (*ausonia*) *ausonia taurica* Röber, [1907]**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995, 7.IV.1995
Previously plotted from Níssiros on a distribution map in Pamperis (1997: 62).

***Pieris brassicae brassicae* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
– 3 km NW Emborió (100 m), 6.IV.1995
Previously reported by Turati (1929: 178), Bernardi (1971: 25), Olivier (1993a: 198 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1111 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 48). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990.

***Pieris rapae rapae* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
Previously reported by Olivier (1993a: 198 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1111 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 50). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki, both on 17.VII.1990 and on 24.VII.1990.

***Pontia* (*daplidice*) *edusa* (Fabricius, 1777)**
No personal field observations. Previously reported by Olivier (1993a: 198 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1111 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 60). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990.

***Satyrium ilicis ilicis* (Esper, [1779])**
– Mandráki (0–50 m), 24.V.1992
– Profítis Ilías (200–450 m), 29.V.1992, 30.V.1992
Previously reported by Olivier (1993b: 21); further plotted from Níssiros on a distribution map in Pamperis (1997: 100).

***Lycaena phlaeas phlaeas* (Linnaeus, 1761)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
– Mandráki (50–150 m), 31.V.1992
– Profítis Ilías (200–450 m), 30.V.1992, 6.IV.1995
Previously reported by Olivier (1993a: 198 [Table 12]); further plotted from Níssiros on a distribution map in Pamperis (1997: 106). Pieper (in litt. 25.VIII.1993) observed the

species on Níssiros on 12–20.III.1970, while Thomson (in litt. 19.VIII.1990) did so in Mandráki on 17.VII.1990 and 24.VII.1990.

***Lampides boeticus* (Linnaeus, 1767)**
– Profítis Ilías (200–450 m), 29.V.1992
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995
Previously reported by Turati (1929: 183), Bernardi (1971: 24), Olivier (1993a: 198 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1111 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 128).

****Leptotes pirithous* (Linnaeus, 1767)**
– Mandráki (0–50 m), 5.IV.1995
– 3 km NW Emborió (100 m), 6.IV.1995
First-ever records for Níssiros.

***Pseudophilotes vicrama schiffermuelleri* (Hemming, 1929)**
– Mandráki (0–50 m), 24.V.1992
– Profítis Ilías (200–450 m), 29.V.1992
Previously reported by Olivier & De Prins (1996: 208) and Olivier (1998a: 29; 1998b: 296); further plotted from Níssiros on a distribution map in Pamperis (1997: 154).

***Polyommatus icarus* (Rottemburg, 1775)**
– Mandráki (0–50 m), 5.IV.1995
Previously reported by Olivier (1993a: 199 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1112 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 234). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990 and 24.VII.1990.

***Danaus chrysippus chrysippus* (Linnaeus, 1758)**
No personal field observations. Recent reports from Kós and Ródos, resp. in 1992 and in 1993 (Olivier & De Prins 1996: 199–200), however, do not preclude the possibility that the species turns up on Níssiros at any time. It had previously been observed there in August 1926 (Turati 1929: 179; Ghigi 1929: 307). Further citations in literature include Bretherton (1966: 19), Bernardi (1971: 27), Olivier (1993a: 116, 199 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 767).

***Kirinia roxelana* (Cramer, [1777])**
– Mandráki (0–50 m), 24.V.1992
– Profítis Ilías (200–450 m), 29.V.1992
Previously reported by Olivier (1993a: 199 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1112 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 434). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990 and 24.VII.1990.

****Lasiommata megera lyssa* (Geyer, [1828])**
– Mandráki (50 m), 7.IV.1995
First-ever record for Níssiros.

****Lasiommata maera* (Linnaeus, 1758)**
– Mandráki (50 m), 5.IV.1995, 7.IV.1995
First-ever record for Níssiros.

***Maniola halicarnassus* Thomson, 1990**
– Mandráki (0–50 m), 24.V.1992
– Mandráki (50–150 m), 31.V.1992
– Profítis Ilías (200–450 m), 30.V.1992
Previously reported by Turati (1929: 181, as "*Epinephele jurtina telmessia* L."), Bernardi (1961: 184, as "*Maniola telmessia* Zeller"; 1971: 27, also as "*Maniola telmessia* Zeller"), Thomson (1992: 204, 210, 213), Olivier (1993a: 199 [Table 12]), 219, 220, 249–250; 1993b: 21, 22; 1998a: 30), Olivier & Coutsis (1993: 114; 1995: 3–7, 10–12, 14–18, 21–22, 25–27, 29, 31 [Plate 2], 33, 35–36, 41–42, 45, 50, 55–57, 59), Hesselbarth, van Oorschot & Wagener (1995: 133, 827, 829, 830, 1112 [Table 27]), Tolman & Lewington (1997: 237) and Pamperis (1997: 398). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990 and 24.VII.1990.

***Hipparchia fatua fatua* Freyer, 1843**
No personal field observations. Previously reported by Turati (1929: 180), Ghigi (1929: 331), Bernardi (1961: 184, as "*Hipparchia allionii* Geyer"; 1971: 28, as "*Hipparchia allioni* Geyer"), Olivier (1993a: 135–137, 199 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1113 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 345). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990 and 24.VII.1990.

***Limenitis reducta herculeana* Stichel, [1908]**
No personal field observations. Previously reported by Turati (1929: 182), Ghigi (1929: 307), Bernardi (1971: 25), Olivier (1993a: 120, 199 [Table 12]), Hesselbarth, van Oorschot & Wagener (1995: 1113 [Table 27]) and Tolman & Lewington (1997: 145); further plotted from Níssiros on a distribution map in Pamperis (1997: 254). Pieper (in litt. 25.VIII.1993) observed the species on Níssiros on 8–21.IX.1981, while Thomson (in litt. 19.VIII.1990) did so in Mandráki on 17.VII.1990 and 24.VII.1990.

***Vanessa atalanta atalanta* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992 (only observed), 5.IV.1995: remarkably common in April 1995. Previously reported by Olivier (1993a: 199 [Table 12]) and Hesselbarth, van Oorschot & Wagener (1995: 1113 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 266). Finally, observed by Thomson (in litt. 19.VIII.1990) in Mandráki on 17.VII.1990.

***Vanessa cardui* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992, 5.IV.1995: very common in April 1995.
Plotted from Níssiros on a distribution map in Pamperis (1997: 268). Pieper (in litt. 25.VIII.1993) observed the species on Níssiros, stating "am 16.3.[1970] Massenzug von *Vanessa cardui* bei Mandraki (…)"

***Polygonia egea* (Cramer, [1775])**
– Emborió (200 m), 29.V.1992 (only observed)
Previously reported by Turati (1929: 183), Hartig (1940: 232 [Footnote (1)]), Bernardi (1971: 27), Olivier (1993a: 193, 199 [Table 12]; 1993b: 21) and Hesselbarth, van Oorschot & Wagener (1995: 1113 [Table 27]); further plotted from Níssiros on a distribution map in Pamperis (1997: 274).

***Nymphalis polychloros polychloros* (Linnaeus, 1758)**
– Mandráki (0–50 m), 24.V.1992 (only observed)
– Profítis Ilías (200–450 m), 29.V.1992, 6.IV.1995
Plotted from Níssiros on a distribution map in Pamperis (1997: 260). Pieper (in litt. 25.VIII.1993) observed the species on Níssiros on 12–20.III.1970.

Unconfirmed record

***Polyommatus agestis* ([Denis & Schiffermüller], 1775)**

Plotted from Níssiros on a distribution map in Pamperis (1997: 180). No other reports of this taxon exist for this island, and as no voucher specimens are at hand to substantiate it, the present record needs confirmation before one can include the species on the Níssiros list (cf. Olivier 1999 for a detailed review of Pamperis 1997). As it has been observed on both Tílos and Kós (Olivier 1993b; Olivier & De Prins 1996), its occurrence on Níssiros is very likely.

Discussion

For a biogeographical analysis of the butterfly fauna of Níssiros, it is important to know that of neighbouring areas as well, in order to discern some distributional patterns in a larger context and to evaluate their significance. Luckily, these areas have been reviewed in detail quite recently (Bodrum Peninsula — Olivier 1998a; Kós — Olivier & De Prins 1996, Olivier 1998b; Tílos — Olivier 1993b; Ródos — Olivier 1993a): a synopsis is presented here on Table 1.

Table 1. Known geographic distribution of the butterflies (Hesperioidea & Papilionoidea) on the Bodrum Peninsula (B) and on the Greek islands of Kós (K), Níssiros (N), Tílos (T) and Ródos (R)

Taxon	**B**	**K**	**N**	**T**	**R**
Thymelicus sylvestris syriacus (Tutt, [1905])	+	+			
Thymelicus acteon acteon (Rottemburg, 1775)	+	+			+
Thymelicus hyrax (Lederer, 1861)	+				+
Gegenes pumilio pumilio (Hoffmansegg, 1804)		+			+
Carcharodus alceae alceae (Esper, [1780])	+	+	+	+	+
Carcharodus orientalis Reverdin, 1913		+	+		
Carcharodus stauderi ambiguus (Verity, 1925)		+	+	+	+
Spialia (*sertorius*) *orbifer orbifer* (Hübner, [1823])	+	+			+
Muschampia proto aragonensis (De Sagarra, 1924)	+			+	
Zerynthia cerisy cerisy (Godart, [1824])	+	+	+		+
Archon apollinus apollinus (Herbst, 1798)		+			+
Iphiclides podalirius podalirius (Linnaeus, 1758)	+	+	+	+	+
Papilio machaon syriacus Eller, 1936	+	+	+	+	+
Colias crocea (Fourcroy, 1785)	+	+	+	+	+
Gonepteryx farinosa farinosa (Zeller, 1847)	+	+		+	+
Gonepteryx cleopatra fiorii Turati & Fiori, 1930					+
Euchloe (*ausonia*) *ausonia taurica* Röber, [1907]	+	+	+	+	+
Aporia crataegi crataegi (Linnaeus, 1758)					+
Pieris brassicae brassicae (Linnaeus, 1758)	+	+	+	+	+
Pieris krueperi krueperi Staudinger, 1860		+			
Pieris rapae rapae (Linnaeus, 1758)	+	+	+	+	+

Taxon	B	K	N	T	R
Pontia (*daplidice*) *edusa* (Fabricius, 1777)	+	+	+		+
Cigaritis ?*cilissa* Lederer, 1861	+				
Favonius quercus quercus (Linnaeus, 1758)					+
Callophrys rubi (Linnaeus, 1758)		+			+
Satyrium ilicis ilicis (Esper, [1779])	+	+	+		
Lycaena phlaeas phlaeas (Linnaeus, 1761)	+	+	+	+	+
Lycaena thersamon (Esper, [1784])	+	+			+
Lampides boeticus (Linnaeus, 1767)	+	+	+		+
Leptotes pirithous (Linnaeus, 1767)		+	+		+
Celastrina argiolus argiolus (Linnaeus, 1758)	+	+			+
Pseudophilotes vicrama schiffermuelleri (Hemming, 1929)		+	+	+	+
Glaucopsyche alexis alexis (Poda, 1761)		+			+
Chilades trochylus trochylus (Freyer, [1844])					+
Plebeius loewii loewii (Zeller, 1847)	+	+		+	+
Polyommatus agestis agestis ([Denis & Schiffermüller], 1775)	+	+		+	+
Polyommatus thersites (Cantener, [1835])		+			+
Polyommatus icarus (Rottemburg, 1775)	+	+	+	+	+
Danaus chrysippus chrysippus (Linnaeus, 1775)		+	+		+
Kirinia roxelana (Cramer, [1777])	+	+	+		+
Pararge aegeria aegeria (Linnaeus, 1758)		+			
Lasiommata megera lyssa (Geyer, [1828])	+	+	+		+
Lasiommata maera (Linnaeus, 1758)		+	+		+
Ypthima asterope asterope (Klug, 1832)					+
Maniola telmessia (Zeller, 1847)	+	+		+	+
Maniola halicarnassus Thomson, 1990	+		+		
Hyponephele lupina intermedia (Staudinger, 1886)	+	+			+
Hipparchia syriaca syriaca (Staudinger, 1871)	+				
Hipparchia syriaca ghigii (Turati, 1929)					+
Hipparchia senthes (Fruhstorfer, 1908)	+	+			
Hipparchia mersina (Staudinger, 1871)	+				
Hipparchia fatua fatua Freyer, 1843	+	+	+	+	+
Pseudochazara anthelea anthelea (Hübner, [1824])	+	+			+
Charaxes jasius jasius (Linnaeus, 1767)	+				+
Limenitis reducta herculeana Stichel, [1908]	+	+	+		+
Vanessa atalanta atalanta (Linnaeus, 1758)	+	+	+	+	+
Vanessa cardui (Linnaeus, 1758)	+	+	+	+	+
Polygonia egea (Cramer, [1775])		+	+		
Nymphalis polychloros polychloros (Linnaeus, 1758)	+	+	+		+
Melitaea trivia trivia ([Denis & Schiffermüller], 1775)	+	+			

Table 2. Species number and relative similarity between pairs of areas reviewed on Table 1. For further explanations see text (both subspecies of *H. syriaca* are treated as one single taxon in the present analysis)

Area	N	K	B	T	R
N	**28**	27	21	14	24
K	*0.563*	**47**	33	18	39
B	*0.447*	*0.611*	**40**	17	32
T	*0.424*	*0.375*	*0.404*	**19**	18
R	*0.451*	*0.709*	*0.582*	*0.375*	**47**

Note.
Bold: number of species known to occur for each area;
regular: number of taxa in common between each area pair;
italics: similarity coefficient between each area pair

Table 2 presents the results of an analysis of faunal similarity (FS) between pairs of areas according to the following formula (cf. de Jong 1976: 206; Olivier 1993a: 197, 203, 205, table 16):

$$FS = \frac{(a,b)}{a + b + (a,b)}$$

where: a = number of taxa restricted to region A
b = number of taxa restricted to region B
(a,b) = number of taxa common to A and B

This formula allows a quick comparison of resemblances between pairs of regions, though it may be less convenient for further statistical processing (but see Dennis, Williams & Shreeve 1991 and Dennis & Shreeve 1996 — who call this the Jaccard similarity coefficient S_J — for further discussion). The fauna of Níssiros thus appears to be most similar to that of Kós, but the data suggest a slightly closer affinity between the faunas of Níssiros and Ródos rather than between those of the former island and the Bodrum Peninsula. Interestingly, Níssiros and Tílos show the lowest relative similarity. These results should, however, be treated with caution. It appears that only islands with a large enough species number (> 35) and with a fauna of approximately the same number yield comparable results. This analysis is therefore not entirely appropriate for the present case. Some of the rather high similarity coefficients (Kós with Ródos, Bodrum Peninsula with Ródos) may only result from the common occurrence in these areas of a significant number of taxa widespread over the adjacent mainland (see Olivier 1988a: 31–32, Appendix 1 for a list of the butterflies of the entire province of Muğla).

The direct analysis of the distribution of single taxa in the area considered in the present analysis seems more promising. Of the 28 species confirmed to occur on Níssiros, no less than 12 (42.86 %) occur in all five areas considered and are thus totally uninformative, and the same can be said of 9 more species (32.14 %), that occur in four out of the five areas considered. Of these, two (*C. stauderi ambiguus* and *P. vicrama schiffermuelleri*) are unknown from the Bodrum Peninsula: since both taxa have also been

recorded from the islands of Kálimnos and Léros (Olivier 1996, 1997), it is quite probable that they have been overlooked rather than really being absent. The 7 other ones are invariably missing on Tílos: this may reflect true absence due either to extinction or to the fact that they never reached this island. Only 25 % of the butterfly fauna of Níssiros is potentially moderately (4 species, i.e. 14.29 %) to highly (3 species, i.e. 10.71 %) informative. The first category includes those that occur in two further areas: of these, *S. ilicis ilicis* also occurs on the Bodrum Peninsula and on Kós, suggesting that it may have reached Níssiros from the latter island (the record from Ródos by Pamperis 1997 is most probably erroneous, cf. Olivier 1999: 79). The three other ones, viz. *L. pirithous*, *D. chrysippus* and *L. maera*, have been recorded from both Kós and Ródos: the first two are well known for their migratory potential and are therefore of no use for the present analysis, while *L. maera* may well have been overlooked on both the Bodrum Peninsula and on Tílos (it has also been found on Kálimnos and Léros, cf. Olivier 1996, 1997). Of the last three species, *C. orientalis* and *P. egea* are further known from Kós only, but probably they have been overlooked on the Bodrum Peninsula (the former is further known from Kálimnos, the latter from both Kálimnos and Léros, cf. Olivier 1996, 1997). *M. halicarnassus* is only known from Níssiros and from the Bodrum Peninsula: interestingly it is replaced by *M. telmessia* (Zeller, 1847) on Ródos, Tílos and Kós, as well as on the the Reşadiye Yarımadası Peninsula (Olivier 1993a, 1993b; Olivier & De Prins 1996; Hesselbarth, van Oorschot & Wagener 1995: 828). There is thus no available evidence for colonization of Níssiros exclusively from the east (Reşadiye Yarımadası Peninsula), nor exclusively from the south (there is not one single butterfly species on Níssiros that also occurs on Tílos and/or Ródos while at the same time being absent on Kós and/or the Bodrum Peninsula). On the contrary, it seems plausible that at least *C. orientalis*, *S. ilicis ilicis* and *M. halicarnassus* (and possibly *P. egea*) arrived from the north (Kós), *M. halicarnassus* subsequently becoming extinct on Kós (Olivier & Coutsis 1995 also considered the possibility of a colonization from the Reşadiye Yarımadası Peninsula), though it still occurs on the Bodrum Peninsula together with *M. telmessia*.

The lack of any taxonomically significant differentiation of any butterfly species on Níssiros and the occurrence of all but one of these on Kós as well, concords with a scenario of a recent arrival from the latter island of most of its current butterfly species and, for those possibly established a longer time, the persistence of at least occasional gene flow with populations from Kós or other areas. Only *M. halicarnassus* from Níssiros is, on average, slightly different from Turkish specimens (↵ larger mean size, ♂ on average with more extended orange-red markings on wing upperside). Statements in support of colonisation of Níssiros mainly from the north have to remain speculative however, as present distributions cannot be interpreted on their own as points of origin and they may have substantially changed in extent since the late Pleistocene, as a result of successive colonisations and extinctions. Comparative data from other animal (and plant) groups would be interesting. It is quite possible that some of the extant butterfly species on Níssiros originated from more than one faunal source area, by more than one single colonisation event, though there are no data at hand to support this.

It is most probable that the colonisation of Níssiros resulted exclusively from dispersal events. Indeed, during the Pliocene the island was immersed entirely (Greuter 1970), emerging only during the Pleistocene though always remaining isolated from the mainland, even at the end of the last glacial maximum (van Andel & Shackleton 1982). At that time Kós was still part of the Anatolian mainland, along with Kálimnos, Léros and some smaller islands, but Níssiros was much larger than today (including the present-day islet of Gialí) and its coastline came very close to Kós. The present-day configuration of these islands dates from less than 9000 BP (van Andel & Shackleton 1982).

Acknowledgments

Thanks are due to Dr. Harald Pieper (Zoologisches Museum Kiel, Germany) and Dr. George Thomson (Lockerbie, Scotland, UK) for the communication of their records. I would further like to express my gratitude to Dr. Roger L. H. Dennis (The Manchester Museum, Manchester University) and Dr. Yuri P. Nekrutenko (Schmallhausen Institute of Zoology, Kiev) for their useful comments on an earlier version of this paper: responsibility for the final result, however, remains solely with me.

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