The phylogenetic relationships of the species and subspecies of the subgenus *Elphinstonia* KLOTS, 1930

(Lepidoptera, Pieridae)

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Abstract: This work presents the results of the first molecular investigations of the subgenus *Elphinstonia* KLOTS, 1930. A 326 bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene was available for the analysis. Monophyly of Elphinstonia is confirmed by the tests, and the further radiation of the subgenus into the "charlonia-group", comprising the species E. penia (FREYER, 1852), E. transcaspica (STAUDINGER, 1882), E. lucilla BUTLER, 1886, E. bazae FABIANO, 1993, E. charlonia (DONZEL, 1842), respectively, and on the other hand the "tomyris-group" including E. lessei BERNARDI, 1957, E. ziayani LEESTMANS & BACK, 2001, and E. tomyris CHRISTOPH, 1884, become apparent. The respective species, represented by several samples of different subspecies and populations, show a conspicuous phylogenetic signal and are unequivocally separable from each other. According to the phenotypic characters published earlier by the first author, it is somewhat surprising that E. penia (FREYER) belongs to the "charlonia-group", and not to the "tomyris-group" Aside from that all recently published taxonomic results are affirmed. Especially E. charlonia (DONZ.), E. penia (FREY.), E. bazae FABIANO, and E. transcaspica (STGR.), confirmed their status as valid species. This is also the fact for E. lessei BERNARDI and E. ziayani LEESTMANS & BACK. Concluding, the re-adjusted taxonomic relationships, the phylogenetic correlation, as well as biogeographic data are presented.

Zusammenfassung: In der vorliegenden Arbeit werden die ersten molekularbiologischen Forschungsergebnisse an der Untergattung Elphinstonia KLOTS, 1930 dargestellt. Für die Untersuchung stand ein 326 bp langes Stück des mitochondrialen Cytochromoxidase Untereinheit I - Gens (COI) zur Verfügung. Die Monophylie von Elphinstonia wird in den Analysen bestätigt und eine weitere Unterteilung einerseits in die "charlonia-Gruppe" mit den Arten E. penia (FREYER, 1852), E. transcaspica (STAUDINGER, 1882), E. lucilla BUTLER, 1886, E. bazae FABIANO, 1993 und E. charlonia (DONZEL, 1842), und andererseits in die "tomyris-Gruppe" mit den Arten E. lessei BERNARDI, 1957, E. ziayani LEESTMANS & BACK, 2001 und E. tomyris CHRISTOPH, 1884, wird deutlich. Die einzelnen Arten, vertreten durch mehrere Proben verschiedener Unterarten und Populationen, zeigen ein deutliches phylogenetisches Signal und sind eindeutig voneinander abgrenzbar. Nach den bereits vom Erstautor veröffentlichten phänotypischen Merkmalen überrascht es etwas, daß E. penia (FREY.) zur "charlonia-Gruppe" und nicht zur "tomyris-Gruppe" gehört. Ansonsten konnten alle zuletzt beschriebenen taxonomischen Resultate bestätigt werden. Insbesondere zeigte sich, daß E. charlonia (DONZ.), E. penia (FREY.), E. bazae FABIANO und E. transcaspica (STGR.) eindeutig als eigene Arten einzustufen sind. Das gilt auch für E. lessei BERNARDI

by

und *E. ziayani* LEESTMANS & BACK. Abschließend werden die neugeordneten taxonomischen Verhältnisse, phylogenetische Zusammenhänge sowie biogeographische Daten erläutert.

Key words: *Euchloe*, *Elphinstonia*, molecular phylogeny, COI, species boundaries, genetic distances.

Introduction: The genus *Euchloe* HÜBNER, 1819, comprises a set of about 25 palaearctic and nearctic species (SAVELA, 2006; ZIEGLER, 2005), which are of interest for taxonomic studies ever since (KLOTS, 1930; BERNARDI, 1945; OPLER, 1966a, b, 1970; REISSINGER, 1990; WINHARD, 2000). Earlier investigations of some *Euchloe* species revealed the existence of two species groups within the genus. Therefore, a splitting into two subgenera had been proposed, viz. *Euchloe* HBN., and *Elphinstonia* KLOTS, respectively (BAKER, 1889; KLOTS, 1930; TALBOT, 1932; BERNARDI, 1945; VERITY, 1947, and others). The assignmet of the described species to the subgenera was, however, incomplete and partially incorrect.

So are, for instance, the taxa *E. charlonia* (DONZ.) and *E. penia* (FREY.) treated as different species in the actual edition of the COLLINS field guide (TOLMAN, 1997) while causes for this taxonomical changes in respect to former issues are missing and the references for the new status is lacking (see BACK, 1991b).

Because of the strongly differing appearance of generations and the very complex life-cycle (up to 5 hibernations, BACK, 1979), misidentifications and misleading interpretations in taxon diagnosis were drawn. Within the last years, breeding studies have given new insights in species biology (STROBINO, 1976; OPLER, 1974; OLIVARES & JIMENEZ GOMEZ, 1996; BACK, 1984a, b, 1991b, 2001), which has led to an excellent starting hypothesis for molecular investigations. Especially the clear differentiation of the species *E. ausonia* (HÜBNER, 1804), *E. simplonia* FREYER, 1829, and *E. crameri* BUTLER, 1869, respectively (BACK, 1991a), as well as the interspecific relationships of species of the "*tagis*-group" [e. g. *E. t. pechi* (STAUDINGER, 1885) and others] and the *Elphinstonia* species (BACK, 1981, 1984a, 1991; BACK et al., 2005) derived from breeding and interbreeding tests lead to a better understanding of the genus *Euchloe* HBN. Most recent molecular analysis (POLLOCK et al., 1998; CHEW & WATT, 2006) elucidated the familial phylogeny of the Pieridae by the use of molecular markers and cleared up the position of Anthocharini within the Pierinae.

Currently there is no universally accepted taxonomic treatment for *Euchloe* HBN. A major cause is the lack of a phylogenetic study. Depending on the author, different described taxa are considered as being valid.

Some implications towards the transfer of molecular investigations within Lepidoptera to taxonomical consequences have been proposed: SPERLING (2003) discussed the species boundaries on the molecular level in *Papilio* LINNAEUS, 1758 species, and HEBERT et al. (2004) refined the species resolution in *Astraptes* HÜBNER, [1819] species.

For our comprehensive molecular investigation we used the existing division of the genus into the two subgenera *Euchloe* HBN., and *Elphinstonia* KLOTS (TALBOT, 1932; BERNARDI, 1945; VERITY, 1947, and others), respectively, as an ingenious working hypothesis. For this first part of the analysis the genotypic interrelationships of species of the subgenus *Elphinstonia* KLOTS are clarified.

Elphinstonia species can be divided into two ecological and bio-geographical groups, the mountain species and the desert species. The former are dispersed in vegetation rich habitats,

mostly mountain landscapes, and are represented by the species *E. penia* (FREY.), *E. lessei* BERNARDI, *E. ziayani* LEESTMANS & BACK, and *E. tomyris* CHRISTOPH, respectively. These species were grouped as the "tomyris-type" The species of the desert and steppe habitats differ by their occurence and biology from the mountain species. They occur mosky in low, hot, dry areas with sparse vegetation. The species are *E. charlonia* (DONZ.), *E. bazae* FABIANO, *E. lucilla* BTL., and *E. transcaspica* (STGR.), respectively. They were grouped as the "*charlonia*-type" The exclusive Palaearctic dispersal of *Elphinstonia* species extends as far as the Canary Islands and Spain in the west, North-Africa to Saudi-Arabia (LARSEN, 1983) and Pakistan as well as from Macedonia, Greece, Turkey to Turkmenistan and Persia.

Our objective is to clarify the relationships within the species of *Elphinstonia* species and subspecies and to solve critical points in taxonomy. At this, the results of this preliminary molecular work proposed are provisionally because of the limited sequence data.

Sample-ID	Genus	Subgenus	Species	Subspecies	Author, year	Locality	GenBank ass. no.
WB002	Euchloe	Elphinstonia	charlonia	charlonia	(DONZEL, 1842)	Spain, Lanzarole, Puerto del Carmen, egg 1.5.1986, e.o. 25.2.1990, leg. W. Back	AM418399
WB003	Euchloe	Elphinstonia	lessei	qohrudicus	BACK & LEESTMANS, 2001	Iran, Yazd, 25.4.2001, leg, J. Klir	AM418400
WB004	Euchloe	Elphinstonia	penia	taleschicus	BACK & LEESTMANS, 2001	N. Iran, Hesarud, E. Ml. Tales, Zanjan prov, 10.5.2001, 1300m. leg. W. Back	AM418401
WB005	Euchloe	Elphinstonia	bazae	iberae	BACK, OLIVARES & LEESTMANS, 2005	Spain, prov. Aragón, Caspe, 16.3.2005, leg. W. Back	AM418402
WB009	Euchloe	Elphinstonia	lessei	qohnudicus	BACK & LEESTMANS, 2001	Iran, E Islahan, Zefre, Wadar-Zefre, Mt. Qohrud 2800m, 21.5.2001, leg. W. Back	AM418403
WB010	Euchloe	Euchloe	ausonia	taurica	Rober, 1907	Armenia, South Zangezur, Megrinski Khrebet, Shwanidzov valley, 1800m, 22.5.2001, leg. A. Dantchenko	AM418404
WB011	Euchloe	Elphinstonia	bazae	bazae	FABIANO, 1993	Spain, prov. Andalusia, Baza, 31.3.2005. leg W. Back	AM418405
WB012	Euchloe	Elphinstonia	bazae	bazae	FABIANO, 1993	Spain, prov. Andalusia. Baza, e. 4.05, leg. W. Back	AM418406
WB013	Euchloe	Elphinstonia	ziayani	ziayani	LEESTMANS & BACK, 2001	N. Iran, Hesarud, E. Mt. Tales, 1300m, Zanjan prov., 27.4.2001. leg. M. Ziayan	AM418407
WB014	Euchloe	Elphinstonia	ziayani	ziayani	LEESTMANS & BACK, 2001	N. Iran, Hesarud, E. Ml. Tales, 1300m, Zanjan prov., 27.4.2001, leg. M. Ziayan	AM418408
WB015	Euchloe	Elphinstonia	Iranscaspica	amseli	GROSS & EBERT, 1975	N. Iran, S of Karaj, Jaroo Mts 1400m, 15.4.2005, leg. A. R. Naderi	AM418409
WB018	Euchloe	Elphinstonia	Denia	thessalica	MEZGER, 1936	Macedonia, Skopje area, gorge Treska. egg/larva 20./24.5.1977, e.l. 11 -15.6.1977, leg. W. Back	AM418410
WB021	Euchloe	Elphinstonia	tomytis	lomyris	CHRISTOPH, 1884	Turkmenislan, Ashkabad, 350m, 31.32.4.1991	AM418411
WB026	Euchloe	Elphinstonia	charlonia	charlonia	(DONZEL, 1842)	SE Egypt, border to Sudan, Jabal Hamalah, app. 1500-1900m, e. March 2003, leg. G. Müller	AM418412
WB029	Euchloe	Elphinstonia	bazae	bazae	FABIANO, 1993	Spain, prov. Andalusia, Baza, 31.3.2005, leg. W. Back	AM418413
WB030	Euchloe	Elphinstonia	penia	thessalica	MEZGER, 1936	Greece, Xirolimol, Kozani, 1000m, 30.4.1990, W. Leg. Fickler	AM418414
WB031	Euchloe	Elphinstonia	penia	thessalica	MEZGER. 1936	Macedonia, Skopje area, gorge Treska, 5.5.1978, leg. W. Back	AM418415
W8032	Euchloe	Elphinstonia	transcaspica	amseli	GROSS & EBERT, 1975	N. Iran, S of Karaj, Jaroo Mts., 15.4.2005, teg. A. R. Naderi	AM418416
W8033	Euchloe	Elphinstonia	penia	taleschicus	BACK & LEESTMANS, 2001	Iran, Hesarud, Zanjan prov., Gilvan, 700-1000m, 16.5.2002, leg. Bostanchi	AM418417
W8034	Euchloe	Euchloe	tagis	granadensis	RIBBE, 1910	Spain, prov. Andalusia, 15km N San Pedro, road to Ronda, 17.4.2001, leg. W. Back	AM418418
WB035	Euchloe	Elphinstonia	charlonia	charlonia	(DONZEL, 1842)	Maroc, Anti-Allas oriental, Tizi-n-Ounzour, djebel Bani, S Agadir-Melloul, 1800-2000m, leg. M. Tarrier	AM418419
WB039	Euchloe	Elphinstonia	lucilla	lucilla	BUTLER, 1886	E Afghanistan, Ghanikhel area, app. 1000m. 14.3.1975, leg. M. Dietz	AM418420
WB050	Euchloe	Elphinstonia	lessei	gohrudicus	BACK & LEESTMANS, 2001	Iran, E Isfahan, Zefre, Wadar-Zefre, Mi. Qohrud 2800m, 21 5.2001, leg. W. Back	AM418421
WB090	Euchloe	Elphinstonia	lessei	zagrosicus	LEESTMANS & BACK, 1992	Iran, Dorud, Lorestan, 6.6.2000, 2700m, leg. Jiri Klir	AM418422
WB091	Euchloe	Elphinstonia	lessei	lessei	BERNARDI, 1957	iran, Dizin, 3000-3200m, 17.6.2004, leg. A. R. Naderi	AM418423

Materials and methods

Table 1: List of specimens and EMBL/GenBank accession numbers

Insect material:

Taxa selection was focused on the Eurasian species of the subgenus *Elphinstonia* (Table 1/ colour plate 13 on p. 515, Figs 1-24; Figure 25). Specimens were taken out of the private collection of WERNER BACK, Freising, Germany (pcWBFS). Samples were stored in pure alcohol, dried or pinned and dried. In some cases, relaxation of wings by the use of a humidity box was applied to specimens before setting. In most cases, three legs were used for further treatment.

DNA extraction, amplification and sequencing

The extraction of sample DNA, amplification and sequencing was performed by kmbs (www.kmbioservices.de). Ground insect tissue was used for the proteinase K procedure with DNeasy tissue kit (OIAGEN), following the manufacturer's protocol for animal tissues with slight modifications. Digestion was performed for 12 hours. Then, DNA was eluted with molecular biology grade water (EPPENDORF). Prior to sequencing, the DNA concentration was measured using a fluorometer (BioRad, VersaFluorTM) and adjusted to 50 ng/ul with molecular biology grade water. Mitochondrial (mtDNA) cytochrome c oxidase subunit I (COI) gene was amplified by PCR (PTC 220 DYAD thermocycler (MJ Research)) using protocols and primers as in SIMON et al. (1994). After generation of some template sequences, primers were designed for *Elphinstonia* species; Forward primer mtD7Pier-kmbs; 5'-CGW ATA AAT'AAT ATA AGW TTT TG-3', reverse primer mtD9Pier-kmbs: 5'-AAT GAW GTA TTA AGA TTA CGA T-3' (BACK et al. 2006). Direct sequencing of dve-labelled templates (BigDye V 1.1, Applied Biosystems) was carried out using an ABI 377 automated sequencer (Applied Biosystems). Single strand sequences were used in both directions to generate a consensus sequence for mismatch detection using Sequence Navigator V 1.0.1 (Perkin Elmer). The sequences were aligned to the reference sequence of *Pieris napi* (LINNAEUS, 1758) (Lepidoptera: Pieridae) (EBI accession number AF170861), see Table 2. The new sequences are deposited at EBI/GenBank. The accession numbers are shown in Table 1.

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AF170861 Pieris nani
WB010 Euchloe ausonia
WB034 Euchloe tagis
WB035 E. charlonia charlonia
WB002 E. charlonia charlonia
WB026 E. charlonia charlonia
WB005 E. bazae iberae
WB011 E. bazae bazae
WB012 E. bazae bazae
WB029 E. bazae bazae
WB039 E. lucilla lucilla
WB015 E. transcaspica amseli
WB032 E. transcaspica amseli
WB004 E. penia taleschicus
WB033 E. penia taleschicus
WB018 E. penia thessalica
WB030 E. penia thessalica
WB031 E. penia thessalica
WB021 E. tomyris tomyris
WB003 E. lessei qohrudicus
WB009 E. lessei qohrudicus
WB050 E. lessei qohrudicus
WB090 E. lessei zagrosicus
WB091 E. lessei lessei
WB014 E. ziayani ziayani
WB013 E. ziayani ziayani
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AF1708	861	Pieris napi
WB010	Euc	chloe ausonia
WB034	Euc	chloe tagis
WB035	E.	charlonia charlonia
WB002	Ε.	charlonía charlonia
WB026	Ε.	charlonia charlonia
WB005	Ε.	bazae iberae
WB011	Е.	bazae bazae
WH012	Ε.	bazae bazae
WR029	Ε.	bazae bazae
WH039	E.	lucilla lucilla
WB015	Ε.	transcaspica amseli
WB0.32	Ε.	transcaspica amseli
WH004	E.	penia taleschicus
100033	E	penia taleschicus
WB018	Ε.	penia thessalica
WB030	Ε.	penia thessalica
WB031	E	penia thessalica
wp021	E	tomyris tomyris
WD0011	Ē	lessei gohrudicus
10000	£.	lessei gohrudicus
10050	F.	lessei cohrudicus
VID030	£.	lessei marceicus
10001	£.	lessei loccoi
10014	- -	ziawani ziawani
10013	5.	ziayani ziayani
WB015	5	ziayani ziayani
AF170	861	Pieris napi
AF170 WB010	861 Euc	Pieris napi chloe ausonia
AF1704 WB010 WB034	861 Euc	Pieris napi chloe ausonia chloe tagis
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AF1704 WB010 WB034 WB035 WB002 WB026 WB005 WB011 WB012	861 Euc E. E. E. E. E.	Pieris napi chloe ausonia checonia charlonia charlonia charlonia charlonia charlonia charlonia bazae iberae bazae bazae bazae bazae
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AF1701 WB010 WB034 WB035 WB022 WB029 WB032 WB032 WB032 WB033 WB033 WB018 WB033 WB018 WB030 WB030 WB090 WB090 WB090 WB091	86100.2020日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日,1995日	Pieris napi chloe ausonis charlonia charlonia charlonia charlonia charlonia charlonia charlonia charlonia bazae bazae bazae bazae bazae bazae bazae bazae bazae baz
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AF170861 Pieris napi	tagaaatata	tcttttgatc	aaataccatt	atttgtatga	tcagtaggaa	ttactgcttt	acttttactt	
WB010 Euchloe ausonia	AT.	A.	TC .	тт.	G.CT.	.AA	.T.A.	
WB034 Euchloe tagis	.AT.	.c	T	.т.	G.	.A	.T.A.	
WB035 E. charlonia charlonia	. AT .	.A.	. TC .	ТТ.	G.TT		.T.AC.T	
WB002 E. charlonia charlonia	.AT.	.A.	.TC.	тт.	G.TT.		.T.AC.T.	
WB026 E. charlonia charlonia	. AT .	.A.	TC,	тт	G.TT.		.T.AC.T.	
WB005 E. bazae iberae	.AT	A.	.TC.	ТТ.	G.TT.		.T.AC.T.	
WB011 E. bazae bazae	AT.	.A.	TC.	ТТ.	G.TT.		.T.AC.T.	
WB012 E. bazae bazae	AT	A	TC.	ТТ.	G.TT.		.T.AC.T	
WB029 E. bazae bazae	. AT .	A.	.TC.	тт.	G.TT		.T.AC.T	
WB039 E. lucilla lucilla	.AT	A	. TC .	ΤΤ.	G.TT.		.T.AC.T	
WB015 E. transcaspica amseli	AT .	.G.	, TC .	тт.	G.T. T.		.T.AC.T	
WB032 E. transcaspica amseli	.AT.	.G.	. TC .	ТТ.	G.TT.		.T.AC.T.	
WB004 E. penia taleschicus	. AT .	.A	.TC.	тт.	G.TT.		GC.T	
WB033 E. penia taleschicus	. AT .	A.	.TC.	ТТ.	G.TT		.GC.T.	
WB018 E. penia thessalica	AT.	.A.	. TC .	тт.	G.TT.		.GC.T.	
WB030 E. penia thessalica	AT .	A.	. TC .	тт	G.TT		GC.T.	
WB031 E. penia thessalica	AT .	.A.:.	. TC .	тт	G.TT.		GC.T	

WB021 E.	tomyris tomyris
WB003 E.	lessei qohrudicus
WB009 E.	lessei qohrudicus
WB050 E.	lessei qohrudicus
WB090 E.	lessei zagrosicus
WB091 E.	lessei lessei
WB014 E.	ziayani ziayani
WB013 E.	ziayani ziayani

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T.A.	. T	Τ.Α.	.AT.	.т.	
Т.А.	. T	Т.А.	.AT.	.т.	
T,A.	. т	Т.А.	. A T.	т.	
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T.A.	. т	T.A.	ТGТ.	.c.	
T.A.	. т	T.A.	ТТ.	.c.	
T.A.	. C	Т.А.	ТАТ.	.T.	
A	.c	Τ.Α.	ТАТ.	. T .	
A.	. C	Т.А.	ТАТ.	. T .	
T.A.	. T	Т.А.	ТА Т.	.C.	
T.A.	. т	Т.А.	ТА Т.	.c.	
Т.А	. T	Т.А	ТАТ.	.C.	
T.A.	. T	Т.А.	ТАТ.	.C,	
T.A.	. T	Τ.Α.	TAT.	.CG.	
T.A.	. T	Т.А.	. Т.	.c.	
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Table 2: Mitochondrial DNA sequences including a 326bp sequence of the cytochrome c oxidase subunit I gene (COI) of the analysed specimens of *Elphinstonia* (WB-numbers) and sequences found in GenBank (remaining numbers).

Sequence Data analysis

For the different analyses 326 basepairs of a homologous fragment of the mitochondrial DNA sequences of the taxa shown in table 1 were used (for sequence data see table 2).

The pairwise genetic distances (Table 3) were calculated using PAUP* software (Phylogenetic Analysis Using Parsimony 4.0 β 10 version, Swofford, 2003).

To infer the phylogenetic relationships among the taxa we executed maximum parsimony (MP) and maximum likelihood (ML) method using PAUP*, *Pieris napi* (L.) was used as outgroup taxon. MP was conducted using the heuristic search option with branch swapping by tree bisection and reconnection (TBR) on 10,000 starting trees with random stepwise addition sequences. Ten replicates were performed within each heuristic search. The ML analysis requires a specific model of sequence evolution to be specified a priori. In order to select the substitution model that describes our data best, sequences were analysed with Modeltest v.3.7 (POSADA & CRANDALL 1998). ML was performed with the heuristic search option, branch swapping by tree bisection and reconnection (TBR) and random stepwise addition sequences by the use of the optimal model defined by Modeltest.

To assess the robustness of relationships, 2,000 bootstrap replications (and 25 random addition sequence replicates for each bootstrap replicate) were performed for MP and 100 for the ML analysis.

Results

Sequence characteristics:

Sequences characteristics show the typical A/T bias known for insect sequences. Base frequencies are 0.2977 A, 0.1605 C, 0.1252 G, 0.4166 T.

Within the complete dataset, including *Pieris napi* (L.), 83 variable positions could be detected (parsimony-informative positions: 61). Within *Elphinstonia* samples 63 positions (parsimony-informative positions: 53) were variable.

DNA sequence divergence

Interspecific genetic differences:

The uncorrected ("p") distance matrix is shown in Table 3. As expected, the outgroup taxon *Pieris napi* (L.) shows rather high a constant genetic distances to the species of *Elphinstonia* ranging between 13.80 % and 15.95 %. *Euchloe tagis* (HÜBNER, 1804) and *Euchloe ausonia* (HÜBNER, 1804) show values of genetic distances to the species of *Elphinstonia* of 7.97 - 11.96 % and 9.55 - 11.35 % respectively.

Within *Elphinstonia* the species show values of interspecific sequence divergence ranging from **1.84**% to **11.04**%. Values below 5% have been found for the species pair groups *P. transcaspical P. penia* (**2.45-3.39**%), *P. lucilla*/*P. penia* (**3.07-3.70**%), *P. lucilla*/*P. transcaspica* (**1.84-2.15**%) and *P. ziayani*/*P. lessei* (**3.68-4.29**%). The interspecific genetic distances between these pair groups are relatively low. The degree of separation of these species will be discussed.

Intraspecific genetic differences

In almost all instances the intraspecific genetic differences between individuals of *Elphinstonia*, including described subspecies, are considerably smaller than the interspecific differences: *E. charlonia*: **0.00-0.31** %; *E. bazae*: **0.00-0.61** %; *E. transcaspica*: **0.31** %; *E. penia*: **0.00-0.61** %; *E. lessei*: **0.00-1.84** %; *E. ziayani*: **0.31** % (Table 3).

Uncorrected ("p") distance

					1	2	3	4	5	6
	Pieri	s.n	api							
	WB010	Eu	chlo	oe ausonia	0.14110					
	WB034	Eυ	chlo	oe tagis	0.11656	0.10123				
4	WB035	Ε.	с.	charlonia	0.15031	0.09509	0.07975			
5	WB002	Ε.	с.	charlonia	0.15031	0.09509	0.07975	0.00307		
6	WB026	Е.	с.	charlonia	0.15079	0.09552	0.08014	0.00313	0.00000	
7	WB005	Ε.	b.	iberae	0.15337	0.10429	0.08282	0.04908	0.05215	0.05256
	WB011	Ε.	b.	bazae	0.15337	0.10429	0.08589	0.05215	0.05521	0.05567
	WB012	Ε.	b.	bazae	0.15337	0.10429	0.08589	0.05215	0.05521	0.05567
10	WB029	E.	b.	bazae	0.15644	0.10736	0.08896	0.05521	0.05828	0.05874
1	WB039	Е.	1.	lucilla	0.13804	0.09509	0.07975	0.05521	0.05215	0.05242
12	WB015	Ε.	t.	amseli	0.14110	0.10429	0.08282	0.05521	0.05215	0.05237

13	WB032	Ε.	t.	amseli	0.14417	0.10429	0.08589	0 05828	0 05521	0 05544
14	WB004	E.	р.	taleschicus	0.14110	0.10736	0.09202	0.05215	0.05521	0.05554
15	WB033	Ε.	г. D.	taleschicus	0.14110	0.10736	0.09202	0.05215	0.05521	0.05554
16	WB018	Ε.	р.	thessalica	0.14110	0.10736	0.09202	0.05215	0.05521	0.05554
17	WB030	Е.	р.	thessalica	0.14417	0.11043	0.09509	0.05521	0.05828	0.05862
18	WB031	Ε.	р.	thessalica	0.14767	0.11393	0.09854	0.05840	0.06147	0.06154
19	WB021	Ε.	t.	tomvris	0.14417	0.09816	0.10429	0.07975	0.08282	0.08338
20	WB003	Ē.	1.	gohrudicus	0.15951	0.11350	0.11963	0.09509	0.09816	0.09880
21	WB009	Е.	î.	gohrudicus	0.16258	0.11350	0.11656	0.09202	0.09509	0.09570
22	WB050	Ε.	1.	gohrudicus	0.15644	0.11043	0.11350	0.08896	0.09202	0.09267
23	WB090	Ε.	1.	zagrosicus	0.15644	0.11043	0.11350	0.08896	0.09202	0.09267
24	WB091	E.	1.	lessei	0.15951	0.11350	0.11656	0.09202	0.09509	0.09574
25	WB014	Ε.	z .	ziavani	0.15644	0.10736	0.10123	0.08282	0.08589	0.08641
26	WB013	Ε.	z.	ziayani	0.15644	0.10429	0.09816	0.07975	0.08282	0.08330
Unco	orrecte	ed	("p'	") distance ma	atrix (cor	tinued)				
_						8	9			
7	WB005	Ε.	b.	iberae						
8	WB011	Е.	ь.	bazae	0.00307					
9	WB012	Ε.	b.	bazae	0.00307	0.00000				
10	WB029	Ε.	ь.	bazae	0.00613	0.00307	0.00307			
11	WB039	Е.	1.	lucilia	0.05521	0.05521	0.05521	0.05828		
12	WB015	Е.	τ.	amsell	0.06135	0.06135	0.06135	0.06442	0.01840	0 00007
13	WB032	Е.	t.	amsell	0.06442	0.06442	0.06442	0.06748	0.0214/	0.00307
14	WB004	Ε.	p۰	taleschicus	0.05521	0.05521	0.05521	0.05828	0.03067	0.02454
15	WB033	Е.	p۰	taleschicus	0.05521	0.05521	0.05521	0.05828	0.03067	0.02454
16	WB018	Ε.	p.	thessalica	0.05521	0.05521	0.05521	0.05828	0.03067	0.02454
17	WB030	Ε.	p.	thessalica	0.05828	0.05828	0.05828	0.06135	0.03374	0.02761
18	WB031	Ε.	p.	thessalica	0.06166	0.06171	0.06171	0.06478	0.03703	0.03079
19	WB021	Е.	t.	tomyris	0.08589	0.08896	0.08896	0.09202	0.09509	0.10123
20	WB003	Ε.	1.	qohrudicus	0.10736	0.11043	0.11043	0.11350	0.10736	0.10736
21	WB009	Ε.	1.	qohrudicus	0.10736	0.11043	0.11043	0.11350	0.10429	0.10429
22	WB050	Ε.	1.	qohrudicus	0.10736	0.11043	0.11043	0.11350	0.10123	0.10123
23	WB090	Е.	1.	zagrosicus	0.10736	0.11043	0.11043	0.11350	0.10123	0.10123
24	WB091	Е.	1.	lessei	0.11043	0.11350	0.11350	0.11656	0.10429	0.10429
25	WB014	Ε.	z.	ziayani	0.09816	0.10123	0.10123	0.10429	0.09202	0.09202
26	WB013	ь.	z.	ziayani	0.10123	0.10429	0.10429	0.10/36	0.08896	0.08896
Unco	orrecte	ed	("p'	") distance ma	atrix (cor	tinued)				
										10
12	60000	F		ameeli	13			16	2	16
13	WB032	E.		amseil	0 02761					
14	WB004	E.		taleschicus	0.02761	0 00000				
10	WB033	с. т		theorealice	0.02761	0.00000	0 00000			
10	WB018	E.		thessalica	0.02761	0.00000	0.00000	0 00307		
10	WB030	ь. г		thessalica	0.03087	0.00307	0.00307	0.00307	0 00020	
10	MB031	E		tomuric	0.03380	0.00613	0.00613	0.00613	0.00920	0 10162
19	WB021	E.		comyris	0.10423	0.09309	0.09509	0.09509	0.09818	0.10163
20	WB003	Е.		qonrudicus	0.11043	0.10/36	0.10/36	0.10/36	0.11043	0.10/91
21	WB009	E.		qonfudicus	0.10/36	0.10429	0.10429	0.10429	0.10736	0.10480
22	WB050	Е.		qonrudicus	0.10429	0.10123	0.10123	0.10123	0.10429	0.10791
23	WB090	Е.		zagrosicus	0.10429	0.10123	0.10123	0.10123	0.10429	0.10/91
24	WB091	Е.		lessei	0.10/36	0.10429	0.10429	0.10429	0.10736	0.11097
25	WB014	Е.		ziayani	0.09202	0.08589	0.08589	0.08589	0.08896	0.09239
26	WB013	Е.		ziayani	0.08896	0.08896	0.08896	0.08896	0.09202	0.09546
Unco	orrecte	ed	("p'	") distance ma	atrix (cor	tinued)				
							21		2.3	
19	WB021	Ε.		tomyris					20	
20	WB003	Ε.		gohrudicus	0.07362					
21	WB009	Ε.		gohrudicus	0.07669	0.00920				
22	WB050	Е,		gohrudicus	0.07055	0.00613	0.01534			
23	WB090	Ε.		zagrosicus	0.07055	0.00613	0.01534	0.00000		
24	WB091	Е.		lessei	0.07362	0.00920	0.01840	0.00307	0.00307	
25	WB014	Е.		ziayani	0.06442	0.04294	0.04294	0.03681	0.03681	0.03988
26	WB013	Е.		ziayani	0.06748	0.03989	0.03988	0.03374	0.03374	0.03681

Uncorrected (...p") distance matrix (continued)

25 WB014 E. ziayani 26 WB013 E. ziayani 0.00307

Table 3. Interspecific pairwise sequence distance matrix of *Elphinstonia* (*E.*) species, *Euchloe tagis* HBN. and *E. ausonia* HBN., and *Pieris napi* (L.). 326 base pairs of the mitochondrial DNA sequences shown in Table 2 were used to calculate the uncorrected ("p") distances.

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Phylogenetic analysis

The MP analysis resulted in two most parsimonious trees (length = 161 steps, CI = 0.69, RI = 0.86) with equal topology. The best fit model under the "Akaike Information Criterion" (AIC) was the general time reversible model, with 6 rate classes, unequal base frequencies and a proportion of invariable sites (GTR+I+G).

The best fit ML model (GTR+I+G) contained the nucleotide substitution rate parameters: [A-C] = 2.0282, [A-G] = 7.3571, [A-T] = 5.2997, [C-G] = 0.0000, [C-T] = 17.0999, [G-T] = 1.0000. The estimated nucleotide frequencies were A = 0.2977, C = 0.1605, G = 0.1252 and T = 0.4166. The proportion of invariable sites (I) was 0.6384. This model of sequence

evolution supports one best tree (-lnL = 1216.9261). Both of the phylogeny reconstruction methods resolved the species entities with high bootstrap support values (Fig. 26). The *Elphinstonia* species *E. charlonia* (DONZEL), *E. bazae* FABIANO, *E. transcaspica* STGR., *E. penia* (FREYER), *E. lessei* BERNARDI, and *E. ziayani* BACK, OLIVARES & LEESTMANS which are represented by more than one individual show monophyly with high support (bootstrap values: 89/84-100/99 MP/ML). At the taxonomic subspecies level there was no phylogenetic signal detectable, with one exception: *E. b. bazae* FABIANO and *E. b. iberae* BACK, OLIVARES & LEESTMANS seem to be on their way to foster their genetic integrity as we detected a weak support for their sistergroup relationship (ML bootstrap 60).

In both calculations (ML and MP) the species were equally arranged into two groups namely the "tomyris-group" (E. tomyris CHRISTOPH, E. lessei BERNARDI and E. ziayani BACK, OLIVARES & LEESTMANS) and in the "charlonia-group" [E. charlonia (DONZEL), E. bazae FABIANO, E. lucilla BTL., E. transcaspica STGR. and E. penia (FREYER)] (Fig. 26). Whereas monophyly of the former is high supported in both analysis (bootstrap values: 89/80 MP/ML), the latter gets weaker support especially from the ML analysis (bootstrap values: 82/52 MP/ML).

In the MP tree the subgenus *Elphinstonia* KLOTS appears monophyletic (bootstrap value: 73, Fig. 26). In the ML tree *E. ausonia* HBN. appears as sister taxon to the "*charlonia*-group" but there is no bootstrap support for this sistergroup relationship. The MP tree defines *Euchloe tagis* HBN. to be the sister taxon of *Elphinstonia*-group. In this case the bootstrap support is barely over 50. Therefore the question of the sistergroup of the subgenus *Elphinstonia* KLOTS cannot be clarified with our phylogenetic data analysis.

Discussion

The subgenus *Elphinstonia* species investigated within this molecular study form a monophyletic group clearly separated from the subgenus *Euchloe* species, i. e. *Euchloe ausonia* HBN. and *Euchloe tagis* HBN., that served as outgroup taxa. There is a clearly supported division of the subgenus *Elphinstonia* KLOTS into the *"charlonia*-group" and the *"tomyris*-group"

The "*charlonia*-group" is comprised of *E. charlonia* (DONZEL), *E. transcaspica* STGR., *E. lucilla* BTL., *E. bazae* FABIANO, and *E. penia* (FREYER). Previously because of its ecological position and its phenootype, *E. penia* (FREYER) had been considered a member of the

"tomyris-group". E. penia (FREYER) is widespread in the Black Sea region and inhabits sites with dense vegetation that include its larval hosts, *Matthiola* R. BR. species, Brassicaceae. The larvae and pupae of this species differ from those of *E. charlonia* (DONZEL), *E. bazae* FABIANO, and *E. transcaspica* STGR., species found in steppe and desert habitats (BACK 1991b, OLIVARES & JIMENEZ GOMEZ 1996). Because the early stages of *E. tomyris* CHRISTOPH, *E. lessei* BERNARDI and *E. ziayani* LEESTMANS & BACK are unknown, their complete assessment must be postponed. Of critical significance is the fact that *E. charlonia* (DONZEL) and *E. penia* (FREYER) are sympatric at the edges of their distributions (J. ad Duruz, S. Syria). Our data shows no evidence of hybridisation and supports the two species' separation.

The validity of the species *E. charlonia* (DONZEL), *E. bazae* FABIANO, and *E. transcaspica* STGR., respectively, as proposed by the first author (BACK, 1991b) by the investigations of interbreeding experiments, is supported by our molecular analysis. This is especially notable for *E. bazae* FABIANO (OLIVARES & JIMENEZ GOMEZ, 1996), which is more closely related to *E. transcaspica* STGR. and *E. penia* (FREYER) than it is to *E. charlonia* (DONZEL) (PÉREZ DE GREGORIO et al., 1992; PÉREZ DE GREGORIO, 1994). The subspecific rank of the newly described *E. bazae iberae* BACK, OLIVARES & LEESTMANS, 2005 is also confirmed by molecular analysis. The widely disjunct distributions of *E. bazae* 's Baza and Zaragoza populations has led to an interruption of gene flow and to isolated independent gene pools.

When we consider *E. charlonia* (DONZEL) our data indicates only negligible genetic difference between the butterflies at Lanzarote and Egypt (border with Sudan). Slightly more genetic differentiation is displayed by the population sample from the Antiatlas (> 2000 m NN) in Morocco. Nonetheless, there is little evidence to indicate the incipient speciation of this high elevation population.

Another point brought out by our data analysis is the relative close genetic relationship among *E. transcaspica* STGR. and *E. lucilla* BTL. despite their clear phenotypic separation. However, as had been proposed by BUTLER (1886), the validity of the species rank is confirmed by genetic analysis.

There was no genetic differentiation between *E. penia thessalica* MEZGER, 1936, a yellow butterfly, and *E. penia taleschicus* BACK & LEESTMANS, 2001, a whitish butterfly, despite their apparent color differences. This points out the problem of overweighting the importance of such "soft" character states when used as the basis for systematic classification or for species separation. Despite this, the subspecific recognition of the whitish populations of *E. penia taleschicus* BACK & LEESTMANS is justifiable because of the stability of this trait (BACK & LEESTMANS, 2001b).

Within the "tomyris-group", the discreteness of the three species *E. tomyris* CHRISTOPH, *E. lessei* BERNARDI, and *E. ziayani* LEESTMANS & BACK, respectively, is confirmed. *E. tomyris* CHRISTOPH is the basal sister taxon to *E. lessei* BERNARDI and *E. ziayani* LEESTMANS & BACK – which had been proposed based on phenotypic characters. There was an unexspectedly large amount of heterogeneous genetic variability between populations of *E. lessei qohrudicus* BACK & LEESTMANS, 2001a.

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Figure 25. Distribution of species and subspecies of Elphinstonia (E.)



Figure 26. Phylogenetic tree of *Elphinstonia* species and subspecies, two *Euchloe* taxa and one outgroup. The tree (length 161 steps, CI 0.69, RI 0.86) derived from a maximum parsimony analysis of the COI sequence data shown in Table 2. Maximum parsimony Bootstrap values > 50 % are shown above or below branches (2000 replications). Bootstrap values using ML distance setting > 50 % (100 replications) are shown below the MP bootstrap values.

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Abb. 1: Nordgriechenland: Der Kerkini-See (A), südwestliche Uferregion (70 m) im Strimonas-Flußtal, eingebettet zwischen dem Kerkini-Grenzgebirge (bis 2031 m) zu Bulgarien im Norden, dem Disoro-Gebirge (bis 767 m) im Westen und dem Mavrovouni-Gebirge (bis 1179 m) im Süden. Foto: 2.VII.1995. Fundort von u. a.: *Colobochyla salicalis* D. & S. (7), *Dysgonia torrida* GN. (35), *Heliothis maritima bulgarica* DRAUDT (137), *Pyrrhia umbra* HUFN. (142), *Eucarta amethystina* HBN. (185), *Cosmia pyralina* D. & S. (190).

Abb. 2: Nordgriechenland: Südwest-Ausläufer des Vermio-Gebirges östlich Kozani, Zentral-Makedonia, in der Nähe des Dorfes Kilada (D), 700 m. Foto: 10.V.2000. Fundort von u. a.: *Gonospileia triquetra* D. & S. (51), *Agrochola wautieri* DUFAY (197), *Agrochola osthelderi* BRSN. (199), *Episema glaucina* ESP. (203), *Episema lederi* CHRISTOPH (205), *Noctua orbona* HUFN. (288).

Abb. 3: Nordgriechenland: Östlicher Katara-Pass im Pindos-Gebirge, nordwestliches Thessalia, 30 km westlich Kalambaka. Blick über das Malakassiatiko-Flusstal auf einen Südhang mit dem Dorf Trigona (H), 750 m. Foto: 29.VI.1996. Fundort von u. a.: *Cryphia amygdalina* BRSN. (74), *Pyrrhia umbra* HUFN. (142), *Pyrrhia purpurina* ESP. (143), *Paradrina wullschlegeli schwingenschussi* BRSN. (156), *Eremodrina pertinax* STGR. (158), *Lithophane ledereri* STGR. (209), *Nonagria typhae* THNBG. (235), *Leucania herrichi* H.-S. (264), *Noctua janthe* BKH. (294), *Noctua haywardi* TAMS (297).

Abb. 4: Mittelgriechenland: Das Pargas-Gebirge (im Süden bis 927 m) erstreckt sich entlang der nördlichen Ipiros-Küste von Igoumenitsa über etwa 60 km bis Parga. Hier ein für die Umgebung Plataria typischer Süd-Osthang (J). Foto: 24.VI.1997. Fundort von u. a.: *Protodeltote pygarga* HUFN. (87), *Trichoplusia circumscripta* FRR. (103), *Spodoptera cilium* GN. (167), *Spodoptera littoralis* Bsd. (168).

Abb. 5: Mittelgriechenland: Ionische Insel Lefkada, südliche Küstenregion bei Evgiros (IS-W), bis 450 m. Foto: 24. Mai 2000. Fundort von u. a.: *Nycteola siculana* FUCHS (57), *Spodoptera cilium latebrosa* LED. (167), *Spodoptera littoralis* BSD. (168).

Abb. 6: Mittelgriechenland: Halbinsel Pilion. Region östlich Visitsa (M), bis 650 m. Macchie mit u. a. *Spartium junceum* (Pfriemenginster), *Arbutus* (Erdbeerbaum) und *Cotinus coggygria* (Perückenstrauch). Foto: 18.V.1999. Fundort von u. a.: *Calophasia opalina* Esp. (118), *Xanthia aurago* D. & S. (194), *Dryobotodes tenebrosa* Esp. (213), *Nonagria typhae* THNBG. (235), *Noctua janthe* BKH. (294), *Noctua haywardi* TAMS (297). Fotos: PIATKOWSKI.



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Abb. 1: Mittelgriechenland: Das Kaliakouda-Gebirge (bis 2100 m), Umgebung Karpenissi, südlich Mega Hori (N). Foto: 27.V.1999. Fundort von u. a.: *Catocala promissa* D. & S. (19), *Cryphia amygdalina* BRSN. (74), *Polyphaenis subsericata* H.-S. (176), *Agrochola gratiosa* STGR. (200), *Apamea anceps* D. & S. (225), *Apamea sordens* HUFN. (226), *Lacanobia contigua* D. & S. (244), *Lacanobia suasa* D. & S. (245), *Noctua interposita* HBN. (289).

Abb. 2: Mittelgriechenland: Arahova (P), 1150 m, Parnassos-Südhang, Sterea Ellada. Foto: 19.IX.2001. Fundort von u. a.: Cryphia maeonis LeD. (81), *Cornutiplusia circumflexa* L. (100), *Cucullia blattariae* Esp. (110) Raupen und Imagines, *Omphalophana antirrhinii* HBN. (118), *Spodoptera littoralis* BsD. (168), *Episema korsakovi* CHRISTOPH (206), *Leucania obsoleta* HBN. (262), *Ochropleura flammatra* D. & S. (284).

Abb. 3: Mittelgriechenland: Uferregion des Vouliakmeni-Sees (P), 0-30 m, am Kap Ireo, nordwestlich Korinthos und Loutraki. Foto: 7.VI.2005. Fundort von u. a.: *Lophoterges hoerhammeri* F. WAGNER (123).

Abb. 4: Südgriechenland: Dimitsana (S) im Zentral-Peloponnes westlich Tripoli (1000 m). Foto: 22.VII.2002. Fundort von u. a.: *Hadena filigrama* Esp. (255), *Hadena syriaca* OSTHLD. (258).

Abb. 5: Südgriechenland: Südöstliche Ausläufer des Lakonia-Gebirges im südöstlichen Peloponnes. Südhang mit *Euphorbia dendroides* nördlich Monemvasia (T). Foto: 22.V. 2003. Fundort von u. a.: *Ophiusa tirhaca* CR. (33), *Amephana dalmatica* RBL. (124).

Abb. 6: Südgriechenland: Halbinsel Mani in der Mitte des südlichen Peloponnes, Sangias-Gebirge (bis 1075 m), ein Ausläufer des Taigetos, Region südlich Vathia (T). Foto: 25.V.2003. Fundort von u. a.: *Ophiusa tirhaca* CR. (33), *Prodotis stolida* F. (37), *Odice suava* HBN. (89), *Trichoplusia circumscripta* FRR. (103), *Copiphana lunaki moreana* THURNER. (121), *Oria musculosa* HBN. (237). Fotos: PIATKOWSKI.



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Bei den Farbtafeln 3-6 verweisen die Zahlen in Klammern hinter den Artnamen auf die Numerierung der Arten im systematischen Teil, dort weitere Anmerkungen im Text.

Abb. 1: Habitat von *Cucullia verbasci* L. mit *Verbascum sinuatum, V. undulatum* und *V. longifolium*. Vatolakos (C), 800 m, 16 km N Grevena, Makedonia. Foto: 25.V.2005.

Abb. 2: Habitat von *Cucullia verbasci* L. mit *Verbascum densiflorum (thapsiforme)*. Agiokambos (E), 20 m, 50 km E Larissa, Ossa-SE, Thessalia. Foto: 2VI.2005.

Abb. 3: *Cucullia verbasci* L. (114). Erwachsene Raupen. Links: (lateral) an *Verbascum densiflorum*. Agiokambos (E), 20 m, 50 km E Larissa, Ossa-SE, Thessalia, 2.VI.2005. Rechts: (dorsal) an *V. sinuatum*. Vatolakos (C), 800 m, 16 km N Grevena, Makedonia, 25.V.2005.

Abb. 4: Habitat von *Cucullia verbasci* L. und *Cucullia thapsiphaga* TR. Ossa-Gebirge (bis 1272 m). Osthang bei Agiokambos, südlich Koutsoupia (E). Foto: 16.V.2000.

Abb. 5: *Cucullia verbasci* L. (114). Erwachsene Raupe (lateral, dorsal) an *V. sinuatum*. Vatolakos (C), 800 m, 16 km N Grevena, Makedonia, 25.V.2005.

Abb. 6: Habitat von *Cucullia verbasci* L. Timfristos-Gebirge (bis 2104 m) nordwestlich Karpenissi (N). Foto: 7.VI.1998.

Abb. 7: *Cucullia verbasci* L. (114). Erwachsene Raupen an *V. densiflorum*. Links: (lateral) Karpenissi (N), 1000 m, Timfristos, Sterea Ellada-NW, 7.VI.1998. Rechts: (dorsal) Asprangeli (G), 1100 m, Vikos-Schlucht, Ipiros-NE, 10.VI.1996. Fotos: PIATKOWSKI. Alle Raupenabbildungen sind Freilandaufnahmen.



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Abb. 1: Habitat von *Cucullia thapsiphaga-*, *C. verbasci-* und *C. blattariae-*Raupen. Koukouli 2 km W (G), 950 m, östlich Asprangeli, Mitsikeli-Gebirge, Vikos-Schlucht, Ipiros-NE. Foto: 4.VI.1997.

Abb. 2: *Cucullia thapsiphaga* TR. (112). Erwachsene Raupen (lateral, dorsal) an *Verbascum lychnitis*. Koukouli 2 km W (G), 950 m, Vikos-Schlucht, Ipiros-NE, 11.VII.2004.

Abb. 3: Habitat von *Cucullia blattariae* Esp. Südliches Mittelgriechenland. Hochebene im südlichen Parnassos bei Desfina (P), 900 m, südlich Arahova, am nördlichen Golf von Korinth. Foto: 20.V. 2000.

Abb. 4: *Cucullia blattariae* Esp. (110). Erwachsene Raupe (dorsolateral) an *Scrophularia canina* und Kokons. Arahova (P), 1150 m, Parnassos, Sterea Ellada, 23.V.1999.

Abb. 5: Habitat von Cucullia lychnitis RBR. Pilio 3 km W (Q), 150 m, Insel Evia-Nord, Sterea Ellada-NE. Foto: 5.VII.2004.

Abb. 6: *Cucullia lychnitis* RBR. (113). Erwachsene Raupen (lateral, dorsal) an Verbascum lychnitis und Kokon. Pilio 3 km W (Q), 150 m, Insel Evia-Nord, 5.VII.2004. Fotos: PIATKOWSKI. Alle Raupenabbildungen sind Freilandaufnahmen.



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Abb. 1-4: *Simyra nervosa* D. & S. (72). Abb. 1 und 2: Raupen vor und nach der letzten Häutung an *Euphorbia*-Blüten, -Blättern und -Stielen. Platanakia (A), 340 m, 75 km W Serres, 15 km W Kerkini-See, Makedonia-NE, 24.V.1998.

Abb. 3: Junge Raupen. Katara-Pass-E (H), 1700 m, 60 km W Kalambaka, Pindos, Thessalia-W. 24.VI.1992. Kokon aus Platanakia (wie Abb. 1 u. 2).

Abb. 4: Erwachsene Raupen (lateral, dorsolateral). Eptalofos (G), 800 m, 60 km SW Kastoria, Pindos-NE, Makedonia-W, 12.VI.1996.

Abb. 5: *Acronicta euphorbiae* D. & S. (68). Kokon und erwachsene Raupe (dorsolateral, ventral) an *Trifolium* (!). Neo Dermati (N), 700 m, 15 km S Karpenissi, Kaliakouda-NE, Sterea Ellada-NW, 5.VI.1998.

Abb. 6: *Apopestes spectrum* Esp. (42). Kokon und erwachsene Raupen. Links: (dorsolateral) Kalamaki (M), 450 m, 40 km SE Volos, Halbinsel Pilio-E, Thessalia-SE, 19.V.1999. Rechts: (dorsolateral) Davlia (P), 30 km NW Livadia, Parnassos-E-Ausläufer, Sterea Ellada-S-Mitte, 20.V.2000. Fotos: PIATKOWSKI. Alle Raupenabbildungen sind Freilandaufnahmen.



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Abb. 1–6: *Euclidia glyphica* L. (50). Die Individuen der griechischen Populationen (Abb. 1-4) sind gegenüber denen der mitteleuropäischen (Abb. 5, 6) deutlich größer, die Grundfarbe der Hinterflügel ist kräftiger orangebraun, das gesamte Erscheinungsbild ist dunkler. Abb. 1: σ, Trigona (H), 750 m, 30 km W Kalambaka, Katara-Pass-E, Thessalia, 17.VII.1991. Abb. 2: ♀, Galaxidi (O), 30 m, 30 km S Amfissa, Sterea Ellada-S-Mitte, 24.V.1999. Abb. 3: σ, Aniada (N), 1160 m, 30 km SE Karpenissi, Kaliakouda, Sterea Ellada-NW, 28.V.1999. Abb. 4: ♀, Kilada (D), 700 m, 18 km E Kosani, Makedonia, 23.VII.1991. Abb. 5, 6: σ, ♀, Deutschland, Hanau, 90 m, 18 km E Frankfurt, Hessen, 21.V., 6.VI.1975.

Abb. 7: *Catocala nymphagoga* Esp. (24). σ , aberrativ, Mega Hori (N), 750 m, 18 km S Karpenissi, Sterea Ellada-NE, 15.-17.VII.1995.

Abb. 8: *Polypogon simplicicornis* ZERNY (4). σ , Limni Vouliakmenis (P), 15 m, 20 km NW Loutraki, Sterea Ellada-SW, 7.-8.VI.2005.

Abb. 9: *Nonagria typhae* THNBG. (235). J, aberrativ, Visitsa (M), 550 m, Halbinsel Pilio, Thessalia-SE, 5.-10.VII.1995. Die 3 vom Autor bisher in weit voneinander entfernt liegenden Regionen Griechenlands gefundenen Exemplare gehören alle dieser Form mit schwarzbraunen Vorderflügeln an.

Abb. 10–12: *Ophiusa tirhaca* CRAMER (33). Etwa 70% aller vom Autor in Griechenland gesammelten oder vor Ort überprüften Exemplare weisen, geschlechterübergreifend, stark reduzierte Hinterflügelbänder auf (Abb. 10, 11).

Abb. 10: σ , aberrativ, Limni Vouliakmenis (P), 15 m, 20 km NW Loutraki, 7.-8.VI.2005. Abb. 11: σ , aberrativ, Trigona (H), 750 m, Katara-Pass-E, Thessalia, 11.VIII.1994. Abb. 12: φ , Habitus typisch O. tirhaca CR., Vathia (T), 100 m, Halbinsel Mani, Peloponnisos, 26.V.2003.

Abb. 13–15: *Minucia lunaris* D. & S. (31). Abb. 13: σ , als dunkle Form typisch für Griechenland, Asprangeli (G), 1050 m, 30 km N Ioannina, Mitsikeli, Ipiros-NE, 3.-7.V.2000.

Abb. 14: 9, ein Exemplar mit atypisch verlaufenden Querlinien, Mega Peristeri (H), 700 m, 35 km E Ioannina, Lakmos-NW, Pindos, Ipiros-E, 13.V.1999.

Abb. 15:9, Habitus typisch lunaris, Asprangeli (G), 1050 m, 30 km N Ioannina, Ipiros, 5.V.2000. Fotos: PIATKOWSKI. Alle Abbildungen im Maßstab 1:1.



Colour plate 7 / Farbtafel 7 3 5 6

Figs. 1-2: *Spilarctia hypogopa hypogopa* (HAMPSON, 1907) σ , Indonesia, West Sumatra, Harau valley, h=700 m, V.2004, native collector leg. (SZMN); 1 – upperside, 2 – underside.

Figs. 3-4: *Spilarctia hypogpa hypogopa* (HAMPSON, 1907) &, Malaysia, Borneo, Sarawak, G. Serapi, 29.IV.1990, coll. Y. KISHIDA; 3 – upperside, 4 – underside.

Figs. 5-6: *Spilarctia hypogopa mentawaica* DUBATOLOV **subsp. nov.**, σ , holotype, Indonesia, Mentawai isls., Siberut isl., Bojakan, IX.2004, native collector leg. (SZMN); 5– upperside, 6: underside.

Fig. 7: Spilarctia moorei (SNELLEN, 1879) J, figure from the original description.

Fig. 8: *Spilarctia moorei* (SNELLEN, 1879) &, lectotype, [Indonesia], Celebes, Lokka [National Natural History Museum (Naturalis) in Leiden], by courtesy of Dr. J. DE JONG and Dr. R. DE VOS.

Colour plate 8 / Farbtafel 8



Figs. 9-10: Spilarctia moorei (SNELLEN, 1879) &, Indonesia, Sulawesi, Rantepao, Tondok-Litak, 17. VIII.1984, N. KASHIWAI leg., coll. Y. KISHIDA; 9: upperside, 10: underside. Figs. 11-12: Spilarctia philippina DUBATOLOV & KISHIDA spec. nov., holotype &, Philippines, Negros I., Mt. Canlaon, IX.1997, native collector leg. (National Science Museum, Tokyo); 11: upperside, 12: underside. Figs. 13-14: Spilarctia philippina mindanaoica DUBATOLOV & KISHIDA subspec. nov., holotype &, Philippines, Mindanao I., Mt. Busa, 11-18. VI.1997, native collector leg. (National Science Museum, Tokyo); 13: upperside, 14: underside. Figs. 15-16: Spilarctia philippina mindanaoica DUBATOLOV & KISHIDA subspec. nov., paratype &, Philippines, Mindanao I., Mt. Busa, 11-18. VI.1997, native collector leg., coll. Y. KISHIDA; 15: upperside, 16: underside.

Colour plate 9 / Farbtafel 9



Fig. 1: *Spilarctia (punctata) siberuta* **spec. nov.**, paratype σ , Indonesia, Mentawai isls, Siberut isl., Bojakan, IX.2004, native collector leg. Fig. 2: *Spilarctia punctata* (MOORE, 1859) σ , Indonesia, E Java, Mt. Argapura, IV.1995, anonymous leg., received from coll. Y. KISHIDA. Fig. 3: *Spilarctia (punctata) procedra* (SWINHOE, 1907) σ , Indonesia, West Sumatra, Harau valley, 700 m, V.2004, native collector leg. Fig. 4: *Spilarctia (punctata) congruenta* (THOMAS, [1993]) σ , Indonesia, Java, Buitenzorg., 27-29.VII.1907, BAR. BRÜGGEN leg. Fig. 5-6: *Spilarctia (nanda) irina* **spec. nov.**, holotype σ , Indonesia, West Sumatra, Mt. Sanggul, 1300 m, VII.2004, native collector leg., upperside (5), underside (6). Fig. 7-8: *Spilarctia ananda* (ROEPKE, 1938) σ , Indonesia, Bali, Tamblingan, VI.2004, native collector leg., upperside (7), underside (8).

Colour plate 10 / Farbtafel 10



Fig. 9-10: Spilarctia (postrubida) flavorubida spec. nov., holotype of, Indonesia, Bali, Tamblingan, VI.2004, native collector leg., upperside (10), underside (11). Fig. 11-12: Spilarctia postrubida (WLEMAN, 1910) of, Taiwan (Formosa), Nan Tow, Wushe, 1966, received from coll. Y. KISHIDA, upperside (11), underside (12). Fig. 13-14: Spilarctia postrubida (WLEMAN, 1910) of, Vietnam, Ninh Binh, Gia Vien, Cuc Phuong, 160 m, 20-21.III.1998, K. YAZAKI leg., coll. Y. KISHIDA, upperside (13), underside (14). Fig. 15: Spilarctia postrubida (WLEMAN, 1910) of, Nepal, Mechi, Godok, 14.IV 1993, coll. Y. KISHIDA. Fig. 16: Spilarctia moorei (SNELLEN, 1879) of, figure from the original description by SNELLEN, 1879.



Fig. 17-18: *Spilarctia hypogopa* (HAMPSON, 1907) σ , Indonesia, West Sumatra, Harau valley, 700 m, V 2004, native collector leg., upperside (17), underside (18). Fig. 19-20. *Spilarctia hypogopa* (HAMPSON, 1907) σ , Indonesia, Bali, Tamblingan, VI.2004,

Fig. 19-20. *Spilarctia hypogopa* (HAMPSON, 1907) σ , Indonesia, Bali, Tamblingan, VI.2004, native collector leg., upperside (19), underside (20).



Melanosphecia auricollis (ROTHSCHILD, 1912), Sarawak, Gunung Gading N.P., 23.-26. 10. 2003 leg. W. MEY.

Colour plate 12 / Farbtafel 12



Fig. 1: Ahlbergia clarolinea spec.nov. Holotype 9 upperside (left half) and underside (right half).
Fig. 2: Ahlbergia clarolinea spec.nov. Paratype of upperside (left half) and underside (right half).
Fig. 3: Ahlbergia clarolinea spec.nov. Paratype of upperside (left half) and underside (right half).
Fig. A: Colandia uemurai motuoa subspec. nov. holotype of Upperside (left half) and Underside (right half).

Colour plate 13 / Farbtafel 13

BACK, W., KNEBELSBERGER, TH. & M. A. MILLER: The phylogenetic relationships of the species and subspecies of the subgenus *Elphinstonia* KLOTS, 1930 (Lepidoptera, Pieridae). - Atalanta **37** (3/4): 469-482, Würzburg (Dezember 2006).

Abbreviations: E.: Elphinstonia, c.: charlonia, p.: penia, t.: transcaspica, Gen.: generation. Same scale for 1-24. Localities: 1: Env. Tiznit, Maroc, 100m, Anti-Atlas occ., 1.-15.3. [19]99. M. R. TARRIER (129). 2: Env. Tiznit, Maroc, 100m, Anti-Atlas occ., 16.-30.4.1999, leg. M. R. TARRIER (129). 3: Umg. Caspe, Aragon, Spanien, 14.-16.3.05, W BACK, FS. 4: Prov. Granada, Baza, 900m, Hoya de Baza, 31.5.2004, W. & Co. BACK, FS. 5: Turkmenia mer. Kopetdag Mts., Kara Kala, 400m, 1.IV.1992, L. BIEBER coll. 6: USSR, Turkmenia, Kopet-Dag Mts., 400-600m, 58°05'E, 37°59'N, 15.-19-IV.1991, No. L1, leg. G.Csorba, GY. Fábián, B. HERCZIG, M. HERBIAY & G. RONKAY. 7: Dalaki, Straße Bushir-Kazerun, 15.-21.3.1971 (19.), W. BACK, FR, Leist. 8: Dalaki, Straße Bushir-Kazerun, 15.-21.3.1971 (19.), W. BACK, FR, Leist.9: Afghanistan, Jalalabad-Torkham, 500m, 18.4.1976, leg. Dr. RESHÖFT. 10: O-Afghaniatan, Ghanikhel Umg., ca. 1000m, 14.3.1975, leg. M. DIETZ. 11: Treska-Schlucht, Umg. Skopje, Mazedonien, 5.5.1978, leg. W. BACK, FR. 12: Treska-Schlucht, Umg. Skopje, Mazedonien, e. l. 25.5.-10.6.[19]77, R. 20.5.[19]77, leg. W. BACK FR. 13: Iran, Zanjan prov., östl. Mt. Tales, 1100-1300m, 9.-30.5.2003, leg. M. ZIAYAN, coll. W. BACK, FS. 14: Iran, Zanjan prov., östl. Mt. Tales, 1100-1300m, 9.-30.5.2003, leg. M. Ziayan, coll. W. BACK, FS. 15: Iran, Tehran prov., Khor-Sijan, 2400-2900m, 23.V.2001, leg. W. BACK, FS. 16: N. Teheran, Darband (Tochal), Elburs, 2700m, 11.6.1999. 17: Iran, Lorestan, Dorud, 15km S, 33°25' N, 49°08' E, 2700m, 4.-6.6.2000, leg. JIRI KLIR. 18: Iran, Lorestan, Dorud, 15km S, 33°25' N, 49°08' E, 2700m, 4.-6.6.2000, leg. JIRI KLIR.19: Iran, Esfahan prov., Wadar-Zefre, Mt. Qohrod, 2400-2900m, 21.V.2001, leg. W. BACK, FS. 20: Iran - centr. Esfahan prov., Qohrud, Mts. Zefre, 2400-2900m, 18.6.1999, leg. V. MAJOR. 21: Iran, Zanjan prov., östl. Mt. Tales, 1100-1300m, 31.5.2002, leg. M. ZIAYAN, coll. W. BACK, FS. 22: Iran, Zanjan prov., östl. Mt. Tales, 1100-1300m, 31.5.2002, leg. M. ZIAYAN, coll. W. BACK, FS. 23: Turkmenistan, Ashkhabad, 10.4.89. 24: Turkmenien, Kopetdagh, Aschchabad, 400m, 1.-10.IV.1991, leg. V. LUKHTANOV.

Colour plate 13 / Farbtafel 13

Plate 1 (Figs 1-24): species and subspecies of Elphinstonia



FISCHER, H. & S. LEWANDOWSKI: Die Geometriden- Fauna von Zypern – eine Überarbeitung aller bisher bekannten Arten. (2. Teil: Orthostixinae und Larentiinae) (Lepidoptera: Geometridae, Orthostixinae, Larentiinae). - Atalanta 37 (3/4): 329-344, Würzburg (Dezemmber 2006).

Abb. 1: Orthostixis cinerea Rebel, 1916, σ , Zypern, Foini, 11.VI.2002, leg. Lewandowski & Fischbacher.

Abb. 2: *Aplocera plagiata* (LINNAEUS, 1758), σ , Zypern, Agridia, 28.IX.2000, leg. FISCHER, H & S. LEWANDOWSKI.

Abb. 3: *Aplocera plagiata* (LINNAEUS, 1758), 9, Kreta, Umg. Anogia, 20.IV.1994, ca. 1000 m ex larva, leg. CHRISTINE & HEINZ FISCHER.

Abb. 4: *Aplocera plagiata* (LINNAEUS, 1758), 9, Korsika, Col de Vergio, 19.V.1996, 800 m, leg. FISCHER, H & C. ZEHENTNER.

Abb. 5: Larentia clavaria pallidata (Staudinger, 1901), J, Zypern, Kathikas, 1.XI.2002, leg. Fischer, H & S. Lewandowski.

Abb. 6: Larentia clavaria pallidata (Staudinger, 1901), 9, Zypern, Gialia, 2.XI.2002, leg. Fischer, H & S. Lewandowski.

Abb. 7: Larentia clavaria clavaria (HAWORTH, 1809), σ , Malta, St. Julian's, 1.III.1998, 5 m, e.l., leg. Lewandowski & Tober.

Abb. 8: Larentia clavaria clavaria (HAWORTH, 1809), 9, Malta, St. Julian's, 1.III.1998, 5 m, e.l., leg. Lewandowski & Tober.

Abb. 9: *Xanthorhoe fluctuata* (LINNEAUS, 1758), J, Zypern, Latsi bei Polis, 31.V.2000, leg. Lewandowski & Tober.

Abb. 10: Xanthorhoe oxybiata (MILLIÈRE, 1872), 9, Zypern, Kathikas, 1. XI. 2002, leg. FISCHER, H & S. LEWANDOWSKI.

Abb. 11: Catarhoe hortulanaria palaestinensis (Staudinger, 1895), J, Zypern, Kathikas, 1. XI. 2002, leg. Fischer, H & S. Lewandowski..

Abb. 12: *Catarhoe permixtaria* (HERRICH-SCHÄFFER, 1856, σ , Zypern, Nikoklela, 1.- 8.V.2000, 150 m, leg. FISCHER, H & S. LEWANDOWSKI.

Abb. 13: Protorhoe unicata (GUENÉE, 1857), &, Zypern, Nikoklela 25.-31.III.2001, 150 m, leg. HENTSCHOLEK.

Abb. 14: Camptogramma bilenatum bohatschi (AIGNER, 1902), Typus &, Zypern, Larnaca, 30.IV.[19]01, coll. MNHU.

Abb. 15: *Camptogramma bilenatum bohatschi* (AIGNER, 1902), *Q*, Zypern, Kidasi, 6.-12.VI.2002, 300 m, leg. HENTSCHOLEK.

Abb. 16: Camptogramma bilenatum bohatschi (AIGNER, 1902), o, Lesbos, Umg. Plomari 28.V.2005, 180 m, leg. Svetlana & HEINZ FISCHER.

Abb. 17: *Antilurga adlata* (Staudinger, 1895), Q, Zypern, Mylikouri, 3.XI.2002, leg. Fischer, H & S. Lewandowski.

Abb. 18: *Nebula ablutaria* (BOISDUVAL, 1840), J, Zypern, Kathikas, 1.XI.2002, leg. FISCHER, H & S. LEWANDOWSKI.



FISCHER, H. & S. LEWANDOWSKI: Die Geometriden- Fauna von Zypern – eine Überarbeitung aller bisher bekannten Arten. (2. Teil: Orthostixinae und Larentiinae) (Lepidoptera: Geometridae, Orthostixinae, Larentiinae). - Atalanta 37 (3/4): 329-344, Würzburg (Dezemmber 2006).

Abb. 1: Nebula schneideraria (LEDERER, 1855), Typus Q, Beirut, X. 1911, leg. PUNG.[ELER], coll. MNHU.

Abb. 2: Myinodes shohami Hausmann, 1994, J, Zypern, Limassol, Ypsonas, 30.I.2003, 50 m, leg. GEORGIOU.

Abb. 3: *Oulobophora externaria* (HERRICH-SCHÄFFER, 1848), 9, Zypern / West, Nikloklela / Paphos, 25.-31.III.2001, 150 m, leg. HENTSCHOLEK.

Abb. 4: Chesias rhegmatica PROUT, 1937, J, Zypern, Latsi bei Polis, 28.II.1999, leg. LEWANDOWSKI & TOBER.

Abb. 5: Lithostege palaestinensis AMSEL, 1935, J., Zypern, Lefkosia, Archangelos, 3.IV.2002, leg. MAKRIS.

Abb. 6: *Thera variata subtaurica* (WEHRLI, 1932), J, Zypern, Pano Amiantos Umg., 27. IX 2002, 1640 m, leg. HENTSCHOLEK.

Abb. 7: Gymnoscelis rufifasciata (HAWORTH, 1809), σ , Zypern, Latsi bei Polis, 10.VI.2000, leg. LEWANDOWSKI & TOBER.

Abb. 8: Gymnoscelis rufifasciata (Haworth, 1809), 9, Zypern, Kathikas, 1.XI.2002, leg. Fischer, H & S. Lewandowski.

Abb. 9: Eupithecia dubiosa DIETZE, 1910, J, Zypern, Latsi bei Polis, 28.II.1999, leg. Lewandowski & Tober.

Abb. 10: *Eupithecia reisserata* PINKER, 1976, σ , Griechenland, Parnassos Oros Umg. Delphi, 16.IV.1979, Li, 500-700 m, G. BAISCH, coll. ZSM.

Abb. 11: *Eupithecia quercetica* Prout, 1938, o, Zypern, Latsi bei Polis, 28.II.1999, leg. Lewandowski & Tober.

Abb. 12: Eupithecia centaureata ([DENIS & SCHIFFERMÜLLER], 1775), σ , Zypern, Latsi bei Polis, 28.II.1999, leg. LEWANDOWSKI & TOBER.

Abb. 13: Eupithecia breviculata (Donzel, 1837), J. Zypern, Nikoklela, 1.-8.V.2000, 150 m, leg. Hentscholek.

Abb. 14: Eupithecia cerussaria (LEDERER, 1855), J, Syrien, Beyrouth, leg. O. STAUDINGER, coll. ZSM.

Abb. 15: Eupithecia ultimaria BOISDUVAL, 1840, 9, Zypern, Nikoklela, 25.-31.III.2001, 150 m, leg. HENTSCHOLEK.

Abb. 16: *Eupithecia ericeata* RAMBUR, 1833, J, Zypern, Kathikas, 1.XI.2002, leg. FISCHER, H & S. LEWANDOWSKI.

Abb. 17: Eupithecia schiefereri Bohatsch, 1893, J, Lesbos, Umg. Plomari, 24.V.2005, 180 m, leg. Svetlana & Heinz Fischer.

Abb. 18: Orthonama obstipata (FABRICIUS, 1794), 9, Zypern, Gialia, 2.XI.2002, leg. FISCHER, H & S. LEWANDOWSKI.

Abb. 19: Perizoma bifaciata melanaria subspec. nov., Holotypus J, Zypern, Lefkara, Umgebung, 29.IX.2004, 800 m, leg. LEWANDOWSKI & TOBER.

Abb. 20: *Perizoma bifaciata melanaria* subspec. nov., Paratypus 9, Zypern, 2 km südlich von Agridia, 28.IX.2000, 1060 m, leg. FISCHER, H & S. LEWANDOWSKI.

Alle Falter coll. S. Lewandowski & H. Fischer, außer Tafel 14, Abb. 14: coll. MNHU, Tafel 15, Abb. 1: coll. MNHU, Abb. 2: coll. Makris, Tafel 15, Abb. 10: coll. ZSM, Abb. 14: coll. ZSM. Alle Fotos S. Lewandowski & H. Fischer, außer Tafel 15, Abb. 2: Makris.





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