

A revision of the infraspecific structure of *Erebia euryale* (Esper, 1805) (Nymphalidae: Satyrinae)

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Abstract. A systematic analysis of the geographic variation of both valve shape and wing pattern reveals that the subspecies of *Erebia euryale* can be clustered into three groups, characterised by their valve shape. The *adyte*-group comprises the Alpine ssp. *adyte* and the Apenninian *brutiorum*, the *euryale*-group includes the Alpine subspecies *isarica* and *ocellaris*, and all remaining extra-Alpine occurrences. The third group (*kunzi*-group), not recognised hitherto, is confined to a restricted, entirely Italian, part of the southern Alps. It comprises two subspecies: ssp. *pseudoadyte* (**ssp. n.**), hardly distinguishable from ssp. *adyte* by its wing pattern, and ssp. *kunzi*, strongly melanistic and even exceeding ssp. *ocellaris* in this respect. The ssp. *pseudoadyte* territory is surrounded by the valleys of the rivers Adda, Rio Trafoi and Adige, and ssp. *kunzi* inhabits the eastern Venetian pre-Alps, the Feltre Alps and the Pale di San Martino. The intervening region (the western Venetian pre-Alps, the Cima d'Asta group and the Lagorai chain) is inhabited by intermediate populations. It is argued that these are probably not hybrid populations, but represent a third morphological unit within the *kunzi* group. A contact area of the *adyte* group and the *kunzi* group exists between Trafoi and Sulden, whereas the *kunzi* group and the *euryale* group almost meet at Passo Rolle. Indications of gene flow between groups were found only near Trafoi.

Zusammenfassung. Aus einer systematischen Analyse der geographischen Variation von sowohl Valvenform als auch Flügelzeichnung geht hervor, dass die Unterarten von *Erebia euryale* sich in drei Gruppen, die sich genitaliter voneinander unterscheiden, einordnen lassen. Zur *adyte*-Gruppe gehören die Unterarten *adyte* (in den Alpen) und *brutiorum* (Apennin). Die *euryale*-Gruppe umfasst die alpinen Unterarten *isarica* und *ocellaris* und alle weiteren außeralpinen Vorkommen der Art. Die dritte, bisher nicht erkannte Gruppe (die *kunzi*-Gruppe) umfasst zwei Unterarten: die ssp. *pseudoadyte* (**ssp. n.**), die sich in der Flügelzeichnung kaum von ssp. *adyte* unterscheidet, und ssp. *kunzi*, deren Melanisationsgrad sogar den der ssp. *ocellaris* übertrifft. Ihr Areal beschränkt sich auf einen Teil der italienischen Südalpen. Die ssp. *pseudoadyte* ist heimisch im Gebiet, das von den Tälern von Adda, Rio Trafoi und Etsch umschlossen wird, während die ssp. *kunzi* die östlichen Venezianer Voralpen, die Feltre Alpen und die Pale di San Martino bewohnt. Das dazwischen liegende Gebiet (westliche Venezianer Voralpen, Cima d'Asta-Gruppe und Lagorai Kette) wird von intermediären Populationen besiedelt. Es gibt Argumente dafür, dass letztere keine Hybridpopulationen darstellen, sondern als eine dritte morphologische Einheit innerhalb der *kunzi*-Gruppe zu betrachten sind. Eine Kontaktstelle der *adyte*-Gruppe und der *kunzi*-Gruppe findet sich zwischen Trafoi und Sulden, während die Areale der *kunzi*-Gruppe und der *euryale*-Gruppe sich am Rollepass berühren. Hinweise für Genfluss zwischen zwei Gruppen wurden nur bei Trafoi gefunden.

Riassunto. Un'analisi sistematica della variazione geografica nella forma della valva e del disegno alare rivela che le sottospecie d'*Erebia euryale* si raggruppano in tre gruppi, caratterizzati dalla forma della valva. Il gruppo *adyte* comprende le ssp. *adyte* (nelle Alpi) e *brutiorum* (negli Appennini). Il gruppo *euryale* include le sottospecie alpine *isarica* e *ocellaris* e tutte le altre sottospecie extraalpine. Il terzo gruppo (il gruppo *kunzi*) è indigeno di una ristretta parte – unicamente italiana – del versante Sud delle Alpi. Questo gruppo comprende due sottospecie: la ssp. *pseudoadyte* (**ssp. n.**), a malapena distinguibile da *adyte* per il disegno alare, e la ssp. *kunzi*, estremamente melanizzata, tanto da superare la ssp. *ocellaris* in questo aspetto. Il territorio della ssp *pseudoadyte* è delimitato dalla Valtellina, Val di Trafoi, Val Venosta e Val d'Adige, mentre la ssp. *kunzi* abita le Prealpi Venete orientali, le Vette Feltrine e la Pala di San Martino. Le Prealpi Venete occidentali, la Cima d'Asta e la catena del Lagorai sono abitate da popolazioni intermedie. È argomentato come queste ultime probabilmente non siano di origine ibrida, ma vadano considerate una terza entità morfologica nel gruppo *kunzi*. Un sito di contatto dei gruppi *adyte* e *kunzi* esiste tra Trafoi e Solda, mentre gli areali dei gruppi *kunzi* e *euryale* si toccano al Passo Rolle. Segni di scambio di geni sono trovati solo presso Trafoi

Introduction

Erebia euryale (Esper, 1805) is one of the most common and most widespread European *Erebia* species. It has a western Palaearctic, arctic-alpine disjunct distribution. The arctic subarea ranges from eastern Finland to the Urals (Lukhtanov & Lukhtanov, 1994; Tatarinov & Dolgin 1997), the alpine (oreal) subarea covers almost all European mountain systems (Warren 1936). This fragmented distribution pattern has led to the description of a large number of subspecies. These are traditionally clustered into three groups (Fig. 1): the *euryale* group, the *adyte* group and the *ocellaris* group (von Goltz 1933; Verity 1953; Arnscheid & Roos 1977, Sonderegger 2005).

In the Alps, the *adyte* group is represented by ssp. *adyte* (Hübner, 1822), the *euryale* group by ssp. *isarica* Heyne, 1895, and the *ocellaris* group by ssp. *ocellaris* Staudinger, 1861. Where two groups come into contact, they behave differently. The subspecies *adyte* and *isarica* remain separated in most contact sites. Intermediate individuals have been found (Rezbanyai-Reser 1991; Sonderegger 2005), but gene flow is strongly limited (Geiger & Rezbanyai 1982). Between the ssp. *ocellaris* and *isarica*, on the other hand, extensive hybrid zones have been described (von Goltz 1933; Arnscheid & Roos 1977). They seem to intermingle and interbreed wherever they meet. Contact sites of ssp. *adyte* and ssp. *ocellaris* have never been reported. Recently it has been demonstrated that the three morphologic groups, at least in the Alps, do not represent three genetic lineages: genetically, ssp. *ocellaris* fits perfectly into the east-Alpine *isarica* populations (Schmitt & Haubrich 2008). Two more subspecies have been described in the Alps. Their descriptions, though, are based on a single population, and their geographic boundaries have never been properly defined: ssp. *etobyma* Fruhstorfer, 1909 and ssp. *kunzi* Heinkele, 2007.

The differences between subspecies and between groups of subspecies are entirely based on wing pattern. Genital characters, which are not subjected to ecologic adaptation and thus are less variable, yield more stable taxonomic criteria than wing pattern does. Differences in male genital anatomy between the Alpine subspecies of *E. euryale* have been described (Arnscheid & Roos 1977, Sonderegger 2005), but their geographic variation has never been studied systematically. Genital morphology thus plays no role in the infraspecific taxonomy of *E. euryale*. This paper presents the results of a morphologic analysis of a large number of populations, covering the whole geographic range of the species, and involving both wing pattern and male genital characters. The results yield the basis for a revision of the infraspecific structure of *E. euryale*.

Material and methods

Wing pattern was studied in 2695 males and 858 females from 86 locations, 15 of which outside the Alps (Fig. 2), with an emphasis on the contact regions *adyte/ocellaris* and *isarica/ocellaris* in the south-eastern Alps (Tab. 1). In samples 87–114, added later, wing pattern was used for determination of the morphologic group only, without being quantified. Genital characters were studied in 772 males from 72 populations, as a rule of 10 males per sample. The choise of the measured parameters, both for

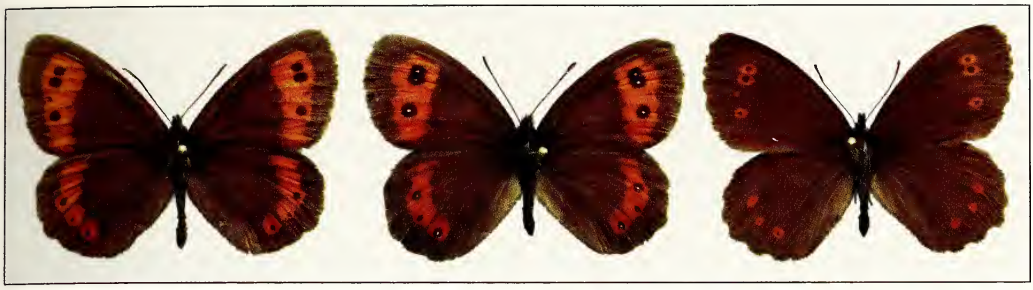

Fig. 1. The traditional tripartition: typical representatives of the *euryale* group, the *adyte* group and the *ocellaris* group (from left to right).

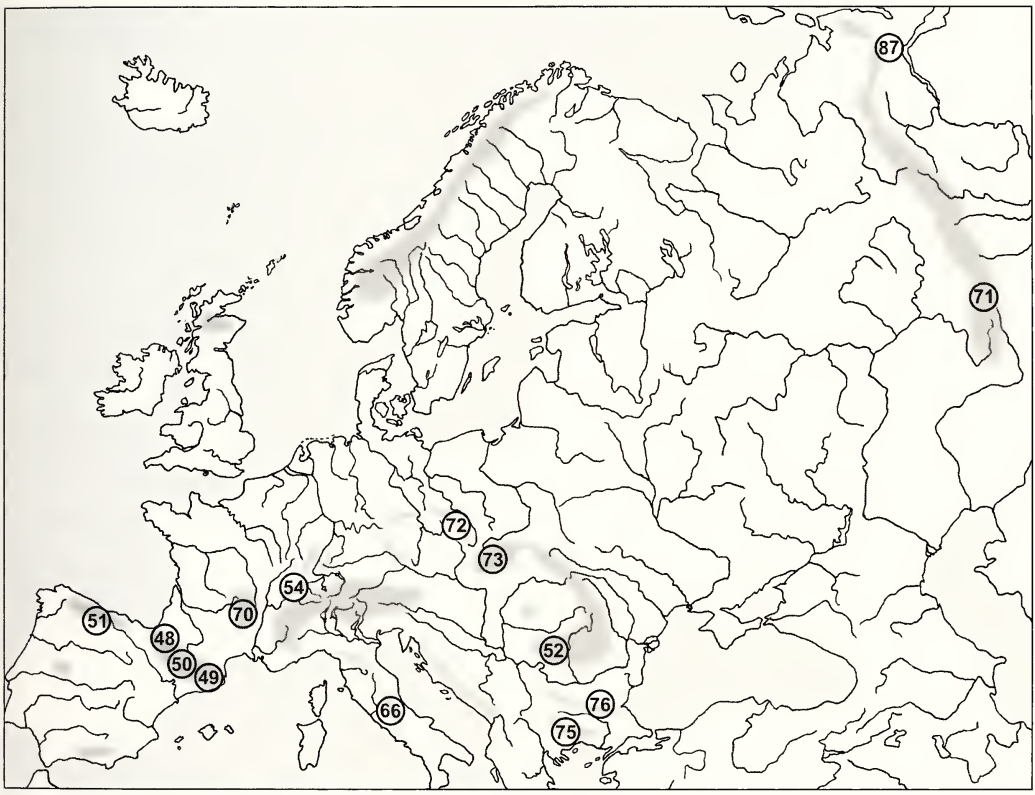

Fig. 2. The extra-Alpine sample sites. Sample numbers refer to Tab. 1. Grey area: mountain systems.

wing pattern and for valve shape, was based on current knowledge of the differences between the groups (Appendix 1). Diagnostic features, characteristic of individual subspecies within these groups, were disregarded.

Wing pattern. Nine wing pattern elements were quantified and scored (quantification criteria in appendix 2).

(i) Development of the postdiscal band on forewing upperside, forewing underside and hindwing upperside (males and females).

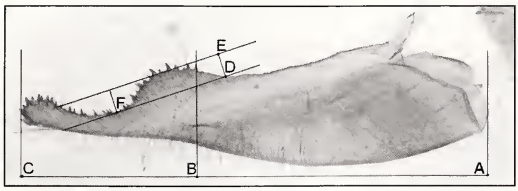

Fig. 3. Valve of *E. euryale*. Illustration of measured values. Shoulder Index = DE/DF. Position of first tooth = AB/AC.

(ii) Development of ocelli (absent, black or pupilled) on forewing upperside, forewing underside and hindwing upperside (males and females).
(iii) Development of the ocelli on the hindwing underside (absent, without or with brown ring) (males only).
(iv) Development of the white postdiscal streak on hindwing underside (males only).
(v) Colour of the postdiscal band on the hindwing underside (females only).

Valve shape. Abdominal tips were macerated in KOH 10% at 100 °C for 15 min, dissected, then dehydrated in ethanol 96% for 5 min and embedded in euparal. Three parameters were calculated from measured values:
(i) Shoulder Index: the height/width ratio of the dorsal shoulder (DE/DF in Fig. 3).
(ii) First Tooth: the relative position of the most proximal tooth (AB/AC in Fig. 3).
(iii) Tooth Length: the length of the longest tooth on the shoulder, measured on its distal slope, as a percentage of the valve length.
For (i) and (ii) a measuring microscope was used (magnification × 30, reading accuracy 10 microns), for (iii) calibrated microphotographs were measured on screen (final magnification x 1000).

Statistics. For cluster analysis variables were standardized (mean=0 and sd=1), squared Euclidian distances were measured, and four algorithms were applied: Ward-method, Average Linkage within groups, Average Linkage between groups and Nearest Neighbour. Equality of distributions (2 samples) was tested with Student's t-test (for $N>30$ and normal distribution), otherwise with Mann-Whitney U test; distributions of more than 2 samples were tested by one-way ANOVA for Gaussian populations with equal variances, otherwise by Kruskal-Wallis H test. Homogeneity of variances was tested with Levene's test, normal distribution with Kolmogorov-Smirnov test or (if $N<50$) Shapiro-Wilks test. All statistical tests were performed with the SPSS 12.0 package. Structuring of the Alps and nomenclature of the mountain groups are according to Marazzi (2005).

Abbreviations

Fw = forewing; Hw = hindwing; Up = upperside; Un = underside; B = postdiscal band; Oc = ocelli; ZMAN = Zoological Museum Amsterdam (NL); LMD = Löbbecke Museum Düsseldorf; CFC = Collection Frans Cupedo, Geulle (NL).

Material deposition

The material is deposited in LMD (sample 61), ZMAN (samples 36 p.p., 52 p.p., 74, 75, 76 p.p., 86) and CFC (remaining samples).

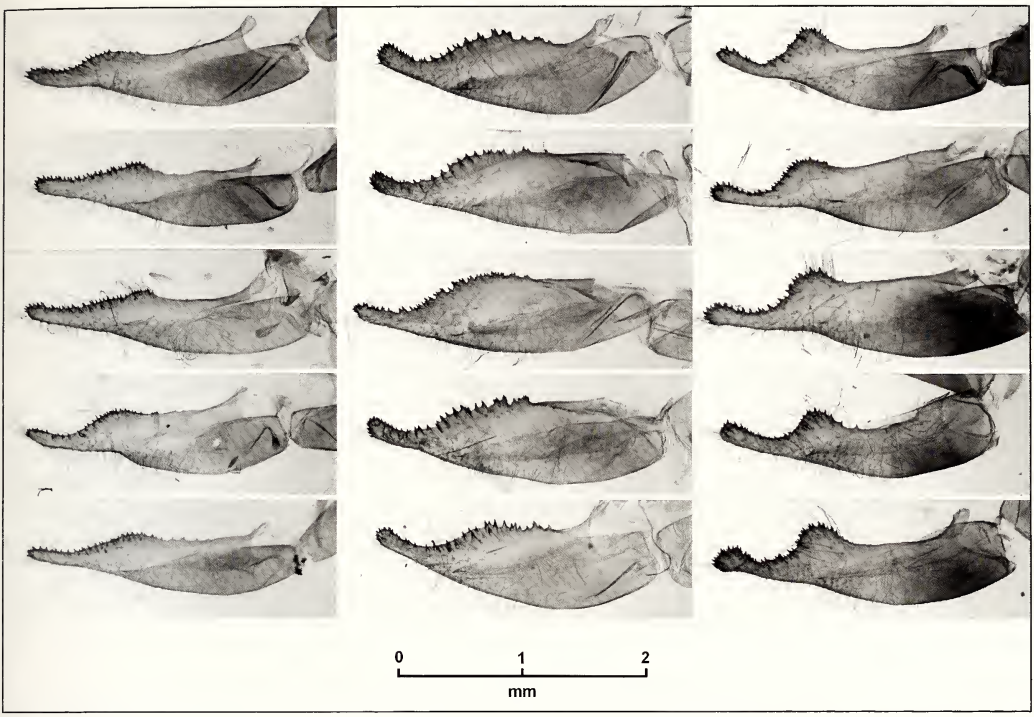

Fig. 4. *Erebia euryale*, valve type 1 (left), type 2 (middle) and type 3 (right).

Results

1 Male genital characters

Population level. A hierarchic cluster analysis based on population means for Shoulder Index, First Tooth and Tooth Length resulted in three clusters, whatever algorithm was used (not figured). These clusters are provisionally named group 1, 2 and 3. Their valve shapes are shown in Fig. 4. The valve of group 1 is slender, the spines are fine and separate, the valve has a large spine-free proximal part. Valve type 2 is broad, the dorsal ridge is convex and bears irregularly placed spines of unequal size, 2 or 3 of them often being fused. The spine-free part is decidedly shorter than in type 1. Type 3 is slender, with a knob shaped apex. Spine length is intermediate between both foregoing types. Its most characteristic features are (i) the prominent, hump-shaped shoulder and (ii) the spine-free proximal part of the valve, which is longer than in both other types. Differences between the three groups are highly significant ($p<0.001$ for each character by Kruskal-Wallis and Bonferroni corrected Mann-Whitney's U test). The boxplots (Fig. 5) visualise that each population is unambiguously attributable to one of the three groups on the basis of the measured parameters. Each algorithm except Nearest Neighbour showed group 1 and 3 more related to each other than to group 2.
Individual level. On the individual level, each parameter shows considerable spread, resulting in overlap between groups. An individual cannot be identified if all three

Tab 1. List of sample sites and sample sizes, the population means and standard deviations of valve characters. N(M) = sample size for male wing characters; N(F) = sample size for female wing characters; N(G) = sample size for genital characters. Population means: FT = First Tooth; SI = Shoulder Index; TL = Tooth Length. sd = standard deviation.

Nr	Sample	Massif	Locality	N(M)	N(F)	N(G)	FT	sd	SI	sd	TL	sd
1	Kaiser	Kaiser Mountains	Wilder Kaiser	22	0	0						
2	Karwendel	Karwendel Mountains	Seefeld	50	4	10	43.45	4.56	12.27	3.07	2.23	0.39
3	Kitzbüheler A	Kitzbühel Alps	Wildschönau	18	6	0						
4	Steinernes M	Berchtesgaden Alps	Dießbachtal	30	8	10	43.79	3.91	13.55	3.43	2.02	0.44
5	Stubaier A	Stubai Alps	Pinnistal	25	12	10	46.63	4.12	12.25	4.37	2.51	0.37
6	Zillertal A	Zillertal Alps	Mayrhofen	11	0	0						
7	H Tauern (N)	High Tauern	Rauris	18	0	10	43.57	3.20	11.59	3.06	2.06	0.31
8	N Tauern	Seckauer Tauern	Knittelfeld	14	7	10	42.72	3.46	11.29	2.35	2.37	0.47
9	Gurktal A	Gurktaler Alps	Turracher Höhe	36	7	10	43.58	5.70	12.77	3.29	2.31	0.30
10	Goldeck	Gailtal Alps	Goldeck	10	2	0						
11	Julian A (C)	Julian Alps	Triglav	36	9	10	42.38	3.54	10.14	1.97	1.99	0.48
12	Julian A (W)	Julian Alps	Sella Nevea	17	1	0						
13	Fleisstal	High Tauern	Grosses Fleisstal	50	6	0						
14	Ötztal A (S)	Ötztal Alps	Vermoispitze	26	13	10	45.47	5.42	9.81	2.89	2.32	0.54
15	P Rolle (W)	Pale di San Martino	Paneveggio	48	12	30	44.60	4.80	11.72	3.10	2.24	0.45
16	Sappada	Carnic Alps	Col Siera	21	0	0						
17	Cavallo	Belluno pre-Alps	Monte Cavallo	50	24	10	56.37	4.84	25.33	3.77	1.94	0.39
18	Tuxer A	Tuxer pre-Alps	Zillertal west side	23	3	0						
19	Geisler G	Geisler Group	Wolkenstein	50	15	10	45.35	3.81	9.77	2.71	2.18	0.31
20	Aurine G	Zillertal Alps	Altmühltal	50	10	0						
21	Defereggen G	Defereggen Alps	Thurntaler	50	7	0						
22	Hochschober	Schober Group	Debanttal	50	18	0						
23	Kreuzeck	Kreuzeck Group	Scharnik	50	18	0						
24	Feltre	Feltre Alps	Vette di Feltre	50	3	10	59.51	3.43	22.55	2.60	1.56	0.41
25	P. Rolle (E)	Lagorai	East of Passo Rolle	50	50	30	56.69	4.32	25.55	5.85	1.84	0.37
26	P Mauria	Carnic pre-Alps	Passo Mauria	30	50	10	45.79	4.40	12.72	3.37	2.19	0.28
27	Lienzer Dol	Gailtal Alps	Lienzer Dolomites	50	8	0						
28	Carega	Piccole Dolomiti	Passo Campogrosso	50	31	10	57.17	5.02	20.69	3.59	1.79	0.31
29	Lavarone	Altipiani Group	Lavarone	50	3	10	56.05	6.18	23.22	5.86	1.99	0.29
30	P Malghen	Lagorai	Passo Malghen	25	32	10	57.46	4.93	22.87	4.40	1.64	0.21
31	Pasubio	Piccole Dolomiti	Monte Pasubio	12	1	0						
32	Sesto	Sesto Dolomites	Sesto	50	4	10	45.16	3.03	12.24	4.31	2.34	0.28
33	Plöckenpas	Carnic Alps	Plöckenpass	38	7	10	42.97	2.01	13.16	3.18	1.93	0.43
34	Val Malga	Adamello Group	Val Malga	24	6	10	60.21	4.81	23.59	4.84	1.83	0.40
35	Croce Domini	Brescia pre-Alps	Passo Croce Domini	21	6	10	59.96	2.21	25.14	4.99	1.80	0.18
36	M Baldo	Garda pre-Alps	Monte Baldo	50	20	10	60.98	2.00	20.19	3.72	1.58	0.26
37	M Tremalzo	Garda pre-Alps	Monte Tremalzo	43	6	10	60.45	3.46	23.52	3.16	1.54	0.30
38	Val Concei	Garda pre-Alps	Val Concei	27	3	10	61.22	4.39	21.81	1.80	1.63	0.39
39	Trafoi-1	W Vinschgau Alps	Trafoi	22	0	10	49.65	6.33	15.54	2.11	1.42	0.18
40	Martelltal	Ortler Alps	Martelltal	48	17	10	60.60	5.77	20.43	5.11	1.77	0.34
41	M Legnone	Western Orobie Alps	Monte Legnone	27	12	10	59.03	3.69	20.80	5.49	1.85	0.32
42	Pzo Redorta	Central Orobie Alps	Pizzo Redorta	14	2	0						
43	Presolana	Bergamasque pre-Alps	Presolana Group	32	14	10	60.47	4.10	20.79	4.40	1.97	0.32
44	Lautaret	Dauphiné Alps	Col du lautaret	36	0	10	46.24	5.45	13.14	2.47	1.44	0.21
45	Oulx	Montgenèvre Alps	Oulx	34	13	10	50.70	6.82	15.13	2.59	1.42	0.38
46	Valdieri	Eastern Maritime Alps	Valle Gesso	44	50	10	51.52	5.20	13.68	2.47	1.47	0.25
47	Cottian A	Monviso Alps	Les Orres	33	34	10	45.51	5.27	11.26	3.19	1.46	0.19
48	Pyrenees (W)	Western Pyrenees	Col Marie Blanque	19	0	10	42.03	7.36	11.84	3.21	2.11	0.30
49	Pyrenees (E)	Eastern Pyrenees	Mont Canigou	62	0	10	44.57	4.14	9.93	2.53	2.05	0.33
50	Pyrenees (C)	Central Pyrenees	Val d'Aran	35	0	0						
51	Cantabria	Sierra Cantabrica	Puerto san Glorio	28	0	10	42.84	4.16	10.91	2.87	1.88	0.40
52	Retezat	Southern Carpathians	Muntii Retezat	33	5	15	42.60	2.53	8.29	2.38	2.28	0.38
53	Grindelwald (S)	Bernese Alps s.s.	Kleiner Scheidegg	18	0	0						
54	Jura	Jura	La Dôle	18	12	10	42.63	4.85	10.05	2.39	2.03	0.34

Tab 1. Continuation.

Nr	Sample	Massif	Locality	N(M)	N(F)	N(G)	FT	sd	SI	sd	TL	sd
58	Val di Vizze	Zillertal Alps	Val di Vizze	27	9	0						
59	Ridnaun	Stubai Alps	Ridnauntal	24	2	0						
60	Tessin	Ticino Alps	Campo Tencia	50	33	0						
61	Mendelpass	Nonsberger Alps	Mendelpass	8	12	8	62.22	2.04	24.61	6.32	1.78	0.38
62	Val Tinée	Western Maritime Alps	Val Tinée	34	16	0						
63	M Tamaro	Como pre-Alps	Monte Tamaro	26	14	10	52.95	6.89	12.67	2.96	1.35	0.22
64	Drôme	Diois pre-Alps	Several localities	29	6	10	46.00	4.35	10.69	3.39	1.27	0.30
65	Pralognan	Vanoise Alps	Pralognan	13	7	10	49.25	7.29	14.44	2.68	1.40	0.31
66	Gran Sasso	Gran Sasso	Gran Sasso	47	11	10	44.15	4.90	13.81	1.73	1.37	0.30
67	Brenta	Brenta Group	Brenta	10	15	10	60.17	2.98	21.83	4.48	1.77	0.34
68	Paganella	Brenta Group	Paganella	16	2	10	61.05	2.98	21.99	2.93	1.77	0.35
69	Pradilago	Presanella Group	Pradilago	24	38	10	58.51	4.86	20.74	3.81	1.90	0.24
70	Massif Central	Massif Central	Mont Meygal	44	7	10	43.35	4.64	12.57	3.00	2.61	0.81
71	Urals	Urals	Mont Iremel	25	6	10	40.82	3.87	11.26	6.25	2.23	0.67
72	Praded	Sudety Mountains	Praded	38	8	10	42.84	3.25	7.78	3.37	2.21	0.29
73	H Tatra	High Tatra	Pod Banske	26	2	10	41.85	3.16	10.73	2.38	2.29	0.17
74	Bohinj	Julian Alps	Bohinj	20	0	0						
75	Falakron	Falakron Mountains	Drama	21	0	12	40.79	3.37	9.91	3.19	2.28	0.52
76	Rila	Rila Mountains	Bulgaria	22	3	11	41.66	3.54	10.83	3.83	2.60	0.36
77	Cimonega	Feltre Alps	Cimonega	46	11	10	56.76	5.19	25.32	6.27	1.62	0.33
78	Visentin	Belluno pre-Alps	Col Visentin	46	6	10	60.47	2.08	24.46	2.37	1.83	0.22
79	Frassenè	Pale di San Martino	Monte Agner	12	1	10	58.69	5.57	28.05	6.92	1.77	0.39
80	M Serva	Zoldo Dolomites	Monte Serva	17	7	10	44.63	4.40	10.72	3.08	2.02	0.37
81	V Zemola	Carnic pre-Alps	Val Zemola	14	8	10	42.04	3.55	10.18	2.61	2.28	0.45
82	S Martino	Pale di San Martino	Sentiero dei Cacciatori	50	26	30	57.87	4.45	24.24	4.46	1.84	0.34
83	Depaoli	Pale di San Martino	Sentiero Depaoli	50	16	10	58.66	2.90	26.21	4.60	1.73	0.36
84	Trafoi-2	W Vinschgau Alps	Madatsch Gletscher	25	0	30	50.95	8.06	14.31	2.80	1.51	0.23
85	Sulden	Ortler Alps	Sulden Legerwand	7	0	7	63.91	2.90	22.89	6.32	1.60	0.43
86	Polar Ural	Polar Ural	Harp settlement	15	5	10	46.19	2.52	10.98	2.88	1.95	0.25
87	V Cavargna	Como pre-Alps	M Stabiello	4	0	0						
88	Serfaus	Samnaun Group	Serfaus	7	2	0						
89	Fimbertal	Samnaun Group	Fimbertal	2	0	0						
90	Kaunertal	Ötztal Alps	Kaunertal	8	0	0						
91	Jaufenpass	Sarntal Alps	Jaufenpass road	2	2	0						
92	Kurzras	Ötztal Alps	Schnalstal	11	1	0						
93	M Stivo	Garda pre-Alps	M Stivo	5	1	0						
94	Cima d'Asta	Cima d'Asta	Val Regana	5	0	0						
95	Lagorai	Lagorai	Cermis	7	50	0						
96	Segantini	Pale di San Martino	Baita Segantini	5	0	3	41.43	2.47	13.09	1.61	2.42	0.86
97	Valles	Passo Valles	Catena di Bocche	4	0	0						
98	S Pellegrino	Marmolada Group	Passo S pellegrino	10	9	5	46.67	2.39	11.69	3.84	2.35	0.44
99	Gares	Pale di San Martino	Val di Gares	16	9	14	59.07	6.12	23.25	4.35	1.91	0.61
100	Zoldo	Zoldo Dolomites	Val di Zoldo	2	0	4	42.26	3.36	8.65	4.39	2.50	0.75
101	Pordoi	Marmolada Group	Passo Pordoi	15	0	3	46.12	3.88	9.83	2.50	2.56	0.52
102	Plattkofel	Sasso Lungo Group	Plattkofel	7	2	0						
103	Rosengarten	Catinaccio	Val delle Feide	17	22	0						
104	M Grappa	Belluno pre-Alps	Monte Grappa	13	0	13	57.44	4.28	23.71	3.35	1.71	0.47
105	Zell am See	Zillertal Alps	Schmittenhöhe	8	0	0						
106	Bagozza	Bergamasque pre-Alps	Bagozza Group	6	1	0						
107	Melag	Ötztal Alps	Langtauferertal	20	15	0						
108	Gößgraben	High Tauern	Ankogel Group	51	0	0						
109	Goldberg	Gailtal Alps	Goldbergsattel	12	5	0						
110	Gemona	Julian pre-Alps	Malga Cuarnan	20	14	0						
111	Mallnitz	High Tauern	Ankogel Group	5	3	0						
112	Falcade A	Marmolada Group	Falcade Alto	6	8	0						
113	Pejo	Ortler Alps	Val di Pejo	3	2	3	58.40	4.22	16.76	3.12	2.11	0.21
114	M Stabiello	Como pre-Alps	Val Cavargna	4	0	4	54.56	5.08	13.35	2.67	1.37	0.10

parameters lie in the overlap zone of two groups. The portion of such total transitions, in the Alpine populations, ranges from 12% (groups 2 and 3) to 29% (groups 1 and 3). To test whether this is due to inadequacy of the parameters or to lack of morphological signal, the right valves of all total transitions were photographed, randomised and identified by visual examination. Misidentifications, including doubts, range from 1.8% (groups 1 and 2) to 4.1% (groups 1 and 3). This demonstrates that valve shape (Fig. 4) offers reliable microscopic identification criteria, but that the parameters (derived from the poor pre-existing knowledge) insufficiently cover the differences between the groups on the individual level. They are appropriate, though, for identification of even a small sample (N = 10).

2 Wing pattern

None of the three groups, based on valve shape, coincides with any of the traditional wing morphologic groups. Valve type 1 is found in all populations of the *adyte* group, except those that live east of the Valtellina – Val di Trafoi line. Valve type 2 is associated with all (Alpine and extra-Alpine) populations of both the *euryale* group and the *ocellaris* group, except those in the Pala Group, the Feltre Dolomites and the Venetian pre-Alps. Valve type 3 is found in the remaining populations, i.e. in (i) a group of populations that were hitherto attributed to *adyte*, (ii) a group of populations hitherto considered *ocellaris*, and (iii) a group of morphologically intermediate populations. Grouping based on valve shape and grouping based on wing pattern thus do not match. From now on, valve morphology will be the leading criterion.

The geographic range of group 1 includes the type locality of ssp. *adyte*, and the range of group 2 includes the type locality of ssp. *euryale*. Consequently, groups 1 and 2 retain the names *adyte* group and *euryale* group. The type locality of ssp. *ocellaris* lies within the group 2 area, hence *ocellaris* is the valid name of the melanistic Alpine populations of the *euryale* group.

Both the *euryale* group and group 3 thus consist of melanistic and non melanistic populations. In both cases, intermediate populations do exist. These need to be recognised and separated before the wing pattern of the three groups and their (melanistic and non-melanistic) subgroups can be described.

Intermediate populations in the *euryale* group. In table 2A all Alpine populations of the *euryale* group (i.e. ssp. *isarica*, ssp. *ocellaris* and the intermediate populations) were ranked according to decreasing band development. For comparison the melanistic populations of group 3, hitherto considered *ocellaris*, were included. Tab. 2 breaks up into four sections, corresponding to four geographically coherent groups of populations. (i) Numbers 1–11 are pure *isarica* populations. (ii) Numbers 12–21 are intermediate between *ocellaris* and *isarica*. (iii) Numbers 22–31 are typical *ocellaris* populations. (iv) The last five populations belong to group 3. There are no intermediate populations here: the values drop abruptly after population 31.

Geographic range. The intermediate *isarica/ocellaris* populations are found in a continuous belt along the southern slopes of the southern Ötztal Alps, the Zillertal Alps and the High Tauern (Fig. 6A). Its western limit is the Weisskugel-Hochalt chain

Tab 2. The Alpine and Pyrenean/Cantabrian populations of the *euryale* group, arranged according to decreasing development of the postdiscal band (sum of the mean scores for forewing upperside, forewing underside and hindwing upperside). Melanistic populations of group 3 are included in the Alpine series for comparison (in italics).

Rank	Locality	Sample	Band
	A. Alps		
1	Steinernes M	4	11.53
2	Karwendel	2	11.52
3	Kitzbüheler A	3	11.33
4	N Tauern	8	11.29
5	Kaiser	1	11.27
6	H Tauern (N)	7	11.11
7	Tuxer A	18	11.04
8	Stubaier A	5	11.00
9	Goldeck	10	10.80
10	Grindelwald (S)	53	10.72
11	Gurktal A	9	10.50
12	Ötztal Alps (S)	14	9.54
13	Zillertal A	6	9.45
14	Ridnaun	59	9.21
15	Julian A (C)	11	9.00
16	Kreuzeck	23	7.92
17	Julian A (W)	12	7.65
18	Fleisstal	13	7.20
19	Hochschober	22	7.10
20	Val di Vizze	58	7.00
21	Aurine G	20	6.50
22	Defereggen G	21	5.84
23	P Mauria	26	5.73
24	Sesto	32	5.54
25	Sappada	16	5.52
26	P Rolle (W)	15	5.46
27	Lienzer Dol	27	5.42
28	Plöckenpas	33	5.26
29	Geisler G	19	5.06
30	V Zemola	81	4.57
31	M Serva	80	4.35
32	*Frassenè*	*79*	*1.92*
33	*Feltre*	*24*	*1.56*
34	*Cavallo*	*17*	*1.24*
35	*Cimonega*	*77*	*1.24*
36	*Visentin*	*78*	*0.96*
	B. Pyrenees/Cantabria		
1	Pyrenees (E)	49	10.15
2	Cantabria	51	9.25
3	Pyrenees (C)	50	7.31
4	Pyrenees (W)	48	4.42

(samples 14 and 92), its eastern limit is the Ankogel-Reißeck chain (sample 111). West of the former (Matschertal) and east of the latter (sample 108) flies pure *isarica*. From there it bends south, through the central Gailtal Alps (sample 109) into the western Julian Alps (samples 11, 12 and 110). One intermediate population is found north of the High Tauern chain (sample 6). The transitional belt thus separates the *isarica* range and the *ocellaris* range across its entire length, which is typical of a hybrid zone.

A second hybrid zone in the *euryale* group is found in the Pyrenees (Table 2B). The melanistic ssp. *antevortes* (sample 48) lives in the north-western Pyrenees. The Spanish side and the eastern Pyrenees are inhabited by the non-melanistic ssp. *pyraenaeicola* (sample 49). Hybrid populations are found in between (sample 50), but sampling density was insufficient to delimit the respective distribution areas. Ssp. *cantabricola* (Cantabrian Mountains, sample 51) is morphologically close to ssp. *pyraenaeicola*.

Intermediate populations in group 3. In table 3, all populations of this group were ranked according to (i) decreasing band development and (ii) decreasing value for ocelli development. For both characters, the 13 highest ranking populations are those with an *adyte* habitus. These are provisionally designated as group 3a. The five lowest ranking populations, in both cases, are the melanistic ones (from now on designated as group 3b). Populations 14–20 are transitional in both characters: they show a tendency towards loss of the white pupil in the forewing and hindwing ocelli, and to reduction of the postdiscal bands (Fig. 7).

Geographic range. The geographic borderline between group 3a and the transitional zone is sharp, and coincides with the Adige valley south of the confluence with the Avisio (Fig. 6A). The eastern borderline of the tran-

Tab 3. Group 3 populations, arranged according to decreasing development of the postdiscal band (left), and according to decreasing development of the white pupilled ocelli (right). Band = sum of the mean scores for forewing upperside, forewing underside and hindwing upperside. Ocelli = sum of the mean scores for forewing upperside and hindwing upperside.

Rank	Locality	Sample	Ocelli
1	Pradilago	69	3.79
2	M Legnone	41	3.44
3	Val Concei	38	3.44
4	Val Malga	34	3.42
5	Pzo Redorta	42	3.14
6	Croce Domini	35	3.14
7	M Tremalzo	37	3.14
8	M Baldo	36	3.12
9	Presolana	43	3.03
10	Paganella	68	3.00
11	Brenta	67	2.70
12	Martelltal	40	2.63
13	Mendelpass	61	2.50
14	Carega	28	2.38
15	P. Rolle (E)	25	2.32
16	Pasubio	31	2.29
17	P Malghen	30	2.08
18	Lavarone	29	2.04
19	S Martino	82	2.04
20	Depaoli	83	1.82
21	Feltre	24	1.26
22	Cimonega	77	1.02
23	Frassenè	79	0.83
24	Cavallo	17	0.74
25	Visentin	78	0.61

Rank	Locality	Sample	Band
1	Val Malga	34	11.33
2	M Legnone	41	10.96
3	Pzo Redorta	42	10.93
4	Croce Domini	35	10.90
5	Presolana	43	10.59
6	Val Concei	38	10.56
7	M Baldo	36	10.52
8	Paganella	68	10.44
9	M Tremalzo	37	10.14
10	Pradilago	69	10.04
11	Mendelpass	61	10.00
12	Brenta	67	9.90
13	Martelltal	40	9.83
14	Lavarone	29	9.06
15	Carega	28	8.36
16	Pasubio	31	8.14
17	P Malghen	30	7.72
18	P. Rolle (E)	25	5.18
19	S Martino	82	5.02
20	Depaoli	83	3.22
21	Frassenè	79	1.92
22	Feltre	24	1.56
23	Cavallo	17	1.24
24	Cimonega	77	1.24
25	Visentin	78	0.96

sitional group follows the Cismon valley and the Brenta valley south of the confluence with the Cismon.

Wing characteristics of groups and subgroups (Tab. 4)

Wing characteristics of the *adyte* group and the *euryale* group were adequately described long ago (Warren 1936). Hence, differentiating characteristics of group 3 will be emphasised here.

Group 1 (the *adyte* group) is characterised by the white pupilled apical ocelli (males 90%, females 100%) and the reduced white postdiscal scaling on the male hindwing underside, which is often absent or confined to a white wedge on nerve 4 (81%).

Group 2. Common characteristics of all (melanistic and non-melanistic) subspecies in the *euryale* group are the blind apical ocelli on the forewing upperside (males 98%, females 71%) and the brown ringed ocelli on the hindwing underside (males 89%, females 81%).

Tab. 4. Results for wing pattern elements, summarised per group, in percent. Col = colour of the postdiscal band on the female hindwing underside.

	FwUpOc			HwUpOc			FwUnOc			HwUnOc			FwUpB						HwUpB					FwUnB				HwUn White				Col	
	0 (no ocelli)	1 (ocelli without white pupil)	2 (ocelli with white pupil)	0 (no ocelli)	1 (ocelli without white pupil)	2 (ocelli with white pupil)	0 (no ocelli)	1 (black ocelli)	2 (black with white pupil)	0 (no ocelli)	1 (black spots)	2 (black with brown ring)	0 (no band)	1 (rings around ocelli)	2 (drop shaped spots)	3 (band broken up)	4 band continuous, constricted)	5 (band continuous, straight)	0 (no band)	1 (rings around ocelli)	2 (band broken up)	3 (spots touching)	4 (continuous band)	0 (no band)	1 (separate spots)	2 (interrupted band)	3 (complete band)	0 (no white scaling)	1 (wedge on nerve 4)	2 (more than wedge)	3 (white streak from costa to n4)	1 white	2 yellow
MALES																																
Alpine subspecies																																
ssp. *adyte*	0	8	92	3	5	92	0	0	100	7	80	13	0	0	0	4	94	1	0	0	1	27	72	0	0	0	100	33	48	14	4		
ssp. *isarica*	2	93	4	7	88	5	2	48	50	2	1	97	0	0	4	10	24	62	0	1	11	44	44	0	0	2	98	13	44	30	14		
transitional *isarica / ocellaris*	5	94	1	8	92	1	1	73	26	6	3	92	0	9	50	20	14	6	2	18	46	28	7	0	1	15	84	32	41	24	3		
ssp. *ocellaris*	2	97	1	8	92	0	2	71	27	11	4	85	1	44	49	5	1	0	5	62	32	1	0	0	5	41	54	46	31	21	2		
euryale group	3	95	2	8	90	2	1	64	34	6	2	91	0	19	34	11	12	22	2	28	29	23	17	0	2	18	78	31	38	20	6		
ssp. *pseudoadyte*	0	23	77	12	38	49	0	1	99	19	77	4	0	0	0	7	79	13	0	1	11	53	34	0	0	1	99	14	17	36	33		
transitional *pseudoadyte / kunzi*	3	46	51	47	44	9	4	11	85	67	30	2	7	17	29	22	23	2	25	25	24	24	1	4	6	33	57	18	31	35	16		
ssp. *kunzi*	34	49	18	93	7	0	37	17	46	92	8	0	67	31	2	0	0	0	92	8	0	0	0	51	18	25	5	61	25	14	0		
kunzi group	9	37	54	44	33	24	10	8	81	53	44	2	19	13	10	11	41	6	31	11	13	30	15	14	6	13	62	27	24	21	19		
All subspecies																																	
adyte group	0	10	90	6	7	87	0	0	100	10	78	12	0	0	0	4	95	1	0	0	1	31	67	0	0	0	100	33	48	14	4		
euryale group, non melanistic	2	93	4	9	85	6	1	47	51	2	1	96	0	0	5	14	25	57	0	2	17	41	39	0	0	2	98	21	42	29	7		
euryale group, transitional	5	94	1	8	91	1	1	73	25	10	7	84	0	8	48	21	13	10	2	18	48	27	5	0	1	14	86	38	39	20	3		
euryale group, melanistic	2	97	1	10	90	0	2	73	26	13	5	81	2	43	49	5	1	0	6	61	31	1	0	0	5	41	53	48	30	20	2		
euryale group	3	94	2	9	88	3	1	61	37	7	4	89	1	14	29	13	15	28	2	23	29	26	19	0	2	14	82	33	38	20	4		
FEMALES																																	
Alpine subspecies																																	
ssp. *adyte*	0	0	100	0	1	99	0	0	100	6	91	3	0	0	0	1	98	1	0	0	2	33	65	0	0	0	100					87	13
ssp. *isarica*	2	56	42	2	58	41	2	11	87	3	5	92	0	0	0	3	41	56	0	0	7	53	41	0	0	0	100					84	16
transitional *isarica / ocellaris*	0	68	32	1	81	18	0	15	85	3	26	70	0	13	31	27	17	12	0	12	42	39	7	0	0	0	100					67	33
ssp. *ocellaris*	0	90	10	0	94	6	0	14	86	11	11	77	0	44	47	7	0	1	0	67	31	2	0	0	1	14	86					50	50
euryale group	0	75	25	1	81	18	0	14	86	7	14	79	0	24	31	13	15	18	0	33	29	26	12	0	0	4	94					63	37
ssp. *pseudoadyte*	0	1	99	7	16	76	0	0	100	17	83	0	0	0	1	4	80	15	0	3	12	56	29	0	0	0	100					86	14
transitional *pseudoadyte / kunzi*	1	5	94	43	33	25	1	1	98	62	36	1	4	18	38	21	16	3	30	41	19	9	1	0	1	16	82					91	9
ssp. *kunzi*	20	18	62	96	4	0	18	2	80	89	11	0	73	24	2	0	0	0	98	2	0	0	0	13	13	49	24					76	24
kunzi group	3	5	92	34	22	44	3	1	97	46	53	1	11	11	18	11	42	8	26	20	14	28	13	2	2	7	83					87	13
All subspecies																																	
adyte group	0	0	100	1	2	98	0	0	100	9	89	3	0	0	0	2	98	1	0	1	4	34	62	0	0	0	100					86	14
euryale group, non melanistic	1	52	47	3	51	46	1	9	90	4	4	91	0	0	1	12	34	52	0	3	10	47	40	0	0	0	100					68	32
euryale group, transitional	0	68	32	1	81	18	0	15	85	3	26	70	0	13	31	27	17	12	0	12	42	39	7	0	0	0	100					67	33
euryale group, melanistic	0	90	10	0	94	6	0	14	86	11	11	77	0	44	47	7	0	1	0	67	31	2	0	0	1	14	86					50	50
euryale group	0	71	28	1	76	22	0	13	87	7	12	81	0	21	28	15	16	21	0	30	28	27	15	0	0	3	94					61	39

Group 3a (differences with ssp. *adyte*). Both have basically the same wing pattern. In group 3a most wing pattern elements are somewhat less developed, both in males and in females. Some 23% of the group 3a males lack the white pupil in the apical ocelli on the forewing upperside (8% in *adyte*), and 65% of them have a discontinuous band on the hindwing upperside (28% in *adyte*). On the hindwing underside, on the other hand, a white streak from the costa at least to nerve 4 is present in 33% of the group 3a males, as opposed to 4% in *adyte*. These differences, in combination, will enable identification of a population; identification on the individual level will often require genital examination.
Group 3b (differences with ssp. *ocellaris*). The resemblance between both is superficial, as group 3b is an adytoid form, *ocellaris* an euryaloid one. Melanisation is more extreme in 3b than in *ocellaris*. In many individuals there is no trace of the postdiscal band on the forewing upperside (males 67%, vs. 1% in *ocellaris*, females 73% vs. 0%), on the forewing underside (males 51% vs. 0%, females 13% vs. 0%) and on the hindwing upperside (males 92% vs. 5%, females 98% vs. 0%). Most conspicuous are the males that, apart from the checked fringes, have a completely black upperside, without any trace of ocelli or postdiscal banding (32% vs. 0%)*, or only deep black apical spots on a black background (33% vs. 0%)*. In the individuals with apical spots on the forewing upperside, though, white pupils are present in 26% of the males and 77% of the females (1% and 10% in *ocellaris*). A further difference is the black instead of dark brown ground colour in the males, even on the hindwing underside. (Percentages marked with * are not directly readable from Table 4).

Genital differences between subgroups

After delimitation of the groups and subgroups, the latter were tested for differences in their genital characters. This revealed (i) that ssp. *isarica* and ssp. *ocellaris* do not exhibit significant differences, and (ii) that group 3a has a significantly lower Shoulder Index value and a significantly higher First Tooth value than group 3b (Table 5). (iii) The transitional group 3 populations are not intermediate in this respect, but equal group 3b.

Contact sites between groups

Contact site of group 3 and the *adyte* group. The area of the non-melanistic group 3 populations is surrounded by deep valleys of the rivers Adda, Rio Trafoi and Adige. The only possible contact zone with ssp. *adyte* is the Stelvio region. East of the pass *adyte* populations occur on the left bank of Rio Trafoi (sample 39 and 84), whereas group 3 was found above Sulden (sample 85), less than 9 km east (Fig. 6B). To test for gene flow, sample 85 was compared with the remaining group 3a populations, and samples 39 and 84 were each compared with the remaining *adyte* populations. Both sample 39 and 84 differed significantly from the control group in a single parameter (Table 5), which might well result from (former) interbreeding. The higher

Tab. 5. Pair wise comparison of samples or groups of samples. * = p with equal variances not assumed (Levene's $p < 0.05$). Significant differences in bold (significance level = 0.05).

Groups compared	N	Test	First Tooth	Shoulder Index	Tooth Length
			p	*p*	*p*
ssp. *isarica*	60	Student's t	0.501	0.114	0.700
ssp. *ocellaris*	105				
group 3a	128	Student's t	**<0.001***	**<0.001**	0.928*
group 3b	77				
group 3a	128	Student's t	**<0.001**	**0.001**	0.204
group 3 trans.	100				
group 3b	77	Student's t	0.144	0.667	0.386*
group 3 trans.	100				
sample 39	10	Mann-Whitney H	0.968	**0.025**	0.822
ssp. *adyte*	104				
sample 84	30	Mann-Whitney H	0.430	0.069	**0.031**
ssp. *adyte*	104				
sample 85	7	Mann-Whitney H	**0.005**	0.597	0.230
group 3a	121				
sample15	30	Student's t	0.757	0.585	0.758
ssp. *ocellaris*	75				
sample 25	30	Student's t	0.564	0.078	0.551
group 3 trans.	40				
sample 82	30	Student's t	0.637	0.389	0.477
group 3 trans.	40				

First Tooth value in sample 85, on the other hand, is opposite to the expected effect of gene flow.

Contact site of group 3 and the *euryale* group. Contact sites of ssp. *ocellaris* and group 3b populations can be expected near the Passo Rolle, and in the Biois valley between Valle di Gares and Falcade. Four samples were available from the Passo Rolle region (see Fig. 6C). Populations of group 3 live south of the pass height, both in the glades of the *Larix* wood (sample 82) and above the timberline (sample 25), whereas ssp. *ocellaris* is common on its north side, in the clearings of the *Picea* wood (sample 15) and above the tree line (sample 96). The shortest distance between populations of both groups is 1.5 km (samples 25 and 96). Group 3 populations on the southern side of the pass are transitional melanistic/non-melanistic populations. A wide range of intermediate individuals occur, some of which would not be distinguishable from ssp. *ocellaris* by their upperside wing pattern. None of them, though, has the brown ringed ocelli on the hindwing underside, typical of the *euryale* group. In an attempt to detect gene flow in genital characters, sample 15 was compared with the remaining *ocellaris* populations, and samples 25 and 82 were each compared with the remaining transitional group 3 populations. No significant differences were found (Tab. 5). Thus genital characters do not reveal any sign of intermingling here. As far as can be judged from the available data, the ranges of the *euryale* group and group 3 are in contact without building a hybrid zone.

Discussion

The taxonomical implications

1 The valid names of the subspecies of group 3

The melanistic subspecies. Verity (1953: 217) was the first to recognise the peculiar character of the melanistic populations of group 3, when he described the population in the Valle di Gares as subrace *totenigra*. This name is not available, though, as Verity explicitly gave it infra-subspecific rank (ICZN 2000, art. 45.6.1). Heinkele (2007) described a population of the eastern foothill of the Monte Cavallo (Pala Fontana) as ssp. *kunzi*. The type locality lies within the range of group 3b, so *kunzi* is the only available and thus the valid name of the eastern (melanistic) subspecies of group 3.

Distribution. The territory of ssp. *kunzi* comprises the eastern Venetian pre-Alps (Monte Grappa, Col Visentin and Monte Cavallo), the Feltre Dolomites and the Pale di San Martino, as far north as the Passo Rolle – Falcade line.

The non-melanistic subspecies. For the western (non-melanistic) subspecies of group 3 no name is available within its geographic range. Dannehl's *mendolana* (Dannehl 1927) from the mountains around the Mendelpass (sample 85) is not available, as it is explicitly published as an aberration. Hence the non-melanistic populations of group 3 are described here as **ssp. n.**

***Erebia euryale pseudoadyte* ssp. n.** **(Fig. 8)**

Material. Holotype: ♂, 'Monte Baldo (It)'|'Mte Altissimo di Nago'|'1500–1700m.'|'12.VII.2001'|'F. Cupedo leg.', CFC; – Paratypes: 37♂, 4♀, same label, CFC; 7♂, 1♀, same label, coll. ZMAN; 16♂, 8♀, 'Monte Baldo (It)'|'Mte Altissimo di Nago'|'1700–2000m.'|'12.VII.2001'|'F.Cupedo leg.', CFC; 5♂, 6♀, same label, coll. ZMAN.

Description. Valve shape. Male valve with a prominent, hump-shaped shoulder on its dorsal edge. The part of the dorsal ridge proximal to the shoulder is free of spines. Wing pattern. Male forewing length 21–23 mm, androconial scales absent. Fringes checked black and white. Postdiscal band distinct, reddish brown, often contracted below the apical spots. The apical ocelli bear a white pupil in 77% of the individuals. Postdiscal band on hindwing upperside broken up into isolated spots, whose inner edge is suffused. Hindwing underside with a white streak from the costa at least to nerve 4 in a third of the males. Female upperside basically as in males, banding and ocelli more developed. Postdiscal band on hindwing underside either white or yellow/orange, variable in width.

Diagnosis. Differs from all ssp. of the *euryale* group and the *adyte* group by the pronounced shoulder on the dorsal edge of the valve, and the longer spine-free proximal part of the valve. Differs from ssp. *kunzi* by its non-melanistic wing pattern.

Etymology. The name refers to the strong similarity, in its wing pattern, with ssp. *adyte*.

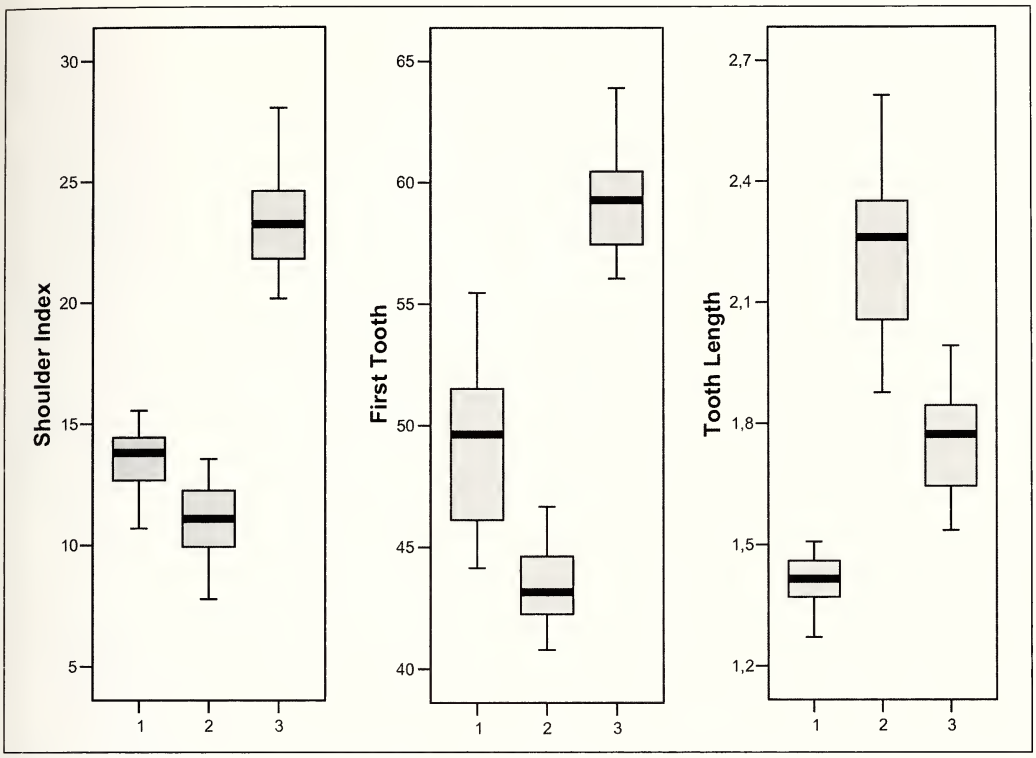

Fig. 5. Boxplots per group of populations for each genital parameter. X-axis: group number.

Distribution. ssp. *pseudoadyte* inhabits the Southern Rhaetian Alps (Ortler, Adamello-Presanella, Brenta and Nonsberger Alps); the Bergamasque Alps and pre-Alps; the Brescian and Garda pre-Alps (see Fig. 6A).

The transitional populations. The Venetian pre-Alps west of the Canale di Brenta (Altipiani, Piccole Dolomiti and Monti Lessini), the Lagorai chain and the Cima d'Asta group in the south-western Dolomites are inhabited by populations that are intermediate between ssp. *pseudoadyte* and ssp. *kunzi*. The transitional zone is separated from the territories of both subspecies by natural barriers, which makes a hybrid origin less obvious than in the case of *isarica/ocellaris*. Three observations even contradict a hybrid origin. (i) Populations 25, 82, 83 and 77 show a clinal variation in all wing characters on the eastern slope of the upper Cismon valley (Tab. 3). This is an indication of former infiltration from the Lagorai chain into the Pala group, and not vice versa. (ii) The white/yellow ratio in the colour of the postdiscal band on the female hindwing underside is different in the sister taxa *pseudoadyte* and *kunzi*, as it is in the sister taxa *isarica* and *ocellaris*. In contrast with the *euryale* group, though, transitional populations in group 3 do not show an intermediate value (Tab. 4), suggesting that these populations have independently been subjected to genetic drift. (iii) With respect to genital differences between groups 3a and 3b, the transitional populations are not intermediate either, but fit into group 3b. These

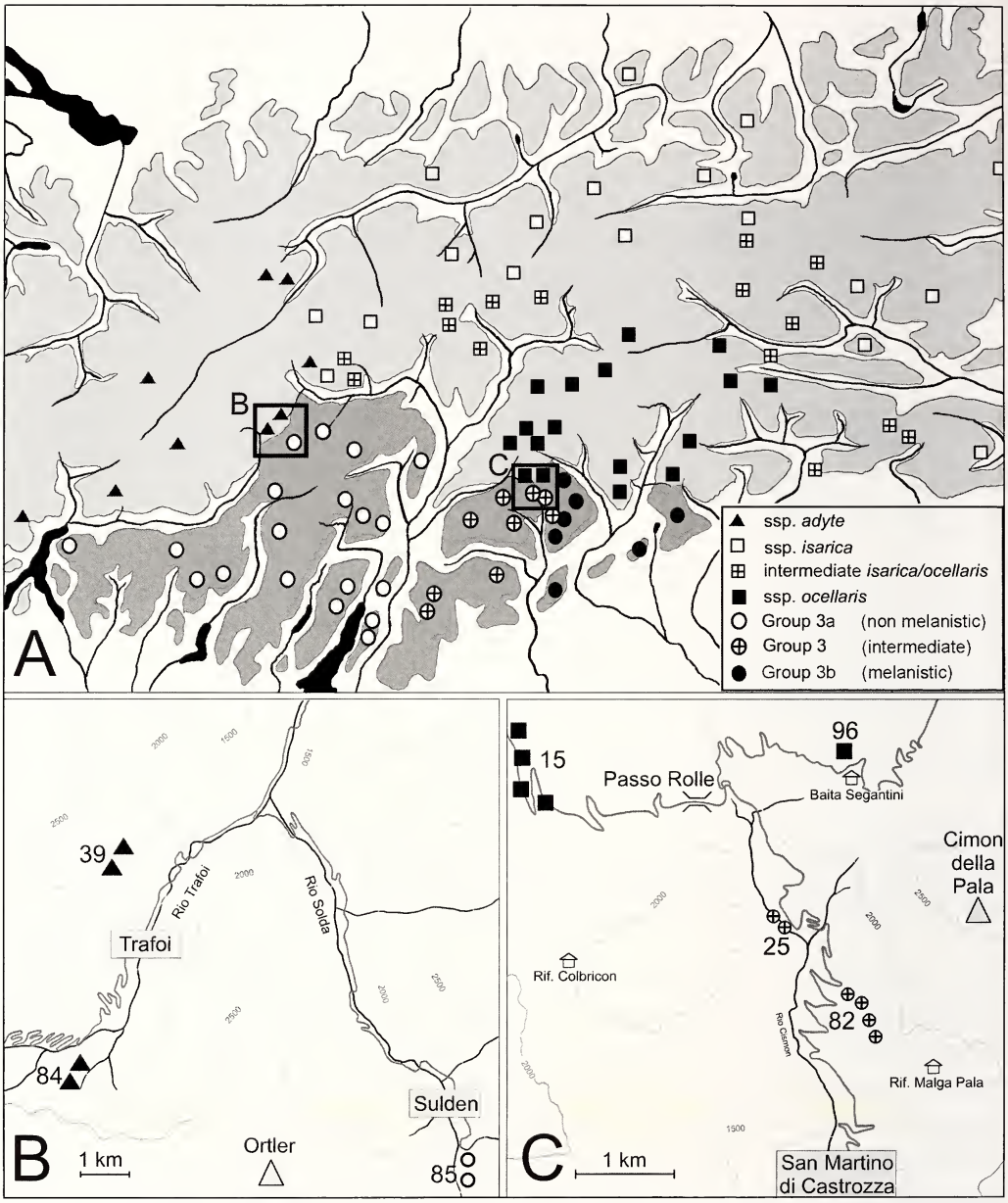

Fig. 6. A. Distribution of the groups and their subgroups in the eastern Alps. Light and dark grey: mountains above 1000 m. Dark grey: distribution area of group 3. Squares: contact areas. B. Contact area near Sulden. Grey: roads. C. Contact area at Passo Rolle. Grey: roads.

arguments cast doubt on the hybrid character of the transitional populations, and are suggestive of an autochthonous origin. Because morphologic data alone cannot be decisive here, the the transitional populations are, provisionally, placed within ssp. *kunzi*. This choice is based on the corresponding values for the genital parameters.

Fig. 7. Variation range in group 3. Row 1: non-melanistic population (sample 36). Row 2+3: transitional populations (samples 28 and 82). Row 4: melanistic population (sample 24).

2 The valid names of the three groups

The populations of *E. euryale* split up into three genital-morphologic, geographically coherent groups of populations. There is limited, if any, gene exchange between these groups. Each of them comprises more than one subspecies. Where two subspecies of one group meet, hybrid populations occur. The groups thus represent a differentiation level between species and subspecies. This kind of hierarchic structuring is expressed

Fig. 8. Left: *E. euryale pseudoadyte* **ssp. n.** (Monte Baldo, I, sample 36). Right: *E. euryale adyte* (Ticino, CH, sample 60). Row 1: males upperside; 2: males underside; 3: females upperside; 4: females underside. Upper left, row 1+2: holotype.

in nomenclature by inserting a group name, in parenthesis, after the species name in the trinomen. According to art. 6.2 of the Code (ICZN 2000) the groups should be named *Erebia euryale* (group *euryale*), *Erebia euryale* (group *adyte*) and *Erebia euryale* (group *kunzi*). The slender shaped valve and the weak differentiation of wing pattern suggest closer affinities of the *kunzi* group to the *adyte* group than to the *euryale* group.

Conclusions

The infraspecific variation in *Erebia euryale* is hierarchically structured in two levels: wing pattern based subspecies are clustered in groups that are defined by their genital anatomy. In the genus *Erebia* this is a recurrent pattern, which was described earlier in the *E. sudetica/melampus* complex, in *E. manto* and in *E. pandrose* (Cupedo 1996, 1997, 2007).

The combined genital/wing morphologic approach revealed two longstanding misinterpretations that affected the existing subspecific classification of *E. euryale*: (i) the melanistic populations in the southern Alps, hitherto considered a coherent group and known as ssp. *ocellaris*, are not monophyletic but result from convergent adaptations, and (ii) the "*adyte* habitus" remained practically unchanged during the divergence of the *adyte* group and the *kunzi* group, giving the false impression of one, morphologically well-defined taxon. These misconceptions being corrected, the infraspecific structure reconstructed here is expected to reflect the phylogenetic relations more accurately than earlier classifications did.

Checklist

This list aims to rearrange the described subspecies of *E. euryale* into three group. It is no taxonomic revision; the justification of subspecies remains undiscussed.

1 *Erebia euryale* (group *euryale*)

Diagnosis: male valve broad, dorsal edge with irregular spines, short proximal spine-free part. Postdiscal ocelli on male hindwing underside black with a brown ring.

E. euryale (euryale) euryale (Esper, 1805) (LT. Giant Mountains, CZ.)
E. euryale (euryale) isarica Heyne, 1895 (LT. Mountains surrounding the Isarvalley, Tyrol, A.)
E. euryale (euryale) syrmia Fruhstorfer, 1909 (LT. Trebević, Bosnia-Herzegowina.)
E. euryale (euryale) tramelana Reverdin, 1918 (LT. Tramelan, Jura, CH.)
E. euryale (euryale) phoreta Fruhstorfer, 1918 (LT. Mont Dore, Auvergne, F.)
E. euryale (euryale) antevortes Verity, 1927 (LT. Cauterets, Hautes Pyrenées, F.)
E. euryale (euryale) pyraenaeicola v.d. Goltz, 1930 (LT. Vernet-les-Bains, Pyrenées Orientales, F.)
E. euryale (euryale) cantabricola Verity, 1927 (LT. Puerto Pajares, Asturias, E.)
E. euryale (euryale) euryaloides Tengström, 1869 (LT. Finland.)
E. euryale (euryale) arctica Poppius, 1906 (LT. Kanin peninsula, RU.)
E. euryale (euryale) ocellaris Staudinger, 1861 (LT. Carinthia, A.)

2 *Erebia euryale* (group *adyte*)

Diagnosis: male valve slender, dorsal spines fine and separate, with a large spine-free proximal part.

E. euryale (adyte) adyte (Hübner, 1822) (LT: Wallis, CH.)
E. euryale (adyte) etobyma Fruhstorfer, 1909 (LT: Col de Tende, Alpes Maritimes, F.)
E. euryale (adyte) brutiorum Turati, 1911 (LT. Gran Sasso, Abruzzo, I.)

3 *Erebia euryale* (group *kunzi*)

Diagnosis: male valve slender, with a prominent shoulder and a spine-free proximal part that reaches to the base of the shoulder.

E. euryale (kunzi) kunzi Heinkele, 2007 (LT. Pala Fontana, Monte Cavallo, Friuli-Venezia Giulia, I.)

E. euryale (kunzi) pseudoadyte **ssp. n. (**LT. Monte Baldo, Trentino, I.)

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Appendices

Appendix 1

Morphologic differences between the traditionally recognised groups in *E. euryale*: the *euryale* group, the *adyte* group and the *ocellaris* group.

Male wing pattern (according to Warren 1936)
(i) The *euryale* group.
Forewing upperside: ocelli without white pupils. Postdiscal band complete.
Hindwing underside: postdiscal band conspicuous. Ocelli with a brown ring.
(ii) The *adyte* group.
Forewing upperside: ocelli with prominent white pupils. Postdiscal band complete, restricted below the apical spots.
Hindwing underside: postdiscal band faintly indicated. Ocelli without brown ring. White streak lining the discal field often reduced to a small tooth, projecting basad along nervure 4.
(iii) The *ocellaris* group.
Forewing upperside: ocelli without white pupils. Postdiscal band reduced, broken up into spots around the ocelli.
Hindwing underside: ocelli black with brown ring.
Female wing pattern
Upperside wing pattern as in males, but more luxurious.
Underside hindwing: the colour of the postdiscal band is either white or yellow (nuances disregarded).
Valve morphology
Valvae of ssp. *adyte* are slender, with a dorsal shoulder; in ssp. *ocellaris* and ssp. *isarica* (*euryale* group) they are broader without marked shoulder (Arnscheid & Roos 1977).
In ssp. *adyte* the valvae bear fine and regularly spaced spines, in ssp. *isarica* (*euryale* group) these are larger, irregularly in shape and arrangement. The proximal spine-free part of the valve is larger in ssp. *adyte* than in ssp. *isarica*. (Sonderegger 2005)

Appendix 2

Quantification criteria for wing pattern elements.
Postdiscal band on forewing upperside (males and females)
0 = absent.
1 = narrow ring around ocelli (ocellaroid). As a rule no spot in cell 3.
2 = rings stretched drop shaped, but separated. As a rule a spot in cell 3.
3 = incomplete band. Spots in cell 2 and 3 not united, or spot in cell 3 strongly constricted (narrower than high).
4 = band continuous, outer margin concave.
5 = band continuous, outer margin straight or convex.

Postdiscal band on forewing underside: (males and females)
0 = absent.
1 = spots separated, band often incomplete.
2 = band complete, strongly constricted or disrupted in cell 3
3 = complete band.
Postdiscal band on hindwing upperside (males and females)
0 = absent.
1 = ocellaroid.
2 = spots united at least in cells 4-5-6, detached in cells 2 and 3.
3 = band continuous.
Ocelli on forewing upperside, forewing underside and hindwing upperside (males and females)
0 = absent
1 = black
2 = pupilled white
Ocelli on hindwing underside (males)
0 = absent
1 = without brown ring
2 = with brown ring
White pattern on hindwing underside (males)
0 = absent
1 = white tooth on nerve 4
2 = additional white along costa, even if weak
3 = a continuous white streak from costa to at least nerve 4
Colour of postdiscal band on hindwing underside (females)
1 = white
2 = yellow or orange