Colour polymorphism of *Callimorpha dominula* (Linnaeus, 1758) in Italy, and the problem of polytopic subspecies

(Lepidoptera, Arctiidae, Callimorphinae)

Von Alberto Zilli

Abstract

Relict populations of *Callimorpha dominula* (Linnaeus, 1758) from Sicily are characterized by individuals virtually indistinguishable from those occurring in the Alps and northwards. This is in profound contrast with the phenotypes found in peninsular Italy (subsp. *persona* Hübner, 1790). The nominate subspecies becomes, therefore, a polytopic subspecies. A general review of the colour polymorphism of the species in Italy is also provided. Following a critical discussion of some pathways through which reoccurrence of characters between distant populations of a same species may occur, particular emphasis is laid upon the possibility that, in special cases, the reoccurrence is not independent, as claimed so far. It is put forward that some cases of polytopism might be parsimoniously explained considering the shift toward a different array of characters of the populations interposed between others, subject to stabilizing selection. It is suggested that archaic *dominula* populations in peninsular Italy underwent melanism and flavism, as now observed in *persona*, and started being involved with a 'southern' Müllerian mimicry ring based on yellow and black patterns. Because of the paucity of the day-flying moths bearing the yellow/black pattern in Sicily, due to a lack of colonization from the mainland, the *dominula* populations in the island would not have met the proper ecological context for undergoing a similar shift. A brief discussion on the subspecies concept tries to show how misused the subspecies category is in taxonomy, not least because of confusion between inductive and deductive processes while circumscribing subspecies and deficiencies in the concept itself. Events of character reoccurrence, and hence polytopic subspecies, are believed to represent a valid reason for abandoning the use of the subspecies category as scarcely informative or even misleading.

Contents

1 Introduction

The Scarlet Tiger Moth, *Callimorpha dominula* (LINNAEUS, 1758), is a well-known and outstanding western palaearctic species which has been a favourite subject for genetical and populational studies. In fact, after the pioneeristic work by STANDFUSS (1896), much research has been carried out on the formal and ecological genetics of *dominula*, among the others by eminent researchers such as CLARKE, GOLDSCHMIDT, COCKAYNE, KETTLEWELL, FISHER, FORD, OWEN, and SHEPPARD.

Details on the bionomics of the species can be drawn from several sources (e.g. WENZEL 1936, KETTLEWELL 1943, FISHER & FORD 1947, COOK 1959, 1961a, 1961b, 1961c, 1962a, COOK & KETTLEWELL 1960, OWEN 1993, 1994, 1996), however it is of interest to stress two main features, namely the day-flying habits of the moth (which is also partially night-active) and the tendency to form local, isolated colonies (KETTLEWELL 1943, FORD 1971). In particular, a spotted distribution of the populations is well-pronounced along peninsular Italy, the species there becoming decisively linked to mountainous areas as it does not tolerate the xeric conditions characteristic of low altitude mediterranean-type ecosystems.

The outstanding pattern of *dominula* (fig. 1) and the way of being displayed, e.g. while flying or resting upon flowers in the sunshine, are particularly characteristic of a distasteful, aposematic organism. The species was in fact shown to be provided with toxic substances (ROTHSCHILD 1961, KAY et al. 1969, EDGAR et al. 1980) and, accordingly, is rejected by natural predators such as birds (FRAZER & ROTHSCHILD 1960, ROTHSCHILD 1985).

According to recent revisionary work (FREINA & WITT 1987), the European populations of *C. dominula* should be split into four well delimited subspecies, namely *dominula* (s.str.), *pompalis* NITSCHE, 1926, *persona* (HÜBNER, 1790), and *bithynica* STAUDINGER, 1871. The main differences between these subspecies are summarised in table 1. Except for *bithynica*, the other three subspecies meet in Northern Italy, originating polymorphic populations in the contact zones (ROCCI 1913, TURATI 1919, 1923, KETTLEWELL 1943, COOK 1962b, E. BERTACCINI, in litt.) (fig. 1).

The remarkable distribution of the colour polymorphism shown by the Scarlet Tiger Moth gives a fine opportunity of reviewing the puzzling phenomenon of the polytopic subspecies and its consequences in taxonomy.

2 The Italian populations

Broadly speaking, nominate *dominula* occurs in North-West Italy, whereas melanic populations (ssp. *pompalis* NITSCHE, 1926) are found more easterly along the Alpine range, in the Dolomites and surroundings. *Callimorpha dominula persona* (HÜBNER, 1790) is exclusive to peninsular Italy, ranging from the Tusco-Aemilian Apennines to Calabria (fig. 1).

The *persona* phenotypes greatly differ from those of the other european subspecies, being characterized by hindwings and abdomen in which the usual red colour of the background is replaced by yellow and by much more conspicuous black markings. The melanism of *persona* is clearly polygenic, in fact several phenotypic classes along a continuum can be recognized, and in the extreme forms the black markings are entirely spread over the hindwings and the abdomen. The forewing apex is also stated to be more acute than in the nominate subspecies (FREINA & WITT 1987), but this trait is so unconstant that other authors maintained the contrary (e.g. TREITSCHKE 1834). Also the forewings are affected by the melanism, as evidenced by the reduced size of their pale spots, but only to a limited extent.

Because of the striking phenotypic differences between *persona* and nominate *dominula* some earlier

Table 1. Main differences between the European subspecies of *Callimorpha dominula* (LINNAEUS) currently recognized. FW, forewing; HW, hindwing.

subsp.	FW spots	HW colour	abdominal stripe	HW melanism
dominula	normal	red	narrow	no
pompalis	reduced	red	wide	yes
persona	reduced	yellow	wide	yes
bithynica	reduced	red	narrow	no

authors even put forward that they represent two distinct species (e.g. ESPER 1794, BOISDUVAL 1834, 1840, TREITSCHKE 1834, DUPONCHEL 1836, HERRICH-SCHÄFFER 1845). KETTLEWELL's (1943) credit is to have critically weighted the two alternative hypotheses about the conspecificity of *dominula* and *persona* through a remarkably elegant reasoning from a methodological standpoint, which is here briefly summarised.

Objectively, some evidence would agree with the existence of two species, above all the low fertility and larval viability of the crosses *dominula* (s.str.) × *persona*, as well as the assortative matings occurring when *dominula* (s.str.) males are given the choice between both types of females (STANDFUSS 1896, GOLDSCHMIDT 1924). On the other hand, the occurrence over large extensions of North Italy of populations in which the diagnostic characters of *persona*, i.e. melanism and flavism, are no more linked is definitely unsubstantial with the existence of more than one species (KETTLEWELL 1943). As a matter of fact, polymorphic populations with yellow unmelanic individuals are known in both the western and eastern districts of North Italy (Piedmont and Friuli), whereas *pompalis* populations, in short 'red *persona*', occur over most of the central-eastern Alpine sector (ROCCI 1913, NITSCHE 1926, DANNEHL 1928, KETTLEWELL 1943, COOK 1962b, FREINA & WITT 1987). Last but not least, *dominula* males are in any case attracted by *persona* females, whenever *dominula* females should be absent, and copulate with them producing some viable offspring, also obtainable through the reverse crosses (KETTLEWELL 1943).

Owing to the scanty data available, it cannot be ascertained whether the assortative matings between *dominula* and *persona*, as well as the lower fertility of their crosses, reveal the occurrence of two differentiated evolutionary lineages. The situation might in fact represent no more than a simple distance effect independent of the subspecies identified by taxonomists, e.g. a case of outbreeding depression coming out from the cross of differently coadapted genotypes sampled from distant populations (cf. OLIVER 1972, ENDLER 1977, TEMPLETON et al. 1986). Research on the courtship behaviour of the Scarlet Tiger Moth, involving a complex array of visual, chemical and acoustic signals (cf. BRAKEFIELD & LIEBERT 1985: 238), and crossing experiments between same phenotypes (e.g. *dominula* × *dominula*) from different areas would be decisive. Interestingly, some experiments on mate choice in a *dominula* population from England evidenced preferential matings between different genotypes (SHEPPARD 1951, 1952, SHEPPARD & COOK 1962, FORD 1971), being one of the few known cases of disassortative mating (PARTRIDGE 1983).

Despite the remarkable amount of work on the genetics of *dominula* in England, although contradictory (e.g. COCKAYNE 1928, KETTLEWELL 1943, FISHER & FORD 1947, WRIGHT 1948, 1978, SHEPPARD 1951, 1952, 1953, 1956, KETTLEWELL 1952, COOK & KETTLEWELL 1960, WILLIAMSON 1960, SHEPPARD & COOK 1962, FORD & SHEPPARD 1969, LEES 1970, FORD 1971, WHITE 1985, JONES 1989, 1993, CLARKE et al. 1990, 1991, 1993, OWEN & CLARKE 1993, OWEN & GOULSON 1994), far fewer data are available on the colour polymorphism of the Italian populations. From museum material it is evident that many amateurs had just crossed specimens north and south of the Alps to obtain beautiful hybrids for their collections. However more rational approaches were followed by STANDFUSS (1896), OBERTHÜR (1911), GOLDSCHMIDT (1924), COCKAYNE (1928) and KETTLEWELL (1943). Unfortunately, most of the experimental crosses were partial or with contradictory results, so a thorough picture of the genetics of the colour polymorphism in Italy is still wanting. It is not the aim of this paper to summarise again the old data available (cf. for reviews COOK 1962b, FORD 1971, ROBINSON 1971), nevertheless, attention should be focused on the normal red colour of *dominula* which is seemingly incompletely dominant over the yellow of the Italian forms (the true situation being probably quite complex), while the gene responsible for the yellow aberrations of *dominula* (s.str.), occurring throughout the species' range, behaves as totally recessive. It remains to be ascertained, therefore, whether the gene responsible of the yellow of the Italian forms is actually different from the *dominula* yellow gene, as suggested by KETTLEWELL (1943), possibly more than one gene being involved, or the discrepancy may be due to differential expression of the same gene in differentiated gene complexes such as those of distant populations, as mooted by FORD (1937).

Regarding the melanism of *persona*, the trait is fairly well described by incompletely dominant genes with additive effects in a two-loci system (GOLDSCHMIDT 1924). However, KETTLEWELL (1943) stressed the difference between yellow *dominula* and unmelanic *persona*, namely the enlarged black dorsal stripe of the abdomen of the latter (often blackening totally the urites), and referred to that character, exclusive to most of the Italian populations, as a 'primary melanistic factor'. This factor is usually associated with 'secondary' ones, i.e. those darkening the hindwings, but it is inherited independently.

Owing to the great variability of the species, affecting also many other traits such as forewing spotting (e.g. number, shape, size, colour, etc.), several authors tried to distinguish by nomenclature any kind of form (cf. BRYK 1937). The names were often misapplied, sometimes conferring to an individual aberration the role of a geographical race or, conversely, applying the name of a local race to vaguely resembling aberrations collected elsewhere. Other sources of errors were homonyms used to depict different forms, misidentifications

and application to wild specimens of names the use of which should have been restricted to laboratory hybrids. The main consequence is that it is a difficult task today to try to elucidate to which phenotypic classes belonged specimens reported in faunistic literature without adequate illustrations. For the sake of clearness it is therefore suggested avoiding using names of the forms and to directly relate to their morphological features. Moreover, mislabelling of bred specimens preserved in museums, particularly in the case of artificial hybrids (e.g. treating *dominula* × *persona* as if they were collected in the wild or in the place of residence of the breeder), is also something that prejudices a careful appreciation of the actual distribution of the colour forms.

2.1 Situation in North Italy and periphery

A satisfactory picture of the colour polymorphism in North Italy will be probably never attained as the current pattern of geographic variation suggests complex dynamics in space and time. The distribution of the melanism, in particular, is clearly mosaic-like in a spatially heterogeneous area such as that of the southern Alps. We find polymorphic populations with specimens ranging from normal *dominula* to *pompalis* east and west of the core area of the so-called ssp. *pompalis* (e.g. Friuli; Lombardia and Ticino). As one might expect, normal *dominula* do also occur within the range of *pompalis* (DANNEHL 1928, COOK 1962b) and viceversa, i.e. *pompalis* phenotypes well outside its putative range (TURATI & VERITY 1912, E. BERTACCINI, in litt., A. ZILLI pers. obs. in Liguria). Even in the populations clearly referable to nominate *dominula* from Piedmont and Friuli a number of the individuals show one or more of KETTLEWELL's melanistic factors.

Regarding the red/yellow polymorphism, yellow specimens have often been reported from Piedmont and Liguria (TURATI & VERITY 1912, ROCCI 1913, KETTLEWELL 1943) and are so frequent in Friuli that yellow monomorphic populations are the rule for many areas (COOK 1962b, C. MORANDINI pers. comm.).

It can also be noted that all the unmelanic specimens south of the Alps, when compared to samples north of the alpine range (e.g. North Switzerland, Bavaria), show some reduction of the size of forewing spots.

Concerning the situation of colour polymorphism in areas peripheral to Italy, most of the populations correspond to the nominate subspecies. It might be worth noting, however, that specimens with golden forewing spots are reported from Wallis (KETTLEWELL 1943) and in part of Slovenjia orange hindwinged individuals are present. The species has also been reported in Corsica (FREINA & WITT 1987: 631), but this datum has not been confirmed by RUNGS (1988).

Under these circumstances it should be clear how misleading the naming of subspecies is for a correct appreciation of the geographic variation of the Scarlet Tiger Moth in nature.

2.2 Situation in peninsular Italy

Roughly south of the Tusco-Aemilian Apenninic watershed the situation is quite simple, as only *persona* phenotypes are found up to Calabria (e.g. COSTA 1842, STANDFUSS 1885, CALBERLA 1887, STAUDER 1916, FREINA & WITT 1987, BERTACCINI et al. 1994). Differences do however occur between populations as to the frequency of the various melanistic morphs.

Despite some red or reddish specimens preserved in public and private collections, clear evidence of any of such individuals collected in the wild south of the very northern Apennines seemingly exists only in STAUDER's (1925) report. This was believed by KETTLEWELL (1943) to represent a new mutation. The rare occurrence of reddish specimens due to northern alleles in peninsular Italy is, on the contrary, well in agreement with populational thinking.

2.3 Situation in Sicily

The recent rediscovery of populations of the Scarlet Tiger Moth in Sicily gave impetus to evaluate critically the theoretical problems of the polytopic subspecies and of their taxonomic treatment.

2.3.1 Literature data

As based on literature, only one specimen of the Scarlet Tiger Moth had ever been collected with certainty in Sicily (MARIANI 1937). However, *persona* had been generically reported for Sicily by DUPONCHEL (1836), SPULER (1906) and KETTLEWELL (1943), all of whom seemingly made reference to ESPER's (1794) and TREITSCHKE's (1834) quotations. Nevertheless, there is strong evidence that, as happened in a long list of nominal taxa, the authors were confusing South Italy and Sicily because these regions once jointly belonged to the single Kingdom of the two Sicilies, being nonetheless known also as the Kingdom of Naples and the Kingdom of Sicily. TREITSCHKE (1834) did not explicitly state that *persona* was occurring in Sicily, but that the dealer G. DAHL obtained some specimens bred ex larvae after his expeditions in South Italy and Sicily ("in Neapel und Sicilien"). The exact collecting site of DAHL is therefore unknown. As a matter of fact, no specimen in TREITSCHKE's collection (Natural History Museum, Budapest) is labelled "Sicilien" as other species collected by DAHL in Sicily are (L. RONKAY, in litt.). HÜBNER (1790, quoted by OBERTHÜR, 1911), who apparently examined the same material in coll. J.C. GERNING (Frankfurt) like ESPER (1794) did later, was more precise in stating that the specimens of *persona* had been sent from the district of Naples to Frankfurt by the King and Queen of the two Sicilies. It is important to note that no specimen of *persona* from Sicily has been found up to now in the Natural History Museum of Vienna, where the material by GERNING is preserved (HORN et al. 1990).

MARIANI's (1937) record is from a beechwood of M. Soro at m 1700 a.s.l. in the Nebrodi range (North-West Sicily). This record was largely overlooked due to both the scanty circulation of the relevant bulletin and MARIANI's misidentifications. This led the singleton to be linked to ssp. *persona*, since at that time *persona* was probably acritically considered as the valid name for every population south of the Po Valley. In fact, MARIANI (1937) first identified the specimen as *romanovi* (name of some hybrids *dominula* × *persona*), and later considered it to represent a variety of *persona* (MARIANI 1939, and specimen's label). Contrary to the expectations, that specimen (preserved in Museo Civico di Storia Naturale di Terrasini, prov. Palermo) fully conforms to nominate *dominula*, as also evidenced by MARIANI's (1937) description and illustration.

2.3.2 Field data

Recently, several specimens of the Scarlet Tiger Moth have been collected in Sicily by S. BELLA, E. BERTACCINI, G. FIUMI, B. GIANDOLFO, W. HOGENES, and F.P. ROMANO, all from Nebrodi Mts, and correspond to *dominula* (s.str.) (e.g. BERTACCINI et al. 1994).

As a matter of fact, the Sicilian specimens, being characteristic of the nominate subspecies, are not only 'taxonomically' unrelated to *persona*, still present in the southernmost tip of Calabria (STAUDER 1916), but also to the other two red-hindwinged southern subspecies, viz. *pompalis* and *bithynica*. The range of *dominula* (s.str.), hence, passes over peninsular Italy and includes Sicily (at least some part of the island). For that reason *C. dominula dominula* (LINNAEUS 1758) becomes a polytopic subspecies.

Last but not least, the Sicilian specimens show traits characteristic of *dominula* north of the Alps. In fact, features like the wide forewing spots, the very small black spots of the hindwing and the extremely narrow black abdominal stripe are all unusual characteristics for any *dominula* population from North Italy.

3 Polytopic subspecies

In a polytypic species, a subspecies should be defined as polytopic when it reoccurs in widely separated areas among which populations belonging to other subspecies are found. Such a reoccurrence is said to be independent according to WILSON & BROWN (1957), MAYR (1963) and MAYR & ASHLOCK (1991). In particular, MAYR (1963) states: "...The distribution of the subspecies will be determined largely by the correlation between the diagnostic characters and the environment; consequently the range of a subspecies may sometimes be discontinuous (polytopic subspecies).". Successively MAYR (1969) writes: "...it may happen that several unrelated and more or less widely separated populations acquire an identical phenotype. The evolutionist knows that such populations are not identical genetically, but since the subspecies is not an evolutionary concept, taxonomists sometimes combine such visually identical populations into a single subspecific taxon. Such a geographically heterogeneous subspecies is called a polytopic subspecies. The only alternative to its recognition is not to recognize any subspecies in such a species.".

In modern evolutionary biology the subspecies concept is generally thought to have outlived its usefulness (e.g. WILSON & BROWN 1953, MINELLI 1994), being of some use only for taxonomic convenience, e.g. in the classification of population samples (MAYR 1969), to depict cases of categorical geographic variation (THORPE 1987) or subjectively perceived partitions of continuous variability (CRACRAFT 1992). The conceptual difficulties engendered by the traditional subspecies concept led BÖHME (1978, 1979) to revisit it from an ecological point of view, aiming at establishing a new role, possibly more linked to the reality of biological phenomena. Alternatively, some taxonomists refused a priori the subspecies as a taxonomic category without natural counterpart in the wild (e.g. POOLE 1989). Nevertheless, the study of intraspecific geographic variation is of great evolutionary interest. Within this context, a rather neglected issue is represented by the character states (hereafter 'characters', for the sake of brevity) which are only shared by distant populations of a species.

3.1 Origin of character reoccurrence

It is evident that only the polytopism of the characters can be observed in nature; any reference to subspecific entities would in fact represent an abstraction subject to severe criticism (e.g. WILSON & BROWN 1953). Therefore, for the sake of naturalness, the present section is chiefly devoted to characters and their states. Nevertheless, to allow effective extension of any comment to the subspecies problem, the discussion is restricted to characters discontinuously varying on a regional scale (e.g. *Leucodonta bicoloria* [DENIS & SCHIFFERMÜLLER], 1775, across the Palaearctic Region, cf. SCHINTLMEISTER 1989), even though, possibly, through transition zones with polymorphic populations or intermediate individuals. In fact, under these circumstances the geographic requisites necessary for delimiting subspecies are clearly met. Aiming at circumventing the conceptual and operational difficulties for subspecies recognition due to the existence of transition zones, it is worth noting the arbitrary proposal of the so called 'seventy-five per cent rule', that is to say the recognition of different subspecies in case at least 75 % of the individuals of adjacent subspecies are determinable (AMADON 1949).

In other cases, the distribution of different morphs can be mosaic-like according to the uneven presence of some alternative ecological factors on a local scale (e.g. f. *statices* and f. *heuseri* of *Procris statices* LINNAEUS, 1758, cf. REICHL 1964, ALBERTI 1978, TARMANN 1979). Such a tight correspondence may be due either to direct habitat selection by the relevant genotypes, or to habitat correlation induced by external agents (e.g. differential predation on alternative phenotypes according to the environmental patches which are chosen for resting, environmental induction, etc.) (WEINS 1976, ALDRIDGE et al. 1993, JONES et al. 1993, FRAIERS et al. 1994). In the extreme cases these processes can even lead contiguous populations to show sharp discontinuities as to striking characters, but the canonical geographical requisites for delimiting subspecies are clearly missing.

From a theoretical point of view, any within-species reoccurrence of characters in distant populations can be due to: ecological determinism, environmental induction during development, chance, and common genealogy. Such causes will now be reviewed separately, although joint presence or overlaps between them might theoretically occur in nature, not least when more than two sites are involved.

3.1.1 Ecological determinism (selection)

This point corresponds to MAYR's (1963, 1969) idea. The independent evolution of identical traits due to similar selective pressures is a rather common phenomenon and most of the taxonomists' polytopic subspecies derive from this kind of events. KUDRNA (1977) defines the same basic phenomenon as 'pseudopolytypism', hopefully to circumvent the conceptual problems arising when a taxonomist finds it difficult to make a decision.

Almost any character is a possible candidate for polytopism, including physiological and biochemical ones. However, the effects of ecological determinism are easily observed in certain cryptic moths choosing stones for resting which, matching with the local rock colours, may show recurrent 'adjustment to background' (cf. FORD 1955) (e.g. species undergoing albinism when they settle in calcareous or chalky areas). A model for the evolution of phenotypic similarity is well represented by some bark-camouflaging species that independently developed melanic patterns in several industrialized districts of Europe (cf. KETTLEWELL 1973). Episodes of altitudinal or thermal melanism (MANI 1968, KETTLEWELL 1973), if not exclusively due to environmental induction, can also produce similarity through selectionistic processes (e.g. between separated mountain populations in contrast with lowland ones).

Character polytopism, determined by community differences between areas, can occur in Batesian mimics, whenever matching with different models, or else Müllerian comimics, possibly following differential selection associated with changes of the abundance of the different pattern types in which the comimics themselves are involved.

The selection responsible of the character reoccurrence may act either on different genes producing an equivalent phenotypic effect or on a same unit (e.g. a rare but widely distributed allele) which is therefore fixed in two or more distant areas. It is noteworthy that many earlier authors admitted that phenotypes characteristic of particular geographic races occurred elsewhere as aberrations across the species' ranges. An excellent account on the dilemma between homologous and analogous genes determining character reoccurrence within- and between species is LATTIN's (1961).

3.1.2 Environmental induction during development

Totally different kind of environmental influences capable of leading to phenotypic similarity between separated areas is evidenced by traits which represent products or by-products of the interaction between genes and external factors during the organisms' developmental pathways. The morphological response to environmental stimuli can fall within the limits of the norm of reaction of given genotypes or represent true phenocopies, i.e. developmental aberrations which often resemble wild mutants or phenotypes particular to special regions (NIJHOUT 1991). Laboratory experiences demonstrated the possibility of obtaining imagines resembling those particular to given regions by manipulating parameters such as light, temperature and humidity (STANDFUSS 1896, KÖHLER & FELDOTTO 1935, ROBINSON 1971). Deposition of melanin as well as other pigments is often correlated with photoperiodic response or fluctuations of other factors (VUILLAUME 1969, WATT 1969, HOFFMANN 1973, KETTLEWELL 1973, SHAPIRO 1976, DOUGLAS & GRULA 1978, BRAKEFIELD & MAZZOTTA 1995). Similarly, the presence or the absence of given substances in the diet can determine dramatic phenotypic effects (PICTET 1905, WIGGLESWORTH 1972, WILSON 1985, 1986). Therefore, should the range of species show a particular shape, the reoccurrence of a given character might be due to differential expression (switching, penetrance, etc.) of genes according to external factors varying geographically, so that similar epiphenotypes are locally produced on a scattered basis.

3.1.3 Chance (probabilistic events)

Although stochastic events should always be considered as possible determinants of biological phenomena, the probability of character polytopism exclusively due to chance appears decisively low. An accidental arousal of a trait common to other populations might theoretically happen in a population (concordant mutation). However, that character will be likely to face different selective regimes because of the diversity of the relevant ecological scenarios. Accordingly, should that character increase in frequency and attain fixation, more likely ecological explanations should be tested, unless it is a neutral character, viz. not affecting the adaptive levels of its bearers. Hypothetically, neutral characters could persist in some populations and even attain fixation by genetic drift or, following the different route of founder's effect, a new colony could originate from bearers of the mutant trait. There are, however, conceptual and operational difficulties in establishing whether or not one character is adaptive. In any case genetic analyses should be carried out to ascertain the possibility of linkage between the relevant genes (possibly even slightly disadvantageous) and others greatly enhancing the fitness of the bearers (e.g. some physiological trait), in which case selectionists hypotheses would again explain the phenomenon (cf. KOJIMA & LEWONTIN 1970).

Contrary to a long held opinion, there is some evidence that genitalic pieces not involved in lock-and-key mechanisms (or in choosing substrata for oviposition) do not have a high adaptive significance (CESARONI et al. 1994), being comparatively free from functional restraints. Therefore, to a certain extent they should be unaffected by strong selective pressures such as those modelling other characters, e.g. wing pattern characteristics, which are amongst the most important ones in relating an individual to its environment (abiotic, biotic, and sexual). Therefore, they could theoretically be selected to test stochastic hypotheses of character reoccurrence between distant populations. However, this would require the existence of sharp discontinuity in the genitalia between adjacent populations of the same species, which is in conflict with being recognized as conspecific. In fact, due to the clearly polygenic nature of such morphological traits, any abrupt gap between morph types provides indirect evidence of genetic divergence of a certain extent.

3.1.4 Common genealogy (phylogenesis)

The possibility of closer kinship between some widely separated populations rather than the neighbouring ones is not necessarily invalid. It follows that the reoccurrence of characters is not independent, as claimed by WILSON & BROWN (1953), MAYR (1963, 1969) and MAYR & ASHLOCK (1991), but derives from a tighter genetic and phylogenetic continuity at infraspecific level. At least three models can be proposed.

3.1.4.1 Geographic vicariance

Sharing the same traits would be the result of past gene flow within one group of populations, upon which ordinary biogeographic events acted by fragmenting its range and allowing the derived subgroups to contact other conspecific populations. From the original group of populations derive two or more separated subgroups, scattered in a continuum of conspecific but lesser related populations having experienced partially different histories. The closer genealogy among the sub-groups is inferred, indeed, by the characters which remain shared, at least for some time.

3.1.4.2 Dispersal

When long distance dispersal is taken into account, the possible constitution of a polytopic complex is evident. For example, following prevailing wind directions a given territory can be colonized not by the nearmost populations, but by individuals from distant populations which thence introduce the characters of their own population (founder's effect).

3.1.4.3 'Shift' of the in-between populations

It is unnecessary always to invoke moving individuals or complex range dynamics to explain non-independent character reoccurrence. Given a geographic continuum of homogeneous populations, a pseudovicariant pattern may arise from the shift of the middle ones toward a different array of characters, with the populations at both extremities remaining unaffected.

The phenomenon is complementary with the one accounted for by ecological determinism, although decisively more probable. In fact, instead of being two distant groups of populations converging in response to similar selective pressures, it is the group in-between which undergoes changes because of different ecological conditions. Ecology still plays a major role, but does not produce independent polytopism but rather the diversification of some populations interposed between conservative ones, at the same time becoming a polytopic complex. Under these circumstances it is a fruitless discussion to separate paleoecological factors (i.e. historical types) from current ecology, as this distinction hinders the temporal continuity of a same phenomenon. A progressively changing ecological background allows both the shift toward new character states and their maintenance.

A similar reasoning was followed by SHEPPARD et al. (1985) while reconstructing the hypothetical ancestral pattern of *Heliconius melpomene* (LINNAEUS, 1758) and *H. erato* (LINNAEUS, 1758). The authors rejected considering the patterns occurring in the Amazon basin as ancestral, not least because of the similarity of patterns between populations north and south of that basin. In fact, if this similarity had been independent, it would have required admitting highly improbable phenomena of convergence and assuming, if not independent, dispersal over thousands of kilometres along the Andean rim of the basin. SHEPPARD et al. (1985) parsimoniously concluded that the Amazonian patterns were secondarily derived and the extra-Amazonian ones close to the ancestral.

4 How to explain the presence of nominate *dominula* in Sicily?

It should be noted that authoritative discussions on the polytopic subspecies (e.g. MAYR et al. 1953, MAYR & ASHLOCK 1991) did not even take into account the possibility of character reoccurrence in more than one character, since reoccurrence of more characters would have represented a probabilistic and biological

absurdity. The close matching between the Sicilian and northern specimens, when compared to *persona*, is therefore particularly surprising, when considering the number of the characters involved and the degree of their genetic/ontogenetic independence (hindwing background colour, width of the abdominal black stripe, hindwing melanism and width of the forewing spots). THORPE (1987), in fact, has properly pointed out that while studying geographic variability the actual congruence of different characters is of value only if they are genetically/ontogenetically independent. Moreover, with characters mutually independent, high levels of congruence between samples from distant areas would suggest underlying vicariance-events as responsible (viz. phylogenetic kinship), whereas low congruence would indicate control by present-day ecological factors (THORPE 1987).

To interpret the occurrence of *dominula* phenotypes in Sicily, what is known about the genetics of the colour forms and the presence of *persona* phenotypes in the southernmost tip of Calabria immediately permit discarding any hypothesis of environmental induction. Stochastic explanations are also hazardous, as the characters involved are so many. Therefore, assuming an archaic presence of *persona* on the Nebrodi Mts, to return back to nominate *dominula* would have required too many character reversals.

Nevertheless, according to the canonical working hypothesis for the character polytopism, analogous selective regimes would have engendered the proper ecological context for such character reversals. For this to be true, it would have required such marked ecological similarities between the Sicilian biotopes and the main European part of the species' range that all the traits characterizing *persona* would have been subject to strong directional selection to obtain a 'new' *dominula* on the island. Nonetheless, the number of the characters involved, as well as their genetic/ontogenetic independence, make again a precise turning back to *dominula* from *persona* a highly improbable event.

As for the remaining hypotheses, the proposal of a vicariance model would require an exageratedly complicated theory of crustal movements and land bridges, not supported by the tertiary and quaternary geological history of the Central Mediterranean (cf. AZZAROLI & CITA 1980, CATALANO et al. 1995). As the Scarlet Tiger Moth is absent in the central and southern Iberian Peninsula and the whole of North Africa, a colonization of Sicily from the south can reasonably be excluded. The species is also absent from other Mediterranean islands and in the East Mediterranean it shows a different combination of characters. The possibility of accidental introduction is also lessened, as the Sicilian records are not from coastal areas near ports and towns, but from well preserved inner mountain zones. It should also be noted that the larvae do not feed upon trees used in reforestation.

According to the 'shift of the in-between model', the Nebrodi populations would represent the descendants of normal red unmelanic *dominula* which, spreading from the north, colonized whole peninsular Italy and Sicily. In fact, several northern species reached Sicily through the Apenninic range and currently survive on the island's mountain massives with relict populations. Once the colonization of Sicily was assessed, it would have been the Apenninic group of populations that diverged, giving rise to the *persona* phenotypes. Therefore, instead of claiming highly improbable theories in order to interpret the presence of nominate *dominula* in Sicily, the question basically moves to the origin of *persona* in peninsular Italy, a more parsimonious hypothesis which will be tentatively discussed in the next paragraph.

4.1 Melanism and the shift red-yellow in Apenninic day-flying moths

The origin of *persona* in peninsular Italy still needs adequate explanation; nevertheless, some bizarre congruences which occur in the Apennines throw some light on the phenomenon. In the Italian Peninsula, in fact, two other aposematic day-flying moths replaced an archaic red/black-unmelanic pattern (R/m), widely spread in the northern areas of their ranges, with a yellow/black-melanic one (Y/M), namely *Zygaena ephialtes* (LINNAEUS, 1767) and *Z. transalpina* (ESPER, 1782). The fact that in both species the Y/M pattern is more recent than the R/m one can easily be inferred through outgroup comparison with the patterns characteristic of other *Zygaena* species, particularly those more related phylogenetically. As a matter of fact, both *Zygaena dorycnii* OCHSENHEIMER, 1808 (sister species of *Z. ephialtes*) and *Z. angelicae* OCHSENHEIMER, 1808 + *Z. hippocrepidis* (HÜBNER, [1799]) (making up an Artenkreis together with *Z. transalpina*) (cf. NAUMANN & TREMEWAN 1984, HILLE & NAUMANN 1992) show the pattern R/m.

In *Zygaena ephialtes* the archaic R/m pattern is widespread from France to central Asia, even though populations with individuals bearing a Y/m pattern are found occasionally. With the exception of the Turkish populations (R/m), the melanic patterns (R/M and Y/M) are characteristic of the southern part of the species' range, from Spain to southern Russia. However, the four main patterns of *ephialtes* (R/m, R/M, Y/M, and,

scarcer, Y/m) coexist over large extensions, the species showing also many more types of pattern in particular contact zones, e.g. intermediate melanics or orange specimens due to multiallelism with differential penetrance and the disruption of differently coadapted genotypes (BOVEY 1941, 1966, 1983, REICHL 1958, 1959, DRYJA 1959, BULLINI et al. 1969, GABRIELE 1990).

As for Italy, the situation is rather simple throughout the peninsula. Apart from some 'relictual' presence of the R/M pattern in North Tuscany (VERITY 1930), all along the Apennines monomorphic Y/M populations occur (the polymorphism relevant to the number of forewing spots not being considered here). The distribution of the colour polymorphism in North Italy is more mosaic-like, with Y/M, R/M, and, occasionally in the western Alps, even R/m populations (GABRIELE 1990) (fig. 2).

The situation of *Zygaena transalpina* in Italy is, on the contrary, remarkably complex as the contact zone between northern (R/m) and southern patterns (Y/M) is somehow streaked along the Apennines. R/m patterns characteristic of central Europe and the Alps do approximately occur over most of North and Central Italy up to the Tiber Valley. It is noteworthy that, like for *dominula*, in Friuli polymorphic populations with red/yellow and unmelanic/melanic individuals occur (REICHL 1962, BOVEY 1981) (interestingly, in the surroundings of Tarnova also *Z. angelicae* shows populations with abundant Y/m individuals, L. MORIN pers. comm.). From Central Italy southwards, the R/m pattern becomes progressively restricted to inner mountain and eastern zones, leaving out the western part of the peninsula. Accordingly, Y/M and R/M patterns are increasingly frequent from the western hills of central Italy to the mountains of South Italy (fig. 3).

Because of the spacial heterogeneity due to the orientation of Apenninic ridges, isolation effects or geographically asymmetric gene flow, as well as the polygenic nature of the melanism and multiallelism for background colouration (BOVEY 1981, REICHL 1992), each *transalpina* population shows in practice a peculiar combination of phenotypic frequencies of colour forms. Highly polymorphic populations with all sort of intermediates are particularly frequent along the southern half of the Peninsula where the two main bulks of populations meet.

Two more aspects deserve further attention, i.e. the presence of R/M populations chiefly linked to low altitude areas from Liguria to Tuscany, similar to many other species of *Zygaena*, and mainly consisting of stout-bodied individuals (COSTANTINI 1916, VERITY 1930, BURGEFF 1951, ALBERTI 1971), and of relict R/m offshoots of these populations in some littoral localities of central Italy.

Despite the complexity of the colour polymorphism of the Italian *transalpina*, there is little doubt that the Y/M patterns represent a purely southern situation, the presence of yellow and of melanic phenotypes being positively associated with warmer and southern areas. This is also demonstrated by a transect in a favourable area at the border between Latium and the Abruzzi, where two parallel mountain ridges, respectively west and east of Roveto Valley, show a NW-SE orientation. At the south-western foothills of both ridges, noticeably warmer than the north-eastern ones, Y/M individuals prevail. The frequency of yellow specimens, as well as melanic ones (both R/M and Y/M), decreases going up the mountains. On the top and on the cooler north-eastern slopes of both ridges R/m individuals are distinctly more abundant.

The ecological background allowing the shift of the R/m pattern of *Zygaena ephialtes* toward the Y/M one was identified as a change of the relative abundance of two Müllerian mimicry rings during the Pleistocene period. According to the proposed model, in South Italy *ephialtes* would have diverged from a main European ring, involving several species of *Zygaena* sharing a R/m pattern, and entered into a more Mediterranean ring based on a Y/M pattern, in which the most abundant comimics are thermophilous species belonging to the genus *Syntomis* (BULLINI et al. 1969, TURNER 1971, SBORDONI et al. 1979). There is strong evidence that the same basic phenomenon has occurred in *Zygaena transalpina*, although incompletely.

The general appearance of *Callimorpha dominula* objectively looks quite different from that characteristic of the *Zygaena* or the *Syntomis* species, particularly in size. Nevertheless, biochemical, eco-ethological, and colour pattern congruences (FRAZER & ROTHSCHILD 1960, ROTHSCHILD 1961, 1985, KAY et al. 1969) suggest that they are all involved in the same Müllerian rings. As a matter of fact, ROTHSCHILD & LANE (1960) showed that some insectivorous species of birds are unable to perceive the difference between *C. dominula* and species of *Zygaena* and *Tyria jacobaeae* (LINNAEUS, 1758), so the birds, having experienced the latter species, try to reject or even escape when either *dominula* or species of *Zygaena* are offered to them.

In peninsular Italy, the two alternative mimicry rings are not mutually exclusive, but coexist over large extensions. However, as there is a distinct trend for the Y/M ring to become progressively scarcer northwards or at higher altitudes, it can be supposed that it attained its current species composition, including ancestral *dominula* populations which once were red unmelanic, in xerothermic refugial areas of southern Italy during the Pleistocene glaciations. It is noteworthy that Sicily remained unaffected by the shift R/m-Y/M, apparently because of unsuccessful colonization by some species. In fact, if is compared the lepidopteran species

Fig. 1: Distribution of the colour polymorphism of *Callimorpha dominula* (LINNAEUS) in Italy.

composition of both mimicry rings between the southern Apennines and Sicily, a particular paucity of Y/ M species in the island will be evident (tab. 2).

To go into deeper detail, in Sicily both *Zygaena ephialtes* and *Z. transalpina* are missing and of the three species of *Syntomis* occurring in south Italy only *S. kruegeri* RAGUSA, 1904 is present (old reports of *S. phegea* LINNAEUS, 1758 being misidentifications by earlier authors). *Syntomis kruegeri* is objectively very common in Sicily. Nonetheless, in contrast to peninsular Italy, in the island the species is on the wing much earlier

(March-May) than *dominula*, the flying period of which (July) is synchronous with that of most *Zygaena* species (June-July). Accordingly, for any Sicilian R/m *dominula* shifting toward the Y/M pattern would have represented an evolutionary step largely devoid of selective advantage.

5 Remarks on the subspecies concept

Nearly every aspect of the subspecies problem has been thoroughly reconsidered after WILSON & BROWN's (1953) famous critique of the subspecies concept (cf. for reviews STARRETT 1958, SIMPSON 1961). However, even a rapid look at recent literature will reveal that the subspecies concept is so differently interpreted that the subspecies category is currently misused to depict a heterogeneous array of situations. Nevertheless, most of the interpretations of the concept fall within one of two classes of meanings, which could be defined as 'evolutionary' or 'descriptive'. In fact, subspecific names are either used as a synthetic way of referring to one group of populations deemed to make up a natural assemblage by virtue of their closer relatedness (genetical and/or genealogical) respecting other populations of the species, or merely relate to the discontinuous geographic variation shown by some characters, viz. the 'diagnostic' ones. In other words, confusion between subspecies as an evolutionary lineage or as a category of convenience arises. It is worth noting that the state of the characters employed for subspecies recognition do not need to be meristic or discontinuous in a strict sense, should 'metacharacters' such as quantitative descriptors obtained through statistical processing of rough data (e.g. continuously varying traits, allomorphic differences) be discriminant.

Despite repeated emphasis that the subspecies concept is not an evolutionary one (e.g. SIMPSON 1961, MAYR 1969, MAYR & ASHLOCK 1991), evolutionary value is frequently conferred on the subspecies and 'subspeciation' processes are even claimed to occur in nature. It is also occasionally deemed that subspecies should represent preliminary steps towards complete reproductive isolation (HAFFER 1986) or incipient species, at least potentially (cf. ASKEW 1970, AMADON & SHORT 1976, BÖHME 1978, 1979).

Undoubtedly, many of the described subspecies do actually coincide with evolutionary lineages, but, according to eminent commentaries on the subspecies problem (e.g. SIMPSON 1961, MAYR 1963, 1969, MAYR & ASHLOCK 1991), it is not the aim of the subspecies concept to depict such units, independent of the keenness of the methodology which, in such cases, has led to subspecies recognition (e.g. genetic analyses, multi-

Table 2. Differences between southern Italy and Sicily regarding the species composition and patterns of day-flying moths involved in Müllerian mimicry rings. R, red; Y, yellow; M, melanic; m, unmelanic.

Species	southern Apennines	Sicily
Zygaena punctum OCHSENHEIMER	R/m	R/m
Z. rubicundus HÜBNER	R/m	–
Z. erythrus HÜBNER	R/m	R/m
Z. minos DENIS & SCHIFFERMÜLLER	R/m	–
Z. purpuralis BRÜNNICH	R/m	R/m
Z. carniolica SCOPOLI	R/m	R/m
Z. loti DENIS & SCHIFFERMÜLLER	R/m	–
Z. oxytropis BOISDUVAL	R/m	R/m
Z. romeo DUPONCHEL	R/m	R/m
Z. viciae DENIS & SCHIFFERMÜLLER	R/m	R/m
Z. ephialtes LINNAEUS	Y/M	–
Z. transalpina ESPER	R/m, R/M, Y/m, Y/M	–
Z. filipendulae LINNAEUS	R/m	R/m
Z. trifolii ESPER	–	R/m
Z. lonicerae SCHEVEN	R/m	R/m
Callimorpha dominula LINNAEUS	Y/M	R/m
Euplagia quadripunctaria PODA	R/m	R/m
Tyria jacobeae LINNAEUS	R/m	R/m
Syntomis phegea LINNAEUS	Y/M	–
S. ragazzii TURATI	Y/M	–
S. kruegeri RAGUSA	Y/M	Y/M

variate morphometrics, eco-ethological and physiological comparisons, systematist's intuition, etc.).

As a matter of fact, most of the ambiguity on the subspecies concept is simply due to the confusion between two different euristic processes, namely induction and deduction. For example, following current populational approaches, evolutionary significant units within species can admittedly be circumscribed and, whenever the pattern of geographic variation allows it, these units are often distinguished as subspecies. In this case, through the analysis of real elements (genes, characters, individuals, etc.), the existence of a more general entity, which is (unfortunately) called a subspecies, is inferred. On the contrary, evolutionary speculations are often acritically advanced on conventional subspecies confident that they have intrinsic evolutionary value, as they would relate to groups of populations fitting into the subspecies' definition. Here, the naturalness of given nominal taxa of subspecific status is deduced as a consequence of a general assumption. Odd as it may seem, the deductionists' assumption of the reality of subspecies as natural elements, and hence of nominal subspecies under consideration, is apparently corroborated by the induction-ists' circumscription of admittedly significant units from an evolutionary viewpoint to which the subspecies category is attributed. In contrast, it should be evident how considering conventional subspecies real because of some natural units, which can be called subspecies, represents an incorrect transference of philosophical qualities between two basically different elements bearing a same name.

Objectively it is the concept itself which, at least after its more famous formalizations, engendered the major source of misunderstanding. MAYR (1963, 1969) and MAYR & ASHLOCK (1991), with minor modifica-tions, define the subspecies as "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species.". In this definition the crucial words are 'differing taxonomically'.

A historical review of the taxon concepts would go far beyond the limits of this study. However, as, in the light of both the cladistic and, at least recently, the evolutionary school (MAYR & ASHLOCK 1991: 116-117), taxa are monophyletic groups of organisms and as the practice of taxonomy aims at classifying organisms through the recognition of groups deemed to be taxa, which are thereafter ranked into a hierarchical order of inclusiveness, on the basis of MAYR & ASHLOCK's definition, subspecies cannot be deprived of the taxon status, which is an ontological condition. Therefore, the common approach of treating conventional subspecies as natural units (also in cladograms) is at least legitimate on a formal ground.

It is not surprising that the contradictory position of the subspecies led these to be considered as false-taxa or pseudotaxa (e.g. BLACKWELDER 1967), although other taxon concepts such as SIMPSON's (1961) and MAYR's (1969), being more conventional, are more compatible with the notion of subspecies.

The ambivalence of MAYR's concept of subspecies is long dated. In fact, it should be noted that in earlier formalizations of the concept by MAYR (1942, MAYR, LINSLEY & USINGER 1953) subspecies were stated to be "genetically and taxonomically different". Later (MAYR 1963, 1969), the term 'genetically' was removed from the definition in order to highlight that subspecies are not genetically coadaptive systems (and, inter alia, because every population is genetically different from the other ones in bisexual species).
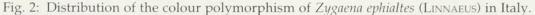
MAYR & ASHLOCK (1991: 44) also introduced an operational limitation stating that 'differing taxono-mically' is to be intended as "by sufficient diagnostic morphological characters": a perplexing opinion which would limit taxonomy to mere morphology. On this subject, it has to be recalled that morphologically indistinguishable species, viz. sibling species, are formally recognized both in taxonomic theory and practice.

5.1 Polytopic subspecies and their outshots on the subspecies concept

Besides the questionable euristic value of the subspecies concept even for appreciating biological phenomena (WILSON & BROWN 1953, GILLHAM 1956, BLACKWELDER 1967, LA GRECA 1987, THORPE 1987, MINELLI 1994), events of character polytopism within species severely affect any residual velleity of the concept itself. Of course, the possibility of independent reoccurrence of characters due to ecological determinism is clearly unconsistent with the recognition of subspecies as evolutionary or natural units (polyphyletic taxa would be named). Even if a polytopic complex had arisen by common genealogy, the application of the subspecies category would now be unacceptable, since the requirement of the geographic uniquity highlighted in the subspecies' definition would be missing. Also the overemphasized role of subspecies as taxonomic conven-ience is definitively flawed by character polytopism, since the use of trinomens would not represent any pattern of geographic variation in the diagnostic characters.

One might argue that the subspecies category could be still used, leaving aside cases of polytopism as oddities. KUDRNA (1977) indeed suggests that when particular phenotypes are shared by widely separated

Fig. 2: Distribution of the colour polymorphism of *Zygaena ephialtes* (LINNAEUS) in Italy.

populations within a species, the relevant populations do not represent one or more subspecies but that the species is pseudopolytypic, i.e. it shows a kind of geographic variation different from both the categorical and clinal ones. The notion of pseudopolytypism is to be disregarded because the categorical variation of one or more characters occurring between two groups of populations is a phenomenon in itself, the appreciation of which cannot depend upon the accidental discovery of other populations, sharing the same character with a group, in another district of the species' range.

Fig. 3: Distribution of the colour polymorphism of *Zygaena transalpina* (ESPER) in Italy.

Avoiding recognition of any polytopic subspecies in a polytypic species would lead, for the sake of homogeneity, to not recognizing any subspecies in such a species and, by the same criterion, not recognizing subspecies in any species, unless it is definitively decided that taxonomy should not operate within a unitarian conceptual framework.

Acknowledgements

Literature

ALBERTI, B. 1971: Sur les zygènes du versant sud du Grand Caucase et remarques sur l'hypothèse du mélanisme littoral (Lep. Zygaenidae). - Bull. Soc. entomol. Mulhouse **juillet-août**, 53-58.

– – 1978: Zur Artfrage von *Procris* forma *heuseri* REICHL (Lepidoptera, Zygaenidae). - Nachrbl. bayer. Ent. **27**, 13-16.

ALDRIDGE, D., JONES, C.W, MAHAR, E., MAJERUS, M.E.N. 1993: Differential habitat selection in polymorphic Lepidoptera in the Forest of Dean. - Entomol. Rec. J. Var. **105**, 203-214.

AMADON, D. 1949: The seventy-five per cent rule for subspecies. - Condor **51**, 250-258.

AMADON, D., SHORT, L. L. 1976: Treatment of subspecies approaching species status. - Syst. Zool. **25**, 161-167.

ASKEW, R. R. 1970: Infraspecific categories in insects. - Biol. J. Linn. Soc. **2**, 225-231.

AZZAROLI, A., CITA, M. B. 1980: Geologia stratigrafica **3**. - Cisalpino Goliardica, Milano.

BERTACCINI, E., FIUMI, G., PROVERA, P. 1994: Bombici e Sfingi d'Italia (Lepidoptera Heterocera) **1**. - Natura-Giuliano Russo Editore, Monterenzio.

BLACKWELDER, R. E. 1967: Taxonomy, a text and reference book. - Wiley & Sons, New York.

BÖHME, W. 1978: Das KÜHNELT'sche Prinzip der regionalen Stenözie und seine Bedeutung fur das Subspezies-Problem: ein teoretischer Ansatz. - Z. zool. Syst. Evolut.-forsch. **16**, 256-266.

– – 1979: KÜHNELT's principle and the subspecies-problem: a reply to L. BOTOSANEANU. - Z. zool. Syst. Evolut.-forsch. **17**, 243-246.

BOISDUVAL, J. A. 1834: Icones historique des Lépidoptères nouveaux ou peu connus **2**. - Roret, Paris.

– – 1840: Genera et index methodicus europaeorum Lepidopterorum. - Roret, Paris.

BOVEY, P. 1941: Contribution à l'étude génétique et biogéographique de *Zygaena ephialtes* L. - Rev. Suisse Zool. **48**, 1-90.

– – 1966: Le problème des formes orange chez *Zygaena ephialtes* (L.). - Rev. Suisse Zool. **73**, 193-218.

– – 1981: Résultats de croisements entre formes rouges et jaunes de *Zygaena transalpina* ESP.. - Mitt. Schweiz. entomol. Ges. **54**, 371-375.

– – 1983: Que représentent les formes orange chez *Zygaena ephialtes* (LINNÉ)? - Alexanor **12** (1982), 349-361.

BRAKEFIELD, P. M., LIEBERT, T. G. 1985: Studies of colour polymorphism in some marginal populations of the aposematic jersey tiger moth *Callimorpha quadripunctaria*. - Biol. J. Linn. Soc. **26**, 225-241.

BRAKEFIELD, P. M., MAZZOTTA, V. 1995: Matching field and laboratory environments: effects of neglecting daily temperature variation on insect reaction norms. - J. Evol. Biol. **8**, 559-573.

BRYK, F. 1937: Arctiidae, Subfam. Callimorphinae et Nyctemerinae. In: BRYK, F., Lepidopterorum Catalogus **82**, 1-105.

BULLINI, L., SBORDONI, V., RAGAZZINI, P. 1969: Mimetismo mülleriano in popolazioni italiane di *Zygaena ephialtes* (L.) (Lepidoptera, Zygaenidae). - Archiv. zool. Ital. **54**, 181-214.

BURGEFF, H. 1951: Die Meeralpengrenze der Zygaenen (Lep.), eine mit Hilfe der Populationsanalyse der Arten der Gattung *Zygaena* (Lepidoptera) durchgeführte Untersuchung über die Lokalisation und die Bedeutung geographischer Rassen in ihrem Zusammenhang mit der Eiszeit. - Biol. Zbl. **70**, 1-23.

CALBERLA, H. 1887: Die Macrolepidopterenfauna der römischen Campagna und der angrenzenden Provinzen Mittelitaliens (Rhopalocera; Heterocera, Sphinges, Bombyces). - Corr. blatt entomol. Ver. Iris **1** (4), 119-158.

CATALANO, R., DI STEFANO, P., SULLI, A., VITALE, F. P. 1995: Evoluzione paleogeografica e strutturale della Silicia e dei mari adiacenti. - Naturalistica sicil. (4) **19**, 143-187.

CESARONI, D., LUCARELLI, M., ALLORI, P., RUSSO, F., SBORDONI, V. 1994: Patterns of evolution and multidimensional systematics in graylings (Lepidoptera: *Hipparchia*). - Biol. J. Linn. Soc. **52**, 101-119.

CLARKE, C. A., CLARKE, F. M. M., COOK, L. M. 1990: Gene frequency in an artificial colony of the Scarlet Tiger Moth, *Panaxia dominula* (L.), after 28 years. - Linnean **6**, 13-16.

CLARKE, C. A., CLARKE, F. M. M., OWEN, D. F. 1991: Natural selection and the scarlet tiger moth, *Panaxia dominula*: inconsistencies in the scoring of the heterozygote, f. *medionigra*. - Proc. R. Soc. Lond. (B) **244** (1311), 203-205.

- - 1993: Gene frequencies in an artificial Wirral colony of the Scarlet Tiger Moth (*Panaxia dominula* L.) in the four years after its rediscovery: 1989-1992. - Linnean **9**, 18-20.

COCKAYNE, E.A. 1928: Variation in *Callimorpha dominula*, L. - Entomol. Rec. J. Var. **40**, 153-160.

COOK, L. M. 1959: The distribution in Britain of the scarlet tiger moth, *Callimorpha* (*Panaxia*) *dominula* L. - Entomologist **92**, 232-236.

- - 1961a: Influence of larval environment on adult size and fecundity in the moth *Panaxia dominula* L.. - Nature **192** (4799), 282.

- - 1961b: Food-plant specialization in the moth, *Panaxia dominula* L.. - Evolution **15**, 478-485.

- - 1961c: Differential mortality between larvae of *Panaxia dominula* (L.) (Lep. Hypsidae) from different colonies. - Entomologist **94**, 135-136.

- - 1962a: Some observations on the condition of over-wintering larvae of the scarlet tiger moth, *Panaxia dominula* (LINNAEUS). - Entomologist **95**, 47-50.

- - 1962b: Evolution in the scarlet tiger moth in Northern Italy. - Syst. Zool. **11**, 17-21.

COOK, L. M., KETTLEWELL, H. B. D. 1960: Radioactive labelling of lepidopterous larvae: a method of estimating late larval and pupal mortality. - Nature **187** (4734), 301-302.

COSTA, A. 1842: Note sur les *Callimorpha dominula* et *donna*. - Ann. Soc. entomol. Fr., **11**, 239-241.

COSTANTINI, A. 1916: Sinossi delle forme della "*Zygaena Transalpina*" ESP. del Modenese e Reggiano. - Atti. Soc. natural. matem. Modena (5) **3**, 25-29.

CRACRAFT, J. 1992: Species concepts and speciation analysis. In: ERESHEFSKY, M., The units of evolution: essays on the nature of species, 93-120.

DANNEHL, F. 1928: Beiträge zur Lepidopteren-Fauna Südtirols (Fortsetzung). - Entomol. Z. Frankf. a.M. **42**, 130-134.

DOUGLAS, M. M., GRULA, J. W. 1978: Thermoregulatory adaptations allowing ecological range expansion by the pierid butterfly, *Nathalis iole* BOISDUVAL. - Evolution **32**, 776-783.

DRYJA, A. 1959: Badania nad polimorfizmem Krasnica Zmiennego (*Zygaena ephialtes* L.). - Warszawa.

DUPONCHEL, P.-A.-J. 1836: Histoire naturelle des Lépidoptères ou papillons de France, Supplément **3**. - Méquignon-Marvis, Paris.

EDGAR, J. A., CULVENOR, C. C. J., COCKRUM, P. A., SMITH, L. W., ROTHSCHILD, M. 1980: Callimorphine: identification and synthesis of the Cinnabar moth "metabolite". - Tetrahedron Letters **21**, 1383-1384.

ENDLER, J. A. 1977: Geographic variation, speciation, and clines. - Princeton University Press, Princeton.

ESPER, E. J. C. 1794: Die Schmetterlinge in Abbildungen nach der Natur. Der europäischen Schmetterlinge **4**. Theil, 2. Band, 2. Abschnitt. - Erlangen.

FISHER, R. A., FORD, E. B. 1947: The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. - Heredity **1**, 143-174.

FORD, E. B. 1937: Problems of heredity in the Lepidoptera. - Biol. Reviews **12**, 461-503.

- - 1955: Moths. - Collins, London.

- - 1971: Ecological genetics. - (3rd edn) Chapman & Hall, London.

FORD, E. B., SHEPPARD, P. M. 1969: The *medionigra* polymorphism of *Panaxia dominula* (Lep., Hypsidae). - Heredity **24**, 561-569.

FRAIERS, T., BOYLES, T., JONES, C., MAJERUS, M. 1994: Short distance form frequency differences in melanic Lepidoptera across habitat boundaries. - Brit. J. Entomol. nat. Hist. **7**, 47-52.

FRAZER, J. F. D., ROTHSCHILD, M. 1960: Defence mechanisms in warningly-coloured moths and other insects. - Verhandl. XI. Int. Kongr. Entomol., Wien 1960, **3**, 249-256.

FREINA, J. J., de, WITT, T.J. 1987: Die Bombyces und Sphinges der Westpalaearktis **1**. - Forschung & Wissenschaft, München.

GABRIELE, F. 1990: Distribuzione geografica del polimorfismo cromatico in *Zygaena ephialtes* L. (Lepidoptera: Zygaenidae). - II Università degli Studi di Roma (Tesi di laurea).

GILLHAM, N. W. 1956: Geographic variation and the subspecies concept in Butterflies. - Syst. Zool. **5**, 110-120.

GOLDSCHMIDT, R. 1924: Erblichkeitsstudien an Schmetterlinge IV. Weitere Untersuchungen über die Vererbung des Melanismus. - Z. indukt. Abstamm. Vererbungslehre **24**, 229-244.

GOULD, S. J., JOHNSTON, R. F. 1972: Geographic variation. - Ann. Rev. Ecol. Syst. **3**, 457-498.

HAFFER, J. 1986: Superspecies and species limits in vertebrates. - Z. zool. Syst. Evolut. -forsch. **24**, 169-190.

HERRICH-SCHÄFFER, G. A. W. 1845: Systematische Bearbeitung der Schmetterlinge von Europa **2**. - bei G. J. Manz, Regensburg.

HILLE, A., NAUMANN, C. M. 1992: Allozyme differentiation in *Zygaena transalpina* (ESPER, 1780) (Lepidoptera: Zygaenidae). In: DUTREIX, C., NAUMANN, C. M., TREMEWAN, W. G., Recent advances in burnet moth research (Lepidoptera: Zygaenidae), 59-87.

HOFFMANN, R. J. 1973: Environmental control of seasonal variation in the butterfly *Colias eurytheme*. I. Adaptive aspects of a photoperiodic response. - Evolution **27**, 387-397.

HORN, W., KAHLE, I., FRIESE, G., GAEDIKE, R. 1990: Collectiones entomologicae. - Akademie der Landwirtschaftswissenschaften der DDR, Berlin.

JONES, C. W., MAJERUS, M. E. N., TIMMINS, R. 1993: Differential habitat selection in polymorphic Lepidoptera. - Entomologist **112**, 118-126.

JONES, D. A. 1989: 50 years of studying the scarlet tiger moth. - Trends Ecol. Evolut. **4**, 298-301.

– – 1993: The phenotype and frequency of f. *medionigra* and *Panaxia dominula* L. (Lepidoptera: Arctiidae) at Cothill, Oxfordshire, England, 1988-1991. - Biol. J. Linn. Soc. **49**, 305-316.

KAY, D., ROTHSCHILD, M., APLIN, R. 1969: Particles present in the haemolymph and defensive secretions of insects. - J. Cell Sci. **4**, 369-379.

KETTLEWELL, H. B. D. 1943: A survey of the insect *Panaxia* (64) (*Callimorpha*) *dominula*, L. - Proc. Trans. S. Lond. entomol. nat. Hist. Soc. **1942-1943**, 1-49.

– – 1946: Further observations on *Panaxia dominula*. - Entomologist **79**, 31-32.

– – 1952: Use of radioactive tracer in the study of insect populations. - Nature **170**, 584-585.

– – 1973: The evolution of melanism. - Clarendon Press, Oxford.

KÖHLER, W., FELDOTTO, W. 1935: Experimentelle Untersuchungen über die Modifikabilität der Flügelzeichnung, ihrer Systeme und Elemente in den sensiblen Perioden von *Vanessa urticae* L., nebst einigen Beobachtungen an *Vanessa io* L. - Arch. Julius Klaus-Stift. (VerebForsch.) **10**, 313-453.

KOJIMA, K., LEWONTIN, R. C. 1970: Evolutionary significance of linkage and epistasis. In: KOJIMA, K., Mathematical topics in population genetics, 367-388.

KUDRNA, O. 1977: A revision of the genus *Hipparchia* FABRICIUS. - Classey, Faringdon.

LA GRECA, M. 1987: L'uso delle categorie sistematiche sottogenere e sottospecie in tassonomia, alla luce della ricerca biogeografica. - Boll. Ist. Entomol. Univ. Bologna **41**, 159-171.

LATTIN, G., de, 1961: Über die genetischen Grundlagen der Merkmalsparallelität. - Zool.Anz. **166**, 357-390.

LEES, D. R. 1970: The *medionigra* polymorphism of *Panaxia dominula* in 1969. - Heredity **25**, 470-475.

MANI, M. S. 1968: Ecology and biogeography of high altitude insects. - W. Junk, The Hague.

MARIANI, M. 1937: Nuove specie e forme di Lepidotteri di Sicilia ed un nuovo parassita degli agrumi. - Giorn. Sci. nat. econom. Palermo **39**, 1-15.

– – 1939: Fauna Lepidopterorum Siciliae. - Mem. Soc. entomol. Ital. **17** (1938), 129-187.

MAYR, E. 1942: Systematics and the origin of species from the viewpoint of a zoologist. - Columbia University Press, New York.

– – 1963: Animal species and evolution. - The Belknap Press of Harvard University Press, Cambridge, Mass..

– – 1969: Principles of systematic zoology. - McGraw-Hill, New York.

MAYR, E., ASHLOCK, P. D. 1991: Principles of systematic zoology. - McGraw-Hill, New York.

MAYR, E., LINSLEY, E. G., USINGER, R. L. 1953: Methods and principles of systematic zoology. - McGraw-Hill, New York.

MINELLI, A. 1994: Biological Systematics, the State of the Art. - Chapman & Hall, London.

NAUMANN, C. M., TREMEWAN, W. G. 1984: Das Biospecies-Konzept in seiner Anwendung auf die Gattung *Zygaena* FABRICIUS, 1775 (Insecta, Lepidoptera, Zygaenidae). - Spixiana **7**, 161-193.

NIJHOUT, H. F. 1991: The development and evolution of Butterfly wing patterns. - Smithsonian Institution Press,Washington & London.

NITSCHE, J. 1926: [...Lepidopterologische Sammelergebnisse aus den Dolomiten vom Sommer 1924]. - Verhandl. zool. -bot. Ges. Wien **74/75** (1924/1925), (62)-(65) (Sitzbericht).

OBERTHÜR, C. 1911: Notes pour servir à établir la Faune Française et Algérienne des Lépidoptères (suite). - Études Lépid. comparée **5**, 11-182.

OLIVER, C. G. 1972: Genetic and phenotypic differentiation and geographic distance in four species of Lepidoptera. - Evolution **26**, 221-241.

OWEN, D. F. 1993: *Equisetum*-feeding larvae of *Panaxia* (*Callimorpha*) *dominula* (Lepidoptera: Arctiidae). - Entomol. Gaz. **44**, 163-166.

– – 1994: Increase in larval foodplant diversity during a population explosion of the moth, *Panaxia dominula* (L.) (Lepidoptera: Arctiidae). - Nota lepid. **16**, 267-273.

– – 1996: Larval food shortage and adult dispersal in *Callimorpha dominula* (L.) (Lepidoptera: Arctiidae). - Nota lepid. **18** (1995), 281-288.

OWEN, D. F., CLARKE, C. A. 1993: The *medionigra* polymorphism in the moth, *Panaxia dominula* (Lepidoptera: Arctiidae): a critical re-assessment. - Oikos **67**, 393-402.

OWEN, D. F., GOULSON, D. 1994: Effect of temperature on the expression of the *medionigra* phenotype of the moth *Panaxia dominula* (Lepidoptera: Arctiidae). - Oikos **71**, 107-110.

PARTRIDGE, L. 1983: Non-random mating and offspring fitness. In: BATESON, P., Mate Choice, 227-255.

PICTET, A. 1905: Influence de l'alimentation et de l'humidité sur la variation des papillons. - Mém. Soc. Phys. Hist. nat. Genève **35**, 45-127.

POOLE, R. W. 1989: Noctuidae. In: HEPPNER, J.B., Lepidopterorum catalogus (n.s.) **118**, i-xii, 1-1314.

REICHL, E. R. 1958: *Zygaena ephialtes* L. I. Formen-Verteilung und Rassengrenzen im niederösterreichischen Raum. - Z. Wien. entomol. Ges. **43**, 250-265.

– – 1959. *Zygaena ephialtes* L. II. Versuch einer Deutung der Rassen- und Formenverteilung auf populationgenetischer Basis. - Z. Wien. entomol. Ges. **44**, 50-64.

– – 1962: Populationsgenetische Untersuchungen an *Zygaena transalpina* ESP. I. Ssp. *tilaventa* HOLIK. - Biol. Glasn. **15**, 141-156.

– – 1964: *Procris heuseri* spec. nov. und *Procris statices* L., zwei Arten in statu nascendi? (Lepidoptera, Zygaenidae). - Nachrbl. bayer. Ent. **13**, 89-95, 99-103, 117-120.

– – 1992: Populationsgenetische Untersuchungen an *Zygaena transalpina* (ESPER, 1782) (Lepidoptera: Zygaenidae). II. Die Rassen Mittelitaliens. In: DUTREIX, C. et al., Recent advances in Burnet Moth research (Lepidoptera: Zygaenidae), 88-100.

ROBINSON, R. 1971: Lepidoptera genetics. - Pergamon Press, Oxford.

ROCCI, U. 1913: Contribuzione allo studio dei Lepidotteri del Piemonte, 3. - Atti Soc.ligust.Sci.nat. **24**, 131-216.

ROTHSCHILD, M. 1961: Defensive odours and Müllerian mimicry among insects. - Trans. R. entomol. Soc. Lond. **113**, 101-121.

– – 1985: British aposematic Lepidoptera. In: HEATH, J., EMMET, A.M., The Moths and Butterflies of Great Britain and Ireland **2**, 9-62.

ROTHSCHILD, M., LANE, C. 1960: Warning and alarm signals by birds seizing aposematic insects. - Ibis **102**, 328-330.

RUNGS, C.E.E. 1988: Liste-inventaire systématique et synonymique des Lépidoptères de Corse. - Alexanor **15** (Suppl.), 1-86.

SBORDONI, V., BULLINI, L., SCARPELLI, G., FORESTIERO, S., RAMPINI, M. 1979: Mimicry in the burnet moth *Zygaena ephialtes*: population studies and evidence of a Batesian-Müllerian situation. - Ecol. Entomol. **4**, 83-93.

SCHINTLMEISTER, A. 1989: Zoogeographie der palaearktischen Notodontidae (Lepidoptera). - Neue entomol. Nachr. **25**, 1-103.

SHAPIRO, A. M. 1976: Seasonal polyphenism. - Evolutionary Biol. **9**, 259-333.

SHEPPARD, P. M. 1951: A quantitative study of two populations of the moth *Panaxia dominula* (L.). - Heredity **5**, 349-378.

– – 1952: A note on non-random mating in the moth *Panaxia dominula* (L.). - Heredity **6**, 239-241.

– – 1953: Polymorphism and population study. - Symp. Soc. exp. Biol. **7**, 274-289.

– – 1956: Ecology and its bearing on population genetics. - Proc. R. Soc. Lond. (B) **145** (920), 308-315.

SHEPPARD, P. M., COOK, L. M. 1962: The manifold effects of the *medionigra* gene of the moth *Panaxia dominula* and the maintenance of a polymorphism. - Heredity **17**, 415-426.

SHEPPARD, P. M., TURNER, J. R. G., BROWN, K. S., BENSON, W. W., SINGER, M. C. 1985: Genetics and the evolution of Muellerian mimicry in *Heliconius* butterflies. - Phil. Trans. R. Lond. (B) **308**, 433-610.

SIMPSON, G. G. 1961: Principles of animal taxonomy. - Columbia University Press, New York.

SPULER, A. 1906: Arctiidae. In: SPULER, A., 1903-1910, Die Schmetterlinge Europas **2**, 128-152.

STANDFUSS, M. 1885: *Callimorpha* v. *Persona* HB. - Corr.blatt entomol. Ver. Iris **1** (2), 23-29.

– – 1896: Handbuch der paläarktischen Gross-Schmetterlinge für Forscher und Sammler. - G. Fischer, Jena.

STARRETT, A. 1958: What is the subspecies problem? - Syst. Zool. **7**, 111-115.

STAUDER, H. 1916: Lepidopteren aus dem Aspromontegebirge. Material zu einer Zusammenstellung der südkalabrischen Schmetterlingsfauna (Fortsetzung u. Schluß). - Z. wiss. Insektenbiol. **12**, 109-112.

– – 1925: Lepidoptera aus Unteritalien II (Fortsetzung). - Soc. entomol. **40**, 5-7.

TARMANN, G. 1979: Die *statices*-Gruppe des Genus *Procris* F. (Lepidoptera, Zygaenidae). - Mitt. Münch. Ent. Ges. **68** (1978), 45-108.

TEMPLETON, A.R., HEMMER, H., MACE, G., SEAL, U. S., SHIELDS, W. M., WOODRUFF, D. S. 1986: Local adaptation, coadaptation, and population boundaries. - Zoo Biology **5**, 115-125.

THORPE, R. S. 1987: Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. - Boll. Zool. **54**, 3-11.

TREITSCHKE, F. 1834: Die Schmetterlinge von Europa, Supplement **10** (1). - E. Fleischer, Leipzig.

TURATI, E. 1919: A 1000 metri sull'Appennino Modenese. Note di lepidotterologia e descrizione di tre nuove specie di micri. - Atti Soc. Ital. Sci. nat. **58**, 147-187.

− − 1923: Cinque anni di ricerche nell'Appennino modenese (Note di Lepidotterologia). - Atti Soc. Ital. Sci. nat. **62**, 4-74.

TURATI, E., VERITY, R. 1912: Faunula Valderiensis nell'alta valle del Gesso (Alpi Marittime). Heterocera. - Bull. Soc. entomol. Ital. **43** (1911), 168-233.

TURNER, J. R. G. 1971: Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies. In: CREED, E. R., Ecological genetics and evolution, 224-260.

VERITY, R. 1930. Descrizione di varie razze italiane e di una portoghese di *Zygaena* e dell'eserge scozzese della *Z. fulvia* F. chiamata a torto *achilleae* ESP. - Mem. Soc. entomol. ital. **9**, 12-29.

VUILLAUME, M. 1969: Les Pigments des Invertébrés. - Masson, Paris.

WATT, W. B. 1969: Adaptive significance of pigment polymorphisms in *Colias* butterflies, II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. - Proc. nat. Acad. Sci. Amer. **63**, 767-774.

WEINS, J. A. 1976: Population responses to patchy environments. - Ann. Rev. Ecol. Syst. **7**, 81-120.

WENZEL, G. 1936: Eine *Callimorpha dominula* L.-Massenzucht (Macrolep.). - Entomol. Z. Frankf. a.M. **49**, 561-564.

WHITE, R. J. 1985: Some population study methods illustrated with the Scarlet Tiger Moth. In: COOK, L. M., Case studies in population biology, 27-60.

WIGGLESWORTH, V. B. 1972: The principles of insect physiology. - (7th ed.) Chapman & Hall, London.

WILLIAMSON, M. H. 1960: On the polymorphism of the moth *Panaxia dominula* (L.). - Heredity **15**, 139-151.

WILSON, A. 1985: Flavonoid pigments in marbled white butterfly (*Melanargia galathea*) are dependent on flavonoid content of larval diet. - J. chem. Ecol. **11**, 1161-1179.

− − 1986: Flavonoid pigments and wing color in *Melanargia galathea*. - J. chem. Ecol. **12**, 49-67.

WILSON, E. O., BROWN, W. L. 1953: The subspecies concept and its taxonomic application. - Syst. Zool. **2**, 97-111.

WRIGHT, S. 1948: On the roles of directed and random changes in gene frequency in the genetics of populations. - Evolution **2**, 279-294.

− − 1978: Evolution and the genetics of populations 4. Variability within and among natural populations. - The University of Chicago Press, Chicago & London.

Author's address:

Dr. Alberto ZILLI
Museo Civico di Zoologia
Viale del Giardino Zoologico 20
I-00197 Rome
Italy

Zilli, Alberto. 1996. "Colour polymorphism of Callimorpha dominula (Linnaeus, 1758) in Italy, and the problem of polytopic subspecies (Lep. Arctiidae, Callimorphinae)." *Mitteilungen der Münchner Entomologischen Gesellschaft* 86, 79–98.