The two subspecies of Polyommatus icarus (Rottemburg) in Lebanon; a probable case of multiple invasion (Lep.; Lycaenidae)

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The presence of two distinct subspecies of *Polyommatus icarus* (Rottemburg) in Lebanon was known since the beginning of this century. From that time they have provided rich food for speculation and controversy (Zerny 1932, Ellison & Wiltshire 1939, Higgins 1964, Paulus & Rose 1971, Larsen 1974 and Nakamura & Benjamini in press). I included both as genuine subspecies in my book on the Lebanese butterflies (Larsen 1974). With the recent welcome trend towards applying a geographic approach in the definition of subspecies (e. g. Mayr 1963, and in more consequence by de Jong 1972) my decision has been informally criticized by some colleagues on the grounds that two subspecies of the same butterfly could not fly on the small territory of Lebanon. I hope to show in this paper that not only are the two valid subspecies, but that their largely allopatric distribution within Lebanon may be explained without undue problems as the result of an invasion of a subspecies with a different mode of ecological adaptation.

#### **Taconomic status**

Polyommatus icarus is a common and variable species with a wide distribution in the Palaearctic region. A multitude of subspecies have been described, many unnecessary, and the species is clearly in need of an enlightened taxonomic study. The two taxa present in Lebanon are: ssp. zelleri Verity, a name which is conventionally but not necessarily convincingly used for all Mediterranean populations, and ssp. juno Hemming, described after speciemens from the Cedar Mountain, 2000 m, and endemic to Lebanon. The two are very different; ssp. zelleri resembles nominate icarus except in the summer broods which have very neat undersides with well-marked orange marginal lunules and little or no basal blue suffusion; ssp. juno is characterised by an almost total reduction of the marginal orange lunules, and partial reduction or disapperance of the black spotting; specimens are usually slightly larger than zelleri and with more pointed wings. It is possible to tell them apart at a glance. Both are figured in colour

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in my book on the Lebanese butterflies (Larsen 1974, plate: 161); the male underside is from an unusually small and dark specimen.

Zerny (1935), in a postscript to his 1932 paper on the Lebanese Lepidoptera, took strong exception to Hemming's (1933) description of ssp. *juno*, considering it to be synonymous with *persica* Bienert, which flies in Iran and Afghanistan, but they are not identical although they share reduction in underside markings, a similarity which could be due to parallel response to ecological conditions. However the possibility that all *persica*-like populations share a common ancestor cannot be ruled out entirely since their overall area of distribution is the same as that of other species of Iranian origin, such a *Pseudochazara pelopea* Klug.

The genitalia of the two subspecies are similar and the chromosome numbers are identical, n = 23 (Larsen 1975).

### **Ecology**

Ssp. zelleri is widespread and common all over Lebanon from sea level to 1500 m, becoming progressively rarer higher up, and rarely surpassing 2000 m. On the coast it flies in a series of ill-defined broods almost all year round while there are two to four broods in the mountains, depending on altitude. It feeds on a wide selection of Leguminosae in spring, but judging from personal observation the main food plant during the hot and dry summer is hardy species of Ononis. At low levels the butterfly can be found nearly everywhere, though grassy areas are preferred; at higher, and especially at the highest, levels wet meadows and agricultural land with permanent moisture are preferred. Such spots are far from common and zelleri becomes increasingly local as altitude increases.

Ssp. juno is found from about 1500 m to 3000 m in both the Lebanon and Antilebanon ranges, and it almost replaces ssp. zelleri above the level of 1800 m. At lower levels there are two well defined broods (June and late July/early August), above 2300 m or so only a single brood. The preferred habitat is the large expanses of open land dominated by thorny Astragalus, Onobrychis cornuta and Berberis libanotica which are so charicteristic of the subalpine and Syrian montane vegetation zones of the high mountains in Lebanon (described in detail in Larsen 1974). Unfortunately I did not manage to find the larvae, but all indications are that they feed on one of the subalpine Astragalus or Coronilla.

In consequence of this difference in ecological preference ssp. *juno* is found only in the high Lebanon and Antilebanon in two disjunct populations, surrounded on all sides by much more extensive populations of ssp. *zelleri*, which extend as far east as the Syrian and Jordanian deserts and as far south as the Sinai.

### Distribution and sympatry

I had planned a detailed study of the interesting situation described above, including aspects such as food plant choice, cohabitation, ecological preferences and breeding experiments, but I was unfortunately forced to leave the Lebanon before this was possible. However, sufficient information was gathered to allow for some fairly precise conclusions to be drawn.

In general the two subspecies do not fly together even in the zone of transition, mainly because their choice of habitat differs so substantially. The zone of transition stretches from about 1500 m to 2000 m; at higher or lower levels all populations are unequivocally attributable to *juno* and *zelleri* respectively. Even here cases of exact sympatry and/or hybridisation are rare since either species lives in discrete colonies on ground which appears unfavourable to the other. A few examples are given below.

In the area leading up the steep road from the village of Faraya, 1400 m, to the Faraya Mzaar Hotel, 1800 m, and the Jabal Kesrouan, 2000 m, icarus was investigated in the course of extensive general collecting during the 1973 and 1974 seasons. At the village itself and up to 1600 m only ssp. zelleri was found on agricultural land bordering colonies of ssp. zelleri was found on agricultural land bordering springs, while equally local colonies of ssp. juno appeared on dry ground. Most of this area is dominated by an association of Phlomis, Carduus and Eryngium which seems equally unfavouable to both subspecies. There was a fairly large, well-watered meadow in one spot which adjoined a hill-side with extensive vegetation dominated by Astragalus and Onobrychis. The meadow contained a flourishing colony of ssp. zelleri while the hillside had a smaller colony of ssp. juno, and there was a fair amount of mixing at the flowery edge of the meadow. On 15. VI. 1974 I caught about 30 zelleri and a dozen juno, none of which were in the least intermediate. From 1800 m onwards, over the undulating plateau of the Jabal Kesrouan which stretches for more than ten kilometres of pure subalpine vegetation, juno is the sole representative till zelleri suddenly reappears in the hashish fields of the eastern foothills of the Lebanon range, bordering the Begaa Valley.

In northern Lebanon, at the village of Bscherré, 1500 m, ssp. zelleri is common. There is also a small colony at about 1700 m at the Aiglon Hotel on sandy soil. At the famous Cedar Grove at 2000 m ssp. juno is extremely common, but a few specimens of zelleri could always be found, especially in the gardens of the village near the actual grove and along watering canals in the area. In late June and early July of 1973 and 1974 I checked hundreds of typical juno inside the walls of the Cedar Grove where they spent the night in communal

roosts with other species of Lycaenidae (Larsen 1973). I noted only a single specimen of *zelleri* inside the walls of the grove; this was a female and it was in copula with a male *juno* though female *juno* were already out in forcel! A small colony of *zelleri* existed some 200 m from the grove, but I never observed any intermediate specimens.

There is also a zone of overlap near Laklouk, 1800 m, on an undulating plateau surrounded by mountains, whose vegetation is not as typically subalpine as the higher parts of the two other areas. I did not visit this area frequently enough to study the situation in detail, but I did get the impression that *zelleri* had three broods and *juno* only two, and that they were not quite synchronic at any time of the year. Two or three clearly intermediate specimens were taken over the years.

On the Barouk Mountain in the southern half of the country, which rises to only just over 1800 m, ssp. zelleri flies to the very summits. Ssp. juno inhabit the same summits but it is rare to find typical specimens. They are normally smaller, with darker undersides and with better developed orange marginal lunules; some are clearly intermediate to zelleri. The general impression is that juno is gradually being replaced by zelleri. The reason may be that these dry, limestone mountains of relatively moderate elevation are not suitable habitats for juno; certainly many of the subalpine species with which juno is associated further north are rare or missing on the Barouk. Nakamura & Benjamini (in press) found both subspecies to be common on the Mt. Hermon in the southern Antilebanon and they found no clear intermedate specimens. The high parts of the northern Antilebanon have not been explored by entomologists, but the same situation is almost certain to prevail.

The overall picture may be summarised thus: ssp. zelleri is common and widespread in Lebanon and the neighbouring countries up to an altitude of 1500 m, more rarely to 2000 m, especially in moist localities at higher levels; ssp.juno is locally common in defined colonies in the high mountains. The zone of contact is relatively narrow and even here there are ecological barriers to frequent cases of exact sympatry. The ecological barriers may be further reinforced by asynchronic emergence of the broods of the two subspecies. Interbreeding does occur, but it is rare and specimens which which cannot confidently be allocated to either of the two are infrequent.

## Biogeographic aspects

In nature ssp. juno is closely associated with a number of species having a similar geographical and ecological distribution in the Le-

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banon and Antilebanon, most of which have either speciated or developed characteristic subspecies in Lebanon. Notable examples are: Leptidea duponcheli xanthochroa Verity. Colias libanotica Lederer, Aglais urticae turcica Staudinger, Satyrus ferula makmal Higgins, Strymonidia myrtale Klug, Lycaena asabinus asabinus Herrich-Schäffer, Lycaena ochimus ochimus Herrich-Schäffer, Lycaena thetis zahaltensis Graves, Agrodiaetus poseidon mesopotamica Staudinger, Agrodiaetus alcestis alcestis Zerny. Lysandra syriaca Tutt, Spialia phlomidis hermona Evans and Hesperia comma pallida Staudinger. Most of these are confined to the subalpine and Syrian zones of both the Lebanese mountain ranges and live widely separated from neighbouring populations in the Taurus of southern Turkey and in Kurdistan. We must assume that these species were isolated in a Syrian refuge (sensu de Lattin 1967) during the Pleistocene with ecological conditions roughly similar to those of the high Lebanese mountains to-day. With the gradually increasing temperatures of the last 10.000 years this group of species has been forced up the mountains in Lebanon, Iraq and Turkey.

Ssp. zelleri is probably a more recent arrival from a Pontomediterranean refuge area. Its current distribution in the area closely resembles a number of other species which do not manage to penetrate the subalpine zone to any significant extent, such as Papilio machaon syriacus Verity, Gonepteryx cleopatra taurica Staudinger, Polygonia egea egea Cramer, Melitaea phoebe telona Fruhstorfer, Aricia agestis agestis Denis & Schiffermüller among others. Once P. icarus is subjected to a careful monographic review, it would not be surprising if a distinct Pontomediterranean element could be detected. P. icarus is an ecologically adaptable species and one of the most common and widespread of the Polyommatini in the western Palaearctic. Why then was the original resident, the ancestor of ssp. juno, not able to establish itself in all of Lebanon? The answer proably is that during the Pleistocene it adapted narrowly, but succesfully, to the conditions under which it and its associated species now fly; it was forced to specialise to an ecxtent which other icarus subspecies were not, and in consequence it lostpart of its adaptive powers. We do not know specialise to an ecxtent which other *icarus* subspecies were not, and in consequence it lostpart of its adaptive powers. We do not know whether *juno* retrenched voluntarily or whether it was forced into its present restricted range in competition with the more dynamic *zelleri*. Judging from the strict ecological requirements of *juno* it is quite likely that the retrenchment was spontaneous and that *zelleri* moved in to fill a void and that the zone of contact is very recent. However, *juno* is definitely on the defensive; there is evidence that it is being crowded off the Barouk Mountains and its ecological requirements severely restricts its distribution elsewhere; but on true home ground it has sufficient advantage over *zelleri* to predominate.

#### Conclusion

it has been suggested that *juno* should be considered a bona species rather than a subspecies of *icarus*, and indeed some of the evidence given here could be used to support such a view. However, there is very little distributional overlap, there is evidence of interbreeding between *juno* and *zelleri*, and *icarus* populations in Iran and Afghanistan have some resemblance to *juno*. Similar situations are found in other taxa, notably *Euphydryas aurinia debilis* Oberthür in the Alps.

On the whole the best solution would appear to be to consider the two Lebanese forms genuine allopatric subspecies which evolved in isolation in separate refuge areas at some point of the Pleistocene and which have later re-established contact. The fact that ssp. juno is surrounded on all sides by ssp. zelleri is no objection to such a view; ssp. juno may be considered the original inhabitant which has adapted to rather specialised conditions, while ssp. zelleri is a more flexible and dynamic invader. The raising of juno to specific rank would obscure an interesting dynamic relationship without conferring any compensatory benefits.

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