The natural history, ecology and distribution of *Turanana panagaea* (Herrich-Schäffer, [1851]) and *Lycaena thetis* (Klug, 1834) in Greece (Lepidoptera : Lycaenidae)

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Abstract. The larval host-plant of *Turanana panagaea* and *Lycaena thetis* in Greece has been established as *Acantholimon androsaceum* (Plumbaginaceae). Strong circumstantial evidence indicates that both butterfly species are monophagous. Experiences in the captive rearing of *T. panagaea*, which hibernates as a pupa, and *L. thetis*, which hibernates as a small larva, are described. Larval feeding regimes indicate negligible or nil inter-species competition. Both species display a high order of adaptation to their larval host-plant, the implications of which are discussed in detail. Observational evidence indicating rapid evolutionary development of *thetis* relative to its congeners is shown to be consistent with theoretical expectation: taxonomic implications are noted. All larval stages of *L. thetis* appear to be myrmecoxenous. Larvae of *T. panagaea* were not observed in nature but other evidence indicates little or no myrmecophily. The absence of larval parasitism noted for *thetis* is contrasted with the high frequencies observed in the larvae of 47 other Greek lycaenids studied in the same, two year period. The observation of *A. androsaceum* on mountains in northern Greece is reported and its significance discussed. The rediscovery of *thetis* on Mount Tymphristos is reported, as is the recent discovery of *thetis* on the Giona mountain by Mr. Jos Dils of Antwerpen at his request.

Samenvatting. De biologie, ecologie en verspreiding van *Turanana panagaea* (Herrich-Schäffer, [1851]) en *Lycaena thetis* (Klug, 1834) in Griekenland (Lepidoptera : Lycaenidae)
De voedselplant van de rups van *Turanana panagaea* en van *Lycaena thetis* in Griekenland is *Acantholimon androsaceum* (Plumbaginaceae). Op basis van de beschikbare gegevens wordt verondersteld dat beide soorten strikt monofaag zijn. Kweekresultaten van *T. panagaea*, die als pop overwintert, en van *L. thetis*, waarvan de jonge rups overwintert, worden beschreven. Voedingsgewoonten de rupsen duiden op weinig of geen concurrentie tussen de soorten. Beide soorten vertonen een hoge aanpassingsgraad aan hun voedselplant en de implicaties daarvan worden in detail besproken. Waarnemingen van een snellere ontwikkeling van *L. thetis* in vergelijking met de verwante soorten staven de theoretische verwachtingen en taxonomische gevolgtrekkingen worden genoteerd. Alle larvale stadia van *L. thetis* blijken myrmecoxenisch te zijn. Rupsen van *T. panagaea* werden in de natuur niet geobserveerd, maar andere waarnemingen duiden op weinig of geen myrmecofilie. Het ontbreken van parasieten bij *L. thetis* staat in schril kontrast met de hoge graad van parasitering bij 47 andere Griekse Lycaenidae soorten, die in dezelfde periode van twee jaar werd vastgesteld. *A. androsaceum* werd aangetroffen in de bergen van Noord-Griekenland en de betekenis daarvan besproken. De herontdekking van *L. thetis* op de Tymfristos wordt vermeld alsook de recente ontdekking van *L. thetis* op de Giona door Jos Dils (Antwerpen).

Résumé. De la biologie, de l'écologie, et de la répartition de *Turanana panagaea* (Herrich-Schäffer, [1851]) et de *Lycaena thetis* (Klug, 1834) en Grèce (Lepidoptera : Lycaenidae)
En Grèce, la plante nourricière de *Turanana panagaea* et de *Lycaena thetis* est *Acantholimon androsaceum* (Plumbaginaceae). Il est prouvé que les deux espèces sont strictement monophages. Les résultats d'élevages, de *T. panagaea* (qui hiverne à l'état de chrysalide), et de *L. thetis* (dont la jeune chenille hiverne) sont décrits. Les exigences alimentaires des deux espèces prouvent qu'il n'existe aucune concurrence entre elles. Les deux espèces montrent un haut degré d'adaptation à leur plante nourricière et les implications sont commentées en détail. L'évolution plus rapide de *L. thetis*, par rapport aux espèces voisines, confirme certaines théories et des conclusions taxonomiques sont mentionnées. Tous les stades larvaires de *L. thetis* semblent myrmecoxéniques. Les

chenilles de *T. panagaea* n'ont pas été observées in situ, mais d'autres observations démontrent peu ou pas de myrmécophilie. L'absence de parasites chez *L. thetis*, est en flagrante contradiction avec le haut degré de parasitage de 47 autres espèces grecques, observées durant la même période de deux ans. *A. androsaceum* vit dans les montagnes du nord de la Grèce, et la signification en est donnée. La redécouverte de *L. thetis*, sur le mont Tymphristos, ainsi que la découverte de cette espèce sur le Mont Giona, par Jos Dils (Antwerpen), sont mentionnées à sa demande.

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The larval host-plant of *Turanana panagaea* (Herrich-Schäffer, [1851])

The first, personal encounter with *Turanana panagaea* (Herrich-Schäffer, [1851]) was in June 1984 on the Chelmos mountain in the northern Peloponnesos, Greece. Close to a ridge at 2000 m, a small number of fresh adults were noted frequenting an area of no more than 3000 m². Acting on the premise that the extreme localisation of the butterfly corresponded to a restriction in the occurrence of its larval host-plant, the biotope was examined systematically for all plant species not in evidence beyond its bounds. Two such species were noted. One was a prostrate *Erodium*, the other, cushion-forming, with dense rosettes of tough, sharply-pointed leaves and dark, pinkish flowers: its identity was later established as *Acantholimon androsaceum* ([Jaub & Spach]. Bois, 1846) (Plumbaginaceae). A prolonged search for ova and larvae was unsuccessful.

The next encounter with *T. panagaea* was in June 1987, again on Chelmos but in a different part of the mountain: here too, *A. androsaceum* was in evidence. The butterfly was not common and, due to a strong wind which persisted for much of the day, these small, vulnerable-looking insects were largely deterred from flying. No eggs or larvae were found. In an effort to improve upon this result, a captive female was kept cool and in darkness for a few hours: confining a female lycaenid in this way, so it has been noted on previous occasions, often stimulates the insect to oviposit when eventually given the opportunity. This incitement would seem to be a natural response to depreviation and, indeed, may be seen in close parallel to the diurnal behavioural pattern of all gravid female butterflies, namely, the early morning ritual of warming, feeding and ovipositing, which - weather conditions permitting - invariably follows night-time inactivity. Regardless of the validity of this hypothesis, the efficacy of the device itself was, on this occasion, well demonstrated. On being released, late afternoon in very warm, still conditions, the female immediately began feeding on the flowers of Thyme. A few minutes later, she flitted to an adjacent plant of *A. androsaceum* where she deposited two eggs on a single rosette of leaves. She then retired to a nearby stone and, with wings fully open, was still sunning herself upon my departure some 10 minutes later.

Later that evening, I met up with my companion, Mr. Charles Derry, who had been collecting in a different part of the biotope. Even before he had chance to relate his day's experience, I noticed in his hand, a small sprig of *A. androsaceum*: this contained two ova that he had seen laid by *T. panagaea* earlier in the day. These had been deposited deep between leaves, in which position they were rather difficult to see. The eggs were retained but failed to hatch. In any event, there would have been no realistic chance of following the development of the species to maturity owing to the presumed impracticability of removing and maintaining even a small specimen of the deeply rooted host-plant.

The larval host-plant of *Lycaena thetis* (Klug, 1834)

In July 1986, a visit to Chelmos was made for the express purpose of learning something of the early stages of *L. thetis* (Klug, 1834). Having located the site where, according to several friends, the appearance of the butterfly could be guaranteed, 15 or so specimens of both sexes were noted in the first day of searching. However, failure to locate a single representative of the Polygonaceae - the Dock family - which, so it had been assumed, was certain to provide sustenance for the caterpillars of *thetis*, resulted in disappointment and more than a little surprise. In the following 2 days, a much intensified search for plants and ovipositing females proved equally fruitless. To add to the frustration, 3 captive females expired without laying a single egg on any of the potted Polygonaceae species which had been taken to the mountain as insurance against the risk of not finding wild ova or larvae. (The in situ removal and use of host-plants for this purpose is often impracticable). At this juncture, concern with *thetis* lapsed for some 5 years.

In April 1991, the search was resumed in the same Chelmos biotope, this time, of course, for the dual purpose of acquiring hibernated/hibernating larvae of *thetis* as well as its host-plant. During 2 days of searching, efforts were hampered by unseasonably low temperatures and a penetrating wind. An unproductive first day was devoted mainly to the area, at about 1550 m, where most of the females had been noted in 1986. The search area was greatly extended on the second day, covering about 3 km² and an altitude range of 1500-2100 m. Near the upper limit of this range, a colony of the host-plant of *panagaea* was located: a search for the larvae of this species was negative. Within this colony, a small patch of *Rumex acetosa* Linnaeus was found. The 10 or so plants were thoroughly examined as were nearby clumps of grasses, stones and, indeed, everything in the vicinity suspected of offering a winter refuge for lycaenid larvae: none were found, and it was later concluded that the *Rumex* plants were of no more than spurious occurrence as no others were found subsequently in a day which concluded with the temperature falling well below zero. Faced with the imminent prospect of falling snow, all concerns with Chelmos were hastily relinquished in favour of the *thetis* biotopes of the more southerly Taygetos Mountains, where, it was hoped, better weather conditions prevailed. Here, unfortunately, the threat of snow

had already given way to actuality and the search for *thetis*, conducted between 1500 and 2200 m, was abandoned after 2 days, As on Chelmos, no member of the Polygonaceae, recognisable as such, was found in the *thetis* biotopes of the Taygetos Mountains.

Discouraged by the difficulties and disappointments, the idea of reverting by the original option of seeking out an ovipositing female and staying with her until she laid an egg, became increasingly attractive. In the event, no such alternative proved necessary for the very remarkable reason that, even before initiating the search for hibernated *thetis* larvae, one of these was already in my possession, feeding happily in a plastic box in the relative comfort of my own car! The explanation for this extraordinary situation is intimately connected with the search for hibernated larvae of *panagaea* which had been conducted concurrently with that for *thetis*. Immediately prior to the search of the *thetis* biotopes on Chelmos, 3 days had been spent looking for *panagaea* larvae on the same mountain. Towards the end of this period, after a total of 18 hours of searching in bitterly cold conditions, a very small, well camouflaged lycaenid larva was found at rest on a leaf of *A. androsaceum*. This was assumed to be that of *panagaea*, the apparent scarcity of larvae being attributed to the prevailing temperature - it was assumed that most larvae were still in hibernation. It was at this point and for this reason that attention turned to the potentially more profitable pursuit of the *thetis* host-plant. Whilst searching for this in the Taygetos Mountains, several colonies of *A. androsaceum* were found between 1500 and 2150 m. A total of 12 small lycaenid larvae, identical to the one originating from Chelmos, were recovered from these plants. At this point, there was no reason to suppose that the larvae were anything other than those of *panagaea*, but, as the weeks passed, and the larvae continued to grow, so did the skepticism concerning their identity. By the time of their pupation, in June, all residual doubt that the larvae from the *panagaea* host-plant were not, in fact, those of *panagaea* had long since been dispelled. In July, the issue was finally resolved when the first imago of *thetis* emerged.

The immature stadia of *T. panagaea*

Having established *A. androsaceum* as the shared larval host-plant of *panagaea* and *thetis*, it was reasoned that *panagaea* most probably hibernates as a pupa. Whilst part of this reasoning related directly to the failure to find over-wintered larvae, a more compelling argument arose from the perceived, ecological vulnerability of both *panagaea* and *thetis*. This perception derives largely from the implications of their apparent restriction to a single host-plant species, which, from all appearances, is itself highly specialised and represented only by small, localised colonies at high altitude. Assuming the validity of this inference, it follows that neither *panagaea* nor *thetis* is likely to disadvantage itself further by utilising the same larval food resource at the same time, given that such competition is unnecessary: here, the adoption of different feeding regimes affords an opportunity of minimising the risk to

both species. As the feeding requirement of hibernated *thetis* larvae coincides with the earliest stage of seasonal development of the host-plant, when only the leaves are available, it follows that competition with *panagaea* would be unavoidable, if this too were to hibernate as a larva. Greater risk - indeed, one potentially lethal to the species - would, of course, incur from *panagaea* hibernating in the ovum stage on the leaves of its host-plant.

In deferring to the foregoing considerations, no further searches were dedicated to hibernated *panagaea* larvae when the next opportunity to examine *A. androsaceum* plants arose in the spring of 1992. Indeed, attention to the host-plant, at this time, centred on *thetis* and it is sufficient to record here that no *panagaea* larvae were found, either on Chelmos or in the Taygetos Mountains.

On Chelmos in July 1992, towards the end of the flight-period of *panagaea*, a concerted effort was made to locate the immature stages of the species. At the time, it was a matter of some surprise that no larvae were found. However, an appreciable number of ova, deposited almost exclusively on the flower bracts, were acquired. The ovum is less than 1 mm diameter, white and discoidal. A depressed area around the micropyle appears slightly grey in comparison to the reticulated surfaces and is large in proportion to the size of the egg. The only ovum whose deposition was witnessed, hatched after 8 days. The newly-hatched larva is a uniform pale yellowish colour and sparsely clothed with whitish hairs. The head is black and shiny.

In its manner of feeding, the *panagaea* larva is quite remarkable. The newly-hatched larva secrets itself immediatly within the flower panicle containing the ovum and does not emerge for 10 or more days, by which time it is about 3 mm long and significantly changed in appearance. At no time during this stage does the larva give the slightest indication of its presence within the flower. A careful examination of the flowers failed to identify the points of ingress and egress of the larvae, but both sites would appear to be the receptacle. Dissection of a discarded flower revealed that all internal tissues down to the base of the calyx were consumed. Upon exiting the flower, the colouration of the juvenile larva (Fig. 4) is closely compatible with that of the tube of the calyx which is of a stiff, papery texture, conically-fluted and off-white with dark-purplish veins. Aligned longitudinally within the calyx of dead flowers, small larvae at rest or in preparation for ecdysis are rendered virtually undetectable. In this connection, it is speculated that egg-laying sites are selected to ensure that the emergence of larvae from the flowers and the skin-change which immediately follows, coincides with the loss of the flower petals. In subsequent instars, larvae refused flowers, preferring, instead, leaf rosettes. However, feeding occurs only at the base of the leaves where these ajoin the stem. Being substantially removed from light, the plant tissue at this location is devoid of chorophyll. In the process of feeding, the larva systematically amputates every leaf except those comprising the outer ring of the rosette before transferring to fresh leaves. The larva betrays neither its presence, nor the consequence of its activity, since the amputated leaves give

every visible indication of being intact - the reality can only be established by jostling or inverting the rosettes. It will be clear, of course, that the outer ring of leaves, which are invariably ignored, serve as a retaining wall - a miniature conical basket - for the severed leaves. Having regard to the figures in Plate 1, it should be noted that larvae were placed upon leaf-rosettes of a much more open structure than is typical of the host-plant in order to gain photographic access.
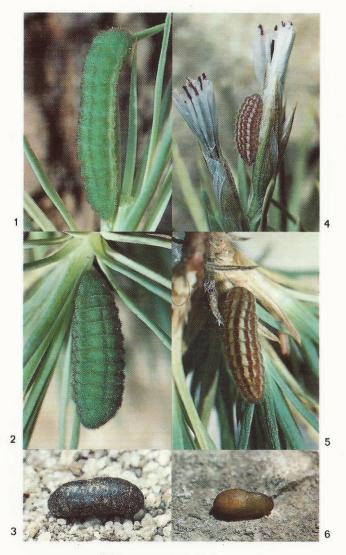
As the larva matures (Plate 1, Fig. 5), its ground colour becomes progressively darker and yellower. This, in conjunction with the dark segmental markings, provides effective camouflage in later skin-changes, which, in captivity, occurred amongst the dead leaves of the plant stems. Unfortunately, circumstances did not permit the close attention required to determine the number of instars with certainty, but there are at least four. The larval stage lasts for about 4 weeks. In the 3 days before pupation, the ground-colour reverts progressively to off-white. A dorsal nectary organ could not be detected even in mature larvae and, in the field, very few foraging ants were noted on host-plants at a time when these were certain to have contained an appreciable number of larvae.

Pupation occurred with no attachment amongst the dense matrix of dead leaves of the host-plant. The species hibernates as a pupa (Plate 1, Fig. 6).

The larva and pupa of *L. thetis*

The *thetis* larvae found shortly after hibernation measured 4-7 mm. Some colour variation was noted, the smaller specimens being generally darker and greyer, occasionally with a rust-coloured sub-spiracular line and a more general diffusion of similar colouration on the anterior and posterior segments. In this livery, the small larvae were well matched to the greyish winter leaves, many of which were also rust-coloured at the tips and edges, evidently the results of weather damage. Very small larvae feed on the upper cuticle of the leaves with the head towards the leaf-tip. Ecdysis occurs with the small larva tightly compressed within the cavity created in the leaf by its feeding. Larger caterpillars (Plate 1, Fig. 1) consume the entire leaf, except for the terminal spine, from the tip downwards. Ecdysis in later instars took place on the underside of the leaf-rosettes. In nature, the feeding station is changed frequently and only 1 or 2 leaves of each rosette are eaten. As the larvae grow, they become brighter green and lose the reddish variegation, thereby matching the fresher appearance of the developing spring leaves. It is noteworthy that the combination of leaf and feeding larva tends to resemble a developing flower panicle: analogically, the leaf and larva correspond, respectively, to the flower stem and flower-buds, whilst the dark, segmental markings of the larva bear close resemblance to the dark edges of the regularly spaced, overlapping flower bracts. The overall impression is further enhanced by the rather cylindrical form of the larva. The mature, non-feeding larva does, however, have a more typical lycaenid shape (Plate 1, Fig, 2). Captive

Plate 1

Figs 1-3: *Lycaena thetis* (Klug, 1834); 1. Half grown larva, 2. Last instar larva, 3. Pupa.
Figs 4-6: *Turanana panagaea* (Herrich-Schäffer, [1851]); 4. Half grown larva, 5. Last instar larva, 6. Pupa.

larvae pupated after 8 to 9 weeks: the post-hibernation larval stage in nature is probably 12 to 13 weeks. A few, half-grown larvae placed on *Rumex acetosa* Linnaeus and *Rumex acetosella* Linnaeus for 24 hours refused to feed.

As in the case of *panagaea*, myrmecophilous glands appear to be lacking and no field associations with ants were noted despite ample opportunity for observation in all stages of larval development. It may be relevant to note in this connection, that no examples of parasitism were observed amongst the 21 successfully reared larvae taken for study in the 1991 and 1992 seasons.

Pupation occurred amongst the dead stem-leaves of the host-plant without attachment. The pupa is shown in Plate 1 Fig. 3. The pupal stage lasted 2-3 weeks.

As the ovum of *thetis* is apparently unknown, the preferred site of its deposition is of some interest in so far as it relates to the potential for competition with *panagaea*. However, the flight periods of the two species are well separated and it is likely that most *panagaea* larvae will have pupated before *thetis* females make their appearance, this allowing *thetis* the choice of leaves or flowers. In the event of some overlap, competition may still be avoided since, as noted earlier, *panagaea* larvae restrict themselves to the leaves in later instars, thereby leaving the flowers free for *thetis*.

It may be noted in passing, that considerable difficulty was experienced in the rearing of *thetis* and *panagaea* larvae owing to the problem of maintaining cut pieces of the host-plant in healthy condition. Deterioration was especially rapid at the higher ambient temperatures of low altitude.

Comparative frequencies of parasitism observed in Greek lycaenids

In sharp contrast to the absence of parasitism noted in *thetis*, the average incidence of confirmed infestation amongst the wild larvae of 47 other lycaenid species collected in Greece, also in 1991 and 1992, was 63%. That this result probably underestimates the full, general extent of infestation, derives from the significant proportion of wild larvae lost through undetermined causes, one of which may be secondary effects of parasitism, e.g., microbiological attack, which could lead to the premature demise of parasite and host alike. Supportive evidence obtains from an observation of 46 wild larvae of *Callophrys rubi* (Linnaeus, 1758), acquired from Drama, northern Greece in 1991. Of the 25 larvae which died emaciated for no certain cause, every one displayed, at the time of its acquisition, a solitary, small, dark spot somewhere on its surface. This, it is surmised, was the site of bacterial infection coinciding with a wound caused by parasitic attack. The presence of parasites was confirmed in 5 larvae, and of the 16 pupae, 4 produced hibernated dipterans: the confirmed incidence of parasitism was, therefore, calculated as 43%. However, if the uncertainty attaching to the surmised cause of death of the other 25 larvae could be removed, the incidence of parasitism in this example would rise to 74%.

Whilst it may be argued that most of the *thetis* larvae were acquired very early in their post-hibernation development, implying a much reduced

opportunity for infestation, experiences with other lycaenids indicate that the period of exposure to the risk is far from proportional to its consequence. Indeed, it would appear that the highest incidence of infestation, for some lycaenids at least, occurs before hibernation. This conclusion derives from high-altitude field studies of hibernating, in contradistinction to hibernated larvae. By definition, the origin of parasites observed in captivity reared larvae, subsequent to their removal from hibernation, cannot be attributed to events in the post-hibernation period. Concomitantly, the probability of infestation during diapause, is adjudged to be small or zero because of the presumed inactivity or absence of adult parasites at high altitudes in winter. The situation affecting *Polyommatus (Agrodiaetus) damon* ([Denis & Schiffermüller], 1775) on Mount Tymphristos at 2000 m in early May 1992 (a very retarded season) exemplifies the general disparity in the pre- and post-hibernation incidence of infestation. Of 49 hibernating, first and second instar larvae removed to captivity, 34 contained parasites, 3 perished from unidentified causes and 12 produced butterflies. Thus, in nature, the maximum loss which could have been incurred by this sample in the post-hibernation period, would have been less than half that for the pre-hibernation and hibernating phases combined.

On the basis of the above field observations, it is adjudged, that, whilst the vast majority of Greek lycaenids are highly susceptible to parasitism, despite the benefits of myrmecophily which apply to most of them, *thetis* appears to have been remarkably successful in adapting to its circumstances unaided by ants.

The distribution of *A. androsaceum, T. panagaea* and *L. thetis* in Greece

According to *Flora Europaea* (Tutin et al., 1964), *Acantholimon ancrosaceum* is the sole European representative of the genus: its distribution is given as: the mountains of the southern part of the Balkan peninsula; Albania, Yugoslavia, Greece and Crete. In addition to this same information, Polunin (1980) cites the eastern Aegean island of Samos. Personal observations correspond to an altitudinal range of 1500-2300 m, but the plant shows a marked preference for consolidated limestone formations which are more prevalent in the upper half of this range. In this connection, it is worth recording that a few colonies of *panagaea* were found in the Taygetos Mountains between 1500 and 1700 m - well below 2000 m which Higgins & Riley (1984) specify as the minimum for the species in Greece.

The establishment of *androsaceum* as the larval host-plant of *thetis* and *panagaea* in southern Greece, where it appears to be known only from the Aroania and Taygetos Mountains, provides very convincing, albeit circumstantial evidence for the occurrence of *androsaceum* in central Greece on mountains known to contain *thetis*. By the same token, the co-habitational existence of *panagaea* on these same mountains became a possibility worthy of investigation, and although some effort in this direction was made in the

spring of 1992, poor weather rendered the negative results far from conclusive.

Interestingly, Mount Typhristos (Veluchi) was found to contain an abundance of *androsaceum*: a lengthy search secured a single *thetis* larva at 1950 m. The butterfly's occurrence on this mountain is mentioned in Higgins & Riley (1984) but this appears to relate to a very old record, dating 1870, by Staudinger (Olivier 1988). On returning to the mountain in August, in the company of Mr. Jos Dils, no imagines were seen. Also in this period, searches were made of the Kaliakouda mountain where both *androsaceum* and *thetis* were found at 1700-1900 m. On being shown a sample of *androsaceum*, its presence on the Giona mountain was kindly confirmed by a shepherd: no plants were found, but the shepherd's botanical awareness was, nonetheless, suitably demonstrated by Mr. Dils who captured a male and female of *thetis* at 1900 m: this seems to be a new record for this mountain. The only other mountain in central Greece to hold *thetis*, appears to be Iti (Olivier 1988) which is some 20 km to the north of Giona. In view of these records, it is curious that *thetis* has not been reported from the much visited Mount Parnassos, 30 km or so the the south east of Giona. Neglect of the appropriate biotopes in higher parts of the massif by butterfly collectors, sufficiently late in the season, would, of course, explain the situation. Whilst the absence of the host-plant would automatically account for the absence of the host, assuming monophagacity, this in itself would pose an interesting biogeographical problem. An equivalent problem would obtain if the host-plant was present without the host.

The occurrence of *A. androsaceum* on Crete and Samos provides for the possibility, of course, for the occurrence of either or both butterfly species on either of both of these islands.

The ecological and taxonomic status of *L. thetis*

Present information indicates that *L. thetis*, in Greece, is represented by small colonies, typically of the order of 3000 m^2, isolated at altitudes above 1500 m. The correlation of the local distribution of the butterfly with *A. androsaceum*, coupled with the observed intimacy of the host/host-plant relationship, suggests total dependence on a plant species, which, from all appearances, is itself highly specialised. Monophagacity is also implied by the rejection of *Rumex* by captive larvae: in this context, the negative results of searches for Polygonaceae - the most probable larval food alternative - in areas frequented by the butterfly, assume some significance. Collectively, these observations concert in presenting *thetis* as a highly adapted insect confined to a narrow range of conditions, which, in turn, implies a proportionately high order of ecological vulnerability. This conclusion has, moreover, some - possibly considerable - relevance regarding the rate at which *thetis* has evolved to its present-day level of adaptation: the specific situation is perhaps best illustrated by the relativies of the general case.

A species confined to small, isolated territories is relatively more vulnerable than one which is wide-ranging, since, by definition, a less restricted species is adaptable to a wider range of conditions; it may, for example, depend on a common, wide-spread host-plant or be polyphagous. Subject to the stresses of adverse environmental forces, it has, therefore, both the potential and opportunity to contract into suitable refugia pending a return to circumstances favouring the recolonisation of areas deprived by local extinction. Here, a critically important corollary is the absence of any imperative to adapt closely to any specific set of conditions: quite the contrary, the versatility of a wide-ranging species is the very means by which it is able to maintain itself. The same cannot apply to an isolated and localised species which could easily become extinct if precautionary measures - close adaptation - were not taken to compensate for the general disadvantage under which it exists. Mereover, the obvious need to achieve security before extinction can occur, implies urgency as well as care in making the adjustment. In short, not only would such a species be obliged to make the best of a bad situation, it would need to do so as quickly as possible. Synonymously, higher evolutionary rates are to be expected for an isolated species than for one which is wide-ranging.

There is, therefore, substantial basis in theory for believing that *thetis* has undergone rapid evolutionary change, relative, that is, to a far less restricted cogener such as *Lycaena thersamon* (Esper, [1874]). That there is significant observational evidence supporting this view, has, of course, already been intimated, and whilst the theoretical argument cannot, obviously, validate these results, its presentation here serves the useful purpose of demonstrating the consistency between expectation and observation.

In noting that all members of the European Lycaeninae except *thetis*, rely solely on Polygonaceae in their larval stage, the apparent absence in the present-day *thetis* biotopes of this, the only plant family expected to afford a transitional role during adaptation, indicates an evolutionary process more in the nature of a «quantum» leap (mutagenesis?) than one of progressive change influenced by the forces of natural selection. This view must, however, be tempered by consideration of the common taxonomic origin of the Polygonaceae and Plumbaginaceae, which, according to Cronquist (1988) is the Caryophyllaceae: the implication here, is that the chemistry of *A. androsaceum* and, for example, *Rumex acetosa* may not be so dissimilar as the enormous disparity in the physical structure of these plants might suggest. Nevertheless, the complete rejection of *Rumex acetosa* by *thetis* larvae is an important experimental result which must, concomitantly, be reconciled with all other considerations in achieving a refined and self-consistent argument. No doubt other problems exist, and, indeed, with regard to the overall situation, the inextricably associated evolutionary histories of *thetis* and *panagaea* is a further complication evoking intense curiousity - certainly, it would be interesting to know, for example, the chronology of these adaptations.

Whatever its mechanism, some consequences of this evolution are clearly visible. For the adult insects, the superficial dissimilarities between *thetis* and its European cogeners are quite distinct, indicating a degree of divergence. To this may now be added the departure of *thetis* from other European Lycaeninae - most notably its cogeners - in its choice of larval host-plant. Whether the overall, observed divergence creates doubt regarding the generic classification of *thetis*, depends, of course, on the parameter set used to define the genus: here, the taxonomic relevance of further biological and ecological evaluations of an extended range of congeneric and other, closely allied species is clear.

It should be mentioned that the Greek race of *thetis*, delineated from its Asiatic counterparts by Dils & van der Poorten (1985), is referable to ssp. *hephestos* (Dils & van der Poorten, 1985).

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