The lifecycle of *Nymphalis vaualbum* ([Denis & Schiffermüller], 1775) in Serbia including new records and a review of its present status in Europe (Lepidoptera: Nymphalidae)

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Abstract: We describe the biology of the complete life cycle of *N. vaualbum* in Serbia, including a detailed account of its preimaginal stages, larval hibernation, courtship behaviour, mating, and oviposition. We publish new records from the Republic of Serbia and review its present status in Europe. In addition, we discuss the climatic requirements for hibernation and larval development and compare its preimaginal stages and adult behaviour with *Polygonia c-album* (Linnaeus, 1758).

Der Lebenszyklus von *Nymphalis vaualbum* ([Denis & Schiffermüller], 1775) in Serbien einschließlich neuer Nachweise und eine Überprüfung des derzeitigen Status dieser Art in Europa (Lepidoptera: Nymphalidae)

Zusammenfassung: Die Biologie des gesamten Lebenszyklus von *N. vaualbum* in Serbien wird beschrieben, einschließlich einer detaillierten Darstellung von Präimaginalstadien und Raupenüberwinterung, Balzverhalten, Paarung und Eiablage. Neue Nachweise aus der Republik Serbien werden gegeben, dazu wird der aktuelle Status dieser Art in Europa zusammengestellt. Darüber hinaus werden die klimatischen Anforderungen für die Überwinterung und die Entwicklung der Raupen diskutiert und die Präimaginalstadien und das Verhalten der Falter mit denen von *Polygonia c-album* (Linnaeus, 1758) verglichen.

Introduction

Although described as widespread in the eastern part of its range, *N. vaualbum* is local and rare in the western part of its range, where it is reported to be in decline (see Fig. 1, map). In the present 27 countries of the European Union (= EU27), the species distribution has declined by 46% over the last ten years and a strong decline in distribution or population size of more than 30% has been reported from Romania and Ukraine. The reasons for these declines are unclear but it is possible that this could be part of long-term natural fluctuations (van Swaay et al. 2010). The species frequently forms temporary populations across Europe outside Russia, with fluctuating abundance and irruptive population dynamics (Mihoci et al. 2012). *N. vaualbum* is still considered to be a native species in Albania, Belarus, Bosnia and Herzegovina, Croatia, Montenegro, Romania, the Russian Federation, Serbia and Ukraine, but the species is now thought to be extinct in Austria, the Czech Republic, Estonia, Hungary, Slovenia and Slovakia (van Swaay et al. 2010). Within the last few years, there have been a number of new observations from the European part of its range. With the exception of Serbia and perhaps Bulgaria and Croatia, where the species is possibly a resident, it is hard to verify whether these sightings are those of vagrant individuals, or if the species has become a temporary resident. In most instances, these new records have only been single observations and possibly the result of recent immigration and subsequent population increase.

According to van Swaay et al. (2010), larval hostplants are definitively not a limiting factor, as *N. vaualbum* utilizes common plant species such as birches (*Betula* spp.), willows (*Salix* spp.), poplars (*Populus* spp.) and elms (*Ulmus* spp.). *Populus tremula* L. and *Salix* spp. are reported as hostplants in the Urals, and in the Far East (including Sakhalin): *Ulmus propinqua* Koidz., *Ulmus laciniata* Trautv. and *Betula mandshurica* Regel (Gorbunov & Kosterin 2007). For Amur Province, *Urtica urens* L. has been reported (Gorbunov & Kosterin 2007). In addition *Populus tremuloides* Michx. (Bird et al. 1995), *Hippophae rhamnoides* L. (Ćelik et al. 2005), *Salix cinerea* L. *Salix fragilis* L. and *Betula alba* L. (Abafi-Aigner 1905, Gozmány 1968), *Alnus* Mill, *Tilia* L., *Acer* L., *Humulus* L., *Rumex* L., *Fraxinus* L., *Morus* L., *Spiraea* L., *Rosa* L., *Sorbus* L. and *Rubus* L. have been quoted in literature (Korshunov & Gorbunov 1995).

An account of the life cycle of this butterfly in the former Soviet Union was described (in Russian) by Y. Korshunov & P. Gorbunov and translated into English by O. Kosterin (1995), and there have been several other brief descriptions of its life history (Buszko & Maslowski 2008, Bird et al. 1995, Pyle 1981), but we are unaware of any detailed accounts of its preimaginal development in Europe.

During 2010–2012, the authors visited the Stara Planina region on several occasions with the aim of studying the habits and habitat of *N. vaualbum* and obtaining live specimens for a rearing experiment. The objective of the study is to provide an account of the species' life cycle in Serbia. We also add new records from Serbia and in addition write a review of the current status of the species in Europe.

Abbreviations used

MGP, CW, MĐ and DT:
Abbreviations of the authors of the present publication in text, legends and table.

Field observations

June 2010

MĐ and DT surveyed a number of habitats in Serbia between 14. vi. and 26. vi. 2010, including Taor (Zlatibor District), Jošanička Banja (Raška District), Kladnica (Moravica), Golija (Moravica) and the Stara Planina (Zaječar District), and *N. vaualbum* was observed at all of these sites. The first specimen was seen 2.5 km NW of Donji Taor (at an altitude of 1049 m) on 14. vi. Further specimens were recorded 7.1 km NE of Kladnica (1 ♂ on 17. vi.), 4.4 km SE of Budoželja (1 ♀ on 18. vi.), 5.3 km NE of Jošanička Banja (1 specimen on 18. vi.), 4.9 km NE of Jošanička Banja (♂♂ and ♀♀ on 19. vi.) and 2.2 km W of Babin Zub Hotel, Stara Planina (2 ♂♂ on 21. vi.).

April–May 2011

Three authors (MGP, DT and CW), accompanied by C. J. Luckens and A. C. Derry, visited Serbia between 28. iv. and 8. v. 2011. Despite surveying various habitats at Jošanička Banja (Raška District), Topli Do (Pirot District) and in the Stara Planina (Zaječar District), no specimens were observed. On 30. iv. 2 ♂♂ of *N. xanthomelas* (Esper, 1781) were captured and released along with several specimens of *Nymphalis polychloros* (Linnaeus, 1758) next to the Toplodolska River, 5 km SW of Topli Do (595 m). The specimens were extremely worn, indicating that the post-hibernating nymphalids had been on the wing for a long period and that egg batches had already been oviposited.

June–July 2011

DT visited Serbia between 3. vii. and 9. vii. 2011. One adult was recorded 4.9 km NE of Jošanička Banja on 3. vii. and over 20 specimens in the vicinity of the Stara Planina at various altitudes from Kalna (400 m) to the Babin Zub Hotel (1565 m) between 5. and 9. vii. He observed several butterflies puddling along the road to the new Stara Planina hotel, taking salts from damp patches along the gravel track. He described the flight as ‘very skittish’ with a tendency for butterflies to skip from one patch to another when disturbed, only resting for brief periods. They had a habit of retreating into shady areas, preferring not to fly in full sunshine, typically flying in dappled sunlight. Despite this observation, butterflies appeared only to fly on hot days and were often seen basking in the morning sunshine. In these sultry conditions specimens were primarily observed between 8:30 and 12:00 h with virtually no activity reported after midday, apart from at Jošanička Banja where one specimen was seen flying at 16:00 on 3. vii. This concurs with a remark made by Gorbunov & Kosterin (2007): “In summer the butterflies usually occur from 9:00– 10:00 h to 18:00–

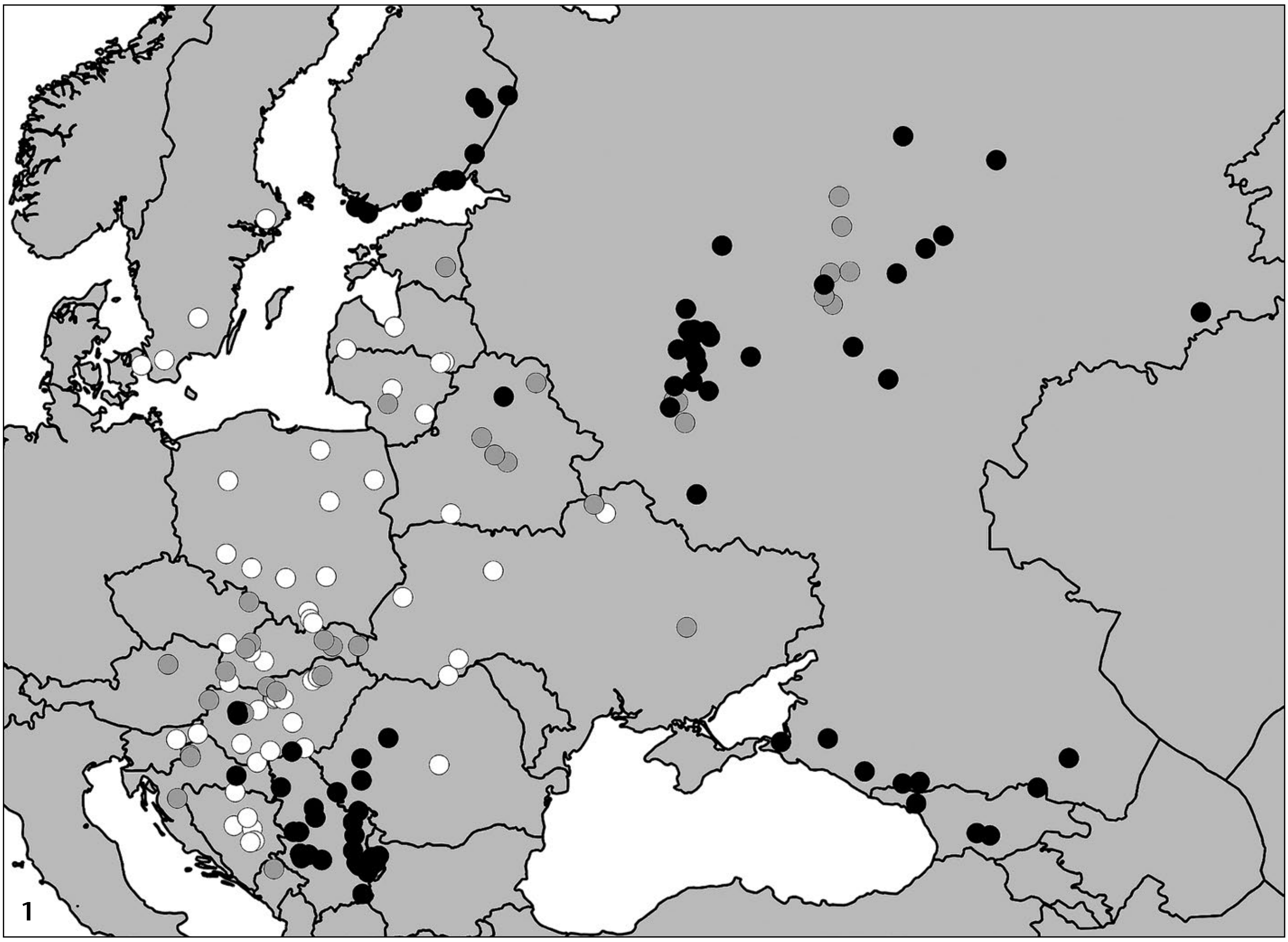

Fig. 1: Distribution of *Nymphalis vaualbum* in Europe. White dots represent records from 1900–1950; grey dots denote records from 1950–2000 and black dots represent records from 2000–2013. — Map prepared by MĐ.

19:00 h, on cold spring days mostly from 11:00–13:00 h." DT reports that a majority of the specimens preferred the partial cover of the tree canopy where conditions were cooler and damper, apart from one specimen that was observed in full sunshine puddling at an open gravel area at 8:30 near the Bigar waterfall, 7.1 km south of Kalna. This comment also agrees with Gorbunov's & Kosterin's observation: "They fly under the canopy of open forests or along edges, and rest in the spots of light on tree trunks at 1–2.5 m above the ground or, more rarely, on bare ground." According to Popović (pers. comm.), *N. vaualbum* also has a habit of guarding its territory.

Summer June–July 2012

MGP, accompanied by C. Orpin, visited Mt. Mučanj (Moravica) on 19. vi.–20. vi. and made over 20 sightings at altitudes ranging from 1150–1350 m on a southeastern approach to the summit (Figs. 2a, b). The butterflies were notably strong, fast fliers, ascending steeply when confronted by large obstacles, and disappearing erratically over the tree canopy if disturbed. Butterflies settled only occasionally when puddling at damp patches at the edge of forest tracks; both ♂♂ and ♀♀ adopted this behaviour. Three Blendon traps were set up and a concoction of rotting bananas enriched with molasses was used as bait. MĐ had previous success in attracting specimens to traps using banana bait in 2010 (MĐ pers. obs.), but on this occasion they failed to attract any specimens. Apart from one ♀ that was observed in an open area close to a spring (1355 m) at 16:00 h, a majority of the sightings were made between 9:00 and 12:00, and along rides in shady woodland. The Golija Biosphere Reserve, SE of Ivanjica, was visited after midday on 20. vi. (Fig. 3). In late afternoon sunshine a ♀ *N. vaualbum*, accompanied by several other nymphalid species, was seen puddling at a forest track, circa 1150 m. It was skittish and flew off when approached.

Between 22. vi. and 30. vi., various habitats in the Stara Planina region were surveyed (Figs. 4a–c). On 25. vi. a fresh specimen was observed flying along a woodland ride north of Janja at an altitude of 590 m. It was flitting between damp patches where other nymphalids were congregating, including: *Argynnis paphia* (Linnaeus, 1758), *Apatura ilia* ([Denis & Schiffermüller], 1775), *Apatura*

Plate 1, Figs. 2–4: Localities of *N. vaualbum* in Serbia. **Figs. 2a–2b:** Mt. Mučanj, Moravica, 19. vi. 2012. **Fig. 3:** Golija Biosphere Reserve, Moravica, 20. vi. 2012. **Figs. 4a–4c:** Babin Zub, Stara Planina, 23.–28. vi. 2012 — Photographs: MGP.

iris (Linnaeus, 1758) and *Araschnia levana* (Linnaeus, 1758). They were similarly imbibing the mineral salts along the track. On 26. vi. a ♀ specimen was recorded at a spring just east of the Babin Zub Hotel (1570 m), and the following day a ♂ was observed flying in the immediate vicinity of the hotel. On the same date C. Luckens and A. C. Derry, who were revisiting the region, observed a ♂ butterfly 1.6 km SE of Crni Vrh, Babin Zub, and a ♀ at the spring, east of the Babin Zub hotel (Fig. 4c). On 29. vi. 2 ♂♂ were recorded just south of the road leading to the Stara Planina hotel close to the new reservoir, alt. 1450 m (Fig. 4b). One further sighting was made on 5. vi. in the Golija Biosphere Reserve, alt. 1134 m, by MGP, CW and J. E. Pateman, a ♀ flying along a track very close to the spot where the observation was made on 20. vi.

Rearing report 2011–2012

Pre-hibernation

5 ♂♂ and 2 ♀♀ of *Nymphalis vaualbum* were captured by DT during early July 2011. The butterflies were kept in individual cardboard boxes and left in a cool, damp shady place during DT's stay in Serbia. If disturbed, they displayed thanatosis, adopting a lifeless pose, motionless with legs drawn up to their bodies. Once back in the UK the specimens were transferred to a wooden half-barrel. The top of this barrel was covered with fine Nylon netting and several wooden slats were placed over half of the netted area, providing some shade from direct sunlight, and protection from the rain. In addition, a wire frame was constructed over the top of the barrel to safeguard against intrusion from cats and other predators. The tub was positioned in a well-ventilated, shady place that allowed partial sunshine during the day. Several cotton pads containing a fructose rich solution (diluted 20%) were placed on top of the exposed netting, allowing the butterflies to feed undisturbed. Adults were observed imbibing from these pads up until the beginning of August, when they commenced a period of aestivation, positioning themselves under the shade of the wooden slats. The butterflies remained dormant until mid-September when they resumed feeding on the fructose pads. By mid-October the butterflies had stopped feeding and commenced hibernation. In nature they reportedly feed on rotten fruit and decaying organic material. Gorbunov & Kosterin (2007) wrote: "These butterflies rarely visit flowers, being attracted mostly by organic solutions such as tree sap or excrement."

Hibernation

Throughout the hibernation period, the butterflies remained in the half-barrel in a shady, but partially exposed, well-ventilated location. They positioned themselves under the wooden slats, allowing some protection from direct exposure to the elements (temperatures as low as −6°C in Farnham during January 2012). The butterflies were monitored throughout the winter months, and CW reports that that they remained torpid until the following spring. In the wild, *N. vaualbum* are believed to hibernate in wood stacks, old redundant farm buildings, anywhere where dry, dark, cool, well-ventilated conditions can be maintained.

Post-hibernation

♂♂ became active and re-commenced feeding five days before the ♀♀ at the end of February 2012. Unseasonably mild temperatures in the U.K. during February almost certainly stimulated this re-emergence. On 1. iii. the two ♀♀ were each placed into individual 70 cm diameter × 120 cm high cylindrical cages. Three ♂♂ were placed in one of these cages, two ♂♂ in the other. Cotton pads impregnated with a Fructose-Glucose-Sodium chloride solution were placed at both the top and bottom of each cage. In addition, a sheet of card was positioned on the roof of both cages to provide shade.

Pairings and oviposition

Large water-filled vessels containing stems of *Ulmus procera* Salisb. and *Salix daphnoides* Vill. were placed into each of the cylindrical flight cages so that their shoots were in contact with the roof and sides of each enclosure. The cages were kept in an unheated greenhouse and in a predominantly sunny aspect. The first pairing was witnessed by CW on 8. iv., a sunny day when temperatures were well in excess of 20°C in his greenhouse. CW observed that the coupling adults were situated at the top of the flight cage in the shade, and had manoeuvred into an acute 'V'-shaped position, i.e. at 45°to each other. At 18:00, copulation was still in progress and once the pairing had terminated all five ♂♂ were assigned to the cage containing the second ♀. Although a pairing was not observed, the abdomen of the second ♀ was inspected on the evening of 10. iv., at which time she was discovered to have a sphragis. However, despite having a sphragis all the eggs laid by the second ♀ failed to hatch, possibly a result of low fertility after a mild winter (see discussion).

All the egg batches were laid on *Ulmus procera* (in preference to *Salix daphnoides*) and unlike *N. polychloros* and *N. xanthomelas,* all the eggs were laid on the shady (north facing) side of terminal twigs. In addition, a few single eggs were deposited on the side netting.

Regarding courtship in nature, Gorbunov & Kosterin (2007) commented: "Mating and oviposition occurs in spring, mostly in May. Before copulation, the ♂ flies for a long time 20–40 cm behind the more or less straight-flying ♀. At last the ♀, and then the ♂, lands on a tree trunk, the ♂ crawls to the ♀ from behind, and either copulation starts or she takes to the air and the courtship flight resumes."

Rearing programme

All equipment used for the breeding programme, including cages and bottles, were sterilized prior to the start of the experiment, and all plant-stem cuttings were checked for predators and potential signs of diseases.

CW reports that the first cluster of eggs was laid on 15. iii. and eclosion took place on 30. iii., fifteen days after oviposition. The ensuing larval batch was transferred to fresh cuttings of *Ulmus procera* and left in a sunny position on a window sill in CW's conservatory. This exposure to direct sunlight incited an adverse reaction, and the larvae, clearly agitated, demonstrated discomfort by arching their abdomens. Resulting from this remonstration, a number of larvae were observed 'abseiling' off their perches attached only by a silken thread, necessitating reattachment using a fine paintbrush. When the larvae were transferred to a shady position, the larvae settled and commenced feeding. This may explain why, in nature, ♀♀ were frequently observed flying in shady, dappled light.

MGP acquired two egg batches from CW on 2. iv. (Fig. 5), the smallest cluster containing 18 eggs, the largest 25 eggs. Both egg batches were pinned onto stem cuttings of *Salix daphnoides* and these were transferred to a glass water-filled receptacle. The containers were placed inside a 25 cm × 25 cm breeding cage and sited at the back of a conservatory in a shady, cool environment. The conservatory roof vents were left open to circulate air and to regulate the temperature.

On 5. iv. eggs from the smallest batch had darkened (Fig. 6), and by the morning of 6. iv. 16 larvae had emerged (Fig. 7). An entire leaf of *Salix daphnoides* had been consumed by the morning of 7. iv., and on 8. iv. one further larva hatched out. CW and DT noted that batch hatchings were not synchronised. At this early stage of development they positioned themselves on the underside leaves of their foodplant in small groups (Fig. 8). Their behaviour is similar to that of *P. c-album*, and in appearance not dissimilar to the larvae of the notodontid moth *Phalera bucephala* (L., 1758).

The larvae spun a very fine 'mesh' of silken webbing over the terminal leaves and twigs of their hostplant forming a protective barrier against predators (Fig. 30). If disturbed, the larvae had a curious habit of posturing, with their heads elevated away from the leaf surface, clinging to their chosen leaf using only their abdominal and anal prolegs. This display appeared to initiate a simultaneous chain reaction from the rest of the batch. CW reports that both *N. polychloros* and *N. xanthomelas* share this curious habit. On 9. iv. the larvae split into two groups of 8, and had grown to 4 mm. By 11. iv. they had reached 4.5 mm in length and appeared to be approaching skin change. In their first instar, the larvae suffered a high rate of mortality, many perishing when being transferred to fresh cuttings.

On 12. iv. the first L_2 larva emerged, 4 mm in length. The larvae fed communally in their first instar but by L_2 they had started to disperse and live a solitary existence, mostly on the undersides of leaves. The larval size increased to 4.5–5 mm on 13. iv., 6 mm on 15. iv. (Fig. 9) and 8.5–9 mm on 16. iv. prior to ecdysis. Apart from two larvae, all had developed to L_3 by 18. iv. The larvae at this stage measured 9.5–10.5 mm in length (Fig. 10), increasing to 12 mm by 21. iv. (Fig. 11). As an experiment, fresh cuttings of *Ulmus glabra* Huds., *Betula pendula* Roth. and *Carpinus betulus* L. were placed into the cage, and the larvae, reputedly polyphagous, commenced nibbling leaves of all three species, but with a noticeable preference for elm.

On 24. iv. several of the larvae were noticeably inactive, remaining motionless throughout the day, and little eating was observed. The largest larva measured 14 mm, but they appeared to be growing at different rates. In an attempt to induce feeding, some of the larvae were transferred onto a growing specimen of *Ulmus glabra* contained within a 25-litre pot. 30. iv. was a warmer day and some eating was observed, but there were further losses. On 1. v. the largest L_4 larva was measured at 19 mm and there were further skin changes (Fig. 13). On 2. v. there were several L_3 to L_4 skin changes and the largest L_4 larva measured 21 mm, but the larvae were still not eating gregariously, feeding was sporadic, and further losses occurred. On cold, wet days, a small percentage of the larvae remained torpid for long periods, resting on their silken pads, refusing to eat, and several perished at this time. Dull and drizzly weather prevailed over the next few days so it was decided to introduce a supplementary light source in an attempt to induce feeding.

On 3. v. there were further (L_3 to L_4) skin changes, and the largest L_4 larva had grown to 22.5 mm in length, increasing to 23 mm by 7. v. by which time it appeared to be moulting. It had constructed a silk pad suspended just above the leaf surface, where it remained motionless. By 9. v. several other larvae had followed suit (Fig. 14), and by 10.v. the first L_5 larva emerged. Eclosion occurred in the early hours of the morning, and by late afternoon (16:00) a second larva had moulted (to L_5). On 13. v. the largest L_5 larva measured 33 mm in length increasing to 38–39 mm on 15. v. In their final instar, larvae fed at different times throughout the day, and, under laboratory light conditions, appeared to be growing at different rates. Unlike the preceding instars, L_5 larvae do not weave silken pads to rest on when not feeding. On 17. v. the largest L_5 larva measured 42 mm (Figs. 17–18). It had increased in size to 46 mm on 19. v., and by 20. v. it was observed wandering around in a restless manner searching for a place to pupate. It proceeded to spin a silken pad on one of the leaves of its hostplant from which it suspended itself (Fig. 19), and by the following day, pupation had taken place (Figs. 20–22). According to Gorbunov & Kosterin (2007) pupation takes place "on host tree branches near the trunk, or on other trunks, sticks, or fences, at about eye-level or higher; rarely herbs". On 30. v. an adult ♂ hatched out, nine days after pupation (Figs. 26–27), and on 31. v. a female emerged (Figs. 28–29).

The duration of the larval stage varies considerably and appears to be weather-dependent. The larvae were more active on warm, sunny days, preferring to feed during the morning and evening, remaining motionless during the heat of the day. However, in their final instar larvae appear restless, eating at various times throughout the day, from dawn to dusk. Larvae were observed feeding as early as 05:00 in the morning, when the temperature was 14°C, and up to 22:00 at night, when the light level was very poor. On hot days (in excess of 21°C) the conservatory door was left ajar to create an airflow; while on cooler days all doors and windows were closed to help increase the ambient temperature. CW had also extended the day length of his breeding programme (supplemented by a light in his conservatory). Similarly, he reported that larvae fed more readily on warm, sunny days. Throughout the entirety of his experiment, all larvae were reared on *Salix daphnoides*.

Description

Ovum

Size 0.9 mm in length and 0.7 mm in diameter, laid in cylindrical batches of ca. 15–50 on the terminal twigs and branches of its hostplant. The egg is barrel-shaped with a depression at the apex and has 11 or 12 longitudinal ribs and a series of transverse spherical keels (a small percentage of eggs have eleven ribs, but the majority twelve). Initially yellowish-green in colour, the developing ovum becomes translucent, and the embryo, with brown-beige speckling, is clearly visible beneath the eggshell (Fig. 5). Prior to eclosion the ova appears (superficially) beige-grey in colour but, on closer inspection, a black head can clearly be seen at the depression, and pale buff-coloured abdominal segments are visible beneath the chorion (Fig. 6).

Larva

L_1 stage

2 mm in length at eclosion with a glossy black head and a milky-grey cervix. The abdominal segments are sandy-buff in colour, slightly paler underneath. Each segment is ringed by a series of black, long protruding, primary setae (Fig. 7). As the larva develops, it appears muddy-brown in colour but on closer examination the abdominal wall is transparent and concealed beneath, a dull-ochre body with a series of (three) muddy-olive coloured longitudinal stripes. The thoracic legs, prothoracic shield and the anal plate are black and each abdominal hair is attached to a dark prominent wart-like protrusion (Fig. 8). Size of larva: 4.5 mm prior to ecdysis.

L_2 stage

Head: The head capsule retains its glossy black colour but now reveals an abundance of small milky-white warts and fine white setae. Two horn-like protections protrude from the vertex. The hairs have developed into large chitinous multi-branched spines. The dorsal spines are variable in colour, ranging from a pale, muddy-brown to black, and appear noticeably darker anteriorly. A dark brown ring encircles the base of each of these spines and the branches of these spinal protrusions are tipped black. In contrast, the lateral and ventral spines are white, flushed yellow at the base. The ground colour of the body is buff becoming paler, almost milky white, below the subdorsal band. The milky-white ventral area is irrorated with chocolate brown specks and blotches.

A conspicuous dark brown stripe runs the full length of the dorsum (Fig. 9); and a row of dorsal spines intersects this band. In the centre of abdominal segments 3–11 a series of 'Y'-shaped markings connects the dorsal line to a broad dark-brown subdorsal band. This wide brown band is solid but interrupted by a pattern of pale blotches at each intersegmental fold. Below this band, the body colour is paler, almost white. A row of dark brown (virtually black) spiracles, each encircled by a creamy-white 'eye', are contained within a dark brown spiracular band. This band is fragmented, and tapers at each intersegmental fold.

The thoracic legs remain black; the abdominal and anal prolegs are milky-grey in colour with dark-grey crotchets. As the L_2 larva matures, all longitudinal stripes and spines become darker. Prior to skin moult the larva measured 9 mm in length and the head capsule 0.9 mm (± 0.1 mm) in width.

L_3 stage

The head capsule, spines (each tipped black), anal plate, anal claspers, thoracic legs, abdominal and anal prolegs are pale-yellow immediately after ecdysis, turning black within two hours.

The two horn-like projections are now multi-branched and have increased in size. All warts, ocelli and setae remain white but are now more conspicuous and protrude farther out from the head capsule.

Generally, the ground colour is lighter than in L_2 stage and all dark stripes and bands appear black and are more extensive (Fig. 10). In some specimens the lateral bands are virtually unbroken but in others, incomplete and fragmented, disrupted by an irregular series of small white dashes and blotches at the intersegmental fold. The spiracular band, now black, is wider, and the spiracles (encircled white), more conspicuous.

The multi-branched spines above the spiracular band are jet-black in colour, and white, tipped pale yellow, below this band. The thoracic legs are black. The abdominal and anal prolegs are greyish yellow, covered with fine, porcelain-white setae and dark-grey crotchets. When fully mature, L_3 larvae display extensive armature and appear predominantly black with two contrasting pale yellow conspicuous subdorsal stripes (Fig. 11).

Pre-moult larvae measure 12 mm in length with head capsule 1.3 mm (± 0.1 mm) in width.

L_4 stage

In appearance, not significantly different from the previous instar.

Similar to L_3 larvae, the head and aforementioned abdominal parts are pale-yellow immediately after ecdysis turning black within a few hours. Many of the white epicranial warts on the head capsule have transformed into conical shaped projections tipped with long white protruding hairs (Fig. 12). The basal row of multi-branched spines is pale yellow, and is linked together by a narrow white subspiracular band. The anal plate is similarly yellow (Fig. 13).

Each thoracic leg has a black pretarsal claw and dark chestnut-brown coxa. In comparison, the abdominal prolegs are greyish-yellow. During skin change the pale yellow cervix is clearly visible. L_4 head capsule: 2.3 mm (± 0.1 mm) in width; larva measured at 24 mm in length prior to moulting (Fig. 14).

L_5 stage

As with previous larval stages, the aforementioned abdominal parts are sulphur yellow in colour becoming black within two hours of ecdysis (Fig. 15). The maxillary palps and antennae are black, the labrum is rusty-red, the clypeus is grey-white, and the spinneret a dull pale-ochre colour (Fig. 16).

The abdominal prolegs have rusty-red crochets, porcelain-white planta, and pale-ochre coloured coxa. Apart from a dark brown pretarsal claw, the thoracic legs are ochre in colour. Compared with the previous instar, the most obvious change regarding the abdomen is the extensive orange-ochre coloured 'haloing' (Figs. 17–18). This is most obvious at the mid-section of each abdominal segment, which is tinged with a rusty-ochre suffusion. This haloing is more extensive at segments A9 and A10. In addition, there is a rusty-ochre coloured suffusion surrounding the basal area of each spine. The ventrum is milky-white with a reticulated pattern of traverse pale chocolate-brown striae (Fig. 16).

Pre-pupal larvae measure 46 mm (± 2 mm) in length with a head capsule 2.8 mm (± 0.1 mm) in width.

Larval defence

Larvae may have a chemical defence effective against birds (or other predators), and it is possible that their strong contrasting colours are aposematic. Their conspicuous branching spines could also act as a defence against predators rendering them unpalatable. In an experiment undertaken by Nylin et al. (2001), domestic chicks (*Gallus gallus domesticus* L.) were presented with 5th instar larvae of *P. c-album*. The chicks were offered larvae with spines and with spines removed. Those without spines were readily eaten whilst those that were protected by spines were avoided. Strong spines are found very commonly in nymphalid larvae, often together with contrasting bright colours. In direct contrast to this theory, CW noted that Great Tits (*Parus major* L.) had a habit of trying to attack a cage containing final instar larvae of *N. vaualbum*, and in one instance a larva was critically injured.

Prepupa

All dark bands are 'washed out' and have an olive hue (Fig. 19). The section below the subdorsal band is creamy-white (including the basal row of spines) and all dark markings are greatly reduced, barely visible. The spiracles are black but the surrounding white rings are now inconspicuous, concealed within the body colour. The dorsal spines remain black. The spines above and below the spiracles are flushed yellow at their bases. The thoracic, abdominal prolegs and anal prolegs are a dull, pale ochre colour. There is extensive ochre colouration at segments A9 and A10.

Pupa

Polymorphic. Varying from pale beige-coloured with a smooth, faintly irrorated surface (Figs. 20–21) to pearl-grey with a strongly reticulated pattern (Fig. 22). Size: 25–26 mm.

The pupa has a series of dorsal cones emanating at the metathorax and extending along abdominal segments 1–8. The tips of the cones at A2 project further out from the body than the other cones. The cones at A1 and A2 and the metadorsal cone are mother-of-pearl coloured, resembling metallic patches. The cones at segments 3–8 vary in colour. Pearl-grey pupae have cones with ochre tips and black rings at the base of these protrusions while the pale beige pupae similarly have ochre tips, but are generally paler and with extensive suffusion.

An outline of the outer margin of the adult forewing is clearly visible beneath the pupal case. The distal edge of the cell, the rim of the eye and all spiracles are also delineated in black. The dorsal keel is shaped like a fin. The pointed horn is falcate and there is a dark stripe along the ventral surface of the cremaster.

Adult

Adult external characteristics have been described in many publications. One distinguishing feature that, as far as we are aware, has not been mentioned in any description, relates to the legs. The middle and hindlegs of *N. vaualbum* are light buff in colour, considerably paler than those of *N. xanthomelas*, but the forelegs of *N. vaualbum* are not only paler, but have an obvious black stripe running down the tibia. In comparison, *N. xanthomelas* has dark brown forelegs and, by contrast, all legs of *N. polychloros* are uniformly dark brown (Figs. 23a–c).

In addition, the labial palpi of *N. vaualbum* are buff coloured in contrast to the darker coloured palps of *N. xanthomelas* and *N. polychloros*.

Variation

The ground colour of ♂♂ undersides varies, either a grey-brown or a buff brown (Figs. 24a, b). There is clear demarcation between the dark discal and paler postdiscal areas. The postdiscal area can be heavily suffused with white scales, particularly where adjoining the discal band. In comparison, other specimens have little, or no, white scaling and this is substituted by a pale buff colour patternation. Regardless of the colouration, there is great contrast between the dark chocolate-brown discal region and the paler postdiscal area.

♀♀ undersides also show dimorphic colouration, but the overall pattern is more uniform and unmarked (Figs. 25a–c). There is marginal variation in colour between the discal and submarginal areas but this is not nearly as obvious as in ♂♂. The hindwings of both sexes have a 'V'-shaped white mark adjoining the cell at S4. In some specimens this 'V' is present in the form of a dash, an 'L', a 'C' or a 'J' and in other specimens this mark is barely visible and only comprises of a few white scales, or can be absent altogether. This marking is far more prominent in ♂ specimens.

Wing measurements

The forewings of 17 ♂♂ were measured (basis to apex) with spans ranging from 30 mm to 32.5 mm; on average: 31.35 mm ± 0.74 mm. Forewing measurements from 3 ♀♀ were taken and these varied between 33 and 34 mm with an average of 33.5 mm ± 0.5 mm.

As a comparative study, the wing measurements of 9 ♂♂ Russian specimens were measured: 5 ♂♂ from Kuldur (Birobidzhan); 2 ♂♂ from Chabarovsk (Siberia); and 2 ♂♂ from Kuvandyk (S Urals). Measurements ranged from 29–31 mm with a mean of 30.1 mm ± 1.07, on average 4.15% smaller than ♂♂ specimens from Serbia.

Foodplants

Salix daphnoides, *Ulmus glabra* and *Ulmus procera* were used in our experiment and were readily accepted by *N. vaualbum* larvae. In addition to these species, the larvae nibbled on leaves of *Betula pendula* (Roth.), *Carpinus betulus* and *Salix caprea* L. (DT pers. obs.). Once larvae had started eating a particular species, they were reluctant to change their choice of foodplant.

Individual country records including archived observations

Historical records show that the species has been recorded in 23 European countries. Based on published records, the observations mentioned below are the most up to date sightings from each of these nations (compare Fig. 1, map).

Denmark: Only four specimens of *N. vaualbum* have ever been recorded, all from 1901. One of them, which is deposited in the Zoological Museum of Copenhagen, was captured at Strandvejen, north of Copenhagen. It is accredited to Mr. V. Thomsen, but according to T. B. Langer, the specimen was recorded by a Mr. Wulff. The three other sightings were from Sønderby near Ebberup on Fyn made by a teacher, Mr. P. Jørgensen. He first saw a specimen in a window on 29. vii. 1901, and later that year he captured two specimens in the same area (Stoltze 1996).

Sweden: The species has only been recorded on three separate occasions, 1906 in Scania (Skåne), 1913 in Uppland and 1914 in Småland (Elmquist pers. comm.).

Finland: *N. vaualbum* is scarce in Finland, and occurs only in very low numbers (Kaitila pers. comm.). The most recent observation is from Eestiluoto, Sipoo (Nyland), between 1.–11. vii. 2013 made by M. Varesvuo, and during the last decade there have been many other sightings: Hamina (Karelia australis) 22. vii. 2012 by J. Halme; Kråkvik, Kemiönsaari (Regio aboënsis) 21. vii. 2011 by M. Cygnel; Uddskatan, Hanko (Nyland) between 15. vii.–27. vii. 2010 by K.-E. Lunddsten; Rääkkylä (Karelia borealis) in 2006, 2008 and 2010 by T. Peltotalo; Rääkkylä (Karelia borealis) in 2001 by M. Marienberg; Kesälahti (Karelia borealis) in 2007 by H. Colliander; two individuals at Kitee (Karelia borealis) in viii. 2006 by K. Nupponen; two individuals at Tohmajärvi (Karelia borealis) in 2006 by K. Nupponen (Kaitila, pers. comm.); Meltola, Imatra (Savonia australis) on 25. iv. 2006 by T. Klemetti; Liperi (Karelia borealis) on 26. viii. 2004 by A. Karhu and Virolahti (Karelia australis) on 15. v. 2001 by E. Hallikainen (Observation List *Nymphalis vaualbum* 2013).

Estonia: The last observation was at Tartu in 1959 (Šulcs & Viidalepp 1974), Vladimir Skvortsov (deceased 1993) was the collector. His home remained on the Russian side of the border after the political changes and his collection is not accessible and may be lost (Tammaru pers. comm.). Before World War II the species was a permanent resident (Ounap pers. comm.)

Latvia: The last records are from Ilukste in 1902, Riga in 1901, Vainode in 1900, 1902 and 1906 and in Laši in 1902 (Šulcs & Viidalepp 1974). Two specimens collected from Riga in 1900 and 1902 are housed in the Museum of Natural History for Latvia, Riga (Savenkov pers. comm.).

Lithuania: The last observation from this country was 16. vi. 1953 at Kvesai village, Kaunas district, made by R. Kazlauskas. Prior to this, Kazlauskas recorded a damaged ♂ from Vilnius on 16. v. 1948 and A. Lesinskas reported that the species was abundant at Dutnuva in the Kedainiai district on 1. vii. 1947. A fresh imago was encountered in the Pasiliai Forest in the same district on 8. vii. 1940 by A. Palionis (Ivinskis pers. comm.).

Poland: *N. vaualbum* is considered a rare vagrant species and there are only a dozen historical records: Pomorskie; Warmińsko-Mazurskie; Podlaskie; Mazowieckie; Swiętokryskie; Dolnośląskie; Opolskie; Śląskie and Malopolskie (Buszko & Nowacki 2000). It was last sighted in 1945 at Ochotnica Dolna, a village in the Gorce Mts. in Southern Poland (Błeszyński et al. 1965). Prior to this sighting, three specimens were caught in 1938 at Krościenko and are currently housed in the Museum of the Pieniny National Park in Krościenko (Kwiczala pers. comm.).

Czech Republic: The last observation was near Opava in the Moravian-Silesian region in the early 1960s (Babočka bílé 2013). At one time, the species was established near Hodonin in South Moravia (Kudrna 1974).

Slovak Republic: The most recent record is from Štúrovo, Nové Zámky District, Nitra, 150 m, on 17. vii. 1993 (Bozano & Floriani 2012). Prior to this observation, the species had not been seen in the Slovak Republic since the 1960s (probably much earlier). Reported sightings by K. Hrubý from: Inovec; Nové Mesto nad Váhom; Branisko; Bratislava; Remetské Hámre; Tisovec; údolie Hornádu and Zlatovce, were published in 1960 but without the years of observation. (Kalivoda pers. comm.).

A photo of an adult *N. vaualbum*, reputedly taken by M. Jagelka at Labske jazero, Slovakia, in vii. 1995, appears in Mazzei at al. (2013). This same photo can be seen on another website (Jagelka 2013) but is credited there as having been taken at McKellar, Ontario, Canada, in 1997. In addition, Jagelka (2013) reports that a ♂ was collected from the Zahorie Area, north of Bratislava, close to Austrian border on iv. 2005. In view of these contradictions, this photo and the accompanying information must be considered dubious and requires confirmation.

Germany: There were three records from Bavaria; two of these observations were from the extensive woodland and Naturpark "Südlicher Steigerwald", close to Uffenheim. However these records have been declared false and have been deleted from the data bank of the Bavarian State Agency of Environment (Kudrna pers. comm.).

Austria: Vienna is the designated type locality ([Denis & Schiffermüller] 1775), but there have been very few observations in the last 100 years. The last specimen was recorded from St. Nikola, Donau (Danube river), Oberösterreich, 48°13.48′ N, 14°54.0′ E on 3. viii. 1981 by Brunner (Gusenleitner pers. comm. 2012, referenced in ZOBODAT, Biogeographical data record number: 2136485) and prior to this observation there have been no new records since 1923.

Slovenia: *N. vaualbum* is now considered extinct. The last observations were more than 70 years ago. There have been only a few sightings, mostly from the beginning of the 20th century. It was found in the east of the country in the Gorjanci Mountains, in the surroundings of Podturn at Dolenjske Toplice by Hafner in 1909, and near the towns of Ljutomer and Slovenske Konjice in the Štájerska (Styria) region by Hofmann & Klos in 1914. In addition, there is a specimen from Pokojišče, located at the southern edge of the Ljubljana basin, in the collection of the Natural History Museum of Slovenia caught in 1932 by R. Rakovec. This is the last reliable record from Slovenia (Ćelik et al. 2005, translation by R. Verovnik).

Croatia: The most recent observation from Croatia is from Mt. Papuk. A single ♂ specimen was collected near a spring at the Dubočanka stream (45°30′18″ N, 17°41′ 13″ E) on 18. vii. 2004 by M. Krištovič. Despite intensive surveys by I. Mihoci and M. Šašić, the species was not observed at any of its historical sites, but has been reconfirmed on Mt. Papuk in the past few years (Mihoci et al. 2012). Prior to these new sightings, the last observation was by Moucha in Plitivički Ljeskovac in 1964 (Mihoci et al. 2012) and by Lorković at Pustodol on 7. vii. 1963 (Mihoci et al. 2012). In Lorković's diary, there is an unpublished record that mentions a sighting along the Kraljičin zdenac to Černomerec (Mt. Medvednica) hiking track on 25. vii. 1950 (Mihoci et al. 2012).

Bosnia and Hercegovina: *N. vaualbum* was last recorded in 1972 (Lelo 2008). However, there is no reference as to the exact locality. The following place names are also cited by Lelo (2008): Mt. Motajica, Travnik, Vareš, surroundings of Sarajevo, Vrelo Bosne, Zavidovići, but again without references.

Serbia: Over the last decade there have been many sightings. Prior to 2006, observations were very scattered and sporadic. The situation changed dramatically in 2009 when *N. vaualbum* was recorded on nine occasions in six different localities. Since then there have been over one hundred confirmed sightings. The presence of fresh adults indicates that the species is breeding in Serbia, at least in limited numbers (Popović & Đurić 2010) (details see Table 1).

Montenegro: A single ♂ was captured by P. Cribb at Crno Jezera, west of Žabljak, on 9. vii. 1972 (Bretherton 1973) but we can find no recent records.

Albania: R. Verovnik has informed the authors that *N. vaualbum* is not listed in any of the summary works and faunistic reports from this country. According to van Swaay et al. (2010), *N. vaualbum* is considered to be a native species in Albania, but this may be erroneous (Verovnik pers. comm.).

Bulgaria: There have been several recent records from the Bulgarian side of the Stara Planina. This comes as no surprise if one considers the number of sightings from just over the border in the Serbian part of the range. In early vi. 2011, a ♂ was observed, photographed and captured in the Western Stara Planina at ca. 1600 m by Z. Kolev and N. Shtinkov. The specimen was seen flying along a road in beech forest with some willows (Kolev pers. comm.). Another specimen was captured above Gorni Lom Village, on the road to Martinovo, W Stara Planina (43°26′ 11″ N, 22°44′5″ E), at an altitude of 690 m on 12. ix. 2011 by S. Beshkov & M. Beshkova. It was flying near a river next to which *Salix* and *Corylus* were growing (Beshkov pers. comm.). Recent reports from the Sveti Nikola pass and Kamen peaks need confirmation (Beshkov pers. comm.).

Plate 2, Figs. 5–22: *N. vaualbum* from Stara Planina, Zaječar, Serbia. **Fig. 5:** Ova, 3. IV. 2012. **Fig. 6:** Ova (near hatching), 5. IV. 2012. **Fig. 7:** L_1 (one-day old) larvae on *Salix daphnoides*, 6. IV. 2012. **Fig. 8:** L_1, 3.5 mm larvae, 9. IV. 2012. **Figs. 9:** L_2, 6 mm larvae, 15. IV. 2012. **Fig. 10:** L_3, 10 mm larva posturing, 19. IV. 2012. **Fig. 11:** L_3, 12 mm larva, 21. IV. 2012. **Fig. 12:** L_4 head capsule detail, 1. V. 2012. **Fig. 13:** L_4, 19 mm larva, 1. V. 2012. **Fig. 14:** L_4, 24 mm larva skin changing on *Ulmus glabra*, 10. V. 2012. **Fig. 15:** L_5, 24 mm, yellow colouration after moult, 10. V. 2012. **Fig. 16:** Head detail, ventral view, of L_5, 33 mm larva, 13. V. 2012. **Figs. 17–18:** L_5, 40–42 mm larva, on *Ulmus glabra*, 17. V. 2012. **Fig. 19:** L_5 hanging up to pupate, 20. V. 2012. **Figs. 20–21:** Buff coloured 26 mm pupa, 22. V. 2012. **Fig. 22:** Grey coloured 25 mm pupa, 22. V. 2012. — Photographs: MGP.

Plate 3, Figs. 23–31: *N. vaualbum* from Stara Planina, Zaječar, Serbia. **Fig. 23:** Nymphalid leg comparisons; **a:** *N. vaualbum;* **b:** *N. xanthomelas;* **c:** *N. polychloros*. **Fig. 24:** *N. vaualbum* ♂♂ uns comparisons. **Fig. 25:** *N. vaualbum* ♀♀ uns comparisons. **Figs. 26–27:** Adult ♂♂, ex ovo, 30. V. 2012. **Figs. 28–29:** Adult ♀♀, ex ovo, 31. V. 2012. **Fig. 30:** Silk webbing on *Salix daphnoides*, 19. IV. 2012. **Fig. 31:** Head capsule comparisons; **a:** *P. c-album;* **b:** *N. vaualbum;* **c:** *N. polychloros;* **d:** *N. antiopa*. — Photographs: MGP.

Hungary: The species was never reported as common in Hungary (at least not in the last 100 years), and old records are usually based on very few specimens, most probably vagrants. There were, however, many scattered localities; Baja (Pandúr), Kecskemét, Budakeszi (Sorrentó), Budapest (Hűvösvölgy, Normafa, Margitsziget, Savanyúvíz- forrás), Pécel, Szeged, Felsőtárkány (Oldalvölgy), Bükkszentkereszt (Hór-völgy), Mosonmagyaróvár (Bálint et al. 2006), and the species was considered a resident up until the 1960s–1970s. The strongest colony was at Nádasdi-erdő, near Kaposvár, and a long bred series from this locality, reared by M. Nattan, is housed in Hungarian Natural History Museum in Budapest (Bálint pers. comm.), and in the collection of the City Museum of Pécs (Németh-Bóka pers. comm.). The last specimen from this haunt was observed on 20. vi. 1946 by G. Lengyel (Bálint pers. comm.).

Table 1: Sightings of *Nymphalis vaualbum* in Serbia since 2010. There have been over a hundred confirmed sightings in total. The presence of fresh adults indicates that the species is breeding in Serbia, at least in limited numbers. — Table prepared by MGP.

Date	Location	Lat.	Long.	Stage	Approx. altitude	Observer
14. vi. 2010	2.5 km. NW of Donji Taor, Zlatibor District	44°6.665′ N	19°47.448′ E	Adult	1049 m	MĐ, DT
16. vi. 2010	6.8 km SE of Niška Banja, Nišava District	43°15.583′ N	22°4.670′ E	Adult	444 m	M. Popović
17. vi. 2010	7.1 km NE of Kladnica, Moravica	43°26.437′ N	20°4.613′ E	Adult	1334 m	MĐ, DT
18. vi. 2010	4.4 km SE of Budoželja, Moravica	43°31.394′ N	20°19.061′ E	Adult	1155 m	MĐ, DT
18. vi. 2010	5.3 km NE of Jošanička Banja, Raška District	43°24.092′ N	20°47.659′ E	Adult	745 m	MĐ, DT
19. vi. 2010	4.9 km NE of Jošanička Banja, Raška District	43°23.985′ N	20°47.540′ E	Adult	721 m	MĐ, DT
21. vi. 2010	2.2 km W of Babin Zub Hotel, Stara Planina, Zaječar District	43°22.091′ N	22°35.624′ E	Adult	1509 m	MĐ, DT
3. vii. 2010	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.473′ N	22°36.974′ E	Adult	1569 m	MĐ, V. Pavković, R. Verovnik
3. vii. 2010	7.1 km S of Kalna, Zaječar District	43°21.066′ N	22°26.566′ E	Adult	539 m	M. Popović, F. Franeta
3. vii. 2010	0.9 km SE of Mezdreja, Knjaževac, Zaječar District	43°24.007′ N	22°31.816′ E	Adult	570 m	M. Popović
4. vii. 2010	9.6 km NE of Temska, Pirot District	43°18.708′ N	22°38.545′ E	Adult	740 m	M. Popović, F. Franeta
5. vii. 2010	2.1 km N of Topli Do, Pirot District	43°21.227′ N	22°40.251′ E	Adult	850 m	M. Popović, F. Franeta
6. vii. 2010	Temska, Pirot District	43°15.648′ N	22°32.853′ E	Adult	405 m	M. Popović, F. Franeta
17. vii. 2010	4.9 km NE of Jošanička Banja, Raška District	43°23.987′ N	20°47.554′ E	Adult	723 m	MĐ, K. van de Logt
26. iii. 2011	1 km E of Gornja Vrežina, Nišava District	43°19.807′ N	22°0.520′ E	Adult	346 m	M. Popović
17. vi. 2011	1.8 km W of Babin Zub Hotel, Stara Planina, Zaječar District	43°22.080′ N	22°35.877′ E	Adult	1551 m	F. Franeta
19. vi. 2011	Ravno Vučje, 5.3 km NE of Janja, Knjaževac, Zaječar District	43°26.203′ N	22°33.645′ E	Adult	794 m	MĐ, M. Popović
19. vi. 2011	drinking fountain of Babin Zub hotel, Stara Planina, Zaječar District	43°22.484′ N	22°37.010′ E	Adult	1569 m	T. Hapka
19. vi. 2011	Hotel Babin Zub, Stara Planina, Zaječar District	43°22.475′ N	22°36.973′ E	Adult	1577 m	T. Hapka
20. vi. 2011	Babin Zub, Stara Planina, Zaječar District	43°24.788′ N	22°34.601′ E	Adult	833 m	T. Hapka
3. vii. 2011	4.9 km NE of Jošanička Banja, Raška District	43°23.985′ N	20°47.540′ E	Adult	721 m	DT
5. vii. 2011	7.1 km S of Kalna, Zaječar District	43°21.066′ N	22°26.566′ E	Adult	539 m	DT
5. vii. 2011	Biger's waterfall, 7.1 km S of Kalna, Zaječar District	43°21.299′ N	22°26.609′ E	1 ♂	456 m	DT
5. vii. 2011	7.5 km S of Kalna, Zaječar District	43°21.148′ N	22°26.802′ E	1 ♂	473 m	DT
5. vii. 2011	Babin Zub, Stara Planina, Zaječar District			2 ♂♂	1000/1500 m	DT
6. vii. 2011	Babin Zub, Stara Planina, Zaječar District			3 ♂♂	1000/1500 m	DT
7. vii. 2011	Babin Zub, Stara Planina, Zaječar District			3 ♂♂	1000/1500 m	DT
8. vii. 2011	road leading to Hotel Stara Planina, Stara Planina			4 ♂♂, 3 ♀♀	1475/2000 m	DT
9. vii. 2011	Babin Zub Hotel, Babin Zub, Stara Planina	43°22.473′ N	22°36.974′ E	2 ♂♂, 1 ♀	1569 m	DT
9. vii. 2011	Kalna to Temska road, Zaječar District			Adult	400–600 m	DT
19. iii. 2012	Izvor, Pirot District	43°4.678′ N	22°23.461′ E	Adult	520 m	D. Stojanović
4. iv. 2012	5.2 km W of Bačka Palanka, Vojvodina	45°14.394′ N	19°18.376′ E	Adult	80 m	I. Tot
8. vi. 2012	2.2 km NE of Vršac, South Banat District, Vojvodina	45°7.655′ N	21°20.164′ E	Adult	345 m	A. Vlatković
9. vi. 2012	Divčibare, Kolubara District	44°6.699′ N	19°59.149′ E	Adult	986 m	F. Franeta
17. vi. 2012	Mt. Mučanj, 6.2 km SW of Katici, Moravica	43°33.033′ N	20°1.625′ E	Adult	1310 m	M. Rowlings
19. vi. 2012	Mt. Mučanj, 5.6 km SW of Katici, Moravica	43°33.044′ N	20°1.863′ E	Adult	1278 m	MGP, C. Orpin
19. vi. 2012	Mt. Mučanj, 6.7 km SW of Katici, Moravica	43°32.817′ N	20°1.490′ E	1 ♀	1355 m	MGP, C. Orpin
19. vi. 2012	Mt. Mučanj, 4.8 km SW of Katici, Moravica	43°32.943′ N	20°2.486′ E	Adult	1175 m	MGP, C. Orpin
19. vi. 2012	Mt. Mučanj, 5.4 km SW of Katici, Moravica	43°33.006′ N	20°2.047′ E	Adult	1250 m	MGP, C. Orpin
20. vi. 2012	Mt. Mučanj, 4.8 km SW of Katici, Moravica	43°32.943′ N	20°2.486′ E	Adult	1175 m	MGP, C. Orpin
20. vi. 2012	Mt. Mučanj, 5.6 km SW of Katici, Moravica	43°33.044′ N	20°1.863′ E	Adult	1278 m	MGP, C. Orpin
20. vi. 2012	Golija, 6,2 km E of Budoželja, Moravica	43°31.835′ N	20°20.045′ E	Adult	1154 m	MGP, C. Orpin
21. vi. 2012	5 km SW of Topli Do, Pirot District	43°20.402′ N	22°41.133′ E	Adult	752 m	MĐ, M. Popović
22. vi. 2012	Babin Zub, Stara Planina, Zaječar District	4322′0″ N	2237′56″ E	Adult	1381 m	S. Safian
22. vi. 2012	Babin Zub, Stara Planina, Zaječar District	43°21.916′ N	22°35.118′ E	Adult	1482 m	MĐ, M. Popović
25. vi. 2012	1.8 km N of Janja, Stara Planina, Zaječar District	43°25.345′ N	22°31.805′ E	1 ♂	591 m	MGP, C. Orpin
26. vi. 2012	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.452′ N	22°37.076′ E	1 ♀	1570 m	MGP, C. Orpin

27. vi. 2012	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.452′ N	22°37.076′ E	Adult	1570 m	C. Derry, C. Luckens
28. vi. 2012	1.6 km SE of Crni Vrh, Babin Zub, Stara Planina, Zaječar District	43°23.948′ N	22°35.819′ E	1 ♂	920 m	C. Derry, C. Luckens
28. vi. 2012	Babin Zub Hotel, Babin Zub, Stara Planina	43°22.473′ N	22°36.974′ E	1 ♀	1569 m	MGP, C. Orpin
29. vi. 2012	reservoir below road leading to Hotel Stara Planina, Stara Planina	43°21.983′ N	22°35.239′ E	2 ♂♂	1450 m	MGP, C. Derry, C. Luckens
29. vi. 2012	5.1 km SE of Crni Vrh, Babin Zub, Stara Planina, Zaječar District	43°22.944′ N	22°36.064′ E	1 ♂	1180 m	C. Derry, C. Luckens
5. vii. 2012	Golija, 5.6 km E of Budoželja, Moravica	43°31.734′ N	20°19.747′ E	1 ♀	1134 m	MGP, CW, J. E. Pateman
6. iv. 2013	Krupac village, close to Leskovik, Stara Planina, Zaječar District	43°17.793′ N	22°13.339′ E	Adult	266 m	T. Hapka
15.–16. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°22.472′ N	22°36.947′ E	3 Adults	1570 m	F. Franeta
15.–16. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°21.626′ N	22°34.813′ E	Adult	1450 m	F. Franeta
15.–16. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°23.027′ N	22°35.609′ E	5 Adults	1256 m	F. Franeta
15.–16. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°22.898′ N	22°36.711′ E	5 Adults	1220 m	F. Franeta
19. vi. 2013	Suva Planina, road from Gornja Studena to Bojanine Vode, Niška Banja	43°13.849′ N	22°6.106′ E	Adult	630 m	D. Radevski
19. vi. 2013	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.484′ N	22°37.010′ E	Adult	1569 m	T. Hapka
19. vi. 2013	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.475′ N	22°36.973′ E	Adult	1577 m	T. Hapka
20. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°24.788′ N	22°34.601′ E	Adult	833 m	T. Hapka
20. vi. 2013	Mt. Ozren, near Sokobanja, Zaječar District	43°37.669′ N	21°52.087′ E	Adult	623 m	V. Pavković
21. vi. 2013	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.484′ N	22°36.985′ E	Adult	1576 m	T. Hapka
21. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°22.120′ N	22°36.010′ E	2 Adults	1569 m	T. Hapka
21. vi. 2013	Konjarnik, Babin Zub, Stara Planina, Zaječar District	43°23.068′ N	22°36.406′ E	2 Adults	1155 m	T. Hapka
21. vi. 2013	Babin Zub, Stara Planina, Zaječar District	43°24.719′ N	22°34.548′ E	Adult	830 m	T. Hapka
22. vi. 2013	Mt. Besna Kobila, east of Vranje, SE Serbia	42°33.027′ N	22°13.884′ E	Adult	1625 m	MĐ, K. van de Logt, B. Kranenbarg
23. vi. 2013	Mt. Besna Kobila, east of Vranje, SE Serbia	42°31.634′ N	22°12.012′ E	Adult	1644 m	MĐ, K. van de Logt, B. Kranenbarg
23. vi. 2013	Mt. Besna Kobila, east of Vranje, SE Serbia	42°31.490′ N	22°12.368′ E	Adult	1674 m	MĐ, K. van de Logt, B. Kranenbarg
23. vi. 2013	Debeli Lug, near Majdanpek, Bor District	44°21.733′ N	21°53.904′ E	Adult	273 m	M. Popović
23. vi. 2013	Josanicka Banya, ca. 1km north, Raška District	43°25′ N	20°50.E	2 Adults	1100 m	C. J. Luckens, H. Elston
23. vi. 2013	Golija, Budozela, Moravica	43°32′ N	20°20.E	2 adults	1100 m	C. J. Luckens, H. Elston
27. vi. 2013	Kalna town, Zaječar District	43°24′ N	22°25.E	Adult	365 m	J. E. Pateman, J. Martin
28. vi. 2013	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.465′ N	22°36.979′ E	Adult	1570 m	C. J. Luckens, H. Elston
28. vi. 2013	Crni Vrh (path to Golema Reka), Zaječar District	43°24′ N	22°36.E	2 Adults	ca. 880 m	C. J. Luckens, H. Elston
28. vi. 2013	road from Janja to Ravno Vučje, Zaječar District			4 Adults	530–900 m	J. E. Pateman, J. Martin
29. vi. 2013	ca. 2 km north Janja, Zaječar District	43°25′ N	22°32′ E	4+ Adults	640 m	C. J. Luckens, H. Elston, J. E. Pateman, J. Martin
30. vi. 2013	road from Janja to Ravno Vučje, Zaječar District			3 Adults	530–900 m	J. E. Pateman, J. Martin
6. vii. 2013	Babin Zub Hotel, Stara Planina, Zaječar District	43°22.465′ N	22°36.979′ E	1 ♀	1570 m	CW
8. vii. 2013	road to Ravno Vučje, Zaječar District			1 ♂	ca. 600 m	CW
11. vii. 2013	Golija, Budozela, Moravica			1 ♂		CW

The most recent sighting from Hungary is from Nagyharsány (Szarsomlyo), observed on 15. iv. 2005. A photo of the specimen was taken by B. Horváth and appears on the Greeneye website (2014). Apparently, Horváth noticed the butterfly basking on a rock and took several photographs without determining the species, and it was only later that L. Németh-Bóka identified the butterfly from photos (Németh-Bóka pers. comm.). In early vii. 2001, G. Dietzel reports having seen an individual at Kislőd (Csalánosi völgy), and in early July 2002 a second specimen at Úrkút (Som-út, Kab-hegy) (Dietzel pers. comm.), and there is an unconfirmed report by Dietzel of a specimen from Úrkút (Som-út, Kab-hegy) in early July 2002 (Dietzel pers. comm.). Prior to these observations the Farkas sisters, accompanied by their father, collected specimens in Herend (Fasori Park) in 1955, and A. Rohonyi captured a singleton west of Veszprém (Betekints-völgy) in 1957 (Dietzel 1997). A single specimen was collected at Miskolc (Avas) in NE Hungary on 29. vi. 1963 (Gyulai 1976) and during the same year M. Nyiro collected a further specimen on 14. vii. near Kőszeg, W Hungary (Németh-Bóka pers. comm.), and this is now housed in the HNHM. There is an unconfirmed report that a specimen was seen in the vicinity of Szentendre by K. Gasko in the 1970s (Németh-Bóka pers. comm.). Bálint comments that, despite individual records, there appear to be no permanent populations in Hungary at the present time.

Romania: A strong decline in distribution or population size of more than 30% has been reported from Romania (van Swaay et al. 2010). After 1990, it has only been reported in western and southwestern Romania, and it is not clear if any stable populations are present in the country. It is possibly still found in the vicinity of Căpâlnaş (Arad county) and Caransebeş (Caraş-Severin county) (Székely 2008). A photo of a ♂ specimen captured near Căpâlnaş on 26. vii. 2007 by Heinz Neumann of Timişoara (Bold Process ID: EZRMN419-09) can be found by accessing the "Butterflies of Romania (EZROM)" project on BOLD at www.boldsystems.org (Dincă et al. 2011). In addition, two photographs of a ♂ *N. vaualbum* appear on the www.meloidae.com beetles website (Krejčík 2012). The pictures were taken by Stanislaw Krejčík on 19. vi. 2012, 3 km south of Bigăr, Caraş-Severin county. During the same month in 2012, L. Rákosy photographed a fresh ♂ in the Apuseni Mountains (Băişoara, Mt. Mare) at 1550 m alt. This species was not observed between 1970 and 2007 in Romania but, together with *N. xanthomelas*, *N. vaualbum* has been expanding its range in the last ten years, regaining its former territories (Rákosy pers. comm.).

Belarus: Specimens (possibly migrants) were recorded from the regions of Vitebsk, Minsk and Mogilyov between 1950 and 1980 (Dovgailo et al. 2003, unpubl.). P. A. Donov reported seeing the butterfly on 17. vii. 1957 and 15. vii. 1960 in the vicinity of Vitebsk and a ♂ was collected by I. A. Solodovnuikov on 4. viii. 1988 (Dovgailo pers. comm.). Another ♂ was captured by V. P. Piskunov at Tulovo village, 2 km E Vitebsk on 3. vii. 1987 and a further specimen was recorded by A. A. Goldenkov in the Lepel' district, Nat. boundary Postrezh'e, Berezinskiy Biosphere Reserve, on 10. viii. 1987 (Dovgailo pers. comm.). In the Minsk region, specimens of *N. vaualbum* were recorded by V. Kornilov in Borovlyany village in 1972 and by S. Kakunin in Turin, Pukhovichi district, on 23. vii. 1989 (Dovgailo pers. comm.). In the Mogilev region, A. A. Goldenkov recorded the species at Osipovichi, Osipovichi district, on 30. vii. 1983 (Dovgailo pers. comm.). There have been no observations for the last two and a half decades (Morgun pers. comm., Dovgailo pers. comm.).

Ukraine: Reported as widespread, except in southern Ukraine and in the Crimea (Tshikolovets 2003), but in strong decline (Tshikolovets pers. comm.). Hormuzaki (1897) mentioned: Cernauka: Chornivka, Novoselytsya district; Krasna: Krasnoilsk, Storozhynets district; Kupka, Hlyboka district and Czernowitz (all records from the Chernivtsi region). According to A. Xiezopolski (1911), two or three specimens of this species, were delivered to Mr. Mikhailov from the immediate vicinity of Novograd-Volynsky (Zhytomyr region) in July 1909. Romaniszyn & Schille (1929) wrote that *Nymphalis vaualbum* was recorded from Zolkiew (presently Zhovkva) in the Lviv region. Goloborodko (2011) stated that the species is very rare in Ukraine and cited single records from the Carpathians, Polissya and Dnipropetrovsk region. He reports that in the Dnipropetrovsk region it was recorded only in Dniprovsko-Orilsky reserve (the Dniprovsko-Orilsky reserve is a wooded area between Dnipropetrovsk, Kirovske, Mykolaivka and Dniprodzerzhynsk). In the Red Data book of Ukraine (Shreshurak et al. 2004), *N. vaualbum* is quoted as being very rare in Chernigiv region; one specimen was reported from the vicinity of Luka village, Shchors district, on 11. vii. 1994, P. Shreshurak leg.; the butterfly was collected on oak sap.

European Russia: Reported from the west and central parts of the Great Caucasus (Tshikolovets & Nekrutenko 2012), the southern Urals (where it is rare), the central and northern parts of the Urals (where it can be common) to the Arctic Circle and possibly further north (Tshikolovets pers. comm.). The distribution of *N. vaualbum* has been strongly expanding in Central Russia due to migratory activity, and the populations have remained stable in these new areas.

Regional records. Chuvashia: Lastukhin (2012); Kaluzhskaya: Sosenka village, Kireikovo village Shmytova (2001), Kaluga region Bolshakov (2003), abundant in the Oka River valley, Kaluga Region during vii. 2006, leg. A. Elez (Morgun pers. comm.); Kirovskaya: Shernin (2000); Kursk: Tatarenko (2008); Mordovia: Ruchin (2008); Moskovskaya: Dmitrov on 24. vii. 1967, leg. L. Nikolaevsky (Tuzov 2000); Luzhki on 24. vii. 1973, leg. L. Nikolaevsky (Tuzov 2000) and 29. vii. 1986, leg. G. Samodurov (Tuzov 2000); Moscow region Bolshakov (2003); abundant in the Ruza district during vii. 2006, leg. A. Elez (Morgun pers. comm.); Chekhov in 2008, 2010, leg. N. Dvoeglazov (Lepiforum: *Nymphalis vaualbum* ([Denis & Schiffermüller], 1775) 2013); L'vovskoe forestry, Podol'sky district on 24. vii. 2009, leg. A. Varlamov (Varlamov 2009); abundant at the Prioksko-Terrasny reserve, Serpukhov district, Moscow Region on 17.–18. vii. 2010 and vii. 2011. In one encounter about 50 specimens on five square metres were observed on forest roads in the Reserve. About 10 years ago this species was absent in this district (Morgun pers. comm.); Torbeevo, Lyubertsy, Moscow Region, on 20. vii. 2012 (Morgun pers. comm.); Veselyovo village, Vereisky Forest, Narofominsk district, on 21. vii. 2012, leg. M. Pozdnova (Pozdnova 2012); Hrypan' village, Ramensky district, on 26. vii. 2010, leg. V. Gumenuk (Gumenuk 2010); Zhukovo village, Ramenskoe district, on 17. iv. 2013, leg. A. Ponomarev (Ponomarev 2013). Reported as widespread in 2011–2012, several dense populations were found in the Moscow Region (Morgun pers. comm.); Nizhegorodskaya: Zubovo, Vetluga, Arzamas, Kstovo, Lyskovo, Pustyn' Tschetverikov (1993), Schelokovsky farm, Nizhny Novgorod on 16. iv. 2009, leg. S. Korb (Korb 2009), Yagodnoye (50 km south of Nizhny Novgorod) in 2009, 2010 and 2011, leg. S. Shmelev (Shmelev *in* Lepiforum: Nymphalis vaualbum ([Denis & Schiffermüller], 1775) 2013); Orenburgskaya: abundant at Kuvandyk on 23. vii. 2000 (Morgun pers. comm.); Penzenskaya: Polumordvinov & Monakhov (2002); Ryazan: Bolshakov (2003); Tatarstan Republic: Zelenodolsk, Alekseev, Vysokogorsk, Kukmorsk, Laishev

Shulaev et al. (2005); Tul'skaya: Pesochensky, Matyukhinsky, Chekalin, Fursovo, Okorokovo, Shatovo, Dubna, Novoe Khanino, Khomyakovo, Popovka, Afanasyevo, Mazalki, Shulgino, Egnyshevka (Sviridov & Bolshakov 1997), Tula region (Bolshakov 2003), abundant at Aleksin district during vii. 2005, leg. A. Lisakovsky (Morgun pers. comm.); Udmurtia: Adakhovsky (2001); Yaroslavskaya: Yaroslavl, in vii. 2005, leg. A. Ilyin (Ilyin *in* Mazzei et al. 2005).

Very local, but sometimes common in the Great Caucasus and it is possible to find stable populations in some localities (Tshikolovets pers. comm.): Black Sea coast of Abkhazia (Milyanovskiy 1947); Avadhara, Abkhazia, 8. vii. 1969, leg. E. Milyanovskiy (Tshikolovets & Nekrutenko 2012); Archys, (Arkhyz) (Mironov 1956); Kerigo, Chechen-Ingoosh Republic (Bálint et al. 1996); Malaya Laba River, Umnyr, 3. vii. 1959 (Tshikolovets & Nekrutenko 2012); Awadhara, Malaya Laba River, North Caucasus (Tshikolovets & Nekrutenko 2012); Dzhemagat River, Teberda (Tshikolovets & Nekrutenko 2012); Samegrelo (Chogonia), Georgia (Didmanidze 2004); environs of Gertma, N slope of Salatau range, Dagestan (Ilyina & Morgun 2011). Vicinity of Utchkulan, Kuban riverhead, N. Caucasus, 1600–1800 m on 3. viii. 1997; Daut gorge, Kuban riverhead, N. Caucasus, 1400 m, on 25. vii. 2007; Borgustan ridge, vicinity of Kislovodsk, N. Caucasus, 1100 m, on 20. iv. 2009 (V. V. Tikhonov pers. comm.). Upper Teberda, 2003–2011, leg. B. V. Stradomsky; env. of Kamyshanov, Krasnodar region, 2010–2011, leg. G. M. Shembergera; Azish Tau, Rozhkao, 2004, leg. Shchourov; Abrau Peninsula, 2007, leg. Shchourov (Tikhonov et al. 2014).

Turkey: There are only a handful of records from Turkey and all of these have been from the Asiatic part: Artvin and Erzurum in NE Turkey (Baytaş 2007); 5–15 km NW of Meydancik, Artvin, 1800–2000 m, viii. 1993; Ak Dağ, NE Hinis, Erzurum (Heyne 1895, Hesselbarth et al. 1995).

Nomenclature

There are currently two names commonly used for this species in literature: *Nymphalis vau-album* ([Denis & Schiffermüller], 1775) and *Nymphalis l-album* (Esper, 1781). The name "*vau-album*" (to be united into one word according to the Code: *vaualbum*), along with many other names, was proposed with a very limited description and no figures in the anonymously published "Wiener Verzeichnis" and has nearly always been attributed to Michael Denis and Ignaz Schiffermüller. However, in a paper published in 2005, Kudrna & Beliček presented what they considered to be 'totally convincing' evidence that Schiffermüller alone was the author, a viewpoint strongly contested by Sattler & Tremewan (2009), maintaining there were many flaws in Kudrna & Beliçek arguments.

Several authors have chosen to dispute the validity of original descriptions within the "Wiener Verzeichnis" and consider the name *Nymphalis vaualbum* to be a *nomen nudum* (Koçak 1982, 1984, Kudrna 2002, Kudrna & Beliçek 2005). However, most of the other names in the "Wiener Verzeichnis" were proposed in a similar vague fashion and many are presently in general use (Gillham 1956). Rejection of the name *vaualbum* would in the end lead to the rejection of many well-established names, resulting in an unstable situation in respect to the nomenclature of European Lepidoptera. For the purpose of this paper and in the interest of stability, we have chosen to conform to the long-established accepted practice of attributing the work (and all new names established therein) to [Denis & Schiffermüller], as agreed by the International Commission on Zoological Nomenclature in Opinion 516 (Hemming 1958) and adhered to by the Fauna Europaea [Fauna Europaea 2014, version 2.6.2 of 29. viii. 2013]. Consequently, *l-album* Esper, 1781 falls as a direct synonym of *vaualbum* on the basis of priority (see www.faunaeur. org/full_results.php?id=441669, accessed 27. i. 2014).

Some authors in North America (e.g., Guppy & Shepard 2013) followed the splitting of the genus *Nymphalis* into several smaller genera by some Russian authors and placed the species *vaualbum* into the genus *Roddia* Korshunov & Gorbunov, 1995. In the Zobodat (2012) data bank, the species is listed as "*Polygonia l-album*". As written above, we follow here the systematics of the Fauna Europaea site.

Discussion

Based on the number of fresh specimens that have recently been observed in the summer months in the vicinity of the Stara Planina, it is inconceivable to think that *N. vaualbum* is not breeding in the region, or at least reproducing there in low densities. The species is probably more widespread in Serbia than previously thought and in all likelihood, the paucity of reports can be attributed to the lack of recording effort (Popović & Đurić 2010).

Extensive, semi-contiguous deciduous woodland habitat exists over much of southern Serbia over a varied range of altitudes, presenting an ideal, viable habitat for such a nomadic dispersing species, i.e. an ideal combination of available habitat, suitably continental climate and altitudinal variation. In Hungary, Romania, Poland, and especially the Czech Republic, the woodland cover is far more fragmented, but suitable habitats do still exist in Slovenia, Croatia and the Baltic States; however, as far as we are aware, there are no permanent colonies in these countries. It would appear that native populations in Europe are unable to tolerate mild winters, and records show that, on average, winter temperatures have increased in western Europe. In Japan, however, populations live in mild winter climates (Jürgen Hensle pers. comm.).

Although we now have considerable knowledge regarding the life cycle of the species (at least in Serbia) we have little understanding of the species' requirements in respect to hibernation.

The latest summer record from Serbia is 22. vii., by which time a majority of butterflies are presumed to have commenced aestivation, and the earliest record from the spring is from Mt. Kosmaj on 14. iii. 2007 (Popović & Đurić 2010). There is, however, one record for *N. vaualbum* on the Bulgarian side of the Stara Planina at Gorni Lom Village, on the road to Martinovo at an altitude of 690 m on 12. ix. 2011 by S. Beshkov & M. Beshkova.

Logic would suggest that butterflies are either hibernating at high altitudes (above 1000 m), where they are frequently seen during the months of June and July, or, after a period of aestivation, adults are descending to lower elevations where they hibernate in a more sheltered environment. It is possible, but highly unlikely, that the species has a prolonged aestivation period and remains in a torpid state prior to hibernation, not re-emerging until the following spring.

Although we cannot confirm this behaviour in nature, observations made in captivity indicate that overwintering specimens feed prior to hibernation. In our breeding experiment after a period of 'unforced' aestivation, specimens became active and recommenced feeding in late summer. In September 2011 and October 2012, CW witnessed *N. vaualbum* butterflies nectaring on (diluted) fructose cotton pads, behaviour also shared by both *N. xanthomelas* and *N. polychloros* in captivity. We also know that other hibernating nymphalid species, such as *V. atalanta* and *P. c-album*, are regular visitors to gardens in late summer, feeding on nectar-rich flowers prior to hibernation, and K. Bailey witnessed many specimens of *N. antiopa* feeding on fluids leaching from wooden barrels in Andorra in late ix. 1975 (Bailey pers. comm.).

At what altitude or at what range of altitudes does *N. vaualbum* hibernate?

If we look at the distribution of this species we know that it is widely distributed and occasionally common at higher latitudes and higher altitudes where winter temperatures can exceed –40°C (e.g. Siberia and Mongolia).

We know that winter temperatures in Eastern Europe are generally lower than in Western Europe, where it can often be mild during January and February. There is evidence to suggest that some butterfly species require a cold period to complete their development (Wigglesworth 1939). This may explain why one of our overwintering ♀♀ *N. vaualbum*, despite having paired (the ♀ had a spermatophore), laid infertile eggs. For many species, it would appear that a prolonged cold spell is crucial for development. After the mild winter of 2011/ 2012 in the U.K. the fertility of many captive bred nymphalids (*Nymphalis polychloros* and *Nymphalis antiopa* Linnaeus, 1758) was poor. In comparison, the country experienced prolonged temperatures below freezing in the previous two years and fertility of paired nymphalids was virtually 100% (Bailey pers. comm.; CW pers. obs.).

K. Bailey (pers. comm.), an entomologist with many years' experience of breeding nymphalids, believes it is essential that adults are exposed to freezing temperatures during their hibernation period, and has come to the conclusion that there is very low fertility (in some cases 0%) from pairings after a mild winter. CW concurs with this theory. During the course of his (K.B.'s) studies, pre-hibernated ♂♂ specimens of *P. c-album* were dissected and it was discovered that their gonads were not fully developed. In an experiment to try to confirm his hypothesis, Bailey over wintered several live specimens of *N. antiopa* in a freezer, replicating the temperatures of a typical central Russian winter. Initially the adults were kept in a half-barrel and fed on a 50% glucose–50% fructose mix prior to diapause. They remained in this half-barrel until the beginning of October when they were transferred to a damp (to avoid desiccation) cardboard box, and placed in a Zanussi mini deep-freezer in his garage. The freezer had been modified so that a thermostat could manually control temperatures. Temperatures were modified on a monthly basis, and for a period they were reduced to –14°C. On removing the cardboard box from the freezer in late April/early May the following year, the specimens were lying torpid at the bottom of the box and appeared dead. They were placed into a large flight cage in a greenhouse. They remained motionless for the first few hours but when the sun warmed up the enclosure, one or two butterflies showed signs of life, and by midday several were in an upright position. Within 24 hours they were flying around the cage, and after 48 h they were performing courtship behaviour, chasing each other around the large 2 m square flight cage. On the third day, matings were observed, resulting in batches of (100%) fertile eggs.

J. Kaitila has presented the authors with an alternative explanation regarding overwintering requirements for *N. vaualbum* in Finland. He informed the first author that at the turn of the last century, up until the end of the 1950s, Finland experienced short but warm summers. In the 1960s, however, there was a dramatic change, and summers became not only longer, but also cooler. In the 1990s, Finland continued to experience these longer summers, but (on average) temperatures started to increase once more, and species such as *N. xanthomelas*, *N. vaualbum*, *Borearctia menetriesii* (Eversmann, 1846) and *Acronicta tridens* ([Denis & Schiffermüller], 1775) made a dramatic return to the annual list of Finnish Lepidoptera.

J.K. believes that one of the key factors for a successful life cycle is the sudden transition from winter to spring with no regression back into winter. This would potentially create a more stable environment for developing larvae and this is backed up by CarolinaSarah (2012), who stated: "Early snowmelt can be a false alarm for caterpillars: if they come out of hibernation before the danger of frost has passed, they may perish in a sudden cold snap. Adult butterflies are similarly affected by spring frosts. ♀♀ depend on nectar to produce eggs, and early frosts can kill new shoots, i.e. climate can affect a species in two ways, indirectly through its (*sic*) food chain and directly through temperature stress."

At what altitude or at what range of altitudes does *N. vaualbum* complete its lifecycle?

MĐ reports that the earliest (naturally emerging) summer brood specimen from Serbia was recorded by A. Vlatković on 8. vi. 2012, 2.2 km NE of Vršac, South Banat District. We can calculate with some degree of accuracy that egg batches would have to have been laid no later than mid-March for the butterfly to complete its life cycle and be on the wing in early vi.

Above 1200 m on the Stara Planina the butterfly's hostplants are likely to be in bud at the beginning of May (or later), so it seems highly unlikely that development from ovum to adult can be achieved in such a short period of time. To substantiate this hypothesis, authors 1, 2 and 3 visited the Babin Zub region of the Stara Planina in early v. 2011. At altitudes above 1000 m they noted that familiar *N. vaualbum* hostplant species such as sallow, elm and birch were barely in bud, while at lower altitudes (below 700 m) the aforementioned species had new shoots. Having taken into account the duration needed to complete the life cycle (in captivity a period of 11 weeks elapsed between oviposition and adult eclosion), this would indicate that the butterfly would have to breed at lower altitudes. According to meteorological data, the Babin Zub can regularly be covered in snow during May. To add further evidence, all spring specimens from Serbia have been recorded at relatively low altitudes: Mt. Kosmaj, 333 m, 14. iii. 2007 (Popović & Đurić 2010); Kumodraž, 181 m, 10. iv. 2009 (Popović & Đurić 2010); Jelašnica gorge, 334 m, 16. iv. 2009 (Popović & Đurić 2010); 1 km E of Gornja Vrežina, 346 m, 26. iii. 2011 (MĐ pers. obs.); Izvor, 520 m, 19. iii. 2012, observer Dejan Stojanović (MĐ pers. obs.); 5.2 km W of Bačka Palanka, Vojvodina, 80 m, 4. iv. 2012, observer Ivan Tot (MĐ pers. obs.); Krupac village, 266 m, 6. iv. 2013 (Hapka pers. comm.).

So why have so many observations been made at higher altitudes? We know that hill topping is a common phenomenon adopted by many butterfly species, predominantly ♂♂. However, a high percentage of specimens observed above 1550 m on the Stara Planina (close to the summit) have been ♀♀, and sightings of both sexes have by no means been restricted to higher elevations. It appears that the main requirement for aestivation is a cool, damp habitat where there is plenty of cover. Naturally, this is nearly always in a woodland or forest setting and this kind of habitat is prevalent on the Babin Zub above 1000 m. The situation on Mt. Mt. Mučanj would appear to back up this speculation. Specimens were only seen in damp, moist woodland where there was plenty of tree cover at altitudes between 1175– 1250 m and not at the summit, 200 m higher, where the habitat is substantially drier.

Summary

A study made by Wahlberg et al. (2005) confirms the stable relationship of *Nymphalis vaualbum* with other species of *Nymphalis*. However, our studies revealed many similarities between *N. vaualbum* and *P. c-album*. In the course of our breeding programme, we observed a number of characteristics shared by both *N. vaualbum* and *P. c-album*.

Both *N. vaualbum* and *P. c-album*, for example, lay their eggs in a shady situation, in contrast to *N. polychloros* and *N. xanthomelas* that lay their egg batches in full sunlight (CW observation). The larval head morphology of *N. vaualbum* is significantly different from that of *Nymphalis* larvae, more akin to the genus *Polygonia,* with two conspicuous spiked horns protruding from the head capsule (Figs. 31a–d). During the course of our rearing programme, we noticed that *N. vaualbum* L_1 larvae disperse into small groups, and from L_2, lead a solitary existence, unlike *N. polychloros* and *N. xanthomelas* that live in large communal webs and disperse at L_4 or L_5 stage. The larvae of both *N. vaualbum* and *P. c-album* predominantly feed on the underside surface of leaves of their hostplant and in a shady situation, compared with *N. polychloros* and *N. xanthomelas* that prefer to feed and bask in full sunshine. Another major difference is that the larvae of *N. vaualbum* spin a fine inconspicuous silken 'tent' between terminal twigs (Fig. 30), but do not cohabit within this 'framework'. *N. polychloros* and *N. xanthomelas* on the other hand construct a large web, and they live communally from within. At adult stage the white (cryptic) 'comma' marking on the ventral hindwing is a characteristic of both *N. vaualbum* and *P. c-album* and both *N. vaualbum* and *P. c-album* have (sexually) dimorphic ventral wing colouration (f. *hutchinsoni*).

In recent years there has been a sudden increase in sightings of *N. vaualbum* in Eastern Europe and, like *N. xanthomelas*, it is hoped that this trend continues possibly re-colonising some of its former haunts such as the Baltic States where there are still vast areas of continuous forest.

In Europe (outside Russia) there are, at present, two widely separated areas of occurrence, eastern Finland and Serbia (including its immediate border areas). While in Serbia one could attribute this to increased observer vigilance, this is considered highly unlikely in Finland, where many entomologists have been recording fauna for well over a century.

Due to the species migratory fluctuations, the authors agree with the IUCN Red List of Threatened Species in that they do not consider the species to be under threat.

A suitable continental climate, combined with continuous (not fragmented) areas of viable woodland habitat, appears to be key factors regarding the species' continued resurgence.

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