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The natural history of the Sinai Baton Blue: the smallest butterfly in the world

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ABSTRACT

Knowledge of the ecology and life history of endangered species is necessary for their successful conservation. In this chapter, I provide a detailed account of the natural history of the Sinai Baton Blue butterfly. I review current knowledge of the genus *Pseudophilotes*, and explore the butterfly's phylogeny. This emphasises the paucity of knowledge surrounding the butterfly and related species, and highlights the general differences in its ecology compared with other species used in metapopulation studies. I provide a description of all stages in the butterfly's lifecycle, including its larval stages (which have never before been described). Using quantitative data relating to adult size, I show that the Sinai Baton Blue can justify claims made that it is 'the smallest butterfly in the world'. I also provide considerable quantitative data on the butterfly's behaviour and ecology, and examine aspects of its mating and oviposition behaviour. Colour photographs illustrate its habitus and aspects of its behaviour and ecology.

INTRODUCTION

The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura) has been described as one of the smallest butterflies in the world (Larsen 1990). It occurs only in the high mountain region of the St. Katherine's Protectorate in Sinai, one of Egypt's most recently designated Protected Areas, and its newest UNESCO World Heritage Site. It is here that the only known larval hostplant, the near-endemic Sinai Thyme (Labiatae: *Thymus decussatus* Benth.) is patchily distributed among the mountains. *Pseudophilotes sinaicus* is one of only two endemic animals in the Protectorate (both butterflies), its endemicity making it a world conservation issue. It is therefore a flagship species for the area, highlighted as a priority for the Protectorate (St. Katherine's Protectorate Management Unit, personal communication).

It is a member of the family Lycaenidae - the largest and most biologically diverse family of butterflies, containing more than 6,000 species (30-40% of all butterfly species) (New 1993). The family is divided into nine sub-families (largely based on morphology and ecology): Lipteninae, Poritiinae, Liphyrinae, Miletinae, Theclinae, Curetinae, Lycaeninae, Polyommatinae, and Riordininae (Eliot 1973, 1990; Ackery 1984; de Jong *et al.* 1996; Ackery *et al.* 1999). The genus *Pseudophilotes* belongs in one of the largest of these sub-families, the Polyommatinae (the 'blues'). Eliot (1973) devised a tribal system within each sub-family, and divided the Polyommatinae into four tribes; *Pseudophilotes* belongs in the largest of these tribes, the Polyommatini, an extremely cosmopolitan tribe with at least twenty species in every zoogeographical region. The tribe Polyommatini is further sub-divided into sections (Eliot 1973); *Pseudophilotes* is in the Glaucopsyche section. The higher taxonomy of *Pseudophilotes* and its relationship with other genera in the Glaucopsyche section (Beuret 1958; Pratt 1994) is described in Figure 1.

Nine species have been reported in the genus *Pseudophilotes*, more than half of them since 1970. However, the specific rank of one of the species (*panoptes*) is debatable (Higgins & Riley 1980; Higgins 1982; Tolman & Lewington 1997), and two other species (*jacuticus* and *jordanicus*) require further investigation – *jordanicus* is described from only a single specimen (Benyamini 2000). None of the species has been well studied, and most papers have dealt only with very general aspects of the species' distribution, ecology, or taxonomy (Table 1). The genus is characterised by species that are small, moderately myrmecophilous, and which generally occur on dry, rocky slopes at high altitude where they mainly feed on plants in the family Labiatae (particularly *Thymus* spp.) (Table 2). Because of the paucity of data on this genus, the status of most species is unknown; their distributions are shown in Figure 2. In addition to *sinaicus*, at least one other species is a narrow endemic (*barbagiae*, found only in Sardinia: Grill 2003). The Sinai Baton Blue is likely to be categorised as 'endangered' or 'critically endangered' because of its restricted distribution area (<200 km²: James *et al.*, 2003; Hoyle & James, 2005) and fluctuation in population size (James, 2006c), and because it is 'threatened' (van Swaay & Warren 1999) by overgrazing, climate change, fragmentation / isolation of its habitat, and collection of its larval hostplant (Hoyle & James, 2005).

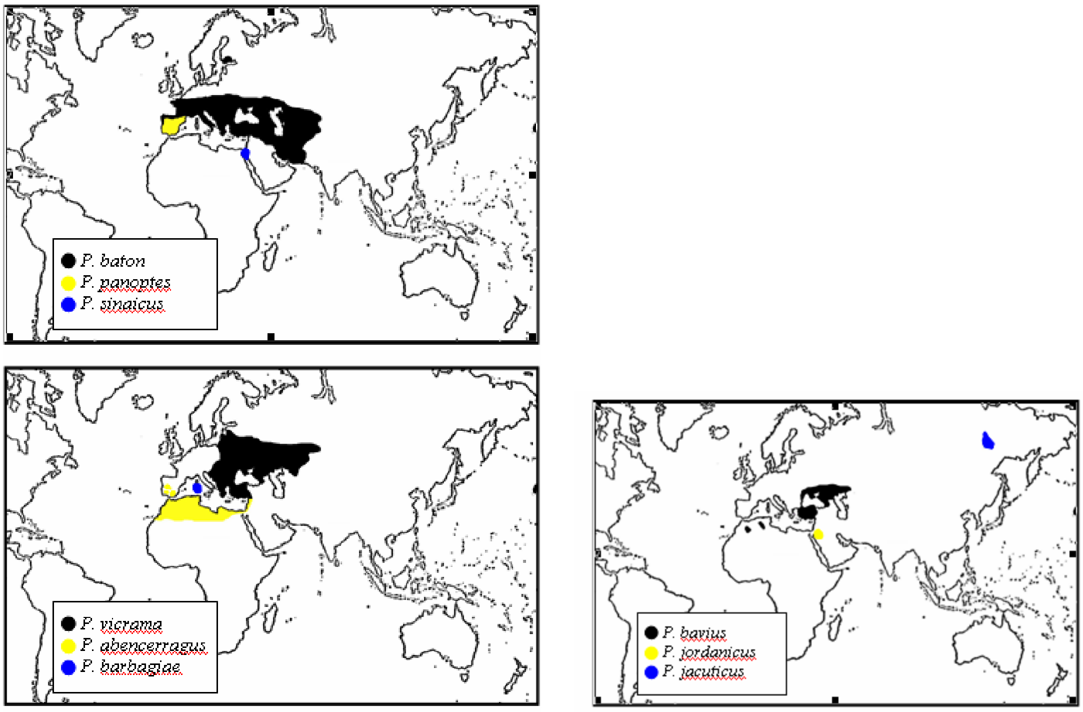

Fig. 2 Distribution of species in the genus *Pseudophilotes*

Table 1 Summary of articles relating to species in the genus *Pseudophilotes*

Species	Summary of subject matter	Reference
Pseudophilotes spp. (*baton*, *vicrama*, *abencerragus, bavius*)	Erecting the genus	Beuret (1958)
P. baton	Description of new species	Bergstrasser (1779)
	Behaviour, ecology (new host plant identified)	Nel (1985)
	Distribution (Hautes-Vosges, France)	Pierrat (1986)
	Biology, conservation (Finland)	Väisänen *et al.* (1994)
	Conservation (Finland)	Marttila *et al.* (1997)
P. vicrama	Description of new species	Moore (1865)
	Distribution (Kos, Greece)	Olivier (1998)
	Conservation (Greece; general)	Grill (2003)
P. abencerragus	Description of new species	Pierret (1837)
	Taxonomy	Agenjo (1984)
	Taxonomy (new sub-species)	Weiss (2000)

P. bavius	Description of new species	Eversmann (1832)
	Behaviour, ecology	Weiss (2000)
P. sinaicus	Description of new species	Nakamura (1975)
P. jacuticus	Description of new species	Korshunov & Viidalep (1980)
P. barbagiae	Description of new species	De Prins & Poorten (1982)
	Behaviour, ecology, distribution	Leigheb & Cameron-Curry (1998)
	Morphology, laboratory rearing	Leigheb *et al.* (2000)
	Conservation, endemism	Grill (2003)
P. panope	Description of new species (assigned specific rank)	Higgins & Riley (1980)
	Taxonomy, distribution	Higgins (1982)
	Behaviour, ecology	Morris (1995)
P. jordanicus	Description of new species	Benyamini (2000)

After the initial description of *Pseudophilotes sinaicus* by Nakamura (1975), very few additional observations have been reported and its status was unknown. In 2001 I discovered 25 local populations, each one occupying a discrete patch of thyme (James *et al.*, 2003). These are likely to represent all, or a large proportion of its worldwide distribution and my estimates suggest the combined total population size in 2001 was approximately 3,000 adults.

I studied these local populations during spring and summer 2001 to 2003, with the main objective of discovering the precise habitat requirements of the species and determining why the butterfly was not present in all of the thyme patches that were located (James *et al.*, 2003; James, 2006b). A second objective was a detailed study on the ecology and behaviour of the larvae and adults in one of the largest local populations (ca. 500 adults: James, 2006c), and I report some of the less obvious of these findings and observations here.

MATERIALS AND METHODS

Study site: In 2002 I studied intensively a local population of butterflies in Farsh Shoeib, a 13,600 m2 patch of thyme bordered on all sides by steep, bare cliffs, close to Gebel Safsafa on the Mt. Sinai massif. The study patch contained 1,212 thyme plants; all were accurately mapped relative to a GPS point (Garmin GPS 12 MAP, + 5 m) using a tape measure and compass. The phenology of each thyme plant was measured weekly: five inflorescences were randomly selected from the most advanced area of the plant and their phenology scored on a 0-7 scale (0 = 100% pre-bud, 7 = >50% seed heads/flowers over: James, 2006b,d). The average of these scores represented the phenological state of the plant. Between 10th June and 24th June (after the main adult flight period but whilst inflorescences were still readily observable), the number of inflorescences on each thyme plant was recorded. On small plants (<200-300 inflorescences) this was done by counting each individual inflorescence, but on large plants it was estimated by taking the average number of inflorescences counted in four randomly placed 10 cm x 10 cm quadrats and extrapolating.

Survey of butterflies: A mark-release-recapture (MRR) study was carried out over 97 consecutive days, from 8th April (the date the first adult was seen) to 13th July (the date the last adult was seen) in Farsh Shoeib; the actual study period extended 7 days either side of this period to make sure that no butterflies were present in the study patch before or after these dates. Every day from dawn to sunset, two field workers actively searched for butterflies whilst continuously walking at a slow pace a pre-determined route that passed every thyme plant and covered the area of the thyme patch. Baton Blues roosted on plants at the edge of the study site and on the tips of dead stalks/dry flower heads, and were easy to find. Thus a search was also made every dawn and dusk at their potential roosting sites. When unmarked butterflies were seen, their location (closest thyme plant), sex, and behaviour were recorded. They were then caught using a butterfly net, given an individual mark on the underwing(s) using permanent marker pens, measured (length of forewing from base to apex), and then released at the point of capture. Newly eclosed adults were easy to identify as they were always near the top of a thyme plant, in pristine condition with particularly bright orange markings, and unable to fly. To reduce the effects of handling no butterfly was caught more than once: when previously marked individuals were seen they were identified using close-focus binoculars (i.e. a 'recapture' was actually a 're-sighting'), and their location and behaviour noted. There were no detectable effects of handling (James, 2006c). To assess the level of disturbance/mortality occurring at night, on 5 separate evenings the exact location of 20 roosting butterflies was noted and these individuals were searched for the following dawn. Because of the intensive marking effort, it is believed that the majority of butterflies were marked at or close to their minimum possible age.

Table 2 Species in the genus *Pseudophilotes*. Doubtful data are preceded by a question mark. §Degree of myrmecophily (see Fiedler 1991): 2 = moderately myrmecophilous (ant associations regularly occur at least with part of the larvae), 3 = steadily mymecophilous (almost all older larvae are nearly permanently attended by ants); ** = larvae with Dorsal Nectary Organ and Tentacular Organ, * = Dorsal Nectary Organ only; symbols and numbers in parenthesis refer to hypothetical assignments based on closely related species. Much information was taken from the 'Finnish IT Centre for Science'¶ and references therein

Species	Habitat & elevation	forewing length (mm)	Lifecycle	Foodplant(s)	Myrmecophily§	Status	Sources
baton Bergstrasser, 1779	sandy meadows, dry slopes, & rocky gullies; to 2000 m	10 - 12	bivoltine (low elevation) univoltine (high elevation) overwinters as pupa	*Thymus* spp. *Satureja* spp. *Mentha* spp.	2** *Lasius* spp. *Myrmica* spp.	rare; locally endangered	Nel (1986); Munguira et al. (1993) Väisänen et al. (1994); Tolman & Lewington (1997); Marttila et al. (1997)
vicrama Moore, 1865	dry meadows, rocky hills, clearings; to 2000 m	10 - 12	bivoltine overwinters as pupa	*Thymus* spp. *Satureja* spp. ?*Mentha* spp.	(2)**	threatened in Europe	Larsen (1980); Grill (2003) Tolman & Lewington (1997)
abencerragus Pierret, 1837	dry, rocky slopes; to 2500 m	10.1	bivoltine (N. Africa) univoltine (Iberian peninsula)	*Thymus* spp. *Salvia* spp. *Medicago* spp. *Cleonia lusitanica*	(2/3**)	-	Mattoni (1980); Tennant (1996); Tolman & Lewington (1997)
bavius Eversmann, 1832	rough ground & meadows; 600 - 1800 m	14	univoltine overwinters as pupa	*Salvia* spp.	2*(*)	vulnerable	Munguira et al. (1993); Tennant (1996); Tolman & Lewington (1997)
sinaicus Nakamura, 1975	dry valleys (wadis); 1500 – 2300 m	9.5	univoltine overwinters as pupa	*Thymus decussatus*	2/3** *Lepisiota* spp.	endangered	Nakamura (1975)
jacuticus Korshunov & Viidalep, 1980	screes, dry meadows & slopes; 500 – 1500 m	-	?univoltine	-	-	-	
barbagiae De Prins & Poorten, 1982	arid, rocky, south facing slopes; >1000 m	11.5	univoltine overwinters as pupa	*Thymus herba-barona*	(2**)	vulnerable	Munguira et al. (1993); Leigheb & Cameron-Curry (1996); Leigheb et al. (2000); Grill (2003)
panope (Eversmann, 1851)	700 – 2000 m	10.8	bivoltine	*Thymus* spp. *Satureja* spp.	(2**)	-	Higgins & Riley (1980); Higgins (1982); Morris (1995); Tolman & Lewington (1997)
jordanicus Benyamini, 2000	sandstone depressions & slopes; 1750m	10	-	?*Satureja nabateorum*	-	-	Benyamini (2000)

RESULTS

Habitat: The Sinai Baton Blue is very local due to its dependence on Sinai Thyme (Plate 1a-c). The plant is patchily distributed, growing only in open areas ('farshes') and dry valleys ('wadis') above ca. 1,500 m and containing relatively well-developed soil. Where it does occur, thyme is often the most abundant species of plant. Forty-one patches of thyme were located in the mountains around the town of St. Katherine (Plate 1d); these were well delimited from the surrounding environment and usually bordered on one or more sides by steep, bare cliffs: patches were separated from one another by ridges, if not mountains. The size of each patch was measured by estimating the amount of thyme (surface area) present (James *et al.*, 2003). Occupied patches varied in size from ca. 5 m² to ca. 400 m², and in altitude from 1,875 to 2,220 m. Butterflies preferred sheltered patches containing relatively large thyme plants and a high diversity of other plant species (James *et al.*, 2003) (Plate 1c). Grazing of thyme by goats and its over-collection for medicinal purposes threaten the patches (Hoyle & James, 2005).

During winter the mountains (up to 2,650 m) are covered in snow, and temperatures on the highest peaks regularly fall below –10 ºC; snowmelt seeps into the ground and provides the area with almost all its water during the dry spring, summer and autumn. The area is classified as arid and in an average year receives <100 mm of precipitation (Greenwood 1997). Between 1st April and 20th July 2002 no rain at all fell in Farsh Shoeib and the temperature ranged from 0 to 35 ºC.

Description of immature stages

Eggs: The small eggs (approximately 0.5 mm in diameter) are pale bluish-white when laid, later becoming white (Plate 1b). They have a generally spherical shape, though are considerably flattened at their top and base. The egg surface is covered with triangular and rectangular cells which are separated by low ridges that meet to form round-topped short projections; the micropyle is slightly depressed and consists of numerous small cells that are symmetrically arranged around the centre (Plate 2a) (Nakamura 1975). Larvae hatch a few days after oviposition (mean number of days to hatching = 4.3 ± 0.6, range 3.0-11.0, n = 17). The main threat to eggs probably comes from goats inadvertently eating them when they graze on thyme buds.

Larvae: I did not breed the Baton Blue in the laboratory, so it is very difficult to identify how many instars the larvae go through and how long each stage lasts. However, field observations suggest larval development takes approximately 21 days, and that there are probably five different size classes. Most lycaenid butterflies have four or five larval instars (Elmes *et al.* 2001), and so I assume each size class that I observed represents a different instar: LI, LII, LII, LIV & LV. Newly hatched larvae (LI) are absolutely tiny (<1 mm long), with a dark brown head and pale body. They eat their way out of the egg through its top surface, but do not eat the rest of the eggshell (Plate 2a). Because they are so small they are difficult to observe under natural conditions. However, on three occasions a newly hatched larva was found inside a thyme bud, having entered it through a small hole on its surface. These larvae presumably ate their way into the bud and continued feeding on it from within (Plate 1b). The second size class of larvae (LII) (Plate 2b) are pale green in colour and covered in long white setae; they are 2-3 mm long. LIII are yellow-green with a pale subspiracular line, ca. 5 mm long, and covered in long white setae (see Plate 4b). LIV (Plate 2c) and LV (Plate 2d) share the same general phenotype: body bright green with a double-row of yellow-green markings along the dorsal ridge and a yellow subspiracular line, a thick cuticle, and a small black head that can be retracted under a well-developed pro-thoracic plate; they are wholly covered in short white setae. Fully developed larvae (ca. 8-9 mm long) are larger than LIV (ca. 7-8mm long) and in some individuals the double-row of yellow-green markings along the dorsal ridge encloses a dull-red line and a line of similar colour runs above the yellow marked subspiracular line.

Larvae were only ever observed feeding on Sinai Thyme. They were never observed moving between thyme plants and hence are likely to be restricted to the plant on which they hatched. Young larvae (LI and LII) feed only on thyme buds, whereas more fully developed larvae (LIII and LIV) feed on thyme buds and flowers; larval feeding damage on buds is very characteristic (see Plate 1b). They feed actively throughout the day and night and were often observed feeding at the top of a plant in the middle of the day when temperature and insolation are at their greatest. There is some evidence of intraspecific competition among larvae: survival rate (egg to adult) was influenced by the density of larvae on a plant (expressed as the number of eggs per plant) (James, 2006b).

The Sinai Baton Blue is a facultative myrmecophile (James, 2006b). Two species of ant were seen tending larvae: *Lepisiota obtusa* and *Monomorium niloticum*. Larvae of all stages were tended by *L. obtusa* (Plates 1b, 3a) and (to a lesser extent) *M. niloticum* (Plate 3b). Seventeen larvae (LIII and LIV) were observed for a total of 87.5 hours: on average each larva was tended 71% of the time (by 1-6 ants). LIV and LV both possess two ant-associated structures; LIII probably possess these structures (Fiedler 1991), but this is yet to be confirmed. The dorsal nectary organ (Plate 3a,c) is located on the dorsum of the seventh abdominal segment and presumably (as is the case in related species: Fiedler 1991; Pierce *et al.* 2002) secretes droplets of simple sugars and amino acids when stimulated by ants via antennation (Plate 3a,b); these are consumed by the attendant ants. The Tentacular Organs (Plate 3b-d) are a pair of epidermal tubes located on either side of the dorsum on the eighth abdominal segment; these are everted when larvae are stimulated by ants or whilst they are crawling about. They are believed to produce volatile secretions that attract and alert attendant ants if a caterpillar is alarmed (Fiedler 1991; Pierce *et al.* 2002).

Larvae are heavily preyed upon when encountered by another species of ant, *Crematogaster aegyptiaca* (Plate 4a,b). This ant appears to be very influential to the local distribution of the butterfly because in areas where it is found, no butterflies survive (James, 2006b). Due to their dependence on thyme buds, larvae risk being eaten/disturbed (they readily drop off an inflorescence if it is shaken) when goats are grazing in the area. I devoted much time to observing larvae, but on only a few occasions saw parasitoids in the vicinity of larvae, and never saw these attacking the larvae. This suggests that rates of larval parasitoid attack are extremely low. On one occasion I observed a larva apparently infected by fungus (Plate 4c).

Pupae: Pupation takes place a few centimetres below the surface of the leaf-litter/soil beneath a thyme plant. It is in this stage that the Baton Blue survives the autumn, winter and early spring – when temperatures regularly drop below freezing and snow is common. It is possible that in drought years pupal diapause can be prolonged, enabling adults to postpone their eclosion for a year or more while waiting for conditions to improve, but this has yet to be confirmed (James, 2006c). Pupae are a uniform light brown with no additional patterning; they are short and blunt (mean length = 6.1 mm ± 0.3, n = 8; mean maximum width = 2.1 mm ± 0.1 , n = 8) (Plate 4d).

Adults and adult size: For a complete description of adults, see Nakamura (1975). In males, the upperside of both wings is brilliant blue (Plate 5a) whereas in females both wings are dark brown (Plate 5b); both sexes have a distinct black bar and the end of the cell of both wings, and a black distal margin (broader in males). The underside of the wings is identical in both males and females (Plate 5c). Figure 3 shows the frequency distribution of male and female sizes (length of forewing). In 2002, the size of 430 individuals (218 females and 212 males) was measured: females had significantly longer forewings than males (mean length females =

9.7 mm ± 0.1, males = 9.4 mm ± 0.1; $t_{428} = 3.0$, $p < 0.01$) (Plates 5c, 6a). It is common for female butterflies to be larger than males (in most British species females are larger and heavier than males: Brakefield & Shreeve 1992). Size was not correlated with day of eclosion in the season for either sex (males, $r_s = 0.06$, n = 191, ns; females, $r_s = 0.13$, n = 182, ns). The smallest individual measured, a male caught in 2003, had a forewing length of 6.25 mm.

Larsen (1990) suggested that the Sinai Baton Blue, "can compete for the title of the world's smallest butterfly." García-Barros (1996, 2000) provides data on the adult size of 1,183 butterfly species in 448 genera, but does not include the Sinai Baton Blue. Using his measure of size (the median of male and female forewing lengths), the Baton Blue is joint sixth smallest butterfly (median forewing length = 9.5 mm) with *Chilades trochylus*, a lycaenid that also occurs in the mountains around the town of St. Katherine. The five smaller species are also lycaenids: *Brephidium exilis* (8.5 mm), *B. metophis* (9.0 mm), *Philotiella speciosa* (8.5 mm), *Actizera stellata* (9.0 mm), and *Paralucia spinifera* (9.3 mm). Some of his data are based on measures taken from just one or a few individuals, and so (unlike my data for the Baton Blue) do not necessarily represent the true extent of variation in adult size (García-Barros: personal communication). Hence, on the basis of this work at least, the Sinai Baton Blue is indeed one of the smallest butterfly species in the world. My smallest individual (6.25 mm) is substantially smaller than any of these medians and therefore there is a real possibility that small individuals are the smallest.

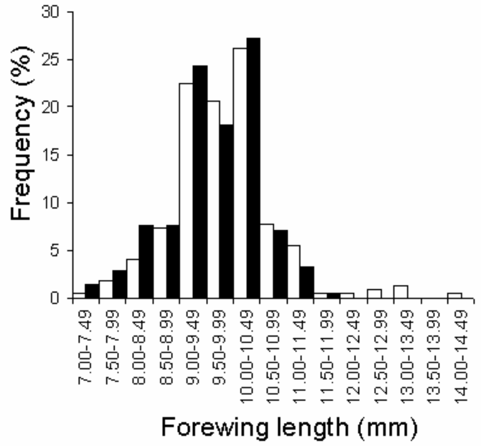

Fig. 3 Frequency distribution of size of individuals caught in Farsh Shoeib in 2002

Assuming the number of eggs laid in Farsh Shoeib in 2001was the same as the number laid in 2002 (estimates of the adult population size in these two years were similar), then survival from egg to adult during 2001-2002 was approximately 0.07. This is almost exactly the same as studies on eight species of British butterfly (mean mortality rate = 94%: Warren 1992). However, the level of mortality is likely to be related to a number of variables, such as the density of larvae (especially given the evidence of intraspecific competition during the larval stages) and weather conditions, and so there is likely to be considerable variation between years and between sites. Indeed, assuming the low numbers of butterflies caught in 2003 (James, 2006c) was due to mortality (and not extended pupal diapause), then mortality in Farsh Shoeib from egg (in 2002) to adult (in 2003) was 99.1%.

Adults occur as a single generation (univoltine) and are on the wing from late March to late July (in 2001, the earliest record was 29th March, and the latest record was 19th July); the precise date varies from year to year (unpublished results) and is also likely to vary from site to site. Timing of the adult flight period corresponds to the phenology of Sinai Thyme (Fig. 4) (James, 2006c,d). Newly eclosed individuals crawl to the surface of the soil and then up to the top of the thyme plant, where they remain (often for several hours) until their wings have expanded and dried (Plate 6b). Most butterflies were first seen during the middle of the morning and probably eclosed in the first half of the morning (Fig. 5), and males did not eclose significantly earlier or later in the day than females (Kruskal-Wallis test, ns). The cue Sinai Baton Blues use to eclose is unknown, but it is likely to involve environmental variables (e.g. soil moisture, temperature, photoperiod etc.) which reliably indicate the presence of thyme buds and flowers. An attempt to re-establish *Maculinea arion* (a related butterfly which also oviposits on thyme buds) failed because the introduced population emerged two weeks later than the main flower-bud period of *Thymus* (Thomas & Elmes 2001). The experiences of immature stages might also affect the timing of eclosion (Leimar 1996). Pratt and Ballmer (1993) demonstrated that the length of pupal diapause in *Euphilotes mattoni* and *Philotiella speciosa* ensured their adult flight periods coincided with the blooming period of their respective hosts at various elevations.

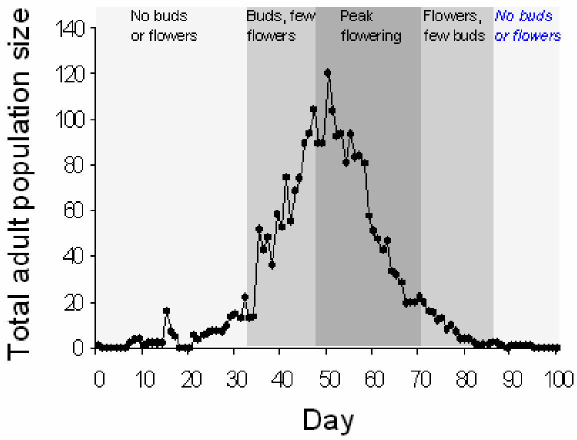

Fig. 4 Phenology of the adult flight period of the Sinai Baton Blue relative to the phenology of Sinai Thyme (different shades of grey)

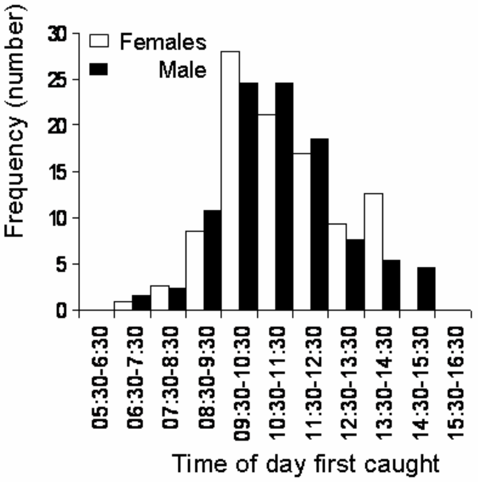

Fig. 5 Time of day (Egyptian time, GMT + 2) that butterflies eclosed. Individuals were caught as they sat on a thyme plant waiting for their wings to expand and dry, so the precise time they eclosed will be 0-2 hours before times recorded

Despite Nakamura's (1975) speculation about a partial second brood, only a single generation was observed in 2001, 2002 and 2003. It is likely that butterflies reported in late July / early August, are old individuals that emerged at the end of the (prolonged) flight period. There is an indication of protandry: significantly more males were recruited during the early flight period than females (James, 2006c). The emergence of males before females is a common strategy in many butterflies and other insects. It could be the result of sexual selection on males to maximise matings, or on females so that the time for oviposition is not reduced (Wiklund & Fagerström 1977; Fagerström & Wiklund 1982). Assuming there is a trade-off between short development time and large adult size (Wiklund *et al.* 1991), protandry may also explain the smaller size of males compared with females, but this trade-off has been disputed (Nylin *et al.* 1993).

The length of time that individuals spent in Farsh Shoeib depended on their sex and when they eclosed (James, 2006d). Most individuals were resident for 3-6 days, and this probably represents their life-span. The maximum residency was 24 (male) and 18 (female) days. There was no correlation between residency and size among individuals first caught on the day that they eclosed (males $r_S = 0.15$, $n = 130$, ns; females $r_S = 0.10$, $n = 118$, ns). Predation is probably the main source of adult mortality: spiders (Plate 6c), praying mantids, birds (especially Scrub Warblers, *Scotocerca inquieta*), and particularly lizards (family Agamidae) (Plate 6d), were all seen attacking Sinai Baton Blues.

Butterflies were active between 0800 to 1600 h (local time), with a peak of activity occurring around midday and lasting for about two hours (Fig. 6); males became active earlier than females (Kruskal-Wallis test, $p < 0.01$) but activity in both sexes ceased at approximately the same time. During the cool, bright weather that typified most mornings in Farsh Shoeib, one would expect small individuals to be active earlier because of their ability to reach optimal body temperature more rapidly (Shreeve 1992); this might explain why males (which are generally smaller than females) became active earlier. In addition to the thermoregulatory restrictions imposed on a butterfly's flight, males are probably also under a selection pressure to become active early in the morning as this would increase their search time for newly emerged (virgin) females (see below). There was a significant negative correlation between the time of day that individuals first became active and the date (males $r_s = -0.23$, $n = 227$, $p < 0.001$; females $r_s = -0.31$, $n = 251$, $p < 0.001$). This is probably because daily temperature increased steadily through the adult flight period (minimum daily temperature $r_s = 0.60$, $n = 97$ days, $p < 0.001$; maximum daily temperature $r_s = 0.78$, $n = 97$ days, $p < 0.001$), and because the sun was rising earlier (74 out of 97 days of the flight period occurred before the summer solstice).

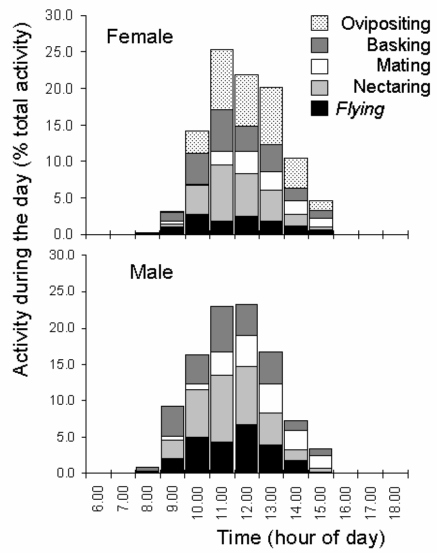

Fig. 6 Activity patterns of butterflies in Farsh Shoeib in 2002 (females = 1342 observations, males = 1193 observations).
All individuals observed but not carrying out one of the activities shown, were roosting

Males were seen flying more often than females ($\chi^2_1 = 31.3$, $p < 0.001$), presumably because in addition to locating thyme flowers from which to take nectar, males also actively searched for newly eclosed females. Identifying territoriality is very difficult, but observations suggest that males may be at least partially territorial: at low male densities male-male interactions (e.g. spiralling flights) were commonly witnessed, but these behaviours were rare at high male densities.

Mating: Males were observed 'patrolling' areas of suitable habitat for newly eclosed (virgin) females, and they were often seen spending more than 10 minutes flying close to and around an individual thyme plant, carefully examining it for females. There is no courtship ritual, so when a female is found the male lands next to her and tries to initiate copulation immediately. Females that have already mated (or that do not want to mate for some other reason) refuse mating by curling their abdomen upwards, spreading their wing out, and walking around the plant (Plate 7a); they fly away if the male becomes too persistent. Patrolling males are apparently unable to determine the sex of an individual if it has its wings folded (so only its underside is visible): a basking male must flash its wings open to signify its sex. Furthermore, males were regularly seen approaching individuals of different species (notably *Lampides* *boeticus*), though it is unclear whether they mistook these individuals for female Baton Blues, or were acting territorially. Mating (Plate 5c) usually lasts for over an hour (mean = 79 minutes ± 16, n = 8 mating pairs), and always terminates with the female pulling the male around the plant for up to 20 minutes prior to uncoupling – apparently in an attempt to detach herself. This characteristic behaviour might indicate a form of mate-guarding, males trying to maximise their chance of fertilising the eggs.

In 2002, 78 different pairs of butterflies (120 different individuals) were observed mating: 32% of all females and 23% of all males were seen mating at least once. In a previous study (James, 2006c), I estimated that 84% of the population in Farsh Shoeib was captured using the method described here, and on average only 15% of the estimated population was missed on a typical day's recording. It is very unlikely that any female remains unmated, so given the comprehensive nature of the MRR study and the long copulation period, it is interesting that only 32% of all females were seen mating. During mating, butterflies are particularly vulnerable to attack by predators and so probably try to remain concealed by staying still and keeping their wings folded (so only the cryptically coloured / patterned underside is visible), and this behaviour may explain the relatively low numbers recorded mating. Females that mate after they are able to fly may choose to mate in a safe / hidden location away from thyme plants, or the male might carry the female to a secluded spot where the pair can remain unmolested (Smith 1984); this would also reduce their chances of being recorded.

Although it is unlikely that all mating pairs were observed, a reasonably high proportion of individuals were seen mating, meaning the data are adequate for an analysis of relative mating success. The distribution of mating frequency for both sexes in shown in Figure 7. Most females mate just once: only 9% (n = 7 females) of mating pairs involved a female that had been seen mating before, and none of these females mated more than twice. This suggests that one mating is usually enough for a female to fertilise all her eggs. In contrast, males seem to mate as many time as possible: 55 of the 78 mating pairs (71%) involved a male that had mated before or would mate again, and three males were recorded mating four times. Females were significantly younger than males when they mated for the first time (independent samples test, $t_{118} = 7.4$, $p < 0.001$) (Table 3). Most females mated for the first time the day they eclosed (65%), and almost all of them (89%) had mated for the first time before they were two days old. This also meant that the number of mating pairs observed had a normal distribution through the season, following the female recruitment curve. As would be expected, females mating a second time were significantly older than females mating for the first time (independent samples test, $t_{76} = 5.5$, $p < 0.001$), and they were also larger (independent samples t-test, $t_{69} = 1.99$, $p < 0.05$) (Table 3). Because of the small number of females observed mating twice, conclusions about multiple mating in females are speculative. However, the relationship between female size and mating frequency has been found in another (unrelated) butterfly species, *Pieris napi* (Bergstrom *et al.* 2002). It is also possible that old females simply require a second mating to fertilise their remaining eggs.

Most males (69%) were two days or older when they mated for the first time, and there was a significant positive correlation between the age of males and the number of times they had mated ($r_s = 0.53$, n = 78, $p < 0.001$).

Virgin females mated very close to the plant where they emerged; indeed, 34 females (47%) mated before they took their first flight. Females that mated a second time were not significantly further from their point of first capture than females mating for the first time (independent samples test, $t_{76} = 1.2$, ns), and this was also true for males; there was no sex difference in this distance either (independent samples test, $t_{23} = 0.3$, ns). Among virgins, the mean distance they were seen mating from the point of first capture (usually the point of eclosion) was significantly less in females than in males (independent samples test, $t_{118} = 2.1$, $p < 0.05$) (Table 3).

Large males have been shown to have a mating advantage in butterfly species in which females mate just once, and also in species exhibiting female polygamy (e.g. Wickman 1985; Wiklund & Forsberg 1991). To understand if size (here measured as forewing length) influenced mating success (number of matings) in male Baton Blues, the mean size of males observed mating at least once was compared with the mean size of males not observed mating: there was no significant difference (independent samples test, $t_{210} = 1.1$, ns) (Table 3). Similarly, there was no significant difference between the size of singly and mutiply mating males (independent samples test, $t_{47} = 0.0$, ns). Males generally mated when they were two or more days old. To disentangle the effect that age might have on mating success, the mean size of males mating at least once was compared with the mean size of males not observed mating but alive (present in the study site) for at least two days: once again there was no significant difference (independent samples test, $t_{126} = 0.9$, ns).

Table 3 Size, age, and distance moved from point of first capture of individuals observed mating

	Females			Males				
Total number of times observed mating (*n* = no. individuals)	0 (*n* = 148)	1 (*n* = 64)	2 (*n* = 7)	0 (*n* = 163)	1 (*n* = 31)	2 (*n* = 10)	3 (*n* = 5)	4 (*n* = 3)
Forewing length (mm)	9.6 ± 0.1	9.8 ± 0.1	10.3 ± 0.3	9.4 ± 0.1	9.5 ± 0.2	9.3 ± 0.2	10.3 ± 0.2	9.0 ± 0.6
Age (days from 1st capture)		0.5 ± 0.1	3.1 ± 1.0		3.1 ± 0.4	5.5 ± 0.5	7.5 ± 1.3	7.7 ± 2.9
Distance from 1st capture (m)		15.4 ± 5.6	44.9 ± 17.3		32.9 ± 6.9	43.2 ± 10.5	36.3 ± 12.1	6.3 ± 0.7

Thus, mating success in males seems to be determined by their residency, and not size. There are many potential explanations for male mating success and female mate-choice (Rutowski 2003) that cannot be assessed using the data of this study. For example females might be selecting males based on their appearance in ultraviolet or polarised light (Rutowski 1998; Sweeney *et al.* 2003), and life-history theory may be important (Fischer & Fiedler 2000); indeed even if female mate-choice was based on size, they are not necessarily using forewing length to assess this: in the butterfly *Bicyclus anynana*, wing size is not a signal for female mate choice (Breuker & Brakefield 2002).

Oviposition: First-instar larvae are absolutely tiny, cannot move far from where they hatched, and only feed on thyme buds; later instars feed on thyme buds and flowers and are almost certainly restricted to the plant on which they hatched. Thus selecting the correct site for oviposition is critical for larvae to access essential resources. Female Baton Blues were only ever seen ovipositing on Sinai Thyme (n = 540 occasions), laying their eggs singly on the inflorescences (n = 336 observations) (Plates 1b, 2a, 7b). Among those inflorescences searched for eggs and on which eggs were found (n = 693 inflorescences), 88% contained only one egg, 10% two eggs, and 2% three or more eggs; the maximum number of eggs seen on an inflorescence was five. The fact that larvae are apparently restricted to one plant would increase the potential for larval competition for resources, and there is evidence that intraspecific competition exists, and that it is important for larval survival. Thus, it would benefit females if they could detect eggs (or larvae) on a thyme plant / inflorescence. In some species, chemical cues are used to detect eggs previously laid on the larval food plants (Dempster 1992; Schoonhoven *et al.* 1990), likewise visual cues may enable females to avoid hostplants containing eggs (Rutowski 2003). The preponderance of inflorescences containing only a single egg, suggest that Baton Blue females possibly can detect other eggs, and preferentially select inflorescences without eggs for oviposition, but such patterns might just as feasibly be the result of chance.

The phenology of inflorescences selected for oviposition was determined by following gravid females. An 'oviposition event' occurred when the female curled her abdomen and started to probe an inflorescence (Plate 7b); such behaviour did not always result in the laying of an egg. After the female left the inflorescence, its phenology was assessed and the presence of an egg recorded. Of 370 'oviposition events' recorded, 228 (62%) resulted in an egg being laid. One hundred and seventy-three (76%) of these eggs were on inflorescences just starting to bud (Fig. 8; Plates 1b, 7b). The proportion of oviposition events that resulted in an egg varied depending on the stage of development of the inflorescence being probed (Fig. 8). In addition to locating a suitable site for attaching her eggs, sensory cues from the ovipositor probing probably enable Baton Blue females to assess the stage of development of the inflorescence. At the range of a few centimetres, females of the butterfly *Battus philenor* use leaf shape to select oviposition sites (Rausher 1978), and female butterflies of other species are attracted to the colour of oviposition substrates (Rutowski 2003).

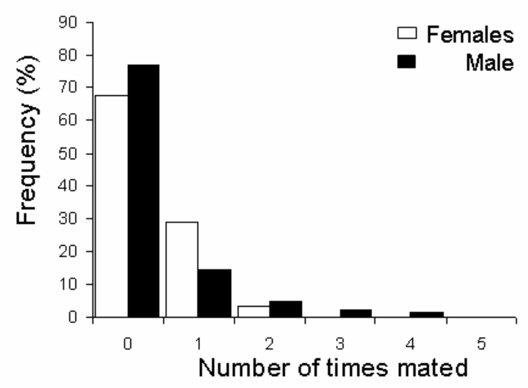

Fig. 7 Frequency distribution of the number of times an individual was observed mating

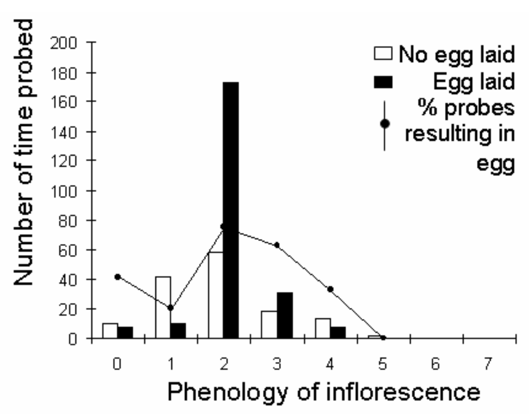

Fig. 8 Phenology of thyme inflorescences used by females during ovipositing behaviour. An 'oviposition event' occurred when a female 'probed' an inflorescence with her abdomen; this did not always result in an egg being laid.

Thus, female Baton Blues are restricted to ovipositing on thyme plants that contain inflorescences in bud. However, within a patch, when all thyme plants that had buds during the adult flight period were surveyed for eggs, egg distribution was found to be non-random: only 35% (n = 287 plants) contained eggs. To understand why ovipositing females preferred some plants and not others, four variables describing thyme plant quality (plant height, condition, green surface area, and number of inflorescences: see James, 2006b) were entered into a logistic regression to explain the occurrence of eggs: only the number of inflorescences entered the model, accounting for 32% of the variation ($b = 0.020 \pm 0.002$, $p < 0.001$). Logic suggests that plants with more oviposition sites (inflorescences) should accumulate more eggs, but the mean number of eggs per inflorescence also increases with the number of inflorescences per plant ($r_s = 0.592$, $p < 0.001$, $n = 817$ plants). Selecting thyme plants with many inflorescences might be a way of reducing the probability of intraspecific competition.

In butterflies that lay clutches of eggs, clutch size has been shown to increase with hostplant quality, e.g. *Battus philenor* females lay larger clutches on plants that contain more edible foliage (Pilson & Rauscher 1988).

In 2002, I estimated that 6,703 eggs were laid in Farsh Shoeib by an estimated 261 females (James, 2006b,c). Thus the average number of eggs laid per female was 26. This (very rough) estimate is similar to *Pseudophilotes barbagiae*, which in captivity lays 20-30 eggs in 2-4 days (Leigheb & Cameron Curry 1998). However, there is bound to be a great degree of variation in the number of eggs laid by individuals in the site, for example as a result of their residency. When I dissected a female of unknown age, I found 36 mature eggs and the remains of six other eggs (that she had presumably already laid).

Feeding: Both sexes feed throughout the day, taking nectar almost exclusively from Sinai Thyme when it is in flower (Plate 7c): of 708 recorded feeding bouts, 92% were on thyme flowers and 4% on flowers of *Globularia arabica* (Globulariaceae). The use of these flowers was separated temporally: all recorded feeding bouts on *G. arabica* occurred prior to 11th May, before Sinai Thyme had started to flower. A further three species of flower were used occasionally: *Tanacetum santalinoides* (Compositae), *Teucrium polium* (Labiatae), *Origanum syriacum* (Labiatae). In both males and females, there is a peak in feeding activity between 1100 and 1200 hrs (Fig. 6) suggesting that this is when Sinai Thyme secretes its nectar.

Roosting: Individuals were selective in where they roosted. They chose the tips of dead stalks/dry flower heads of plants at the edge of the study patch (Plate 7d), and because steep cliffs enclosed the study patch, these plants were often high up its sides. This indicates that they move up to find roosting sites, but the plants chosen also tended to be on slopes that faced west (69%) and therefore remained in the afternoon sun the longest. This might be an important consideration when selecting a roosting site: roosting on plants located on the sides of cliffs, mean that butterflies probably avoid the generally lower temperatures and more humid conditions of the wadi floor and, compared with plants found there, are exposed to the sun until later in the afternoon. This means that they remain potentially active for longer, and also reduces the amount of time that they are exposed to predators when they are inactive.

Of 897 butterflies recorded roosting, 68% were on *Jasonia montana*, 13% on *Tanacetum santalinoides*, 8% on *Artemisia herba-alba*, and 8% on *Pterocephalus sanctus*.

Mortality at night when the individuals are roosting is probably negligible: only one roosting butterfly on the 100 occasions (20 individuals x 5 nights) failed to be seen again in exactly the same location the following morning.

Conservation: In addition to a metapopulation study, an important part of my project was the conservation of the Sinai Baton Blue butterfly. This entailed providing the St. Katherine's Protectorate Management Unit (SKPMU) with the scientific information necessary for it to develop a conservation management plan for the species. It is therefore very rewarding to see that my research is now being applied in a truly practical sense. Using information I provided, the SKPMU prevented grazing in a key area of thyme in 2003, greatly benefiting the conservation of the butterfly. To avoid potential conflict with the local Bedouin they restricted grazing only for the three months that coincided with the time of year that the butterfly depends on thyme. The scheme was such a success that the Bedouin have agreed not to take their goats to the thyme patch during the same period next year (a 'hilf' = a traditional form of set-a-side that was the norm among the Bedouin when they were semi-nomadic, but has been abandoned since their sedentarization). This agreement enables the conservation of the butterfly to succeed with very little financial / logistical input from the SKPMU. The SKPMU is now aware of the location, size and suitability of every patch of habitat for the Sinai Baton Blue, and they can monitor these patches so that the status of the butterfly can be assessed and resources diverted to their conservation if necessary.

Successful conservation requires that the species in question is properly publicised. This publicity informs and educates the public about the species, and increases their awareness of the threats it faces. Over the last 3 years, I have had numerous articles/photographs of the Sinai Baton Blue published, given many lectures/slide-shows about the butterfly, the area, and my research, and succeeded in making the butterfly a centrepiece in the new St. Katherine's visitor centre (see photograph). I sincerely hope my efforts have helped the Egyptian Environmental Affairs Agency to promote the 'world's smallest butterfly' as a flagship species for the area, and that in turn this goes some way to ensuring its long-term future.

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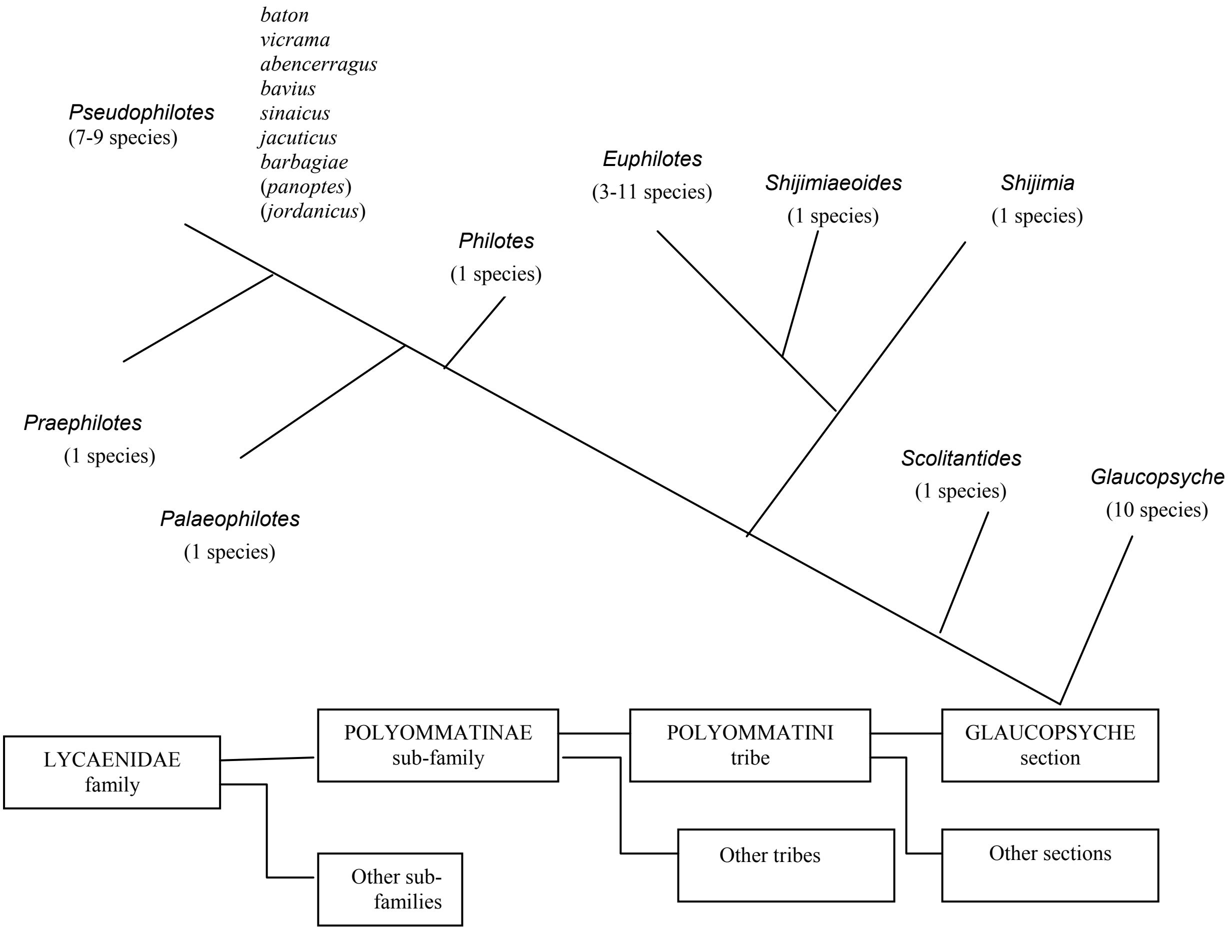

Fig. 1 The higher taxonomy of the genus *Pseudophilotes* and its relationship with other genera in the Glaucopsyche section, constructed from the discussion of Beuret (1958) and Pratt (1994): the diagram is only partly based on a phylogeny supported by characters

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Plate 1
Sinai Thyme (*Thymus decussatus*) in flower
Sinai Baton Blue egg on a thyme bud. The egg has hatched and the young larvae is inside the bud on the right; note the characteristic larval feeding damage on the bud, and the attendant ant (*Lepisiota obtusa*)
A typical patch of habitat: a sheltered area containing large thyme plants
The high mountain region of the St. Katherine's Protectorate in South Sinai. The photograph was taken from the top of the area's highest mountain (Mt. St. Katherine: 2,650 m); the conical peak (right of centre) is Mt. Sinai

Plate 3
(a) Lepisiota obtusa stimulating the Dorsal Nectary Organ (DNO) of a fully developed larvae (LV) via antennation
(b) Monomorium niloticum ants tending LV; note the everted Tentacular Organ (TO) to the left of the head of the bottom ant
(c) SEM (x 65) of the 7th (to the top and right of the picture) and 8th (to the bottom and left of the picture) abdominal segments of LV, showing the position of the ant organs
(d) SEM (x 300) showing the detail of a Tentacular Organ

Plate 4
Crematogaster aegyptiaca ants attacking LIV as it feeds on a thyme flower
(b) C. aegyptiaca carrying LIII in its mandibles
(c) LIV attacked and killed by fungus
(d) Sinai Baton Blue pupae (ca. 6 mm in length) found in soil under a thyme plant

Plate 5
(a) Male Sinai Baton Blue, showing the upperside of the wings; note the brilliant blue wings, broad black distal margin and black cell-end bar in all wings
(b) Female Sinai Baton Blue, showing the upperside of the wings; note the dark brown wings and narrow black distal margin
(c) Mating Sinai Baton Blues (female on left); note that the underside of the wings in both sexes is identical, and the sexual size dimorphism

Plate 6
The size of a male Sinai Baton Blue (minor divisions on the ruler are millimetres)
(b) Newly eclosed male (on thyme plant) with unexpanded wings
(c) Sinai Baton Blue being preyed upon by a spider (unknown species)
(d) Lizards are one of the main sources of adult mortality. This is a female Sinai Agama (Pseudotrapelus sinaitus) – a species regularly seen eating the butterfly

Plate 7
A female refusing to mate with a male; note how she has curled her abdomen upwards to prevent coupling
(b) A female ovipositing on a thyme bud. The red markings on the underside of her forewings were added as part of the identification procedure in a MRR experiment
(c) A Sinai Baton Blue taking nectar from a thyme flower
(d) A typical Sinai Baton Blue roosting site: the butterfly is on the tip of a dead stalk in the centre of a Jasonia montana plant growing on a west facing slope slightly up from the wadi floor