

Integrative evidence reveals the occurrence and parapatric distribution of *Palaeophilotes panoptes* and *P. baton* in southern France

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Abstract

Integrative evidence reveals the occurrence and parapatric distribution of Palaeophilotes panoptes and P. baton in southern France. Biodiversity is dynamic, and faunistics and taxonomy are ever-evolving fields that need constant update and refinement. Thus, species lists and distribution maps may need improvement even for well-studied countries. The current view is that *Palaeophilotes panoptes* is absent from southern France, where only *P. baton* occurs. Using COI mitochondrial genetic sequences, wing morphology, phenology, and conservatively reassigned citizen-science records, we document the presence of *P. panoptes* in a wide area in southeastern Occitanie and delineate a largely parapatric contact with *P. baton* with narrow contact zones. COI data recover three geographically structured lineages (two within *P. baton* and one corresponding to *P. panoptes*). Phenology indicates strict univoltinism in *P. panoptes* versus a partial second generation in *P. baton* at low elevation, while morphology shows consistent population-level trends but no unambiguously diagnostic individual characters. The observed genetic differentiation, spatial distribution and phenological patterns seem to rely on the host-plant specialization of *P. panoptes* on *Thymus vulgaris*, while *P. baton* is more plastic in its trophic preferences.

Key words: *Palaeophilotes baton*, *Palaeophilotes panoptes*, *Pseudophilotes*, DNA barcoding, Citizen science, Parapatric distribution

Introduction

Butterflies of the genus *Palaeophilotes* are small lycaenids typically associated with Lamiaceae, whose anthophagous larvae feed on flower buds. Males usually display bright blue dorsal wings, while females are darker. In Europe, six species are currently recognized within this monophyletic genus (Todisco et al 2018): *P. bavius* (Eversmann, 1832), *P. panoptes* (Hübner, [1813]), *P. baton* (Bergsträsser, 1779), *P. vicrama* (Moore, 1865), *P. barbaggiae* (de Prins & Van der Poorten, 1982), and *P. abencerragus* (Pierret, 1837). The strong morphological resemblance among some species makes their identification particularly challenging, especially since cases of introgression or local hybridization have been documented (Todisco et al 2018). Recent phylogenetic and taxonomic studies have demonstrated that the genus traditionally referred to as *Pseudophilotes* should be treated under the senior and valid name *Palaeophilotes* Forster, 1938 (Lukhtanov et al 2025). We follow this revised nomenclatural framework throughout the present study.

Among these species, the taxonomic status of *P. panoptes* (type locality: Spain) has long been debated. While some

authors historically considered it a subspecies of *P. baton* (type locality: Hanau, Germany) (Mazel 2007), others elevated it to species rank (Vilarrubia 1961, Higgins 1982). More recently, Ebdon et al (2021) confirmed its specific status and estimated its divergence from *P. baton* at approximately 1.97 million years. Although a parapatric distribution of the two species is now generally accepted, their potential contact zones remain poorly documented (Vilarrubia 1961, Olano et al 1989, Redondo 1990, Mazel 2007). Identification relies mainly on external characters (presence of orange spots, coloration of the hindwing underside, integrity of the black fringe lines), as genitalia are generally regarded as indistinguishable (Fernandez-Rubio 1976, De Prins and Van der Poorten 1982, Leraut 2016).

Regarding voltinism, however, these two early-flying species show marked differences. In *P. baton*, the existence of a partial second generation is well documented, except in the highest-altitude populations (Nel 1982, Muñoz Sario 2011, Tshikolovets 2011, Requejo Camiña and Estévez Rodríguez 2013, Lafranchis et al 2015, Leraut 2016, Tolman and Lewington 2021). By contrast, in the Iberian literature, *P. panoptes* is almost unanimously described as strictly univoltine (Vilarrubia 1961, Redon-

do 1990, Muñoz Sariot 2011, García-Barros et al 2013, Requejo Camiña and Estévez Rodríguez 2013, Obregón et al 2014, Vila et al 2018). Reports of a partial second generation exist, although, at least in contact zones with *P. baton*, they are likely the result from misidentifications (Montagud and García-Alamá 2010, Tshikolovets 2011, Lafranchis 2014b, Leraut 2016, Tolman and Lewington 2021). Nevertheless, recent evidence suggests the existence of an occasional partial second generation in the east of Spain (Bernat-Ponce et al 2025).

In southern France, particularly in the departments of Pyrénées-Orientales and Aude, populations with intermediate habitus between *P. baton* and *P. panoptes* have been reported for more than a century. Oberthür (1910) and later Verity (1928) already mentioned mixed forms in Vernet-les-Bains and Corneilla-de-Conflent (Ambollas), while Higgins suggested in 1981 a possible extension of *P. panoptes* into Roussillon (see Mazel 2007). These hypotheses were rejected by Mazel (2007), who, based on a detailed morphological study, concluded that there was unrestricted gene flow between the two entities, treating these populations as subspecies of *P. baton* (*P. baton praepanoptes* in France and *P. b. praebaton* in Spain). This interpretation was later adopted by Leraut (2016) and widely accepted in French national works and checklists (Dupont et al 2013, Lafranchis 2014a). Accordingly, in the current French national taxonomic reference (TAXREF v18.0, Gargominy et al 2025), *Palaeophilotes panoptes* is recognized as a valid taxon but is considered absent from metropolitan France, with all French records traditionally assigned to *P. baton*.

However, the available molecular and ecological evidence calls for a re-evaluation of this interpretation. Rather than revising the taxonomy of the genus, our work aims to document the distributional, ecological and mitochondrial patterns of the *Palaeophilotes baton* / *P. panoptes* complex in southern France within the currently accepted taxonomic framework. More specifically, our objectives are:

- (1) to test whether *P. panoptes* occurs in southern France on the basis of mitochondrial COI data;
- (2) to delimit the distributional boundary and contact zone between *P. panoptes* and *P. baton* in Pyrénées-Orientales and Aude;
- (3) to assess whether morphological, phenological and ecological variation is concordant with the mitochondrial pattern; and
- (4) to evaluate the contribution of conservatively re-assigned citizen-science records to refining the regional distribution of both taxa, as such data are increasingly recognized as a valuable resource in biodiversity research (Mason et al 2025).

To address these objectives, we combine mitochondrial barcoding data (COI), morphological evidence (forewing underside ocelli and wing morphometrics), ecological data (altitude and voltinism), and high-resolution occurrence data from citizen science (faune-occitanie.org and iNaturalist).

Material and methods

A detailed description of the methodology is provided in supplementary material S2, but the main analytical workflow is summarized here. We examined approxi-

mately 350 *Palaeophilotes* specimens from southern France (Occitanie), mainly from the departments of Pyrénées-Orientales, Aude and Hérault, including both recent material (2018–2025) and historical specimens from the Mazel collection, which was taxonomically revised in this study. Complete metadata for all samples are provided in supplementary data 1 (DOI: [10.5281/zenodo.19728264](https://doi.org/10.5281/zenodo.19728264)).

Genetic analyses

For the molecular analyses, we generated COI sequences for 36 individuals of the *Palaeophilotes baton/panoptes* complex and combined them with 22 publicly available French COI sequences. Because the aim of this study was to assess the occurrence of *P. panoptes* in southern France and to delimit its contact zone with *P. baton* in Occitanie, the main molecular dataset was intentionally restricted to French material. Published non-French sequences were used as comparative context in the interpretation of the mitochondrial lineages, but a broader Iberian or European COI analysis was beyond the scope of the present study. Two additional sequences of *P. barbagiae* and *P. abencerragus* were included as outgroups. All sequences were aligned in MAFFT v7.490 (Katoh and Standley 2013) and trimmed to a standard length of 658 bp. Mitochondrial structure was summarized using a maximum-likelihood phylogeny in IQ-TREE v2.0.7 and a TCS haplotype network constructed with the statistical parsimony algorithm implemented in the R package *pegas* v1.4. Pairwise genetic distances were calculated from the COI alignment. The complete dataset is available in BOLD under project code PSEF (DOI: [10.5883/DS-PSEF](https://doi.org/10.5883/DS-PSEF)).

Mapping, phenology, and altitudinal distribution

Citizen-science records of *Palaeophilotes* were compiled from Faune-Occitanie and iNaturalist for the Occitanie region (1986–2024). To ensure consistency between sources, only records with spatial accuracy ≤ 750 m were retained, and a small number of clearly erroneous records were discarded after verification of associated photographs. The final dataset comprised 3,149 records from Faune-Occitanie and 292 from iNaturalist (3,441 records in total). Records were mapped in QGIS v3.44.3 (QGIS Development Team 2025). Species attribution of citizen-science records was performed conservatively and did not rely on phenology. Instead, we used a three-step spatial framework based on genetically confirmed occurrences: (1) initial delimitation of the distribution areas of each taxon; (2) definition of a buffered contact zone (3 km) around the nearest opposing records, which was excluded from attribution; and (3) reassignment of all remaining records to one or the other taxon according to the resulting distribution areas. These data were then used for mapping and for descriptive analyses of phenology and altitudinal distribution.

Wing pattern and morphometry

Morphological analyses focused on two sets of external characters: forewing underside ocelli and wing morphometry. Individuals were assigned either genetically or, outside the exclusion zone, by unambiguous locality. All morphological traits were analysed as population-level

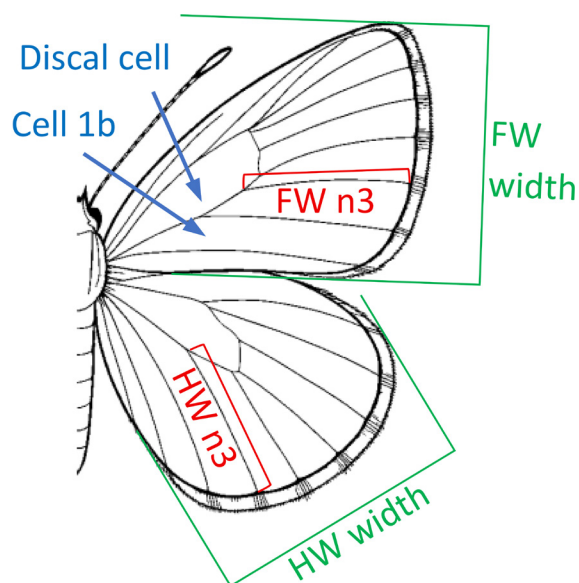


Fig. 1. Schematic diagram of the morphological traits examined. Ocelli positions on the underside of the forewing (discal cell and cell 1b) and morphometric variables measured on the right wings (FW n3, length of forewing vein 3; FW width, forewing width; HW n3, length of hindwing vein 3; HW width, hindwing width) (fig. 1).

trends and were not used as primary criteria for species assignment. Wing-pattern analysis recorded the presence or absence of ocelli in the discal cell and in cell 1b of the forewing underside, and individuals were classified into five recurrent ocellus categories. Wing morphometrics were based on four standardized linear variables: forewing vein 3 length (FW n3), forewing width (FW width), hindwing vein 3 length (HW n3), and hindwing width (HW width) (fig. 1).

All statistical analyses were performed in R v4.5.1 using the packages pegas v1.4, effsize v0.8.1, ggplot2 v4.0.0, tidyverse v2.0.0, readr v2.2.0, readxl v1.4.5, lubridate v1.9.4, dplyr v1.1.4 and car v3.1.5. Differences in forewing underside ocellus frequencies between taxa were first tested across the five recurrent categories using a chi-square test of independence. Ocellus data were then collapsed into a binary trait corresponding to the presence or absence of an ocellus in cell 1b, and species differences were assessed using Fisher's exact test. To test whether this contrast depended on sex, we fitted a binomial generalized linear model including Species, Sex and their interaction. For wing morphometrics, *P. baton* and *P. panoptes* were compared separately in males and females using Welch's t-tests, and effect sizes were estimated using Hedges' g. Normality and homoscedasticity assumptions were evaluated using Shapiro-Wilk and Levene tests, respectively; these diagnostics are reported in supplementary material S3. Phenology and altitudinal patterns were analysed descriptively from dated occurrence records and visualised in relation to elevation and COI-confirmed occurrences.

Results

Genetic analyses

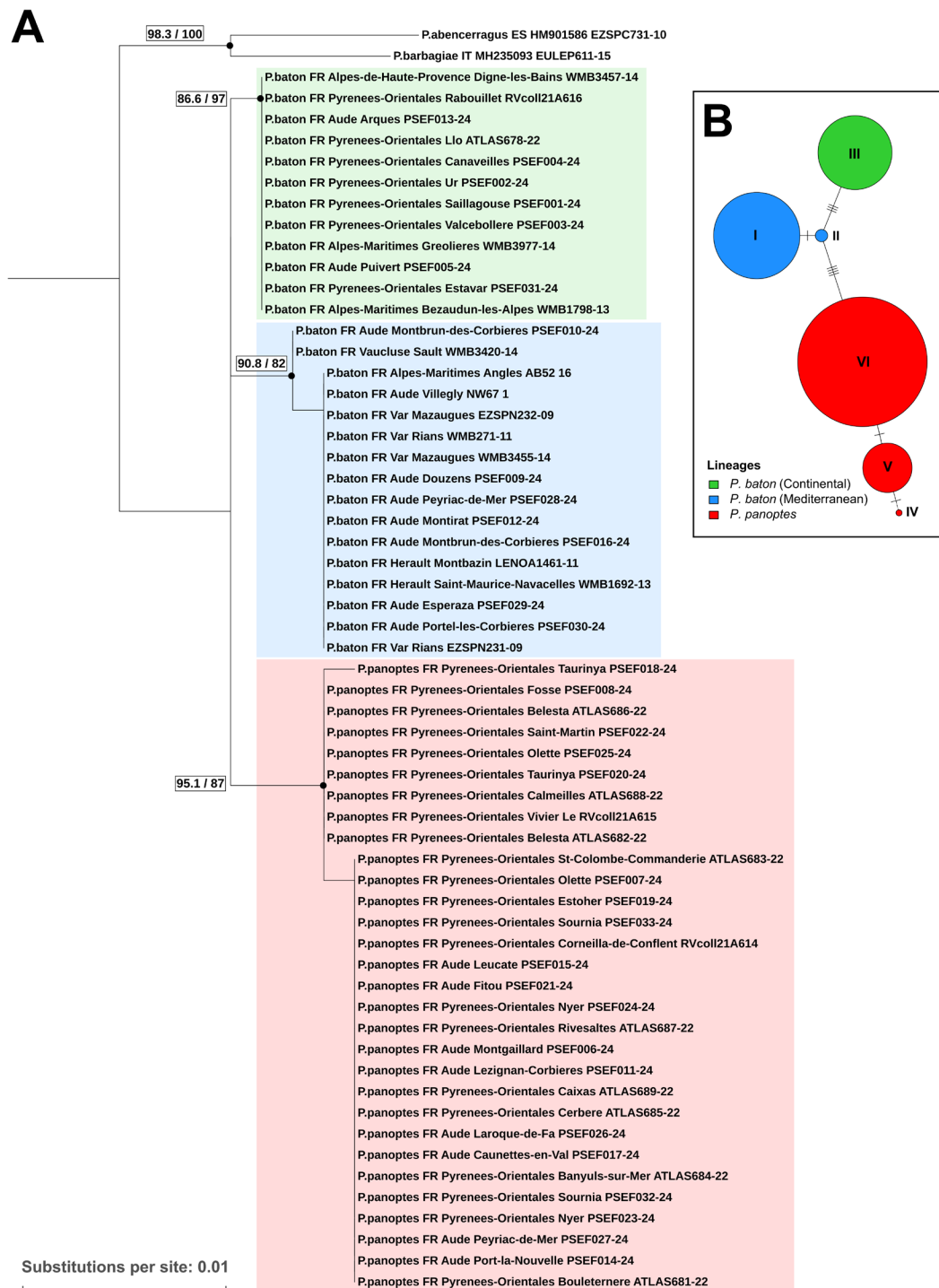
We obtained 58 COI sequences (mostly 658 bp), which grouped into three well-supported mitochondrial clades in the maximum-likelihood phylogeny (fig. 2A) and the TCS network (fig. 2B): (i) a widespread 'continental' lineage of *P. baton* restricted in our study area to Pyrenean and pre-Pyrenean sectors; (ii) a distinct Mediterranean lineage of *P. baton*, confined to low elevations, absent from Pyrénées-Orientales and present across most of Aude, and previously shown to be closer to *P. vicrama* than to the continental *P. baton* lineage (Todisco et al 2018); and (iii) a *P. panoptes* clade, providing mitochondrial evidence consistent with its occurrence in France, widely distributed at low and mid elevations in Pyrénées-Orientales and in the southeastern third of Aude. Outside Occitanie, the limited French sequences available also recover both *P. baton* mitochondrial lineages, consistent with the pattern observed in Occitanie. Pairwise distances indicate low but structured divergence: within *P. baton* 0–0.61%, within *P. panoptes* 0–0.30%, and between *P. baton* and *P. panoptes* 0.61–1.06%; the two *P. baton* lineages differ by 0.46–0.61%. Together, these data support a largely parapatric distribution in southeastern Occitanie (fig. 3), with narrow contact zones: the closest records are separated by 3.5–4.5 km in Conflent, Corbières and Fenouillèdes, and only one locality (Peyriac-de-Mer) provided evidence of syntopy and synchrony (specimens PSEF027–24 and PSEF028–24 in the molecular dataset).

Mapping, phenology, and altitudinal distribution

Late-season observations (records after mid-June below 1,000 m) fall entirely within the distribution range of *P. baton* as established by COI barcoding (fig. 2). Combining barcoding with conservatively reassigned citizen-science records refines the distributions of the two taxa (fig. 3) and their phenology in Occitanie (fig. 4). *P. panoptes* records range from 10 February to 6 June (0–1,280 m), consistent with strict univoltinism. *P. baton* records extend from 25 February to 09 October, with a spring generation followed by a partial and prolonged lowland summer generation; above 1,000 m, records are consistent with a single summer generation. Its altitudinal range spans sea level to 1,850 m (Cerdagne).

Wing pattern and morphometry

Representative ventral wing patterns illustrate a gradual transition from the typical *P. panoptes* phenotype to the typical *P. baton* phenotype, highlighting the absence of fully diagnostic individual characters (fig. 5, localities in supplementary note S1). Forewing underside ocelli differ markedly between taxa (fig. 6). Across five recurrent ocellus configurations, the overall distribution differs significantly between *P. panoptes* and *P. baton* ($\chi^2 = 59.46$, $df = 4$, $p = 3.8 \times 10^{-12}$). When collapsed to a binary trait (ocellus in cell 1b present vs absent), an ocellus in cell 1b is frequent in *P. baton* (53.8%) but rare in *P. panoptes* (15.6%; Fisher's exact test $p = 5.0 \times 10^{-12}$; odds ratio = 6.24, 95% CI = 3.52–11.34). A binomial GLM



including Species, Sex and their interaction indicates that this contrast is consistent in both sexes (non-significant interaction, see supplementary material S3.1).

Wing morphometrics also show consistent size differences between taxa (fig. 7). For all four variables and in

both sexes, *P. baton* individuals are larger on average than *P. panoptes*, with highly significant contrasts and large effect sizes (Hedges' g consistently large; see supplementary table S1 for full descriptive statistics and test outputs and supplementary material S3.2 for assumption checks).

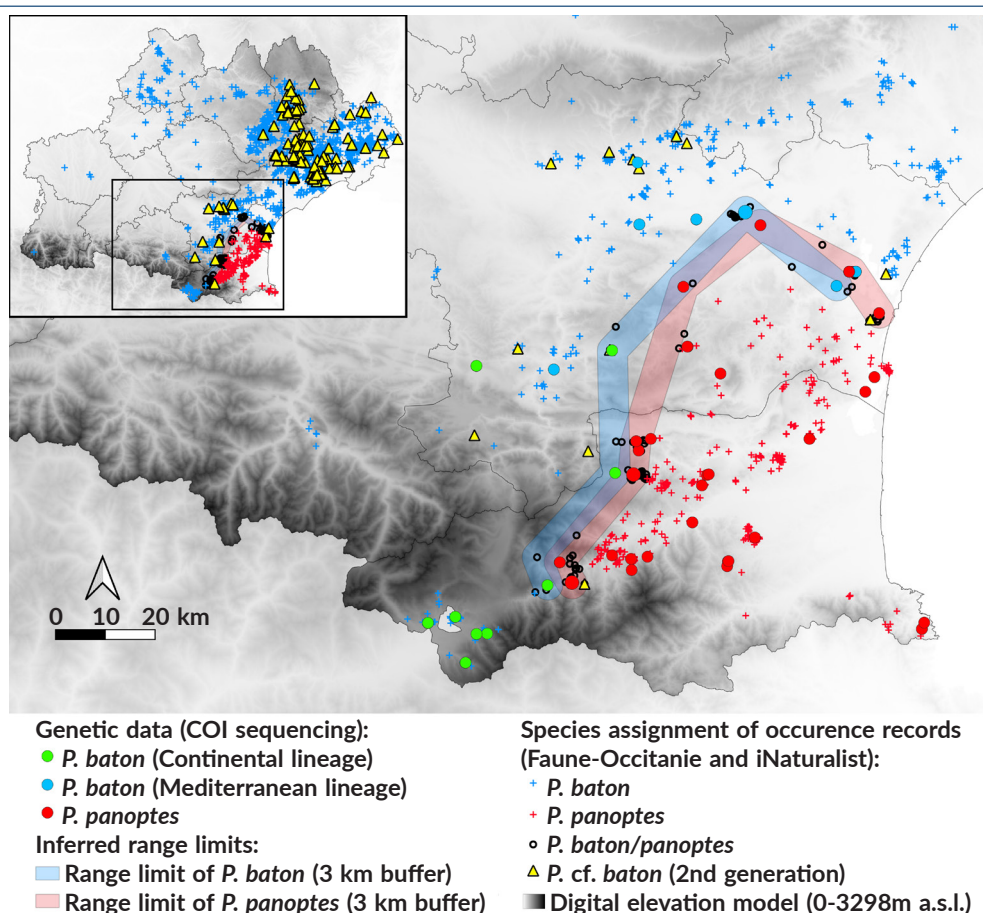


Fig. 3. Distribution of *Palaeophilotes baton* and *P. panoptes* in southeastern Occitanie, based on COI-barcoded individuals and conservatively reassigned citizen-science records (outside contact zone); the inferred contact zone is defined using 3 km buffers for species range limits. Inset: Occitanie (southern France).

Although distributions overlap, the direction of the effect is consistent across traits and sexes. Taken together with wing-pattern results, morphometrics provide an additional population-level signal consistent with the separation of the two taxa in Occitanie.

Discussion

The presence of two distinct *Palaeophilotes* species in France has long been suggested by some authors, but no robust evidence had previously been published to confirm this hypothesis. The main difficulty lies in the absence of reliable morpho-anatomical criteria allowing the two entities to be distinguished. As in earlier studies, detailed examination of genitalia revealed no diagnostic differences (unpublished data). Our own morphological analyses (ocelli and wing morphometry) confirm that confident identification at the individual level is not possible, as character distributions overlap extensively between *P. baton* and *P. panoptes*. However, a clear population-level signal emerges: average wing size and the presence of an ocellus in forewing cell 1b. Such 1b ocelli are uncommon in *P. panoptes* but much more frequent in *P. baton*. Although

these traits cannot serve as strict individual diagnostic markers, they provide a consistent population-level signal when interpreted alongside the genetic, phenological, and ecological evidence presented below. Despite the substantial overlap, these results support the view that *P. baton* and *P. panoptes* represent two distinct taxonomic entities. These interpretations should nevertheless be treated with caution, as they are based on regional material; confirmation from broader sampling and additional contact zones would further strengthen this conclusion.

Throughout this paper, we interpret mitochondrial patterns within the taxonomic framework adopted by Sucháčková Bartoňová et al (2021) and Lukhtanov et al (2025). In our COI dataset, *P. panoptes* is consistently recovered as a mitochondrial lineage distinct from *P. baton*. Because COI is a single mitochondrial marker, these results describe mitochondrial lineage structure rather than providing a taxonomic revision. Within *P. baton*, however, we detect two well-differentiated COI lineages that are geographically structured in our study area. A 'continental' lineage occurs in the Pyrenean and pre-Pyrenean sectors (including Cerdagne in Pyrénées-Orientales and in western parts of Aude), mostly at mid to high elevations.

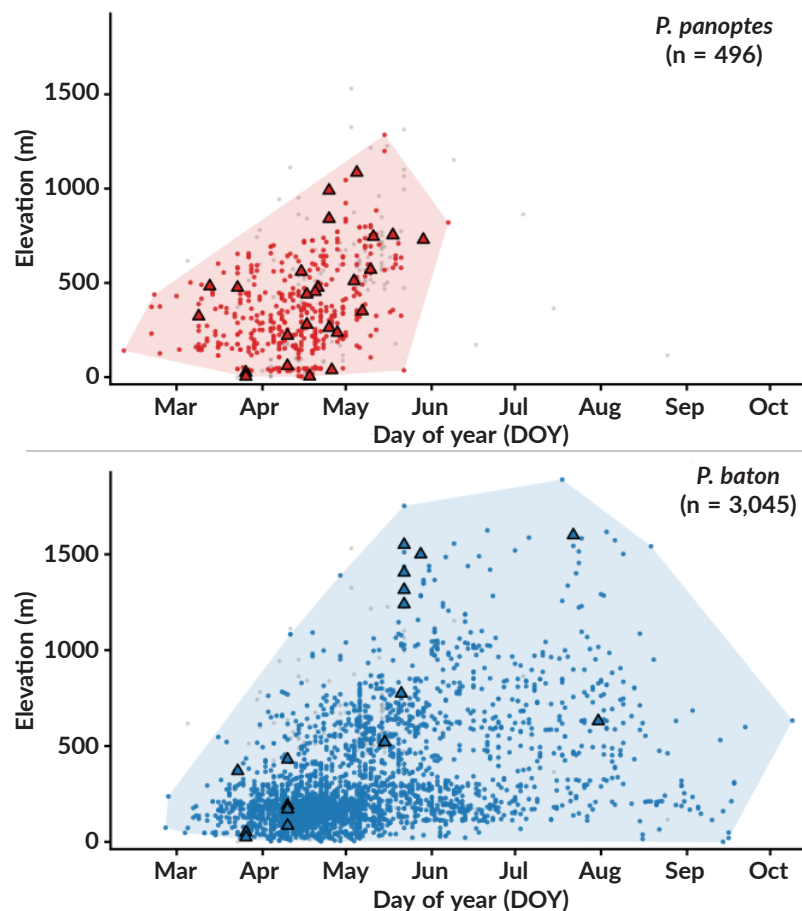


Fig. 4. Phenology of *Palaeophilotes panoptes* and *P. baton* in Occitanie. Dots represent citizen-science records; triangles indicate COI-confirmed records.

By contrast, a 'Mediterranean' lineage is confined to low elevations in North Aude, is absent from Pyrénées-Orientales, and shows a distinctly coastal distribution.

This Mediterranean lineage displays a typical relict pattern *sensu* Dapporto et al (2022): in Occitanie it is represented in our dataset by a largely unique COI haplotype, which is nevertheless closely related to haplotypes found in Corsica and in some coastal localities of southeastern Italy. This indicates that the lineage we observe in southern France is not an isolated artefact but rather the fragmented remnant of a formerly more widespread entity. At the same time, *P. panoptes* shows multiple distinct COI haplotypes mostly concentrated in the Iberian region, whereas *P. baton* overall exhibits shallow maximum COI divergence but strong geographic structuring of haplotypes across its range (Dapporto et al 2022). Taken together, these patterns are consistent with long-term persistence in distinct glacial refugia followed by secondary contact.

The Mediterranean COI lineage of *P. baton* is very close to, and in published datasets can be shared with, *P. vicrama*, and mitochondrial divergence between them can be very low. This pattern raises the possibility that it reflects past mitochondrial introgression rather than

simple intraspecific structuring, a scenario reported in other lycaenids (Talavera et al 2013, Dincă et al 2015) and potentially facilitated by maternally inherited *Wolbachia*, which can promote cytoplasmic sweeps and mitochondrial hitchhiking (Sucháčková Bartoňová et al 2021). *Wolbachia* prevalence appears geographically heterogeneous in the *P. baton* complex, and genomic work indicates that host shifts are frequent and that *Wolbachia* genomes commonly harbour candidate loci associated with reproductive manipulation (Toro-Delgado et al 2025). We therefore cannot fully exclude incomplete lineage sorting, but ancient introgression remains a plausible explanation for the observed pattern. Discriminating between these alternatives would require genome-wide data across a broader geographic range and is beyond the scope of the present study.

By combining COI barcoding data with citizen-science records (faune-occitanie.org, iNaturalist), we refined the respective distributions of the two *Palaeophilotes* species in Occitanie. On this basis, we then characterised their regional phenology, which reveals a pronounced contrast in voltinism within the study area: *P. panoptes* is strictly univoltine, whereas *P. baton* produces a partial second generation. This difference appears directly related to larval



Fig. 5. Ventral wing pattern variation in *Palaeophilotes panoptes* (top) and *P. baton* (bottom).

feeding strategies and host-plant phenology. *Palaeophilotes* larvae are anthophagous and depend on a tight synchrony between larval development and host-plant flowering. In the Roussillon plain (Pyrénées-Orientales), *P. panoptes* emerges with the first flowers of *Thymus vulgaris* L. and disappears by the end of its flowering, usually in early May, thereby being consistent with its strict monophagy in the study area. The species remains confined to patches of *T. vulgaris*, and its altitudinal limit in Pyrénées-Orientales (~1,200 m) closely matches that of its host plant (Gautier 1897). In our study area, *P. panoptes* is only known on *T. vulgaris*. More broadly, however, the species has been reported from several *Thymus* species in the Iberian Peninsula (Muñoz Sarios 1995, Munguira et al 1997), indicating that it should be regarded as oligophagous within this genus rather than strictly monophagous.

By contrast, *P. baton* shows markedly greater trophic plasticity. Up to 1,000–1,200 m, the first generation appears to develop mainly on *T. vulgaris*, but at higher elevations other Lamiaceae are exploited, notably *Thymus serpyllum* L. s.l. (Lhomme 1923, Tshikolovets 2011, Leraut 2016). The partial second generation, which apparently does not occur above 1,000 m, is known to use *Clinopodium nepeta* (L.) Kuntze, 1891 in Provence (Nel 1985). Lhomme (1923) also mentioned *Securigera varia* (L.) Lassen (= *Coronilla varia* L.), but this association should be treated with caution. Some populations also develop on the convolvulaceous *Cuscuta epithymum* (L.) L. in Spain and France (Muñoz Sarios 2011, Gourvil and Sannier 2022). In captivity, the species has been successfully reared on *Lavandula latifolia* Medik. and also accepts *Satureja montana* L. and certain *Mentha* L. species (Nel 1982). Furthermore, other *Thymus* species are also used by *P. baton*, such as *T. nitens* Lamotte, *T. praecox* Opiz, and *T. pulegioides* L. (Konvička et

al 2008, Tshikolovets 2011, Leraut 2016, Buord et al 2017). This dietary flexibility allows *P. baton* to occupy a wide range of habitats, from Mediterranean lowlands to sun-exposed mountain slopes reaching 1,800 m in elevation. This pronounced difference in voltinism and host-plant use implies partial ecological niche segregation between the two taxa in southern France: *P. panoptes* appears closely associated with *Thymus* spp. (and, in our study area, only with *T. vulgaris*), whereas *P. baton* shows substantially broader trophic plasticity, including several documented non-*Thymus* host plants. This ecological differentiation likely contributes to maintaining their parapatric boundary in southern Occitanie.

The question of possible late emergences in *P. panoptes* has been examined in detail, particularly in the Valencian Region, eastern Spain (Bernat-Ponce et al 2025), where so-called 'out-of-season' observations have increased in recent years. However, these records remain confined to areas hosting the subspecies *Thymus vulgaris aestivus* (Willk.) A. Bolòs and O. Bolòs, which shows unusually late flowering. Given the close association of *P. panoptes* with *Thymus*, these authors suggest that this phenomenon may reflect local adaptation to climate warming. These observations illustrate how the interaction between host-plant phenology and climate change can modulate *P. panoptes* population dynamics without challenging its fundamentally univoltine character. Apparent 'late' records therefore do not necessarily indicate a true second generation, but could instead reflect local shifts in host-plant phenology.

The apparently parapatric distribution of *P. panoptes* and *P. baton* raises the question of barriers to gene flow. Our results suggest the existence of two types of contact zones. In fragmented terrain along the inland Pyrenean foothills of Pyrénées-Orientales and western Aude, where

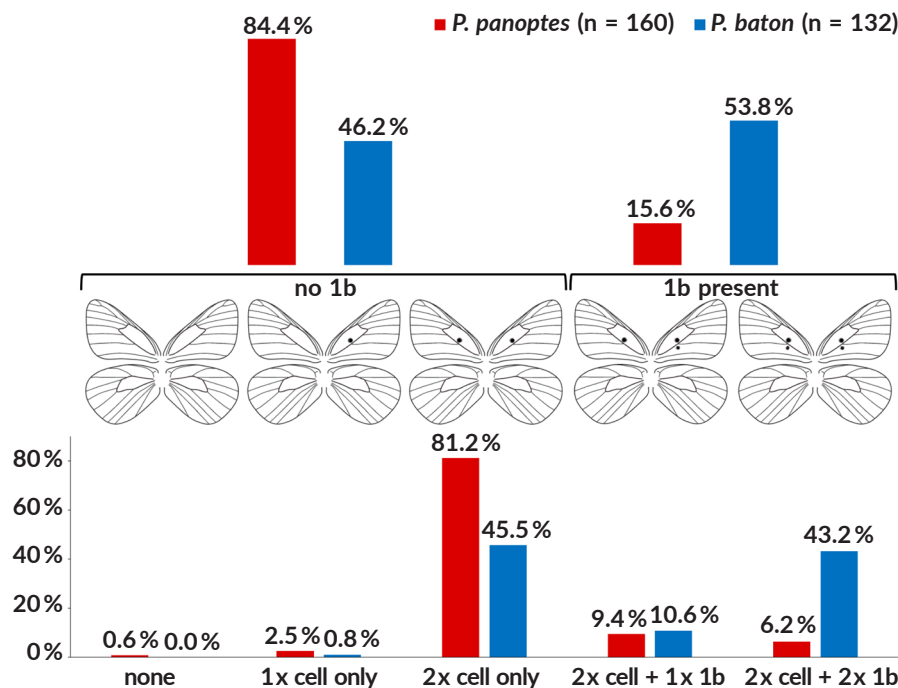


Fig. 6. Forewing underside ocelli in *Palaeophilotes panoptes* (red) and *P. baton* (blue). Top: binary scoring of the presence of a 1b ocellus; bottom: percentages of five recurrent ocellus categories.

suitable habitats are discontinuous within an otherwise unsuitable forest matrix, we observed small areas that appear suitable but hold no *Palaeophilotes*, or only a few isolated individuals (e.g. Canaveilles, Rabouillet, Salvezines). This configuration resembles a 'tension zone' (Barton and Hewitt 1985), in which potential contacts do not result in persistent, viable populations. In the Mediterranean coastal sector around the Bages/Sigean lagoon complex in eastern Aude, by contrast, suitable habitats appear more continuous and topographic barriers weaker. Here, we observed a narrow spatial overlap between the two taxa, confirmed by genetic data, but without population fusion. Notably, in our dataset, the inland contact-zone localities involve the continental *P. baton* mitochondrial lineage, whereas the lagoon complex involves the Mediterranean lineage. This type of overlap may be more widespread in the Mediterranean region, but this remains to be confirmed.

These two contrasting situations are consistent with barriers limiting the establishment of mixed populations, potentially including reproductive interference (postzygotic incompatibilities without a premating barrier) as well as ecological constraints that prevent stable coexistence.

Comparable patterns are found in other species complexes with an Iberian component extending beyond the Pyrenees, such as *Melanargia lachesis* (Hübner, 1790) / *M. galathea* (Linnaeus, 1758) (Habel et al 2017), or *Iphiclides feisthamelii* (Duponchel, 1832) / *I. podalirius* (Linnaeus, 1758) (Gaunet et al 2019), where secondary contact between lineages from distinct refugia is likewise associated with partial reproductive barriers. These parallels suggest that such parapatric distributions may

result from common processes linked to glacial cycles, ecological constraints, and the dynamics of gene flow (Dapporto et al 2019).

Taken together, the *Palaeophilotes* system illustrates how ecological plasticity, historical isolation, and partial reproductive barriers can interact during the divergence process, in line with established theoretical frameworks for the study of hybrid zones (Barton and Hewitt 1985, 1989) and the evolution of host specialization in butterflies (Forister et al 2015).

Finally, documenting the occurrence of *P. panoptes* in France (until now considered a strictly Iberian endemic) has conservation relevance. Its French distribution, restricted to a few areas in southeastern Occitanie and closely tied to that of *T. vulgaris*, may be vulnerable to land-use change and climate warming, both of which affect host-plant availability and flowering phenology. Long-term population monitoring, particularly through citizen science, therefore, appears relevant to detect potential range contractions or shifts. In addition, *P. panoptes* has been tentatively reported from northern Morocco (Tarrier 2019), although this record should be treated with caution given the difficulty of species identification in the group. In any case, our evidence from southern France is sufficient to show that *P. panoptes* is not confined to the Iberian Peninsula.

In summary, our integrative regional dataset documents the occurrence of *P. panoptes* in southern France and delineates a largely parapatric contact with *P. baton* in Occitanie. The two taxa show consistent ecological and phenological differences, which likely contribute to maintaining their distributional boundary. The persistence

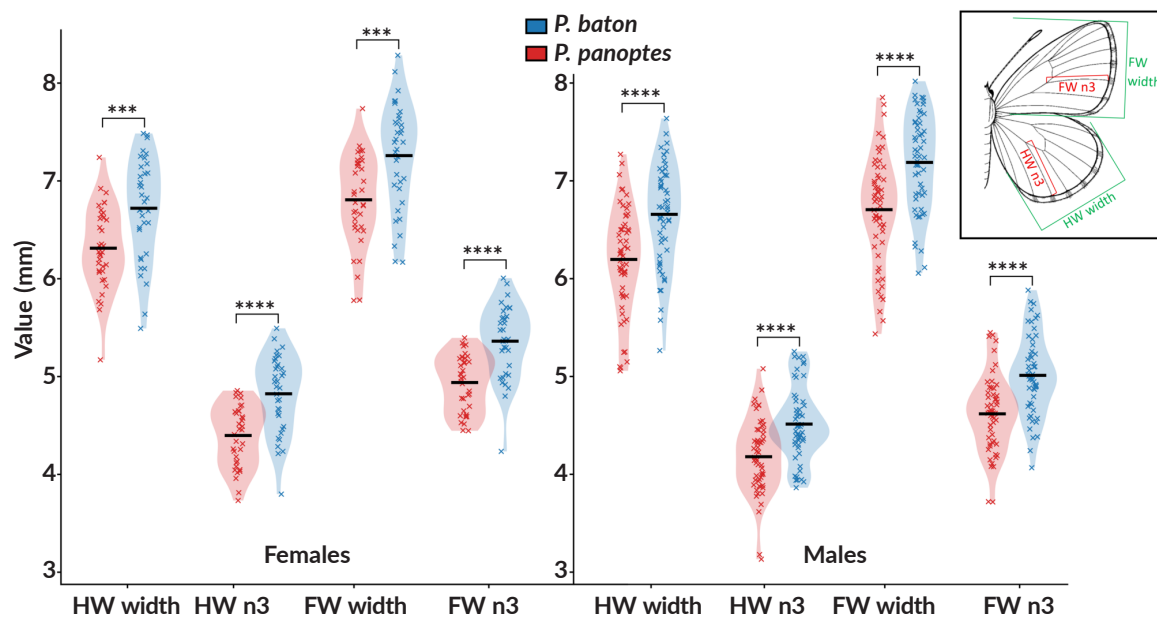


Fig. 7. Wing morphometrics in *Palaeophilotes baton* and *P. panoptes*. Crosses indicate individual values, violins the density, and black bars the mean. Inset shows the four measured variables. Asterisks indicate interspecific statistical significance (** $p < 0.001$; **** $p < 0.0001$).

of narrow contact zones suggests barriers to gene flow, potentially involving reproductive interference as well as ecological constraints, but testing the nature and strength of these barriers will require genome-wide data across multiple contact zones.

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Author contributions

A Gaunet, conceptualization, resources, investigation, data curation, formal analysis, visualization, and writing - original draft; **R Vila**, conceptualization, resources, investigation, supervision, and writing - review and editing. Both authors contributed to the interpretation of the results and approved the final version of the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

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Supplementary material

S1: Supplementary notes

Note S1. Localities of specimens shown in fig. 5.

P. panoptes (top; left to right): Llers (Es: Girona); Caunettes-en-Val (Fr: Aude); Nyer (Fr: Pyr.-Or.); Sournia (Fr: Pyr.-Or.).

P. baton (bottom; left to right): Véraza (Fr: Aude); Moussoulens (Fr: Aude); Salle-en-Beaumont (Fr: Isère); Belin-Béliet (Fr: Gironde).

S2: Detailed Methods

Specimen sampling and preservation

Individuals were collected between 2018 and 2025 in Occitanie (southern France), mainly in the departments of Pyrénées-Orientales, Aude, and Hérault. Most specimens originate from the collection of A. Gaunet (Perpignan, France) and from the collection of R. Vila (Butterfly Diversity & Evolution Laboratory, Barcelona, Spain).

The collection of R. Mazel, assembled as part of his work published in 2007 and currently curated by A. Gaunet (Perpignan, France), was also included and taxonomically revised in this study.

In total, nearly 350 specimens, primarily from the study area, were examined. Complete metadata for all samples are provided in supplementary data 1 (DOI: [10.5281/zenodo.19728264](https://doi.org/10.5281/zenodo.19728264)).

Sequencing and genetic analysis

Extraction and amplification

A total of 36 individuals of the *Palaeophilotes baton/panoptes* complex were newly sequenced for this study. Mitochondrial DNA of the cytochrome c oxidase subunit I (COI) gene was extracted from a single leg of each specimen using standard protocols for Lepidoptera. DNA extraction, PCR amplification, and sequencing were performed in two facilities: (i) the Butterfly Diversity & Evolution Laboratory, following the protocol of de Freina et al (2015), and (ii) Genoscreen, following standard barcoding protocols (Sañudo-Restrepo et al 2013, Todisco et al 2018). PCR amplifications used commonly employed COI primer pairs (UniLepF1/UniLepR1, LCO1490/Nancy, and LepF1/LepR1).

In addition to the newly generated sequences, previously published COI sequences of *P. baton* and *P. panoptes* from France were retrieved from the BOLD and GenBank databases. Two additional COI sequences of *Palaeophilotes barbagiae* and *P. abencerragus* were included as outgroups in the phylogenetic analyses. In total, 60 COI sequences were analysed, comprising 58 sequences of the *P. baton/panoptes* complex and two outgroup taxa.

Detailed information for all sequences included in the analyses is provided in supplementary data 1 (DOI: [10.5281/zenodo.19728264](https://doi.org/10.5281/zenodo.19728264)). All newly generated COI sequences were deposited in BOLD Systems alongside the publicly available sequences used in this study. The complete dataset is available in BOLD under project code PSEF (DOI: [10.5883/DS-PSEF](https://doi.org/10.5883/DS-PSEF)).

Sequence Alignment

All COI nucleotide sequences were aligned together using MAFFT v7.490 with the -auto option to select the most appropriate alignment strategy and the -adjustdirection option to ensure correct sequence orientation. The resulting alignment was manually inspected and trimmed to a standard length of 658 base pairs.

Phylogenetic Reconstruction

Maximum-likelihood (ML) phylogenetic inference was performed using IQ-TREE v2.0.7 on the complete dataset, including the two outgroup taxa. The best-fit nucleotide substitution model was selected using ModelFinder, with TN+I chosen according to the Bayesian Information Criterion (BIC). Node support was assessed using 1,000 ultrafast bootstrap replicates (UFBoot2) combined with 1,000 SH-like approximate likelihood ratio test replicates (SH-aLRT). Ultrafast bootstrap trees were refined using nearest-neighbor interchange (-nni).

Haplotype Analysis

To investigate genealogical relationships and visualize mitochondrial genetic diversity within the *P. baton/panoptes* complex, we constructed a haplotype network using the statistical parsimony TCS algorithm implemented in the R package pegas v1.4 (R v4.5.1; R Core Team 2024). This analysis was conducted on the 58 aligned COI sequences of *P. baton* and *P. panoptes*. Haplotype connections were inferred under a 95% statistical parsimony criterion. Haplotypes were defined as unique DNA sequences and visualized with node sizes proportional to their observed frequencies. The network was colour-coded according to the three mitochondrial lineages identified in the ML phylogeny, and mutational steps separating haplotypes were indicated by hatch marks on the connecting branches.

Citizen science data

With the agreement of the Collectif Faune-Occitanie, we accessed all records of the genus *Palaeophilotes* collected between 1986 and 2024 in the Faune-Occitanie citizen science database (www.faune-occitanie.org; Collectif Faune-Occitanie 2024). These data were complemented with records available for the Occitanie region on iNaturalist (www.inaturalist.org; iNaturalist 2024).

Records are usually entered directly by observers via smartphone and are therefore georeferenced with high spatial accuracy. In Faune-Occitanie, however, some records are localized only to a named site, with a maximum spatial uncertainty of 750 m.

To ensure consistency between datasets, we excluded iNaturalist records with lower spatial accuracy than this threshold. Rare records that were clearly erroneous were also discarded after verification of the associated photographs. The final dataset therefore comprised 3,149 records from Faune-Occitanie and 292 from iNaturalist, for a total of 3,441 records. All analyses were conducted on anonymised occurrence records; retained records are provided in supplementary data 2 (DOI: [10.5281/zenodo.19728264](https://doi.org/10.5281/zenodo.19728264)). Species attribution of citizen-science records was performed using a conservative spatial fra-

mework derived from genetically confirmed occurrences (see below) and did not rely on phenology as a criterion.

Mapping, phenology, and altitudinal distribution

Citizen science data were mapped using QGIS v3.44.3. Records corresponding to a putative second generation of *Palaeophilotes* were plotted separately to assess whether this late-season signal was spatially homogeneous across the study area.

Integration of citizen science data followed a three-step protocol designed to obtain robust species-level attribution without relying on phenological assumptions:

1. Initial delimitation based on genetic data.

Using genetically identified individuals, we delineated the respective distribution areas of each species in QGIS. These reference data were also used to outline the potential contact zone between the two taxa (fig. 3).

2. Definition and exclusion of the contact zone.

To delimit the distributional front of the two species, we drew two lines connecting, for each taxon, the confirmed records closest to the distribution area of the other taxon. A 3 km buffer was then applied around each line. The two resulting bands partially overlapped, and the exclusion zone was defined as the union of these buffers. All citizen science records located within or between these zones were excluded from subsequent analyses. This conservative step aimed to limit attribution errors arising from the immediate proximity of the two taxa and from occasional spatial gaps between genetically confirmed records.

3. Final species attribution of citizen science records.

All remaining observations from Faune-Occitanie and iNaturalist were assigned to one or the other of the two distribution areas defined above.

This deliberately conservative procedure ensured that only the least ambiguous citizen science records were incorporated into downstream phenological and altitudinal analyses. These steps resulted in a detailed map of the inferred distributions of the two species in Occitanie (fig. 3).

To identify records consistent with a putative partial second generation, we defined 'late-season' observations as records obtained after mid-June and below 1,000 m in elevation and mapped these records separately. Finally, we used R v.4.5.1 (R Core Team) (packages tidyverse, lubridate, readr, readxl, ggplot2) to generate a scatterplot showing phenology (day of year) and altitudinal range for each taxon. To illustrate the envelope of each taxon's observations, convex polygons enclosing all points were calculated. Grey circles represent records without species attribution that fall within the contact-zone buffers and were therefore excluded from conservative reassignment (n = 140).

Wing pattern and morphometry

We examined two types of external characters: (i) the pattern of ocelli on the underside of the forewings, and (ii) quantitative wing morphometric variables.

The individuals analysed originate from Occitanie and cover the geographic range of the study populations. Specimens were identified either genetically (COI barcoding) or, when the assignment was unambiguous, by locality

(i.e. outside the exclusion zone defined between the two taxa; see above). The individuals included in each analysis are indicated in supplementary data 1 (DOI: [10.5281/zenodo.19728264](https://doi.org/10.5281/zenodo.19728264)). In all cases, these external characters were analysed as population-level trends and were not used as primary criteria for species assignment.

Wing pattern

For each specimen, we recorded the presence or absence of an ocellus in the discal cell and in cell 1b on the underside of the forewing (fig. 1, blue arrows). Each individual was then assigned to one of the following five ocellus categories:

- no ocellus;
- 1 × cell only: a single discal ocellus on one forewing;
- 2 × cell only: one discal ocellus on each forewing, but no ocellus in cell 1b;
- 2 × cell + 1 × 1b: two discal ocelli plus one ocellus in cell 1b;
- 2 × cell + 2 × 1b: two discal ocelli plus one ocellus in cell 1b on each forewing.

This character, which is only rarely considered in the literature, was examined here because repeated field observations revealed marked and nearly consistent differences between *P. baton* and *P. panoptes*. Ocelli were scored visually on well-preserved specimens. Only ocelli of normal size, clearly visible to the naked eye, with sufficient contrast and sharply defined margins, were counted; very faint traces or minute spots only detectable under magnification were not considered.

We first compared the distribution of the five categories between *P. baton* and *P. panoptes* using a χ^2 test of independence in R v.4.5.1. Because some categories were rare, we then simplified this trait into a more biologically meaningful binary state:

- 'no 1b ocellus' (no ocellus in cell 1b; categories 1-3);
- '1b ocellus present' (at least one ocellus in cell 1b on at least one forewing; categories 4-5).

We compared the frequencies of these two states between species using Fisher's exact test, from which we report the exact *P*-value, the odds ratio, and its 95% confidence interval. To test for a possible effect of sex, we fitted a generalized linear model of the binomial family (logistic regression; R: family = binomial), with the presence of an ocellus in cell 1b (yes/no) as the response variable, and Species, Sex, and their interaction as predictors. The interaction term was not significant, indicating that the difference between species is consistent in both males and females. We therefore pooled sexes for the descriptive summaries and statistical tests presented.

Wing morphometry

We measured four standardized wing variables (fig. 1, red and green measurements):

- length of forewing vein 3 (FW n3);
- forewing width (FW width);
- length of hindwing vein 3 (HW n3);
- hindwing width (HW width).

The use of vein-based landmarks ensures high repeatability, as these reference points are easily identifiable. FW n3 / HW n3 and FW width / HW width were me-

Table S1. Comparative wing morphometric results between *Palaeophilotes baton* and *P. panoptes*. Values are mean $\pm$ SD (n). P-values are from Welch's t-tests. Hedges' g is reported with qualitative interpretation.

Variable	Sex	<i>P. baton</i>	<i>P. panoptes</i>	Difference (Welch's t-test)
FW n3	M	5.01 $\pm$ 0.40 (n = 56)	4.62 $\pm$ 0.38 (n = 56)	$p < 0.0001$; Hedges' g = 0.99 (strong effect)
FW n3	F	5.36 $\pm$ 0.37 (n = 35)	4.95 $\pm$ 0.28 (n = 35)	$p < 0.0001$; Hedges' g = 1.24 (strong effect)
FW width	M	7.19 $\pm$ 0.49 (n = 56)	6.71 $\pm$ 0.56 (n = 56)	$p < 0.0001$; Hedges' g = 0.91 (strong effect)
FW width	F	7.26 $\pm$ 0.54 (n = 35)	6.83 $\pm$ 0.45 (n = 35)	$p = 0.0006$; Hedges' g = 0.86 (strong effect)
HW n3	M	4.51 $\pm$ 0.37 (n = 56)	4.18 $\pm$ 0.38 (n = 56)	$p < 0.0001$; Hedges' g = 0.89 (strong effect)
HW n3	F	4.82 $\pm$ 0.39 (n = 35)	4.41 $\pm$ 0.31 (n = 35)	$p < 0.0001$; Hedges' g = 1.17 (strong effect)
HW width	M	6.66 $\pm$ 0.52 (n = 55)	6.20 $\pm$ 0.54 (n = 56)	$p < 0.0001$; Hedges' g = 0.86 (strong effect)
HW width	F	6.72 $\pm$ 0.52 (n = 35)	6.33 $\pm$ 0.41 (n = 35)	$p = 0.0009$; Hedges' g = 0.82 (strong effect)

asured on a single forewing and a single hindwing that were correctly spread flat, preferentially on the right wings when intact. All measurements were taken at $\times 10$ magnification by the same operator, on sufficiently well-preserved specimens, using a PERFEX Zoom Sc 6.34 LED trinocular stereomicroscope coupled with a TOUPCAM 5.2 MP CMOS camera and Toupview software (version 4.12.29030.20250722). All linear measurements are expressed in millimetres (mm). Specimens with distorted or incomplete wings were excluded from morphometric analyses.

All statistical analyses were conducted in R v.4.5.1. For morphometric variables, *P. baton* and *P. panoptes* were compared separately in males and females using Welch's t-tests (stats package), which do not assume equal variances. Prior to these tests, we assessed normality within each group (species $\times$ sex $\times$ variable) using Shapiro-Wilk tests, and evaluated homogeneity of variances between species using Levene's tests (car package). None of the variables showed marked deviations from normality, and variances did not differ significantly between species.

For each morphometric variable, we report, separately for males and females: the mean $\pm$ SD and sample size for each species, the exact P-value from Welch's t-test, and Hedges' g (effsize package) as an estimate of effect size. Effect sizes were interpreted following Cohen (1988) as small ($|g| > 0.2$), medium ($|g| > 0.5$), or large ($|g| > 0.8$).

S3. Supplementary Results

S3.1. Additional statistical outputs

A binomial GLM including Species, Sex, and their interaction confirmed that this difference between taxa is not driven by sex: the Species $\times$ Sex interaction was not significant. In other words, both males and females of *P. baton* tend to show 1b ocelli much more frequently than *P. panoptes*.

Taken together, these results show that although the presence of an ocellus in cell 1b is not individually diagnostic (both taxa can show it), it provides a clear and repeatable population-level signal: 1b ocelli are common in *P. baton* and remain rare in *P. panoptes*. In addition, for every measured linear wing trait, mean values are higher

in *P. baton* than in *P. panoptes* in both sexes, and the effect sizes (Hedges' g) are consistently large.

S3.2. Assumption checks and diagnostics

Assumption checks:

For each sex $\times$ species $\times$ variable combination, distributions were approximately normal (Shapiro-Wilk $p > 0.05$ in most cases; the only clear deviation was HW n3 in males of *P. baton*, Shapiro-Wilk $p = 0.034$). Variances did not differ significantly between species for any variable (Levene tests, all $p \geq 0.18$). These diagnostics indicate that Welch's t-test comparisons are robust for our data.

Wing size and shape differed consistently between the two taxa in Occitanie (fig. 7; table S1). For all measured variables, *P. baton* individuals were on average larger than *P. panoptes*, in both males and females.

In males, *P. baton* exhibited longer FW n3 (5.01 $\pm$ 0.40 mm vs 4.62 $\pm$ 0.38 mm in *P. panoptes*), broader forewings (FW width: 7.19 $\pm$ 0.49 mm vs 6.71 $\pm$ 0.56 mm), longer HW n3 (4.51 $\pm$ 0.37 mm vs 4.18 $\pm$ 0.38 mm), and broader hindwings (HW width: 6.66 $\pm$ 0.52 mm vs 6.20 $\pm$ 0.54 mm). All differences were highly significant (all $p < 0.0001$), with large standardized effect sizes (Hedges' g between 0.86 and 0.99, all interpreted as 'strong').

Females followed the same pattern, with *P. baton* showing greater FW n3 (5.36 $\pm$ 0.37 mm vs 4.95 $\pm$ 0.28 mm in *P. panoptes*), broader forewings (7.26 $\pm$ 0.54 mm vs 6.83 $\pm$ 0.45 mm), longer HW n3 (4.82 $\pm$ 0.39 mm vs 4.41 $\pm$ 0.31 mm), and broader hindwings (6.72 $\pm$ 0.52 mm vs 6.33 $\pm$ 0.41 mm) than *P. panoptes*. Again, all contrasts were strongly significant ($p \leq 0.001$), and effect sizes were large ($|g| = 0.82\text{--}1.24$).

Although there is visible overlap in the distributions of the measured values for the two species (fig. 7), they are significantly different: for every measured linear trait, mean values are higher in *P. baton* than in *P. panoptes*, and the magnitude of separation between species is consistently large for both sexes. Taken together with the wing-pattern data, the morphometric results reinforce the interpretation that the two taxa correspond to distinct lineages rather than representing intraspecific phenotypic variation.

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