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Fifty Shades of Whites: taxonomic revision of *Talbotia* Bernardi, 1958, *Pieris* Schrank, 1801, and *Artogeia* Verity, 1947, through a review of available anatomical and molecular data

(Lepidoptera, Pieridae)

by

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Abstract: This review focuses on the molecular phylogeny of *Pieris* Schrank, 1801 s. l. The taxonomic relationships between different taxa were determined and revised through a phylogenetic analysis of freely available mitochondrial DNA sequences and a thorough examination of anatomical features described in the literature. Based on the integrated data, this group of butterflies was divided into three distinct genera: *Talbotia* Bernardi, 1958*, Pieris* Schrank, 1801, and *Artogeia* Verity, 1947. Within these genera, a total of seven subgenera were identified: ***Pieris* (*Afropieris*) subgen. nov.**, *Pieris* s. str., ***Artogeia* (*Bernardia*) subgen. nov.**, ***A.* (*Mariania*) subgen. nov.**, ***A.* (*Tadokoroa*) subgen. nov.**, ***A.* (*Sinopieris*) comb. nov.**, and ***Artogeia*** s. str. **comb. rev.** The study included a comprehensive set of mitochondrial DNA sequences from different taxa of ***Artogeia*** s. str. **comb. rev.** ("napi-complex") that are distributed across three different continents. The molecular analysis revealed that ***Artogeia*** s. str. **comb. rev.** comprises a small number of well-distinct species, along with a larger group of highly genetically similar taxa. This latter was referred to as "superspecies-*napi*" and is further subdivided into three species-groups (*marginalis, bryoniae* and *napi* species-group) grossly mirroring the geographical distribution of the included taxa.

Keywords: *Talbotia*, *Pieris*, *Artogeia*, Lepidoptera, Pieridae, Pierinae, new subgenera, new combinations, Holarctic Region, Afrotropical region, Palearctic Asia, phylogenetic analysis, Phylogeny, COI, phenotype, androconia, genitalia.

1. Introduction: Reissinger (in Eitschberger, 1983: XIII) wrote: Jedermann kennt den "Kohlweißling" (Everybody knows the cabbage whites), and indeed, cabbage whites are very common in the northern hemisphere. However, ironically, this group of butterflies has been a subject of disagreement among lepidopterists for more than a century.

Pieris s. l. is a cosmopolitan group of butterflies, with its highest species richness found in the mountainous regions of the Palearctic region. It comprises around 50 species, being the largest group within the subtribe Pierina. These butterflies are typically small to medium-sized, with a white or yellowish-white ground colour and varying proportions of black, brown, and less frequently, yellow or greenish-dark scales. Sexual dimorphism is pronounced, with ♀♀ generally having more heavy markings. While most high-altitude species are univoltine, lowland species often have more than three generations annually. Some species, such as *P. rapae* (Linnaeus, 1758), exhibit slow and feeble flight, while others, like *P. sherpae* (Epstein, 1979), are fast and erratic fliers (Epstein, 1979; Evans, 1932; Talbot, 1905). However, they generally fly at low altitudes and can often be seen visiting flowers or resting on vegetation.

♀♀ lay eggs individually or in groups on the lower part of the leaves of various plant families, including Akaniaceae, Amaranthaceae, Brassicaceae, Capparaceae, Cleomaceae, Resedaceae, Simaroubaceae, and Tropaoleaceae. Occasionally, they may also lay eggs on Aizoaceae, Alliaceae, Apocynaceae, and Asteraceae (Robinson et al., 2023). This wide hostplant usage contrasts with the plant preferences of other butterfly subfamilies, such as Dismorphinae and Coalidinae, which primarily feed on Fabaceae (Braga et al., 2021). Notably, the larvae of some species, like *P. brassicae* (Linnaeus, 1758) and *P. rapae* (L.), are well-known and widespread agricultural pests, often inadvertently introduced to many countries through the trade of brassicaceous crops (Ryan et al., 2019). Unfortunately, the preimaginal stages and the host plants of many species remain to be discovered. Diapause is limited to the pupal stage, and its duration varies from a few weeks to several months, depending on the species and their environment (Eitschberger, 1984).

The limited range of colours and shapes in the adults has made *Pieris* s. l. one of the less attractive groups for collectors of diurnal Lepidoptera. Additionally, the interspecific and seasonal phenotypical overlap among these butterflies makes identifying some species challenging. Despite attempts at intrageneric classification based on phenotypic traits made over 90 years ago, the taxonomy of this group is still not entirely resolved (Mariani, 1937).

1.1. Historical background: After the establishment of the genus *Pieris* Schrank in 1801, the classification of *Pieris* s. l. was primarily based on wing colouration, which led to the placement of some species [e.g. *dubernardi* (Oberthür, 1884)*,* and allies], into various different genera including *Aporia* Hübner, [1819]*, Mancipium* Stephens, 1827*, Parapieris* de Nicéville, 1897*, Pontia* Fabricius, 1807*, Pieris*, and *Syncloe* Hübner, [1818] (Bernardi, 1947a, 1947b; de Nicéville, 1897; Dixey, 1894; Leech, 1892; Oberthür, 1876, 1884). The first description of taxonomically relevant anatomic features in *Pieris* s. l was made by Grote (1900) while studying the wing venation of Pieridae. Dixey (1932) established androconia as a useful feature to distinguish between a group of taxa of the family, and a year later Klots studied the ♂ genitalia of Pieridae to infer the phylogenetic relationships of its subfamilies, tribes, and genera (Dixey, 1894; Klots, 1933).

Mariani (1937) emphasized the usefulness of examining ♀ genitalia to distinguish and classify species of *Pieris* s. l. (see also Petersen, 1901, 1904). He was also the first to propose the division of *Pieris* s. l. into three species groups represented by the species *P. brassicae* (L.), *P. rapae* (L.), and *P. napi* (L.)*,* respectively. Additionally, Mariani (1937) proposed some currently accepted systematic arrangements, such as including both *P. ergane* (Geyer, [1828]) and *P. davidis* (Oberthür, 1876) within the *napi*-group and placing *P. mannii* (Mayer, 1851), *P. canidia* (Spaarman, 1768)*,* and *P. tadjika* Grum-Grshimailo, 1888 in the *rapae*-group.

Bernardi (1947) proposed a systematic arrangement of *Pieris* and *Pontia* species based on the combination of wing venation, the morphology of androconia, and ♂ and ♀ genitalia. He divided the genus "*Pieris"* into three species groups which differed from those proposed by Mariani. These groups were the "*brassicae*-group (*Pieris* s. str.)", "*rapae*-group", and "*naganum*-group". Notably, Bernardi was the first to establish the taxonomic relationship between *M. naganum* (Moore, 1884) and other *Pieris* species, (although he later created the monotypic genus *Talbotia* to include *naganum*. Additionally, Bernardi (1958, 1947b) emphasized the close relationship between the genera *Pieris* and *Pontia*. In the same year, Verity (1947) divided the genus *Pieris* into two subgenera: *Pieris* s. str. with type-species *brassicae* (L.) and *Artogeia*, with type-species *napi* (L.). The latter subgenus also included *ergane* (Geyer)*, mannii* (Mayer)*,* and *rapae* (L.).

Since 1950, and following the seminal works by Müller, lepidopterists began to delve into the intricate taxonomy of *P. napi* (L.) and related taxa, conducting breeding and hybridization experiments to investigate the relationships between the European *P. napi* (L.) and *P. bryoniae* (Hübner, [1806]) (Lorković, 1962a, 1962b; Müller & Kautz, 1939). A significant advancement in understanding the *napi*-group (sensu Mariani, 1937) occurred with the publication of the monumental monography by Eitschberger (1983). In this work Eitschberger analyzed almost all known taxa of the "*napi-bryoniae*-complex" (with the exception of *ergane* and *dubernardi* and allies). He provided comprehensive information on taxonomical features such as colour patterns, genitalia morphology, and biogeography and depicted the anatomic details of hundreds of specimens, discussing their interspecific variation. Eitschberger's monograph is considered one of the key milestones in *Pieris* s. l. research and remains the only dedicated book on the subject.

Geiger and colleagues made significant contributions by conducting ELISA studies to construct the first molecular phylogenetic tree of *Pieris*. They highlighted the marked difference between the genus *Pieris* (including for the first time many American taxa) and *Pontia* and confirmed the presence of three "species groups/subgenera" within the former: *Pieris* s. str. including *brassicae, Artogeia,* including *napi* and a third unnamed group including *rapae.* (Geiger & Scholl, 1985; Geiger & Shapiro, 1992; Mariani, 1937; Porter & Geiger, 1995).

Since 1990, Hao Huang has published a series of works focusing on the identification, anatomy, and biogeography of taxa related to *dubernardi* Obth. Huang revised this group and established the genus *Sinopieris* Huang, 1995, which was later considered synonymous with *Pieris* (Huang, 1995, 1998, 2003, 2019; Tadokoro et al., 2016). In 2013, Tadokoro and colleagues started a comprehensive study of the Asian taxa within the "*napi*-group". They provided molecular data and critically reviewed the existing literature on the group (Tadokoro et al., 2013; Tadokoro et al., 2013). Importantly, Tadokoro et al. demonstrated for the first time that the "*napi*-group" consists of a few anatomically and genetically distinguishable species, along with a larger number of closely related taxa referred to as the "*napi*-complex" (Eitschberger, 1983; Tadokoro et al., 2014, 2016; Tadokoro, Shimokama et al., 2013; Tadokoro, Shinkawa et al.. 2013).

In recent years, several attempts have been made to define the systematics of the family Pieridae, including the "*napi*-complex" (Chew & Watt, 2006; Braby et al., 2006; Wahlberg et al., 2014; Middleton Welling et al., 2020; Dinca et al., 2021; Dapporto et al., 2022; Ge et al., 2023). However, most of them have focused on a limited number of taxa and specific regions within the Palearctic region. Consequently, a comprehensive revision of the higher taxonomy of *Pieris* s. l. is still lacking.

This paper's aim is to conduct a comprehensive review of publicly available genetic data and existing literature related to the taxa included in *Pieris* s. l.*,* which are found in the Holarctic and Afrotropical regions. It will specifically focus on molecular and anatomical data to gather as much information as possible on these taxa. The ultimate goal is to analyze these data, deduce the relationships between these taxa, and propose a comprehensive taxonomic arrangement of the various generic and infrasubgeneric groups within *Pieris* s. l.. This research will contribute to a better understanding of the taxonomic relationships and evolutionary history of these butterflies, and provide valuable insights into the diversity and classification of the *Pieris* s. l.

2. Material and Methods

2.1 Molecular data search: Sequences of the complete mitochondrial genome (CMG) and/or cytochrome c oxidase subunit I (COI) gene were searched in the National Center for Biotechnology Information (NCBI) Taxonomy database under "*Pieris"* (NCBI:txid7115).(Schoch et al., 2020) CMG and COI sequences of *Iphiclides podalirius* (Linnaeus, 1758) (NCBI:txid110791) *Pontia* (*Baltia*) *butleri* (Moore, 1882) (NCBI:txid320288), *Pontia* s. str. *callidice* (Hübner, [1800]) (NCBI:txid320238) and *Pontia* s. str. *edusa* (Fabricius, [1777]) (NCBI:txid345723) were chosen as outgroups. For each taxon, at least one sequence was copied into a dedicated spreadsheet, where was also recorded the collecting place and date of collection of each specimen, if available. Sequences referring to taxa linked to wrong or doubtful collecting data, according to the original description or relevant literature were excluded.

2.2 Phylogenetic analysis

All phylogenetic analyses were carried out with MEGA 11 software (Tamura et al., 2021) using either the Maximum Likelihood method (ML), the Minimum Evolution method (ME), or the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) with 1000 bootstrap replicates to estimate branch support. For analyses carried out with the ML method, initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura-Nei model and then selecting the topology with superior log likelihood value (Tamura & Nei, 1993). In ME and UPMGA analyses, the evolutionary distances were computed using the p-distance method and are in the units of the number of base differences per site (Nei & Kumar, 2000). The ME tree was searched using the Close-Neighbor-Interchange (CNI) algorithm at a search level of 1 (Rzhetsky & Nei, 1992). The neighbor-joining algorithm was used to generate the initial tree (Saitou & Nei, 1987). The methods were differentially employed to gather a richer informational output from the analysis of each group of taxa (Mount, 2008; Munjal et al., 2018).

Molecular distances between taxa were also estimated by calculating the Kimura two-parameter distances (K2P) using MEGA 11 software (Kimura, 1980; Tamura et al., 2021). The K2P distances, in percentage, were interpreted as indicative of generic, infrasubgeneric, specific, or infrasubspecific rank, by adopting the previously reported cut-offs of >10%, 4-10%, 2-3%, and <2%, respectively (Hebert et al., 2003).

Phylogenetic analysis of CMG sequences was first performed on all taxa labeled as "*Baltia* Moore, 1878", "*Pieris*", or "*Pontia*", included in NCBI's Taxonomy database (Schoch et al., 2020). Then, COI sequences of all taxa included in "*Pieris*" (NCBI:txid7115) were analyzed. Unfortunately, it was not possible to align together all the COI sequences of the taxa belonging to the "*napi*-group", as for many of them only a partial (either 5' or 3' end) sequence of COI was available, thus lacking sufficient overlap with other sequences. For this reason, and to retain the highest number of taxa in the study, we separately analyzed a first set of sequences for which was possible an alignment of the 5' end (COI-A) and a second set of all sequences including only the 3' end (COI-B). The latter set contained only the taxa of the *napi*-group, including all the available Asian taxa. *Iphiclides podalirius* (L.) and *T. naganum* (Moore) were respectively selected as outgroups for COI-A and COI-B sets. Eventually, we compared and discussed the results of all the evolutionary analyses.

2.3 Comparison of molecular results and published anatomical data: Descriptions and graphical reproductions of phenotypical features of systematic importance were gathered after a bibliographic search. Specifically, reference works were selected for the analysis of either wing venation (Bernardi, 1958; Dixey, 1894; Grote, 1900), androconial morphology (Dixey, 1894; Tadokoro et al., 2016; Tadokoro, Shimokama et al., 2013, 2014; Warren, 1961, 1963), and ♂ and ♀ genitalia (Drohsin, 1933; Eitschberger, 1983; Ge et al., 2023; Huang , 2019; Mariani, 1937). Description and representation of these structures for each group of taxa were studied, according to the phylogenetic relationships highlighted in the phylogenetic analysis. The results were then discussed to validate our molecular data.

3. Results

3.1 Collected sequences : After manual scrutiny of all the available sequences on NCBI's Taxonomy database, a total of 72 sequences (10 CMG and 62 COI) of *Pieris s.l.* (representing 52 taxa), 2 of *Pontia* s. str. (representing 3 taxa), 1 of *Pontia* (*Baltia*), and 2 of *I. podalirius* (L.) were selected. COI-A and COI-B were respectively composed of 51 and 23 sequences, including the outgroups. Relevant information on the specimens included in the study is summarized in Table 1.

3.2 Molecular phylogeny

3.2.1 Relationship between *Pieris* and *Pontia*: From the evolutionary analyses of CMG sequences (supplementary fig. 1), *Pieris* s. l. was confirmed as the sister group of *Pontia*, (including the subgenus *Baltia*) (Ding & Zhang, 2017; Zhang et al., 2021). The median K2P between the two groups was 11%, ranging between 10.3% and 12.3%. For comparison, *I. podalirius* (L.) showed a median K2P of 18.6% from either group (Supplementary Table 1).

3.2.2. Relationship between infrasubgeneric taxa: In the analysis of COI sequences (fig. 1A), *Pieris s.l.* emerged as a polyphyletic group composed of seven major clusters of taxa, with a K2P ranging between 8% and 15%. (Table 2, Supplementary Tables 1-2) and at least 17 valid species (i.e. K2P>2%, Table 1). The seven clusters generally showed strong internal support (bs>87), while the connection between different branches showed a variable but generally weaker support (39<bs<60). Overall, phylogenetic analysis and K2P values suggested the division of *Pieris s.l.* into 3 genera and 7 subgenera as follows:

1) *Talbotia* Bernardi (1948);
2) *Pieris* (***Afropieris***) **subgen. nov.**;
3) *Pieris* s. str. Bernardi (1947);
4) *Artogeia* (***Bernardia***) **subgen. nov.**;
5) *Artogeia* (***Mariania***) **subgen. nov.**;
6) *Artogeia* (***Tadokoroa***) **subgen. nov.**;
7) *Artogeia* (*Sinopieris*) Huang, 1995 **comb. nov.**;
8) *Artogeia* s. str. Verity, 1947 **comb. rev.**, including a few species, and a large group of taxa with K2P<2% that were included into the (superspecies-*napi*).

Talbotia naganum (Moore) was the first to branch, alone, from the concatenated tree. This taxon was genetically well-separated from others (K2P range: 10-12%, Table 2), validating the monotypic genus *Talbotia* (Bernardi, 1958).

The genus *Pieris* was the second to branch. Interestingly it split into a first sub-branch containing only *brassicoides* Guérin-Méneville, 1849 (K2P of 6% from *brassicae*), for which it was erected the monotypuc subgenus *P.* (***Afropieris***) **subgen. nov..** In the second sub-branch (i.e. *Pieris s.str.*), *deota* (de Nicéville, [1884]) was the first species to stem after *brassicoides*, having a K2P between 2 and 2.9% from other *Pieris* s. str. species at ML but not ME analysis. All other taxa clustered into two closely-related groups i.e. *brassicae* + *azorensis* Rebel, 1917 + *ottonis* ottonis Röber, 1907 (intertaxa K2P range: 0.4-1.3%), and *cheiranthi* (Hübner, 1808) + *wollastoni* (Butler, 1886) + *banchoavensis* Pinker, 1968 (intertaxa K2P range: 0.7-1%), reflecting the Eurasian distribution of the former group, and the geographic isolation in the Canary Islands of the latter (fig. 1A, Supplementary fig. 2). Their intertaxa K2P <2%, confirmed the specific rank of both *brassicae* and *cheiranthi* and the infrasubspecific rank of *azorensis* and *ottonis* and *wollastoni* and *banchoavensis* respectively.

The third major branch of the tree showed an intertaxa K2P ≤10%, but higher distances from both *Talbotia* and *Pieris*. For this reason, the genus *Artogeia* was resurrected. The sub-branches of this last suggested its division into five different subgenera.

The subgenus *A.* (***Bernardia***) **subgen. nov.** was erected to include taxon *krueperi* Staudinger, 1860, clustering alone, as the first sub-branch of *Artogeia* (K2P of 9% from other *Artogeia* subgenera. The second sub-branch of *Artogeia* included 10 taxa for which it was erected the subgenus *A.* (***Mariania***) **subgen. nov.** Based on their K2P, four of these taxa deserve a species rank [i.e. *P. mannii* (Mayer}*, P. rapae* (L.)*, canidia,* and *palaearctica* Staudinger, 1886). Of interest, the two latter Asiatic taxa, clustered together and separately from the cosmopolitan (but originally Middle-eastern) *rapae* and the euro-mediterranean *mannii*. The internal K2P for the two subgroups is 4% between *rapae* and *mannii*, 2.4%, and between *canidia* and *palaearctica*. The K2P distance between subgroups was around 5% (Ryan et al., 2019). The third sub-branch of *Artogeia* was composed of the highly phenotypically divergent taxon *extensa* Poujade, 1888 (K2P 10% from *napi*), included in the novel subgenus *A.* (***Tadokoroa***) **subgen. nov..** Then branched together *davidis*, *gyantsensis* Verity, 1911*,* and *kozlovi* (Alphéraky, 1897), included into the subgenus *A.* (*Sinopieris*) **comb. nov**., previously considered as a separate genus.

Eventually, branched the subgenus *Artogeia* s. str. **comb. rev.**, the richest in species and infrasubspecific taxa of the whole genus. This subgenus was composed of a few well-distinct species, i.e. *melete* Ménétriès, 1857, *melaina* Röber, 1907*,* and *ergane* (Geyer). After these species, the analysis showed a progressive lowering of either K2P (<2%) and of bs values between other taxa, highlighting their increasing genetic similarity. Nevertheless, these taxa showed remarkable phenotypical differences (see below) and were not merely acceptable as subspecies of the type-species *napi.* For this reason, this point was considered the beginning of superspecies-*napi* (*L.*) (Ge et al., 2023; Tadokoro et al., 2014; Tadokoro, Shimokama et al., 2013).

ML on COI-A and UPGMA analysis of COI-B, highlighted a tendency for [superspecies-*napi* (L.)] taxa to merge into three distinct species-groups grossly based on their geographic origin (Supplementary fig. 2A, fig. 1B): (1) a first and smaller species-group, (*marginalis* species-group) was composed of northern American taxa branching separately after the *Artogeia* s. str. **comb. rev.** progenitor and included: *virginiensis* Edwards, 1881), *mcdunnoghi* Remington, 1954, *microstriata* Comstock, 1924, *venosa* Scudder, 1961, and *reicheli* Eitschberger, 1983. These taxa showed a shared ancestor at ME, while in the ML tree, they branched separately; (2) the second, species-group, (*bryoniae* species-group), included all eastern Asiatic taxa [i.e. *dulcinea* (Butler, 1882), *erutae* Poujade, 1888, *kneitzi* Eitschberger, 1983, *latouchei* Mell, 1939, and *reissingeri* Eitschberger, 1983, the central Asian *narina* Verity, 1908 *bryonaie* (Hübner, [1806]), and *wolfsbergeri* Eitschberger, 1983 from Europe, *oleracea* (Harris, 1829) from British Columbia, and "*marginalis* Scudder, 1961" (see below), and *hulda* Edwards, 1869, both from Alaska; (3) finally, the *napi* species-group grouped the majority of Euro-mediterranean taxa (i.e. *adalwinda* Fruhstorfer, 1909, *balcana* Lorković, 1968, *keskuelai* Eitschberger, 2001, *lappona* Rangnow, 1935, *napi* (L.), *pseudorapae* Verity, 1908, *segonzaci* Le Cerf, 1923), together with *muchei* Eitschberger, 1983, *and ochsenheimeri* Staudinger, 1866 from Central Asia. Based on the analysis of two different

COI sequences, *euorientis* Verity, 1908, clustered either in the *bryoniae* (at ML) or *napi* species-group (at UPMGA), reflecting the scarce knowledge on the likely multiple taxa of *Artogeia* s. str., inhabiting the area between southern Siberia and Mongolia.

To investigate the relationships between the American and European taxa included in the "Asiatic" *bryoniae* species-group and the Turkestanian *ochsenheimeri* included in the Euro-mediterranean *napi* species-group, were also calculated the K2P distances between taxa grouped according to their geographic origin i.e. America (*hulda*, *macdunnoughii*, *microstriata*, *oleracea*, *reicheli*, *venosa*, and *virginiensis*), (Central- and Eastern) Asia (*dulcinea*, *erutae*, *euorientis*, *kneitzi*, *latouchei*, *muchei*, *narina*, *ochsenheimeri*, and *reissingeri*), and Europe, including Middle East and northern Africa (*adalwinda*, *balcana*, *bryonaie*, *keskuelai*, *lappona*, *napi*, *pseudorapae*, *segonzaci*, and *wolfsbergeri*). KP2 between taxa within these geographic groups, ranged respectively between 0-2.8%, 0.1-2%, and 0-2.3% (Supplementary Tables 2 and 3) while comparing the groups pairwise, KP2 ranges were 0.2-2.5% between American and Asiatic taxa, 0.6-2.6% between American and European taxa, and 0.5-2.6% between Asian and European taxa. Of interest, in each geographic group emerged at least one highly divergent taxon i.e. *olearacea, hulda,* and "*marginalis*" (KU875897.1) within American taxa (showing a maximum KP2 from *virginiensis*), *ochsenheimeri* within Asian taxa (maximum KP2 from *dulcinea*), and *bryoniae* and its subspecies *wolfsbergeri* within European taxa (maximum KP2 from *napi,* Supplementary Tables 2-3), reflecting their location in the three species-groups at the phylogenetic analysis.

3.3 Morphological correlations

3.3.1. Wing venation : The wing venation pattern in *Pieris s.l.* and *Pontia* species exhibits similarities. In *Pieris* s. l., the forewing cell is typically at least as long as half of the wing's length and generally includes four radial veins. These radial veins consist of the separated R3 (vein 9) and the fused R4-R5 (veins 8+7), all of which arise from the cell (Bernardi, 1947b; Della Bruna et al., 2004; Dixey, 1894; Grote, 1900).

However, in *Pieris* s. str. and *Artogeia* s. str. **comb. rev.**, vein R3 can occasionally be fused with R4-R5. For instance, *P. brassicae* and *A. (Sinopieris) stoezneri* may exhibit three radials, while *deota, cheiranthi, davidis, dubernardi, kozlovi*, and *venata* typically have four radials (personal observation). Moreover, some *Artogeia* species with four radials (e.g. *napi, erutae, melaina*), have a very short vein R3 (personal observation), possibly indicating a tendency toward the complete fusion of veins R5, R4, and R3, as previously highlighted (Grote, 1900). In *Pontia* the forewing cell is slightly shorter than the cell.

Overall, the pattern of wing venation is valuable to distinguish taxa at a genus or suprageneric rank but is of lesser significance for distinguishing infrasubgeneric taxa within *Pieris* s. l. On the other hand, the number of radial veins has a strong taxonomical significance in *Pontia*. Indeed, subgenera *Pontia* s. str. (including taxon *santamarta* Ackery, 1975), and *P.* (*Baltia*), have 4 radial veins, while there are only 3 in *Pontia* (*Pontieuchloia*) Verity, 1929 and *Pontia* (*Sisymbria*) Zhang, 2021 with fused vein R3-R4-R5 (Bernardi, 1947b; Della Bruna et al., 2004; Dixey, 1894; Grote, 1900).

3.3.2. Androconial morphology: The literature distinguishes three different morphological types of androconia in *Pieris* s. l. (Fig 3): (1) small, similar to other wing scales, characterized by a lamina shaped as an irregular convex pentagon with parallel sides; (2) larger and different from the other scales, featuring an elongated lamina, slightly cuneiform or dacriform; (3) medium-sized and markedly different from other wing scales, with an ampulliform or piriform lamina, observed exclusively in *Artogeia*. (Warren, 1961).

Androconia of the first type are described in *Talbotia naganum* and are similar to those of *Pontia* species (with the notable exception of *callidice*, lacking androconia) (Bernardi, 1958, 1947b; Dixey, 1894, 1932). Androconia of the second type are exclusive to species of the genus *Pieris,* while *Artogeia* species have androconia of the third type. In comparison to other subgenera of *Artogeia*, in both *A.* (***Bernardia***) **subgen. nov.**, and *A.* (***Mariania***) **subgen. nov.**, the distal end of the lamina is narrower compared to its proximal part (i.e. more distinctively ampulliform). However, the length of the lamina is considerably shorter in the former subgenus compared to all other genera and subgenera of *Pieris s.l.* (Warren, 1961). In subgenera *A.* (***Todokoroa***) **subgen. nov.**, *A.* (***Sinopieris***) **comb. nov***.,* and taxa other than (superspecies-*napi*) of *Artogeia* s. str*.,* the lengths of the lamina, the arrangement of its "arms" (cornua of Dixley, 1932), and the size of the scent cell hold systematic significance (Tadokoro et al., 2016; Tadokoro, Shimokama et al., 2013; Tadokoro, Wang, et al., 2013). For instance, compared to *napi*, *extensa* has a much shorter and stockier lamina with a smaller scent cell, while *dubernardi* features a more elongated lamina, a medium-sized scent cell, and "open arms" (everted cornua) (Tadokoro et al., 2016). Interestingly *melete* has a lamina similar to other *Artogeia* s. str. **comb. rev.** species, but with a notably larger scent cell (Tadokoro, Shimokama et al., 2013). The same feature was recently reported also in *ajaka* and *melaina*, even though their scent cells were slightly smaller compared to *melete* (Das et al., 2021; Tadokoro et al., 2017). Finally, among the (superspecies-*napi*), androconia are stockier in species related to *bryoniae,* comparing to those related to *napi*, even though more specific and reproducible data are lacking (Warren, 1961). Overall, androconia have a value in the distinction of genera, subgenera, and group of species within *Pieris* s. l.

3.3.3. ♂ genitalia: The valva represents the ♂ genitalia's structure with the highest systematic value in *Pieris* s. l. (fig. 3). This sclerotized structure typically exhibits a subtriangular to subtrapezoid shape, often considerably longer than its height, and with a rounded distal end—a common characteristic among most Pieridae (including *Pontia*). However, a noteworthy exception exists in both, *Talbotia* and *Pieris,* where the valva's distal end is pointed. In *Talbotia*, it assumes a subtriangular shape, while in *Pieris*, it has a sub-trapezoidal appearance. Interestingly, *P.* (*Afropieris*) *brassicoides* displays a valva with a rounded distal end, similar to *Artogeia* (Bernardi, 1958; Chang & Chang, 1963).

The morphology of the aedoeagus, tegumen, and uncus has been reported as highly variable both across and within species, with seemingly limited systematic relevance based on available data. Recently, the tegumen, specifically its convexities and processes, has been recognized as a valuable feature for distinguishing some *Artogeia* s. str. **comb. rev.** species (Ge et al., 2023). Similarly, the thickness of the uncus and the ratio between tegumen and uncus lengths appear to be of taxonomic interest, although the existing literature on this subject remains limited (Ge et al., 2023; Tadokoro et al., 2016; Tadokoro, Shinkawa et al., 2013).

3.3.4. ♀ genitalia. The analysis of ♀ genitalia, particularly the signum ("lamina dentata" of Mariani, 1937) holds significant taxonomic value for distinguishing between genera and subgenera and can occasionally help in species determination (fig 3). In *Pieris* s. l., the signum is consistently positioned on the right dorsolateral side of the corpus bursae, anterior to the entrance of the ductus bursae. It typically consists of two wings ("alette" as described by Mariani) that may be separated by a central unsclerotized and spineless linear space ("spazio non aculeato" according to Mariani) (Mariani, 1937).

The shape of the signum variues among groups within *Pieris* s. l. (Chang & Chang, 1963; Mariani, 1937; Robbins & Henson, 1986).:

1. In *Talbotia*, it is subtrapezoidal.
2. In species belonging to *Pieris* and *Artogeia* (***Bernardia***) **subgen. nov.**, it is condiform.
3. In those belonging to *A.* (***Mariania***) **subgen. nov.**, it appears grossly oval.
4. In *A.* (***Todokoroa***) **subgen. nov.**, *A.* (***Sinopieris***) **comb. nov.**, and *Artogeia* s. str. **comb.rev.**, it is elongated subsagittate/cordiform, often extending into a long, spineless process known as the flagellum ("flagello" by Mariani or "tail" as described by Chang.

At the infrasubgeneric level, the shape of the signum remains relatively constant, although some exceptions have been noted: in *A.* (***Mariania***) **subgen. nov.**, *rapae* and *mannii* have an oval-shaped signum, while *canidia* displays a shield-shaped signum with rounded sides and defined concavities on the longitudinal edges. In these species, the signum lacks the central unsclerotized spineless space. The signum of *palearctica* is not described in the literature. In *tadjika*, a rare species possibly also belonging to *A.* (***Mariania***) **subgen. nov.**, the signum is longitudinally flattened and subcordate but still entirely sclerotized and covered in spines, appearing intermediate between the signum of *Pieris* or **A. (*Bernardia*) subgen. nov.** and that of *A.* (***Mariania***) **subgen. nov.** In *A.* (***Tadokoroa***) **subgen. nov.**, the signum's shape resembles that of *Artogeia* s. str. **comb. rev.** but features a broader central spineless space. In *A.* (***Sinopieris***) **comb. nov.**, the signum exhibits variable shapes, being lanceolate in *wangi* and *dubernardi* and rounded in *kozlovi* and *gyantsensis* (Bernardi, 1947b; Ge et al., 2023; Huang, 2019; Mariani, 1937).

In summary, the signum is highly valuable for distinguishing between genera and subgenera within *Pieris* s. l. but has limited significance in the differentiation of species. Notably, Ge et al. (2023) conducted a systematic examination of the sterigma in *Artogeia* species from Asia, revealing significant differences across these species (Ge et al., 2023). This is particularly noteworthy considering the previously described scarcity of differences in these structures among *Pieris* and *Artogeia* species (Lagnel, 1966).

4. Discussion: *Pieris* s. l. represents a substantial group within the Pieridae family, with its primary center of species diversity located in central and eastern Asia. This group encompasses a wide range of species, including cosmopolitan agricultural pests and highly localized alpine taxa. In this study, the relationship between *Pieris* s. l. and its sister-group, *Pontia*, was analyzed and confirmed. Furthermore, it delves into the previously unexplored phylogenetic relationships among different taxa within *Pieris* s. l. , utilizing evolutionary analysis of CMG and COI sequences (table 2, fig 3) (Bernardi, 1947b; Zhang et al., 2021). The findings from these evolutionary analyses have led to the proposition of several taxonomic changes within *Pieris* s. l., including the confirmation, resurrection, or establishment of three distinct genera, six subgenera, and the identification of one superspecies (fig 3, table 3). This detailed taxonomic arrangement is underpinned by a comprehensive review of anatomical features that were previously deemed significant for taxonomic classification (Bernardi, 1958; Geiger & Shapiro, 1992). In the subsequent sections, we will provide a comprehensive overview of the systematics, biogeography, anatomical characteristics, and unresolved taxonomic matters pertaining to each relevant taxon.

4.1. Genus *Talbotia* Bernardi, 1958: Type-species: *Mancipium naganum* Moore, 1884; J. Asiatic Soc. Bengal **53** Part II (1): 45.

In the concatenated tree, *T. naganum* (Moore) was positioned as the outermost taxon within the *Pieris* s. l. group. It forms a sister-group with *Pieris* and *Artogeia*, collectively representing the sister-group of *Pontia* (Ding & Zhang, 2017; Wei et al., 2023). *Talbotia naganum* (Moore) is distributed across India (Assam), Myanmar, southern and eastern China, Vietnam, Laos, and Taiwan, with four recognized subspecies: *cisseis* Leech, 1890, *pamsi* (Vitalis de Salvaza, 1921), *karumii* Ikeda, 1937, and *aurelia* Monastyrskii & Vu, 2021. Notably, *T. naganum* (Moore), inhabits the southern fringes of the likely speciation center of *Pieris* s. l. and is estimated to have speciated approximately 34 million years ago (Braby et al., 2006).

The proposal to include *Talbotia* within the genus *Pieris* has been a subject of discussion, primarily due to their similar appearance. However, this notion was ultimately rejected based on distinctive anatomical characteristics unique to *Talbotia*. These distinguishing features include (Bernardi, 1958):

1. Forewing Venation: *Talbotia* follows the general schema with four radial veins.
2. Androconia: *Talbotia*'s androconia are small, undifferentiated, and virtually indistinguishable from those of *Pontia*.
3. Valva: The valva in *Talbotia* is subtriangular and distally pointed, a trait shared with *Pieris* s. str. (such as *Ganyra* Billberg, 1820, and *Belenois* Hübner, [1819]).
4. Signum: ♀ *Talbotia* individuals possess a subtrapezoidal signum that is fully covered with spines, differing from *Pieris* s. l. species (Bernardi, 1958).

Another noteworthy feature of *Talbotia* is the presence of a discal spot at the distal end of the forewing cell, a characteristic typically associated with *Pontia*. This feature is absent in other *Pieris* s. l. species, except for *A.* (***Sinopieris***) **comb. nov.** Additionally, *Talbotia* ♂♂ exhibit two premarginal spots in spaces Cu2 (1b) and M2 (3), which in ♀♀ merge into two black bands following the anal vein (1) and M3 (4) from the base of the wing (fig 3).

4.2. Genus *Pieris* Schrank, 1801: Type-species: *Papilio brassicae* Linnaeus, 1758; Systema Naturæ (Ed. 10) **1**: 467.

The genus *Pieris* comprises a group of medium-sized butterflies characterized primarily by two distinctive features: (1) elongated dacriform androconia and (2) subcordate signa with a central longitudinal spineless area, notably lacking the flagellum. In all species within this genus, the upper surface of the wings displays either a white or pale yellow ground colour, devoid of dark scales covering the veins. Additionally, the forewing typically exhibits four radial veins, although an exception exists with *P. brassicae* (L.). Interestingly, in contrast to *Artogeia*, *Pieris* species lay their eggs in clusters. Phylogenetic analysis has provided robust support for the recognition of four distinct species, with one of these species demonstrating greater genetic divergence from the others, warranting its placement in a separate subgenus.

4.2.1. Subgenus *Pieris* (*Afropieris*) subgen. nov.: Type-species: *Pieris brassicoides* Guérin-Méneville, 1849; Voyage en Abyssinie: 365.

Remarkable from many points of view, *brassicoides*, is the only *Pieris* species inhabiting Sub-Saharan Africa. It is limited to central-eastern Africa and has two subspecies: *brassicoides* from Ethiopia and Eritrea, and *marghanita* Hemming, 1941, from Tanzania (Storace, 1956). Even though its speciation remains a biogeographical dilemma, *brassicoides* belongs to the genus *Pieris* and represents its most divergent taxon (K2P: 6-7% from *Pieris* s. str. species). *Pieris* (***Afropieris***) **subgen. nov.** displays unique features among *Pieris* species, such as (1) the presence of heavily black-coloured veins in the hindwing underside, and (2) the absence of a distal tip of the valva in ♂. Nevertheless, size, wing shape, as well as androconia and signum morphology are comparable to those seen in other *Pieris* species (Lagnel, 1966)

4.2.2. Subgenus *Pieris* s. str.: Type-species: *Papilio brassicae* Linnaeus, 1758; Systema Naturæ (Ed. 10) **1**: 467.

This subgenus was first proposed by Bernardi (1947) and subsequently by Korb & Bolshakov (2011), to separate the type-species *brassicae* from palaearctic species with different androconia and genital morphology -i.e. *rapae*- and *napi*-related species-, included in the subgenus "*Pieris* (*Artogeia*)". In this study, evolutionary analysis provided strong support for separating *Pieris* from *Artogeia*. Furthermore, it confirmed the existence of three distinct species within the former subgenus, namely *brassicae*, *cheiranthi*, and *deota* (K2P range: 2-2.9%).

Anatomically, species within the subgenus Pieris s.str. are characterized by the absence of black-coloured veins on both sides of their wings. They possess a valva with a subtrapezoidal shape and a pointed distal end (fig 3). Except for the cosmopolitan and multivoltine species brassicae and its subspecies, this subgenus comprises taxa. found in various regions, including central Asia (*deota*), Azores (*azorensis*,), Madeira (*wollastoni*, currently extinct), or Canary Islands (*cheiranthi*, and *banchoavensis*).

Pieris s. str. *deota* diverged after *P. brassicoides* at ML analysis (bs: 100) and after *P. cheiranthi* and related taxa at ME analysis (bs: 36), as previously reported, albeit with limited support (bs: 60, Wiemers: Die Tagfalter der Kanaren und Madeiras. Available online at: https://www.ufz.de/export/data/10/239123_S5_Wiemers.pdf). However, considering the characteristics and geographical distribution of *P. deota*, the ML results are the most plausible. An associated taxon that could not be included in COI analysis is *P. eitschbergeri* Lukhtanov, 1996. This is a highly localized butterfly from Kyrgyzstan, and is distinguished from *P. deota* by differences in wing colour patterns and the morphology of ♂ and ♀ genitalia. Due to limited available material and literature, further investigation is required to determine whether *P. eitschbergeri* represents a distinct species, a subspecies, or an aberrant form of *P. deota* (Lukhtanov, 1996).

The next taxon to branch from the concatenated tree was *P. brassicae*, a widely recognized and nearly cosmopolitan pest that has extended its range from the Palearctic region to Africa, the Americas, and New Zealand. It is believed to have likely speciated in Europe and subsequently dispersed through agricultural trade routes, much like *P. rapae* (Ryan et al., 2019). Due to limited genetic diversity and relatively little intraspecific phenotypic variation, defining the subspecies within brassicae (e.g. *azorensis*, *nepalensis* Gray, 1846 *ottonis,* and others) proved challenging during COI sequence analysis. Similarly, evolutionary analysis provided substantial support for recognizing *cheiranthi* as a distinct species. This larger species is native to the European Atlantic islands. On the other hand, *banchoavensis* from La Palma and the now-extinct *wollastoni* from Madeira are likely subspecies of *cheiranthi*. Notably, *wollastoni*, despite its habitus resembling brassicae more closely, exhibited a lower K2P genetic distance from *cheiranthi* (approximately 0.6-1%) compared to *brassicae* (approximately 2.3-3%). Hence, it was considered a subspecies of the latter (Wiemers: Die Tagfalter der Kanaren und Madeiras. Available online at: https://www.ufz.de/export/data/10/239123_S5_Wiemers.pdf).

4.3. Genus *Artogeia* Verity, 1947

Type-species: *Papilio napi* Linnaeus, 1758; Systema Naturæ (Ed. 10) **1**: 467.

The inclusion of some *Pieris s.l.* species in the separate genus *Artogeia* has been a subject of extensive discussion in the past. Verity issued the subgenus "*Pieris (Artogeia)"* in 1947, in its work on Italian Rhopalocera, based on *napi* as the type species, but also encompassing *rapae*. Subsequently, Kudrna (1974) and Higgins (1975) elevated *Artogeia* to the generic rank. However, Kudrna later reclassified it as a subgenus (Blab & Kudrna, 1982). Notably, Feltwell & Vane-Wright (1982) raised the possibility that *Artogeia* might not constitute a monophyletic group (see also Robbins & Henson, 1986).

This study contributes new phylogenetic data to complement the existing anatomical evidence. Previous authors had already identified *Artogeia* butterflies within *Pieris* s. l. based on distinctive characteristics, including (1) unique androconial morphology and (2) the presence of a distally rounded valva. Although there are variations in the morphology of the signum and the external appearance of different species within *Artogeia*, they share the common behaviour of laying eggs individually, as opposed to in clusters as observed in *Pieris*.

All *Artogeia* species in this study displayed K2P genetic distances exceeding 10% from both *Talbotia* and *Pieris*, emphasizing their distinctiveness. Additionally, the analysis revealed a progressive clustering of *Artogeia* species into five subgenera, with pairwise K2P genetic distances ranging between 7% and 10% and varying levels of support (bs range: 49-91).

4.3.1. Subgenus *Artogeia* (***Bernardia***) subgen.nov.

Type-species: *Pieris krueperi* Staudinger, 1860; Wiener entomologische Monatsschrift **4** (1): 19.

In the tree resulted from ME analysis, *krueperi* appeared as a solitary branch, diverging after *Pieris* **s. str.** (bs: 55). Conversely, in the ML tree, *krueperi* clustered with ***A.*** (***Mariania***) **subgen. nov.** (bs: 49). Regardless of its specific placement, *krueperi* consistently emerged as a highly genetically distinct species, characterized by (1) its unique wing colour pattern, featuring grayish or greenish patches on both sides of the hindwing, and (2) the distinctive morphology of the signum, which is cordiform and possesses a central unsclerotized, spineless space resembling that of Pieris. Additionally, the forewing of krueperi exhibits four radial veins. The ♂ genetic distance (K2P) between *krueperi* and *rapae* was calculated to be 8.7%, justifying the establishment of separate subgenera. For *krueperi* and its closely related species, the subgenus *A.* (***Bernardia***) **subgen. nov.**, is proposed, paying tribute to the contributions of Georges Bernardi (1922-1999), a distinguished Russian-French entomologist who made significant advancements in the comparative anatomy and systematics of *Pieris* s. l. and *Pontia*.

Regrettably, only COI sequences from the bi- to multivoltine European *krueperi* Staudinger, 1860 were available for analysis, and sequences from subspecies *devta* (De Niceville, 1884) from Turkestan and *persica* Staudinger, 1886 from Ladakh could not be obtained. Additionally, COI sequences for *mahometana* (Grum-Grshimailo, 1888), likely representing a distinct (larger) species with characteristic wing markings inhabiting high-altitude mountain regions between Tajikistan and Afghanistan, could not be retrieved.

4.3.2. Subgenus *Artogeia* (***Mariania***) subgen.nov.

Type-species: *Papilio rapae* Linnaeus, 1758; Systema Naturæ (Ed. 10) **1**: 468.

A fourth monophyletic clade which received strong support in both ME and ML trees (bs range: 95-100), emerged following *A.* (***Bernardia***) **subgen. nov.**. Due to its well-supported status, significant K2P genetic distances, and distinctive anatomical characteristics of the included taxa, a separate subgenus named *A.* (***Mariania***) **subgen.nov.** has been established. This subgenus is dedicated to Mario Mariani (1898-1965), an Italian lepidopterologist and medical entomologist renowned for his work on the ♀ genital anatomy of *Pieris* and ***Artogeia***, where he emphasized its systematic importance (Mariani, 1937).

Phylogenetic analysis involved the study of ten taxa within *A.* (***Mariania***) **subgen. nov.**, which were further organized into two subgroups comprising four bi- to multivoltine species. The first subgroup consisted of *P. rapae* (Linnaeus, 1758) and *mannii* (Mayer, 1851), while the second included *canidia* (Spaarman, 1768) and *A.* (***Mariania***) *palaearctica* Staudinger, 1886 **stat.** et **comb. nov.** Additional sequences of infrasubspecific taxa clustered as follows: *crucivora* Boisduval, 1836, from Eastern Asia and *debilis* Alphéraky, 1889, from central Asia associated with *rapae; alpigena* (Verity, 1911) and *rossii* (Stefanelli, 1900) with *mannii*; *kaolicola* Bryk, 1946 from Korea with *canidia*; and *indica* Evans, 1926 from Pakistan with *palaearctica* (fig 1). Sequences of *tadjika* Grum-Grshimailo, 1888, a last likely valid species were not available for inclusion in the analysis. Evolutionary analysis suggested a full species rank for *palaearctica* (K2P: 2.4% from *canidia*). *Artogeia* (***Mariania***) *palaearctica* **stat. e comb. nov.** exhibits distinct phenotypic characteristics, including smaller size and less pronounced black markings with smaller black spots in both sexes. The question of whether the subspecies described for *canidia* in central and south-eastern Asia represent actual subspecies of *canidia*, *palaearctica*, or are simply synonyms of them remains to be determined.

Anatomically, *A.* (***Mariania***) **subgen. nov.** is set apart from other *Artogeia* subgenera by its distinctively shaped signum, which also helps in distinguishing the two subgroups, *rapae-mannii* and *canidia-palaearctica* (as mentioned above). Additionally, it possesses more ampulliform androconia compared to the more pyriform androconia of the following subgenera.

Artogeia (***Mariania***) **subgen. nov.** has an interesting biogeography. While *canidia* and *palaearctica* inhabit Asia (ranging from Turkestan to Japan and Southern India) together with *tadjika,* from south-western Tajikistan, *rapae* originated from Middle-East, later spreading in Europe, then to Asia, and more recently to America and Australia, and *mannii* speciated in Europe where it may represent an extinguishing relict (Mariani, 1937; Ziegler & Eitschberger, 1999). Overall the common *A.* (***Mariania***) **subgen.nov.** ancestor may have originated in central Asia, and subsequently dispersed eastward to Japan with *palaearctica* and *canidia*, while also spreading westward with *rapae* into the Middle East and with *mannii* into Europe.

4.3.3. Subgenus *Artogeia* (*Tadokoroa*) subgen. nov.

Type-species: *Pieris erutae var. extensa* Poujade, 1888; Bull. Soc. Ent. Fr. (Ser. 6) **8**: XIX.

The fifth branch of the concatenated tree and the third within *Artogeia* consisted solely of *extensa*, which is the largest among all *Pieris* s. l. species, boasting a wingspan of up to 90 mm. This univoltine to bivoltine species is further divided into three subspecies, each with a distinct distribution within a narrow mountainous region: the nominal subspecies ranges across southern Shaanxi, southeastern Tibet, and northern Myanmar; the smaller subspecies *yunnansia* Tadokoro & Wang, 2014 is found in Yunnan; and the subspecies *bhutya* Talbot, 1939 inhabits northeastern Bhutan (Tadokoro & Wang, 2014).

A comparison of K2P genetic distances between *extensa* and other *Artogeia* subgenera suggested a clear separation (table 2). Additionally, *extensa* exhibited numerous distinctive anatomical characteristics, including:

1. Smaller androconia with a subtriangular shape, less pronounced dilation at their base, and the smallest scent cell in the genus (with an average width of 13 µm in subspecies *bhutya* compared to an average of 23 µm in *erutae*).
2. A larger valva (around 2.5 mm compared to 1.2 mm in *erutae*) that is more convex distally and features an inferior concave sinuosity.
3. A large, subsagittate/cordiform signum with flagellated features similar to those in *A.* (***Sinopieris***) **subgen. nov.** and *Artogeia* s. str. **comb. nov.**, but with a significantly larger unsclerotized and spineless central longitudinal area. (Das et al., 2021; Tadokoro et al., 2017).
4. A larger appendix bursae compared to other species, and forewings that are always 4-veined (Das et al., 2021). These distinctive features justify the creation of a separate subgenus named *A.* (***Tadokoroa***) **subgen. nov.**, honoring Teruo Tadokoro, the Japanese lepidopterologist who has significantly advanced our understanding of Asian *Artogeia* and clarified their complex taxonomy.

4.3.4. Subgenus *Artogeia* (*Sinopieris*) Huang, 1995 comb. nov.

Type-species: *Pieris davidis var. venata* Leech, 1891; Entomologist **24** (Suppl.): 58.

The subgenus *A.* (*Sinopieris*) **comb. nov.** encompasses a group of at least eight univoltine and highly localized species that inhabit the high-altitude mountains of the Himalayan range, spanning regions from Nepal, Sikkim, Tibet, Xinjiang, Qinghai, Gansu, Sichuan, to Yunnan. These butterflies can be divided into two distinct groups based on their wing markings: 1. the *dubernardi*-group including *dubernardi*, *chumbiensis* (de Nicéville, 1897), *kozlovi*, *rotschildi* (Verity, 1911), and *wangi* (Huang, 1998); 2. the *davidis*-group consisting of *davidis*, *stoetzneri* (Draeseke, 1924) and *venata* (Leech, 1891).

The taxonomical history of *A.* (*Sinopieris*) **comb. nov.** has been revised over the years (Tadokoro et al., 2016). Initially, due to their wing colour patterns, (e.g. black-marked upperside veins, black discoidal markings of forewings, and prominent black spot on hindwing space 6), these species were either included in the genera *Pontia* (e.g. *dubernardi*) or *Aporia* (e.g. *davidis*) or even placed alongside *Pontia callidice* whitin the genera *Parapieris* de Nicéville, 1897 or *Synchloe* Röber, 1906. One hundred years after the description of *dubernardi*, Huang erected the genus *Sinopieris*, separating these butterflies from *Pieris, Artogeia,* and *Pontia*. Of interest, despite the genus *Sinopieris* initially included the type-species *gongaensis* Huang, 1995 (synonym of *venata*), *davidis*-group taxa were later excluded as they currently are (Huang, 2019; Tadokoro et al., 2016).

Initially, due to their wing colour patterns, [i.e. *davidis*, *kozlovi*, and (*chumbiensis*) *gyantsensis*] were examined. Notably, in all concatenated trees, these taxa clustered together in a distinct clade after *extensa*. The K2P between *davidis* and *kozlovi* was 5.3%, while 6.7% and 7.1% respectively between each species and *napi*. These data suggest that *A.* (*Sinopieris*) **comb. nov.** is a distinct and possibly polyphyletic subgenus, encompassing both the *dubernardi*- and *davidis*-group. Further research is needed to determine whether certain groups within this subgenus represent superspecies or separate species, as indicated by biogeography and phenotype whether some groups of taxa represent further superspecies (e.g. *dubernardi*, and *kozlovi*) or separated species, as suggested by biogeography and phenotype [e.g. *sherpae* and *lhamo* (Kocman, 1999)].

While wing markings have limited utility in species differentiation due to examples of interspecific overlap or cryptic species (e.g. the geographically separated *kozlovi* and *lahmo* Kocman, 1999), the anatomical characteristics of *A.* (*Sinopieris*) **comb. nov.** can help distinguish it from other *Artogeia* subgenera. Notably, the androconia and signa in this subgenus exhibit various shapes and a wide range of interspecific variation. The shape of the signum resembles that of *Artogeia* s. str. **comb. nov.** but is proportionally much longer in *davidis* and *stoetzneri*, stouter in *venata,* cordiform and stout (*chumbiensis*, *rotschildi*), oval-lanceolate (*kozlovi*), and elongated-lanceolate (*dubernardi, wangi*) (Huang, 2019; Vis & Coene, 2012). Overall, the shape of the signum supports the division of *A.* (*Sinopieris*) **comb. nov.** species into the *dubernardi*- and *davidis*-groups.

4.3.5. The subgenus *Artogeia* s. str. comb. rev. Verity, 1947

Type-species: *Papilio napi* Linnaeus, 1758; Systema Naturæ (Ed. 10) **1**: 468.

The subgenus ***Artogeia*** s. str. **comb. rev.** also known as the "*napi*-*bryoniae*-complex" or "*napi*-group," represents one of the most phenotypically diverse and taxonomically challenging groups within *Pieris* s. l. and also the last to branch from the concatenated tree. These butterflies are primarily found in continental Asia, with only a minority of species colonizing Europe or North America. Phylogenetic data support the polyphyly of *Artogeia* s. str. **comb. rev.** meaning that it consists of a few genetically distant species (i.e. *melete*, *malaina*, and *ergane*), and a large group of sometimes highly localized taxa with very low interspecific K2P (median 1.7%). These closely related taxa are grouped together under the concept of (superspecies-*napi*), following articles 6.2, 10.4, 11.9.3.5, and 23.3.3 of the international code of zoological nomenclature (ICZN). The superspecies concept was previously discussed but not applied for *A.* species (Bowden, 1972). Anatomically, *Artogeia* s. str. **comb. rev.** is characterized by having (1) 3 to 4 radial veins and (2) lacking variation of the shape of valva and signa. However, androconia, and especially the size of the scent cell, differ in taxa other than (superspecies-*napi*). Overall, *Artogeia* s. str. **comb. rev.** appears to be polyphyletic, as suggested in previous studies (Feltwell & Vane-Wright, 1982).

4.3.5.1. *melete* Ménétriès, 1857, *ajaka* Moore, 1865, *melaina* Röber, 1907, and *ergane* (Geyer, [1828])

The bi- to multivoltine taxon *melete*, inhabiting Eastern Asia between Northeastern China, Russian Far-east (Ussur, Sakhalin), Korea, and Japan, was previously considered to include also the sympatric *dulcinea* and the allopatric *erutae*. This confusion relied upon the very pronounced intraspecific difference between the seasonal forms of each species, and the great interspecific similarity between the same seasonal form of each of them (Tadokoro et al., 2014, 2017; Tadokoro, Shimokama et al., 2013). However, COI analysis in this study confirmed *melete* as a genetically distinct species with a K2P of 5.6% compared to *napi* (Ge et al., 2023; Tadokoro et al., 2013). Anatomically, *melete* is characterized by (1) pyriform androconia with scent cells that are twice as large as those of *napi* and (2) the presence of two parallel black slender streaks in the cell at the underside of forewings. This last feature is absent in all other sympatric taxa (Tadokoro et al., 2013).

Taxa *ajaka* and *melaina* are likely two closely related Himalayan species. While *ajaka* is more localized and inhabits only the area between north-western Pakistan and Indian Kumaon, *melaina* is distributed from Indian Garhwal (where it is sympatric with *ajaka*) through all the Himalayas, up to Buthan. Both species are likely bivoltine, and comparing biogeography, date of capture, and descriptions of the specimens, we suspect that the recently described *A. tadokoroi* Das et al., 2021 may represent the spring form of *ajaka* (therefore being a synonym of it). Nevertheless, at COI analysis, was only available a sequence of *melaina* from eastern Tibet. This last showed a K2P of 4.6% from *napi*. Of interest, both *ajaka* (including *tadokoroi*) and *melaina* bear androconia with a distinctively larger scent cell compared to taxa included in (superspecies-*napi*), but smaller compared to those of *melete.* The valva and the signum were otherwise indistinguishable from those of other *Artogeia* s. str. **comb. rev.** species (Das et al., 2021). According to the K2P values, and despite the hierarchy that emerged at UPMGA analysis (fig 2), *melaina* seems more closely related to *melete* and *ergane* than to *napi* (see below). Moreover, it should be determined whether *ajaka* and *melaina* represent another superspecies within the subgenus *Artogeia* s. str. **comb. rev.** given their anatomical similarities.

Artogeia ergane is a small butterfly resembling *rapae* in its colour pattern, but being anatomically and genetically closer to *napi*. The K2P distances between *ergane* and *kozlovi*, *melete*, or *napi* were respectively 7.4%, 5.3%, and 4.3%. Moreover, the structure of either androconia or genitalia of *ergane* was superimposable to that of (superspecies-*napi*) taxa*,* further supporting their proximity, and a higher phylogenetic distance between *ergane* and either *melete* or *extensa* (Eitschberger, 1984; Mariani, 1937; Warren, 1961). *Artogeia ergane* flights with two to three generations between Europe (with the nomotypical subspecies) and Middle-East (Turkey to Lebanon with subspecies *detersa* Verity, 1908) up to Iran (subspecies *elbursina* Bytinski-Salz & Brandt, 1937). Of interest, it is still unclear whether the sympatric "*Pieris higginsi* Warren, 1961", and "*Pieris persis* Verity, 1922", are or not synonyms of *elbursina* due to the scarce knowledge on Middle-Eastern *Artogeia* s. str. **comb. rev.** taxa.

4.3.5.2. (superspecies-*napi*) and its species-groups

Mentioned by other authors as the "*napi*-complex", *Artogeia* s. str. (superspecies-*napi*) is a complex group of butterflies with morphologically with morphologically similar androconia and genitalia*,* and very low intertaxa K2P values. Nevertheless, the high variability in the wing colour pattern, seasonality, and biogeography of the taxa included in this group, stimutaled the description of many distinct species (Eitschberger, 1983). While this study does not provide a comprehensive phylogenetic analysis, it does shed light on the relationships between these taxa based on COI analysis.

Interestingly, superspecies-*napi* taxa showed a tendency to group into 3 species-groups, roughly mirroring their geographical distribution: *marginalis, bryoniae* and *napi* species-group (fig. 2-3, Supplementary fig 2). Interestingly enough, five taxa (e.g*.,* *bryoniae, hulda, marginalis* (KU875897.1), *ochsenheimeri* and *oleracea*) merged with geographically distant peers. In other words, phylogenetically distant taxa of the (superspecies-*napi*) without a common immediate ancestor may have converged in the same continent at a certain point of their evolution.

According to phylogenetic analysis, and K2P values, *marginalis* species-group included *venosa* and *microstriata* both from California and Oregon (separated by a K2P of 0.6%), *virginiensis, macdunnoughii,* and *reicheli,* from the western U.S.A. (the two latter having a K2P divergence from *virginiensis* of 1.8% and 1.7% respectively). Three more American taxa (i.e. *marginalis* (KU875897.1), *hulda,* and *oleracea*), clustered in *bryoniae* species-group. COI sequences of two further American taxa -the isolated *acadica* Edwards, 1881 from Newfoundland and *angelika* Eitschberger, 1983, from Russian Yakutia and Alaska- were not retrieved (Chew & Watt, 2006; Eitschberger, 1983).

This taxonomic and biogeographic tangle is complicated by taxon *marginalis*, a widely distributed butterfly, reported to inhabit most of the east coast of Northern America, with several different subspecies. The specimen included in the phylogenetic analysis (KU875897.1) was from Alaska, where are described at least four subspecies of *marginalis* (i.e. *hulda, guppyi* Eitschberger, 1983*, meckyae* Eitschberger, 1983 and *shapiroi* Eitschberger, 1983 sympatric with *oleracea* (extending toward East up to Quebec and Labrador) and *angelika*. Moreover, it should be noted that in the original description, the four subspecies of *marginalis* from Alaska have more heavily marked and dark-coloured ♀♀, compared with the nominal subspecies, and are much more similar to the sympatric *angelika*, as well as to *narina* from Asia and *bryoniae* from Europe. As a matter of fact, COI sequence KU875897.1, clustered in the *bryoniae* species-group together with *bryoniae*, *narina*, and *oleracea*. We thus hypothesize that the nomotypical *marginalis* included in *marginalis* species-group is phylogenetically distant (and taxonomically unrelated) to its "subspecies" inhabiting Alaska and north-western Canada.

The American taxa were thus divided into two different clusters. The *marginalis* species-group includes the most divergent of (superspecies-*napi*), inhabiting the mountain areas of Eastern U.S.A., southern than 47th parallel north, (i.e. *marginalis)*, and the north-western coast of U.S.A (i.e.*virginiensis*) and having mostly unmarked wings. Taxa clustering in the *bryonaie* species-group (i.e. *oleracea, hulda,* and "*marginalis* KU875897.1", possibly representing taxon *guppyi*), inhabit Alaska and British Columbia northern that 47th parallel north and display a *bryoniae*-like colour pattern in ♀♀.

The second species-group of the (superspecies-*napi*) mostly included Asian taxa. Two smaller clusters could be recognized at the ME tree. The first includes (1) *erutae,* a multivoltine and quite common species from Central China, Northern Vietnam, Myanmar, Laos, and Thailand, presenting with at least two subspecies (nomotypical and *reissingeri* from Hunan, with a K2P divergence of 0%), (2) *latouchei,* a recently recognized multivoltine species from East China, and (3) *dulcinea*, a bivoltine, from Russian Far East and north-eastern China, with its subspecies *kneitzi* from Shaanxi (with K2P divergence from *dulcinea* and *erutae* of 0.26% and 0.92% respectively). Of interest, *knetzi* Eitschberger,1983 was described as a subspecies of *erutae*, then recognized as a subspecies of *dulcinea* by Tadokoro (2014) based on phylogenetic data, and eventually re-considered as a subspecies of *erutae* by Ge et.al (2023), basing on the K2P divergence between the three taxa. According to Tadokoro (2014, 2019) a further taxon to be included in this cluster is *pseudonapi* Verity, 1911, flying between Hokkaido (Japan) Sakhalin and Kurili Islands, and emerged as a valid species after phylogenetic investigations.

The second cluster grouped *bryoniae* (with its Italian ssp *wolfsbergeri*) from the Alps, together with *narina* from Kyrgyzstan and Xinjiang, and the three American taxa *oleracea*, *hulda* and "*marginalis* KU875897.1 c.f. *guppyi*". All these are highly localized, univoltine butterflies, inhabiting high mountain ranges, and have dark-coloured ♀♀. Interestingly, the allopatric *bryoniae* and *narina* displayed a much lower distance to *dulcinea* (K2P of 0.6% for *bryoniae* and 0.7% for *narina*), compared respectively to the sympatric *napi* (K2P=2.3%) or *ochsenheimeri* (K2P=1.8%). Thus, as shown by Ge et al. (2023), *narina* should not be considered a subspecies of *ochsenheimeri*, as proposed by Tadokoro et al. (2014).

Further studies should determine whether phenotypical similar taxa (i.e. *caucasica* Lorković, 1968, *turcica* Eitschberger & Hesselbarth, 1977 and *goergneri* Eitschberger, 1986 from Turkey, *kamtschadalis* Röber, 1907 from Kamchatka, *sheljiuzhkoi* Eitschberger, 1983, and *schintlmeisteri* Eitschberger, 1983 from Russian Far East, *mihon* Yakovlev, 2006 from Mongolia and Xinjiang and *sifanica* Grum-Grshimailo, 1895 from Tibet) also belong to this subgroup.

Eventually, a last taxon, *nesis* Fruhstorfer, 1909 from Japan (except northeastern Hokkaido) was previously shown to merge with

taxa merged in the *bryoniae* species-group, but not included in either of the two above-analyzed clusters (Tadokoro, 2019).
The last species-group of the (superspecies-*napi*) also included two clusters. The last grouped the nomotypical *P. napi* (L.) distributed between the Euro-mediterranean region and a broad portion of Western Russia, *adalwinda* from Fennoscandia, the sympatric *lappona* (likely synonym, with K2P divergence= 0%), *keskuelai* from Polar Ural, *balcana* flying from the Balkans to Middle *pseudorapae* (possibly a synonym of the latter, K2P= 0.15%), and *segonzaci*, limited to the higher Atlas in Morocco. The K2P divergence between *napi* and either *balcana* or *segonzaci* resulted respectively 1% and 0.6%.
A second cluster grouped *ochsenheimeri*, a very rare butterfly inhabiting a limited area between Tadjikistan, Uzbekistan, and Kyrgyzstan, *muchei* Eitschberger, 1983 distributed from East Kazakhstan, Uzbekistan, Tajikistan, and Kyrgyzstan, and the less well-defined *euorientis*, inhabiting (at least) Transbaikal Siberia and northern Mongolia. The K2P divergence between *ochsenheimeri* and *napi*, *muchei,* or *euorientis* were respectively 1.2%, 1.3%, and 1.2%, highlighting the very tight phylogenetic relationship of these taxa. A remarkable taxonomic issue related to the *napi* species-group concern the central Asiatic "*P. bryoniae bryonides* Sheljuzhko, 1910", as combined by Eitschberger (1983) and the sympatric "*P. napi muchei* Eitschberger, 1983". While the first flights between May and June, the second is only found between late June and July, therefore possibly representing two seasonal forms of the same species [i.e. *A.* (*napi*) *bryonides* Sheljuzhko, 1910 **comb. nov.**], as previously hypothesized (Eitschberger, 1983; Eitschberger & Dantchenko, 2014; Tadokoro et al., 2014). Eventually, two last taxa of which COI sequences were unavailable and possibly included in the *napi* species-group are *bowdeni* Eitschberger, 1983 from north-eastern Turkey, and *vitimensis* Verity, 1911 from Transkbajkal Siberia.

5. **Conclusions**: This work contributes to the taxonomy of *Pieris* and related genera by combining mitochondrial sequence analysis and anatomical features of systematic importance and provides a unified vision of this group of butterflies. It reveals that *Pieris* s. l. is polyphyletic, comprising three distinct genera: *Talbotia*, *Pieris,* and *Artogeia*. Molecular data supported the division of *Pieris* into two subgenera, and *Artogeia* into five subgenera, giving consistency to many previously recognized groups of species (e.g. "*rapae*-group", "*dubernardi*-group"). Eventually, the subgenus *Artogeia* s. str. **comb. rev.**, was tentatively dissected, validating and expanding the general schema proposed by Tadokoro et al. and proposing a preliminary split of the (superspecies-*napi*) into three grossly geographically-based species-groups (Tadokoro et al., 2014; Tadokoro, Shimokama et al., 2013).
This study has however several limitations mostly related to its design. As it is based on freely available data, it was not possible to analyse the sequences of relevant taxa (e.g. *mahometana*, *tadjika*, and others likely included in superspecies-*napi*) and sequences other than COI and a few CMG. Moreover, and most regrettably, despite the included sequences being carefully selected and checked for coherence between each taxon, and its locality and date of capture, it was not possible to directly examine and determine each specimen. Finally, the analyses were not specifically designed to deal with the fine taxonomical relationships between superspecies-*napi*-taxa, thus these results must be confirmed in future and more comprehensive studies.

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References

Bernardi, G. (1958): Taxonomie et Zoogeographie de Talbotia naganum Moore (Lepidoptera Pieridae). - Revue Française d'entomologie **25**: 123-128, Caen.

Bernardi, G. (1947a): Recherche de la position sistematique exacte de trois especes de Pierini asiatiques. - Bulletin de La Société Entomologique de France **52** (6), 156-159, Paris.

Bernardi, G. (1947b): Revision de la classification del espèces holarctiques des genres *Pieris* Schr. Et *Pontia* Fabr. (Lep., Pieridae). - Miscellanea Entomologica **44** (1), 65-80, Geneve.

Bowden, S. R. (1972): *Pieris napi* L. (Pieridae) and the superspecies concept. - Journal of the Lepidopterists' Society **26**: 170-173, New Haven, Connecticut.

Braby, M, Vila, R. & N. Pierce (2006): Molecular phylogeny and systematics of the Pieridae (Lepidoptera: Papilionoidea): higher classification and biogeography. - Zoological Journal of the Linnean Society **147** (2): 239-275, London. https://doi.org/10.1111/j.1096-3642.2006.00218.x

Braga, M. P., Janz, N., Nylin, S., Ronquist, F. & M. J. Landis (2021): Phylogenetic reconstruction of ancestral ecological networks through time for pierid butterflies and their host plants. - Ecology Letters 24(10), 2134-2145, Paris. https://doi.org/10.1111/ele.13842

Chang, V. C. S. & Chang, V. C. S. (1963). Quantitative analysis of certain wing and genitalia characters of Pieris in western North America. - The Journal of Research on the Lepidoptera **2** (2): 97-125, Arcadia, California. https://doi.org/10.5962/p.333437

Chew, F. S. & W. B. Watt (2006): The green-veined white (*Pieris napi* L.), its Pierine relatives, and the systematics dilemmas of divergent character sets (Lepidoptera, Pieridae). - Biological Journal of the Linnean Society **88** (3): 413-435, London. https://doi.org/10.1111/j.1095-8312.2006.00630.x

Dapporto, L., Menchetti, M., Voda, R., Corbella, C., Cuvelier, S., Djemadi, I., Gascoigne-Pees, M., Hinojosa, J., Lam, N., Serracanta, M., Talavera, G., Dinca, V. E., & R. Vila (2022: The atlas of mitochondrial genetic diversity for Western Palaearctic butterflies. - Global Ecology and Biogeography 1-7, Hoboken, New Jersey. https://doi.org/10.1111/geb.13579

Das. G., Eitschberger, U, Singh, N. & K. Chandra (2021): A new species of the genus *Pieris* Schrank, 1801 (Lepidoptera: Pieridae: Pierinae) with taxonomic notes on the *Pieris napi* group from India. - Zootaxa **5004** (4), Article 4, Auckland, New Zealand. https://doi.org/10.11646/zootaxa.5004.4.1

de Nicéville, L. (1897): On new or little-known Butterflies from the Indo- and Austro-Malayan Regions. - The Journal of the Bombay Natural History Society **66** (II): 543-577, pl.1-4, Bombay.

Della Bruna, C. D., Gallo, E, & V. Sbordoni (2004): Guide to the Butterflies of the Palearctic Region. Pieridae Part I, **31** (2nd ed.), Omnes Artes.

Dinca, V. E., Dapporto, L., Somervuo, P, Voda, R., Cuvelier, S., Gascoigne-Pees, M., Huemer, P., Mutanen, M., Hebert, P., & R. Vila (2021): High resolution DNA barcode library for European butterflies reveals continental patterns of mitochondrial genetic diversity. - Communications Biology **4**: 1-11, London. https://doi.org/10.1038/s42003-021-01834-7

Ding, C., & Y. Zhang (2017): Phylogenetic relationships of Pieridae (Lepidoptera: Papilionoidea) in China based on seven gene fragments. - Entomological Science **20** (1): 15-23, Tokyo. https://doi.org/10.1111/ens.12214

Dixey, F. A. (1894): On the phylogeny of the Pierinae, as illustrated by their wing-markings and geographical distribution.

Transactions of the Entomological Society of London **2**: 249-335, London.

Dixey, F. A. (1932): The plume-scale of the Pierinae. - Transactions of the Royal Entomological Society of London **80** (1): 57-75, London.

Drohsin, J. (1933): Über Art und Rassenunterschiede der männlichen Kopulationsorgane von Pieriden (Lep.). - Alfred Kernen Verlag. Stuttgart.

Eitschbeger, U. (1983): Systematische Untersuchungen am *Pieris napi-bryoniae*-Komplex (s.l.) (Lepidoptera, Pieridae). - Herbipoliana **1** (1): 1-510, **1** (2): 1-602, Eigenverlag, Würzburg.

Eitschberger, U. & A. Dantchenko (2014): Beitrag zur Kenntnis der zentralasiatischen *Pieris napi muchei* Eitschberger, 1983. - Atalanta **45**: 133-138, Würzburg.

Epstein, H. J. (1979): Interesting, rare and new Pierids from the Central Nepal Himalayas- International Nepal Himalaya Expedition for Lepidoptera Palaearctica -INHELP- 1977, Report No. 2. - Entomologist's Gazette **30**: 77-104, Oxford.

Evans, W. H. (1932): The identification of Indian butterflies. - The Bombay Natural History Society **1**: 66-67, Bombay.

Feltwell, J. & Vane-Wright, R. I. (1982): Large White Butterfly; the biology, biochemistry and physiology of *Pieris brassicae* (Linnaeus). - Springer, Dordrecht.

Ge. S.-X., Jiang, Z.-H., Wang, J. Q., Song, K., Zhang, C. & S. J. Hu (2023): A revision of the *Pieris napi*-complex (Lepidoptera: Pieridae) and similar species with distribution in China. - Arthropod Systematics & Phylogeny **81**: 257-287, Sofia. https://doi.org/10.3897/asp.81.e85191

Geiger, H. J. & A. Scholl (1985): Systematics and evolution of holarctic Pierinae (Lepidoptera). An enzyme electrophoretic approach. - Experientia **41** (1): 24-29, Basel. https://doi.org/10.1007/BF02005856

Geiger, H. J. & A. M. Shapiro (1992): Genetics, systematics and evolution of holarctic *Pieris napi* species group populations (Lepidoptera, Pieridae). - Journal of Zoological Systematics and Evolutionary Research **30** (2): 100-122, Frankfurt a.M. https://doi.org/10.1111/j.1439-0469.1992.tb00161.x

Grote, A. (1900): The descent of the Pierids. - Proceedings of the American Philosophical Society **39**: 4-67, Philadelphia.

Hebert, P. D. N., Cywinska, A., Ball, S. L., & J. R. de Waard (2003): Biological identifications through DNA barcodes. - Proceedings. Biological Sciences **270** (1512): 313-321, London. https://doi.org/10.1098/rspb.2002.2218

Huang, H. (1995): Erection of a new genus for the '*dubernardi*-group' and a new species of Pieridae (Lepidoptera: Rhopalocera) in China. - The Bulletin of the Amateur Entomologists' Society **54** (399): 53-58, London.

Huang, H. (1998): Research on the butterflies of the Namjagbarwa Region, S. E. Tibet (Lepidoptera: Rhopalocera). - Neue Entomologische Nachrichten **41**: 207-264, Marktleuthen.

Huang, H. (2003): A list of butterflies collected from Nujiang (Lou Tse Kiang) and Dulongiang, China with descriptions of new species, and revisional notes. Neue Entomologische Nachrichten **55**: 3-114, Marktleuthen.

Huang, H. (2019): New or little known butterflies from China – 3 (Lepidoptera: Pieridae, Nymphalidae, Riodinidae, Lycaenidae et Hesperiidae). - Neue Entomologische Nachrichten **78**: 203–255, Marktleuthen.

Kimura, M. (1980): A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. - Journal of Molecular Evolution **16** (2): 111-120, Heidelberg. https://doi.org/10.1007/BF01731581

Klots, A. B. (1933): A generic revision of the Pieridae (Lepidoptera) together with a study of the male genitalia. - Entomologica Americana **12**: 139-242, Brooklyn, New York City.

Korb S. & L.V. Bolshakov (2011): A catalogue of butterflies (Lepidoptera: Papilionoformes) of the former USSR. - Eversmannia Suppl. **2**: 1-124, Rostov-on-Don.

Lagnel, M. (1966): Note sur l'armure génitale màle et femelle du sous-genre *Pieris* Schrank (Lep. Pieridae). - Bulletin de La Société Entomologique de France **71** (3/4): 91-94, Paris.

Leech, J. H. (1892): Butterflies from China, Japan, and Corea **1**: 1-188), R.H. Porter, London. https://doi.org/10.5962/bhl.title.86314

Lorković, Z. (1962a): The genetics and reproductive isolating mechanisms of the *Pieris napi-bryoniae* group. - Journal of the Lepidopterists' Society **16** (1): 5-19, New Haven, Connecticut.

Lorković, Z. (1962b): The genetics and reproductive isolating mechanisms of the *Pieris napi-bryoniae* group. - *J*ournal of the Lepidopterists' Society **16** (2): 105-116, New Haven, Connecticut.

Lukhtanov, V. A. (1996): Eine neue Art der Gattung *Pieris* Schrank, 1801 aus Kirgisien. - Atalanta **27** (1/2): 211-221, Würzburg.

Mariani, M. (1937): Anatomia e fisiologia degli organi genitali femminili delle *Pieris* Schrk. (Lepidoptera, Pieridae). - Festschrift zum 60. Geburtstag von Prof. Dr. Embrik Strand **3**: 434-450, Riga.

Middleton Welling J., Dapporto, L., García-Barros, E., Wiemers, M., Nowicki, P. P., Plazio, E., Bonelli, S., Zaccagno, M., Šašić, M., Liparova, J., Schweiger, O., Harpke, A., Musche, M., Settele, J., Schmucki, R. & T. Shreeve (2020). A new comprehensive trait database of European and Maghreb butterflies, Papilionoidea. - Scientific Data **7**: 351, London. https://doi.org/10.1038/s41597-020-00697-7

Mount, D. W. (2008): Choosing a method for phylogenetic prediction. - CSH Protocols **2008**, Huntington. https://doi.org/10.1101/pdb.ip49

Müller, L. & H. Kautz (1939): *Pieris bryoniae* O. *und Pieris napi* L. - Kommissionsverlag Otto. H. Wrede, Wien.

Munjal, G., Hanmandlu, M. & S. Srivastava (2018): Phylogenetics Algorithms and Applications. - Ambient Communications and Computer Systems 904: 187-194, Springer. Singapore. https://doi.org/10.1007/978-981-13-5934-7_17

Nei, M., Kumar, S. (2000): Molecular Evolution and Phylogenetics. - Oxford University Press.

Oberthür, Ch. A. (1876): Espèces nouvelles de Lépidopterès recueillis en Chine par M. l'abbé A. David / Lépidoptères nouveaux de la Chine. - Études d'entomologie **2**: 13-34, pl.1-4, Rennes.

Oberthür, Ch. A (1884): Lépidoptères du Thibet. - Études d'entomologie **9**: 7-22, pl. 1-3, Rennes.

Petersen, W. (1901): Zur Morphogenese der doppelten Bursa copulatrix bei Schmetterlingen. - Allgemeine Zeitschrift Fur Entomologie **6**: 323-325, Druck und Verlag von J. Neumann. Neudamm.

Petersen, W. (1904): Die Morphologie der Generationsorgane der Schmetterlinge und ihre Bodeutung für die Artbildung. - Mem Ac St Petersb **8** (16): 84, St. Petersburg.

Porter, A. H. & H. J. Geiger (1995): Limitations to the inference of gene flow at regional geographic scales – an example from the *Pieris napi* group (Lepidoptera: Pieridae) in Europe. - Biological Journal of the Linnean Society **54** (4): 329-348, London. https://doi.org/10.1016/0024-4066(95)90014-4

Robbins, R. K. & P. M. Henson (1986): Why *Pieris rapae* is a better name than *Artogeia rapae* (Pieridae). - **40** (2):79-92, London. http://repository.si.edu/xmlui/handle/10088/2765

Robinson, G. S., Ackery, Ph. R., Kitching, I. J., Beccaloni, G. W. & L. M. Hernández (2001): Hostplants of the moth and butterfly caterpillars of the Oriental Region. - United Selangor Press, Kuala Lumpur. http://www.nhm.ac.uk/hosts.

Ryan, S. F., Lombaert, E., Espeset, A., Vila, R., Talavera, G., Dincă, V., Doellman, M. M., Renshaw, M. A., Eng, M. W., Hornett, E. A., Li, Y., Pfrender, M. E. & D. Shoemaker (2019): Global invasion history of the agricultural pest butterfly *Pieris rapae* revealed with genomics and citizen science. - Proceedings of the National Academy of Sciences of the United States of America **116** (40): 20015-20024, Washington DC. https://doi.org/10.1073/pnas.1907492116

Rzhetsky, A., & M. Nei (1992): A Simple Method for Estimating and Testing Minimum-Evolution Trees. - Molecular Biology and Evolution **9** (5): 945, Lawrence, Kansas. https://doi.org/10.1093/oxfordjournals.molbev.a040771

Saitou, N., & M. Nei (1987). The neighbor-joining method: A new method for reconstructing phylogenetic trees. - Molecular Biology and Evolution **4** (4): 406-425, Lawrence, Kansas. https://doi.org/10.1093/oxfordjournals.molbev.a040454

Schoch, C. L., Ciufo, S., Domrachev, M., Hotton, C. L., Kannan, S., Khovanskaya, R., Leipe, D., McVeigh, R., O'Neill, K., Robbertse, B., Sharma, S., Soussov, V., Sullivan, J. P., Sun, L., Turner, S. & I. Karsch-Mizrachi (2020): NCBI Taxonomy: A comprehensive update on curation, resources and tools. Database: The Journal of Biological Databases and Curation, 2020, baaa062. https://doi.org/10.1093/database/baaa062

Storace, L. (1956): Ropaloceri dell'Africa Orientale -VIII. Su alcune Pieridae, con descrizione di nuove forme (Lep. Rhop.). - Annali Del Museo Civico Di Storia Naturale Di Genova **68**: 335-350, Genova.

Tadokoro, T. (2019): Scientific names of the two *Pieris napi* (Linnaeus, 1758)-related species of Japan. - Atalanta **50** (1-4): 166-174, Würzburg.

Tadokoro, T., Inomata, T. & M. Wang (2016): Taxonomic review of the *Pieris dubernardi*-group, with description of a new subspecies from Northern Sichuan, China (Lepidoptera, Pieridae). - Lepidoptera Science **67** (3-4): 99-114, Tokyo. https://doi.org/10.18984/lepid.67.3-4_99

Tadokoro, T., Shimokama, T. & M. Wang (2013): Primary study of *Pieris napi*-group in East Asia (Part 1) phylogenetic analyses, morphological characteristic and geographical distribution. - Butterflies (Teinopalpus) **64**: 36-43, Tkyo.

Tadokoro. T., Shinkawa T. & M. Wang (2013): Description of a new species of the genus *Pieris* (Lepidoptera Pieridae) from North Yunnan, China. - Lepidoptera Science **64** (1): 1-9, Tokyo. https://doi.org/10.18984/lepid.64.1_1

Tadokoro. T., Shinkawa T. & M. Wang (2014): Primary study of *Pieris napi*-group in East Asia (Part 2) phylogenetic analyses, morphological characteristics and geographical distribution. - Butterflies (Teinopalpus) **65**: 20-35, Tokyo.

Tadokoro. T. & M. Wang (2014): Description of a new subspecies of *Pieris extensa* Poujade, 1888 from north Yunnan, China, and clarification of the seasonal forms in the species(Lepidoptera, Pieridae). - Lepidoptera Science **65** (3): 94-100, Tokyo. https://doi.org/10.18984/lepid.65.3_94

Tadokoro, T., Wang, M. & G. C. Bozano (2013): Description of a new subspecies of *Pieris shangrilla* (Lepidoptera, Pieridae) from Sichuan Province, China. - Lepidoptera Science **64** (3): 87-92, Tokyo. https://doi.org/10.18984/lepid.64.3_87

Tadokoro, T., Wangchuk, S., Wangdi, S., Wangdi, K., Wangdi, S.R., Drukupa, S., Harada, M., Saito, M., Aoki, T., Yamaguchi, S., Igarashi, Y., Watanabe, Y. & M. Yago (2017): Description of a new subspecies of *Pieris erutae* Poujade, 1888 from Eastern Bhutan, with taxonomic notes on the *Pieris napi* group from the Himalayas (Lepidoptera, Pieridae). - Lepidoptera Science **68** (3-4): 81-91, Tokyo. https://doi.org/10.18984/lepid.68.3-4_81

Talbot, G. (1905): Fauna of British India including Ceylon and Burma (Papilionidae & Pieridae) **1** (2nd Ed.). - Taylor & Francis. London..

Tamura, K. & M. Nei (1993): Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. - Molecular Biology and Evolution **10** (3): 512-526, Oxford University Press. Oxford. https://doi.org/10.1093/oxfordjournals.molbev.a040023

Tamura, K., Stecher, G., & S. Kumar (2021): MEGA11 – Molecular Evolutionary Genetics Analysis Version 11. - Molecular Biology and Evolution **38** (7): 3022-3027, Oxford University Press. Oxford. https://doi.org/10.1093/molbev/msab120

Verity, R. (1947): Le Farfalle diurne d'Italia **3**, Divisione Papilionida, Sezione Papilionina, Famiglie Papilionidae e Pieridae. - Marzocco, Firenze.

Vis, R. A. & H. Coene (2012): Contribution to the butterfly fauna of Sichuan, China (Hesperioidea, Papilionoidea). - Deinsea **15** (1): 13-36, Rotterdam.

Wahlberg, N., Rota, J., Braby, M., Pierce, N. & C. Wheat (2014): Revised systematics and higher classification of pierid butterflies (Lepidoptera: Pieridae) based on molecular data. - Zoologica Scripta **43** (6): 641-650, Oslo. https://doi.org/10.1111/zsc.12075

Warren, B. C. S. (1961): The androconial scales and their bearing on the question of peciation in the genus *Pieris*. - Entomologische Tidskrift **82** (3-4): 121-148, Stockholm.

Warren, B. C. S. (1963): The androconial scales in the genus Pieris 2. - Entomologische Tidskrift **84** (1-2): 1-4, Stockholm.

Wei, F., Huang, W., Fang, L., He, B., Zhao, Y., Zhang, Y., Shu, Z., Su, C. & J. Hao (2023): Spatio-Temporal Evolutionary Patterns of the Pieridae Butterflies (Lepidoptera: Papilionoidea) Inferred from Mitogenomic Data. - Genes **14** (1), Article 1, Basel. https://doi.org/10.3390/genes14010072

Zhang, J., Cong, Q., Shen, J., Opler, P. & N. Grishin (2021): Genomics-guided refinement of butterfly taxonomy. - The Taxonomic Report of the International Lepidoptera Survey **9**, Leesburg, Virginia. https://doi.org/10.5281/zenodo.5630311

Ziegler, H. & U. Eitschberger (1999): Der Karstweissling *Pieris mannii* (Mayer, 1851). Systematik, Verbreitung. Biologie (Lepidoptera: Pieridae). - Neue Entomologische Nachrichten **45**: 1-217.

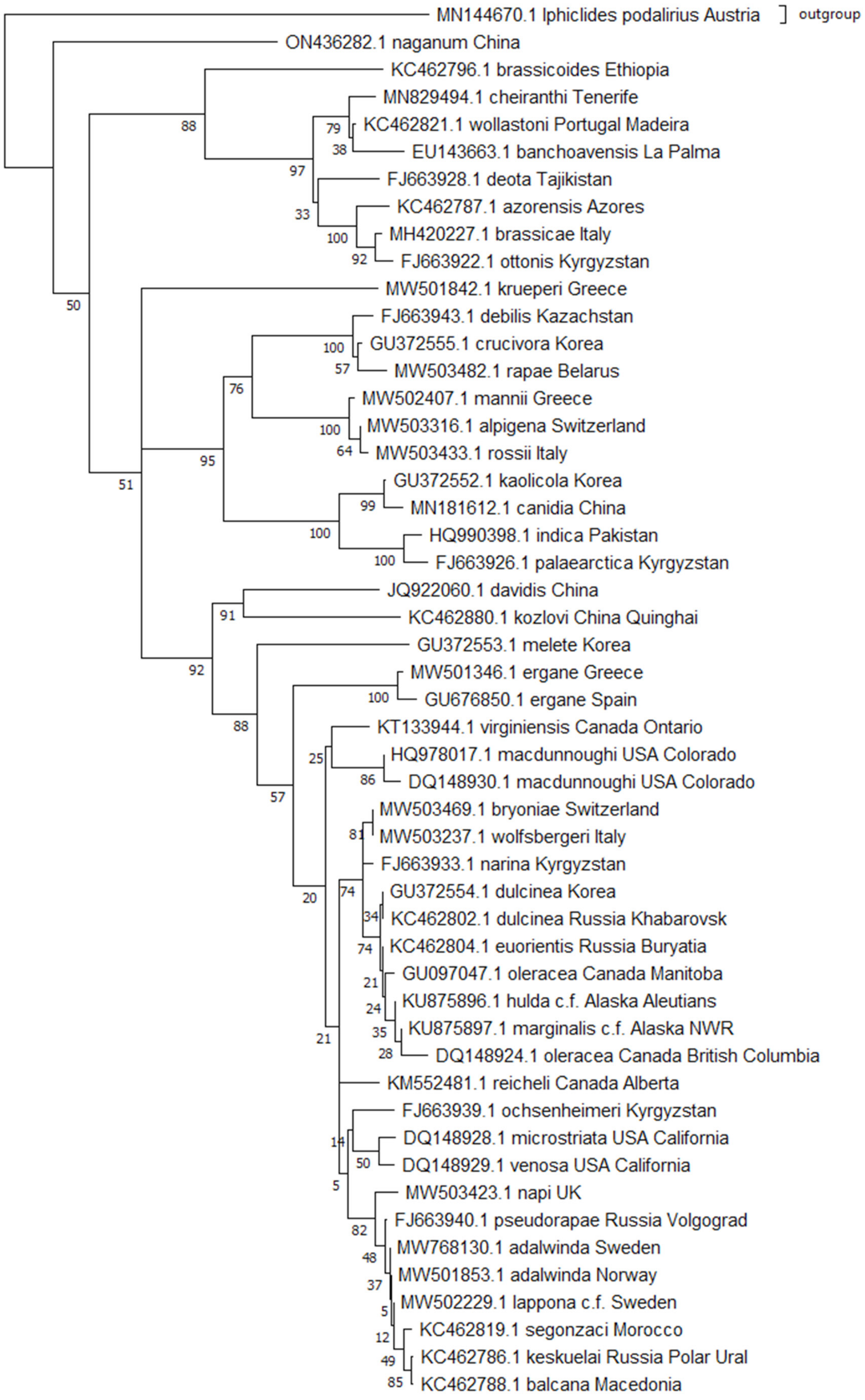


Fig. 1: Phylogenetic tree obtained from the analysis of COI-A sequences set of *Pieris* and *Artogeia* using the minimum evolutiom Method. *Iphiclides podalirius* (Linnaeus, 1758) was included as the outgroup.

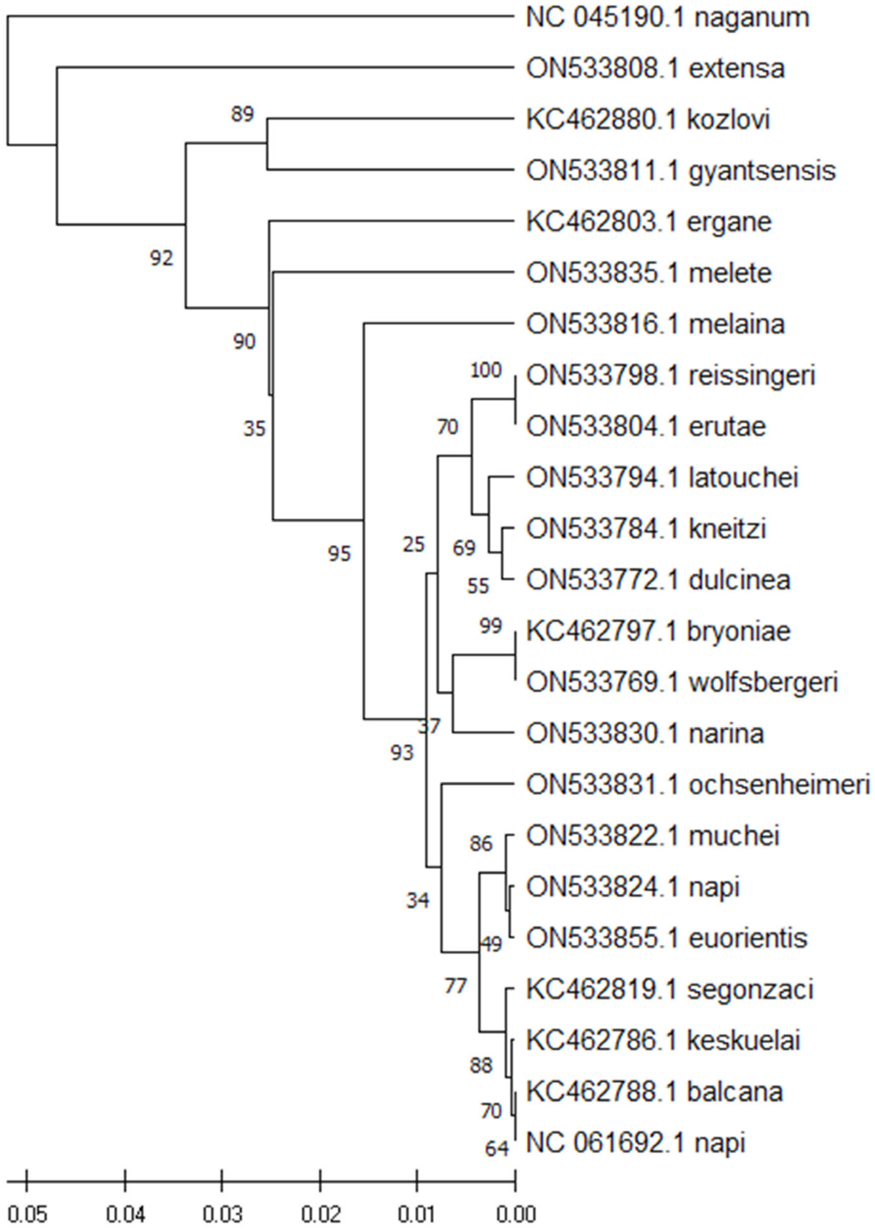


Fig. 2: Phylogenetic tree obtained from the analysis of COI-B sequences set of *Artogeia* (***Tadokoroa***) **subgen. nov.**, *A.* (***Sinopieris***) **subgen. nov.**, and *Artogeia* s. str. using the UPMGA method. *Talbotia naganum* (Moore, 1884) was included as the outgroup.

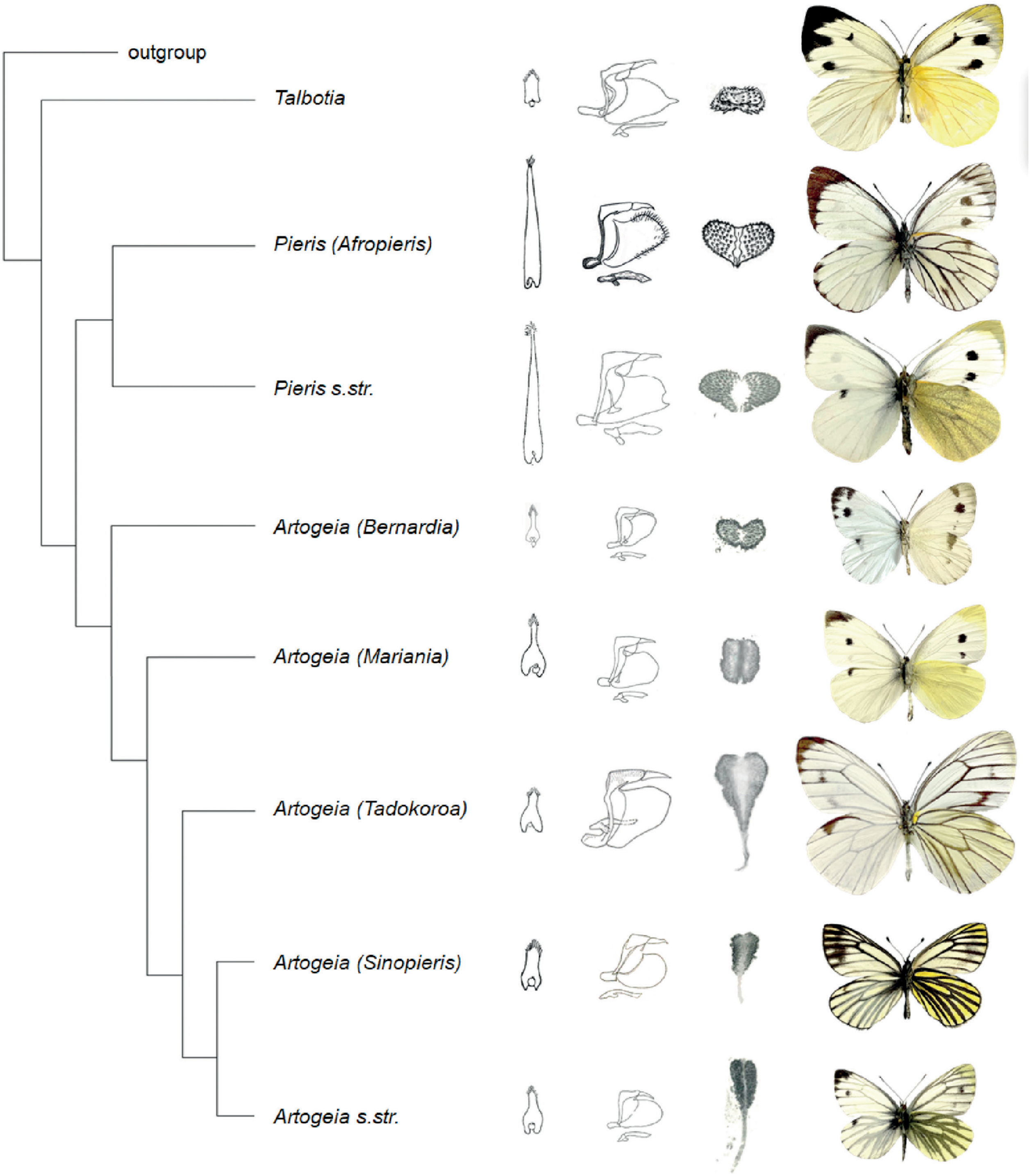


Fig. 3: Phylogenetic relationships between genera and subgenera of *Pieris* s.l., showing for each group (from left to right) androconia, male genitalia, signum, and habitus of adult ♂♂ of the type-species. The anatomical details are modified from Drohsin (1933), Mariani (1937), Bernardi (1947a, 1947b, 1958), and Lagnel (1966), while the pictures of adult specimens are taken from the author's private collection.

#	Genus	Subgenus	Taxon	NCBI:txid	COI sequence	Database	Collection place	Date
1	Talbotia		naganum	320302	NC_045190.1	CMG, B	China: Jiangxi Province Jiulianshan mountains	15-Aug-2009
2	Talbotia		naganum	320302	ON436282.1	A	Taiwan: Jilong City, Ruifeng District, Houtong	
3	Pieris	Afropieris	brassicoides	1343055	KC462796.1	A	Ethiopia: W Ethiopia, Gecha 1600-2200 m	01-Dec-2007
4	Pieris	Pieris s.str.	azorensis	1343050	KC462787.1	A	Portugal: Azores, Ilha do Corvo, Azores, Vila do Corvo (430 m)	18-Aug-2000
5	Pieris	Pieris s.str.	banchoavensis	484400	EU143663.1	A	Spain: La Palma	2006
6	Pieris	Pieris s.str.	brassicae	7116	ON939547.1	CMG		
7	Pieris	Pieris s.str.	cheiranthi	484400	MN829494.1	A	Spain: Santa Cruz de Tenerife, Puerto de la Cruz, Tenerife (50 m)	04-Aug-2017
8	Pieris	Pieris s.str.	deota	596639	FJ663928.1	A	Tajikistan: Gorno-Badakhshan Autonomous Province, 37.733 N 74.85 E	26-Jul-1996
9	Pieris	Pieris s.str.	ottonis	596637	FJ663922.1	A	Kyrgyzstan: Chatkal, 41.667 N 70.867 E	27-Jul-1993
10	Pieris	Pieris s.str.	wollastoni	1343053	KC462821.1	A	Portugal: Madeira, Ribeiro Frio (800 m)	21-Aug-1964
11	Artogeia	Bernardia	krueperi	1343056	MW501842.1	A	Greece: Peloponnesos, Mt. Taygetos (hairpins to Anavriti)	26-May-2014
12	Artogeia	Mariania	alpigena	876065	MW503316.1	A	Switzerland: Raron, Raron	
13	Artogeia	Mariania	canidia	479977	MN181612.1	A	China: Henan, Puyang, Fan County	26-Jul-2016
14	Artogeia	Mariania	crucivora	930006	GU372555.1	A	Korea: Hampyeong, Jeonnam	
15	Artogeia	Mariania	debilis	596644	FJ663943.1	A	Kazakhstan: Semipalatinsk	30-May-1994
16	Artogeia	Mariania	indica	1674290	HQ990398.1	A	Pakistan: Punjab, Murree, Murree	14-Jun-2010
17	Artogeia	Mariania	kaolicola	929992	GU372552.1	A	Korea: Paju, Gyeonggi	
18	Artogeia	Mariania	mannii	876065	MW502407.1	A	Greece: Sterea Ellada, bridge east of Arachova	24-May-2014
19	Artogeia	Mariania	palaearctica	596638	FJ663926.1	A	Kyrgyzstan: Toguz Toro, 41.217 N 73.733 E	08-Jul-1993
20	Artogeia	Mariania	rapae	596645	MW503482.1	A	Belarus: Minsk Region, neighborhood vill. Schemyislitsa	16-Jul-2011
21	Artogeia	Mariania	rapae	596645	NC_015895.1	CMG		
22	Artogeia	Mariania	rapae	596645	NC_015895.1	CMG		
23	Artogeia	Mariania	rossii	876065	MW503433.1	A	Italy: Cesena	
24	Artogeia	Tadokoroa	extensa	441326	ON533808.1	B	China, Sichuan Province, Dujiangyan	15-Jul-2019
25	Artogeia	Sinopieris	davidis	1173054	JQ922060.1	A	China	
26	Artogeia	Sinopieris	gyantsensis	2944397	ON533811.1	B	China, Tibet, Jiangyi County, Karola pass	2-Jul-2020
27	Artogeia	Sinopieris	kozlovi	2944399	KC462880.1	A, B	China: Quinhai, Orindnur Lake	05-Jul-2005
28	Artogeia	Artogeia s.str.	adalwinda	1343049	MW501853.1	A	Norway: Nordland, Andenes	
29	Artogeia	Artogeia s.str.	adalwinda	1343049	MW768130.1	A	Sweden: Abisko	07-Jul-2019
30	Artogeia	Artogeia s.str.	balcana	1343054	KC462788.1	A	Macedonia: Matka canyon, Skopje (300 m)	23-Jun-2002
31	Artogeia	Artogeia s.str.	balcana	1343054	NC462788.1	B		
32	Artogeia	Artogeia s.str.	bryoniae	876064	KC462797.1	B	Austria: Salzburg, Grossglockner, Mitteralm	04-Jul-2006
33	Artogeia	Artogeia s.str.	bryoniae	876064	MW503469.1	A	Switzerland: Interlaken, Bort	
34	Artogeia	Artogeia s.str.	dulcinea	930005	GU372554.1	A	Korea: Mt. Odae, Gangwon	
35	Artogeia	Artogeia s.str.	dulcinea	930005	KC462802.1	A	Russia: Far East Russia, 20 km S Khaborovsk	15-Jul-2007
36	Artogeia	Artogeia s.str.	dulcinea	930005	ON533772.1	B	China, Heilonhjiang Province, Mudanjiang	15-Jun-2019
37	Artogeia	Artogeia s.str.	ergane	1107706	GU676850.1	A	Spain, Teruel	17-May-2009
38	Artogeia	Artogeia s.str.	ergane	1107706	KC462803.1	B	Croatia: Split-Dalmatia, Omis	12-Apr-2006
39	Artogeia	Artogeia s.str.	ergane	1107706	MW501346.1	A	Greece: Peloponnese, Katafigio - Profitis Ilias, Oros Taygetos	09-Jul-2014
40	Artogeia	Artogeia s.str.	erutae	2944400	ON533804.1	B	China, Sichuan Province, Dujiangyan	23-Mar-2020
41	Artogeia	Artogeia s.str.	euorientis	1343051	KC462804.1	A	Russia: Buryatia reg., E Siberia, Gusinoye lake	07-Jun-2007
42	Artogeia	Artogeia s.str.	euorientis	1343051	ON533855.1	B	Russia, Siberia, Repiblic of Buryatia, Kabansy district	20-May-2017
43	Artogeia	Artogeia s.str.	marginalis	345714	KU875897.1	A	Alaska: NWR, Atigun Gorge (600 m)	15-Jul-2002
44	Artogeia	Artogeia s.str.	hulda	345714	KU875896.1	A	Alaska: Aleutians	04-Jul-2007
45	Artogeia	Artogeia s.str.	keskuelai	1343049	KC462786.1	A,B	Russia: Polar Ural Mts, Pimpelis Mt., Paypudinya riv. (700 m)	10-Jul-2002
46	Artogeia	Artogeia s.str.	kneitzi	2944401	ON533784.1	B	China, Shaanxi Province, Ningshan County, Huangguan town	16-May-2020
47	Artogeia	Artogeia s.str.	lappona	596643	MW502229.1	A	Sweden: Norrbotten, Abisko Ostra	
48	Artogeia	Artogeia s.str.	latouchei	2944403	ON533794.1	B	China, Jiangsu province, Nanjing, Liuhe district, Mt. Hengshan	15-Apr-2014
49	Artogeia	Artogeia s.str.	macdunnoghi	345717	DQ148930.1	A	USA: Colorado, Gunnison Co.	
50	Artogeia	Artogeia s.str.	macdunnoghi	345717	HQ978017.1	A	USA: Colorado, Nr Independence Pass	23-Jul-1989
51	Artogeia	Artogeia s.str.	melaina	2944404	ON533816.1	B	China, Tibet, Bomi County	22-Mag-2019
52	Artogeia	Artogeia s.str.	melete	270461	GU372553.1	A	Korea: Paju, Gyeonggi	

to be continued the following page

Tab. 1: Detailed list of the complete mitochondrial genome and COI gene sequences used in the phylogenetic analysis.

53	Artogeia	Artogeia s.str.	melete	270461	NC_010568.1	CMG		
54	Artogeia	Artogeia s.str.	melete	270461	ON533835.1	B	China, Liaoning Province, Fushin, Nanzamu town	27-Apr-2020
55	Artogeia	Artogeia s.str.	microstriata	345715	DQ148928.1	A	USA: California, Mt. Veeder, Sonoma Co	
56	Artogeia	Artogeia s.str.	muchei	2944406	ON533822.1	B	Kyrghyzstan, West Tian-Shan, Chatkal Mt range, Padysha-Ata river ravine	18-Jun-2013
57	Artogeia	Artogeia s.str.	napi	596643	MW503423.1	A	United Kingdom: England, Oxfordshire,	19-May-2016
58	Artogeia	Artogeia s.str.	napi	596643	NC_061692.1	CMG		
59	Artogeia	Artogeia s.str.	napi	596643	ON533824.1	B	Russia, S. Ural, Chelyabisk region, Sheghinsk city	20-Mag-2011
60	Artogeia	Artogeia s.str.	narina	596641	FJ663933.1	A	Kyrgyzstan: Naryn district	04-Jul-1993
61	Artogeia	Artogeia s.str.	narina	596641	ON533830.1	B	Kyrgyzstan, Inner Tian-Shan, At-Bashi Mt. Range, Kynda pass	10-lug-16
62	Artogeia	Artogeia s.str.	ochsenheimeri	596642	ON533831.1	B	Kyrgyzstan, Alai Mt. Range, Gulcha river valley, Kuugandy rivulet	7-Jul-2018
63	Artogeia	Artogeia s.str.	oleracea	345712	DQ148924.1	A	Canada: British Columbia, Alaska Highway at Racing River crossing	
64	Artogeia	Artogeia s.str.	oleracea	345712	GU097047.1	A	Canada: Manitoba	04-Aug-2004
65	Artogeia	Artogeia s.str.	pseudorapae	596643	FJ663940.1	A	Russia, Stavropol	09-Aug-2001
66	Artogeia	Artogeia s.str.	reicheli	345714	KM552481.1	A	Canada: Alberta, Waterton Lakes NP, Maskinonge Lake (1282m)	26-Aug-2008
67	Artogeia	Artogeia s.str.	reissingeri	2944402	ON533798.1	B	China, Huan Province, Anhua County	10-Mar-2020
68	Artogeia	Artogeia s.str.	segonzaci	1343052	KC462819.1	A, B	Morocco: Marrakech, Hoher Atlas, Tizi-n-Tacheddirt (3200 m)	12-Jul-2002
69	Artogeia	Artogeia s.str.	venosa	345716	DQ148929.1	A	USA: California, Big Sur, Monterey Co	
70	Artogeia	Artogeia s.str.	virginiensis	345718	KT133944.1	A	Canada: Ontario, Kawartha, Oliver Ecological Centre	
71	Artogeia	Artogeia s.str.	wolfsbergeri	876064	MW503237.1	A	Italy: Valle D'Aosta, Col du Grand Saint Bernard	
72	Artogeia	Artogeia s.str.	wolfsbergeri	876064	ON533769.1	B	Italy, Valle D'Aosta, Pila	20-Jun-2010
73	Pontia	Baltia	butleri	320288	NC_045189.1	CMG		
74	Pontia	Pontia s.str.	callidice	320238	NC_045191.1	CMG		
75	Pontia	Pontia s.str.	edusa	345723	NC_047456.1	CMG	China	16-Aug-2016
76	Iphiclides		podalirius	110791	MK507891.1	CMG	France	1988
77	Iphiclides		podalirius	110791	MN144670.1	A	Austria: Schwarzau am Steinfeld	23-May-2016

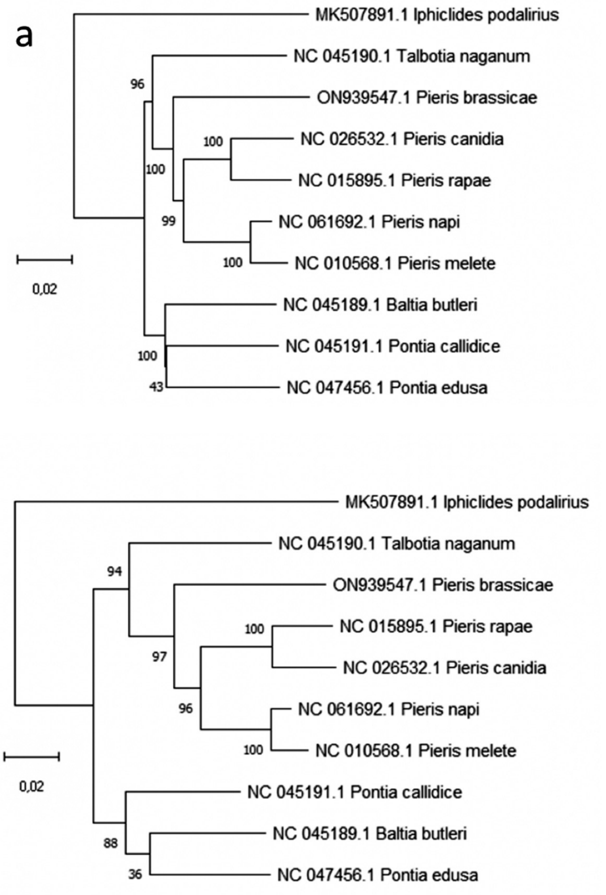
Tab. 1: Detailed list of the complete mitochondrial genome and COI gene sequences used in the phylogenetic analysis.

		1	2	3	4	5	6	7
1	*Talbotia*							
2	*Pieris* (*Afropieris*)	0,12						
3	Pieris s.str.	0,13	0,06					
4	*Artogeia* (*Bernardia*)	0,11	0,11	0,10				
5	*Artogeia* (*Mariania*)	0,10	0,11	0,12	0,09			
6	*Artogeia* (*Tadokoroa*)	0,15	N/A	0,14	N/A	0,10		
7	*Artogeia* (*Sinopieris*)	0,10	0,11	0,12	0,09	0,09	0,08	
8	*Artogeia* s.str.	0,10	0,11	0,11	0,09	0,09	0,10	0,07

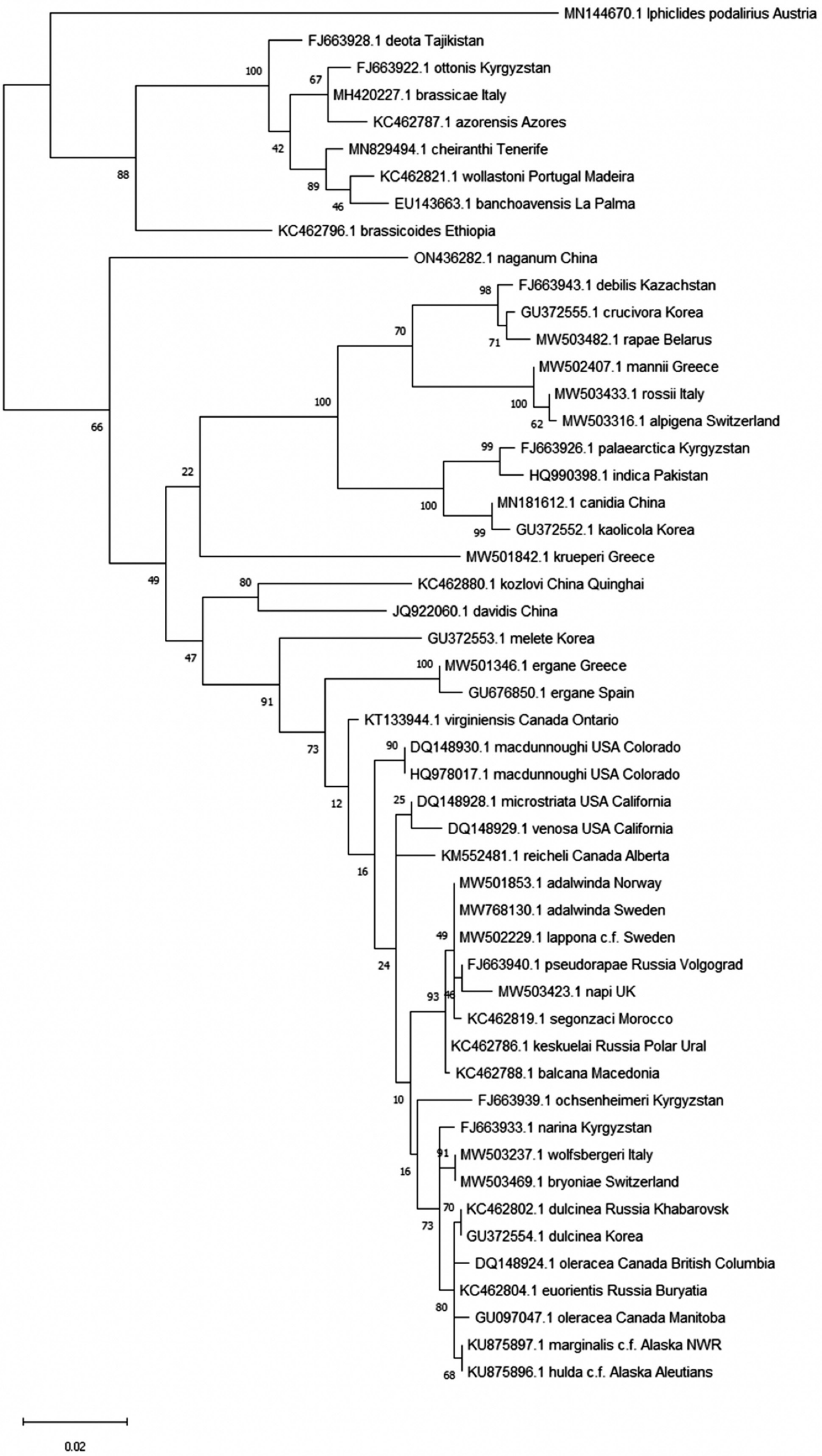
Table 2: Estimates of Evolutionary Divergence between Sequences (K2P). The number of base differences per site between COI sequences of *Talbotia*, *Pieris,* and *Artogeia* are shown. This analysis involved 8 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

	Genus *Talbotia* Bernardi, 1958
1	*Talbotia naganum* (Moore, 1884)
	Genus *Pieris* Schrank, 1801
	Subgenus ***Afropieris* subgen.nov.**
2	*Pieris (Afropieris) brassicoides* Guérin Méneville, 1849
	Subgenus *Pieris s.str.* Schrank, 1801
3	*Pieris s.str. deota* (de Nicéville, [1884])
4	*Pieris s.str. eitschbergeri* Lukhtakov, 1996*§
5	*Pieris s.str. brassicae* (Linnaeus, 1758)
6	*Pieris s.str. cheiranthi* (Hübner, 1808)
	Genus *Artogeia* Verity, 1947
	Subgenus ***Bernardia* subgen.nov.**
7	*Artogeia (Bernardia) krueperi* (Staudinger, 1860)
8	*Artogeia (Bernardia) mahometana* (Grum-Grshimailo, 1888)*§
	Subgenus Mariania **subgen.nov.**
9	*Artogeia (Mariania) tadjika* (Grum-Grshimailo, 1888)*§
10	*Artogeia (Mariania) canidia* (Spaarman, 1768)
11	*Artogeia (Mariania) palaearctica* (Staudinger, 1886) stat. et comb. nov.§
12	*Artogeia (Mariania) rapae* (Linnaeus, 1758)
13	*Artogeia (Mariania) mannii* (Mayer, 1851)
	Subgenus ***Tadokoroa* subgen.nov.**
14	*Artogeia (Tadokoroa) extensa* Poujade, 1888
	Subgenus Sinopieris Huang, 1995 comb.nov. *davidis-group*
15	*Artogeia (Sinopieris) davidis* (Oberthür, 1876)§
16	*Artogeia (Sinopieris) stoezneri* (Draeseke, 1924)*§
17	*Artogeia (Sinopieris) venata* (Leech, 1891)*§
	dubernardi-group
18	*Artogeia (Sinopieris) rothschildi* (Verity, 1911)*§
19	*Artogeia (Sinopieris) chumbiensis* (de Nicéville, 1897)§
20	*Artogeia (Sinopieris) sherpae* (Epstein, 1979)§
21	*Artogeia (Sinopieris) kozlovi* (Alphéraky, 1897)§
22	*Artogeia (Sinopieris) dubernardi* (Oberthür, 1884)*§
23	*Artogeia (Sinopieris) wangi* (Huang, 1998)*§
	Subgenus Artogeia s.str. Verity, 1947
24	*Artogeia* s.str. *melete* (Ménétriès, 1857)
25	*Artogeia* s.str. *ajaka* (Moore, 1865) *§
26	*Artogeia* s.str. *melaina* (Röber, 1907)
27	*Artogeia* s.str. *ergane* (Geyer, [1828])§
	Superspecies-napi *marginalis*-group
28	*Artogeia* s.str.. *(napi) acadica* (Edwards, 1881)*§
29	*Artogeia*s.str. *(napi) venosa* (Scudder, 1961)
30	*Artogeia* s.str. *(napi) virginiensis* (Edwards, 1881)
31	*Artogeia* s.str. *(napi) marginalis* (Scudder, 1861)§
	bryoniae-group
32	*Artogeia* s.str.. *(napi) angelika* (Eitschberger, 1983)*
33	*Artogeia* s.str.. *(napi) olearacea* (Harris, 1829)
34	*Artogeia* s.str. *(napi) pseudonapi* (Verity, 1911)
35	*Artogeia* s.str. *(napi) nesis* (Fruhstorfer, 1909)*
36	*Artogeia* s.str. *(napi) erutae* (Poujade, 1888)
37	*Artogeia* s.str. *(napi) latouchei* (Mell, 1939)
38	*Artogeia* s.str. *(napi) dulcinea* (Butler, 1882)
	Artogeia s.str. *(napi) steinigeri* (Eitschberger, 1983)*§
39	*Artogeia* s.str. *(napi) narina* (Verity, 1908)
40	*Artogeia* s.str.. *(napi) bryoniae* (Hübner, [1790])
41	*Artogeia* s.str. *(napi) caucasica* (Lorkovic, 1968)*§
42	*Artogeia* s.str. *(napi) mihon* (Yakovlev, 2006)*
	napi-group
43	*Artogeia* s.str. *(napi) ochsenheimeri* (Staudinger, 1866)
44	*Artogeia* s.str. *(napi) bryonides* (Sheljuzhko, 1910)§
45	*Artogeia* s.str. *(napi) euorientis* (Verity, 1908)§
46	*Artogeia* s.str. *(napi) napi* (Linnaeus, 1758)
47	*Artogeia* s.str. *(napi) segonzaci* (Le Cerf, 1923)
48	*Artogeia* s.str. *(napi) balcana* (Lorkovic, 1968)
49	*Artogeia s.str. (napi) pseudorapae (Verity, 1908)*
50	*Artogeia s.str. (napi) bowdeni (Eitschberger, 1983)*§*

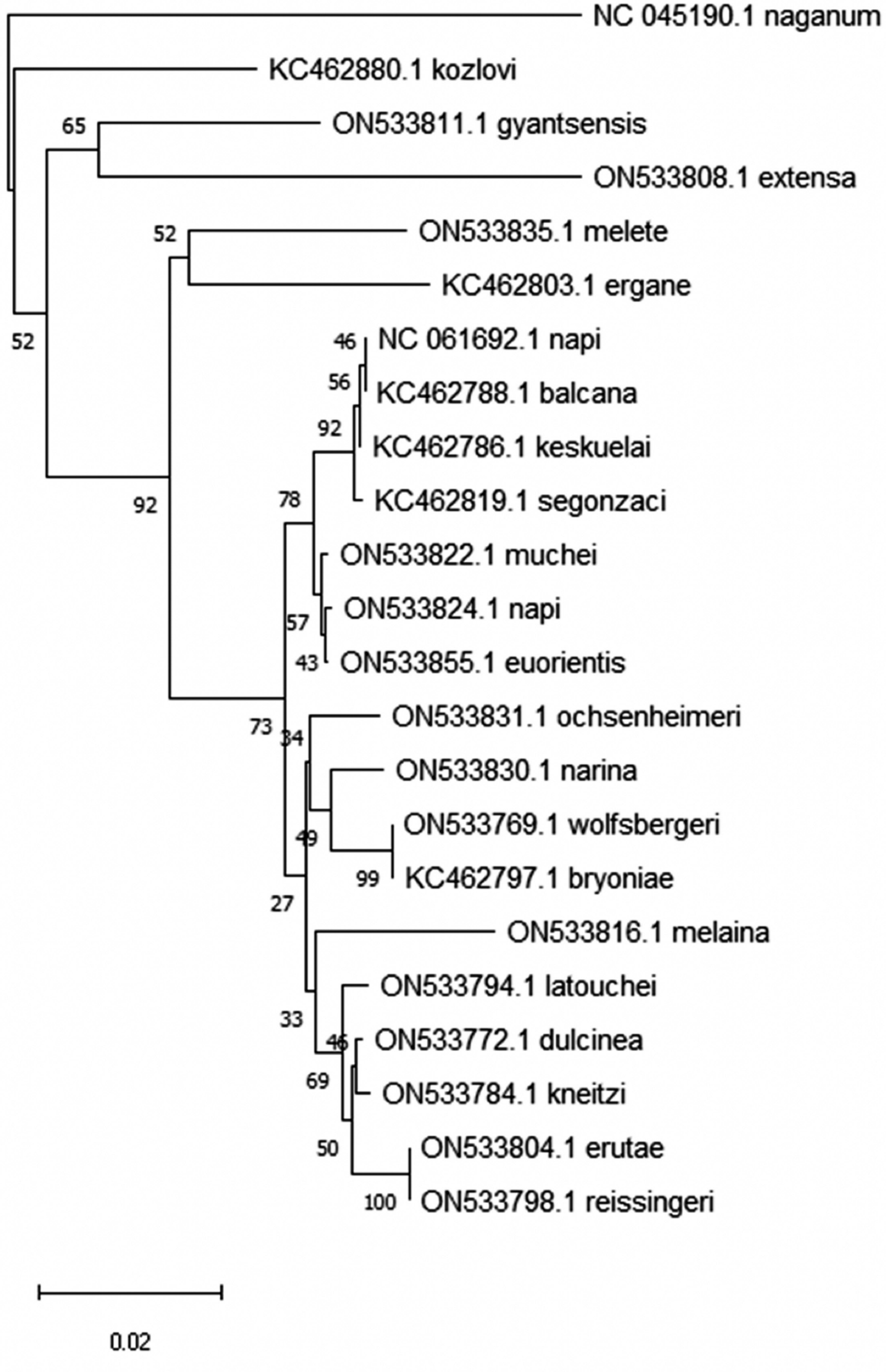
Tab. 3: Summary of the known species of *Talbotia*, *Pieris,* and *Artogeia* arranged according to the taxonomical changes proposed in this work. Taxa are ordered according to their phylogenetic relationship. *=species not included in our phylogenetic analysis; §=taxa needing further investigation to assess their taxonomic rank.



Supplementary Fig. 1: Phylogenic tree obtained from the analysis of complete mitochondrial genome sequences *Talbotia*, *Pieris*, *Artogeia* and *Pontia*. with the maximum likelihood (a) or minimum evolution (b) method. *Iphiclides podalirius* (Linnaeus, 1758) was included as outgroup.



Supplementary Figure 2: Phylogenic tree obtained from the analysis of COI-A sequences set of *Pieris*, and *Artogeia* using the maximum likelihood method. *Iphiclides podalirius* (Linnaeus, 1758) was included as outgroup.



Supplementary Figure 3: Phylogenic tree obtained from the analysis of COI-B sequences set of, *Artogeia* (***Tadokoroa***), *Artogeia* (*Sinopieris*) and *Artogeia* s.s tr. using the minimum evolution method. *Talbotia naganum* (Moore, 1884) was included as outgroup.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
1	MW768130.1_adalwinda_Sweden																																																		
2	KC462788.1_balcana_Macedonia	0,002																																																	
3	KC462787.1_azorensis_Azores	0,113	0,111																																																
4	MH420227.1_brassicae_Italy	0,110	0,125	0,009																																															
5	FJ663922.1_ottonis_Kyrgyzstan	0,111	0,125	0,014	0,005																																														
6	KC462796.1_brassicoides_Ethiopia	0,108	0,123	0,062	0,061	0,062																																													
7	MW503469.1_bryoniae_Switzerland	0,019	0,015	0,110	0,106	0,108	0,104																																												
8	MW503237.1_wolfsbergeri_Italy	0,019	0,015	0,110	0,106	0,108	0,104	0,000																																											
9	MN181612.1_canidia_China	0,093	0,097	0,128	0,126	0,126	0,126	0,091	0,091																																										
10	HQ990398.1_indica_Pakistan	0,103	0,115	0,117	0,115	0,121	0,119	0,097	0,097	0,024																																									
11	GU372552.1_kaolicola_Korea	0,087	0,090	0,123	0,117	0,119	0,115	0,089	0,089	0,004	0,028																																								
12	EU143663.1_banchoavensis_La_Palma	0,108	0,126	0,034	0,024	0,026	0,072	0,108	0,108	0,139	0,121	0,121																																							
13	MN829494.1_cheiranthi_Tenerife	0,108	0,111	0,026	0,020	0,025	0,069	0,104	0,104	0,130	0,117	0,118	0,015																																						
14	JQ922060.1_davidis_China	0,060	0,067	0,103	0,107	0,109	0,105	0,065	0,065	0,103	0,098	0,096	0,117	0,111																																					
15	FJ663928.1_deota_Tajikistan	0,108	0,128	0,030	0,020	0,022	0,060	0,104	0,104	0,130	0,115	0,111	0,026	0,022	0,109																																				
16	GU372554.1_dulcinea_Korea	0,020	0,016	0,105	0,106	0,108	0,108	0,006	0,006	0,091	0,099	0,088	0,108	0,101	0,066	0,104																																			
17	KC462802.1_dulcinea_Russia_Khabarovsk	0,020	0,015	0,113	0,106	0,108	0,108	0,006	0,006	0,091	0,099	0,091	0,108	0,104	0,066	0,104	0,000																																		
18	GU676850.1_ergane_Spain	0,044	0,049	0,113	0,117	0,119	0,113	0,036	0,036	0,098	0,110	0,097	0,117	0,113	0,075	0,111	0,038	0,038																																	
19	MW501346.1_ergane_Greece	0,039	0,042	0,111	0,115	0,117	0,115	0,034	0,034	0,096	0,108	0,096	0,119	0,115	0,069	0,113	0,033	0,033	0,005																																
20	KC462804.1_eurorientis_Russia_Buryatia	0,019	0,015	0,111	0,104	0,106	0,106	0,005	0,005	0,091	0,097	0,089	0,106	0,103	0,064	0,102	0,002	0,002	0,039	0,034																															
21	KC462786.1_keskuelai_Russia_Polar_Ural	0,002	0,001	0,111	0,125	0,125	0,123	0,015	0,015	0,097	0,115	0,089	0,126	0,111	0,067	0,128	0,014	0,015	0,049	0,042	0,015																														
22	KC462880.1_kozlovi_China_Quinghai	0,068	0,074	0,111	0,124	0,126	0,111	0,065	0,065	0,105	0,101	0,091	0,131	0,118	0,053	0,117	0,069	0,072	0,075	0,074	0,070	0,074																													
23	MW501842.1_krueperi_Greece	0,091	0,093	0,099	0,105	0,110	0,110	0,089	0,089	0,100	0,094	0,100	0,118	0,112	0,082	0,112	0,091	0,091	0,093	0,091	0,089	0,093	0,094																												
24	HQ978017.1_macdunnoughi_USA_Colorado	0,020	0,019	0,115	0,110	0,111	0,103	0,014	0,014	0,082	0,096	0,084	0,112	0,108	0,067	0,108	0,019	0,019	0,031	0,030	0,017	0,019	0,059	0,082																											
25	MW502407.1_mannii_Greece	0,077	0,096	0,107	0,107	0,108	0,110	0,079	0,079	0,061	0,066	0,061	0,110	0,103	0,087	0,099	0,082	0,082	0,098	0,096	0,080	0,096	0,087	0,094	0,080																										
26	MW503433.1_rossii_Italy	0,080	0,100	0,110	0,110	0,112	0,112	0,082	0,082	0,065	0,066	0,064	0,114	0,106	0,087	0,101	0,085	0,085	0,097	0,096	0,084	0,100	0,089	0,091	0,084	0,003																									
27	KM552481.1_reicheli_Canada_Alberta	0,017	0,017	0,113	0,110	0,111	0,104	0,014	0,014	0,098	0,103	0,091	0,110	0,108	0,062	0,108	0,020	0,020	0,039	0,037	0,019	0,017	0,059	0,087	0,018	0,077	0,080																								
28	GU372553.1_melete_Korea	0,056	0,049	0,108	0,112	0,114	0,115	0,054	0,054	0,089	0,098	0,088	0,121	0,107	0,074	0,110	0,053	0,056	0,064	0,062	0,054	0,050	0,073	0,100	0,051	0,103	0,107	0,055																							
29	MW503423.1_napi_UK	0,008	0,011	0,113	0,110	0,111	0,108	0,023	0,023	0,093	0,103	0,087	0,110	0,110	0,067	0,108	0,025	0,025	0,046	0,041	0,023	0,011	0,072	0,089	0,025	0,080	0,084	0,022	0,056																						
30	FJ663933.1_narina_Kyrgyzstan	0,019	0,013	0,110	0,106	0,108	0,104	0,006	0,006	0,089	0,097	0,089	0,108	0,104	0,066	0,104	0,008	0,008	0,039	0,034	0,006	0,013	0,072	0,086	0,017	0,079	0,082	0,020	0,054	0,023																					
31	FJ663939.1_ochsenheimeri_Kyrgyzstan	0,022	0,022	0,108	0,111	0,113	0,106	0,019	0,019	0,098	0,099	0,094	0,110	0,110	0,057	0,104	0,020	0,020	0,031	0,030	0,019	0,022	0,072	0,082	0,022	0,085	0,085	0,022	0,056	0,026	0,019																				
32	FJ663926.1_palaearctica_Kyrgyzstan	0,103	0,118	0,121	0,119	0,125	0,115	0,101	0,101	0,024	0,008	0,025	0,124	0,117	0,098	0,119	0,103	0,103	0,107	0,105	0,101	0,118	0,100	0,098	0,096	0,067	0,067	0,103	0,094	0,103	0,101	0,103																			
33	FJ663940.1_pseudorapae_Russia_Volgograd	0,002	0,004	0,113	0,110	0,111	0,108	0,020	0,020	0,093	0,103	0,087	0,108	0,108	0,060	0,108	0,022	0,022	0,042	0,038	0,020	0,004	0,068	0,091	0,022	0,077	0,080	0,018	0,056	0,006	0,020	0,023	0,103																		
34	GU372555.1_crucivora_Korea	0,082	0,089	0,115	0,115	0,117	0,113	0,082	0,082	0,045	0,059	0,062	0,117	0,117	0,090	0,113	0,086	0,085	0,084	0,082	0,084	0,090	0,084	0,094	0,077	0,041	0,044	0,080	0,093	0,085	0,082	0,087	0,056	0,082																	
35	FJ663943.1_debilis_Kazachstan	0,084	0,103	0,115	0,115	0,117	0,117	0,084	0,084	0,049	0,059	0,057	0,119	0,111	0,096	0,113	0,087	0,087	0,089	0,087	0,085	0,103	0,082	0,099	0,078	0,038	0,041	0,082	0,101	0,087	0,084	0,092	0,057	0,084	0,006																
36	MW503482.1_rapae_Belarus	0,087	0,108	0,113	0,117	0,119	0,115	0,087	0,087	0,054	0,062	0,060	0,121	0,113	0,096	0,115	0,090	0,090	0,089	0,087	0,089	0,108	0,085	0,092	0,082	0,044	0,044	0,085	0,101	0,087	0,087	0,092	0,057	0,087	0,006	0,009															
37	KC462819.1_segonzaci_Morocco	0,002	0,004	0,109	0,123	0,123	0,120	0,015	0,015	0,097	0,115	0,087	0,121	0,109	0,072	0,125	0,016	0,015	0,049	0,042	0,015	0,003	0,072	0,093	0,019	0,096	0,100	0,017	0,050	0,006	0,013	0,022	0,118	0,004	0,091	0,103	0,108														
38	3944.1_virginiensis_Canada_Ontario	0,022	0,019	0,111	0,108	0,110	0,104	0,019	0,019	0,091	0,101	0,085	0,110	0,106	0,066	0,106	0,023	0,023	0,031	0,030	0,022	0,019	0,058	0,093	0,014	0,080	0,084	0,017	0,042	0,023	0,022	0,026	0,098	0,020	0,078	0,080	0,084	0,019													
39	KC462821.1_wollastoni_Portugal_Madeira	0,094	0,130	0,030	0,023	0,023	0,073	0,098	0,098	0,108	0,091	0,080	0,010	0,007	0,099	0,020	0,094	0,094	0,113	0,113	0,090	0,130	0,118	0,102	0,102	0,083	0,083	0,098	0,103	0,094	0,094	0,102	0,095	0,094	0,095	0,095	0,095	0,120	0,094												
40	GU097047.1_oleracea_Canada_Manitoba	0,022	0,017	0,115	0,108	0,110	0,110	0,008	0,008	0,093	0,101	0,092	0,110	0,106	0,067	0,106	0,005	0,005	0,042	0,038	0,003	0,017	0,074	0,093	0,020	0,084	0,087	0,022	0,057	0,026	0,009	0,022	0,105	0,023	0,087	0,089	0,092	0,017	0,025	0,094											
41	ON436282.1_naganum_China	0,098	0,108	0,124	0,126	0,128	0,119	0,098	0,098	0,109	0,105	0,105	0,136	0,128	0,120	0,126	0,101	0,101	0,101	0,103	0,099	0,108	0,103	0,114	0,098	0,105	0,105	0,098	0,105	0,098	0,096	0,099	0,105	0,098	0,099	0,101	0,105	0,108	0,099	0,109	0,103										
42	MN144670.1_iphiclides_podalirius_Austria	0,158	0,180	0,138	0,136	0,138	0,127	0,157	0,157	0,164	0,151	0,160	0,146	0,135	0,160	0,138	0,160	0,160	0,170	0,170	0,158	0,180	0,151	0,159	0,162	0,138	0,140	0,157	0,172	0,155	0,157	0,166	0,153	0,157	0,129	0,125	0,131	0,180	0,153	0,116	0,160	0,133									
43	KU875896.1_hulda_c.f._Alaska_Aleutians	0,021	0,017	0,114	0,107	0,109	0,109	0,006	0,006	0,093	0,101	0,092	0,109	0,105	0,062	0,105	0,003	0,003	0,042	0,037	0,002	0,017	0,068	0,091	0,019	0,082	0,085	0,021	0,054	0,026	0,006	0,021	0,105	0,023	0,087	0,089	0,092	0,017	0,024	0,095	0,005	0,102	0,155								
44	MW502229.1_lappona_c.f._Sweden	0,000	0,002	0,113	0,110	0,111	0,108	0,019	0,019	0,093	0,103	0,087	0,108	0,108	0,060	0,108	0,020	0,020	0,044	0,039	0,019	0,002	0,068	0,091	0,020	0,077	0,080	0,017	0,056	0,008	0,019	0,022	0,103	0,002	0,082	0,084	0,087	0,002	0,022	0,094	0,022	0,098	0,158	0,021							
45	KU875897.1_marginalis_c.f._Alaska_NWR	0,017	0,017	0,113	0,105	0,105	0,107	0,007	0,007	0,093	0,105	0,092	0,111	0,107	0,064	0,109	0,004	0,004	0,042	0,036	0,002	0,017	0,067	0,088	0,021	0,088	0,092	0,017	0,056	0,022	0,007	0,023	0,107	0,019	0,092	0,094	0,098	0,017	0,021	0,095	0,004	0,103	0,157	0,000	0,017						
46	DQ148928.1_microstriata_USA_California	0,015	0,012	0,117	0,113	0,117	0,127	0,012	0,012	0,089	0,093	0,093	0,131	0,117	0,046	0,120	0,012	0,012	0,037	0,034	0,012	0,012	0,056	0,079	0,018	0,089	0,093	0,012	0,034	0,018	0,009	0,012	0,099	0,015	0,099	0,106	0,110	0,015	0,015	0,202	0,015	0,093	0,202	0,012	0,015	0,012					
46	DQ148928.1_microstriata_USA_California	0,015	0,012	0,117	0,113	0,117	0,127	0,012	0,012	0,089	0,093	0,093	0,131	0,117	0,046	0,120	0,012	0,012	0,037	0,034	0,012	0,012	0,056	0,079	0,018	0,089	0,093	0,012	0,034	0,018	0,009	0,012	0,099	0,015	0,099	0,106	0,110	0,015	0,015	0,202	0,015	0,093	0,202	0,012	0,015	0,012					
47	DQ148929.1_venosa_USA_California	0,015	0,012	0,113	0,113	0,117	0,127	0,018	0,018	0,082	0,086	0,086	0,131	0,117	0,046	0,120	0,018	0,018	0,043	0,040	0,018	0,012	0,053	0,079	0,018	0,083	0,086	0,018	0,034	0,018	0,015	0,018	0,093	0,015	0,093	0,099	0,103	0,015	0,015	0,164	0,021	0,093	0,202	0,018	0,015	0,018	0,006				
48	DQ148924.1_oleracea_Canada_British_Columbia	0,018	0,015	0,124	0,120	0,124	0,135	0,006	0,006	0,096	0,099	0,100	0,138	0,124	0,053	0,127	0,003	0,003	0,043	0,040	0,003	0,015	0,069	0,093	0,028	0,100	0,103	0,018	0,050	0,024	0,006	0,018	0,106	0,021	0,103	0,110	0,113	0,018	0,028	0,202	0,006	0,099	0,206	0,003	0,018	0,003	0,015	0,021			
49	DQ148930.1_macdunnoughi_USA_Colorado	0,021	0,018	0,124	0,117	0,120	0,120	0,024	0,024	0,079	0,089	0,082	0,135	0,120	0,053	0,124	0,025	0,025	0,034	0,031	0,025	0,018	0,053	0,073	0,000	0,093	0,096	0,024	0,037	0,028	0,021	0,024	0,089	0,024	0,089	0,096	0,099	0,021	0,018	0,202	0,028	0,093	0,206	0,025	0,021	0,025	0,018	0,018	0,028		
50	MW503316.1_alpigena_Switzerland	0,078	0,098	0,108	0,108	0,110	0,110	0,080	0,080	0,063	0,064	0,066	0,112	0,104	0,085	0,103	0,084	0,084	0,096	0,094	0,082	0,098	0,087	0,089	0,082	0,005	0,002	0,079	0,105	0,082	0,080	0,084	0,066	0,078	0,042	0,039	0,042	0,098	0,082	0,083	0,085	0,103	0,138	0,083	0,078	0,090	0,089	0,082	0,099	0,093	
51	MW501853.1_adalwinda_Norway	0,000	0,002	0,113	0,110	0,111	0,108	0,019	0,019	0,093	0,103	0,087	0,108	0,108	0,060	0,108	0,020	0,020	0,044	0,039	0,019	0,002	0,068	0,091	0,020	0,077	0,080	0,017	0,056	0,008	0,019	0,022	0,103	0,002	0,082	0,084	0,087	0,002	0,022	0,094	0,022	0,098	0,158	0,021	0,000	0,017	0,015	0,015	0,018	0,021	0,078

Supplementary Table 2 - Estimates of Evolutionary Divergence between Sequences (K2P). The number of base differences per site from between COI-A sequences of *Talbotia*, *Pieris*, *Artogeia* and *Pontia* are shown. This analysis involved 51 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

		1	2	3	4	5	6	7	8	9
1	NC 045190.1 *Talbotia naganum*									
2	NC 045191.1 *Pontia callidice*	0,109								
3	NC 045189.1 *Baltia butleri*	0,105	0,088							
4	NC 047456.1 *Pontia edusa*	0,110	0,089	0,089						
5	NC 026532.1 *Pieris canidia*	0,108	0,113	0,113	0,111					
6	NC 010568.1 *Pieris melete*	0,107	0,111	0,108	0,112	0,084				
7	NC 061692.1 *Pieris napi*	0,100	0,103	0,100	0,105	0,078	0,022			
8	NC 015895.1 *Pieris rapae*	0,109	0,112	0,112	0,112	0,048	0,082	0,076		
9	ON939547.1 *Pieris brassicae*	0,116	0,119	0,122	0,123	0,103	0,098	0,091	0,102	
10	MK507891.1 *Iphiclid. podalirius*	0,190	0,182	0,185	0,180	0,188	0,186	0,181	0,187	0,191

Supplementary Table 1 - Estimates of Evolutionary Divergence between Sequences (K2P). The number of base differences per site from between complete mitochondrial genome sequences of *Talbotia*, *Pieris*, *Artogeia* and *Pontia*. This analysis involved 10 nucleotide sequences. Codon positions included were 1^{st}+2^{nd}+3^{rd}+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	ON533769.1_wolfsbergeri																						
2	ON533811.1_gyantsensis	0,075																					
3	ON533772.1_dulcinea	0,012	0,071																				
4	ON533804.1_erutae	0,019	0,075	0,007																			
5	ON533784.1_kneitzi	0,012	0,071	0,003	0,009																		
6	ON533798.1_reissingeri	0,019	0,075	0,007	0,000	0,009																	
7	ON533855.1_euorientis	0,017	0,064	0,013	0,017	0,013	0,017																
8	ON533808.1_extensa	0,105	0,082	0,102	0,102	0,102	0,102	0,099															
9	ON533794.1_latouchei	0,016	0,071	0,004	0,011	0,007	0,011	0,012	0,103														
10	ON533816.1_melaina	0,032	0,075	0,026	0,032	0,026	0,032	0,031	0,120	0,024													
11	ON533822.1_muchei	0,016	0,065	0,012	0,016	0,012	0,016	0,001	0,099	0,013	0,030												
12	ON533824.1_napi	0,019	0,065	0,015	0,019	0,015	0,019	0,001	0,100	0,013	0,033	0,003											
13	ON533830.1_narina	0,012	0,073	0,013	0,017	0,013	0,017	0,013	0,103	0,015	0,032	0,015	0,015										
14	ON533831.1_ochsenheimeri	0,017	0,072	0,017	0,024	0,017	0,024	0,012	0,108	0,016	0,032	0,013	0,012	0,013									
15	ON533835.1_melete	0,055	0,075	0,052	0,052	0,055	0,052	0,047	0,096	0,054	0,061	0,046	0,046	0,055	0,051								
16	KC462803.1_ergane	0,055	0,081	0,053	0,058	0,058	0,058	0,048	0,112	0,051	0,051	0,048	0,048	0,053	0,051	0,053							
17	KC462819.1_segonzaci	0,023	0,064	0,017	0,025	0,017	0,025	0,008	0,094	0,019	0,036	0,008	0,006	0,025	0,019	0,051	0,055						
18	KC462788.1_balcana	0,022	0,068	0,016	0,022	0,016	0,022	0,008	0,099	0,018	0,034	0,008	0,006	0,024	0,018	0,051	0,053	0,002					
19	KC462797.1_bryoniae	0,000	0,073	0,014	0,024	0,014	0,024	0,018	0,101	0,016	0,036	0,018	0,020	0,014	0,020	0,053	0,055	0,023	0,022				
20	KC462880.1_kozlovi	0,068	0,053	0,066	0,075	0,070	0,075	0,068	0,092	0,068	0,081	0,068	0,070	0,072	0,072	0,070	0,088	0,066	0,070	0,068			
21	NC_045190.1_naganum	0,115	0,107	0,118	0,120	0,118	0,120	0,107	0,149	0,118	0,133	0,107	0,105	0,112	0,109	0,110	0,119	0,103	0,104	0,104	0,097		
22	KC462786.1_keskuelai	0,022	0,068	0,016	0,022	0,016	0,022	0,008	0,099	0,018	0,034	0,008	0,006	0,024	0,018	0,051	0,053	0,002	0,000	0,022	0,070	0,100	
23	NC_061692.1_napi	0,023	0,069	0,019	0,023	0,019	0,023	0,008	0,102	0,017	0,037	0,009	0,007	0,021	0,016	0,052	0,053	0,002	0,000	0,022	0,070	0,101	0,001

Supplementary Table 3 - Estimates of Evolutionary Divergence between Sequences (K2P). The number of base differences per site from between COI-B sequences of *Artogeia* (***Tadokoroa***), *Artogeia* (*Sinopieris*) and *Artogeia* s. str. are shown. This analysis involved 23 nucleotide sequences. Codon positions included were 1^{st}+2^{nd}+3^{rd}+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

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