Trends in systematics

New insights into systematics of European Green, White-backed and Middle Spotted Woodpecker

The woodpeckers Picidae constitute a well-defined family that includes 34 genera and 236 species (Winkler et al 2020a). They occur in every major biogeographic region except Australasia, Madagascar and Antarctica. The woodpeckers are most often divided into three subfamilies: ***1*** Jynginae, the Eurasian and Sub-saharian wrynecks (two species), are sister to all other woodpeckers; ***2*** Picumninae, the piculets (28 species), a pan-tropical group of small short tailed woodpeckers; and ***3*** Picinae (206 species), the typical woodpeckers. Monophyly of the Picumninae has recently been refuted as Antillean Piculet *Nesoctites micromegas* was found to be more closely related to the typical woodpeckers (Benz et al 2006, Fuchs et al 2007, Shakya et al 2017) than to other piculets. Uncertainties also remain concerning the relationships of the two other piculet genera, *Sasia* and *Picumnus* with respect to the *Nesoctites/Picinae* clade. An almost complete molecular phylogeny of the Picidae has recently been published by Shakya et al (2017), including 203 of 217 described species listed in Dickinson & Remsen (2013), and highlighted three primary subdivisions in Picinae. The Western Palearctic (WP) woodpeckers belong to two of these divisions, the Picini (Grey-headed *Picus canus*, European Green *P viridis*, Iberian Green *P (v) sharpei*, Levaillant's *P vaillantii*, Scally-bellied *P squamatus* and Black Woodpecker *Dryocopus martius*) and the Melanerpini (Eurasian Three-toed *Picoides tridactylus*, Middle Spotted *Dendropicos medius*, Great Spotted *Dendrocopos major*, Syrian *D syriacus*, White-backed *D leucotos*, Lilford's *D (l) lilfordi*, White-winged *D leucopterus*, Sind *D assimilis* and Arabian *Dendrocoptes dorae*, and Lesser Spotted Woodpecker *Dryobates minor*). Molecular studies over the last two decades not only modified our view concerning the higher level relationships among woodpeckers genera but also species limits within some groups (eg, *Chrysocolaptes*, *Melanerpes*; Campbell et al 2016, Llanes-Quevedo et al 2022) and WP woodpeckers are no exceptions (Perktas et al 2011, Pons et al 2011, 2019, 2020, Kamp et al 2019, Schweizer et al 2022). Below, we review these changes for three species (European Green,

White-backed and Middle Spotted) with differing distributions, habitat requirements and abundance.

European Green Woodpecker (hereafter *viridis*) is a common and conspicuous species, frequently encountered by people in western Europe. Surprisingly for such a common bird, the systematics and the evolutionary history of *viridis* remained unclear until recently. The same statement holds for White-backed Woodpecker (hereafter *leucotos*), although it is a much rarer and secretive species which is dependent on old-growth deciduous or mixed forests. Genetic studies also revealed unexpected genetic differentiation within the Middle Spotted Woodpecker (Schweizer et al 2022), a resident habitat specialist characteristic of deciduous forests over much of Europe (except Britain and virtually all of Scandinavia), Anatolia, the Caucasus region and the Zagros mountains of Iran and Iraq. We highlight here the main advances in the understanding of *viridis*, *leucotos* and *medius* systematics based on our genetic studies of these three species complexes.

European Green Woodpecker complex

Until the 2000s, four subspecies were recognised throughout Eurasia (Winkler & Christie 2002): ***1*** *P v viridis* occurring from Britain east to European Russia; ***2*** *P v karelini* (hereafter *karelini*) distributed over Italy, the Balkans, the Caucasus and south-western Turkmenistan; ***3*** *P v innominatus* (hereafter *innominatus*) restricted to south-western Iran and extreme north-eastern Iraq; and ***4*** *P (v) sharpei* (hereafter *sharpei*) in Iberia and southern France. Morphological differences among *innominatus*, *karelini* and nominate *viridis* are very subtle (Cramp 1985, Winkler & Christie 2020). In contrast, *sharpei* differs markedly from the other three subspecies in having a restricted amount of black on the side of the face, often limited to indistinct grey lines on the lore (Short 1982, Cramp 1985). Consequently, it has been suggested that *sharpei* may deserve species rank since the 19th century (Saunders 1872, Redactie Dutch Birding 2002, Winkler & Christie 2020, Commissie Systematiek Nederlandse Avifauna 2025). The taxonomic status of a fifth taxon, *P (v) vaillantii* (hereafter *vaillantii*; plate 430), endemic to northern Africa, has also been debated for long, being successively considered a subspecies (Winkler & Christie 2002) or a separate species (Vaurie 1959a, Voous 1973, Short 1982, Thévenot et al 2003, Commissie Systematiek Nederlandse Avifauna 2025). Based on plumage colouration patterns, it has been suggested that *sharpei* may be an intermediate link between *viridis* and *vaillantii* (Winkler & Christie 2002).

Phylogenetics and phylogeography

Viridis is closely related to the widespread and morphologically diverse Grey-headed Woodpecker and to Black-headed Woodpecker *P erythropygius*, a south-eastern Asian species encountered in dry and deciduous forests (Fuchs et al 2008). Pons et al (2011) inferred the molecular phylogenetics and the phylogeography of the *viridis* complex using four autosomal nuclear introns, one sex chromosome (Z) intron and two mitochondrial protein-coding genes. The results revealed three divergent clades within the complex (figure 1): ***1*** one clade that includes individuals collected from Britain to Russia that belong to *viridis* and *karelini*; ***2*** one Iberian clade (corresponding to *sharpei*); and ***3*** one North African clade (corresponding to *vaillantii*). Both mitochondrial and nuclear data sets strongly supported a sister relationship between *viridis/karelini* and the Iberian clade *sharpei*, showing that the Strait of Gibraltar acted as a strong geographical barrier preventing genetic exchanges between both sides of the Mediterranean Sea. The divergence time analyses indicated that the North African clade *vaillantii* diverged from the European clade during the Pleistocene between 1.6 and 2.2 million years ago (mya). The split between *sharpei* and *viridis/karelini* occurred later, c 0.7-1.2 mya (mid-Pleistocene), and can be explained by a strong reduction in gene flow between the Iberian and the European clades due to the Pyrenees. However, recent unpublished ecological modeling and genomics results (Fuchs et al in prep) suggest a more complex biogeographical scenario in which *sharpei* could also have persisted during the last glacial periods on the north side of the Pyrenees. The important role of Iberia as a glacial refugium for several bird species has been underlined by a number of phylogeographical studies (eg, Iberian Chiffchaff *Phylloscopus ibericus*, Helbig et al 1996; Citril Finch *Carduelis citrinella*, Förschler et al 2011; Savi's Warbler *Locustella luscinioides*, Neto et al 2012; Dunnock *Prunella modularis*, Drovetski et al 2018; and magpies *Pica*, Song et al 2018).

Secondary contact zone in southern France

Geographical distribution of *sharpei* is not strictly limited to the Iberian Peninsula, as its presence north of the Pyrenean range has been documented since the late 19th century (Lacroix 1872-1875, 1877ab). Most authors consider its distribution across southern France to be limited to the department Pyrénées-Orientales, adjacent to the northern Spanish frontier and the Mediterranean Sea (Mayaud 1936), or even to a narrow strip

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430 Levaillant's Woodpecker / Levaillants Specht *Picus vaillantii*, male, Ifrane, Morocco, 19 May 2008 *(Georges Olioso)*. In this species, both male and female have black malar stripe bordered above by fairly broad whitish line. With its black malar stripe and lack of black mask, male *vaillantii* superficially resembles female Iberian Green Woodpecker *P sharpei*, leading some taxonomists to suggest that *sharpei* could be closer to *vaillantii* than to European Green Woodpecker *P viridis*, which is not the case. **431** European Green Woodpecker / Groene Specht *Picus viridis*, male, Mas de la Cure, Camargue, Bouches-du-Rhône, France, 23 June 2010 *(Georges Olioso)*. This male ('e' in figure 2) of typical plumage from population 4 (close *viridis* allopatry) harboured very small proportion of autosomal genes introgressed from Iberian Green Woodpecker *P sharpei*. Black is deep and extends far behind eye. Red moustache is bordered by broad black edge. **432** Iberian Green Woodpecker / Iberische Groene Specht *Picus sharpei*, male, Céret, Pyrénées-Orientales, France, 27 June 2005 *(Georges Olioso)*. This male with typical *sharpei* plumage was captured not far from Spanish border. This male possessed *sharpei* mitochondrial and nuclear genes without any sign of introgression at sampled loci. **433** Green woodpecker / groene specht *Picus*, Mas de Londres, Hérault, France, 26 June 2011 *(Georges Olioso)*. This male ('c' in figure 2) had European Green Woodpecker *P viridis*-type plumage and mixed ancestry with small proportion of Iberian Green Woodpecker *P sharpei* genes.

north of the Pyrenees extending westward to the Atlantic (Dubois et al 2008, Grangé 2008). However, birders visiting the Languedoc-Roussillon region were often puzzled by the appearance of green woodpeckers encountered in this region. Jouard (1928) examined woodpeckers collected in the eastern Pyrenees and found plumage characteristics that distinguished them from both *viridis* (plate 431) and *sharpei* (plate 432). More recently, Beuzard (1997), taking into account the plumage variability of green woodpeckers in museums collected in Languedoc-Roussillon, suggested the existence of a hybridisation zone between *sharpei* and *viridis*, stretching from the eastern Pyrenees to Béziers, Hérault. In addition, analysing the geographical distribution of the mito-

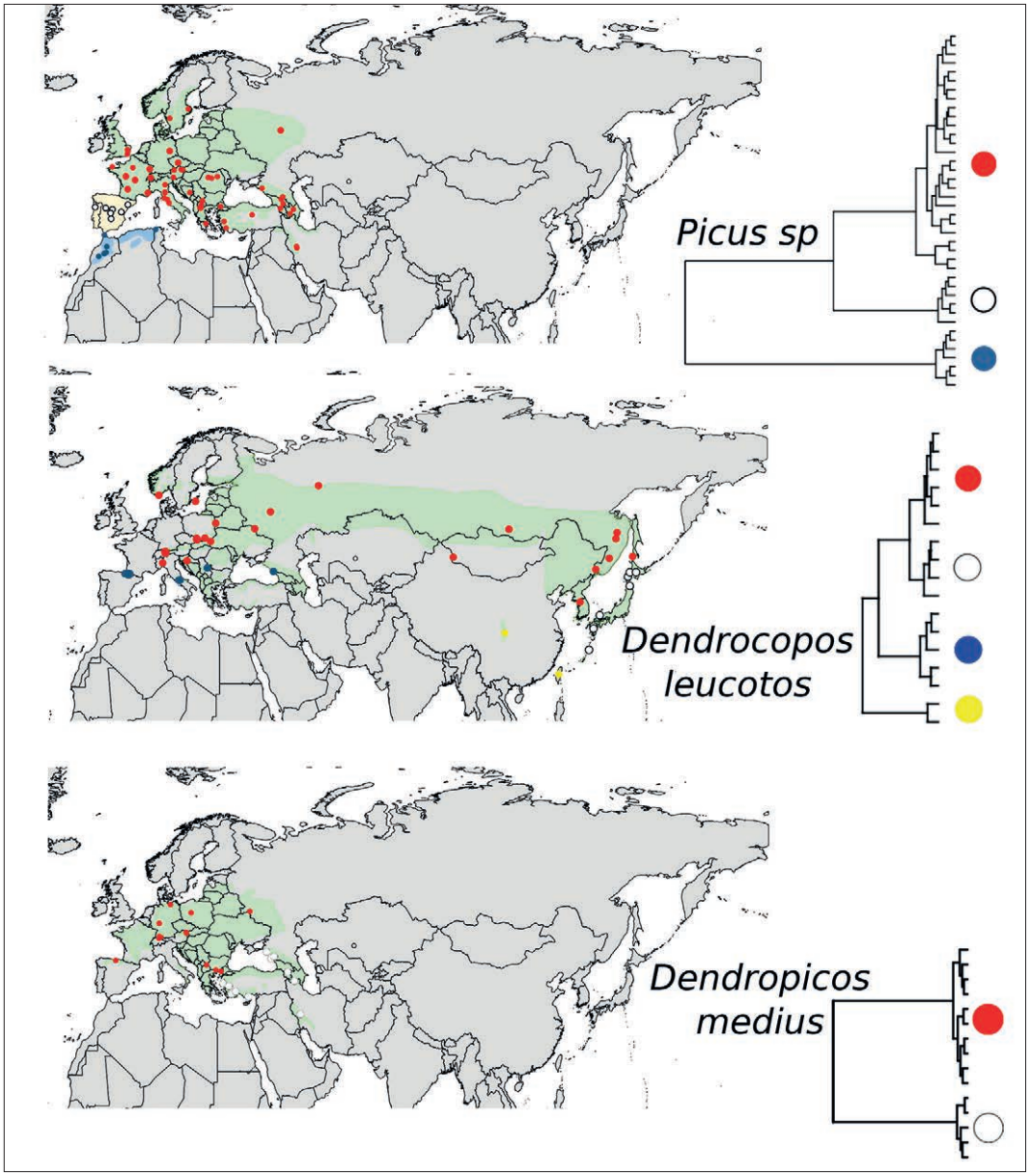


FIGURE 1 Geographical distribution of main mitochondrial clades of European Green *Picus viridis*, Iberian Green *P sharpei* and Levaillant's *P vaillantii* (upper), White-backed Woodpecker *Dendrocopos leucotos* (middle) and Middle Spotted Woodpecker *Dendropicos medius* (lower). Upper: red = *viridis*, white = *sharpei*, blue = *vaillantii*. Middle: red = *leucotos*, white = Japanese subspecies, blue = *lilfordi*, yellow = Chinese subspecies. Lower: red = *medius*, white = Asian subspecies (including Caucasus).

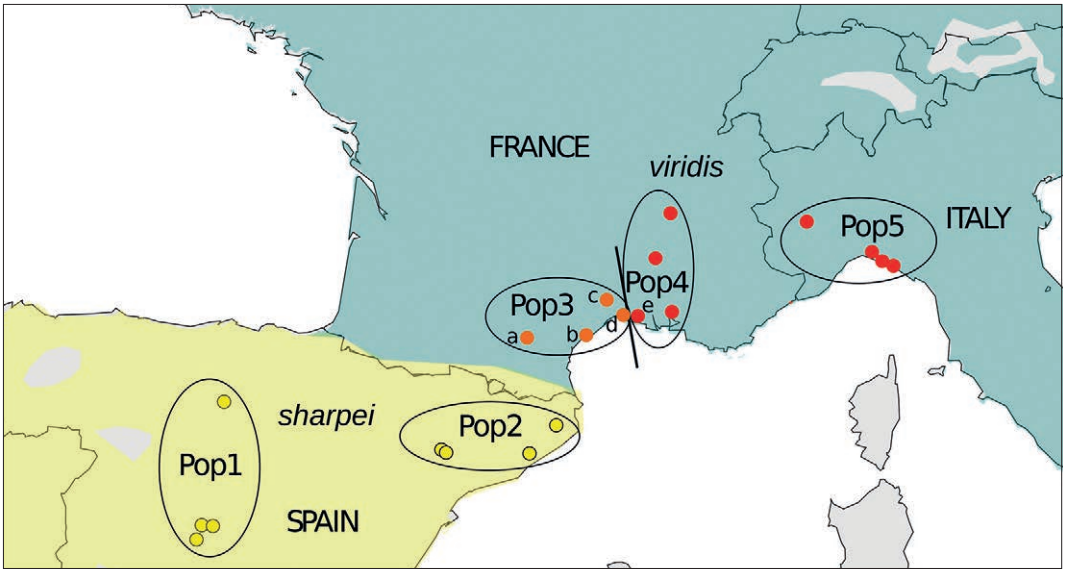


FIGURE 2 Geographic position of sampled individuals (n=20 males) and sampled populations (Pop) (n=5) of Iberian Green Woodpecker *Picus sharpei* and European Green Woodpecker *P viridis* in France, Italy and Spain. Studied contact zone (Pop3) was delimited based on overlap of mitochondrial lineages (Pons et al 2011) and occurrence of individuals with intermediate plumage (Olioso & Pons 2011). Contact zone is located in Languedoc-Roussillon along Mediterranean coast. Lowercase letters (a, b, c, d, e) denote genetically admixed birds, being not 'pure' *viridis* or *sharpei*. All birds were ringed using rings from Centre de Recherches sur la Biologie des Populations d'oiseaux. Modified from Pons et al (2019).

434 Green woodpecker / groene specht *Picus*, 'intermediate' male, Villesèquelande, Aude, France, 18 May 2005 *(Georges Olioso)*. This male ('a' in figure 2) had intermediate plumage and is genetically assigned to Iberian Green Woodpecker *P sharpei* having only small proportion of European Green Woodpecker *P viridis* genes. Dark grey, instead of black as in pure *viridis*, extending around eye; little black around moustache.

435 Green woodpecker / groene specht *Picus*, male, Vias, Hérault, France, 21 June 2009 *(Georges Olioso)*. This male ('b' in figure 2) had Iberian Green Woodpecker *P sharpei*-type plumage and *sharpei* genome with only small proportion of European Green Woodpecker *P viridis* genes. Grey colour restricted to small area in front of and under eye. Red moustache has thin and incomplete greyish edge, not reaching rear part of moustache.

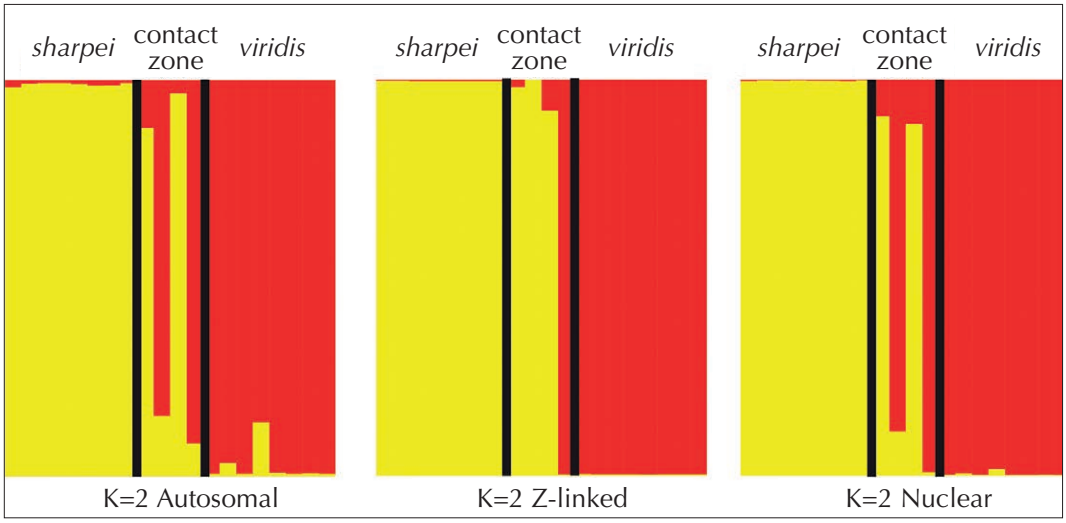


FIGURE 3 Plots performed with STRUCTURE showing genetic structure using 16 autosomal and 18 Z-linked loci across allopatric Iberian Green Woodpecker *Picus sharpei* and European Green Woodpecker *P viridis* populations and across secondary contact zone in Languedoc-Roussillon, France (n=20 males). Model best fitting our data was K=2. Y-axis varies between 0 and 1. Each individual is represented by single vertical line broken into two coloured segments, with lengths proportional to each of the two inferred clusters. Yellow: *sharpei* cluster (Pop1 and Pop2); red: *viridis* cluster (Pop4 and Pop5). Individuals from contact zone showed low levels of genetic admixture. Modified from Pons et al (2019).

chondrial cytochrome b and Z-linked BRM intron-15 alleles in southern France, Spain and Europe, Pons et al (2011) concluded that Iberian and European clades of the green woodpecker complex came into secondary contact along the Mediterranean coast, in Languedoc-Roussillon.

To further assess the geographical limits of the contact zone and gene flow between Iberian and European clades, Pons et al (2019) used 10 Z-linked and nine autosomal loci from seven chromosomes; 20 males (thus possessing two copies of the Z chromosome) from one population distributed across the contact zone in southern France and four allopatric populations were analysed (figure 2). The results of Pons et al (2019) confirmed the existence of a secondary contact zone between *sharpei* and *viridis* clades in southern France. The geographical mixing of *sharpei* and *viridis* alleles, that are clearly differentiated at most Z-linked and autosomal loci, is limited to the contact zone, ie, to an area whose limits can be broadly delimited in the west by the France-Spain border and Camargue, Bouches-du-Rhône, in the east. All males sampled in the contact zone showed signs of slight mixed ancestry (figure 3). The male 'c' sampled on the eastern side of the contact zone (figure 2, plate 433) had a Z-linked *viridis* genotype but harboured a small proportion of *sharpei* autosomal alleles (10%). Similarly, the easternmost juvenile male 'd' of the contact zone possessed a high proportion of *viridis* ancestry with 15% and 5% of autosomal and Z-linked *sharpei* alleles, respectively and *sharpei* mitochondrial DNA (mtDNA). Both males 'a' and 'b' (figure 2, plate 434-435) sampled across the western part of the contact zone harboured a large proportion of *sharpei* ancestry, holding 10% and 5% of autosomal *viridis* alleles, respectively. Overall, the mean proportion of admixture was higher in autosomal loci (10%) than in Z-linked loci (3.2%), in accordance with several studies showing that sex chromosomes are generally less prone to introgression than autosomal chromosomes (see Pons et al 2019 for references). We did not detect any evidence of introgression neither in distant allopatric populations in Italy or Spain nor in close allopatric populations 2 (Catalunya, Spain) and 4 (Provence-Alpes-Côte d'Azur, France) except for one slightly introgressed *viridis* male 'e' (figure 2, plate 431) sampled near the eastern limit of the contact zone in Camargue where only *viridis*-like green woodpeckers are currently observed by local ornithologists. Overall, these results suggest that gene flow is severely restricted and geographically limited to a narrow contact zone revealing a probably well-advanced speciation process. In

order to further study the spatial variation of gene flow through the contact zone, additional studies involving more individuals and genome-wide data are needed.

Species and subspecies limits

The *viridis* complex comprises three divergent clades that occupy distinct geographical ranges in Europe (without the Iberian Peninsula), Turkey and Iran (*viridis*), Spain/Portugal (*sharpei*) and Northern Africa (*vaillantii*). Perktas et al (2011) reached similar results, ie, three primary mitochondrial clades, using another mitochondrial marker (ND2).

In addition to strong genetic differentiation, *vaillantii* exhibits several diagnostic plumage characters (Winkler & Christie 2020). As this clade differs in several functionally independent genetic and phenotypic traits, we consider, in line with previous authors (Peters 1948, Vaurie 1959a, Voous 1973), that a species rank for *vaillantii* (Malherbe, 1847) is the best taxonomic treatment. The specific status of *vaillantii* is now accepted by all major taxonomic authorities (eg Dickinson et al 2013, Christidis et al 2025, Gill & Donsker 2025) as well as woodpecker specialists (Gorman 2014).

Pons et al (2011, 2019) showed reciprocal monophyly of mtDNA and several nuclear loci between *sharpei* and all other green woodpeckers distributed across Europe (*viridis*, *karelini*). *Sharpei* could also be distinguished from other green woodpeckers by several discrete plumage characters (greyish ear-coverts and greyish area around eye, non-barred undertail-coverts; see Cramp 1985, Olioso & Pons 2011, Winkler & Christie 2020) and vocalisations. These two clades differ in the distinctive call given during the breeding season, which is generally higher pitched, faster and differently structured in *sharpei* (Fauré 2013). *Sharpei* would thus clearly deserve species status under the phylogenetic species concept (Cracraft 1983, Helbig et al 2002). In addition, genetic admixture is limited to a narrow geographical region located in southern France between the France-Spain border and the Rhone delta. Reduced gene flow across the contact zone and low levels of admixture of birds sampled in the contact zone suggest that isolating barriers are efficient at limiting interspecific introgression. Although data concerning reproductive isolating mechanisms are currently lacking and more individuals from the contact zone and the Pyrenees should be analysed using genomics data to better evaluate gene flow, the results of Pons et al (2019) lend support to the treatment of Iberian and European green woodpecker clades as two distinct biological species, *P viridis* Linnaeus, 1758 and *P sharpei* (Saunders, 1872), because the interspecific gene flow is probably weak and spatially restricted to an apparently stable contact zone that is narrow relative to the breeding range of each clade (Johnson et al 1999). Aràgena et al (2020), using a COI barcoding approach, found similar mitochondrial genetic divergence between the Iberian and the European clades. This taxonomic rank has already been adopted by most important checklists (del Hoyo & Collar 2016, Christidis et al 2025, Gill & Donsker 2025), although others still consider the Iberian clade as a subspecies (Dickinson et al 2013). Very rarely, *sharpei* individuals located far away from the French border in the Iberian Peninsula show a dark grey tinge around the eye reminiscent of the plumage pattern of introgressed birds from the contact zone (José Luis Copete pers comm). Jean-Marc Pons and Damian Romay (unpublished results) genotyped green woodpeckers (n=25) from Galicia, north-western Spain using one nuclear marker and one mitochondrial marker. All these birds only harboured *sharpei* alleles. We suggest that intraspecific plumage variation may explain such atypical plumage far away from the contact zone, even if more studies would be needed to fully exclude that *viridis* alleles may have dispersed across Iberia.

Further taxonomic subdivisions have been recognised in *Picus viridis* sensu stricto. Birds from Italy and the Caucasus, which are slightly smaller and duller (less yellow, more grey) than the nominate, were assigned to the subspecies *karelini* (Winkler & Christie 2002, 2020). Current genetic data do not lend support to such a taxonomic treatment; all green woodpeckers currently assigned to *karelini* harbour the most common mtDNA haplotype found everywhere across Europe. In addition, both taxa do not significantly differ in voice (Fauré 2013). We thus agree with Vaurie (1959a) and Short (1982), who suggested that the subspecies *karelini* should be synonymised with *viridis*. Perktas et al (2011) proposed to elevate the Iranian subspecies *innominatus* (Zagros Green Woodpecker) to species rank because Iranian woodpeckers possess unique mitochondrial haplotypes not found elsewhere and are thus genetically diagnosable. However, they mention that *innominatus* is not reciprocally monophyletic and genetically very close to the other *viridis* populations. The Iranian birds are only slightly different in plumage from other *viridis* (head side and underparts are slightly paler and upperparts are less green). Unlike *vaillantii* and *sharpei*, Iranian birds do not exhibit any discrete plumage characters

that would differentiate them from other European Green Woodpeckers. Hence, in our opinion, there is currently no strong argument favouring the assignment of species rank to Iranian birds. Pending new genomics studies based on a comprehensive sample size, assigning a subspecific rank to Iranian green woodpeckers is currently the best taxonomic treatment. In line with Zink (2004), we advocate that in most cases a given geographical population should have a recent distinct evolutionary history to be ranked as a subspecies which is the case for *innominatus*, but not for *karelini*.

White-backed Woodpecker complex

White-backed Woodpecker belongs to a large Palearctic and Indo-Malayan radiation of large pied woodpeckers (genus *Dendrocopos*, 10-12 species; Fuchs & Pons 2015, Winkler et al 2020a). Its closest relative is Okinawa Woodpecker *D noguchii*, a dark brown woodpecker, only found on subtropical Okinawa, Japan (Winkler et al 2020b). White-backed is the largest *Dendrocopos* woodpecker and is highly dependent on old-growth deciduous and mixed forests for both foraging and nesting. This dependency of old forests makes its conservation status uncertain in the western part of its distribution.

Geographical distribution

Up to 10-12 subspecies mainly based on plumage variation, corresponding to four mitochondrial clades (figure 1), are currently recognised across its wide distribution over the Palearctic (Grangé & Vuilleumier 2009, Grangé 2022, 2023). Nominate *D l leucotos* (hereafter nominate *leucotos*) has a very wide and continuous range from northern and central Europe to eastern Asia, and the similar *D l uralensis* is distributed from the Ural mountains to Baikal lake. Four subspecies (*D l subcirris*, *D l stejnegeri*, *D l namiyei* and *D l owstoni*) are endemic to the Japanese archipelago from northern Hokkaido up to the small islands in the southern Ryukyu archipelago. *Owstoni* (Amami Woodpecker), which differs from other subspecies by its darker plumage, is only found on Amami Oshima (Ryukyu archipelago) where it inhabits old mature evergreen broadleaved forests.

In the southern part of its range, White-backed Woodpecker has a much more restricted and discontinuous geographical distribution. *D (l) lilfordi* is only distributed in old mountainous forests of the southern Palearctic (Pyrenees, Abruzzo, Balkans, Asia Minor and Caucasia). In China, two endemic allopatric subspecies occur in central (*D l tangi*) and south-eastern mainland (*D l fohkiensis*), respectively, and another subspecies (*D l insularis*) is endemic to Taiwan.

Phylogeny

Pons et al (2020) reconstructed the phylogenetic relationships among nine subspecies (nominate *leucotos*, *uralensis*, *lilfordi*, *subcirris*, *stejnegeri*, *namiyei*, *owstoni*, *insularis* and *tangi*) using one mitochondrial gene and three autosomal nuclear introns. Their results suggest that the endemic Chinese subspecies (*tangi*, *insularis)* were the first to branch off c 0.8 mya (figure 1). The second split separated the southern *lilfordi* subspecies from the northern *leucotos* group which comprises ***1*** two subspecies (nominate *leucotos*, *uralensis*) that were not genetically differentiated from each other at the studied loci; and ***2*** four closely related Japanese subspecies (*namiyei*, *subcirris*, *stejnegeri* and *owstoni*) (figure 1). Within the northern group, the Japanese subspecies form a monophyletic group related to the continental *leucotos/uralensis*.

Western Palearctic phylogeography

Pons et al (2020) used a combination of mtDNA and ecological niche modeling to reconstruct the phylogeography of *leucotos* and *lilfordi* clades. The niche models for current conditions were projected on paleoclimatic layers from the last interglacial (c 130 000 years ago) and the last glacial maximum (21 000 years ago). As for the *viridis* complex, the climatic oscillations of the Pleistocene (2.6-0.012 mya) played a major role in the present-day genetic structure of the White-backed Woodpecker complex in the WP. *Lilfordi* and *leucotos/uralensis* clades diverged during the mid-Pleistocene c 0.6 mya. In contrast with *lilfordi*, whose allopatric small populations are genetically structured and persisted through the Pleistocene climatic oscillations in southern Europe, genetic data suggest that the *leucotos/uralensis* clade shows very weak geographical structure with evidence for recent spatial expansion from a unique refuge. Ellegren et al (1999), based on the sampling restricted to Polish and Scandinavian populations, reached a similar result. Notably, unlike the most common pattern of population expansion following warming of the climate which is oriented from eastern Asian glacial refugia towards Europe in several bird species (see Pons et al 2020 for examples), the geographical distribution of the genetic diversity in *leucotos*, which is the highest in central Europe, suggests a reverse pattern; ie, the persistence of a *leucotos*

436 Lilford's Woodpecker / Lilfords Witrugspecht *Dendrocopos lilfordi*, male, Abruzzo, Italy, 13 May 2024 *(Paul Harris)*. Back of *lilfordi* is characteristic, with number of white transversal bars, six to eight depending on individual, quite thin and well-defined. White-backed Woodpecker *D leucotos* has only four to six transversal bars. Upper bar on top of wing is always thin, unlike that of *leucotos*, which is much thicker. Pink of undertail very extensive in this individual but very variable individually. Pattern of external rectrices (proportion of white/black) varies greatly between individuals and can be used to differentiate them.

437 Lilford's Woodpeckers / Lilfords Witrugspechten *Dendrocopos lilfordi*, female with young male, Arette, Pyrénées-Atlantiques, France, 16 June 2009 *(Pierre Navarre)*. Back has six white transversal bars. Flank heavily streaked down to lower abdomen. Pink of undertail extending to top of legs (character very variable depending on individual, see male in plate 436). Pattern of external rectrices very different from that of male in plate 436. Young male (25-27 days old) has classic matte red crown of adult male and strong streaks of upper flank are visible.

population in a cryptic glacial refugium possibly located around the Carpathians, from which the subspecies may have expanded eastward across Siberia after the last glacial maximum. Consistent with mitochondrial data, climatic niche modeling suggests that suitable climatic conditions might have persisted in central Europe around the Carpathian mountains during the last glacial maximum (Pons et al 2020). Nevertheless, this unexpected biogeographic scenario would deserve to be confirmed using a more densely sampled study based on genome-wide data. Pons et al (2020) also performed isolation-migration analyses to assess historical gene flow between *lilfordi* and *leucotos*. The results strongly indicated that no historical gene flow occurred between the two clades which have probably been fully isolated since their divergence.

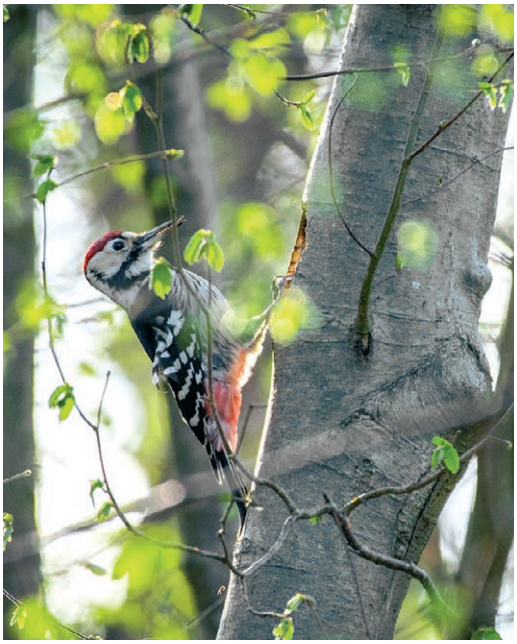
Systematic issues

Three primary clades emerged across the Palearctic in the *leucotos* complex. The current taxonomy that comprised one polytypic species including up to 12 subspecies does not entirely reflect the evolutionary history of the *leucotos* clades. Additional genetic and phenotypic studies, including a much larger number of *leucotos* from China, Taiwan, Siberia and mountains of the southern Palearctic are needed to achieve a comprehensive taxonomic treatment of the complex. Nevertheless, based on the study of Pons et al (2020), it is still possible to draw several systematic propositions pending further studies.

Western Palearctic subspecies lilfordi

Molecular species delimitation methods, mitochondrial reciprocal monophyly and the gene flow analyses gave support for no historical gene

438 Lilford's Woodpecker / Lilfords Witrugspecht *Dendrocopos lilfordi*, juvenile female, Lourdios-Ichère, Pyrénées-Atlantiques, France, 7 May 2017 *(Stéphane Hommeau)*. Crown is pure black and lower back has three to four black bars. **439** White-backed Woodpecker / Witrugspecht *Dendrocopos leucotos*, female, South Korea, 20 October 2018 *(Laurent Joubert)*. This bird is intermediate in plumage between Scandinavian nominate *leucotos* (very little streaking on flank and few transversal stripes on back) and Korean taxa further east (*takahashii* and *quelpartensis*) and Japanese taxa which possess heavily streaked flank. Note wide upper white bar present on all taxa except Lilford's Woodpecker *D lilfordi*. These Korean and Chinese birds have been named *sinicus* by Sergei Buturlin, a taxon no longer recognised today.



440 White-backed Woodpecker / Witrugspecht *Dendrocopos leucotos*, male, Bieszczady mountains, Maniów, Poland, 30 April 2017 *(Guillaume Beloscar)*. This bird has four bars on back, with upper bar wider. Flank finely streaked on white underparts. Generally, *leucotos* appears paler than Lilford's Woodpecker *D lilfordi*, notably on head which is more yellowish in *lilfordi*. **441** Amami Woodpecker / Amamiwitrugspecht *Dendrocopos leucotos owstoni*, Tatsugo, Armani Oshima, Kagoshima, Japan, 2 March 2018 *(William Price)*

flow between *lilfordi* and the northern clades. The sharing of nuclear alleles between *lilfordi* and *leucotos* highlighted in Pons et al (2020) seems to result from incomplete clade sorting of ancestral alleles and not from introgression between both clades. This provides strong support to their independent evolution since the mid-Pleistocene. The COI mitochondrial genetic distance between *lilfordi* and *leucotos* is 2.1%, which compares to the distances between Great Spotted Woodpecker and Syrian Woodpecker (2.8%; Pons et al 2020). *Lilfordi* has a strong sedentary lifestyle, closely linked to beech and humidity in mountainous regions whereas *leucotos* shows greater ecological flexibility in its choice of habitat and expansion tendencies, with erratic habits in some populations (Grangé 2015). Differences in ecology coupled with differences in adult plumage (rump mostly black, back-barred black, pink below more extensive than in *leucotos*) and juvenile plumage (undertail-coverts not reddish and females without red on crown) (see Grangé 2022, 2023 for a detailed description of plumage differences between taxa) and genetic variation suggest that *lilfordi* may be elevated to species rank under the Phylogenetic Species Concept (PSC). However, given that the separation between *lilfordi* and *leucotos* is a fairly recent event at the evolutionary scale and knowing that *lilfordi* and *leucotos* are geographically intertwined in the Balkans (cf Perušek 1991; Hans Winkler unpublished data), Pons et al (2020) also recommend to assess whether both subspecies are ecologically segregated or syntopic and at what level they are reproductively isolated. This would permit to assess the completion of premating and postmating isolating barriers and to determine whether *lilfordi* and *leucotos* behave as biological species or not. The reasons why we recommend that *sharpei* be recognised as a species and *lilfordi* not are summarised in figure 4. Note that *lilfordi* is treated as a separate species by Commissie Systematiek Nederlandse Avifauna (2025); cf Redactie Dutch Birding (2012).

Uralensis is similar to nominate *leucotos* but is much whiter on the wings and the back and less streaked below. Geographic variation in plumage of *leucotos* in Central Asia is currently not well understood and despite lack of difference in mtDNA with *leucotos* and pending further genetic, ecological and morphological studies, Pons et al

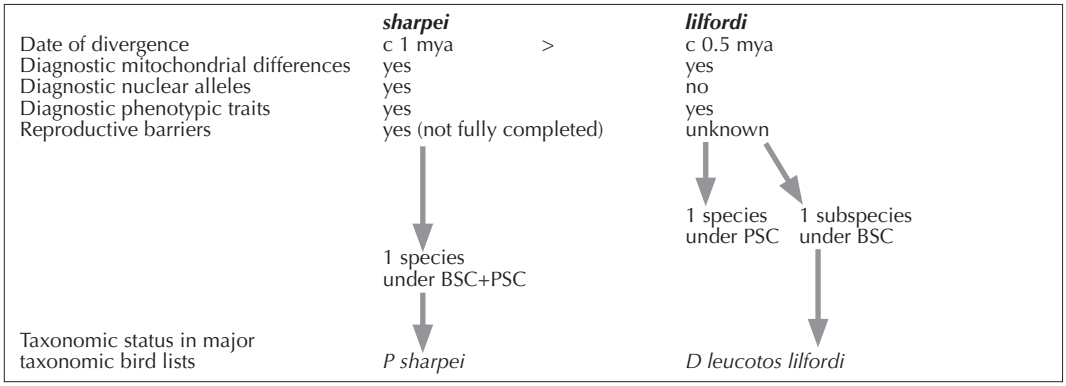


FIGURE 4 Comparative taxonomic status of Iberian Green Woodpecker *Picus sharpei* and Lilford's Woodpecker *Dendrocopos lilfordi* clades following molecular studies by Pons et al (for details see references). Both taxa show comparable level of phenotypic differences. However, date of divergence is probably more ancient for *sharpei* which exhibits clear-cut differences both in mitochondrial and nuclear genes. In addition, our data suggest that partial reproductive barriers exist between European Green Woodpecker *P viridis* and *sharpei* that reduce gene flow across secondary contact in southern France while it is unknown for *lilfordi* and White-backed Woodpecker *D leucotos*. Mya = million years ago, BSC = Biological Species Concept, PSC = Phylogenetic Species Concept.

(2020) advocated maintaining the taxonomic status of *uralensis* unchanged.

Chinese endemic subspecies

The Chinese clade split from other *leucotos* clades during the Mid-Pleistocene (c 0.8 mya) and diversified in three morphological subspecies *tangi*, *insularis* and probably *fohkiensis* which are all darker in plumage than *leucotos/lilfordi*. *Insularis* has an insular range limited to Taiwan while *tangi* and *fohkiensis* are restricted to two relatively small allopatric areas in central and south-east China. *Tangi* is similar to *fohkiensis* but with less black underparts and larger in size. The latter could not be sampled by Pons et al (2020) but based on geography and plumage *fohkiensis* is very likely closely related to *tangi* and *insularis*. The plumage of *insularis* is similar to that of *tangi* but it has a whiter back and wider pink lower parts and a smaller size.

Attributing species status for *lilfordi* under the PSC would imply that species status is also deserved for the Chinese subspecies, otherwise *leucotos* would be paraphyletic. *Insularis* (Gould, 1863) which has priority according to the zoological nomenclature rules would include two mainland subspecies (*tangi*, *fohkiensis*) and the nominate *insularis* subspecies. The probable inclusion of *fohkiensis* into *insularis*, based on morphology (Cheng 1956), geography and plumage has nevertheless to be confirmed using genetic data.

Japanese archipelago endemic subspecies

Four endemic Japanese subspecies formed a monophyletic group of recent origin; the COI mitochondrial marker diverges only by two mutational steps from the continental *leucotos* group. Pons et al (2020), using a molecular species delimitation method and four loci identify the Japanese clade as an independent clade. Although being evolutionary distinct, the Japanese clade is genetically and phenotypically poorly differentiated from *leucotos* and the four Japanese subspecies are distinguished by only minor plumage differences (Grangé 2023). As all Japanese populations share the most common mitochondrial haplotype and are poorly differentiated in plumage, it can be argued that all populations belong to the same subspecies. However, pending further studies needed to evaluate more in depth phenotypic and genomic variability across the archipelago, we advocate to not change the taxonomic status of Japanese White-backed Woodpeckers. *Owstoni* was sometimes treated as full species (del Hoyo & Collar 2014). Based on our results it does not deserve species-level status as it is not genetically differentiated from other Japanese subspecies. Differences in plumage and morphology highlighted for this insular taxon (Grangé 2023) may result from a rapid evolution or phenotypic plasticity related to humid subtropical insular environment and/or drift. However, due to its insular distribution and peculiar ecological niche and its distinctive plumage, *owstoni* deserves in our view subspecies status despite lack of genetic differentiation at the loci analysed by Pons et al (2020).

442 European Middle Spotted Woodpecker / Middelste Bonte Specht *Dendropicos medius medius*, Rafz, Zürich, Switzerland, 10 December 2017 *(Patrick Donini)*. In this individual of nominate *medius* from Europe (European clade), pinkish colouration extends diffusely from rear underparts onto flank and upper belly which is usually not so in individuals from Asian clade. Moreover, streaking on underparts is less prominent than in latter (cf plate 443).

443 Asian Middle Spotted Woodpecker / Aziatische Middelste Bonte Specht *Dendropicos medius anatoliae*, Lesvos, Greece, 24 April 2001 *(René Pop)*. Note that pinkish colouration of rear underparts extends less onto flank and upper belly in this individual of Asian clade. Streaking on underparts is rather prominent, more so than usual in individuals from European clade (cf plate 442).

Middle Spotted Woodpecker

Four subspecies are usually recognised (Christidis et al 2025): ***1*** *D m medius* breeding in Europe except the Caucasus; ***2*** *D m caucasicus* of northern Turkey (excluding European Turkish Thrace), Caucasus, Transcaucasia and probably north-western Iran; ***3*** *D m anatoliae* breeding in western and southern Turkey, Lesvos and north-western Syria; and ***4*** *D m sanctijohannis* of the Zagros mountains of western Iran and north-eastern Iraq. Over its entire range, Middle Spotted Woodpecker displays only slight morphological variation which has been described as being partly clinal in nature (Cramp 1985). In nominate *medius*, the pinkish colouration on the underparts is less restricted to the vent compared with the Asian subspecies and extends diffusely onto the flank and upper belly; the latter is less extensively coloured yellowish. The two outermost visible tail feathers (which equal the second and third outermost ones, the outermost is reduced and normally hidden in woodpeckers) are mainly whitish with limited black markings, while they show black and white bars of approximately even width in the Asian subspecies – there is variation, however. The Asian subspecies *caucasicus* and *anatoliae* are rather similar and have been synonymised (with the former name having priority) (Vaurie 1959b, 1965). The isolated subspecies *sanctijohannis* differs from both by the underparts showing more restricted black streaks and the yellow on the belly being paler and more restricted to the lower parts.

Phylogenetics and phylogeography

Middle Spotted Woodpecker has been variously included in the genera *Dendrocopos*, *Leiopicus*, *Picoides* or *Dendropicos*. However, Fuchs & Pons (2015) showed that it is best treated in *Dendrocoptes* together with its closest relatives, ie, Arabian Woodpecker *D dorae*, endemic to the Arabian Peninsula, and Brown-fronted Woodpecker *D auriceps* from the northern part of South Asia. This is now usually followed (Christidis et al 2025,

but Commissie Systematiek Nederlandse Avifauna 2025 places it in *Dendropicos*; cf Redactie Dutch Birding 2016, Sangster et al 2016). Given the comparatively weak morphological variation in Middle Spotted across its entire range, it was rather surprising when Kamp et al (2019) found pronounced genetic differences, a so-called phylogeographic break, between Asian (including the Caucasus) and European populations. Although nuclear genetic markers were included in the latter study, this separation into an Asian and a European clade was mainly driven by variation in three markers from the mtDNA. The split between the two clades was dated to have happened around 1.5 mya, a level of divergence found, eg, between different species in the *viridis* complex (see above).

This result was surprising in another aspect. The two groups seemed to be separated by the Sea of Marmara with the Dardanelles and Bosporus Straits. Although different subspecies have been described on either side of the Sea of Marmara for a few bird species, including Lesser Spotted Woodpecker (Schweizer 2025), this area should generally not represent a strong physical barrier for a bird species, although this seems not to hold for woodpeckers.

Phylogeographic structure inferred solely based on mtDNA might not necessarily represent the true evolutionary history of clades for various reasons (eg, Schweizer & Burri 2019), consequently, these results were tested with genetic data stemming from the entire genome. Schweizer et al (2022) analysed 2743 variable positions, so-called single nucleotide polymorphisms (SNPs), distributed throughout the genome using samples from Armenia, the Caucasus, Greece, Serbia, Spain and Switzerland. Consistent with previous results based on mitochondrial data, a clear genomic divergence between Asian (including the Caucasus) and European populations was found. However, the data also revealed signatures of gene flow from the Asian into the European populations. It thus suggested that there might be limited or at least unidirectional introgression upon secondary contact between the Asian and the European clade. However, so far, neither the location of a putative secondary contact zone is known nor, if it existed, whether it is stable or not. It must be taken into account that its location must not necessarily coincide with the proposed subspecies borders along the Sea of Marmara.

Despite introgression, the different clades of Middle Spotted Woodpecker could at least be considered as incipient species. However, it is premature to make any taxonomic conclusion before genomic data based on a more comprehensive geographic sampling is available and potential phenotypic differences, eg, in vocalisations are documented. So far, it is not clear which prezygotic isolation factors other than demographic or geographical aspects could limit gene flow between Asian and European populations. At least slight differences in habitat preferences might exist. In mainland Greece, Middle Spotted is mainly found in deciduous woodland dominated by oaks and avoids any other type of vegetation, whereas on Lesvos (close to the Turkish coast), birds are commonly found in olive groves (Handrinos & Akriotis 1997). Olive groves are also inhabited by birds in Turkey but oaks are an important aspect of their habitat there, too (Kirwan et al 2008), hence it is not clear whether there is a strong habitat shift between the two clades.

General comments

Delimiting species remains challenging in many cases because the speciation process, ie, the evolution of reproductive barriers, is a gradual process that most often takes between one and three million years in birds. Hence posing a discrete limit over a continuous process may be problematic especially in case of clades having recently diverged. Young clades whose reproductive barriers are still porous and gene flow not fully stopped are in the so-called 'grey zone' where morphological, ecological and genetic traits evolve at different rates and can lead to different taxonomic inferences. Using an integrative taxonomic framework based on the combination of multiple types of complementary evidences (Sangster 2018, Schweizer et al 2023) may help in correctly delimited young species limits. Incomplete geographic sampling of widespread natural populations is another limiting factor in many systematic studies. For instance, for the *viridis* complex and especially the *leucotos* complex which have a widespread geographical distribution, Pons et al (2011, 2020) did not include representatives of several populations (Iran for *viridis* complex, South-East Asia for *leucotos* complex) that would have been useful to reinforce and enlarge their taxonomic conclusions. Although birds are probably among the best known zoological groups, much more remains to be done to correctly translate their diversity and complex evolutionary history into a natural classification. This means that bird names and bird lists will continue to change as our knowledge progresses. At the same time, taxonomists need to consider that taxonomy re-

quires stability to be workable and that each proposed change must be supported by a set of scientific evidence as robust as possible.

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