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"Phylogeny of the *Garrulus glandarius* complex (Corvidae, Aves) based on mitochondrial marker sequences"

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"Defining subspecies within the Jay … is possibly the most subjective and 'blurred' field any taxonomist can venture into. If the intention is to see a tiny difference and name it, ample opportunities exist. Practically all morphological traits vary clinally *and* individually, creating a quagmire of variation, and even when comparing long series … it is possible to arrive at different conclusions depending on the underlying taxonomic philosophy."

Shirihai & Svensson (2018)

Eurasian Jay – *Garrulus glandarius* by Paul Wolf [https://pbase.com/wolfoto]
Burgenland, Austria
August 2018

In memory of

ANITA GAMAUF

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Abstract

Phylogeny of the *Garrulus glandarius* complex (Corvidae, Aves) based on mitochondrial marker sequences

The avian genus *Garrulus* within the family Corvidae is by most authorities considered to comprise three forest-dwelling species of the Old World. Its most familiar member the Eurasian Jay *Garrulus glandarius* exhibits a complex geographic pattern of morphological variation over its wide, mainly Palearctic, distribution area. The major checklists of the birds of the world do currently accept between 34 and 40 different subspecies that are usually arranged in five to eight groups, of which some recurringly had been proposed to form distinct species. In the present study a phylogeny of the *Garrulus glandarius* complex has been constructed, predominantly based on foot pad samples from museum specimens covering nine subspecies groups of this complex, as well as the two other species of the genus, *Garrulus lanceolatus* and *Garrulus lidthi*. Phylogenetic trees based on sequences of the mitochondrial *cytochrome b* gene and the complete mitochondrial *control region* indicate a subdivision into at least eight major clades within the *G. glandarius* complex, for the most part matching with the established subspecies groups. The insular subspecies, *Garrulus g. taivanus* from Taiwan, additionally represents a very distinct mitochondrial lineage. Notwithstanding the clear genetic differentiation of many taxa within the complex, several possible cases of successful interbreeding between representatives of different subspecies groups have been detected.

Zusammenfassung

Phylogenie des *Garrulus glandarius*-Komplexes (Corvidae, Aves) basierend auf mitochondriellen Markersequenzen

Die Gattung *Garrulus* der Rabenvogelfamilie Corvidae umfasst laut den meisten Autoren drei waldbewohnende Arten von Hähern der alten Welt. Der bekannteste Vertreter, der Eichelhäher *Garrulus glandarius*, weist innerhalb seines weit ausgedehnten, hauptsächlich paläarktischen Verbreitungsgebiets eine stark ausgeprägte geografische Variation auf. Aktuelle Übersichtswerke erwähnen zwischen 34 und 40 anerkannte Unterarten, die üblicherweise in fünf bis acht Unterartengruppen zusammengefasst werden. Für manche deutlich differenzierte Gruppen wurde bereits mehrmals Artstatus vorgeschlagen. Im Zuge dieser Studie wurde, hauptsächlich mittels Proben aus Museumsbälgen von Individuen aus neun Unterartengruppen des *Garrulus glandarius*-Komplexes sowie von den zwei weiteren Arten der Gattung, *Garrulus lanceolatus* und *Garrulus lidthi*, eine umfassende Phylogenie dieses Komplexes erstellt. Die Phylogenetischen Bäume, basierend auf Sequenzen des mitochondriellen *Cytochrom b* Gens und der kompletten mitochondriellen *Kontrollregion*, zeigen mindestens acht klar differenzierte monophyletische Gruppen innerhalb des Eichelhäher (*Garrulus glandarius)*-Komplexes, die überwiegend mit den etablierten Unterartengruppen übereinstimmen. Die Inselform, *Garrulus g. taivanus* von Taiwan repräsentiert eine zusätzliche deutlich differenzierte mitochondrielle Linie. Trotz der großen genetischen Unterschiede zwischen vielen Taxa des Komplexes konnten auch mehrere Hinweise auf erfolgreiche Mischbruten zwischen Individuen aus verschiedenen Unterartengruppen festgestellt werden.

Introduction

The genus *Garrulus* Brisson, 1760 is by most authorities currently considered to comprise three species of forest-dwelling Old World representatives of the avian family Corvidae (e.g. Madge 2009; Dickinson & Christidis 2014), also called the true or typical jays, in contrast to the diverse New World jays (Madge & Burn 1994; Goodwin 1976). Two of these species are each confined to comparatively restricted Asian distribution areas. The woodlands of the western Himalayas are inhabited by the primevally appearing Lanceolated Jay *Garrulus lanceolatus* Vigors, 1831 (von Vietinghoff-Scheel 1992), which recurrently has been placed into separate genera (*Celalyca* Gray, 1855 or *Laletris* Reichenow, 1906) (e.g. Kaup 1855; Salvadori 1872; Reichenow 1914; Hartert 1918; Whistler 1923; Sushkin 1927). Whereas the for long time obscure origin of the elusive Lidth's Jay *Garrulus lidthi* Bonaparte, 1850 at last had been located at the beginning of the twentieth century on two small islands of the Riu Kiu arc south of the major islands of Japan (Hartland 1905; von Vietinghoff-Scheel 1992; Collar et. al 2001). Principally owing to its almost chintzy purple plumage colouration, it has by some been generically separated as well (*Lalocitta* Reichenow, 1906) (e.g. Reichenow 1914; Sushkin 1927; Jahn 1942).

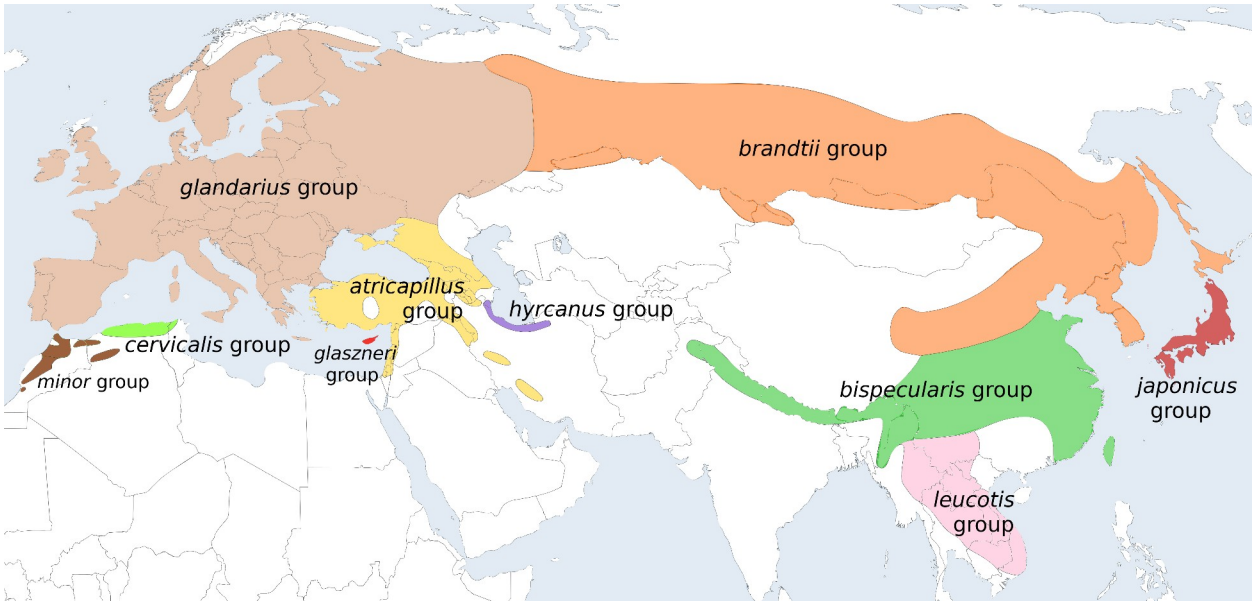

Figure 1. Breeding distribution ranges of the subspecies groups of the Eurasian Jay *Garrulus glandarius* (based on the combined information from del Hoyo & Collar 2016; Shirihai & Svensson 2018; Isenmann & Moali 2000; Johansen 1944).

The widely-ranging Eurasian Jay *Garrulus glandarius* (Linnaeus, 1758), in contrast, inhabits wooded areas from the Atlas Mountains in North Africa, across northern Eurasia to Japan, parts of continental Southeast Asia and the Himalayas, where it co-exists with *Garrulus lanceolatus* (Goodwin 1976; Ali & Ripley 1987; Madge 2009; Figure 1). Within this extensive distribution area, the Eurasian Jay exhibits an astonishing degree of morphological variation. The major checklists of the birds of the world recognise between 34 and 40 subspecies (Clements 2000; Dickinson & Christidis 2014; Gill et al. 2020) and many additional forms have been described, albeit in some cases based on subtle plumage minutiae and by referring to insufficiently large type series of sometimes doubtful origin (cf. Parrot 1907; Keve 1939, Blake & Vaurie 1962; Dickinson et al. 2004b; Shirihai & Svensson 2018).

This array of subspecies has been variably arranged into eight (e.g. Vaurie 1959), seven (Reichenow 1905; Roselaar in Cramp & Perrins 1994), six (Kleinschmidt 1893; Reichenow 1914) or five (Keve 1939; Kuroda 1957; Goodwin 1976), yet each time morphologically distinct, groups either by pursuing typological approaches (Reichenow 1914; Keve 1939; Vaurie 1959) or by taking presumed evolutionary relationships into consideration as well (Kuroda 1957; Goodwin 1976; Roselaar in Cramp & Perrins 1994). Most later synopses have embraced the subdivision into eight subspecies groups (Sibley & Monroe 1990; Haffer 1993; Madge & Burn 1994; Madge 2009; Mitchell 2017), a system first published by Stresemann (1940) in a lively review of Keve (1939). According to these authors the Eurasian Jay *Garrulus glandarius* is comprised of, the European *glandarius* group, the western North African *cervicalis* group, the *atricapillus* group of the Middle East and the Caucasus, the *hyrcanus* group of the Caspian Alborz mountains, the *brandtii* group of most of northern Asia, the *japonicus* group of the Japanese islands Honshu and Kyushu, the *bispecularis* group of southern China and the Himalayas and the *leucotis* group from continental Southeast Asia.

In the present study, by incorporating some of the views of Roselaar in Cramp & Perrins (1994) and Shirihai & Svensson (2018), as well as Keve (1969), the subspecies hailing from the western and southern parts of the Atlas Mountains are separated in the *minor* group and *G. g. glaszneri* from Cyprus forms the *glaszneri* group (Figure 1; Table 1), raising the number of groups to ten.

Table 1. List of subspecies of the Eurasian Jay *Garrulus glandarius* accepted by Dickinson & Christidis (2014) and additional subspecies mentioned in this study, currently not recognised (with quotation marks), arranged in ten groups slightly altered from Madge (2009) and Roselaar in Cramp & Perrins (1994). The type localities and references to the original descriptions are given, for the latter see Appendix III.

G. glandarius **subspecies**	**Type locality**	**Original description**
	glandarius **group**	
glandarius	Sweden	*Corvus glandarius* Linnaeus, 1758
"*sewerzowii*"	Kasan & Simbirsk (Uljanowsk), Russia	[*Garrulus glandarius*] var. *sewerzowii* Bogdanov, 1871
fasciatus	Spain	*Glandarius garrulus fasciatus* Brehm, 1857
"*lusitanicus*"	Linares do Riofrio, Salamanca, Spain	*Garrulus glandarius lusitanicus* Voous, 1953
ichnusae	Sardinia	*Garrulus ichnusae* Kleinschmidt, 1903
rufitergum	Tring, England	*Garrulus glandarius rufitergum* Hartert, 1903
hibernicus	County Wexford, Ireland	*Garrulus glandarius hibernicus* Whiterby & Hartert, 1911
corsicanus	Corsica	*Garrulus glandarius corsicanus* Laubmann, 1912
albipectus	Florence, Tuscany, Italy	*Garrulus albipectus* Kleinschmidt, 1920
cretorum	Mount Ida, Crete	*Garrulus glandarius cretorum* Meinertzhagen, 1920
graecus	Sparta, Taygetos, Greece	*Garrulus glandarius graecus* Keve, 1939
ferdinandi	Burgas, Bulgaria	*Garrulus glandarius ferdinandi* Keve, 1944
	glaszneri **group**	
glaszneri	Troodos mountains, Cyprus	*Garrulus glaszneri* Madarász, 1902
	minor **group**	
minor	Djelfa, Saharan Atlas, Algeria	*Garrulus minor* Verreaux, 1857
"*oenops*"	Taddart, High Atlas, Morocco	*Garrulus oenops* Whitaker, 1897
whitakeri	Tangier, Morocco	*Garrulus glandarius whitakeri* Hartert, 1903
	cervicalis **group**	
cervicalis	Algeria	*Garrulus cervicalis* Bonaparte, 1853
"*koenigi*"	Ain-Draham, Tunisia	*Garrulus glandarius koenigi* Tschusi, 1904
	atricapillus **group**	
atricapillus	Mount Lebanon, Lebanon	*Garrulus atricapillus* Geoffroy Saint-Hilaire, 1832
krynicki	Georgiyevsk, Stavropol Krai, Russia	*Garrulus krynicki* Kaleniczenko, 1839
anatoliae	Asia Minor (cf. Keve 1973)	*Garrulus atricapillus anatoliae* Seebohm, 1883
"*rhodius*"	Monte Ataviro, Rhodes, Greece	*Garrulus rhodius* Salvadori & Festa, 1913
"*hansguentheri*"	Tash-Cupri, near Istanbul, Turkey	*Garrulus glandarius hansguentheri* Keve, 1967
"*susianae*"	Izeh (Mal Amir), Khuzestan, Iran	*Garrulus glandarius susianae* Keve, 1973
iphigenia	Koreis, Crimea	*Garrulus glandarius iphigenia* Sushkin & Ptuschenko, 1914
samios	Samos, Greece	*Garrulus glandarius samios* Keve, 1939
	hyrcanus **group**	
hyrcanus	Mazendaran, Iran	*Garrulus hyrcanus* Blanford, 1873
"*caspius*"	Lankaran, Azerbaijan	*Garrulus atricapillus caspius* Seebohm, 1883
	brandtii **group**	
brandtii	Altai	*Garrulus brandtii* Eversmann, 1842
"*taczanowskii*"	Sakhalin, Russia	*Garrulus glandarius taczanowskii* Lönnberg, 1908
"*pallidifrons*"	Uenai, Iburi, Hokkaido, Japan	*Garrulus glandarius pallidifrons* Kuroda, 1927
pekingensis	Beijing, China	*Garrulus bispecularis pekingensis* Reichenow, 1905
kansuensis	Gansu, China	*Garrulus glandarius kansuensis* Stresemann, 1928

	***bispecularis* group**	
bispecularis	Himalayas, India (Ticehurst & Whistler 1924)	*Garrulus bispecularis* Vigors, 1831
taivanus	Taiwan	*Garrulus taivanus* Gould, 1863
sinensis	Ningbo, China	*Garrulus sinensis* Swinhoe, 1871
"*rubrosus*"	plains north of Yangtze (Wuhan), China	*Garrulus glandarius rubrosus* Keve, 1939
haringtoni	Mt Victoria, S Chin Hills, Myanmar	*Garrulus haringtoni* Rippon, 1905
interstinctus	Darjeeling, West Bengal, India	*Garrulus bispecularis interstinctus* Hartert, 1918
persaturatus	Shillong, Meghalaya, India	*Garrulus bispecularis persaturatus* Hartert, 1918
	***leucotis* group**	
leucotis	Kyaukhnyat, Kayin State, Myanmar	*Garrulus leucotis* Hume, 1874
oatesi	Chin Hills, Myanmar	*Garrulus oatesi* Sharpe, 1896
	***japonicus* group**	
japonicus	Japan (cf. Dickinson et al. 2004a)	*Garrulus glandarius japonicus* Temminck & Schlegel, 1847
"*hiugaensis*"	Nisimera-mura, Kyushu, Japan	*Garrulus japonicus hiugaensis* Momiyama, 1927
orii	Miyanoura, Yakushima, Japan	*Garrulus glandarius orii* Kuroda, 1923
tokugawae	Sado, Japan	*Garrulus glandarius tokugawae* Takatsukasa, 1931

In areas were the ranges of such groups overlap, successful interbreeding between representatives of different groups is suspected due to the existence of birds with mixed characters (Keve 1939; Stresemann 1940; Vaurie 1959; Goodwin 1976; McCarthy 2006), which have often been described as new taxa. For instance, "*G. g. sewerzowii*" from eastern European Russia is now generally regarded to actually consist of variable intergrades between *G. g. glandarius* and *G. g. brandtii* (Stresemann 1919; Johansen 1944; Voous 1945; Keve 1966; Dementiev & Gladkov 1970; Shirihai & Svensson 2018), "*G. g. hansguentheri*" found in the Bosporus area has been suggested to comprise intergrades between *G. g. glandarius* and *G. g. anatoliae* (Roselaar 1995), "*G. g. caspius*" inhabiting the southwestern coast of the Caspian Sea exhibits mixed characters between *G. g. krynicki* and *G. g. hyrcanus* (Buturlin & Dementiew 1933; Voous 1945; Keve 1973), while *G. g. pekingensis* from northeastern China probably consists of intergrades between *G. g. brandtii* and *G. g. sinensis* (Keve 1939, 1969; Voous 1945), and lastly, *G. g. oatesi* as well as *G. g. haringtoni* from northern Myanmar have been suggested to actually comprise intergrades between *G. g. leucotis* and *G. g. interstinctus* or *G. g. persaturatus* of the *bispecularis* group (Baker 1922; Blacke & Vaurie 1962; Dickinson et al. 2004a; cf. Rasmussen & Anderton 2012). However, no studies investigating the extent of interbreeding and gene flow, or the fertility of such intergrades, in any of the contact zones have been published (c.f. Helbig 2005).

Since the general prevalence of trinomial nomenclature in ornithology at the beginning of the twentieth century (cf. Haffer 1992) only few authors opted to treat the subspecies groups of the Eurasian Jay each as species on their own (Reichenow 1905, 1914; Witherby et al. 1944; McCarthy 2006), while specific separation of the two Southeast Asian groups has had more advocates (e.g. Hartert 1918; Baker 1922, 1932; Jones 1947; Whistler & Kinnear 1949; Lavkumar 1956; Abdulali 1980) and several others stated the possibility that at least some groups might require species status (Keve 1939; Sibley & Monroe 1990; Helbig 2005; Shirihai & Svensson 2018; MacKinnon 2022). Quite recently, del Hoyo & Collar (2016), in a piloting list, split the Asian *bispecularis* and *leucotis* group each into distinct species, hence called Plain-crowned Jay *Garrulus bispecularis* and White-faced Jay *Garrulus leucotis* respectively. This decision was based on substantial differences in plumage colouration, biometric measurements and vocal discrepancies (del Hoyo & Collar 2016; Boesman 2016) quantitatively assessed following the "Tobias criteria" (cf. Tobias et al. 2010; del Hoyo & Collar 2014). These taxonomic changes, however, have not been adopted by subsequent versions of other major checklists of the birds of the world (Christidis et al. 2018; Gill et al. 2020; Madge et al. 2020).

Bearing in mind these systematic uncertainties, the numerous taxa defined to comprise the Eurasian Jay *Garrulus glandarius* by most authorities (e.g. Clements 2000; Madge 2009; Dickinson & Christidis 2014) could, for the time being, be referred to as an informal complex. This already has been put into practice by some authors (Dickinson et al. 2004a; Shirihai & Svensson 2018) in line with the recent treatment of several other Palearctic bird groups with controversial taxonomy (e.g. Olsson et al. 2010, 2013; Illera et al. 2011; Opaev et al. 2018; Raković et al. 2019). Throughout the present study, this aggregate of taxa, comprised of ten subspecies groups, is therefore referred to as the *Garrulus glandarius* complex.

Considering that the morphological diversity of the jays of the genus *Garrulus* has fascinated renowned ornithologists for centuries (e.g. Bonaparte 1851; Hume 1874; Wallace 1880; Seebohm 1883; Hartert 1918; Meinertzhagen 1920; Stresemann 1940; Voous 1953; Vaurie 1954), it comes somewhat as a surprise, that no comprehensive phylogenetic analysis has been undertaken so far.

Several genetic studies which investigated the phylogenetic relationships within the family Corvidae indicate that the *Garrulus* jays are closely allied with many other Old World members of the family Corvidae (Cibois & Pasquet 1999; Ericson et al. 2005; Kennedy et al. 2012; Fernando et al. 2017; Liu et al. 2018). Probably depending on the respective taxa covered, differing marker sequences and tree construction methods, the genera *Corvus* Linnaeus, 1758 (Ericson et al. 2005), *Pica* Brisson, 1760 (Kennedy et al. 2012) or *Ptilostomus* Swainson, 1837 (Fernando et al. 2017) have been proposed as sister taxon of the genus *Garrulus*.

Preliminary studies focusing on the phylogenetic relationships within the genus *Garrulus* have been based on partial DNA sequences of the mitochondrial (mt) *control region* (*CR*) and the mt *cytochrome b* gene (*cytb*) (Akimova et al. 2007; Aoki et al. 2018). These studies indicate the existence of several reasonably distinct mt lineages within the *Garrulus glandarius* complex, in so far as individuals of the eastern Palearctic subspecies *G. g. brandtii* and *G. g. japonicus* seem to be clearly differentiated from European jays (Akimova et al. 2007; Aoki et al. 2018). Taking into account the low number of analysed taxa and the incomplete geographical coverage, according to the authors, sampling artefacts could have had influenced the outcome and in consequence, no taxonomic recommendations have been made (Akimova et al. 2007; Aoki et al. 2018). It was nonetheless suggested that these results do corroborate the hypothesis of a Southeast Asian origin of the genus *Garrulus* (Akimova et al. 2007), as had been proposed for the entire family Corvidae (cf. Amadon 1944; Sibley & Ahlquist 1985; Ericson et al. 2005).

The aim of the present study was the construction of a phylogeny of the genus *Garrulus*, with special focus on the *Garrulus glandarius* complex, drawing upon mt DNA sequences of the *cytb* gene and the complete *CR*. This should provide the foundation for a better understanding of the evident diversity within this fascinating group of birds. With the inclusion of museum specimens, a more complete coverage of the described taxa within the *Garrulus* jays has been endeavoured. Besides solving the issue whether the astonishing degree of morphological geographic variation within these birds is reflected also by a corresponding amount of genetic divergence, this study could also provide new insights into the evolutionary history of the entire genus *Garrulus*.

Material and Methods

To uncover the phylogenetic structure within the genus *Garrulus* on the various taxonomic levels, two different mt marker regions were chosen for analysis. The protein-coding *cytb* gene had been proved to provide the basis for molecular phylogenetic reconstructions in an ever-growing number of studies and is considered to provide its best resolution when applied for comparisons on the taxonomic levels of species to genera (Moore & deFilippis 1997). Bearing in mind that *cytb* sequences of many taxa of the family Corvidae are available on GenBank, this marker was deemed suitable for the construction of a phylogeny of the genus *Garrulus*. With sequences of the more variable mt *CR* it was aimed to detect genetic differences on the subspecies and population level within the *Garrulus glandarius* complex. Two of the three domains of the *CR* had been described as hypervariable (Vigilant et al. 1989; Wenink et al. 1993), and should be well suited for this task, as they are considered to be the "fastest" changing regions of the avian mt genome (Baker & Marshall 1997).

As intergradation or hybridisation between taxa has for long been regarded as a common phenomenon within the *G. glandarius* complex, the inclusion of nuclear sequence data could be suggested to detect possible intergrades or even mt introgression following secondary contact (cf. Irwin et al. 2009; Rheindt & Edwards 2011). Unfortunately, numerous nuclear marker sequences have failed to resolve differences between closely related bird taxa in a number of recent studies (e.g. Bonaccorso et al. 2009; Förschler et al. 2009; Olsson et al. 2010, 2013; Song et al. 2018; Raković et al. 2019; Albrecht et al. 2020) and their amplification from old museum skins had been shown to be problematic (e.g. Ericson et al. 2005; Olsson et al. 2010; but cf. Irested et al. 2006). Therefore, nuclear markers were not employed during the present study.

Instead, the plumage features of the sampled museum specimens have been thoroughly assessed and photographically documented (Appendix II) to detect possible mismatches between some morphological characters and genetic results, which could indicate intergradation.

Sampling

Throughout this study the taxonomy and nomenclature of subspecies follows Dickinson & Christidis (2014), while delimitation of the subspecies groups of the *Garrulus glandarius* complex is slightly modified from Madge (2009), Roselaar in Cramp & Perrins (1994) and Shirihai & Svensson (2018). Individuals which exhibit mixed plumage characters between different groups of the *Garrulus glandarius* complex are referred to as intergrades, as the term "hybrid" is generally used to describe birds resulting from interbreeding between undisputed species (e.g. Dickinson et al. 2004a; McCarthy 2006).

The sampling encompasses 87 different individuals of the *G. glandarius* complex, covering most of its distribution range and nine subspecies groups (all but the *minor* group). Additionally, samples from three individuals of *G. lanceolatus* and of two *G. lidthi* could be obtained. Thus, the total number of sampled individuals is 92 (Table 2). From twelve of these samples DNA already extracted during earlier studies (Akimova et al. 2007; Töpfer et. al 2011) was available in the DNA collection of the Natural History Museum Vienna (NMW). The sources of DNA were muscle and liver tissues from 38 individuals stored in 96 % ethanol in the NMW as well as foot pad samples from 54 museum specimens in the NMW, up to 180 years of age, sampled by employees of the Ornithological Collection on three occasions by cutting out small pieces, 2 to 3 mm in diameter, of foot tissue, following the procedure in greater detail described in Töpfer et al. (2011).

Museum specimens have been selected to cover as many described subspecies as possible. Especially in taxa with wide distribution areas it was attempted to include specimens from various locations within their respective ranges. Whenever available, individuals collected in the months June and July were preferred. Most likely due to a combination of breeding activity (Holyoak 1967; Sackl & Samwald 1997) and moulting of flight feathers (Haffer 1993), within this period usually no migration movements of jays can be recorded in central Europe (Gatter 2000) and most individuals are expected to be in the vicinity of to their respective breeding grounds (cf. Grahn 1990; Patterson et al. 1991;Rolando et al. 1995), which might be applicable to other parts of the distribution range as well (Dementiev & Gladkov 1970; Webster 1975; Wassink 2015).

Table 2. List of samples including tissue type (li=liver, mu=muscle, fp=foot pad), collection number (AK=Tissue collection of the Laboratory of evolutionary zoology and genetics, Federal Scientific Center of the East Asia Terrestrial Biodiversity (FSCEATB), Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia, listed samples also stored in the NMW; NMW=Natural History Museum Vienna; G=NMW DNA-tissue collection), the sequenced genetic markers (+=sequenced, -=not sequenced) with GenBank accession numbers, the geographic origin and the date of collection.

Code	Tissue	Collection-Nr.	*cytb*	*CR*	Geographic origin	Collection date
Garrulus glandarius glandarius						
Gglagla-1	li	AK 0128	+	+	Russia, Tula oblast	18.06.1998
Gglagla-2	li	AK 0175	+	+	Russia, Moskau oblast, Zvenigorod	30.06.2001
Gglagla-3	mu	AK 0226	+	+	Russia, Kirov oblast, Zuyevsky district	01.2002
Gglagla-4	li	AK 0381	+	+	France	
Gglagla-5	li	AK 0382	+	+	France, Île-de-France, 77 Fontenaills	
Gglagla-6	mu	G543	-	+	Austria, Upper Austria, Wolfsbach	21.11.2000
Gglagla-7	mu	G544	-	+	Austria, Upper Austria, Wolfsbach	10.12.2000
Gglagla-8	mu	AK 0239	+	+	Russia, Kirov oblast, Zuyevsky district	01.2002
Gglagla-80	mu	AK 0515	-	+	Russia, Kaliningrad oblast	25.10.2003
Gglagla-81	mu	AK 1208	-	+	Russia, Kaliningrad oblast	01.05.2006
Gglagla-82	mu	AK 2165	-	+	Russia, Kaliningrad oblast	18.04.2005
Gglagla-83	mu	AK 2182	-	+	Russia, Kaliningrad oblast	25.10.2003
Gglagla-86	fp	NMW22956	+	+	Poland, Warmia-Masuria	04.06.1898
"Garrulus glandarius sewerzowii"						
Gglasew-1	li	AK 0229	+	+	Russia, Kirov oblast	01.2002
Gglasew-2	mu	AK 1209	-	+	Russia, Kirov oblast	17.12.2004
Gglasew-3	mu	AK 1210	+	+	Russia, Kirov oblast	16.01.2005
Garrulus glandarius fasciatus						
Gglafas-1	fp	NMW45417	+	+	Spain, Castile and León, Salamanca	12.05.1941
Gglafas-2	fp	NMW45413	-	+	Spain, Castile and León, Salamanca	20.04.1941
Gglafas-4	fp	NMW22970	+	+	Spain, Andalusia, Sevilla	15.10.1904
Garrulus glandarius ichnusae						
Gglaich-1	fp	NMW22967	+	+	Sardinia, Province of Nuoro, Belvi	02.1903
Garrulus glandarius rufitergum						
Gglaruf-1	fp	NMW93013	+	+	United Kingdom, Kent, Sevenoaks	24.03.1958
Gglaruf-2	fp	NMW93015	-	+	United Kingdom, Kent, Sevenoaks	20.01.1960
Gglaruf-3	fp	NMW93016	+	+	United Kingdom, Kent, Sevenoaks	13.12.1962
Gglaruf-4	fp	NMW93014	-	+	United Kingdom, Kent, Sevenoaks	25.04.1958
Garrulus glandarius hibernicus						
Gglahib-1	fp	NMW52447	+	+	Ireland, Offaly, Birr	30.11.1910
Garrulus glandarius corsicanus						
Gglacor-1	fp	NMW5710	+	+	France, Corsica, Vico	02.12.1912
Gglacor-2	fp	NMW75744	+	+	France, Corsica, Evisa, Aitone Forest	22.05.1910
Garrulus glandarius albipectus						
Gglaalb-1	fp	NMW22952	+	+	Montenegro, Herceg Novi	01.12.1903
Gglaalb-2	fp	NMW22953	-	+	Montenegro, Herceg Novi	20.09.1903
Garrulus glandarius cretorum						
Gglacre-1	fp	NMW45408	+	+	Greece, Crete, Samaria	17.04.1942
Gglacre-2	fp	NMW45407	+	+	Greece, Crete, Samaria	17.06.1942

Garrulus glandarius graecus						
Gglagrc-2	fp	NMW45409	+	+	Greece, Peloponnes, Vytina	28.06.1942
Gglagrc-3	fp	NMW45411	+	+	Greece, Peloponnes, Vytina	31.05.1942
Garrulus glandarius ferdinandi						
Gglafer-1	fp	NMW72179	+	+	Turkey, Kirklareli Province, Dereköy	07.05.1967
Garrulus glandarius glaszneri						
Gglaglsz-1	fp	NMW22969	+	+	Cyprus, Troodos Mountains	14.06.1903
Garrulus glandarius cervicalis						
Gglacer-1	fp	NMW22972	+	+	Tunisia, Jendouba, Ain Draham	04.1903
Gglacer-2	fp	NMW22976	+	+	Tunisia, Jendouba, Ain Draham	26.02.1912
Gglacer-3	fp	NMW22975	+	+	Algeria, Batna Province	01.05.1892
Garrulus glandarius atricapillus						
Gglaatr-1	fp	NMW76678	+	+	Israel	27.04.1970
Gglaatr-2	fp	NMW76679	+	+	Israel, Haifa district	26.03.1979
Gglaatr-3	fp	NMW89121	+	+	Israel, Northern district, Nir David	15.01.1988
Garrulus glandarius krynicki						
Gglakry-1	li	AK 0111	+	+	Russia, Stavropol Krai, Kislowodsk	27.01.2000
Gglakry-2	li	AK 0125	-	+	Russia, Stavropol Krai, Kislowodsk	02.02.1999
Gglakry-5	mu	AK 2167	-	+	Russia, Krasnodar Krai	01.02.2008
Gglakry-6	mu	AK 2180	-	+	Russia, Krasnodar Krai	02.02.2009
Gglakry-9	fp	NMW73747	-	+	Abkhazia, Sukhumi	04.07.1953
Gglakry-10	fp	NMW43259	-	+	Russia, Stavropol Krai, Pyatigorsk	<1839
Gggk-1		AK 0375	+	+	Russia, Rostov Oblast, Tarasovsky District	23.05.2002
Garrulus glandarius anatoliae						
Gglaana-3	fp	NMW72418	-	+	Turkey, Bolu Province, Abant Gölü	06.07.1968
Gglaana-4	fp	NMW3302	-	+	Turkey, Izmir Province	12.12.1871
Gglaana-7	fp	NMW72419	+	+	Turkey, Ankara Province, Beydili	08.07.1968
Gglaana-8	fp	NMW72420	+	+	Turkey, Antalya Province, Kasaba	17.07.1968
"Garrulus glandarius rhodius"						
Gglarho-1	fp	NMW83689	+	+	Greece, Rhodes, Salakos	03.06.1935
Gglarho-2	fp	NMW83688	+	+	Greece, Rhodes, Salakos	03.06.1935
Garrulus glandarius Iphigenia						
Gglaiph-1		AK 0472	+	+	Crimea, Bakhchysarai Raion, Aromat	19.10.2004
Gglaiph-2		AK 0500	+	+	Crimea, Bakhchysarai Raion, Aromat	19.10.2004
Gglaiph-3	mu	AK 0745	-	+	Crimea	26.10.2004
Gglaiph-4	mu	AK 0746	-	+	Crimea	26.10.2004
Gglaiph-5	mu	AK 1195	+	+	Crimea	14.10.2005
Garrulus glandarius hyrcanus						
Gglahyr-3	fp	NMW22985	+	+	Azerbaijan, Lankaran area	26.02.1880
Gglahyr-4	fp	NMW22986	+	+	Azerbaijan, Lankaran area	01.01.1880
"Garrulus glandarius caspius"						
Gglacas-1	fp	NMW22982	+	+	Azerbaijan, Lankaran area	1887
Gglacas-2	fp	NMW22981	+	+	Azerbaijan, Lankaran area	07.1887
Garrulus glandarius brandtii						
Gglabra-1		AK 0354	+	+	Russia, Primorsky Krai	
Gglabra-3		AK 0346	+	+	Russia, Primorsky Krai, Arsenyev	16.05.2002
Gglabra-4		AK 0386	+	+	Russia, Amur Oblast, Norsk	16.01.2003
Gglabra-5	mu	AK 2169	-	+	Russia, Sakhalin	30.05.2009
Gglabra-6	mu	AK 2172	-	+	Russia, Sakhalin	02.06.2010
Gglabra-7	mu	AK 2178	+	+	Russia, Sverdlovsk Oblast	01.2004
Gglabra-8	mu	AK 2251	+	+	Japan, Hokkaido	01.2014

Gglabra-9	mu	AK 2252	+	+	Japan, Hokkaido	01.2014
Gglabra-10	mu	AK 2253	+	+	Japan, Hokkaido	01.2014
Gglabra-11	mu	AK 2254	-	+	Japan, Hokkaido	01.2014
Gglabra-12	fp	NMW23017	-	+	Russia, Buryatia, Tunkinsky District	18.12.1912
Gglabra-13	fp	NMW96332	+	+	Russia, Zabaykalsky Krai, Bukukun	02.09.2004
Gglabra-14	fp	NMW23003	-	+	Russia, Tomsk Oblast, Kislovka	1898
Gglabra-15	fp	NMW83304	-	+	Japan, Hokkaido	28.09.1908
Garrulus glandarius bispecularis						
Gglabis-1	fp	NMW43258	+	+	India, Himalaya	1831-1836
Gglabis-2	fp	NMW22965	+	+	India, Himalaya	1831-1836
Garrulus glandarius taivanus						
Gglatai-1	mu	AK 1165	+	+	Taiwan	
Gglatai-0		GenBank	AB239527	-	Taiwan	
Garrulus glandarius sinensis						
Gglasin-1	fp	NMW22978	+	+	China, Hubei Province, Wuhan (=Hankou)	19.01.1912
Gglasin-0		GenBank	JN018413	JN018413	China	
Garrulus glandarius leucotis						
Gglaleu-1	fp	NMW45462	+	+	Myanmar, Mandalay Division, Pyin U Lwin	06.12.1937
Gglaleu-2	fp	NMW45463	+	+	Myanmar, Mandalay Division, Pyin U Lwin	07.12.1937
Garrulus glandarius japonicus						
Gglajap-1	mu		+	+	Japan, Honshu	07.03.2003
Gglajap-2	fp	NMW83271	-	+	Japan, Honshu, Chubu Region, Mt Fuji	15.11.1908
Ggaljap-3	fp	NMW94467	+	+	Japan, Honshu, Hyogo Prefecture, Tanba	03.11.1957
"Garrulus glandarius hiugaensis"						
Gglahiug-1	fp	NMW22992	+	+	Japan, Kyushu, Nagasaki Prefecture	10.1887
Garrulus lanceolatus						
Glan-1	fp	NMW46624	-	+	India, Himalaya	12.12.1941
Glan-2	fp	NMW98267	+	+	Afghanistan, Nuristan Province	1969
Glan-3	fp	NMW98268	+	+	Afghanistan, Nuristan Province	1969
Glan-0		GenBank	JQ864504	-	Himalaya	
Garrulus lidthi						
Glid-1		AK 0383	+	+	Japan, Ryukyo Islands	
Glid-2	fp	NMW83348	+	+	Japan, Ryukyo Islands, Amami Oshima	1900-1910
Zavattariornis stresemanni						
Zstr		GenBank	AY395627	-		
Ptilostomus afer						
Pafe		GenBank	U86040	-		
Pica pica pica						
Ppic		GenBank	AY701185	-	Russia, Smolensk oblast	
Pica pica mauritanica						
Pmau		GenBank	MG640744	-	Algeria, Lambese	
Pica hudsonia						
Phud		GenBank	MG640818	-	USA, North Dakota	
Pica nutalli						
Pnut		GenBank	MG640808	-	USA, California	
Podoces biddulphi						
Pbid		GenBank	AY395623	-		
Podoces hendersoni						
Phen-1		GenBank	GU592504	-		
Phen-2		GenBank	AY395624	-		

Laboratory procedures

Extraction

To minimise risk of contamination, DNA extractions were conducted in the cleanroom of the NMW DNA laboratory and standard routines against contamination were obeyed, e.g., regular overnight UV irradiation of the room. Tissue from muscle or liver (hereafter just referred to as "muscle samples") and foot pad samples were never extracted at the same time, and only a maximum of ten samples were extracted simultaneously. For all the extractions, the QIAGEN DNeasy Blood & Tissue Kit (QIAGEN, Venlo, Netherlands) was used according to the manufacturer's instructions. The time until complete digestion for muscle samples varied between one and three hours, while foot pad samples were digested for 46 to 71 hours. Finally, the DNA was eluted in 50 µl PCR grade water in muscle samples and 30 µl in foot pads. Blank extractions, without the addition of tissue, were performed at a ratio of at least 1:10 as well.

PCR amplification

Cytochrome b (*Cytb*)

Muscle samples: From DNA extracted from muscle samples, generally, the amplification of 1 254 base pair (bp)-fragments, comprising the entire *cytb* gene (1143 bp) plus partial sequences of the flanking genes, was conducted. For the amplification of this fragment primers binding in the adjacent genes (*ND5* gene: primer ND5-Gar1+; *tRNA-Thr* gene: primer Thr-Gar2-) were used (Table 3). Polymerase chain reactions (PCRs) were performed in thermocyclers from Eppendorf AG (Hamburg, Germany) in 25 µl reaction volume using the TopTaq Master Mix Kit (QIAGEN) according to the manufacturer's protocol, containing 2.5 µl of 10x TopTaq Buffer, 5 µl of 5x Q-Solution, 0.5 µM of each primer, 0.2 mM of each dNTP, 1 unit TopTaq DNA Polymerase and 1 µl of template DNA. Each set additionally consisted of a negative control without template DNA. PCRs were composed of initial denaturation at 94 °C for 3 min, followed by 40 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s and elongation at 72 °C for 90 s, completed by 7 min of final extension at 72 °C. To check for amplification success, PCR products were analysed by electrophoresis in 1 % agarose gel.

Table 3. Primers used for PCR amplification and for sequencing of the *cytb* gene. The orientation of each primer is indicated by a "+" (forward) or a "-" (reverse) at the end of its name. For specific primers, targeted taxa are indicated, general = used for all taxa.

Primer	Primer sequence (5'-3')	Taxon	Source
ND5-Gar1+	GGATCATTTGCCCTATCAATC	general	Aoki et al. 2018
Thr-Gar2-	GCCTTCAATCTTTGGTTTACAA	general	Aoki et al. 2018
Cytb-Gar3-	CGAATTAGTCATCCGAATTGTAC	general	This study
Cytb-Gar4+	CTAGCCATACACTACACAGCAGA	general	This study
Cytb-Gar40+	CTAGCTATACACTATACAGCAGA	*G. g. bispecularis*	This study
Cytb-Gar5-	TTAGTGATAACTGTAGCCCCTC	general	This study
Cytb-Gar50-	GTCATTCTACTAGTGTTTGTCC	general	This study
Cytb-Gar6+	CCCTGATAGCAACCGCCTTCGTAGG	general	This study
Cytb-Gar60+	CTAATAGCAACTGCTTTCGTAGG	*G. lidthi*, *G. lanceolatus*	This study
Cytb-Gar7-	TAAGGGTGGAATGGGATTTT	general	This study
Cytb-Gar70-	GTAGGGGTGGAATGGAATTTT	*G. lidthi*, *G. lanceolatus*	This study
Cytb-Gar8+	CGAGACAGGATCAAACAACCCA	general	This study
Cytb-Gar80+	GAAACAGGGTCGAACAACCCA	*G. lanceolatus*	This study
Cytb-Gar9-	TAGAAATAGGACTAGGACTGAAGC	general	This study
Cytb-Gar90-	AGAAATAGGATTAGGACTGAAGC	*G. lanceolatus*	This study
Cytb-Gar10+	CCTAACAAACTAGGAGGAGT	general	This study

Foot pads: For amplification of DNA from foot pad samples a variety of internal primers was designed (Table 3), with the aim to obtain the same total sequence length (1254 bp) as with the external primer pair used for amplification in muscle samples, but in this case with the combination of five overlapping fragments, each with a length of about 300 bp (Figure 2a). With most samples the following primer combinations were used: ND5-Gar1+/Cytb-Gar3-, Cytb-Gar4+/Cytb-Gar5-, Cytb-Gar6+/Cytb-Gar7-, Cytb-Gar8+/Cytb-Gar9- and Cytb-Gar10+/ Thr-Gar2-. For some taxa it was necessary to create additional specific primers. PCR conditions were the same as those used for the amplification of the long fragment, but annealing temperatures varied depending on the primer combination and elongation time was reduced to 30 s. PCR products of these shorter fragments were analysed on 2 % agarose gels. When no bands were detectable, PCR was repeated with 2 or 3 µl of template DNA of the respective sample. Amplification of DNA originating from foot pads was generally not conducted together with that from muscle samples, but in some cases a single positive control was added.

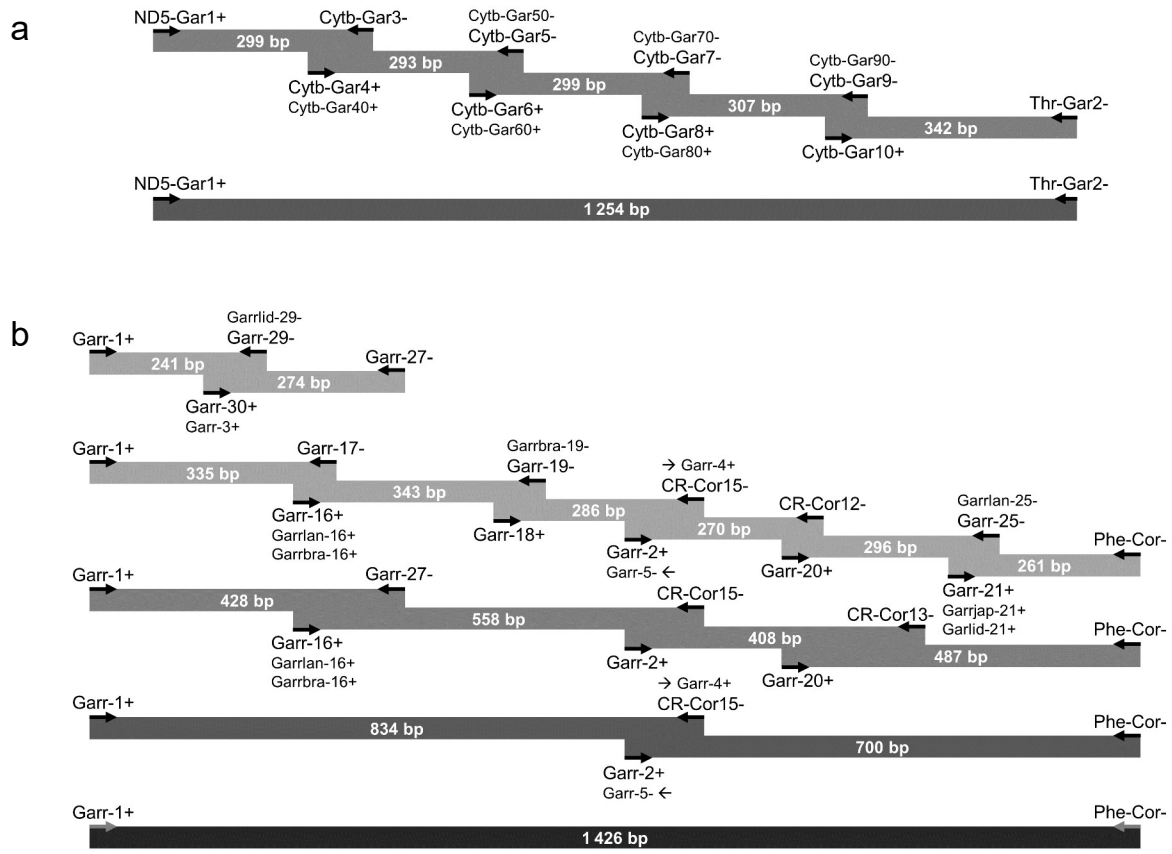

Figure 2. Binding sites of **(a)** *cytb* and **(b)** *CR* primers and resulting PCR fragments with lengths in base pairs (bp) referring to the individual Gglacor-2.

Control region (CR)

Muscle samples: From DNA of muscle samples the complete *CR* was amplified as one fragment employing primers (Table 4, Figure 2b) that bind in the adjacent genes *tRNA-Glu* (Garr-1+) and *tRNA-Phe* (Phe-Cor-). The amplified fragments (1426 bp, referring to the individual Gglacor-2) therefore contained 71 bp of 5'-flanking sequence (*tRNA-Glu* gene plus spacer between tRNA gene and the *CR*), the 1313 bp long *CR* as well as 42 bp 3'-flanking sequence (spacer plus *tRNA-Phe* gene). PCRs were performed as described for *cytb*, but instead the programme consisted of two steps. The first comprised 3 min of initial denaturation at 94 °C followed by five cycles of denaturation at 94 °C for 30 s, annealing at 63 °C for 30 s and elongation at 72 °C for 90 s. The second step contained 35 cycles of denaturation at 94 °C for 30 s, annealing at 56 °C for 30 s and elongation at 72 °C for 90 s, completed by 7 min of final extension at 72 °C. PCR products were analysed by electrophoresis in 1 % agarose gel. When no or only very weak bands were visible PCR was repeated with 2 to 5 µl of template DNA.

Table 4. Primers used for PCR amplification and for sequencing of the *CR*. The orientation of each primer is indicated by a "+" (forward) or a "-" (reverse) at the end of its name, (s) = used for sequencing only. For specific primers taxa are indicated, general = used in all taxa.

Primer	Primer sequence (5'-3')	Taxon	Source
Garr-1+	GTTCCTACCTGGACCCTCCCCAA	general	modified from CR-Cor16+ (Kryukov et al. 2017)
Phe-Cor-	TTGACATCTTCAGTGTCATGC	general	Kryukov et al. (2004)
Garr-2+	GATCGCGGCATCCGACCGCC	general	This study
CR-Cor15-	GATGTACACGTCAAGAGGAAG	general	Kryukov et al. (2017)
Garr-3+ (s)	GCATACAATTCTTGTCCAC	general	This study
Garr-4+ (s)	CTTCCTCTTGACGTGTACATC	general	This study
Garr-5- (s)	GGCGGTCGGATGCCGCGATC	general	This study
Garr-30+	TCTTTGCATACAATTCTTGTCCAC	general	This study
Garr-29-	GAGTTTGGTTAGGTCTTGCATTAC	general	This study
Garrlid-29-	GATTTTGGTTAGGTATCACATTAC	*G. lidthi*	This study
Garr-17-	GTTAGGTAGGATTATTTGGGTTT	general	This study
Garr-16+	GGAAACCTCTAGGCACATCCCCA	general	This study
Garrbra-16+	GAAACTTCCAGGCACATTCCCA	*G. g. brandtii*, *G. g. bispecularis*	This study
Garrlan-16+	AACAACTTCCAGGCACATTCCCA	*G. lanceolatus*, *G. lidthi*, *G. g. japonicus*	This study
Garr-27-	GAGAATTCATTGGGGTACTAGGA	general	This study
Garr-18+	CGACGTAGATGCTACCCACGG	general	This study
Garr-19-	TGCAAGTTGTGCGAGGGTGTA	general	This study
Garrbra-19-	GCAAGTTGTGCGAGGGTGTA	general	This study
CR-Cor14+	GGAGTTATCTTCCTCTTGAC	general	Töpfer et al. 2011
Garr-20+	TGGGTCCCCCAGCTACCTAT	general	This study
CR-Cor12-	GAAACATGTCCGGCAACCAT	general	Töpfer et al. 2011
Garrjap-22+	ATCGTTTCATTTTTATCTTGTCA	*G. g. japonicus*	This study
CR-Cor13-	GGTGGTTTGGATAATGTAGGT	general	Töpfer et al. 2011
Garr-21+	CTACTTTCCCCCTATTCCA	general	This study
Garrlid-21+	CCTCTATCTTCCTCCTATTCCAT	*G. lidthi*	This study
Garrjap-21+	CTCTACATTCCCCCCATTCCA	*G. g. japonicus*	This study
Garr-25-	TTTGTTAAATGGGGTGTTAAAAC	general	This study
Garrlan-25-	AAATGGGGTGTTAAAGTGACG	*G. lanceolatus, G. lidthi*	This study

Foot pads: For foot pad samples several internal primers were designed (Table 4). The most frequently used primer combinations were Garr-1+/Garr-17-, Garr-16+/Garr-19-, Garr-18+/CR-Cor15-, Garr-2+/CR-Cor-12-, Garr-20+/Garr-25- and Garr-21+/Phe-Cor-. Thus, the complete *CR* was amplified with up to seven overlapping fragments with a length of about 300 bp (Figure 2b). With samples from more recent specimens, various primer combinations resulting in longer fragments between 400 and 700 bp were used. PCRs were performed in 50 µl reaction volume containing 5.0 µl AmpliTaq Gold 360 Buffer 10x, 2 µl 360 GC Enhancer, 25 mM magnesium chloride, 1.25 units AmpliTaq Gold 360 DNA Polymerase (all from Thermo Fisher Scientific, Waltham, Massachusetts, USA), 0.2 mM of each dNTP, 0.5 µM of each primer and between 1 and 3 µl of template DNA. Initial denaturation took place at 95 °C for 10 min and each of the following 40 cycles contained 30 s of denaturation at 95 °C, 30 s annealing and elongation at 72 °C for 30 s, followed by 7 min final extension at 72 °C.

The PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN) following the protocol and eluted in PCR grade water.

Sequencing

While the laboratory work described above was conducted by the author in the Central Research Laboratories of the NMW, Sanger sequencing was performed by Microsynth AG (Balgach, Switzerland). *Cytb* sequencing was done with the amplification primers. For sequencing of the *CR*, initially the primers Garr-1+ and Phe-Cor-, as well as the two primers binding in the middle of the *CR*, Garr-2+ and CR-Cor15-, were used. Due to a C-stretch close to the 5'-end of the *CR* the primer Garr-1+, although working fine for PCR, was not useful as a sequencing primer, as downstream of the C-stretch no reliable base calling has been achieved. In consequence, the new primer Garr-3+, which binds just downstream after the problematic C-stretch, was used for sequencing instead. Additionally, a T-stretch in the middle of the *CR*, between the binding sites of the primers Garr-2+ and CR-Cor15-, hampered the successful use of these internal primers for sequencing. Instead, the primers Garr-4+ (reverse sequence of CR-Cor15-) and Garr-5- (reverse sequence of Garr-2-) were used.

Data analysis

The obtained sequences were checked, edited, assembled and manually aligned using Bioedit 7.2.3 (Hall 1999). In addition to the *cytb* sequences obtained from the 64 different individuals (Table 2) in the course of this study, a sequence of *G. glandarius* originating from China, supposedly of the subspecies *G. g. sinensis* (accession number JN018413), and one of each *G. g. taivanus* (AB239527) as well as of *G. lanceolatus* (JQ864504) were included in the alignment from GenBank. Furthermore, following a phylogenetic analysis conducted with *cytb* sequences of all taxa of the family Corvidae available on GenBank (see Appendix I), nine cytb sequences of eight species were added to the alignment as an outgroup (Table 2). Since the sequenced parts of the adjacent genes were left out for the final *cytb* alignment, it had a length of 1143 positions and contained 76 sequences.

Concerning the *CR* alignment, one sequence supposedly of *G. g. sinensis* (JN018413) available from GenBank was added as well. To avoid alignment difficulties, owing to sequence length variations within the domain III of the *CR*, no taxa beyond the genus *Garrulus* were included into the *CR* alignment. As noted above, sequencing of a short fragment at the 5'-end of the *CR* proved to be problematic due to a C-stretch. In 71 individuals the short sequence upstream of this segment (48 bp *tRNA-Glu* gene, 33 bp *CR*) therefore could not be determined. Hence, the final alignment used for construction of the phylogenetic trees and networks was trimmed to start with the C-stretch and included about 1260 bp of the *CR* plus 21 bp of 3'-flanking sequence of the *tRNA-Phe* gene. This resulted in the final *CR* alignment with a length of 1340 positions, including alignment gaps, comprising 93 sequences.

Genetic distances were calculated with MEGA X (Kumar et al. 2018) using the pairwise deletion option for alignment gaps treatment. Prior to the construction of phylogenetic trees, the best-fitting models of nucleotide substitution were selected according to the Bayesian Information Criterion out of 24 substitution models with MEGA X (Kumar et al. 2018) and out of 88 different models using the programme jModelTest 2.1.7 (Darriba et al. 2012; Guindon & Gascuel 2003). For the *cytb* as well as the *CR* dataset HKY+Γ+I has been determined as the best-fitting substitution model by each of these programmes.

In addition, for the *cytb* data substitution models were determined separately for the three codon positions. Each of the programmes, jModelTest 2.1.7 and MEGA X, selected K2P+Γ as the best-fitting substitution model for the first, HKY+I for the second and HKY+ Γ for the third codon position.

Maximum likelihood (ML) analyses were conducted with RAxML v8.2.10 (Stamatakis 2014) using the graphical user interface raxmlGUI 2.0.0-beta.3 (Edler et al. 2020). GTR+Γ+I was selected for both marker genes, as the HKY substitution model could not be combined with the models +Γ+I in this programme. The robustness of the received topologies was assessed with 1 000 thorough bootstrap replications. Additional ML trees were constructed with MEGA X, as this programme allowed the selection of the preferred HKY+Γ+I model, with 1 000 bootstrap replications.

Bayesian inference (BI) analyses were undertaken with MrBayes 3.2.7 (Ronquist et al. 2012), employing the default priors. For the *CR* dataset HKY+Γ+I (nst=2, rates=invgamma) was used as substitution model, for *cytb* the settings nst=2 rates=gamma were used for the first and third, and nst=2 rates=propinv for the second codon position. Starting each analysis from random trees, two independent runs each consisting of 20×10^6 generations of four Markov chain Monte Carlo chains were performed and sampled every 100 generations. After checking of the output of the *CR* analysis, the first 100 000 generations were discarded as "burn-in", while for the *cytb* analysis the first 200 000 generations were left out. Based on the remaining iterations posterior probability values and consensus trees were generated. A BI tree was also constructed from a concatenated *cytb* and *CR* dataset amounting to a total of 2 483 positions (2 423 bp in Gglacor-2), with the same settings as above, but with 25×10^6 generations instead, of which the first 250 000 were discarded.

The resulting phylogenetic trees were visualised with FigTree v1.4.4 (Rambaut 2018). Additionally, haplotype networks were constructed using the median-joining inference method (Bandelt et al. 1999) implemented in the programme Popart 1.7 (Leigh & Bryant 2015).

Results

Amplification and sequencing success

Sequences with an unambiguous base calling could be obtained from all the 92 sampled individuals. Moreover, amplification and sequencing of the complete marker sequences in one fragment was successful for all the muscle samples (*cytb*: 23 individuals, *CR*: 38 individuals). With DNA extracted from many foot pad samples various primer combinations, resulting in different fragment lengths, have been tested for amplification of the *CR* (cf. Figure 2b.). Whereas in many samples from individuals collected in the twentieth century fragments with a length of more than 500 bp were amplified and sequenced successfully, only fragments of about 300 bp of length worked in most of the ninetieth century samples (Figure 3). From the oldest specimens (Gglabis-1, -2), collected between 1831 and 1836, nonetheless 343 bp fragments were amplified and sequenced successfully. Such with a length of 428 bp were obtained from specimens collected as far back as in the year 1892 (Gglacer-3), while 558 bp and 619 bp fragments were successfully sequenced from samples of specimens from 1935 (Gglarho-1, -2) and 1967 (Gglafer-1), respectively.

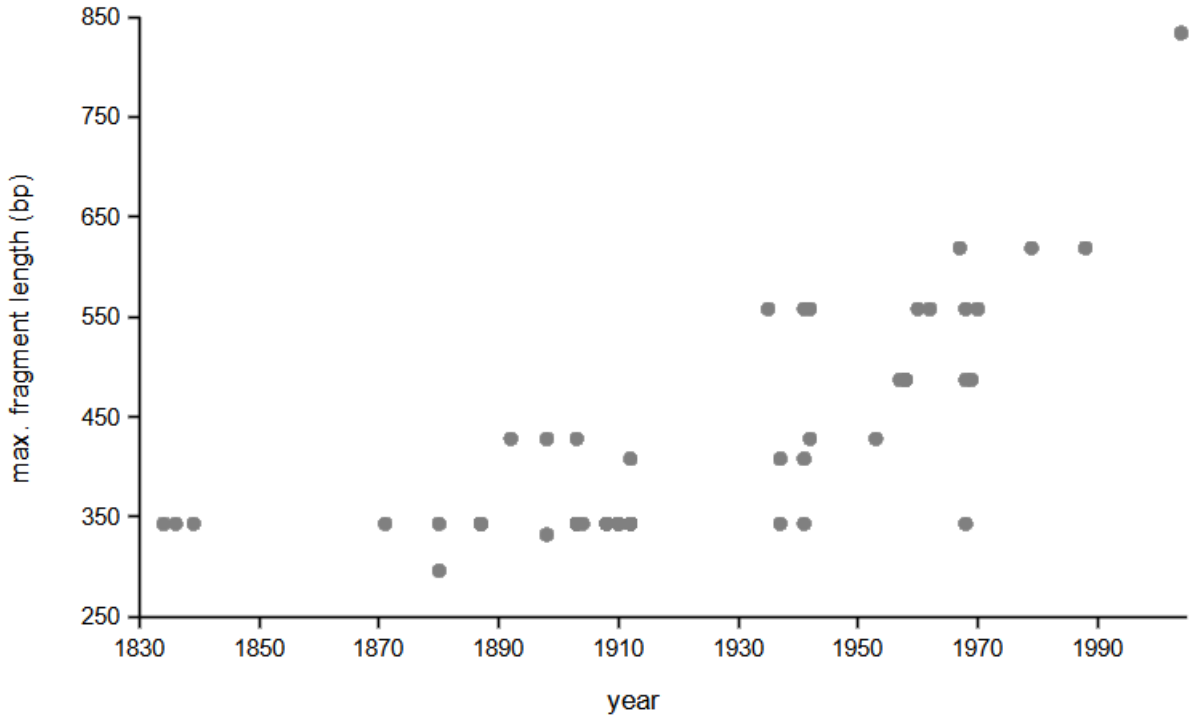

Figure 3. Maximum length, in base pairs (bp), of successfully sequenced *CR* fragments from DNA extracted from foot pad samples of 49 specimens with year of collection.

The *cytb* marker region was sequenced from 64 individuals (Table 2). From 63 of those, sequences of the complete *cytb* gene were obtained, which has been achieved by combining several 300 bp long fragments in museum specimens. Only from one individual (Gglahyr-3, collected in 1880) just a single fragment (307 bp of length, including the primers Cytb-Gar8+ and Cytb-Gar9-) was successfully amplified and sequenced. No non-coding segments or misplaced stop codons can be detected in these sequences. The final *cytb* alignment used for further analysis, hence, contains 76 sequences, comprising 63 1143 bp sequences and one 261 bp sequence obtained during this study, as well as 12 sequences from Genbank.

The complete *CR* marker sequence with a length of 1382 bp, after removing the external primers Garr-1+ and Phe-Cor-, was successfully sequenced from only one individual (Gglacor-2, collected in 1910), which is therefore used as the reference sequence. In the remaining samples, as explained above, a continuous C-stretch close to the 5'-end of the *CR* hampered successful sequencing of the full marker sequence. Yet, the sequencing reaction with the primer Garr-1+ was tried in 21 individuals, although, except for Gglacor-2, producing reliable sequences of only about 100 bp of length, which at least made the complete *CR* available for these individuals. Its length varies between 1 309 bp (*G. g. brandtii*) and 1 318 bp (*G. g. taivanus*) within the *Garrulus glandarius* complex and amounts to 1 315 bp in *G. lidhti*. For the remaining 71 individuals about 1 260 bp of the *CR* and 21 bp of 3'-flanking sequence were sequenced successfully using the primer Garr-3+ instead. The final *CR* alignment has a length of 1 340 bp, including alignment gaps, and contains 93 sequences of various taxa of the genus *Garrulus*, 92 obtained in the present study and one added from GenBank.

Sequence variability

Without the nine outgroup sequences the 1143 bp *cytb* alignment with 67 sequences yields 48 different haplotypes (71.6 % of all sequences). It contains 237 variable sites (20.7 % of all positions) of which 212 are parsimony informative and 25 are singletons. About 81 % of the variable sites are located at the third codon positions (cf. Figure 4), where 193 (50.7 %) of the 381 positions are variable, compared to 37 (9.7 %) at the first and 7 (1.8 %) at the second positions.

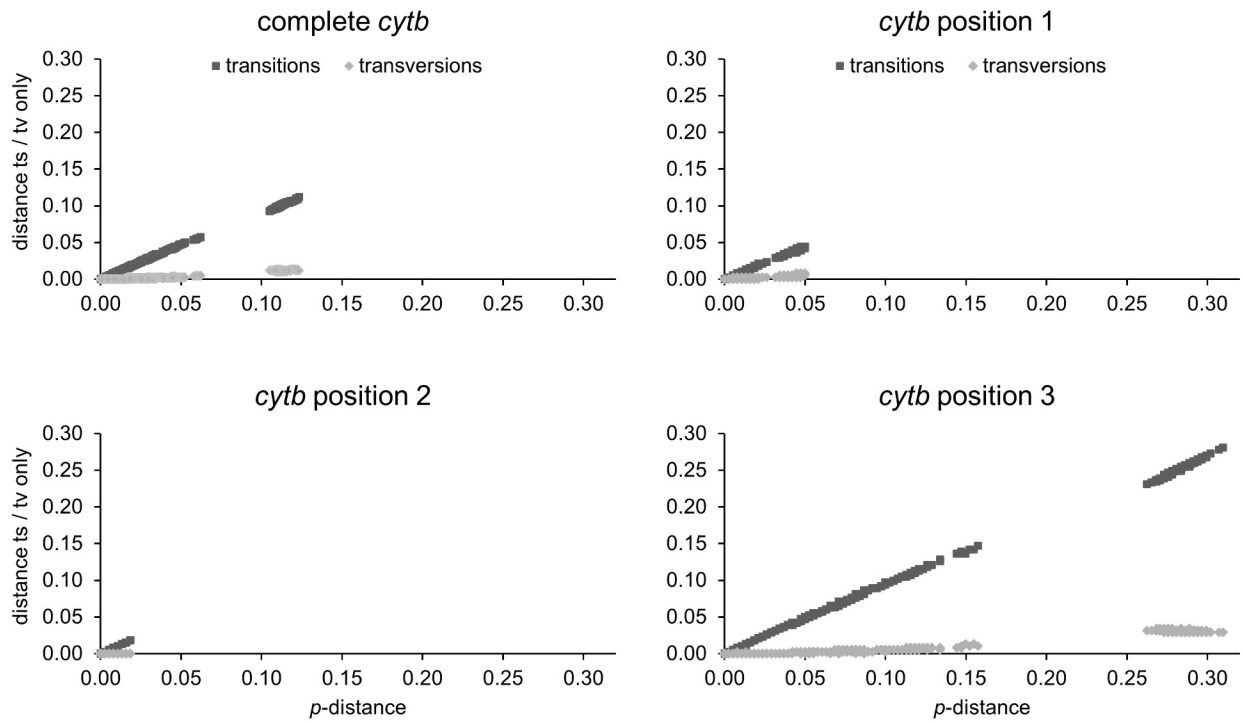

Figure 4. Sequence variability within the *cytb* dataset of the genus *Garrulus* comprising sequences of 66 individuals (Gglahyr-3 excluded), illustrated as pairwise comparisons of transitions (ts) and transversions (tv) with *p*-distances for the entire 1143 bp *cytb* gene and its three codon positions. The separated points at the upper right end of the graph, especially pronounced at the third codon position, depict the genetic distances between the *Garrulus glandarius* complex and the species *G. lanceolatus* and *G. lidthi*.

The 93 *CR* sequences of the genus *Garrulus* yield 82 (88.2 %) different haplotypes. Of the 1340 total positions of the *CR* alignment 288 (21.5 %) are variable, of which 253 are parsimony informative and 35 constitute singletons. The variable sites are not evenly distributed across this genetic marker region (Figure 5), based on their frequency, the *CR* can be roughly divided into three parts. Of the 404 bp of the first third of the *CR* alignment (mainly corresponding to domain I) 31.2 % (126) are variable sites, in the central second part (alignment positions 405-887) (domain II) only 7.5 % (36) of 483 sites are variable and the 432 positions of the 3'-third of the *CR* (positions 888-1315) (domain III) contain 28.7 % (124) variable sites. Two more variable sites can be found in the sequenced part of the flanking *tRNA-Phe* gene but are not included in this analysis.

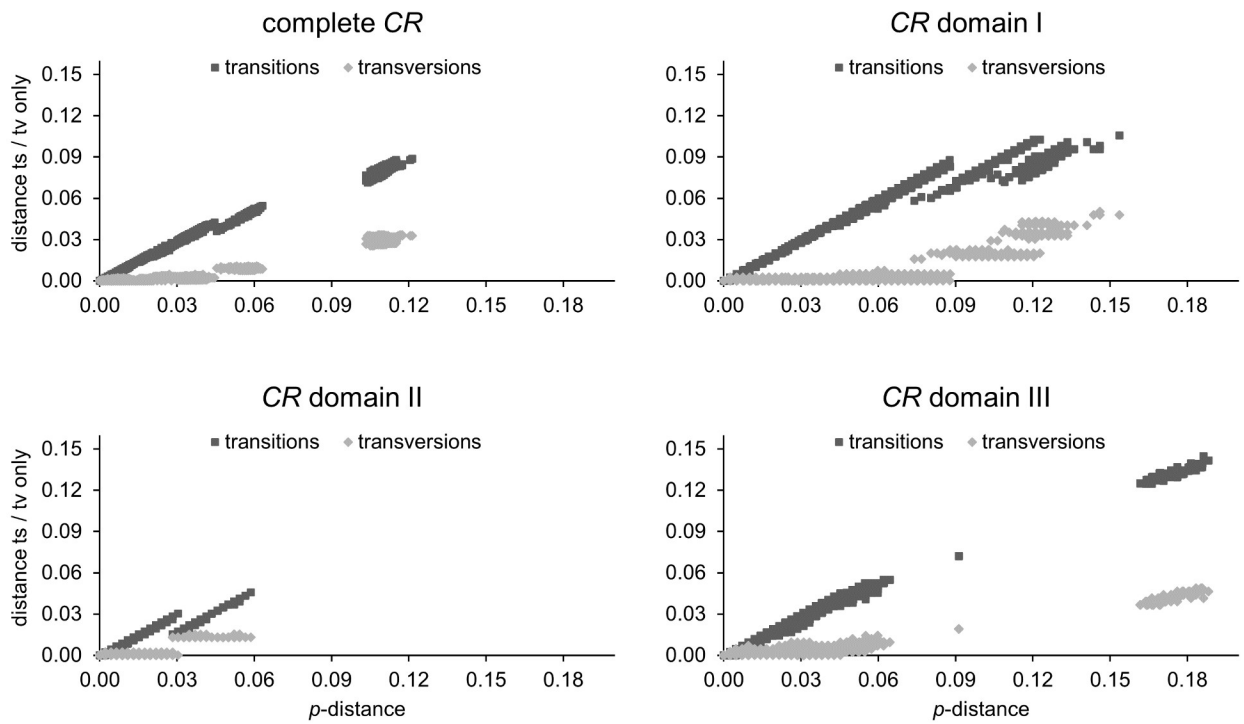

Figure 5. Sequence variability within the *CR* dataset of the genus *Garrulus* comprising sequences of 93 individuals illustrated as pairwise comparisons of transitions (ts) and transversions (tv) with *p*-distances for the entire 1340 bp *CR* alignment and its three domains. The separated points at the upper right end of the graph, especially pronounced in domain III, depict the genetic distances between the *Garrulus glandarius* complex and the species *G. lanceolatus* and *G. lidthi*.

The high concentration of variable sites in two comparatively short segments is even more pronounced in comparisons within single subspecies groups of the *Garrulus glandarius* complex. Considering only the 37 sampled individuals of the *glandarius* clade (see below), the hypervariable segment in the 5′-half of the *CR* (domain I) contains 44 (64.7 %) of the total 68 variable sites and the second variable part at the 3′-end of the *CR* (domain III) contains 16 (23.5 %) variable sites. Similar distributions can be observed in the other two subspecies groups with more than ten sampled individuals. Within the *atricapillus* clade (n=19) 21 (67.7 %) out of 31 variable sites are located in domain I and 7 (22.6 %) in domain III, while in the *brandtii* clade (n=15) as well 21 (67.7 %) of 31 variable sites are in domain I and only 6 (19.4 %) in domain III. In these comparisons within subspecies groups an even stronger concentration of variable sites in domain I of the *CR* can be observed, with about two-thirds of all variable sites in this just about 300 bp long segment.

Phylogeny of the genus *Garrulus*

Phylogenetic trees constructed with the respective *cytb* and *CR* datasets as well as with the concatenated dataset, overall show very similar topologies independently of the tree construction method (ML and BI) used. However, support values of some nodes vary considerably depending on the genetic marker sequence and the phylogenetic tree construction approach. Generally, the highest support values have been achieved with the BI analysis of the concatenated dataset. As for most outgroup taxa only *cytb* sequences have been available (cf. Appendix I), the results regarding the phylogeny of the genus *Garrulus* are described by referring to the *cytb* trees (Figure 6).

The monophyly of the genus *Garrulus* is highly supported in all phylogenetic reconstructions of the *cytb* dataset (Figure 6). Based on the available sequences and considering the mainly weak support values in these trees, the sister group of the genus *Garrulus* could be either *Zavattariornis stresemanni* Moltoni, 1938, the genus *Pica* or even *Ptilostomus afer* (Linnaeus, 1766), while two species of the genus *Podoces* Fischer von Waldheim, 1821 are more distantly related to these taxa. When referring to uncorrected genetic distances (*p*-distances) of *cytb* (Table 5), amongst these taxa the Ethiopian Bush-Crow *Z. stresemanni* is on average the most similar to the various taxa of the genus *Garrulus*, followed by *P. afer* and representatives of the genus *Pica*. The BI tree (Figure 6a) depicts a clade containing *Zavattariornis stresemanni* and the genus *Pica* as sister clade to the genus *Garrulus*, while in the ML tree *Z. stresemanni* is shown as the single sister species of the latter genus (Figure 6b). However, the relationships among those lineages are poorly supported in both trees.

Within the genus *Garrulus* a highly supported and clearly differentiated clade comprising the species *Garrulus lanceolatus* and *Garrulus lidthi* forms the sister clade of the *Garrulus glandarius* complex in BI and ML trees (Figure 6). Uncorrected genetic distances between each of these species and the various taxa of the *G. glandarius* complex vary between 10.7 and 12.2 % for *cytb* and 10.5 and 11.8 % for the *CR*. The mean *p*-distances between *G. lanceolatus* and *G. lidthi* are about 6 % for both marker genes (Tables 5, 6).

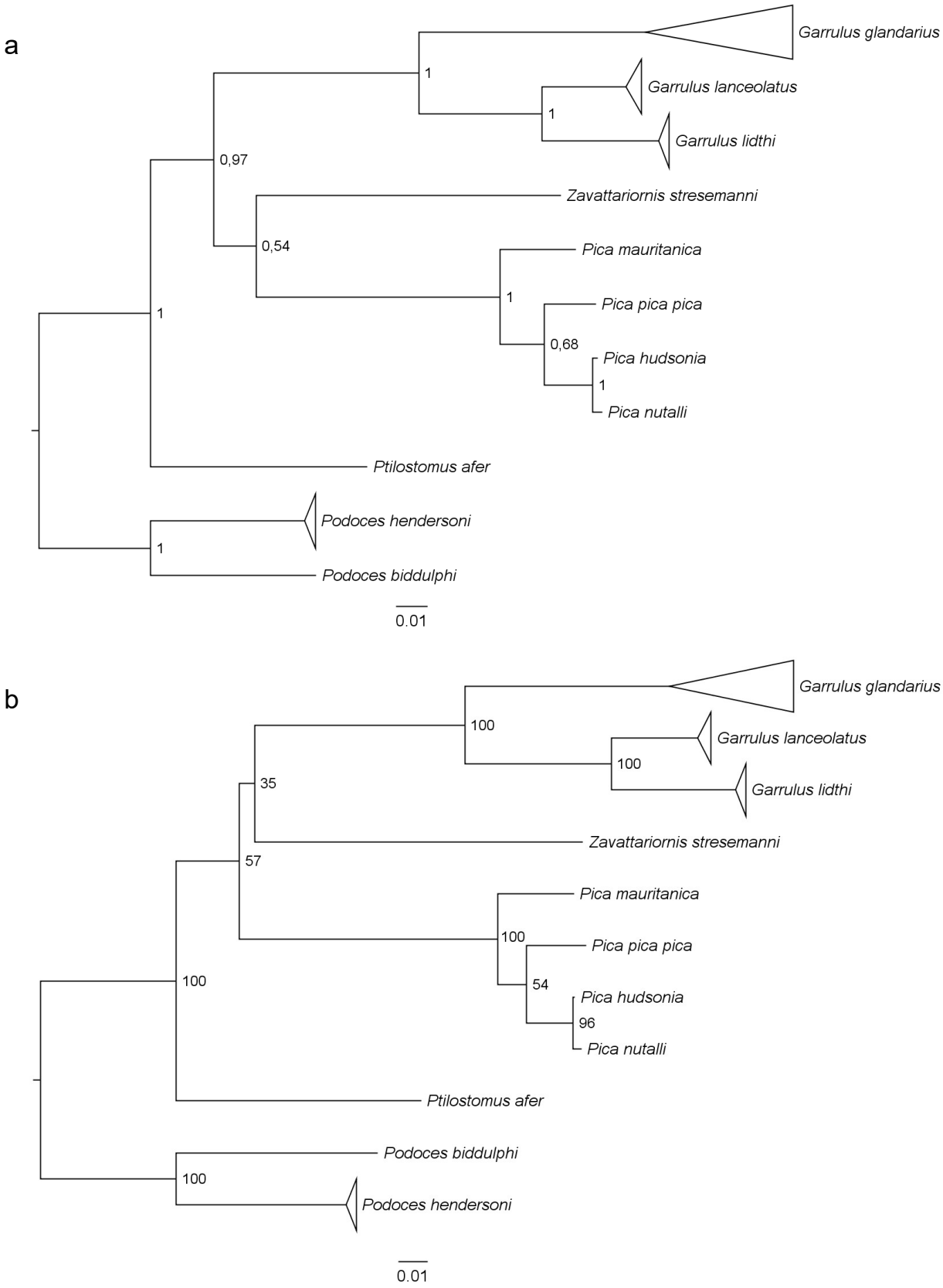

Figure 6. (a) Bayesian tree based on *cytb* sequences of the genus *Garrulus* and several related taxa (76 sequences, 1143 alignment sites) and **(b)** a ML tree constructed with RAxML based on the same dataset. Posterior probability (BI) and bootstrap (ML) values of the major nodes are shown.

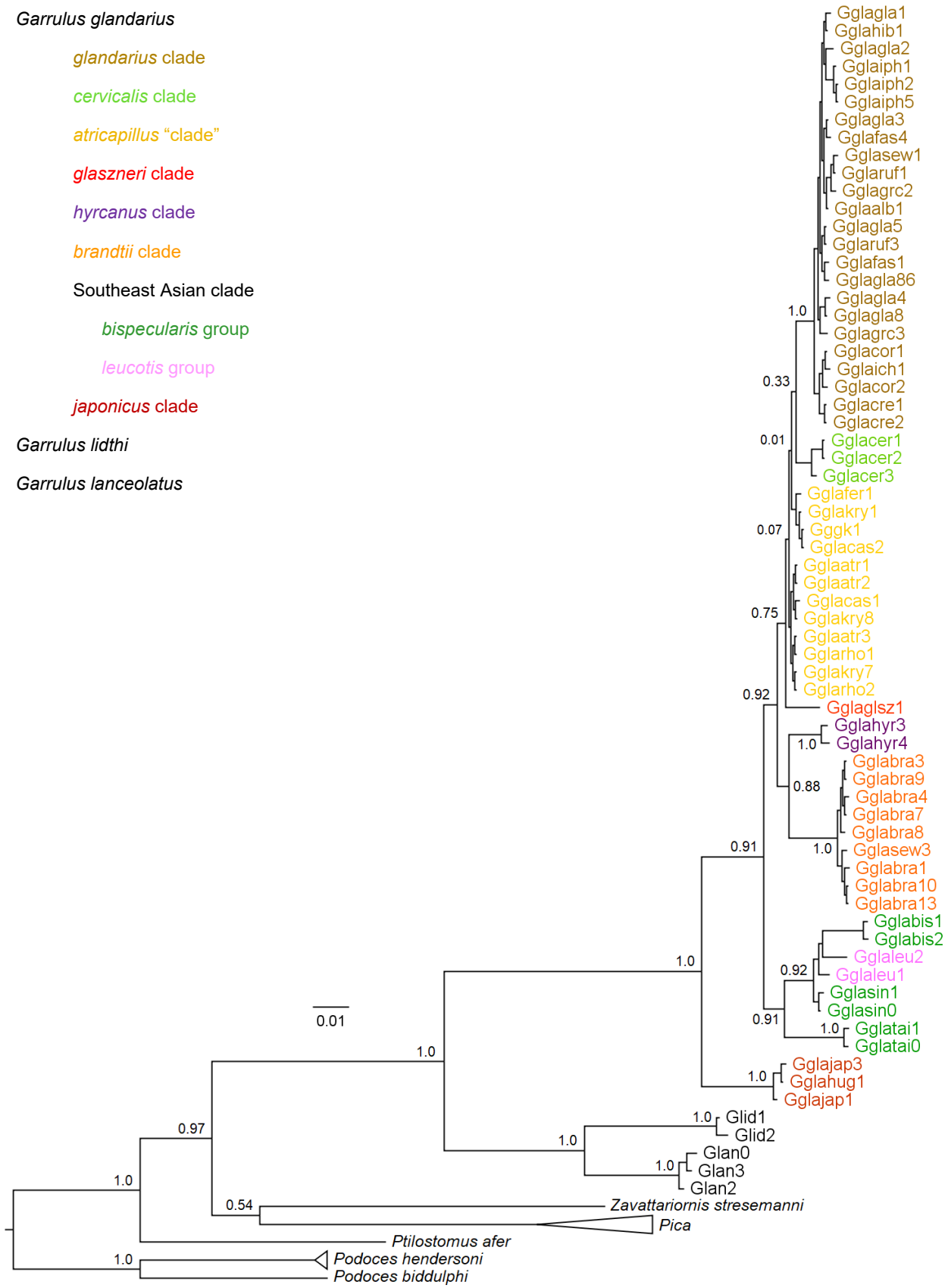

Figure 7. Bayesian tree based on the same *cytb* dataset as Figure 6, showing all individual seuqences of the genus *Garrulus*. Posterior probability values of major nodes are shown. The colours mostly correspond to subspecies groups.

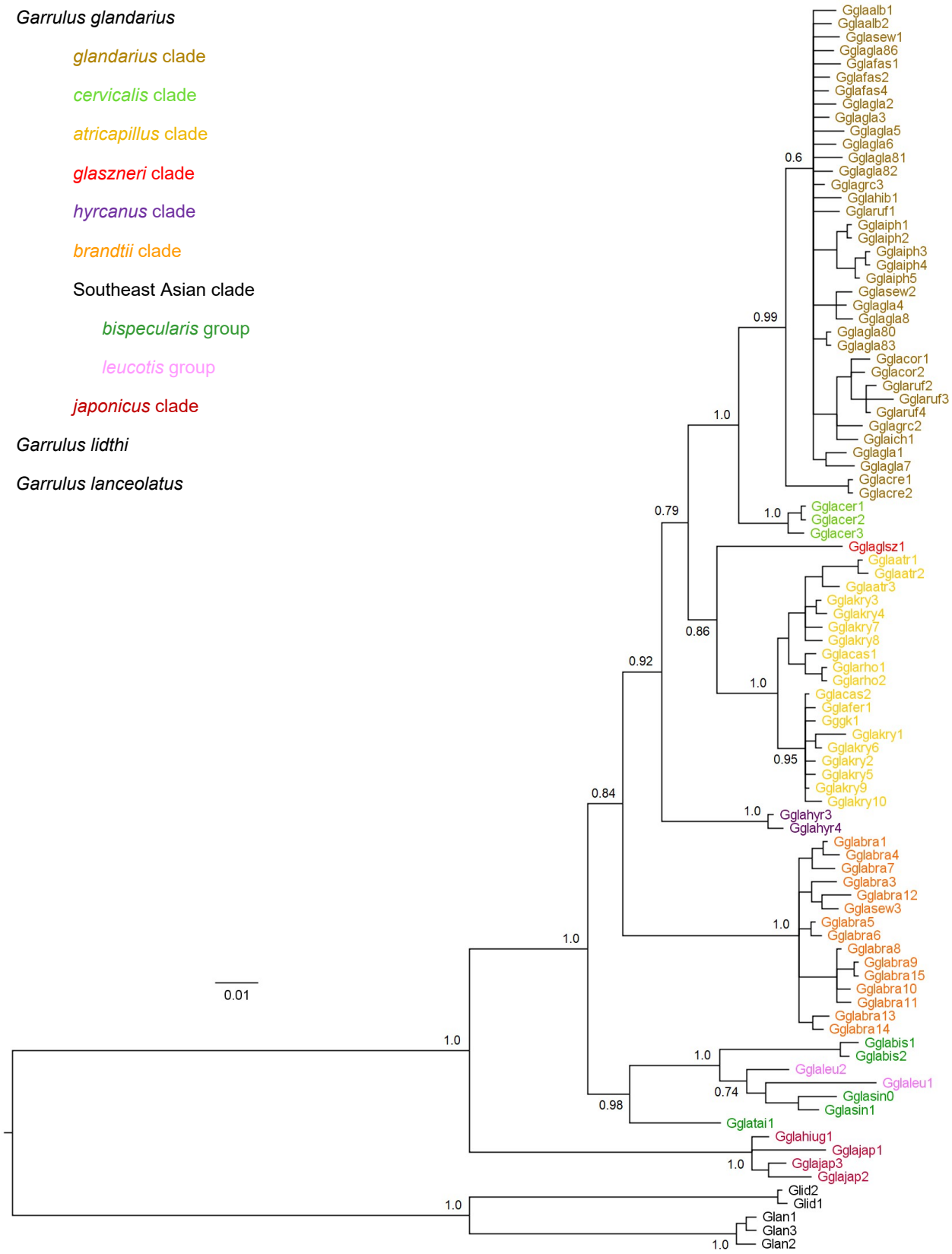

Figure 8. Bayesian 50 % majority-rule consensus tree based on 93 *CR* sequences (1340 alignment sites) of the genus *Garrulus*. Posterior probability values of selected nodes are shown, major clades as well as some additional individuals of the *Garrulus glandarius* complex are denoted by different colours.

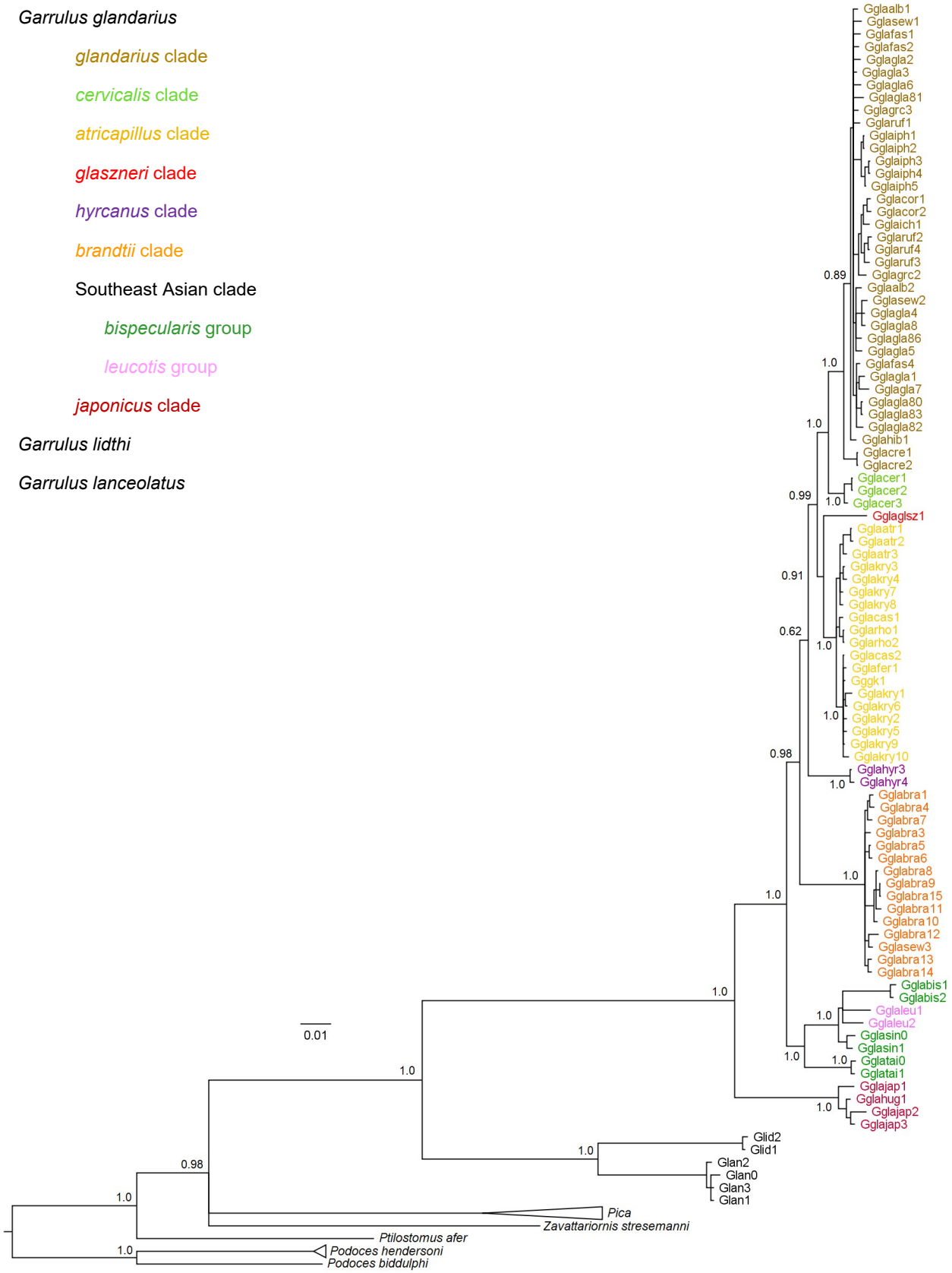

Figure 9. Phylogeny of the *Garrulus glandarius* complex in the form of a Bayesian 50 % majority-rule consensus tree constructed with the concatenated *cytb* and *CR* dataset (2483 alignment sites), comprising sequences of 95 individuals of the genus *Garrulus*. Posterior probability values of the major nodes are shown.

Table 5. Genetic *p*-distances in % between the major clades as well as selected genetically distinct subspecies of the *Garrulus glandarius* complex, *Garrulus lanceolatus*, *Garrulus lidthi*, *Zavattariornis stresemanni* and *Pica pica pica*, calculated from *cytb* sequences with MEGA X using the pairwise deletion option. Mean *p*-distances between clades/taxa are shown below the diagonal, the diagonal depicts sequence variability within each clade (*in italics*) and the ranges of *p*-distances between taxa are given above the diagonal.
In this table the *glandarius* clade does not include the subspecies *G. g. cretorum* which is shown separately, the individual Gglahyr-3 of the *hyrcanus* clade was excluded as the obtained *cytb* sequence is only 261 bp long and the respective taxa of the Southeast Asian clade are presented separately.

Taxon/clade	gla	cre	glsz	cer	atr	hyr	bra	bis	sin	leu	tai	jap	Glan	Glid	Zstr	Ppic
***glandarius* clade** (n=22)	*0.3*	0.1-0.3	1.4-1.7	0.9-1.2	0.5-0.9	1.8-2.0	2.1-2.6	3.2-3.4	2.3-2.5	2.5-3.2	3.1-3.3	4.2-4.5	11.0-11.5	11.4-11.8	13.2-13.5	14.3-14.5
G. g. cretorum (n=2)	0.3	*0.0*	1.3	0.9-1.0	0.5-0.7	1.8	2.2-2.4	3.2	2.3-2.4	2.4-3.1	3.1	4.2-4.4	11.1-11.4	11.3-11.5	13.1	14.4
***glaszneri* clade** (n=1)	1.6	1.3	/	1.5-1.7	1.0-1.1	2.4	2.5-2.7	3.5	2.4-2.5	2.5-2.8	3.4	4.5-4.6	10.8-11.0	11.3-11.5	13.0	14.3
***cervicalis* clade** (n=3)	1.1	1.0	1.6	*0.3*	0.5-0.9	1.8-2.0	2.0-2.3	3.2	2.2-2.4	2.4-3.1	3.0-3.1	4.2-4.5	11.1-11.4	11.6-11.8	12.8-13.1	14.4
***atricapillus* clade** (n=12)	0.7	0.6	1.0	0.7	*0.3*	1.3-1.6	1.7-2.0	2.9-3.0	1.8-2.0	2.1-2.6	2.6-2.7	3.8-4.1	10.8-11.3	11.4-11.7	12.8-13.1	14.1-14.3
***hyrcanus* clade** (n=1)	1.9	1.8	2.4	2.0	1.5	/	2.3-2.4	3.8	3.0-3.1	3.2-3.5	3.4	4.6-5.0	11.0-11.3	12.2-12.3	13.2	14.6
brandtii clade (n=9)	2.4	2.3	2.6	2.1	1.8	2.4	*0.3*	3.7-3.9	2.8-3.1	3.1-3.7	3.8-3.9	4.4-4.6	10.9-11.5	11.7-12.2	12.6-12.9	13.8-14.2
G. g. bispecularis (n=2)	3.3	3.2	3.5	3.2	2.9	3.8	3.8	*0.2*	1.4-1.5	1.5-1.7	3.2-3.4	4.6-5.2	10.5-10.9	10.8-10.9	12.2	13.0-13.2
G. g. sinensis (n=2)	2.4	2.3	2.5	2.3	1.9	3.0	3.0	1.4	*0.1*	0.4-1.0	2.5-2.6	4.3-4.5	10.8-11.1	10.8-11.0	12.7-12.8	13.6
G. g. leucotis (n=2)	2.9	2.8	2.7	2.8	2.3	3.4	3.4	1.6	0.7	*1.0*	2.8-2.9	4.5-5.0	10.6-11.2	10.7-10.9	12.6-12.8	13.5-13.6
G. g. taivanus (n=2)	3.3	3.2	3.4	3.1	2.7	3.4	3.9	3.4	2.6	2.8	*0.2*	5.1-5.3	11.4-11.6	11.5-11.8	12.9-13.1	13.9
***japonicus* clade** (n=3)	4.4	4.3	4.5	4.4	4.0	4.8	4.5	4.9	4.4	4.8	5.2	*0.3*	10.8-11.1	11.3-11.5	13.6-13.9	13.6-13.8
G. lanceolatus (n=3)	11.3	11.2	10.9	11.2	11.0	11.1	11.2	10.7	10.9	10.9	11.5	10.9	*0.5*	5.8-6.2	14.0-14.2	12.4-12.8
G. lidthi (n=2)	11.6	11.4	11.4	11.7	11.5	12.2	12.0	10.8	10.9	10.8	11.6	11.4	6.0	*0.3*	13.7-14.2	13.3-13.4
Z. stresemanni (n=1)	13.3	13.1	13.0	12.9	13.0	13.2	12.7	12.2	12.7	12.7	13.0	13.7	14.1	14.0	/	12.1
Pica p. pica (n=1)	14.4	14.4	14.3	14.4	14.2	14.6	14.0	13.1	13.6	13.5	13.9	13.7	12.6	13.3	12.1	/

Table 6. Genetic *p*-distances in % between the major clades as well as selected genetically distinct subspecies of the *Garrulus glandarius* complex, *Garrulus lanceolatus* and *Garrulus lidthi*, calculated from *CR* sequences with MEGA X using the pairwise deletion option. Mean *p*-distances between taxa/clades are shown below the diagonal, the diagonal depicts sequence variability within each clade (*in italics*) and the range of *p*-distances between taxa is given above the diagonal.

In this table the *glandarius* clade does not include the subspecies *G. g. cretorum* which is shown separately as are the respective taxa of the Southeast Asian clade.

Taxon/clade	gla	cre	glsz	cer	atr	hyr	bra	bis	sin	leu	tai	jap	Glan	Glid
***glandarius* clade** (n=35)	*1.3*	1.1-1.5	2.2-2.8	1.3-2.1	2.0-3.2	1.6-3.2	3.1-4.1	3.5-4.2	3.1-4.1	3.4-4.2	2.9-3.5	5.1-6.3	10.5-11.1	10.9-11.1
G. g. cretorum (n=2)	1.3	*0.0*	2.8	1.5	2.4-2.8	2.0-2.8	3.3-3.6	4.1-4.2	3.5-3.9	3.4-3.7	3.0	5.7-6.2	10.8-11.0	11.0-11.1
***glaszneri* clade** (n=1)	2.5	2.8	*/*	2.5-2.6	2.1-2.7	2.2-3.2	3.2-3.8	3.6-3.8	3.5-3.9	3.7-3.9	3.3	5.1-5.8	11.3-11.4	10.8-10.9
***cervicalis* clade** (n=3)	1.6	1.5	2.6	*0.2*	2.1-2.7	1.6-2.5	3.1-3.7	3.6-3.9	3.2-3.9	3.4-3.8	2.4	5.3-6.2	10.9-11.1	11.0-11.1
***atricapillus* clade** (n=19)	2.5	2.5	2.3	2.2	*1.2*	1.0-2.3	3.0-4.0	3.8-4.5	3.2-3.8	3.4-4.0	2.8-3.2	5.1-6.2	10.8-11.3	10.4-10.9
***hyrcanus* clade** (n=2)	2.4	2.4	2.7	2.0	1.7	*0.1*	3.0-4.2	3.4-4.1	2.3-3.1	2.6-3.3	2.2-2.7	4.7-6.2	10.3-10.8	10.3-11.1
***brandtii* clade** (n=15)	3.5	3.5	3.4	3.4	3.5	3.5	*1.2*	3.6-4.1	3.4-3.9	3.5-4.2	3.5-3.9	5.2-6.2	11.0-11.5	10.6-11.3
G. g. bispecularis (n=2)	3.8	4.2	3.7	3.8	4.0	3.8	3.9	*0.2*	2.1-2.4	1.9-2.8	3.2	5.4-5.6	10.6-10.7	10.4-10.5
G. g. sinensis (n=2)	3.5	3.7	3.7	3.6	3.4	2.7	3.5	2.3	*0.6*	1.0-1.9	2.5-2.9	4.5-5.2	11.0-11.2	11.0-11.2
G. g. leucotis (n=2)	3.7	3.5	3.8	3.7	3.6	2.9	3.8	2.3	1.4	*1.8*	2.5-3.0	4.7-5.9	11.0-11.2	11.0-11.2
G. g. taivanus (n=1)	3.2	3.0	3.3	2.4	2.9	2.4	3.6	3.2	2.7	2.8	*/*	5.4-5.7	10.5-10.6	10.5-10.6
***japonicus* group** (n=4)	5.8	6.0	5.5	5.9	5.7	5.4	5.7	5.5	4.9	5.3	5.6	*1.5*	10.7-11.5	11.6-12.1
G. lanceolatus (n=3)	10.8	10.9	11.3	11.0	11.1	10.6	11.3	10.8	11.1	11.1	10.5	11.1	*0.3*	5.9-6.0
G. lidthi (n=2)	11.0	11.1	10.8	11.0	10.6	10.7	10.8	10.5	11.1	11.1	10.5	11.8	6.0	*0.1*

Phylogeny of the *Garrulus glandarius* complex

The monophyly of the *Garrulus glandarius* complex is highly supported in all the phylogenetic reconstructions (Figures 6-9). Within the *G. glandarius* complex at least eight major clades are distinguishable (Figures 7-9), mostly corresponding to the morphologically defined subspecies groups. The most basal split separates the highly supported *G. g. japonicus* (*japonicus* group) from the remaining taxa of the complex, which is consistent for all trees constructed and highly supported by BI analysis of the *CR* and the concatenated dataset (posterior probability (pp)=1.0), but less so by *cytb* data (pp=0.91) and ML analysis (MEGA X: bootstrap *cytb*=0.89, *CR*=0.93; ML trees not shown). The next clade includes members of the morphologically distinct *bispecularis* and *leucotis* group and is hence called Southeast Asian clade. Individuals of the *brandtii* group form another monophyletic group as do two individuals of the subspecies *G. g. hyrcanus* (*hyrcanus* group). The succession of these two splits though remains uncertain, but in most trees the *brandtii* clade branches off a more basal node than the *hyrcanus* clade. Lastly, several comparatively close related clades which mainly correspond to the *atricapillus* group, the *cervicalis* group, the *glandarius* group and the *glaszneri* group are assembled in a well-supported "western clade".

The maximum uncorrected genetic *p*-distances between individuals within the *G. glandarius* complex are 5.3 % for *cytb* and 6.3 % for the *CR* (Tables 5, 6), each from comparisons including individuals of the *japonicus* group. The genetic distances between the clades become gradually smaller from east to west, with the most differentiated clade comprising the *japonicus* group and smaller *p*-distances between the Western Palearctic clades. As somewhat of an exception the single individual sampled of the subspecies *G. g. glaszneri* from Cyprus is well differentiated from all the other clades (see Tables 5, 6).

Phylogenetic structure of subspecies groups within the *G. glandarius* complex

japonicus group

The genetically most distinct clade within the *G. glandarius* complex comprises sequences of four individuals originating from the Japanese main islands Honshu and Kyushu, thus matching with the *japonicus* group. Mean *p*-distances

between the *japonicus* clade and the remaining clades of the *G. glandarius* complex vary between 4.0-5.6 % for *cytb* and 4.9-6.0 % for the *CR*. Each of these individuals represents a unique haplotype for both marker genes. The single individual from the southern main island Kyushu (subspecies "*G. g. hiugaensis*") is embedded with the remaining jays from Honshu (*G. g. japonicus*) (haplotype network not shown).

Southeast Asian clade (*bispecularis* and *leucotis* group)

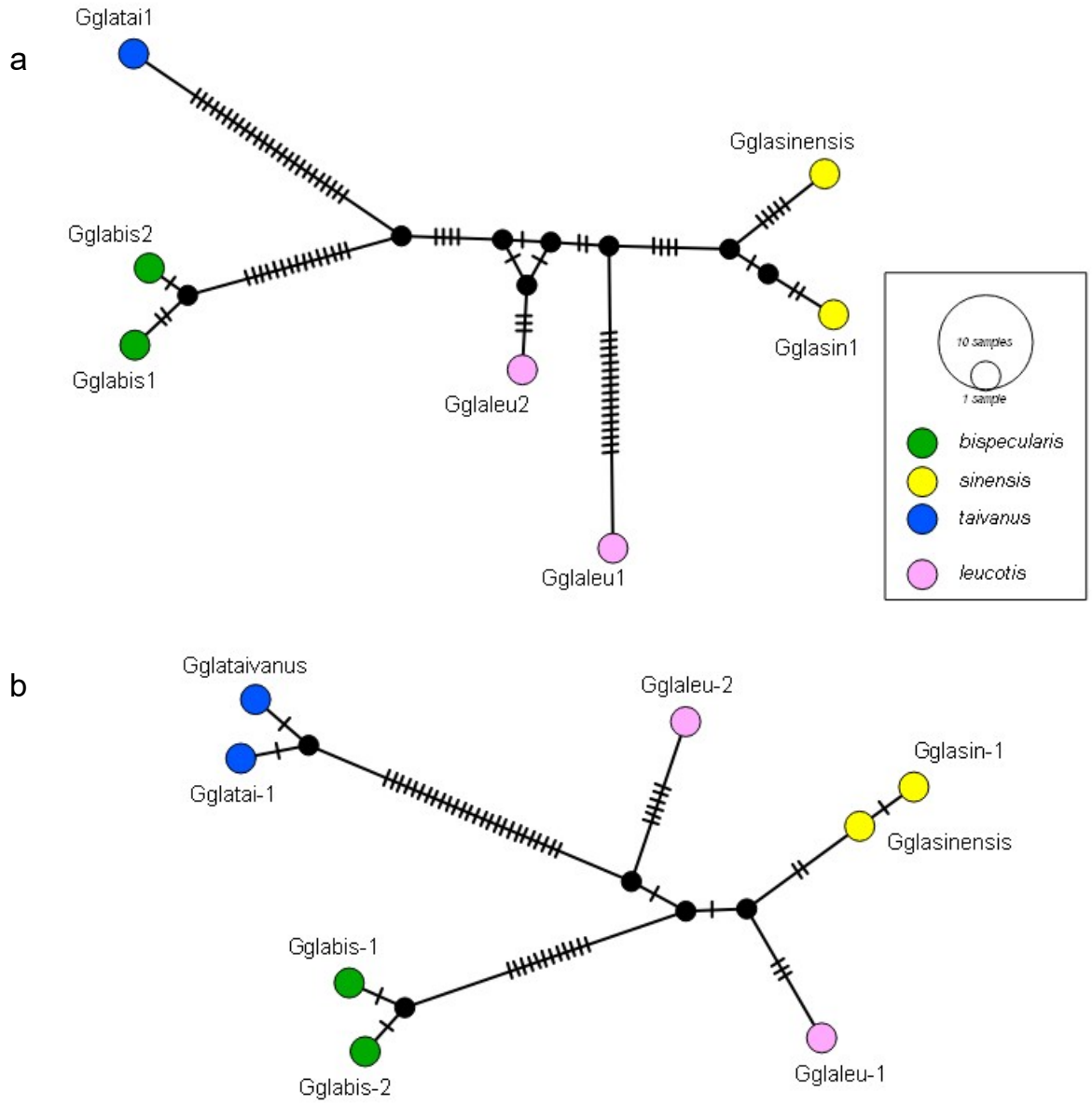

Figure 10. Median joining networks of the Southeast Asian clade comprising **(a)** *CR* sequences of seven individuals and **(b)** *cytb* sequences of eight individuals.

The sampled individuals of these two groups cluster together in one very diverse clade, referred to as Southeast Asian clade (Figures 7-9). The *bispecularis* group is here represented by *G. g. bispecularis*, *G. g. sinensis* and *G. g. taivanus*. In the trees the most basal branching within this clade separates *G. g. taivanus* from Taiwan from the other taxa. This subspecies is genetically very distinct, which is clearly illustrated in haplotype networks (Figure 10) and phylogenetic trees (Figures 7-9). *P*-distances to the other sampled taxa within the clade range between 2.5 % (to *G. g. sinensis*) and 3.4 % (*G. g. bispecularis*) for *cytb* and between 2.5-2.9 % (to *G. g. sinensis*) and 3.2 % (*G. g. bispecularis*) for the *CR*. Furthermore, the subspecies *G. g. bispecularis* proves to be well separated from *G. g. sinensis*, with *p*-distances from 1.4 to 1.5 % for *cytb* and 2.1 to 2.4 % for the *CR*.

The two sampled individuals of the subspecies *G. g. leucotis*, which is usually placed into a separate subspecies group, cluster between the taxa of the *bispecularis* group. The sequences are particularly close to those of *G. g. sinensis*, from which they are separated by *p*-distances of 0.4-1.0 % for *cytb* and 1.0-1.9 % for the *CR*. Moreover, the two individuals of *G. g. leucotis* do not cluster closely together in the haplotype networks (Figure 10). The *p*-distances between the two samples are on the same scale as those between these individuals and *G. g. sinensis*, with 0.9 % for *cytb* and 1.8 % for the *CR*.

brandtii group

Jays of to the *brandtii* group form a distinct clade with more than 1.6 % *cytb* and a minimum of 3.0 % uncorrected *CR* sequence divergence from all the other taxa within the *G. glandarius* complex. A sample assigned to "*G. g. sewerzowii*" from the Kirov oblast in European Russia clusters within this clade. The haplotype network illustrates that the clustering of individuals from continental Asia shows no obvious geographical pattern (Figure 11) for samples from the Urals (Sverdlovsk oblast), western Siberia (Tomsk) and the Russian Far East (Primorsky krai). *CR* sequences of two samples from the Sakhalin islands ("*G. g. taczanowskii*") cluster together and differ by a minimum of four base substitutions from jays of mainland Asia. Even more distinct are five individuals from Hokkaido ("*G. g. pallidifrons*"), which differ by a minimum of eight substitutions from the geographically close Sakhalin jays and by a minimum of

ten substitutions from the mainland *G. g. brandtii* (Figure 11). Yet, the distinctiveness of these two forms is not evident from the *cytb* data (haplotype network not shown).

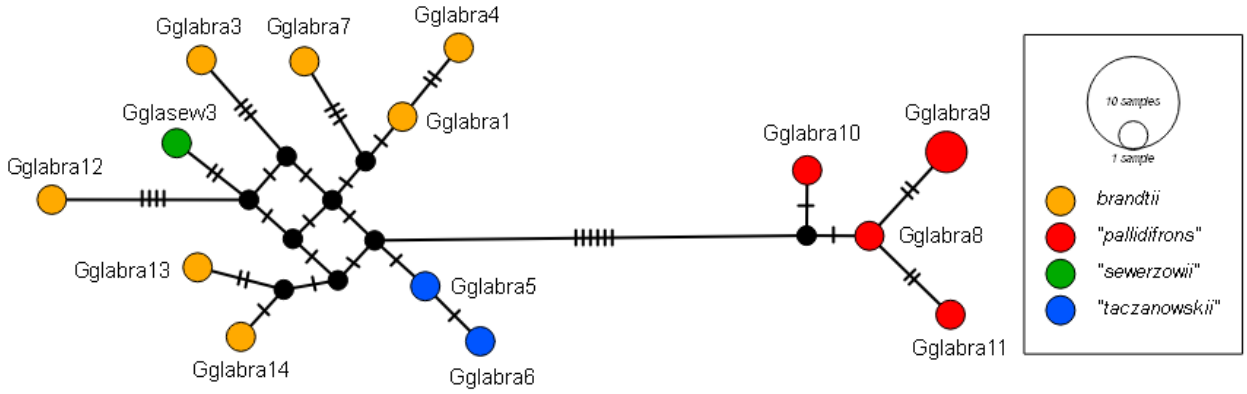

Figure 11. Median joining network based on *CR* sequences of 15 individuals of the *brandtii* clade. Haplotypes from mainland Asia (*G. g. brandtii*) are coloured in orange, those from eastern European Russia ("*G. g. sewerzowii*") in green, from the Sakhalin islands ("*G. g. taczanowskii*") in blue and Hokkaido ("*G. g. pallidifrons*") in red. The individuals Gglabra-9 and Gglabra-15 exhibit identical haplotypes.

hyrcanus group

Sequences of two individuals originating from the Lankaran area in present day Azerbaijan, which exhibit morphological characters of the subspecies *G. g. hyrcanus* (see Appendix II) form a well separated clade. *P*-distances to all the other sampled taxa are higher than 1.3 % for *cytb* and more than 2.0 % for the *CR*. Two more specimens collected in the same area assigned to "*G. g. caspius*", exhibiting intermediate plumage characters between the present subspecies and representatives of the *atricapillus* group, cluster with the latter (Figure 13).

Table 7. Numbers of haplotypes for each marker gene for the major clades of the *Garrulus glandarius* complex with more than 10 sampled individuals (n=number of samples).

clade	*glandarius*	*atricapillus*	*brandtii*
Cytb haplotypes / n	17 / 24	4 / 12	6 / 9
%	70.8 %	33.3 %	66.6 %
CR haplotypes / n	33 / 37	17 / 19	14 / 15
%	89.2 %	89.5 %	93.3 %

Western clade

Whereas the abovementioned subspecies groups form very distinct clades, the subclades within the "western clade" are genetically much less differentiated. Nevertheless, in most phylogenetic trees all the Western Palearctic subspecies groups can be assigned to well supported clades (Figures 8, 9). Only in some *cytb* trees the "*atricapillus* clade" forms a paraphyletic assemblage (Figure 7), which, however, is not evident in haplotype networks (Figure 12).

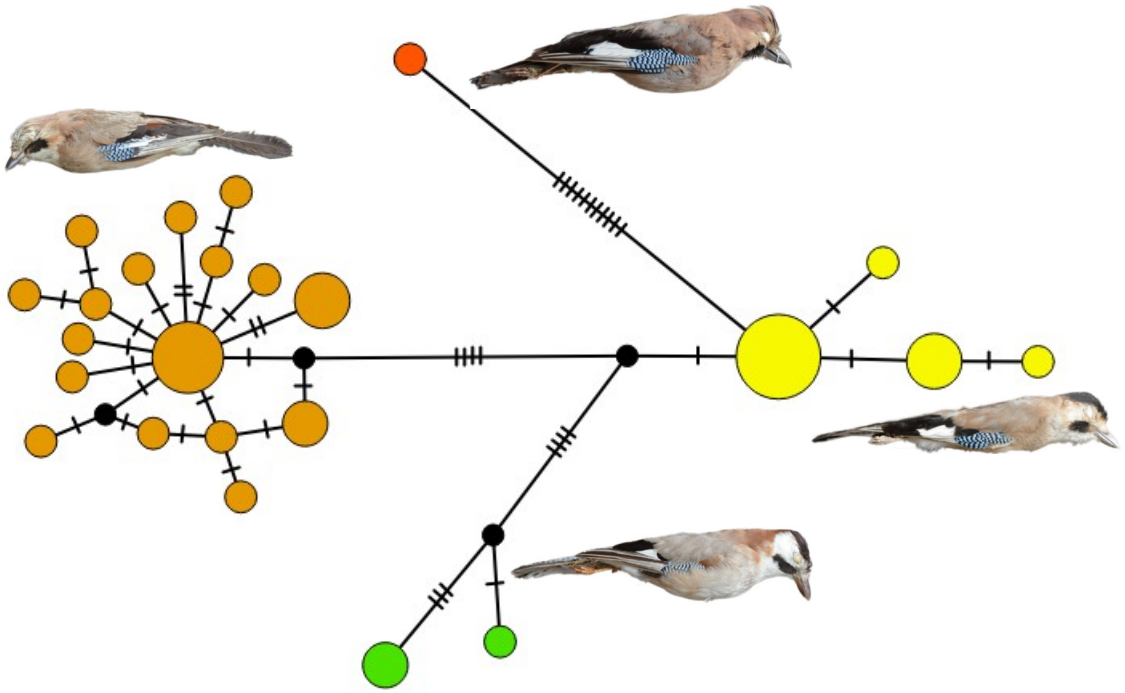

Figure 12. Median joining network of the "western clade", comprising *cytb* sequences of 40 individuals of the *glandarius* group (brown), the *cervicalis* group (green), the *atricapillus* group (yellow) and the *glaszneri* group (red).

atricapillus group

Within the *atricapillus* clade, mostly matching with the *atricapillus* group, the *CR* provides a detailed resolution at the subspecies level. The three specimens of *G. g. atricapillus* cluster together in phylogenetic trees and networks of the *CR* dataset (Figure 12a) and are separated by a minimum of five substitutions from jays of the subspecies *G. g. anatoliae*. The two birds from the island Rhodes ("*G. g. rhodius*") are separated by a minimum of eight substitutions from the

geographically adjacent *G. g. anatoliae*, but only by three from an individual from Azerbaijan (Gglacas-1). A well differentiated Caucasus clade, mainly comprising the subspecies *G. g. krynicki*, is separated by a minimum of seven substitutions from all the other samples of this clade and forms a well-supported subclade in all the phylogenetic trees of the *CR* data (combined dataset: pp=1.0, *CR*: pp=0.95). This separation of the individuals from the Caucasus area can also be observed in the *cytb* data (Figures 7, 12b), albeit the distance to the other taxa within the clade is just one substitution. A jay from European Turkey of the subspecies *G. g. ferdinandi* of the *glandarius* group clusters within this well supported Caucasus clade. Of the two specimens of "*G. g. caspius*", from present day Azerbaijan, one clusters within the Caucasus clade, while the other one exhibits a quite distinct haplotype close to *G. g. anatoliae*. None of the five samples from the Crimean *G. g. iphigenia*, which is assigned to the *atricapillus* group, clusters within the *atricapillus* clade, instead they form a subclade of the *glandarius* clade.

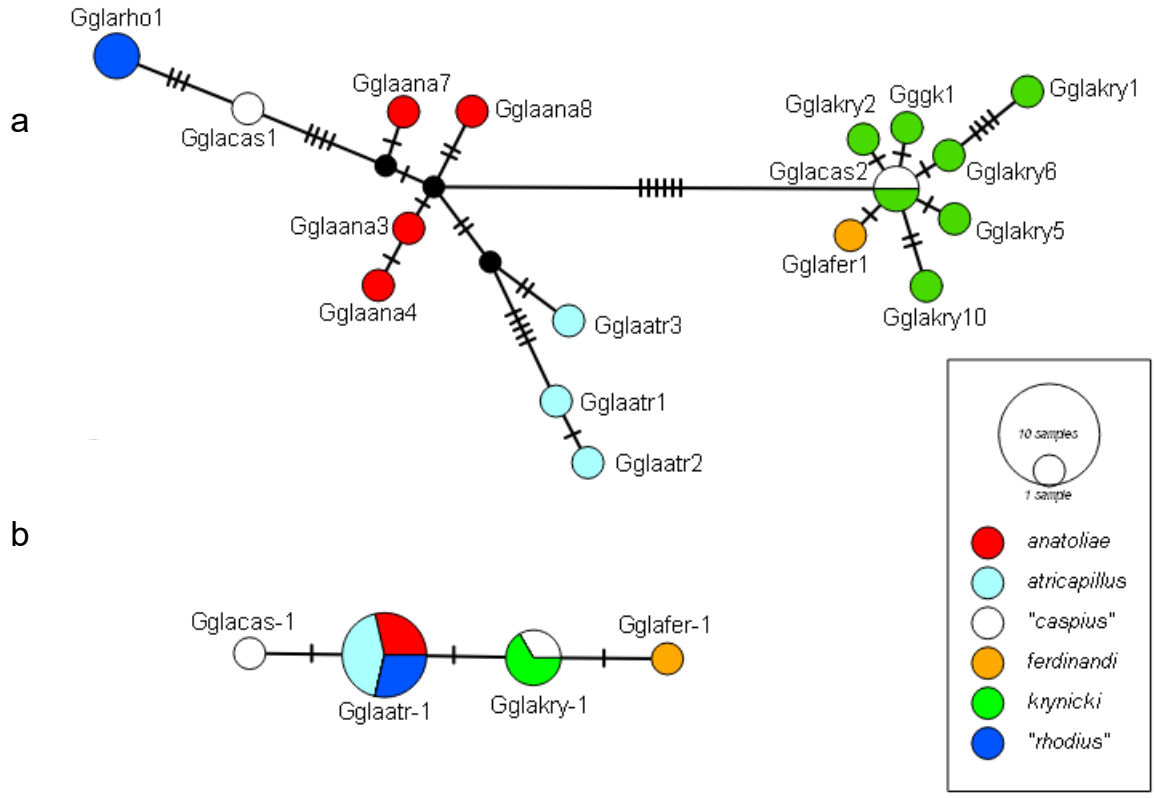

Figure 13. Median joining networks of the *atricapillus* clade comprising **(a)** *CR* sequences of 19 individuals and **(b)** *cytb* sequences of 12 individuals.

cervicalis group

Sequences of the three specimens of the North African subspecies *G. g. cervicalis* form the sister clade of the European *glandarius* clade. Despite the morphological distinctness of the subspecies, it is genetically very similar to jays of the *glandarius* group, with *p*-distances of 0.9-1.2 % for *cytb* and 1.3-2.1 % for the *CR*. In the *cytb* dataset sequences of *G. g. cervicalis* are even closer to those of the *atricapillus* clade, with *p*-distances of 0.5-0.8 %, while these two clades are separated by 2.1-2.3 % in the *CR* data. For the three samples of the *cervicalis* group a clear differentiation between two specimens from Tunisia ("*G. g. koenigi*") and one from Algeria can be detected for both marker genes (Figures 7-9).

glandarius group

Among the sequences of the 37 individuals forming the *glandarius* clade, in the *CR* data 33 (89 %) different haplotypes can be found, while the *cytb* sequences from 24 individuals yield 17 (71 %) haplotypes (Table 7). No evident clustering according to their respective subspecies assignment or collecting locations can be observed for samples from the European mainland (Figure 13), but the insular subspecies *G. g. corsicanus*, *G. g. ichnusae* and *G. g. cretorum*, each exhibit unique haplotypes for both analysed marker genes, which cluster together in haplotype networks. Three of the individuals of the English *G. g. rufitergum* cluster together as well. A single specimen of the Irish subspecies *G. g. hibernicus* yields a quite distinct *CR* haplotype which is not closely allied with those of the English Jays.
The most differentiated subspecies within the *glandarius* clade according to *CR* data is *G. g. cretorum* from the island Crete. Sequences of the two sampled individuals are identical and form the sister clade to the other subspecies of the *glandarius* clade (Figures 8, 9), from which they are separated by at least 15 substitutions in the *CR*, but just one in *cytb*.

Except for one individual, which belongs to the *brandtii* clade, all the samples from European Russia cluster within the *glandarius* clade. Interestingly, five samples from the Crimean subspecies *G. g. iphigenia*, usually included in the *atricapillus* group, form an own subclade within the *glandarius* clade. This distinctness of the Crimean jays can be detected with both marker genes.

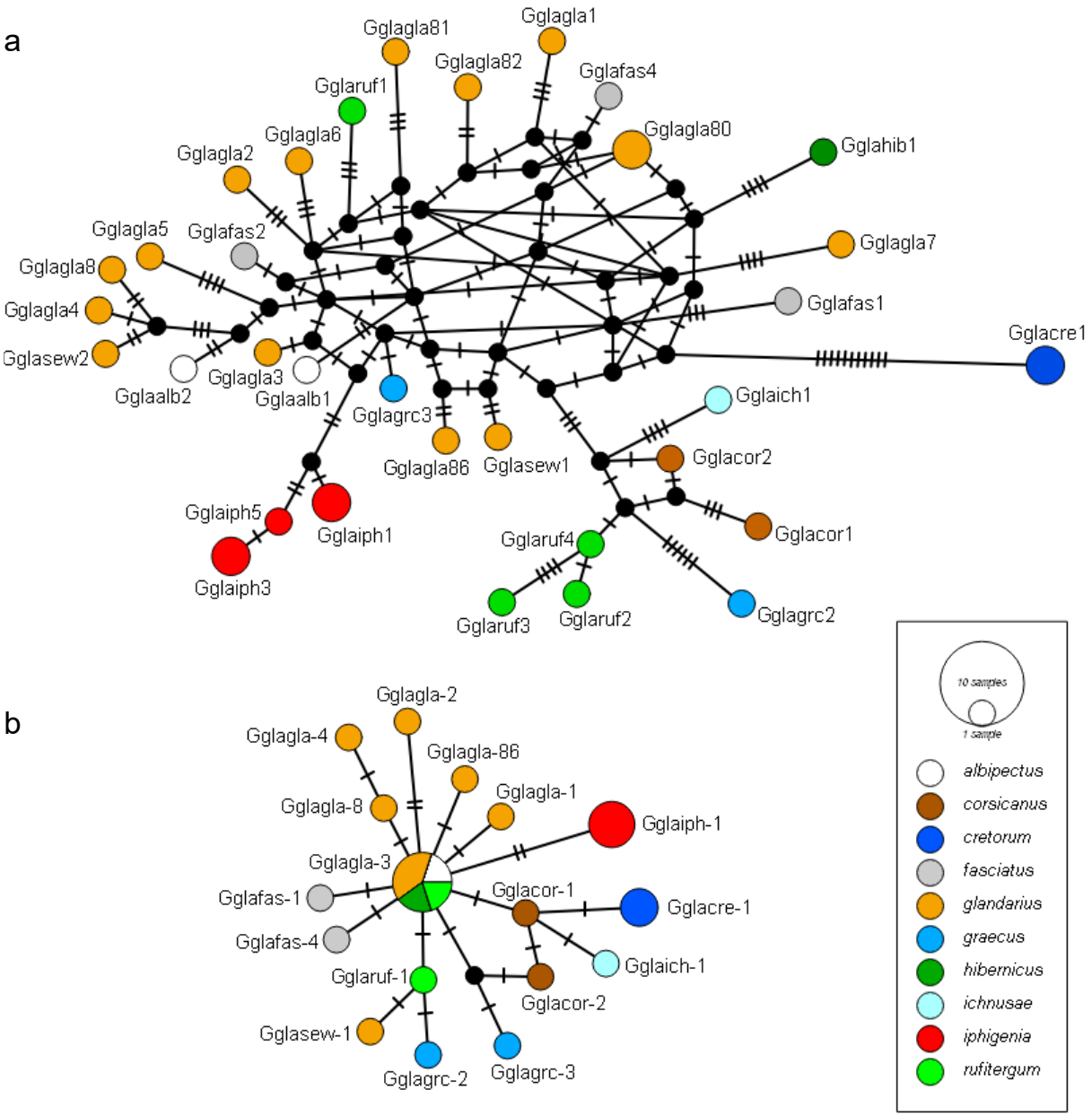

Figure 14. Median joining networks of the *glandarius* clade based on **(a)** *CR* sequences of 37 individuals and **(b)** *cytb* sequences of 24 individuals.

glaszneri group

A single sampled individual of the subspecies *G. g. glaszneri* from the island Cyprus is genetically the most distinct taxon within the whole "western clade" (Figures 7-9, Tables 5, 6). In most of the phylogenetic reconstructions it forms the sister taxon of the *atricapillus* clade, from which it is separated by more than 0.9 % sequence divergence in *cytb* and more than 2.0 % in the *CR*. *P*-distances to the *glandarius* clade are even higher, with more than 1.3 % for *cytb* and a minimum of 2.2 % for the *CR*.

Discussion

Amplification and sequencing success

Successful extraction, amplification and sequencing of both genetic markers from all the sampled museum specimens in the present study underlines the suitability of foot pads to recover mt DNA even from old specimens. The method of cutting off a small piece of the foot or toe pad of a preserved bird specimen is often regarded as a non-destructive way to obtain tissue samples (e.g. Mundy et al. 1997), but feathers have been suggested as alternative sources (Leeton et al. 1993; cf. Graves & Braun 1992). Moreover, the use of museum specimens ensures a good documentation of the sampled individuals.

Although no systematic investigation of degradation of DNA has been undertaken during this study, amplification of *CR* fragments of various lengths has been attempted with many individuals. These trials show an evident trend towards decreasing PCR fragment lengths with increasing age of the sampled specimens (Figure 3). Nevertheless, even from the oldest specimens, which at least had been collected around 1830, fragments of about 340 bp of length have been sequenced successfully. Many samples from the twentieth century would even be suited for efficient sequencing of longer marker regions with fragments of 500 to 600 bp. Decreasing PCR amplifiability with increasing age of foot pad samples already has been well documented by Glenn et al. (1999) and Töpfer et al. (2011). Besides age, individual preservation conditions of sampled bird specimens may influence PCR success as well (cf. Töpfer et al. 2011). In several specimens of whom only about 300 bp fragments could have been amplified, although they did not belong to the oldest specimens sampled, the foot tissue appeared especially hard and dry.

Sequence variability

The results of this study clearly illustrate that the *cytb* gene provides considerably less resolution on the subspecies level than the complete *CR*. Despite very similar percentages of variable sites for both markers (*cytb*: 20.7 %, *CR*: 21.5 %), more than 88 % of the sampled individuals yield unique haplotypes in the *CR* dataset but only 71.6 % for *cytb*. As the individuals for sequencing of the latter marker were selected to provide a complete taxon sampling, this

difference might even be more pronounced if sequences of all the individuals would have been analysed. The comparatively high percentage of variable sites in the *cytb* data within the genus *Garrulus* is probably due to the strong differentiation of *G. lanceolatus* and *G. lidthi* from *G. glandarius* at the third codon positions (Figure 4).

In contrast to these general results, when comparing genetic *p*-distances between some taxa they proved to be slightly higher for *cytb* than for the entire *CR*. For example, *cytb* sequences of *G. lanceolatus* and *G. lidthi* differ by 10.7 to 12.2 % from those of the *G. glandarius* complex but *CR* sequences only by 10.5 to 11.8 % and within the complex the subspecies *G. g. taivanus* differs from *G. g. bispecularis* by 3.4 % in *cytb* but only by 3.2 % in the *CR* data (Tables 5, 6). As in each of these cases *CR* distances are just slightly lower than for *cytb*, it could be an artefact created by chance due to the stochasticity involved in base substitutions, especially in the *CR*. An additional explanation could be the low proportion of variable sites in the conserved middle section of the *CR*, where only 7.5 % are variable, compared to 20.7 % for the complete *cytb* gene. When a certain amount of divergence is reached, the slowly evolving central domain, in combination with increasing numbers of undetected multiple substitutions in the hypervariable domain I of the *CR*, where first effects of saturation can already be observed (cf. Figure 5), could lead to lower *p*-distances in comparisons using the entire *CR* than for *cytb*.

The unequal distribution of base variability within the *CR*, with a conserved central part flanked by more variable segments, is well documented for many vertebrate taxa (e.g. Vigilant et al. 1989; Wenink et al. 1994; Lee et al. 1995; Baker & Marshall 1997). That the highest substitution rates are to be found in domain I of the *CR* is in line with the results of several intraspecific studies on birds (Wenink et al. 1993; Baker et al. 1994; Glenn et al. 1999), whereas in comparisons on higher taxonomic levels domain III exhibits slightly more variability (Wenink et al. 1994; Saunders & Edwards 2000). These observations hold good for the *CR* dataset of the genus *Garrulus* where variable sites are about equally distributed between the two peripheral domains when the total alignment is examined but accumulate in the first third when only single subspecies groups are considered. So, to summarise, it can be noted that the two peripheral domains of the *CR*

evolve noticeably faster than the *cytb* gene, underlining their superiority for intraspecific phylogenetic analyses. However, in many comparisons on the taxonomic levels of genera or families the complete *CR* might not generally be expected to be the most variable part of the mitochondrial genome.

The length of the *CR* slightly varies between some taxa in the genus *Garrulus*, ranging from 1 309 to 1 318 bp. This is quite large in comparison to other bird species, as according to Baker & Marshall (1997) the average length of the avian *CR* amounts to 1 168 bp. Yet, this length appears to be typical for corvid birds. In a comparison including 21 species of the family Corvidae *CR* lengths vary between 1 310 and 1 354 bp (Saunders & Edwards 2000) and it comprises 1 346 bp in *Urocissa erythroryncha* Boddaert, 1783 (Liu et al. 2018). In many bird species short tandem repeats can be observed in the 3'-third of the *CR*, often resulting in considerable intraspecific sequence length variation (Wenink et al. 1994; Berg et al. 1995; Gibbs et al. 1996; Mundy et al. 1996). This is not evident for the *Garrulus* jays and has not been reported for other corvid genera by neither Saunders & Edwards (2000) nor Haring et al. (2012) or Kryukov et al. (2017).

Phylogeny of the genus *Garrulus*

Phylogenetic trees including several outgroup taxa (Figure 6) (also see Appendix I.) support a comparatively close relationship between the genera *Garrulus* and *Pica*. Sequences of the latter taxon were already used to root phylogenetic trees of the genus *Garrulus* by Akimova et al. (2007) and Aoki et al. (2018). In the present study, a single *cytb* sequence of the Ethiopian Bush-Crow *Zavattariornis stresemanni* clusters with these two genera, concurring with the tree depicted in Jønsson et al. (2020). The phylogenetic position of this extraordinary Ethiopian endemic has for long been debated. Originally described as a corvid bird (Moltoni 1938), it has been suggested to be placed within the starling family Sturnidae (Benson 1942; Fry et al. 2000) or was considered to form a separate family on its own (Lowe 1949). Nevertheless, most authors have continued to treat it as a member of the Corvidae with suggested affinities to the genera *Podoces*, *Nucifraga* Brisson, 1760, *Pica* and *Garrulus* (cf. Amadon 1944; Ripley 1955; Goodwin 1976; Madge & Burn 1994), which was

supported by an initial genetic study (Ericson et al. 2005). The available *cytb* data now suggests that *Zavattariornis stresemanni* is the sister species of either the genus *Pica* or *Garrulus*, with further affinities to *Ptilostomus afer* and the genus *Podoces* (Figure 6).

Monophyly of the genus *Garrulus* is backed by the available *cytb* data (see Figure 6). Uncorrected genetic distances of more than 10.5 % for both analysed marker genes between the *G. glandarius* complex and the clade comprising the species *G. lanceolatus* and *G. lidthi* indicate that the genus *Garrulus* involves two very distinct mt lineages. Nevertheless, the placement of *G. lanceolatus* into an own genus as proposed by Kaup (1855) and Reichenow (1906, 1914) appears not practical, but has been "appreciated" by Hartert (1918), based on some plumage features, and tentatively approved by Sushkin (1927). Yet, many reversionary plumage aberrations recorded in different taxa of the *G. glandarius* complex (Horváth 1976; 1981) as well as vocal and behavioural similarities (Goodwin 1952) indicate a comparatively close relationship between *G. glandarius* and *G. lanceolatus*. The separation of the morphologically even more distinct *G. lidthi* into its own genus *Lalocitta* (cf. Reichenow 1906) has had more advocates (Hartert 1918; Kuroda 1926; Sushkin 1927; Jahn 1942). Sushkin (1927), who moreover suggested a New World origin of this species, referred to morphological differences to support his claim, while Jahn (1942) gave a detailed description of the peculiar nesting habits in tree cavities, but still noted many similarities with the Eurasian Jay. Both lines of reasoning have been dismissed by other authors, as the morphological differences do mainly concern plumage colouration (e.g. Goodwin 1976) and nesting in tree hollows has in exceptional cases also been recorded in *G. glandarius* (e.g. Tutt 1953; Haffer 1993). Genetic data confirms that *G. lidthi* represents the sister species of *G. lanceolatus*, as already presumed by Goodwin (1952, 1976) and Haffer (1993). The uncorrected genetic distances between the two species of about 6 % for both analysed marker sequences are only slightly above the range of genetic variation within the whole *G. glandarius* complex (cf. Tables 5, 6).

Phylogeny of the *Garrulus glandarius* complex

All the phylogenetic reconstructions implemented during this study clearly support the monophyly of the *Garrulus glandarius* complex (Figures 6-9). Total sequence variability of 4.5 % in *cytb* and 6.3 % in the *CR* data within the whole *G. glandarius* clade demonstrate the high amount of genetic variation within the complex. A clear subdivision into at least eight major clades is discernible, which mainly corresponds to the morphological subdivision into eight subspecies groups (cf. Stresemann 1940; Vaurie 1959; Haffer 1993; Madge 2009), but is also compatible with the division into ten groups applied in the present study.

In all the phylogenetic trees (Figures 6-9) the *japonicus* group forms the sister clade of the remainder of the complex, a result in line with the previous studies of Akimova et al. (2007) and Aoki et al. (2018). The inclusion of several samples of the *bispecularis* and *leucotis* group from the southeastern parts of Asia distinguishes the present study from the aforementioned. Although jays from these two groups fall into a distinct clade, they are not as well differentiated as the *japonicus* group and closer related to the remaining taxa of the complex. In consequence a split of each of these two groups into full species as proposed by del Hoyo & Collar (2016) would render the remaining species *Garrulus glandarius* (sensu del Hoyo & Collar 2016) polyphyletic based on mt DNA. The *brandtii* and the *hyrcanus* group as well do represent distinct mt lineages, which supports their respective separation into different subspecies groups. The remainder of the Western Palearctic taxa are comparatively closely related, which already has been suspected by Kuroda (1957) and Goodwin (1976), who have united the *glandarius*, *atricapillus* and *cervicalis* group into one western group. Nevertheless, each of these three groups forms a separate mt clade, which, together with their morphological distinctness, supports their placement into different subspecies groups.

Hence, it can be noted that, given the clear division of the *Garrulus glandarius* complex into several distinct lineages, its subdivision into major subspecies groups is well supported by mt genetic data. For the time being, this system appears to provide a realistic depiction of the genetic diversity within the *G. glandarius* complex. A more clinal geographic variation without a clear

separation into groups, as proposed by some authors (e.g. Keve 1939; Keve & Doncev 1967; Keve 1973) does not describe the true relations of diversity within the whole complex. Although there may exist broad areas with jays exhibiting clinal variation of some plumage features within some groups (e.g. Hartert 1918; Voous 1945, 1953, 1954; Austin & Kuroda 1953), mt DNA supports the existence of, by means of morphological examination, already by many ornithologists detected, evolutionary units above the level of subspecies within the *G. glandarius* complex.

Albeit such aggregates of subspecies could be formally described following Article 6.2. of the International Code of Zoological Nomenclature (ICZN 1999), this approach appears not suitable for the situation at issue, as it would concurrently determine species rank for the entire complex, which, as outlined throughout this work, is not altogether clear (e.g., proposed species rank for some groups).

Phylogenetic structure of subspecies groups within the *G. glandarius* complex

japonicus group

A clade comprising four sequences from the Japanese main islands Honshu and Kyushu matches with the *japonicus* group and differes considerably from all other taxa of the *G. glandarius* complex. Due to the low number of samples analysed in the present study only limited conclusions concerning the diversity within the group can be drawn. One individual from the island Kyushu, by some considered to be inhabited by a separate subspecies "*G. g. hiugaensis*", clusters between the samples from Honshu. This is in line with the results of Aoki et al. (2018), who analysed *cytb* and partial *CR* sequences of 25 individuals of the *japonicus* group, but did not include the fast-evolving domain I of the *CR*.

bispecularis group

The three sampled subspecies of this group *G. g. bispecularis*, *G. g. sinensis* and *G. g. taivanus* each display distinct mt lineages. The differentiation between these subspecies is higher than between most Western Palaearctic subspecies groups (see Tables 5, 6). This considerable genetic diversity is in strong contrast to the morphological uniformity of the *bispecularis* group (Goodwin 1976; Madge 2009).

The subspecies *G. g. taivanus* from the island Taiwan is, besides *G. g. japonicus*, the genetically most distinct subspecies of the whole complex. These genetic structures indicate long lasting isolation of several representatives of the group, although presently the *bispecularis* group is supposed to have a continuous distribution range and all mainland subspecies seem to be connected through intermediate birds (Hartert 1918; Keve 1939). The sampling in the present study covered only two of these subspecies from both ends of the range of the *bispecularis* group, *G. g. bispecularis* from the western Himalayas and *G. g. sinensis* from eastern China. A more complete coverage including jays from localities in between the aforementioned would be needed to clarify the exact distribution of the already detected mt lineages and whether even additional genetically distinct subspecies exist.

leucotis group

Quite surprisingly, the two samples of the subspecies *G. g. leucotis*, which often has even been regarded as a separate species (e.g. Hartert 1918; Baker 1922; del Hoyo & Collar 2016), cluster within the individuals of the *bispeclaris* group. Moreover, the fact that the two samples do not cluster closely together, but seem to represent two different mt lineages, appears even more puzzling. As the sampled specimens had been collected in central Myanmar in peripheral parts of the subspecies distribution range, close to a putative intergradation zone with the *bispecularis* group (Blacke & Vaurie 1962), several explanations are possible:

1) The *leucotis* group is closely related to the *bispecularis* group and at the same time exhibits considerable variation between its own representatives.

2) One of the sampled individuals is an intergrade with a member of the *bispecularis* group and carries the mt DNA of a representative of the *bispecularis* group currently not covered by the sampling. The other individual represents the mt lineage of *G. g. leucotis* which is very closely related to the *bispecularis* group.

3) Both sampled individuals are intergrades but with different representatives of the *bispecularis* group, carrying their respective mt DNA. This would mean that

the authentic mt lineage of *G. g. leucotis* has not been detected in the present study.

4) The *leucotis* group does presently not possess a distinct mt lineage but might have had so in the past. Large scale introgression of mt DNA from the adjacent *bispecularis* group replaced this formerly unique mt lineage.

Based on the results of the present study concerning other groups and subspecies of *G. glandarius* explanation 1) appears least probable. Taxa with comparatively small to medium sized distribution areas that exhibit distinct mt lineages usually exhibited only weak genetic differentiation between different individuals. As the morphological differentiation between *G. g. leucotis* and the *bispecularis* group is very pronounced and include plumage features as well as some biometric measurements explanation 2) does not seem reasonable as well.

This leaves explanations 3) and 4) as probable reasons for the lack of a distinct mt lineage of *G. g. leucotis* in the present study. Both explanations presuppose that interbreeding between jays of the *leucotis* group and the *bispecularis* group does occur where the breeding distribution areas of these groups come into contact in northern Myanmar. This has been widely acknowledged on the basis of individuals with intermediate characters (Baker 1922; Keve 1939; Blake & Vaurie 1962; Goodwin 1976; Dickinson et al. 2004a; del Hoyo & Collar 2016). As they seem to occur in comparatively large areas in the contact zone of the two subspecies groups, they even led to the description of still widely recognised subspecies (e.g. *G. g. oatesi*, *G. g. haringtoni*).

To test these hypotheses, individuals from the central and southern areas of the distribution range of the *leucotis* group need to be sampled. If they represent a distinct mt lineage, the two individuals sampled in the present study are very likely the result of recent interbreeding with jays of the *bispecularis* group. When mt sequences then still cluster with the *bispecularis* group, additionally nuclear markers could be used to test for mitochondrial introgression after secondary contact. This phenomenon is scarce in birds but has been suggested for some Palaearctic taxa (e.g. Irwin et al. 2009). If nuclear markers, with adequate substitution rates, reveal no differentiation of the *leucotis* group, explanations 1) and 2) might again be considered.

brandtii group

Jays belonging to the *brandtii* group form a very distinct clade within the *G. glandarius* complex. Eight individuals from the Asiatic mainland cluster together. Although the sampling covered the full west-east expanse of the distribution range from the Urals to the Far East, individuals do not cluster corresponding to their geographic origin. This would oppose the sometimes raised doubts about the degree of genetic distinctness of the *brandtii* group as a whole (cf. Shirihai & Svensson 2018), as previous genetic studies only sampled birds of this group from the Russian Far East (Akimova et al. 2007; Aoki et al. 2018). A sequence of a jay assigned to the presumed "hybrid"-subspecies "*G. g. sewerzowii*" clusters within the *brandtii* clade. As the sample was collected in the Russian Kirov region in January, it documents that birds with mt DNA of *G. g. brandtii* can at least in winter occur far west into European Russia.

Jays from two Far Eastern islands revealed to form separate clusters in haplotype networks of the *CR* dataset. Samples from individuals collected on the Russian Sakhalin island (described as "*G. g. taczanowskii*") differ only slightly from those of the mainland. More individuals would be needed to verify the genetic distinctness of this form. *CR* sequences of Jays from the northernmost Japanese main island Hokkaido ("*G. g. pallidifrons*") differ considerably from individuals from the Asiatic continent and the geographically close Sakhalin island. A weak genetic differentiation of the Hokkaido jays was already recorded by Aoki et al. (2018), who discussed a possible independent refugium on Hokkaido during the last glacial period. Interestingly, the differentiation of both island forms is only visible in the *CR* dataset and nearly all diagnostic substitutions occur in domain I. In the *cytb* dataset these island forms share their respective haplotypes with various individuals of mainland origin. These results nicely illustrate the suitability of the *CR*, especially its hypervariable domain I, for phylogenetic inferences on the level of subspecies and populations.

hyrcanus group

The mt genetic distinctness of this poorly known subspecies was revealed on the basis of two specimens originating from the Lankaran area in present-day Azerbaijan, which clearly exhibit the morphological features of this subspecies

(referring to Blanford 1876; Keve & Doncev 1967; Shirihai & Svensson 2018; see Appendix II). At the southwestern coast of the Caspian Sea, the distribution areas of the *hyrcanus* group and the *atricapillus* group overlap. Birds with varying intermediate characters between these two groups have been recorded in this area, which were described as "*G. g. caspius*" (Buturlin & Dementiew 1933; Dementiev & Gladkov 1970; Keve 1973; Shirihai & Svensson 2018). The two intermediate birds analysed in the present study cluster within the *atricapillus* clade. The fact that these jays with intermediate characters exist in this region, but according to their mt DNA cluster with one of the accepted subspecies, strongly suggests that these birds are indeed intergrades.

Western clade

A comparatively close relationship of the western Palearctic subspecies groups was already suggested by Kuroda (1957) and Goodwin (1976) based on morphological data. Consequently, they unified the *glandarius*, *atricapillus* and *cervicalis* group into one western group, named *glandarius* group, which however was not widely accepted. Although this close relationship is confirmed by genetic data of the present study, as well as by Akimova et al. (2007) and Aoki et al. (2018), each of these three groups still represents a distinct monophyletic entity.

atricapillus group

Within this clade, mainly corresponding to the *atricapillus* group, a clear subdivision can be observed. The three main subspecies of the group *G. g. atricapillus*, *G. g. anatoliae* and *G. g. krynicki* are each identifiable on the basis of *CR* sequences. A particularly strong differentiation exists between jays from the Caucasus (*G. g. krynicki*) and the remaining subspecies of the group. This could be explained by an independent refugium in the Caucasus during the glacial period. Besides the recognised subspecies two specimens from the island Rhodes ("*G. g. rhodius*") yield separate haplotypes closely related to *G. g. anatoliae*. In line with the results of Akimova et al. (2007) a total of five samples from the Crimean Peninsula assigned to the subspecies *G. g. iphigenia*, which is usually placed in the *atricapillus* group, cluster with the *glandarius* group instead.

As no morphological data regarding the sampled individuals exists it is difficult to interpret these surprising results (see below).

Another interesting result is that sequences from a specimen of the subspecies *G. g. ferdinandi* from European Turkey cluster within the *atricapillus* clade. This subspecies is usually included in the *glandarius* group as it is very similar the nominate form (Keve & Doncev 1967; Rokitansky & Schifter 1971). The fact that a jay exhibiting morphological characters of the *glandarius* group clusters genetically with the *atricapillus* group could be interpreted as a result of interbreeding between these groups. This has been suggested to be the reason for the occurrence of birds exhibiting mixed plumage features between these two groups in the Bosporus area (Roselaar in Cramp & Perrins 1994; Roselaar 1995). However, *CR* and *cytb* sequences of this individual cluster within the well-defined Caucasian clade, which considerably complicates this otherwise conclusive interpretation. If the specimen information can be considered reliable, at least two explanations might be considered. (1) The separation of the Caucasian clade within the *atricapillus* clade could be a sampling artefact created by the low number of analysed individuals. This is deemed very unlikely due to the comparatively high amount of differentiation in the *CR* dataset. Another explanation could be that (2) the black-headed Caucasus jays once had a more extensive distribution range along the northern and western coast of the Black Sea. This is illustrated in old distribution maps from Wallace (1880) and Kuroda (1957), while Dombrowski (1912) recorded dark-capped jays similar to the Turkish subspecies in southeastern Romania. Even though the plumage feature of the black cap may have been lost in many individuals of this region they still could carry mt DNA of their ancestors. A sample of a Jay collected in the plains of the Russian Rostov oblast in May (Gggk-1) exhibiting a Caucasian haplotype, indicates that individuals with mt DNA of the Caucasus subclade of the *atricapillus* clade can be recorded far north of the acknowledged distribution range even during the breeding period. Together with the surprising clustering of the Crimean samples, these results highlight the need for a detailed combined genetic and morphological study of the Jays around the Black Sea.

Sequences of two specimens from Azerbaijan ("*G. g. caspius*") cluster within the *atricapillus* clade. As these birds exhibit intermediate plumage features between

jays of the *atricapillus* group and the subspecies *G. g. hyrcanus*, this indicates successful interbreeding between these two groups. One of these presumed intergrades clusters within the Caucasus clade, but the second yields a quite distinct haplotype similar to *G. g. anatoliae*. This could point towards the existence of another distinct mt lineage within the *atricapillus* group. A possible candidate could be the population of the Iranian Zagros Mountains, described as "*G. g. susianae*" Keve, 1973. It furthermore illustrates that *G. g. hyrcanus* might interbreed with individuals of two quite distinct lineages of the *atricapillus* group at the southwestern coast of the Caspian Sea.

cervicalis group

Three specimens of the North African subspecies *G. g. cervicalis* yield sequences which form a separate clade close to the nominate *glandarius* group. The finding that two samples from Tunisia cluster separately from an Algerian one for both genetic markers underline that different mt lineages exist in northern Africa. This assumption is backed by a considerable number of subspecies described from different localities of the Atlas mountain range (Hartert 1895; Parrot 1907; Vaurie 1954). Morphologically particularly distinct are jays from the western part of the Atlas Mountains (*G. g. minor*, *G. g. whitakeri*). These birds resemble those of the European *glandarius* group, from which they are separated by the Strait of Gibraltar but share some features with the black-capped *G. g. cervicalis*. In consequence, their exact affinities are debated. While some included these jays in the European *glandarius* group (Stresemann 1940; Voous 1953), others placed them in the *cervicalis* group (Vaurie 1954, 1959; Keve 1969; Haffer 1993; Madge 2009) or proposed to arrange them into a separate group (Roselaar in Cramp & Perrins 1994; Shirihai & Svensson 2018; this study). Unfortunately, no specimens from this area have been available for analysis.

glandarius group

The numerous subspecies of the European *glandarius* group have been comparatively well covered in the present study. Interestingly, no consistent clustering according to subspecies affiliation or geographic origin can be observed in samples from the European mainland. This could be interpreted to support the morphological results of Vaurie (1954) and Shirihai &

Svensson (2018) that variation on the European continent is mainly clinal and only a certain percentage of individuals can be confidently assigned to described subspecies. Yet, Vaurie (1954) was able to detect certain discontinuities of clinal plumage variation, which were attributed to isolation in different refugia during the Pleistocene glaciations. Specifically, an Iberian refugium as well as a second refugium comprising the Balkan and Italian peninsulas were proposed. Genetic data from the present study shows no such division, as neither samples of the Iberian subspecies *G. g. fasciatus* nor jays of the Balkan subspecies *G. g. albipectus* and *G. g. graecus* do cluster together. Instead they are scattered between samples from central Europe and European Russia. In combination with the high genetic diversity within the *glandarius* clade, this pattern could suggest that isolation into different glacial refugia did not last for periods long enough to be detectable with mt DNA sequence data (cf. Avise & Walker 1998).

In addition, migration could have considerably affected the outcome of the present study. While at least parts of the populations of Europe perform annual migration movements in autumn (Gatter 1974; Haffer 1993; Cramp & Perrins 1994), in some years large scale influxes, so-called invasions, evasions, eruptions or irruptions, of jays of north-easterly origin occur (Küchler 1932; Gatter 1974, 2000; Zink 1981; Heine et. al. 1999). The whereabouts of these birds are not yet completely understood (Gatter 1974; Haffer 1993). Considerable return passage after evasions suggests that many birds migrate back to their respective breeding grounds (Küchler 1932; Geyr von Schweppenburg 1956; Gatter 1974; 1977; Posse 1999; Armbruster et al. 2005). But it is not clear if, or to what extent, birds which migrated southwards in autumn do stay in their respective winter quarters in central or southern Europe for breeding with local birds in subsequent seasons. Such behaviour could lead to considerable gene flow between populations in Europe, especially after large scale evasions. Moreover, as autumn migration starts at the end of August and spring migration does continue throughout May (Küchler 1932; Gatter 1974, 2000; Werner et al. 2020), jays collected within this timespan could, at least in Europe, add considerable noise to the results of genetic studies. Based on ringing results it was estimated that a third of the jays present in Czechia and Slovakia in the winter months had been of foreign origin (Cepák et al. 2008). In the present

study many individuals collected outside of the months June and July are included, thus the results concerning the population structure within Europe could have been affected by such migrating individuals.

In contrast to the sampled jays from the European mainland, individuals from different Mediterranean islands as well as most individuals from the English subspecies *G. g. rufitergum* cluster according to their geographic origin. While the subspecies *G. g. corsicanus* from Corsica and *G. g. ichnusae* from Sardinia are only slightly differentiated, two individuals of *G. g. cretorum* from Crete exhibit a very distinct haplotype in the *CR* dataset, suggesting a long-lasting isolation of this subspecies. Interestingly, the differentiation of this subspecies was much less pronounced in the *cytb* dataset.

Sequences of the five individuals from the Crimean Peninsula cluster within the *glandarius* clade. Morphologically, the local subspecies *G. g. iphigenia* is by all authors included in the black-capped *atricapillus* group. Unfortunately, no morphological data for these individuals is available, as only muscle tissue was provided. The fact that the five individuals clustered together in all phylogenetic reconstructions could indicate that indeed local breeding birds were sampled. However, in the winter half-year of 2004/05, when all but one of these individuals have been sampled, a major irruption occurred in large parts of Europe (e.g. Maumary et al. 2007; Dierschke et al. 2011; Teufelbauer et al. 2017; Chylarecki et al. 2018). It can therefore not fully be excluded that the sampled birds originate from more northern breeding grounds.

glaszneri group

Usually placed in the nominate *glandarius* group (e.g. Haffer 1993; Madge 2009), the peculiarity of this subspecies from the island of Cyprus has already been noted by some authors (Keve 1969; Roselaar in Cramp & Perrins 1994; Shirihai & Svensson 2018). Mt genetic data indicates that it is not closely related to the *glandarius* group but constitutes the most distinct mt lineage within the "western clade" and does therefore warrant a separate group. These results would support the idea that it represents an isolated relict of a formerly more widespread form (Roselaar in Cramp & Perrins 1994).

Evolutionary history

Most authors have proposed an origin of the *Garrulus* jays in the tropical rainforests of Southeast Asia (Sushkin 1927 except for *G. lidthi*; Keve 1969; Ericson et al. 2005; Finlayson 2011). Out of this area they presumably had spread across the Palearctic into cooler and drier habitats (Ericson et al. 2005), allegedly assisted by the uplift of the Himalayan-Tibetan plateau, but still retained their forest-dwelling habits (Finlayson 2011). The two species *G. lanceolatus* and *G. lidthi* had become isolated in the Himalayas and the Ryu Kyu Islands respectively, while one dominant species *G. glandarius* had occupied wooded areas across the Palearctic (Finlayson 2011).

Initial genetic studies of the genus *Garrulus* have been interpreted to support the hypothesis of a Southeast Asian origin of the genus, as the most distinct mt lineages had been found in eastern Asia (Ericson et al. 2005; Akimova et al. 2007). The taxonomically more complete dataset of the present study allows a re-evaluation of these hypotheses. In the constructed phylogenetic trees, the succession of the splits within the *G. glandarius* complex does almost exactly follow an east-west gradient (Figures 6-9), with the most distinct lineages in eastern Asia and less well distinguished lineages in the Western Palearctic (Tables 5, 6). Furthermore, the two species forming the sister clade of the complex are confined to distribution areas in the eastern half of Asia. Simply following Darwin's "centres of creation" concept (Darwin 1859; Bremer 1992), these findings would support an evolutionary origin of the genus *Garrulus* in southeastern parts of Asia.

The analysis of the *cytb* dataset including several outgroup taxa points towards a more entangled biogeographical history than outlined above. If the genus *Garrulus* had evolved directly out of tropical Southeast Asia, it would be expected that its next relatives were to be found in this area. The available genetic data shows that the corvid genera which are (still) confined to the (sub-) tropical forests of the Oriental region (*Crypsirina* Vieillot, 1816, *Temnurus* Lesson, 1831, *Platysmurus* Reichenbach, 1850, *Dendrocitta* Gould, 1833, *Cissa* Boie, 1826, *Urocissa* Cabanis, 1851) form the sister group of the remainder of the family Corvidae (except *Pyrrhocorax* Tunstall, 1771) but have no close affinities to

the *Garrulus* jays (Ericson et al. 2005; Fernando et al. 2017). Although this pattern could support a Southeast Asian origin of the whole family Corvidae (but note the position of *Pyrrhocorax*), this might not necessarily hold for the genus *Garrulus*. *Platylophus galericulatus* Cuvier, 1816, a jay-like bird from Southeast Asia, with a distribution range adjacent to that of the *G. glandarius* complex (cf. Madge & Burn 1994, Madge 2009), does exhibit some similarities with the species of the genus *Garrulus* (Amadon 1944), but initial genetic data indicated that it might not belong to the family Corvidae at all (e.g. Jønsson et al. 2012). Moreover, it appears counterintuitive that no *Garrulus* jays do exist on the Indian subcontinent, the Malay Peninsula and the Sunda Islands, although the latter were repeatedly connected with continental Southeast Asia over the last 250 000 years (cf. Voris 2000) as well as in the Miocene and early Pliocene (Hall 2013)

According to mt DNA, the genus *Garrulus* clusters in a clade which comprises the genera *Pica*, *Zavattariornis*, *Ptilostomus* and *Podoces* (Appendix I.; cf. Ericson et al. 2005; Fernando et al. 2017), that inhabit arid open landscapes of Asia, Africa and North America (Madge 2009). The *Garrulus* species are the only forest-dwelling taxa within this clade. Conveniently, the Himalayan species *G. lanceolatus*, which has by some been regarded as a relictual form of a formerly more widespread ancestor of the *Garrulus glandarius* complex (e.g. Goodwin 1952, Horváth 1976), does occur in comparatively open woodlands (Goodwin 1976, Madge 2009). Even though the ancestor of the whole assemblage of aridity-adapted corvids might had initially dispersed out of tropical Southeast Asia, the generic radiation within this assemblage probably took place along the mid-latitude belt (cf. Finlayson 2011). The emergence of the savanna and desert inhabiting corvid genera *Pica*, *Podoces*, *Ptilostomus* and *Zavattariornis* could be attributed to the cooling (cf. Zachos et al. 2001) and general aridification of Eurasia and Africa which at the latest commenced in the early Miocene about 20 million years ago (Mya) (Jacobs et al. 1999; Guo et al. 2002) and further intensified around 14 Mya (Flower & Kennett 1994;) and 8 Mya (Quade et al. 1989; Cerling et al. 1997). The separation between the *Garrulus glandarius* complex and the other two *Garrulus* species was dated to about 8 Mya by Aoki et al. (2018), which coincides with a global vegetation change towards more open habitats (cf. Cerling et al. 1997). Within the closely related genus *Pica* the

spatial separation between the North African lineage and the remainder of the genus was suggested to have occurred about 5 Mya (Song et al. 2018). The presently wide geographic spread of the different genera of this assemblage of aridity-adapted Corvidae from the Sahel zone to North America, combined with the suggested early splits within the genera *Garrulus* and *Pica* at the opposite ends of Eurasia, could indicate that also the possible common ancestor of the whole assemblage, as suggested for the genus *Garrulus* by Wallace (1880) and Goodwin (1952), already had a wide Eurasian distribution area. Fossil remains from the middle Miocene assigned to the extinct *Miocorvus larteti* (Milne-Edwards, 1871), similar in dimensions to modern *Garrulus glandarius*, have been found in various localities across Europe (Gál & Kessler 2006; Kessler 2020) and could be interpreted in favour of these assumptions.

Based on the available genetic data as well as the mentioned biogeographic, ecological, geological and paleontological aspects, the geographic origin of the present genus *Garrulus* can therefore at the moment not be restricted to tropical Southeast Asia, it might as well have had emerged in more northern regions of Eurasia. In this light, the current biogeographical pattern of the genus *Garrulus* could rather reflect the distribution of ancient woodland refugia and not a comparatively recent radiation out of tropical Southeast Asia.

Taxonomic conclusions

The results of the present study clearly show that the morphological subspecies groups are the main entities of mt genetic diversity within the *G. glandarius* complex and are monophyletic in most of the phylogenetic trees. Additionally, within the groups, many subspecies form separate haplotype clusters. In recent years several authors have indicated that some of the subspecies groups could warrant species status (e.g. Helbig 2005; Shirihai & Svensson 2018). The decision of del Hoyo & Collar (2016) to split just the *bispecularis* and the *leucotis* group each into separate species is not supported by the available mt genetic data, because it would render the remainder of *Garrulus glandarius* polyphyletic, owing to the strong genetic differentiation of the *japonicus* group. Genetic distances between the *japonicus* group and the remaining taxa of the *G. glandarius*

complex are only slightly lower than between the two other species of the genus *G. lanceolatus* and *G. lidthi*. Several more Asiatic subspecies groups have reached levels of mt genetic differentiation which are in the range of those between many closely related species within the family Corvidae (cf. Haring et al. 2012; Cohn-Haft et al. 2013; and with circumspection Ericson et al. 2005).

Nevertheless, both morphological as well as genetic data imply that the taxa of the *G. glandarius* complex share a common evolutionary origin and the subspecies groups are basically different geographic counterparts with probably parapatric or slightly overlapping distribution ranges. Successful interbreeding seems to occur regularly wherever individuals of different groups come into contact (Stresemann 1940; Vaurie 1959; McCarthy 2006). However, no detailed studies investigating the extent of interbreeding and possible gene flow in any contact zone exist, making a thorough evaluation difficult. For example, strongly differing reports about the extent of the most often mentioned contact zone between the European *glandarius* group and the Asiatic *brandtii* group have been published. According to Voous (1945, 1953) and Harrison (1982) it stretches across whole European Russia, while Shirihai & Svensson (2018) in line with Wallace (1880) limit it to the eastern half of European Russia and others have stated that intergradation is restricted to a narrow area at the western foot of the Ural Mountains (Laubmann 1914; Stresemann 1919; Keve 1966; Dementiev & Gladkov 1970; Dickinson & Christidis 2014). Assessing the frequency of intergrades between groups might also be impeded by the possibility that they could be overrepresented in many museum collections, as their variable morphology often led to the description of new taxa. Together with the fact that possible differences in vocalisations between some subspecies groups (cf. Goodwin 1952; Ali & Ripley 1987; Boesman 2016) have not been studied in-depth, these uncertainties hinder a comprehensive taxonomic re-evaluation of the *G. glandarius* complex.

Splitting of distinct forms with restricted ranges into species, although from a taxonomical and conservational point of view disputed, has been used for decades as a tool to increase conservation efforts (cf. Hazevoet 1996; Collar 1997; Gamauf et al. 2005; Peterson 2006; Pratt 2010; Raposo et al. 2017). All the three species (sensu del Hoyo & Collar 2016) of the *G. glandarius* complex are currently

not considered globally threatened. The present study indicates that two morphologically strong differentiated island subspecies, *G. g. glaszneri* from Cyprus and *G. g. taivanus* from Taiwan represent very distinct mt lineages. Although interbreeding with adjacent forms is very unlikely in both cases, splitting of these subspecies into species appears premature, especially considering that it would have far reaching consequences for the taxonomic status of many more taxa within the *G. glandarius* complex. To maintain the monophyly of the *glandarius* group, the subspecies *G. g. glaszneri* should be treated as a separate informal subspecies group. This would furthermore highlight its considerable genetic and morphological differentiation and could raise awareness regarding conservation issues of this every so often unappreciated island endemic. Assuming species status for the Cyprus Jay *G. g. glaszneri*, this would probably lead to its classification as a globally threatened species (cf. IUCN 2012), considering that forest fragmentation (Hellicar et al. 2014), corvid shooting (Hadjisterkotis 2003) and illegal bird trapping (Birdlife Cyprus 2020) might still represent major conservation issues on this small island. For conservation purposes it might therefore be advisable to treat the subspecies groups of the *G. glandarius* complex and *G. g. taivanus*, which might warrant an own group as well, as Evolutionary Significant Units (cf. Moritz 1994; Avise 1989).

For the time being at least, considering the available genetic data and the various systematic uncertainties it might be suggested to continue to treat the *Garrulus glandarius* complex as one species comprised of several informal groups of subspecies. As not all taxa of the complex were covered by the present study and many subspecies and groups were represented by just one or two individuals, it appears inappropriate to proclaim far reaching taxonomic changes. Further studies could analyse even more sampled specimens per taxon from geographically more widespread locations. Of special interest would be the genetic identity of the *leucotis* group and *G. g. minor* as well as the extent of interbreeding and gene flow between subspecies groups.

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Appendix I

Searching for the sister taxon of the genus *Garrulus*

A phylogeny of the family Corvidae based on *cytochrome b* sequence data

To reliably test for monophyly in molecular phylogenetic studies a complete taxon sampling (Graybeal 1998; Johnson 2001) as well as an appropriate outgroup (Smith 1994; Grant 2019) are essential. Previous genetic studies of the Corvidae provide only limited insights (Cibois & Pasquet 1999) or depict slightly varying phylogenetic positions of the genus *Garrulus* (Ericson et al. 2005; Kennedy et al. 2012; Fernando et al. 2017; Liu et al. 2018). A phylogenetic tree of the family Corvidae was therefore constructed specifically for the present study, to determine the best-suited outgroup sequences available for the *cytb* dataset.

Cytb sequences from all the corvid taxa available on GenBank as well as from three outgroup taxa were selected for the analysis (Table I). The alignment contains 151 sequences of 78 species (taxonomically following Dickinson & Christidis 2014) and has 1 143 positions. Following the determination of the best-fitting substitution model independently for each codon position with the programme jModelTest 2.1.7 (Darriba et al. 2012), the settings nst=6 rates= invgamma were applied for all codon positions for BI analysis with MrBayes 3.2.7 (Ronquist et al. 2012). Starting from random trees, two independent runs each consisting of 20×10^6 generations of four Markov chain Monte Carlo chains were performed and sampled every 100 generations. After checking of the output, the first 500 000 generations were discarded as "burn-in".

The resulting phylogenetic tree (Figure I) reveals that the genus *Garrulus* clusters in a clade with the taxa *Pica*, *Zavattariornis stresemanni*, *Ptilostomus afer* and *Podoces*. Although this clade is poorly supported, the surrounding nodes exhibit high posterior probability values, thereby supporting the assumption that this assemblage represents close relatives of the genus *Garrulus*. In consequence, nine *cytb* sequences of these taxa were added to the *cytb* dataset of the genus *Garrulus* as outgroups.

Figure I. Phylogeny of the family Corvidae in form of a Bayesian 50 % majority-rule tree based on 151 *cytb* sequences (1143 alignment sites) of 78 species. Posterior probability values of the major nodes are shown.

Table 1. *Cytb* sequences with GenBank accession numbers (GB-Nr.) used for the present phylogenetic tree of the family Corvidae.

Species	GB-Nr.	Species	GB-Nr.	Species	GB-Nr.
Platysmurus leucopterus	KY492612	*Pica nutalli*	MG640808	*Aphelocoma woodhouseii*	HQ123846
Temnurus temnurus	AY395626	*Nucifraga columbiana*	KF509923		HQ123849
Crypsirina temia	AY395618	*Nucifraga caryocatactes*	JQ864510		HQ123853
Dendrocitta formosae	MK875763		KJ456365		HQ123855
Dendrocitta cinerascens	KY492611		U86041		HQ123857
Dendrocitta frontalis	JQ864495	*Corvus monedula*	KJ456237		HQ123859
Pyrrhocorax pyrrhocorax	JQ864523		U86033		HQ123860
	KY378773	*Corvus ossifragus*	HQ535807	*Aphelocoma insularis*	HQ123829
	U86044	*Corvus hawaiiensis*	AY005928	*Aphelocoma californica*	U77335
Pyrrhocorax graculus	NC025927	*Corvus frugilegus*	Y16885	*Cyanocitta cristata*	X74258
	JQ864522	*Corvus albicollis*	AY527263	*Cyanocitta stelleri*	AY030113
Urocissa caerulea	NC037486	*Corvus corax*	AY527266		EU075428
Urocissa erythroryncha	KJ456508		AY527269		EU075438
	U86038		JQ864490	*Cyanocorax violaceus*	GU144879
	NC020426	*Corvus cryptoleucus*	AY527265		GU144881
Cissa chinensis	JQ864486	*Corvus ruficollis*	KY378740	*Cyanocorax cyanomelas*	GU144858
	U86037	*Corvus albus*	AY527262	*Cyanocorax cristatellus*	GU144883
Cissa thalassina	KY492609	*Corvus brachyrhynchos*	AY030112	*Cyanocorax caeruleus*	GU144878
Perisoreus canadensis	U77331	*Corvus caurinus*	EF210778	*Cyanocorax morio*	DQ912593
	AY509654	*Corvus corone*	HE805700		AY395625
Perisoreus infaustus	U86042		HE805701	*Cyanocorax colliei*	DQ912591
Perisoreus internigrans	AY395621		HE805754	*Cyanocorax formosus*	U77336
Cyanopica cyanus	AY701174	*Corvus pectoralis*	MN310552	*Cyanocorax yncas*	KJ456245
	AY701177	*Corvus moneduloides*	CM018859		GU144888
	AY701180	*Corvus orru*	FJ498999		GU144889
	AY701181		FJ499000	*Cyanocorax mystacalis*	GU144872
	KT934323	*Corvus coronoides*	AF197837		GU144874
Garrulus glandarius	AB239527	*Corvus splendens*	JQ864493	*Cyanocorax dickeyi*	GU144886
	AB242559		KY018671		GU144887
	EF602122	*Corvus macrorhynchos*	HE805911	*Cyanocorax affinis*	GU144867
	LC332889		HE805915		GU144869
	LC332917	*Corvus kubaryi*	AY005930	*Cyanocorax heilprini*	GU144875
Garrulus lanceolatus	JQ864504	*Cyanolyca mirabilis*	DQ912592	*Cyanocorax cyanopogon*	GU144876
Garrulus lidthi	U86035	*Cyanolyca viridicyanus*	U77333		GU144877
Zavattariornis stresemanni	AY395627	*Gymnorhinus cyanocephalus*	U77332	*Cyanocorax chrysops*	GU144863

Ptilostomus afer	U86040		AY030115		GU144865
Podoces hendersoni	GU592504	*Aphelocoma unicolor*	HQ123865	*Cyanocorax cayanus*	GU144854
	AY395624		HQ123868		GU144856
Podoces biddulphi	AY395623		HQ123871	*Cyanocorax melanocyaneus*	GU144897
Pica pica	KJ456399		HQ123873	*Cyanocorax sanblasianus*	GU144893
	AY701184		HQ123877		GU144894
	AY701185	*Aphelocoma ultramarina*	HQ123803	*Cyanocorax beecheii*	GU144895
	MG640712		HQ123814		GU144896
	MG640744		HQ123818	*Corcorax melanoramphos*	AY064274
	MG640750		HQ123824	*Melampitta lugubris*	AY443253
	MG640762		HQ123825	*Megalampitta gigantea*	AY443252
	MG640820	*Aphelocoma wollweberi*	HQ123810		
Pica hudsonia	MG640818	*Aphelocoma coerulescens*	HQ123862		
			HQ123863		

Appendix II

Photographic documentation of the sampled museum specimens of the genus *Garrulus*

The remarkable geographic variation of plumage features in the *Garrulus* jays, especially within the *Garrulus glandarius* complex, has fascinated ornithologists for centuries, resulting in a mass of publications. Important contributions came from O. Kleinschmidt, with a deep delve into the individual variation of the European jays (Kleinschmidt 1893), a topic further investigated by K. Voous in a detailed study of the clinal variation of plumage colouration in Europe (Voous 1953). The most papers devoted to the geographical variation of *Garrulus glandarius* probably have been written by A. Keve. An extensive review comparing the numerous forms of the Eurasian Jay and including descriptions of several new subspecies (Keve 1939) has been followed by articles on the taxonomy of the jays of the Balkan Peninsula (Keve & Doncev 1967) and the Middle East (Keve 1973) amongst others, as well as a monograph of *G. glandarius* (Keve 1969). Further notable contributions came from C. Parrot and C. J. Vaurie respectively, with synopses including many of the Palaearctic forms (Parrot 1907; Vaurie 1954). In addition, some handbooks contain extensive sections on the morphological variation of the jays of the genus *Garrulus*, for instance "Die Vögel der Paläarktischen Fauna" (Hartert 1910), "The Birds of the Western Palearctic" (C.S. Roselaar in Cramp & Perrins 1994) as well as the "Handbook of Western Palearctic Birds" (Shirihai & Svensson 2018).

The following pages do not claim to provide a systematic morphological re-examination of the *G. glandarius* complex, which is long overdue and would have to include many of the type specimens as well. It is a commented photographic documentation of the specimens in the NMW examined during the present genetic study, focused on plumage features essential for identification. Of each of the individuals a photograph showing a lateral view from a slightly elevated position is presented. It has been endeavoured to include all the important plumage features in one picture. Therefore, the bird's crown, the head side, parts of the upperside, the wing as well as parts of the breast and flank should be

visible. Keep in mind that the photographs have been taken on six different occasions between 14.11.2018 and 23.09.2019 under slightly varying light conditions. In the text it has therefore been attempted to focus on general plumage patterns and not on slightly differing colour hues.

Eurasian Jay *Garrulus glandarius* (Linnaeus, 1758)

glandarius group

The various subspecies of the *glandarius* group share a white forecrown with black streaks and a white secondary patch (Goodwin 1976; Madge & Burn 1994), while the colouration of most of the remaining body plumage varies considerably depending on the geographic origin (Voous 1953). The bill is entirely dark, extent and size of the black crown-streaks are very variable (Kleinschmidt 1893).

Garrulus glandarius glandarius (Linnaeus, 1758)

Gglagla-86, NMW 22 956, Poland, Warmia-Masuria, 04.06.1898

The nominate form is probably the most variable of all the subspecies of *Garrulus glandarius* (Shirihai & Svensson 2018). In the specimen Gglagla-86 the rufous neck is quite sharply demarcated from the greyish-brown mantle, which also applies for the transition between the clean white area on the throat and the brown breast. The crown-streaks are comparatively narrow in this individual and the mantle exhibits almost the same colour tone as the underparts. Unfortunately, no birds from the apparent type locality in Sweden have been available for comparison.

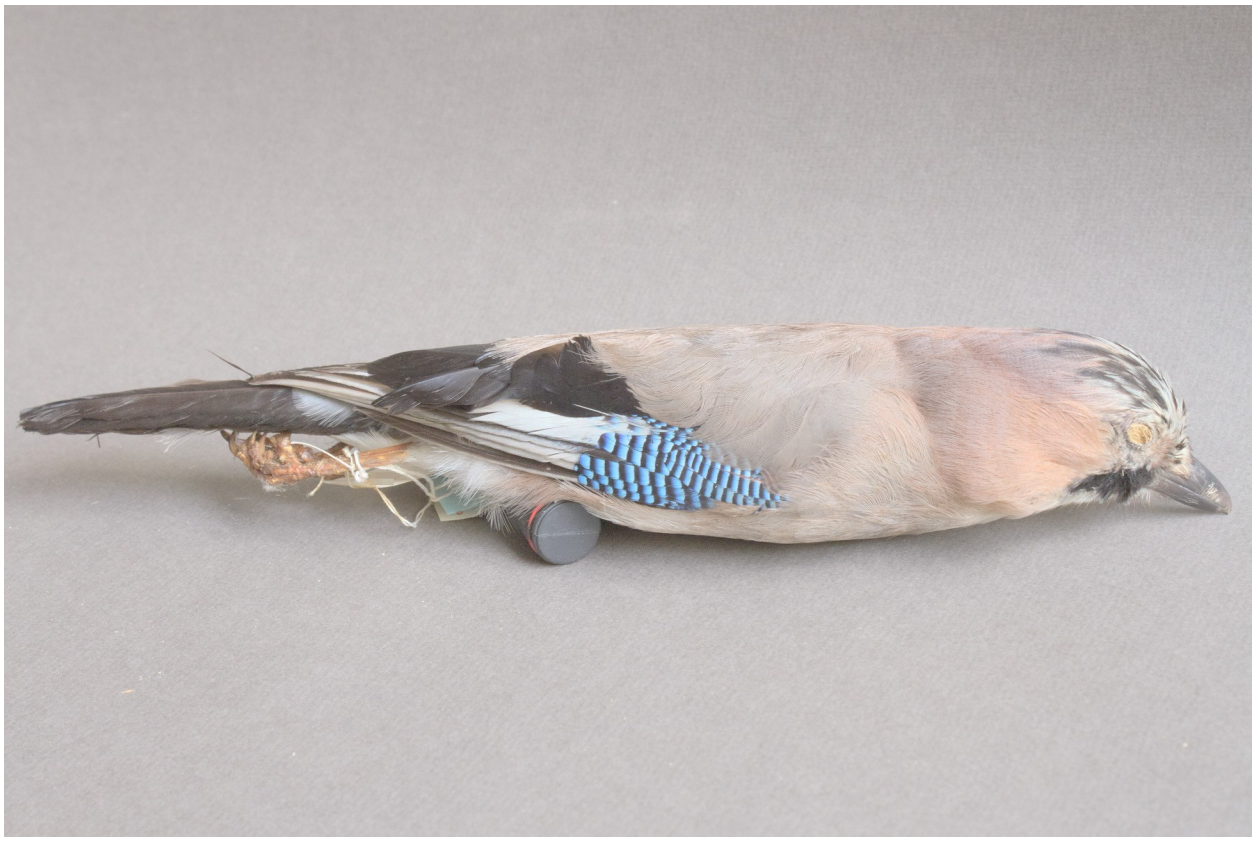
Garrulus glandarius fasciatus (Brehm, 1857)

Compared with central European birds, the back and the mantle of the Iberian subspecies are notably greyer (Voous 1953), creating a contrast to the reddish-brown neck, while the underparts are lighter coloured. Although the specimen Gglafas-2 shows less grey on the upperside than Gglafas-1, it is still greyer than most central European individuals (cf. Gglagla-86). The two mentioned specimens originate from the type locality of the subspecies "*G. g. lusitanicus*" Voous, 1953, which was described to be slightly paler than birds from south-eastern Spain (Voous 1953) and thereby very similar to *G. g. albipectus* (Keve 1939). This holds when the two individuals are compared with the specimen from southern Spain (Gglafas-4). Note the extensive white area on the head, which includes the head sides well behind the eye in "*G. g. lusitanicus*". However, this subspecies from north-western Iberia is usually not accepted by other authors.

Gglafas-4 is a typical individual of the subspecies *G. g. fasciatus* with a dark and grey appearance as well as broad black crown-streaks. The grey area on the back does even extend towards the hind-crown. Compared with the previous two specimens the body plumage is noticeably darker and the white area on the head is more restricted, resulting in mostly rufous-brown head sides.

Gglafas-1, NMW 45 417, Spain, Castile and León, Salamanca, 12.04.1941

Gglafas-2, NMW 45 413, Spain, Castile and León, Linares de Riofrio, 20.04.1941



Gglafas-4, NMW 22 970, Spain, Andalusia, Sevilla, 15.10.1904

Garrulus glandarius albipectus Kleinschmidt, 1920

Gglaalb-1, NMW 22 952, Herceg Novi (Castelnuovo), Montenegro, 01.12.1903

Gglaalb-2, NMW 22 953, Herceg Novi (Castelnuovo), Montenegro, 20.09.1903

The subspecies *G. g. albipectus* has been described as overall paler than most of the other South European taxa (Kleinschmidt 1920), which otherwise belong to the darkest forms (Voous 1953). Compared to the similar "*G. g. lusitanicus*" the white area on the head is more restricted and does barely extend behind the eye in the examined specimens. The greyish area of the upperside does reach the hind-crown, resulting in a lack of contrast between the mantle and the nape. The individual Gglaalb-2 has a less grey mantle and is thus very similar to the English subspecies *G. g. rufitergum*. But the latter is overall slightly darker and usually lacks any traces of grey on the upperparts. Unfortunately, specimens from the Apennine Peninsula, the type locality of *G. g. albipectus*, have not been available for comprison with the birds from the eastern coast of the Adriatic Sea.

Garrulus glandarius graecus Keve, 1939

Gglagrc-2, NMW 45 409, Greece, Peloponnes, Vytina, 28.06.1942

Gglagrc-3, NMW 45 411, Greece, Peloponnes, Vytina, 31.05.1942

This subspecies was described by referring to its darker grey upperside and more whitish underparts compared to the nominate *G. g. glandarius* (Keve 1939). The individual Gglagrc-2 appears quite pale and the back has only a slight greyish tinge making it probably indistinguishable from many central European birds. The plumage of Gglagrc-3 is darker and more in accordance with the original description, as it shows very broad crown-streaks. It is similar to *G. g. fasciatus,* but the underparts are paler, and the white area on the head sides does extend further behind the eye.

Garrulus glandarius ferdinandi Keve, 1944

Gglafer-1, NMW 72 179, Turkey, Kirklareli Province, Dereköy, 07.05.1967

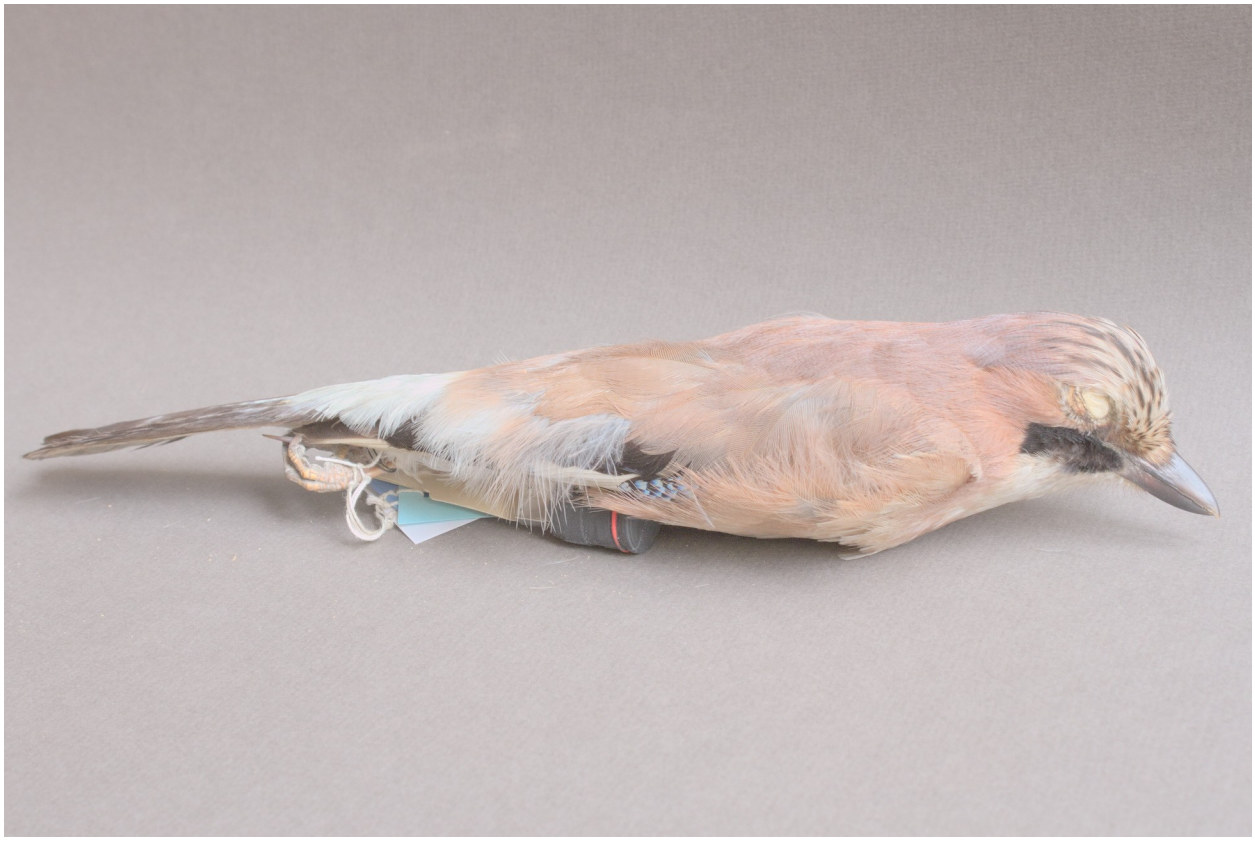
The subspecies *G. g. ferdinandi* was described as being paler and more reddish than the nominate form and *G. g. graecus* (Keve 1944). The mt DNA of this individual does cluster with that of the jays of the *atricapillus* group. The comparatively large white area on the head with narrow black streaks on the forehead which become broader towards the hind-crown is a morphological indication of this affinity. Without genetic evidence this individual probably would have passed through as a bird of the nominate subspecies *G. g. glandarius* (cf. Rokitansky & Schifter 1971).

Garrulus glandarius rufitergum Hartert, 1903

Gglaruf-1, NMW 93 013, United Kingdom, Kent, Sevenoaks, 24.03.1958

The English subspecies can be distinguished from the various forms of the mainland of Europe by the absence of greyish feathers on the back, thus exhibiting no contrast between the mantle and the neck (Hartert 1903). The overall colouration has been described as more vinaceous-pink than in the nominate *G. g. glandarius* (Shirihai & Svensson 2018), while the head sides are usually brown. Gglaruf-1, which does not cluster with the other individuals of this subspecies in the *CR* network, has a greyish tinge on the upperside and is extensively white behind the eye. Both features are more typical for birds from mainland Europe, which however can look very similar to *G. g. rufitergum* in the northwestern parts of France and the Low countries (cf. Voous 1953). Gglaruf-2 and Gglaruf-3 exhibit typical features of the present subspecies, while Gglaruf-4 is quite pale and owing to some greyish feathers on the upperside reminiscent of *G. g. albipectus*, but the head sides are uniform brown behind the eye and the nape is pinkish-brown.

Gglaruf-2, NMW 93 015, United Kingdom, Kent, Sevenoaks, 20.01.1960



Gglaruf-3, NMW 93 016, United Kingdom, Kent, Sevenoaks, 13.12.1962

Gglaruf-4, NMW 93 014, United Kingdom, Kent, Sevenoaks, 25.04.1958

Garrulus glandarius hibernicus Whiterby & Hartert, 1911

Gglahib-1, NMW 52 447, Ireland, Offaly, Birr, 30.11.1910

The present specimen of the Irish Jay is easily distinguishable from the English *G. g. rufitergum*. The plumage of *G. g. hibernicus* is uniformly dark brown and it shows hardly any contrast between the mantle and the underparts of the body. The head exhibits almost no white, with pure white feathers being restricted to a small area on the throat (Witherby & Hartert 1911; McGeehan & Wyllie 2012). Overall, it appears similar to the Caspian *G. g. hyrcanus*, which is even darker brown (Shirihai & Svensson 2018) with fewer white feathers on the crown.

Garrulus glandarius corsicanus Laubmann, 1912

Gglacor-1, NMW 5 710, France, Corsica, Vico, 02.12.1902

This is an overall quite dark subspecies, similar to the other Mediterranean forms *G. g. fasciatus* from southern Spain, *G. g. graecus* from Greece and *G. g. ichnusae* from Sardinia, but very different from the geographically close pale Italian form *G. g. albipectus* as it exhibits a clear contrast between the mantle and the neck (Voous 1953). The head sides of the present subspecies are usually entirely brownish, even in front of the eye, a feature not found in the specimens of the other southern European forms, except for *G. g. ichnusae* and *G. g cretorum*.

Gglacor-2, NMW 75 744, France, Corsica, Evisa, Aitone Forest, 22.05.1910

Garrulus glandarius ichnusae Kleinschmidt, 1903

Gglaich-1, NMW 22 967, Sardinia, Province of Nuoro, (Barbagia di) Belvi, 02.1903

The Sardinian subspecies *G. g. ichnusae* has been described to be similar to *G. g. corsicanus* but slightly paler (Laubmann 1912). The upperside and the underparts exhibit nearly identical greyish-brown colour tones (Kleinschmidt 1903). In contrast to the examined specimens of *G. g. corsicanus* the white feathers on the crown are restricted to the forehead.

Garrulus glandarius cretorum Meinertzhagen, 1920

This subspecies exhibits a strong contrast between the uniform grey back and the reddish-brown neck and head (Meinertzhagen 1920), which makes it quite easily distinguishable from the examined specimens of the adjacent *G. g. graecus*. It is overall comparatively dark and the white area on the crown is restricted to the forehead, with pure white only to be found on the throat. Some individuals of this subspecies (e. g. Gglacre-1) are similar to *G. g. glaszneri*, but the present subspecies exhibits noticeably more white feathers on the head, especially the white area on the throat is more extensive and the underparts are lighter coloured as well. The specimen Gglacre-2 appears somewhat aberrant, as it exhibits extremely broad black crown-stripes and a monstrous bill.

Gglacre-1, NMW 45 408, Greece, Crete, Samaria, 17.04.1942

Gglacre-2, NMW 45 407, Greece, Crete, Samaria, 17.06.1942

glaszneri group

Garrulus glandarius glaszneri Madarász, 1902

Gglaglsz-1, NMW 22 969, Cyprus, Troodos Mountains, 14.06.1903

Although often included in the *glandarius* group, *G. g. glaszneri* is morphologically a very distinct taxon (e.g. Keve 1939; Shirihai & Svensson 2018) and therefore, backed up by mt genetic data, here considered to form a separate group. It exhibits a strong contrast between the grey mantle and the uniform reddish-brown area on the head and neck. The underparts are similarly brown and thereby darker than in most subspecies of the *glandarius* group. White on the head is restricted to a very small area on the throat (Madarász 1902; Meinertzhagen 1920). The specimen shown was collected a year after the type specimen of this taxon at the same locality and does morphologically correspond with the type series (cf. Madarász 1902; Keve 1939).

cervicalis group

The taxa of this North African group exhibit a strong contrast between the grey upperside and the dark reddish neck (Madge & Burn 1994), the crown is entirely black with black feathers extending to the forehead.

Garrulus glandarius cervicalis Bonaparte, 1853

Gglacer-1, NMW 22 972, Tunisia, Jendouba Governorate, Ain Draham, 04.1903

Gglacer-2, NMW 22 976, Tunisia, Jendouba Governorate, Ain Draham, 26.02.1912

Gglacer-3, NMW 22 975, Algeria, Batna Province, 01.05.1892

The plumage of *G. g. cervicalis* is characterised by a grey upperside, a reddish-brown neck and pale greyish-brown underparts (Keve 1939). The specimens Gglacer-1 and Gglacer-2 hail from the type locality of the generally not accepted "*G. g. koenigi*" in north-western Tunisia (Tschusi 1904). It differs from *G. g. cervicalis* by a paler plumage coloration and more white feathers on the forehead, which holds in comparison with Gglacer-3. In that specimen the head sides are creamy white, and the hind-crown exhibits some brown feathers, reminiscent of *G. g. whitakeri* (cf. Keve 1939).

atricapillus group

Representatives of this group share a black hind-crown, while the forehead is white. The body plumage is uniform greyish-brown (Madge & Burn 1994).

Garrulus glandarius atricapillus Geoffroy Saint-Hilaire, 1832

Gglaatr-1, NMW 67 678, Israel, 27.04.1970

This subspecies is the palest of the group. The white area on the head extends far to the rear (Shirihai & Svensson 2018) ending with a sharp contrast to the greyish-brown body plumage, particularly noticeable in the specimen Gglaatr-2. In the individuals Gglaatr-1 and Gglaatr-3 the head sides are creamier white.

Gglaatr-2, NMW 76 679, Israel, Haifa district, 26.03.1979

Gglaatr-3, NMW 89 121, Israel, Northern district, Nir David, 15.01.1988

Garrulus glandarius krynicki Kaleniczenko, 1839

Gglakry-9, NMW 73 747, Abkhazia, Sukhumi, 04.07.1953

Gglakry-10, NMW 43 259, Russia, Stavropol Krai, Pyatigorsk, before 1839

Compared with *G. g. atricapillus* the white area on the head is more restricted in *G. g. krynicki* and the head sides have a brownish tinge (Shirihai&Svensson 2018). No abrupt contrast between the white head and the brownish body plumage can therefore be observed.

Garrulus glandarius anatoliae Seebohm, 1883

Gglaana-3, NMW 72 418, Turkey, Bolu Province, Abant Gölü, 06.07.1968

This subspecies exhibits in some respects intermediate plumage features between *G. g. atricapillus* and *G. g. krynicki*. The head sides and the throat are white but do not extend as far to the rear as in *G. g. atricapillus*. Note the contrast between the greyish-brown upperside and the rufous-brown neck, which is not found in any other subspecies of the *atricapillus* group. Moreover, some black feathers do reach the forehead in this subspecies (Roselaar 1995). Both features are slightly reminiscent of the north African subspecies *G. g. cervicalis*. As these individuals have been collected in north-western Anatolia, these characters could be the result of intergradation with the adjacent *glandarius* group. Gglaana-4 is a comparatively dark individual, similar to *G. g. krynicki*, but note the black feathers on the forehead, usually not found in that subspecies.

Gglaana-4, NMW 3 302, Turkey, Izmir Province, 12.12.1871

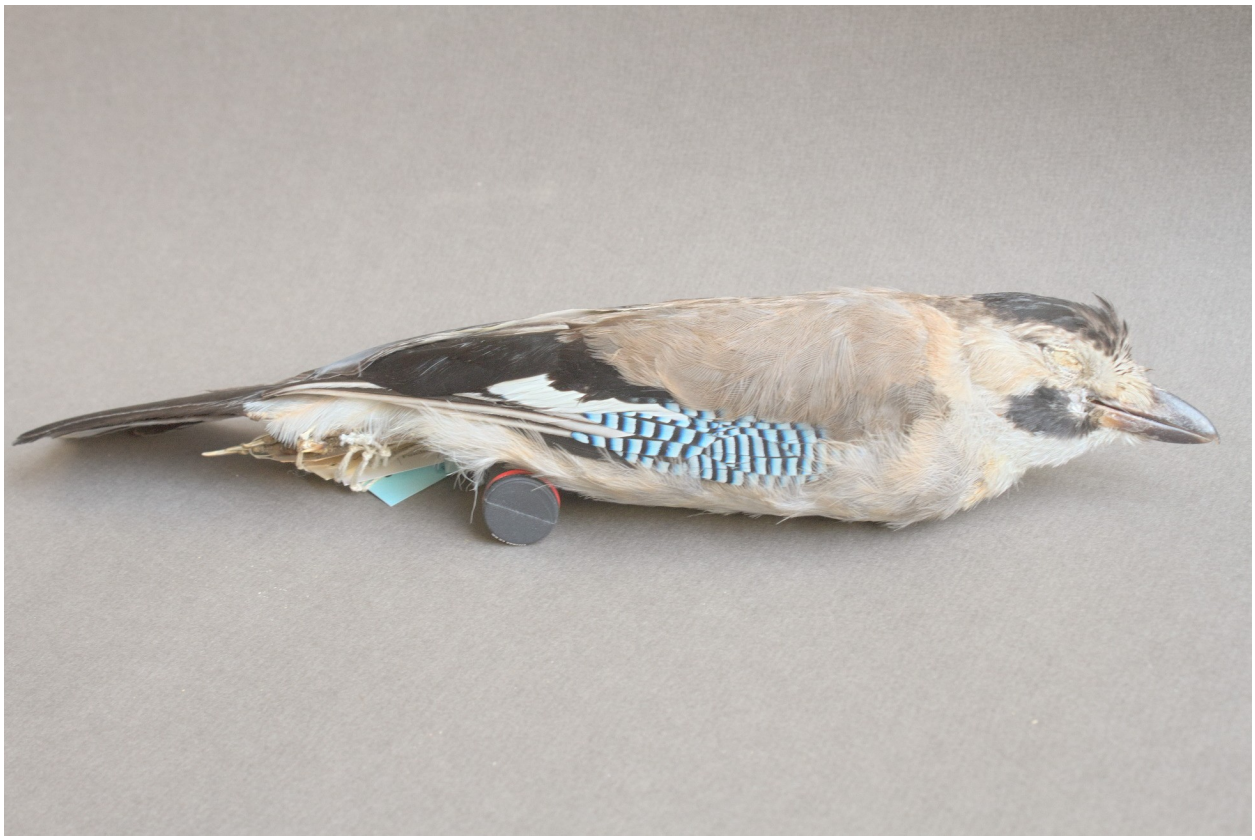
Gglaana-7, NMW 72 419, Turkey, Ankara Province, Beydili, 08.07.1968

Gglaana-7 is an individual with a more whitish forehead, but still note single black feathers. It differs from *G. g. atricapillus* by the lack of a sharp demarcation between the pure white throat and the greyish-brown underparts, which instead smoothly merge into each other. The quite pale underparts distinguish this individual from *G. g. krynicki*, note the rufous neck as well. In Gglaana-8 the clean white throat is comparatively well demarcated from the brown underparts, but the rufous-brown tinge on the head sides, extending forward to the bill, distinguishes this individual from *G. g. atricapillus*.

Gglaana-8, NMW 72 420, Turkey, Antalya Province, Kasaba, 17.07.1968

"*Garrulus glandarius rhodius*" Salvadori & Festa, 1913

It appears similar to *G. g. anatoliae*, but it is overall slightly paler, and the back is greyer (Keve 1973). The specimen Gglarho-1 is a freshly fledged bird (cf. Ghigi 1929), in which the plumage is very variable (Keve 1973), it should therefore not be considered as a typical individual of this subspecies. The individual Gglarho-2 appears very similar to *G. g. atricapillus* but note the rufous zone between the head and the mantle, comparable to *G. g. anatoliae*.



Gglarho-1, NMW 83 689, Greece, Rhodes, Salakos, 03.06.1935

Gglarho-2, NMW 83 688, Greece, Rhodes, Salakos, 03.06.1935

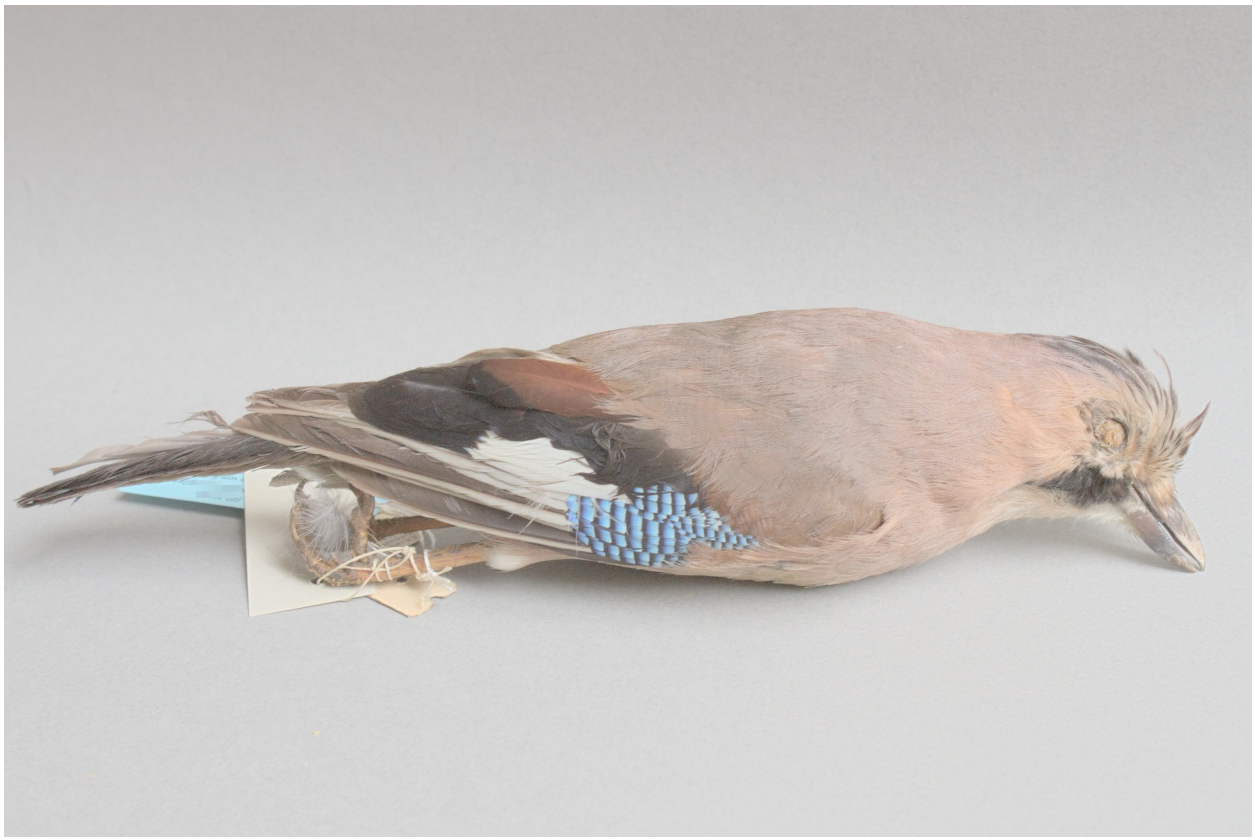
hyrcanus group

This group exhibits a uniform dark brown body plumage and a streaked crown (Blanford 1876; Keve & Doncev 1967; Shirihai & Svensson 2018). Individuals with all-black crowns, as illustrated in Madge & Burn (1994), del Hoyo et al. (2009) and del Hoyo & Collar (2016) are probably the result of intergradation with jays of the *atricapillus* group. While the extent of black crown-streaks does vary considerably between individuals within the *glandarius* group it seems to be an important plumage feature to correctly identify *G. g. hyrcanus*.

Garrulus glandarius hyrcanus Blanford, 1873

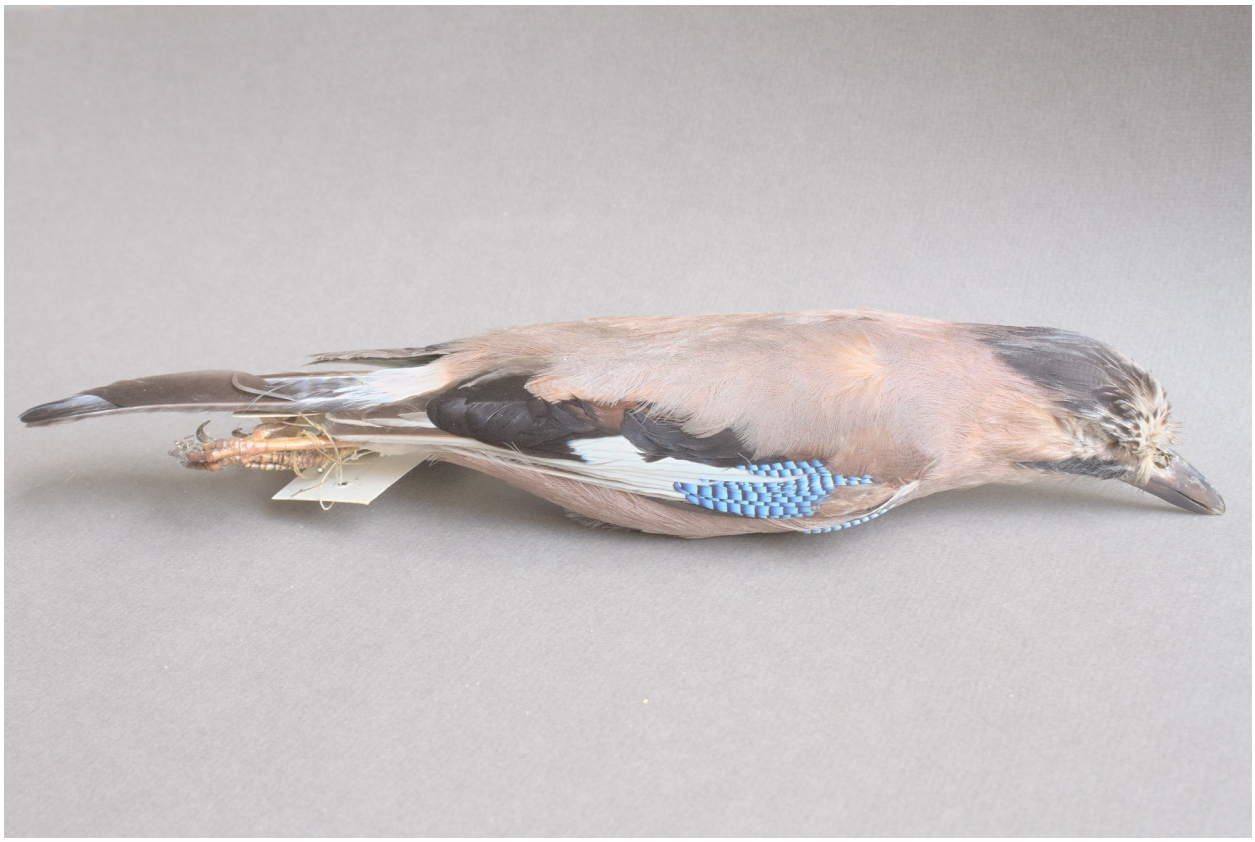
Gglahyr-3, NMW 22 985, Azerbaijan, Lankaran area, 26.02.1880

Note the uniformly dark brown body plumage and the densely streaked crown with the broadest streaks on the forecrown (cf. Hüe & Etchecopar 1970). Pure white on the head is restricted to a very small area on the throat. The head of Gglahyr-4 is slightly paler with single white feathers on the forehead and head sides. The black crown-stripes become gradually broader towards the hind-crown. These characters could be a result of intergradation with the *atricapillus* group. Mt DNA sequences of this individual cluster with Gglahyr-3.



Gglahyr-4, NMW 22 986, Azerbaijan, Lankaran area, 01.01.1880

"*Garrulus glandarius caspius*" Seebohm, 1883



Gglacas-1, NMW 22 982, Azerbaijan, Lankaran area, 1887

This taxon probably consists of intergrades between *G. g. hyrcanus* and jays of the *atricapillus* group (Seebohm 1883; Keve 1973; Shirihai & Svensson 2018). The specimen Gglacas-1 is very similar to *G. g. krynicki* but note the overall darker body plumage, almost no white on the headsides and the black feathers on the white forehead. The individual Gglacas-2 exhibits almost exactly intermediate characters between *G. g. hyrcanus* and *G. g. krynicki*. Only a small area of the hind-crown is entirely black, while the rest of the crown is densely streaked. The amount of white on the head is less than in *G. g. krynicki* but more than in *G. g. hyrcanus*. The body plumage is not entirely uniform dark brown but a slight contrast between the dark mantle and the more rufous neck and headsides is visible. Mt DNA of these individuals clusters with the *atricapillus* group.

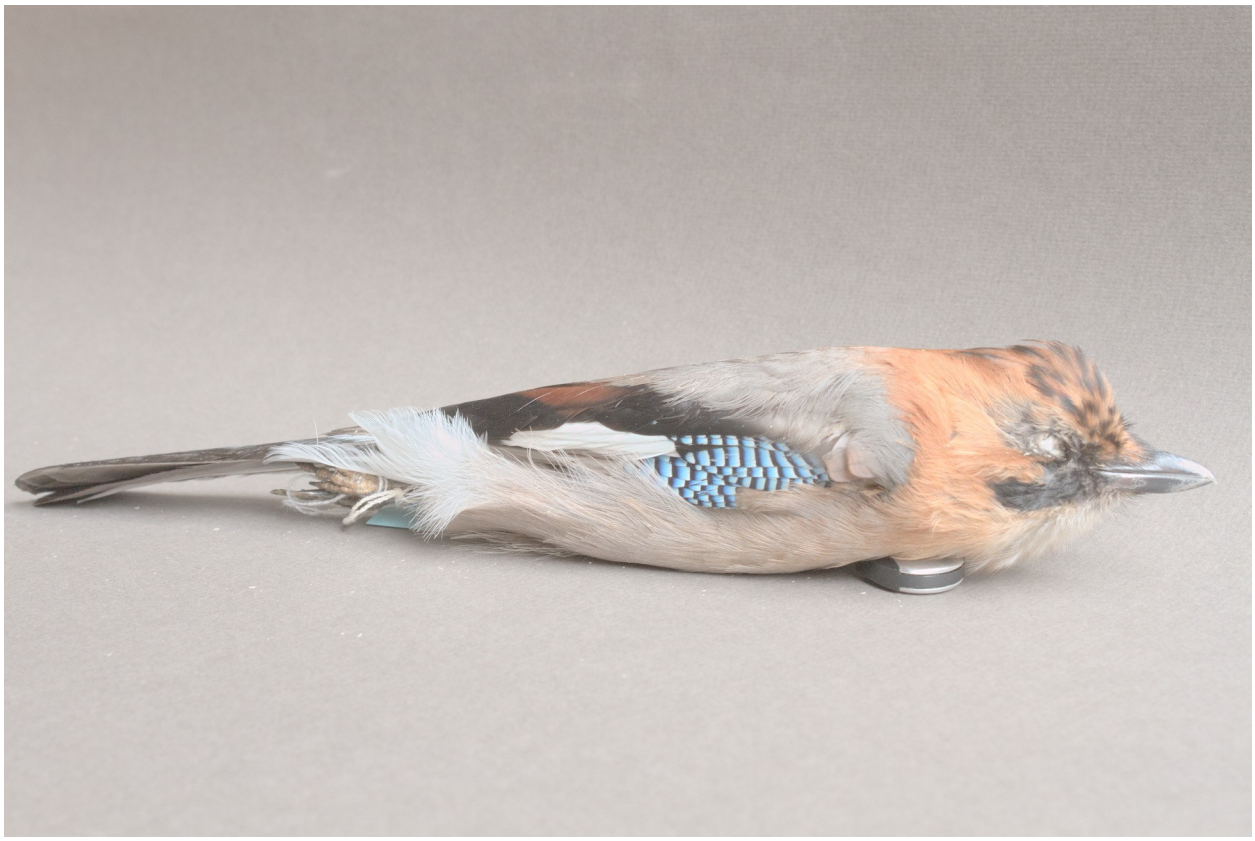
Gglacas-2, NMW 22 981, Azerbaijan, Lankaran area, 07.1887

brandtii group

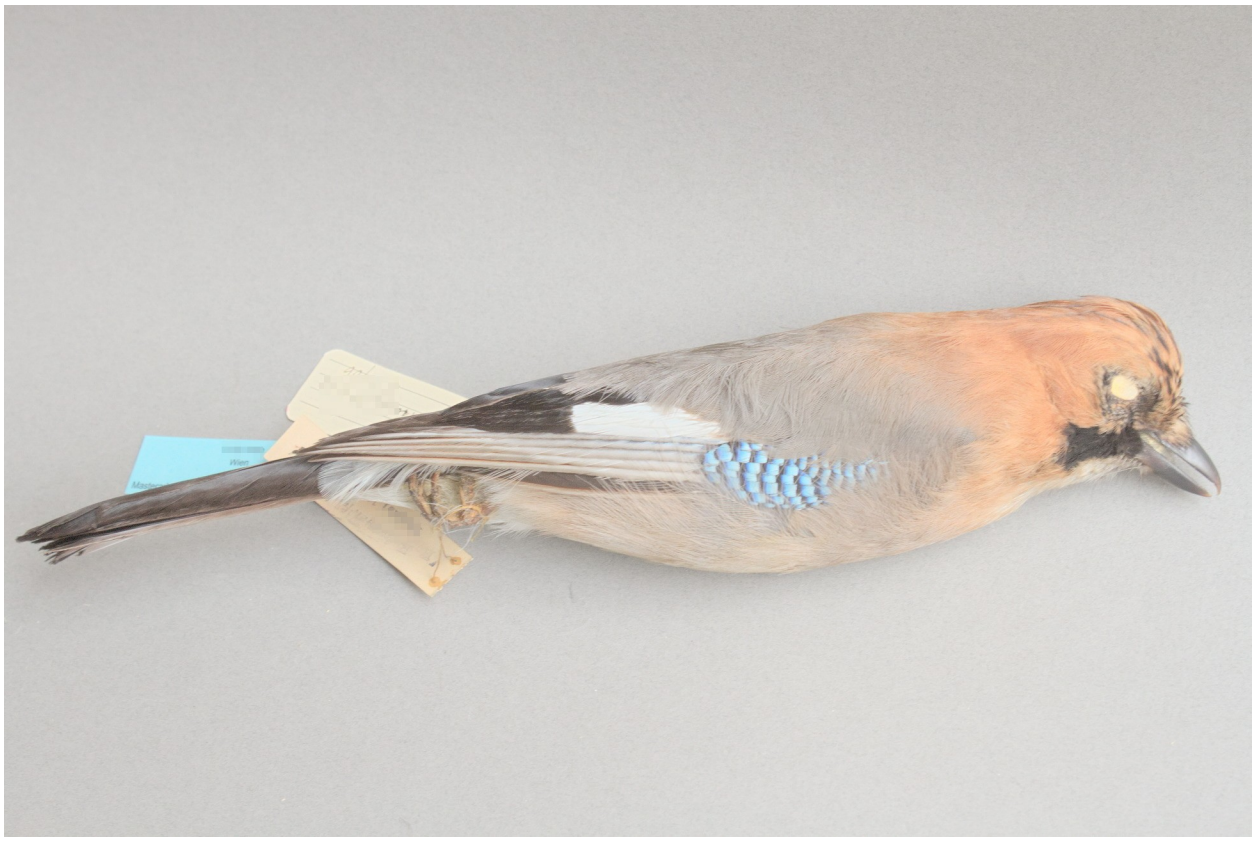
Jays of this group are characterised by a uniform grey upperside contrasting with the rufous-orange head, whereas the underparts are uniform pale greyish-brown. The rufous crown is densely streaked and pure white feathers on the head are confined to the throat (Madge & Burn 1994, Shirihai & Svensson 2018).

Garrulus glandarius brandtii Eversmann, 1842

Gglabra-12, NMW 23 017, Russia, Buryatia, Tunkinsky District, 18.12.1912



Gglabra-13, NMW 96 332, Russia, Zabaykalsky Krai, Bukukun, 02.09.2004



Gglabra-14, NMW 23 003, Russia, Tomsk Oblast, Kislovka, 1898

Gglabra-15, NMW 83 304, Japan, Hokkaido, 28.09.1908

The Jays from Hokkaido were described as the subspecies "*G. g. pallidifrons*", which is currently not accepted. The foxy-red of the head should be duller while the forehead and the underparts appear slightly paler than in other taxa of the *brandtii* group (Kuroda 1927). Austin & Kuroda (1953) recognise this form, but by referring to a "lavender-brown cast to the gray of the back". This character is also visible in the specimen Gglabra-15, which also exhibits quite pale underparts and a lighter coloured head. *CR* sequences of this form are very distinct.

bispecularis group

The body plumage of the subspecies of this group is uniform brown and the crown usually not streaked. The secondary patch is blue with black bars, compared to clean white in the hitherto illustrated groups (Madge & Burn 1994).

Garrulus glandarius bispecularis Vigors, 1831

Gglabis-1, NMW 43 258, India, Himalaya, 1831-1836

In the subspecies of the western Himalayan mountains note the uniform brown body plumage, the lack of crown streaks and the banded secondary patch. The underparts are slightly paler than the upperside, the throat is creamy white. In live birds the iris is chestnut, not blue (Goodwin 1976).

Gglabis-2, NMW 22 965, India, Himalaya, 1831-1836

Garrulus glandarius sinensis Swinhoe, 1871

Gglasin-1, NMW 22 978, China, Hubei Province, Wuhan (=Hankou), 19.01.1912

The plumage colour tones of *G. g. sinensis* are quite variable (Keve 1939). The present individual is the cotype of the generally not accepted subspecies "*G. g. rubrosus*", which is slightly paler than typical *G. g. sinensis*, making it very similar to *G. g. bispecularis* from which it differs by a slight greyish tinge on the back (Keve 1939), as well as by a pale cream iris, which is usually encircled by a dark ring (Tai & Fan 2004).

leucotis group

As in the *bispecularis* group, the secondary patch is blue-black banded. The body plumage is less uniform, the head is pure white, strongly contrasting to the brown body, and the hind-crown is uniformly black (Madge & Burn 1994).

Garrulus glandarius leucotis Hume, 1874

Gglaleu-1, NMW 45 462, Myanmar, Mandalay Division, Pyin U Lwin, 06.12.1937

Somewhat surprisingly, the mt DNA of both sampled individuals clustered with the *bispecularis* group. As both specimens were collected close to the northern boundary of the distribution area attributed to *G. g. leucotis* this could be due to intergradation with some representatives of the *bispecularis* group.

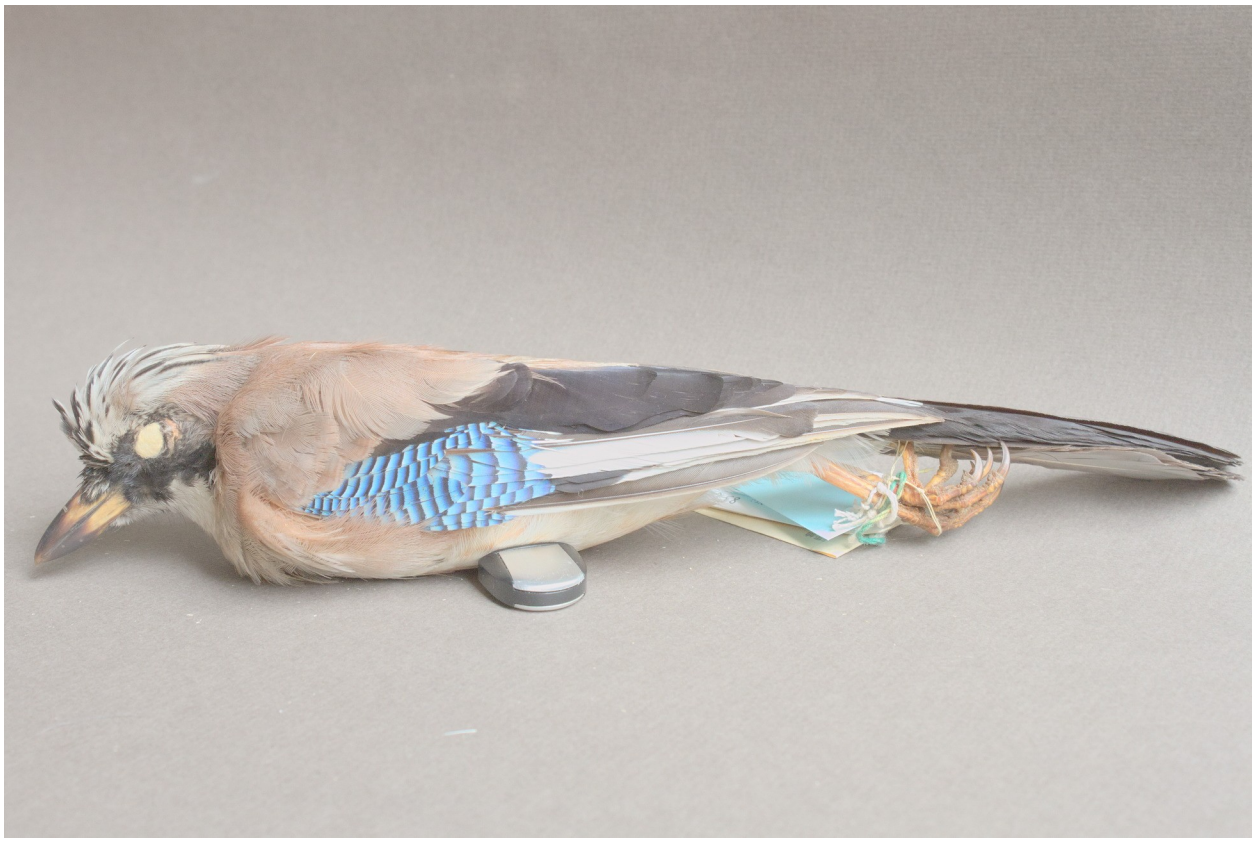
Assuming that in jays inhabiting the core breeding distribution area of *G. g. leucotis* the black crown streaks do extend onto the forehead (Baker 1922; King et al. 1975; Robson 2002), the pure white forecrowns of the present specimens could be phenotypical results of interbreeding. This feature is especially pronounced in the individual Gglaleu-2 where the all black hindcrown does abruptly end above the eye, while Gglaleu-1 exhibits scattered, albeit brown, streaks on the forehead.

Gglaleu-2, NMW 45 463, Myanmar, Mandalay Division, Pyin U Lwin, 07.12.1937

japonicus group

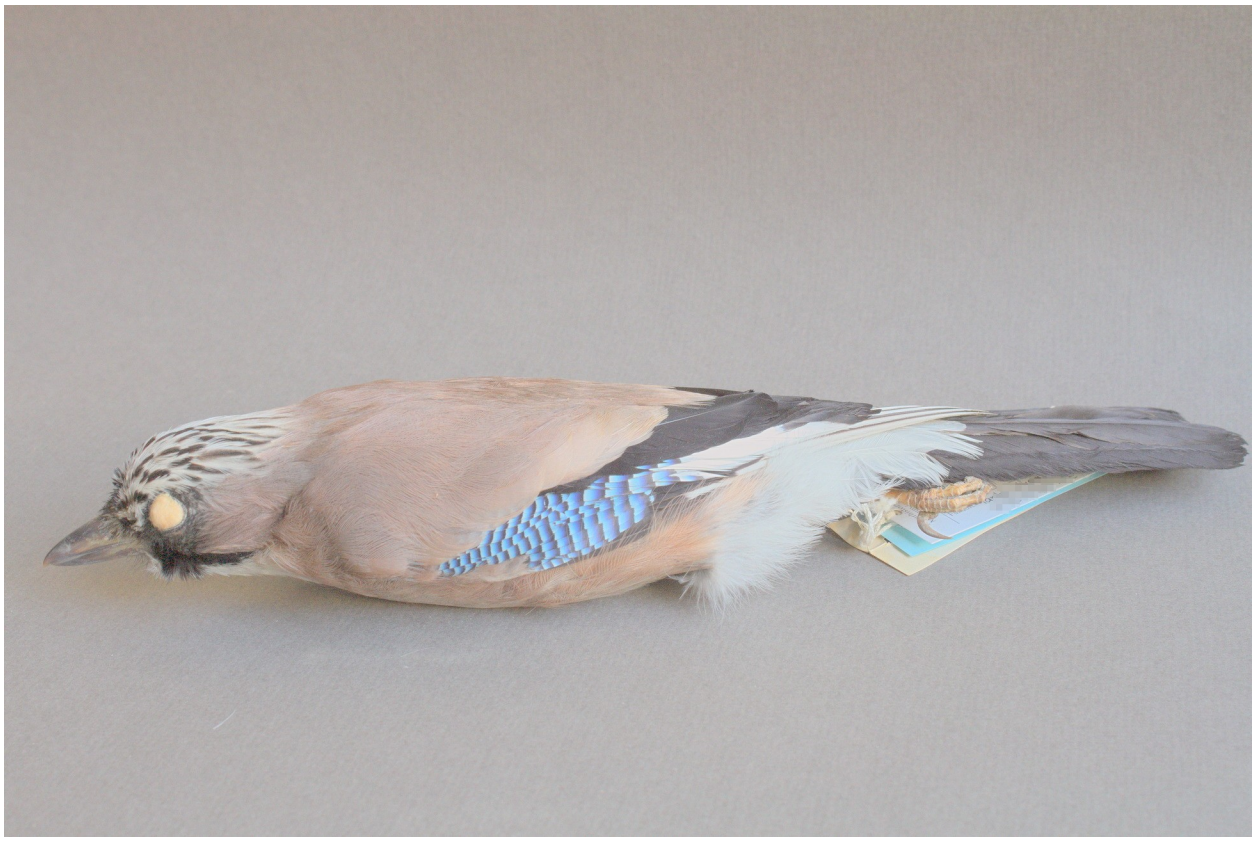
The taxa of this group are superficially very similar to the European *glandarius* group with a streaked crown and a white secondary patch. In live birds, the pure white iris is a striking feature (Shimba 2018), which separates the group from all the other taxa of the *G. glandarus* complex. The plumage pattern of the head is more contrasting, the white secondary patch much larger (Madge & Burn 1994) and individual variation is much less pronounced than in the *glandarius* group. These differences could indicate that the superficially similar plumage features probably evolved independently of the *glandarius* group.

Garrulus glandarius japonicus Temminck & Schlegel, 1847

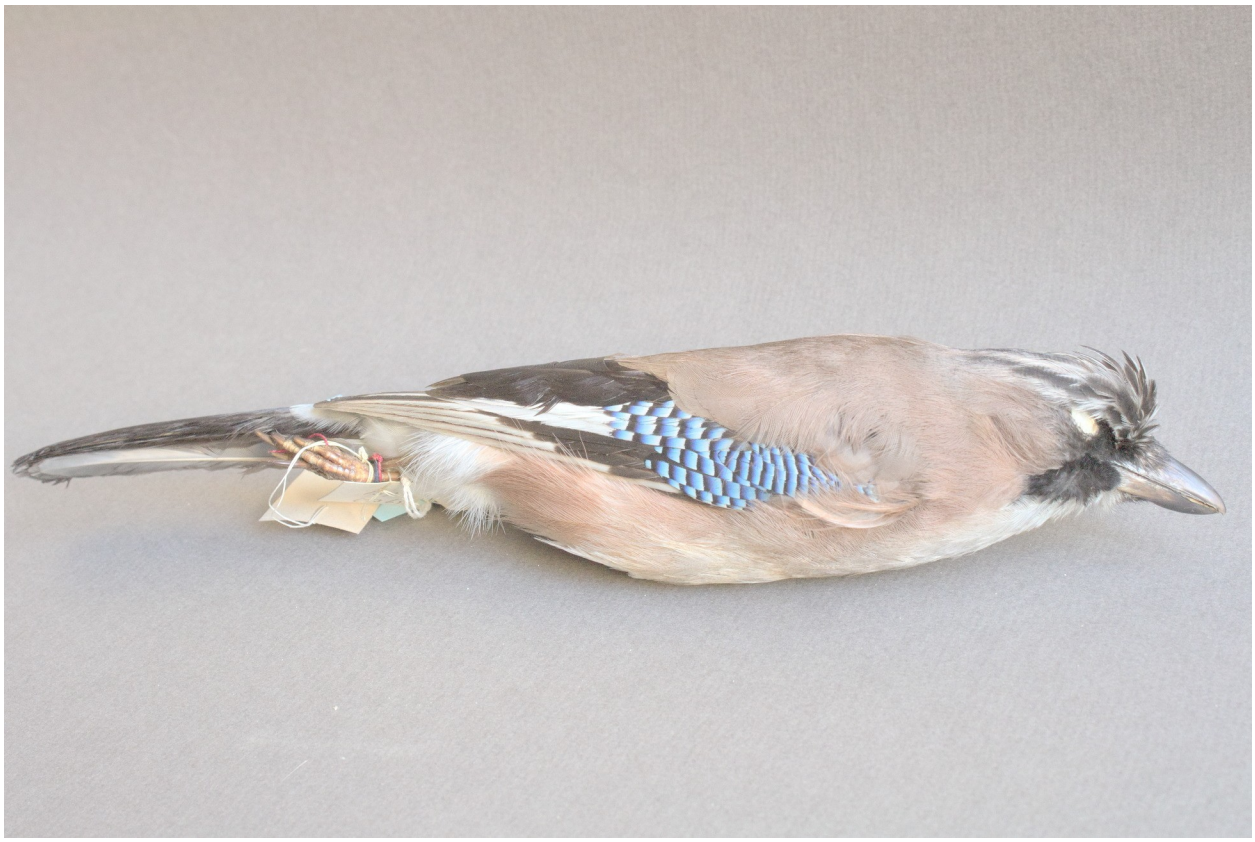


Gglajap-2, NMW 83 271, Japan, Honshu, Chubu Region, Mount Fuji, 15.11.1908

Superficially, it is similar to the *glandarius* group, but the white area on the crown is sharply demarcated from the uniform brown body plumage. The area in front of the eye and the nasal bristles are completely black, the head sides behind the eye brown. The base of the bill is pale, whereas it is completely dark in all the other groups. Note the extensively white secondaries and primaries as well.
In the individual Gglajap-3 the black area in front of the eye is less extensive and the white secondary patch smaller. Note the well demarcated white area on the crown and the brown head sides behind the eye.
The Jays from Kyushu are sometimes separated as "*G. g. hiugaensis*", which was described to be generally darker than *G. g. japonicus* (Momiyama 1927). This is evident when the specimen Gglahiug-1 is compared with the two formers. The mantle is darker and more greyish, the black crown-streaks are noticeably broader and the black area around the eye is more extensive, while the clean white area on the throat extends comparatively far to the rear in this individual. The subspecies *G. g. hiugaensis* is recognised by Austin & Kuroda (1953) owing to its darker head.



Gglajap-3, NMW 94 467, Japan, Honshu, Hyogo Prefecture, Tanba, 03.11.1957

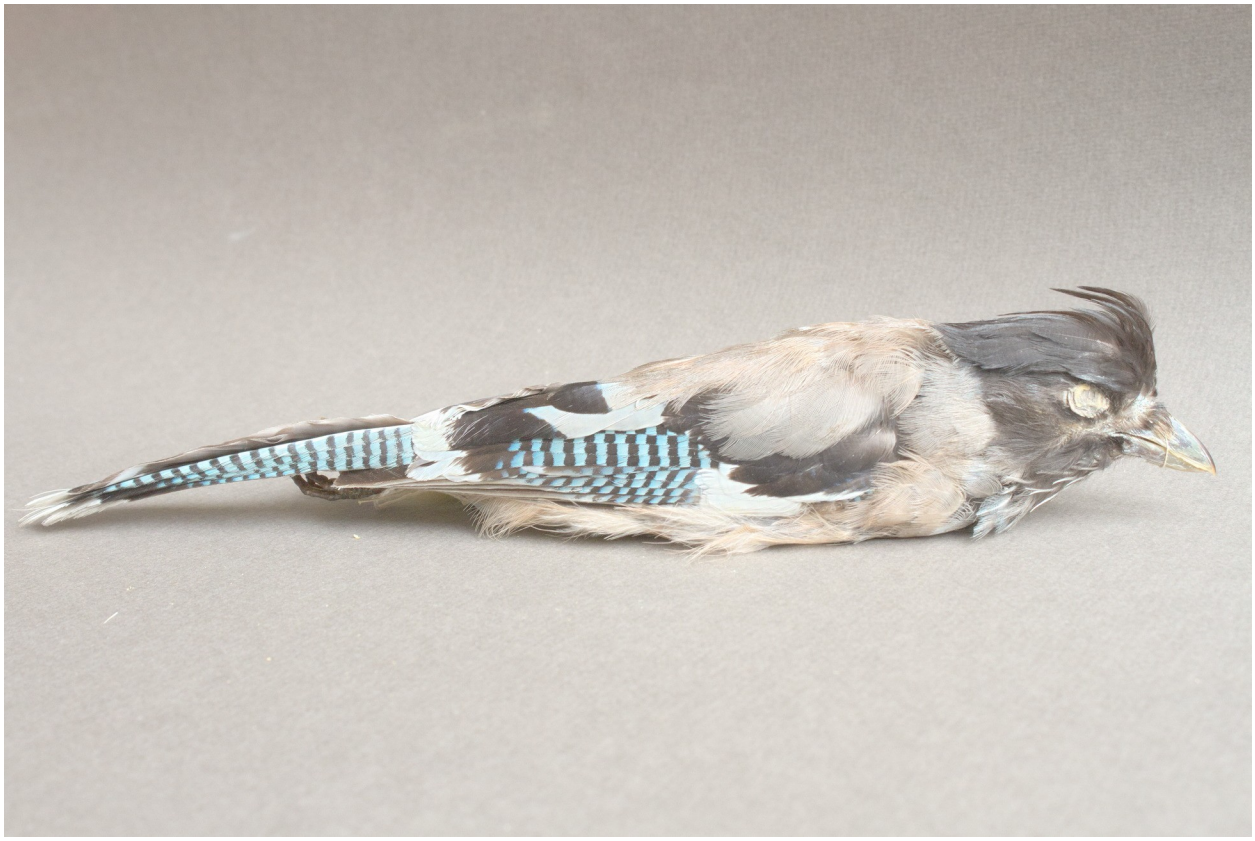


Gglahiug-1, NMW 22 992, Japan, Kyushu, Nagasaki Prefecture, 10.1887

Black-headed Jay *Garrulus lanceolatus* Vigors, 1831

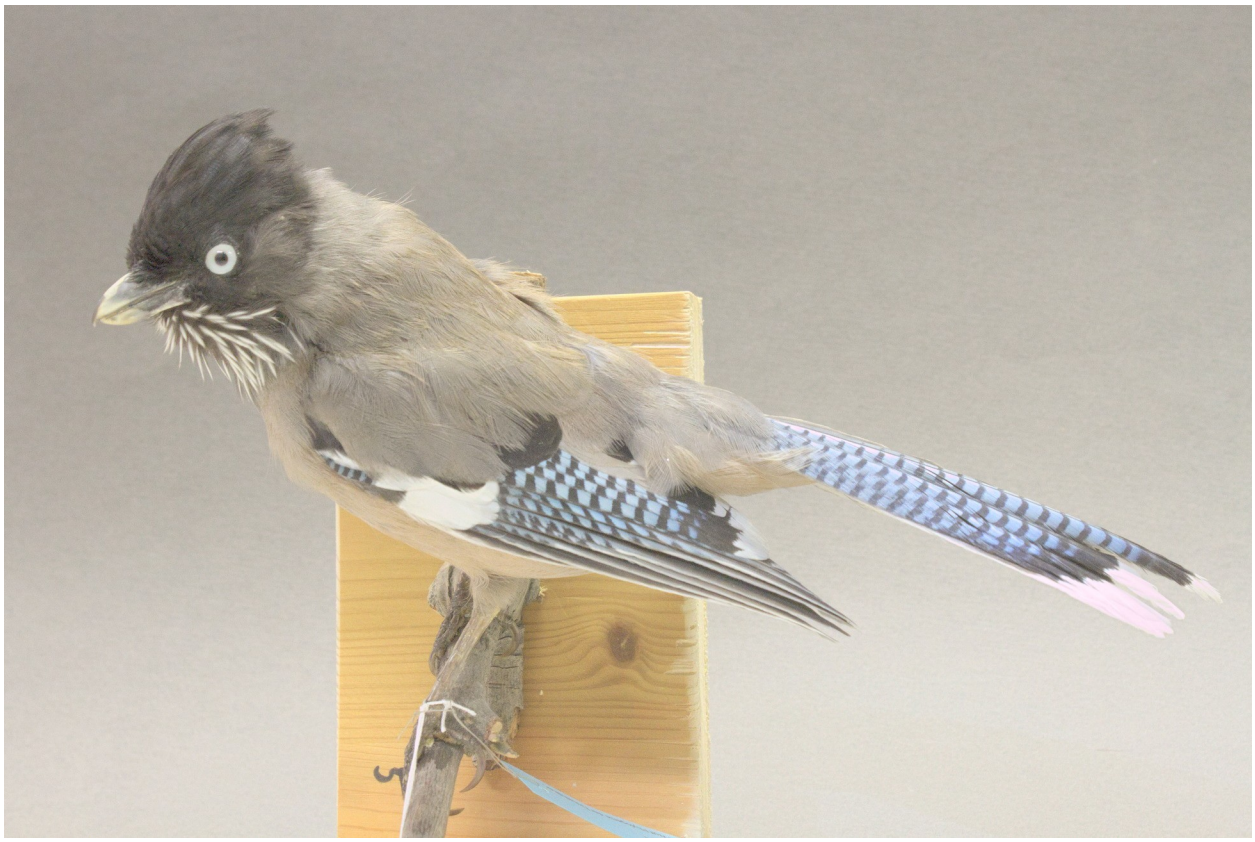
This distinctive species shares with the taxa of the *Garrulus glandarius* complex the brown body plumage and the blue-black bands on the wing and the tail, but the blue bands on the tailfeathers, whose tips are clean white, extend further to the rear. On the wing, the alula is blue-black striped and separated by the pure white primary coverts from the other banded flight feathers. The head is mostly black, while the black throat exhibits white lanceolate streaks.

Interestingly, the typical barring of the tail and the secondaries of this species, can also be observed in some individuals of *G. glandarius* (cf. Kleinschmidt 1924; Horváth 1976; 1981). For instance, extensively banded tail feathers can be found in the *cervicalis* group, while traces of blue-black bands on the secondaries, which are typical for the *bispecularis* and *leucotis* group, can be observed in some individuals of the *glandarius*, *glaszneri*, *atricapillus* and *hyrcanus* group (see images above). Considering these similarities with the taxa of the *G. glandarius* complex and the genetic affinity, it appears unnecessary to place this species into a separate genus as proposed by Kaup (1855) and Reichenow (1906).



Glan-1, NMW 46 624, India, Himalaya, 12.12.1941

Glan-2, NMW 98 267, Afghanistan, Nuristan Province, 1967-1969



Glan-3, NMW 98 268, Afghanistan, Nuristan Province, 1967-1969

Lidth's Jay *Garrulus lidthi* Bonaparte, 1850

This species is easily distinguished from all the other taxa of the genus *Garrulus* by its remarkably purple-blue plumage coloration. With *G. lanceolatus*, to which it is genetically closely related, it shares the black bars on the wing coverts and the white streaks on the throat.

Glid-1, NMW 83 348, Japan, Ryukyo Islands, Amami Oshima, 1900-1910

Note the black bars on the wing coverts and some secondaries, while the white streaks on the throat are hardly visible in this individual. Only the anterior part of the head is black, and the bill is entirely pale.

Appendix III

References of original scientific descriptions

The sources of the original descriptions of all the taxa mentioned in the main study and Appendix II are listed below. For scientific descriptions of additional taxa mentioned in Appendix I see del Hoyo et al. (2007, 2009).

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