The Arctic Warbler *Phylloscopus borealis* – three anciently separated cryptic species revealed

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The Arctic Warbler *Phylloscopus borealis* breeds across the northern Palaearctic and northwestern-most Nearctic, from northern Scandinavia to Alaska, extending south to southern Japan, and winters in Southeast Asia, the Philippines and Indonesia. Several subspecies have been described based on subtle morphological characteristics, although the taxonomy varies considerably among different authors. A recent study (T. Saitoh *et al.* (2010) *BMC Evol. Biol.* **10**: 35) identified three main mitochondrial DNA clades, corresponding to: (1) continental Eurasia and Alaska, (2) south Kamchatka, Sakhalin and northeast Hokkaido, and (3) most of Japan (Honshu, Shikoku, Kyushu). These three clades were estimated to have diverged during the late Pliocene to early Pleistocene (border at *c.* 2.6 million years ago). Differences in morphometrics have also been reported among members of the three clades (T. Saitoh *et al.* (2008) *Ornithol. Sci.* **7**: 135–142). Here we analyse songs and calls from throughout the range of the Arctic Warbler, and conclude that these differ markedly and consistently among the populations representing the three mitochondrial clades. Kurile populations, for which no sequence data are available, are shown to belong to the second clade. To determine the correct application of available scientific names, mitochondrial DNA was sequenced from three name-bearing type specimens collected on migration or in the winter quarters. Based on the congruent variation in mitochondrial DNA, morphology and vocalizations, we propose that three species be recognized: Arctic Warbler *Phylloscopus borealis* (*sensu stricto*) (continental Eurasia and Alaska), Kamchatka Leaf Warbler *Phylloscopus examinandus* (Kamchatka (at least the southern part), Sakhalin, Hokkaido and Kurile Islands), and Japanese Leaf Warbler *Phylloscopus xanthodryas* (Japan except Hokkaido).

Keywords: cryptic species, cytochrome-*b*, phylogeny, taxonomy, vocalizations.

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The Arctic Warbler *Phylloscopus borealis* breeds from northern Scandinavia to Alaska and south to Japan, and winters in Southeast Asia, the Philippines and Indonesia (Ticehurst 1938, Watson *et al.* 1986, Chrabryj *et al.* 1991, Cramp 1992,
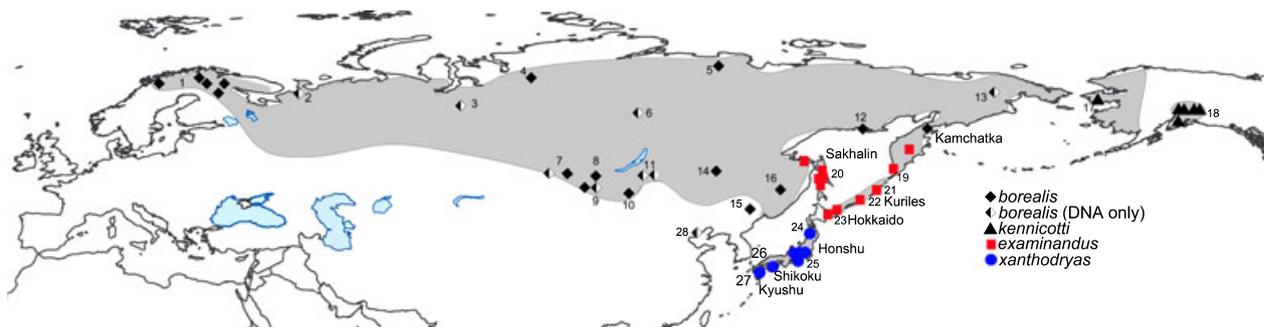
Figure 1. Distribution of the Arctic Warbler (grey shading) based on Chrabryj *et al.* (1991), Cramp (1992) and Lowther (2001). The circumscription of the taxa are based on the results of the present study (mostly in agreement with Ticehurst 1938), except that *kennicotti* is here recommended to be treated as a junior synonym of *borealis*. Sample sites for the sound recordings are marked by symbols and numbers (see Supporting Information, Appendix S1 for explanation); the three symbols lacking numbers (two *examinandus*, one *borealis*) refer to sound recordings obtained after the detailed analyses were completed (see Discussion). For *borealis*, DNA sampling sites are indicated by bicoloured symbols; for *kennicotti*, all DNA samples are from site number 18; whereas for *examinandus* and *xanthodryas*, the DNA sampling sites mostly coincide with the sound sampling sites, except for numbers 21 and 22, from which no DNA samples were available.

Dickinson 2003, Bairlein *et al.* 2006; Fig. 1). In the breeding season it is found in coniferous, deciduous and mixed forests, although in most of its range it prefers broadleaved forest, e.g. Birch *Betula* spp. and Poplar *Populus* spp. It also occurs in Willow *Salix* spp. and other scrub on tundra, as well as at or just above the tree limit in mountains (up to 2500 m in Japan). The winter habitats are more diverse, and include various rather open forest habitats, parks, plantations and mangrove (Dement'ev & Gladkov 1968, Brazil 1991, Chrabryj *et al.* 1991, Cramp 1992, Lowther 2001, Bairlein *et al.* 2006).

Morphological variation within the large breeding distribution of the Arctic Warbler is slight (Ticehurst 1938, Williamson 1967, Cramp 1992, Bairlein *et al.* 2006), although Saitoh *et al.* (2008) found consistent differences in morphometrics between some populations. A variable number of subspecies are usually recognized, although there is much disagreement among authors regarding the circumscription and distribution of these taxa (Table 1). For example, Ticehurst (1938) and Dement'ev and Gladkov (1968) propose completely opposite views of the breeding ranges of the subspecies *xanthodryas* and *examinandus*, whereas others treat the latter as a junior synonym of the former.

Saitoh *et al.* (2006) reported preliminary results from a study of mitochondrial cytochrome-*b* from eastern Asia and Alaska. They found four clades representing: (a) Kamchatka and Hokkaido (northern Japan), (b) Siberia and Alaska, (c) Sakhalin, and (d) Honshu, Shikoku and Kyushu (central and south Japan). Three of these (a, b and d) were considered sufficiently different to warrant treatment as separate species (it was not stated to which species clade c should belong). Later, Reeves *et al.* (2008) analysed mitochondrial ND2 sequence data from 88 individuals across the species' range except Japan, and confirmed the presence of a European/Siberian/Alaskan clade and a much divergent Kamchatka/Sakhalin clade. They found only slight divergence within the former clade, although the samples from northeast Siberia and Alaska formed a weakly supported and poorly differentiated subclade. In a further study of cytochrome-*b* sequences from 113 individuals from throughout the range of the Arctic Warbler, Saitoh *et al.* (2010) identified three main clades representing: (a) Europe, Siberia and Alaska, (b) Kamchatka, Sakhalin and Hokkaido, and (c) the rest of Japan (Honshu, Kyushu, Shikoku). They inferred that these clades diverged during the late Pliocene or early Pleistocene (border between these periods at *c.* 2.6 million years ago; International Commission on Stratigraphy 2009). They also confirmed the existence of a northeast Siberia/Alaska subclade within the European/Siberian/Alaskan clade first noted by Reeves *et al.* (2008).

In this paper we analyse songs and calls from throughout the range of the Arctic Warbler. We also analyse mitochondrial cytochrome-*b* sequences from three nominal types collected away from the breeding grounds (*examinandus*, *xanthodryas* and *flavescens*), and morphometrics from two of these. We propose that three species be recognized:

Table 1. Taxonomy of *Phylloscopus borealis* according to different authors. Note especially the differences with respect to the subspecies *xanthodryas* and *examinandus*.

	Ticehurst (1938)	Williamson (1967)	Dement'ev and Gladkov (1968)	Watson *et al.* (1986)	Cramp (1992)	Dickinson (2003), Bairlein *et al.* (2006)
borealis Blasius, 1858; type from Sea of Okhotsk, 59°38'N, 147°30'E	Continental Eurasia (not Kamchatka)	Continental Eurasia (probably not Kamchatka)	Continental Eurasia S to 59/60°N (not Kamchatka)	NE Siberia	Continental Eurasia (not Kamchatka)	Continental Eurasia (not Chukotka and Kamchatka)
talovka Portenko, 1938; type from headwaters of the Sertynya river, northern Urals	–	–	–	Scandinavia to Yenisey R., Nizhnyaya Tunguska R. and L. Baykal	–	–
transbaicalicus Portenko, 1938; type from Borzya, Zabaykalsky Krai, Russia (c. 50°23'N, 116°31'E)	–	–	–	Nizhnyaya Tunguska R., E to Yakutsk, S to Transbaikalia, N Mongolia and Stanovoy range	–	–
hylebata Swinhoe, 1861; type from Amoy (=Xiamen), Fujian province, China (c. 24°36'N, 118°44'E)	–	–	SE part of continental Eurasian range, S of 60°N (not Kamchatka); Sakhalin Isl.	SE Russian Far East, NE China	–	–
kennicotti Baird, 1869; type from St. Michael, Norton Sound, Alaska (c. 63°28'N, 162°W)	Alaska	Alaska	Alaska	Alaska	Alaska	Alaska
xanthodryas Swinhoe, 1863; syntypes from Amoy (=Xiamen), Fujian province, China (c. 24°36'N, 118°44'E)	S Kuril Isl., Japan (Hondo (=Honshu), Hokkaido)	S Kuril Isl., Japan; probably Kamchatka	Kamchatka, Commander Isl., N Kurile Isl.	N Sea of Okhotsk, Kamchatka, Commander Isl., Kurile Isl., Japan	Kamchatka, Commander Isl., Kurile Isl., Sakhalin Isl., Japan	'Chukotka and Kamchatka to Sakhalin and Japan'
examinandus Stresemann, 1913; lectotype from Bali, Indonesia	Kamchatka, Commander Isl., N Kurile Isl. (Sakhalin?)	–	S Kuril Isl., Japan	–	–	–

Arctic Warbler *P. borealis* (*sensu stricto*) (continental Eurasia and Alaska), Kamchatka Leaf Warbler *P. examinandus* (Kamchatka (at least southern part), Sakhalin, Hokkaido and Kurile islands), and Japanese Leaf Warbler *P. xanthodryas* (Japan except Hokkaido).

METHODS

Taxonomy

For the circumscription and distribution of the different taxa we preliminarily follow Ticehurst (1938; Table 1, Fig. 1). The population on Sakhalin was only tentatively placed in *examinandus* by Ticehurst (1938).

DNA

To determine the relationships of the taxa *examinandus* Stresemann, 1913, *xanthodryas* Swinhoe, 1863, and *flavescens* Gray, 1860, which were collected on migration or in the winter quarters, incomplete mitochondrial cytochrome-*b* sequences were obtained from toe-pads of the lectotype of *examinandus* (in the American Museum of Natural History, New York, USA; 609 bp), and of two of the three syntypes of *xanthodryas* (214 bp), and both syntypes of *flavescens* (578 bp; the two latter taxa in The Natural History Museum, Tring, UK) (Supporting Information Appendix S1). These were compared with 41 different cytochrome-*b* haplotypes from throughout the range of the Arctic Warbler obtained from Saitoh *et al.* (2010), as well as three haplotypes obtained from migratory birds in northeast China and Russia (Fig. 1, Appendix S1). DNA from the toe-pads was extracted and sequenced following the protocols in Irestedt *et al.* (2006) and Svensson *et al.* (2008), although with different taxon-specific primers (available from P.A.).

The phylogenetic analyses of the mitochondrial haplotypes were performed as in Saitoh *et al.* (2010), except that the program BEAST was not used for any analyses. Pairwise HKY + I distances were estimated using TREEFINDER (Jobb *et al.* 2004, Jobb 2008), and uncorrected p-distances were calculated in PAUP* (Swofford 2002); only complete (1012 bp) sequences were used, and hence the partial sequences of the types were not included. The HKY + I model was selected by the Akaike Information Criterion (Akaike 1973) calculated by

MRMODELTEST2 (Nylander 2004) in conjunction with PAUP* 4.0b10 (Swofford 2002), with the outgroups excluded.

Vocalizations

Sound recordings of song of 94 individuals and of calls of 53 individuals from throughout the breeding range of Arctic Warbler were obtained (Fig. 1, Appendix S1). Sonograms of these vocalizations were produced using RAVEN version 1.3 (Cornell Laboratory of Ornithology). The song terminology is explained in Figure 2. The following measurements were taken on entire song strophes and calls: Δ time (s) = duration; Δ frequency (Hz) = frequency range; mean frequency; and highest and lowest frequency (in case of doubled calls, only the main note was measured). In addition, the number of syllables/strophes was counted. Moreover, for each male's unique strophe(s), the following was noted: type, number and order of syllables; number of A and B syllables; and number of thin elements at beginning of (or inside) syllables. A factor analy-
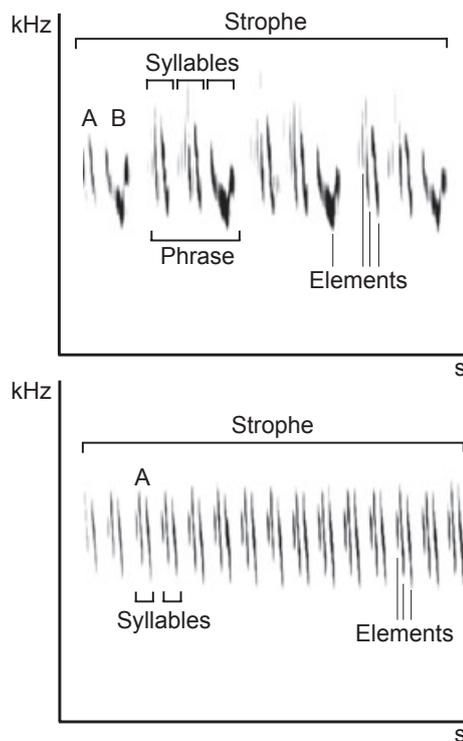
Figure 2. Song terminology (top *examinandus*, bottom *borealis*). Strophes are separated by pauses of varying length. The term 'note' refers to any discrete sound.

sis was performed in STATISTICA 9 (Statsoft Inc., Tulsa, OK, USA) based on the variables 'number of elements/unique A syllable', 'number of elements/unique B syllable' (lacking in *borealis* and *kennicotti*; counted as zero), 'number of syllables/strophe', 'bottom frequency of strophe', 'top frequency of strophe', 'Δ time of strophe', 'number of unique syllables/unique strophe', and 'number of thin elements/unique multi-element A syllable'.

Morphology

Four type specimens (three syntypes of *xanthodryas* and one syntype of *flavescens*) were measured in The Natural History Museum, Tring, UK (Appendix S1). These were compared with measurements of 55 adult males from across the eastern part of the species' breeding range (Saitoh *et al.* 2008). We followed the methodology of Saitoh *et al.* (2008) by performing canonical discriminant analysis (CDA). We only used characters with a correlation coefficient between the characters ($r < 0.6$) to avoid multi-collinearity. Therefore, we used only four characters: natural wing-length (NW), tarsus-length, total head-length and length of primary number 10 (counted descendently) in relation to the tips of the primary coverts. One of the three syntypes of *xanthodryas* had a damaged bill, and therefore was not included in the CDA (Appendix S1).

RESULTS

Mitochondrial gene tree

In the cytochrome-*b* tree (Fig. S1) the lectotype of *examinandus* is nested in the Kamchatka–Sakhalin–Hokkaido clade; the haplotype representing the two syntypes of *xanthodryas* is in the Honshu–Shikoku–Kyushu clade, and one of the syntypes of *flavescens* is in the continental Eurasia clade (we failed to obtain a sequence from the second syntype).

Genetic distances

The pairwise cytochrome-*b* distance between the three main clades identified in the gene tree (Supporting Information Fig. S1) was 4.0–6.7% (mean 5.3 ± 0.65%) HKY + I corrected, or 3.6–5.6% (mean 4.6 ± 0.49%) uncorrected p-distance. In contrast, the divergences within each of the three primary clades are considerably lower, 0–0.9% (mean 0.35 ± 0.17%) HKY + I corrected, or 0–0.9% (mean 0.34 ± 0.17%) uncorrected.

Songs

There are three main song types, representing different geographical areas: (1) continental Eurasia (except Kamchatka) and Alaska (*borealis/kennicotti*); (2) Hokkaido, Kuriles, Kamchatka and Sakhalin (*examinandus*); and (3) Honshu, Shikoku and Kyushu (*xanthodryas*). These three groups are diagnosably different, and every individual studied has been unambiguously placed in one of them. The differences between *borealis/kennicotti* and the two other taxa are especially striking, whereas the differences between *examinandus* and *xanthodryas* are less immediately apparent, although with practice they are easily discernible by ear and can be clearly distinguished via inspection of their respective sonograms. A factor analysis including eight song variables results in the separation of *xanthodryas* from the two remaining taxa according to factor 1, which explained 44.8% of the variation, and moderate separation of *borealis/kennicotti* from *examinandus* by factor 2, which explained 22.4% of the variation (Supporting Information Fig. S6a). If the variable 'number of thin elements/unique multi-element A syllable' is excluded from the analysis, factor 1 explained 47.8% and factor 2, 20.9% of the variation, and the separation between *borealis/kennicotti* and *examinandus* increased (Fig. S6b).

The song of *borealis* (Fig. 3a–f, Supporting Information Fig. S2, Table S1 and Audio S2, S3 and S16) is a 0.6–4.6 s (mean 2.08 ± 0.58 s) slightly harsh, fast rattling *rererererererererere* or, differently transcribed, *zezezezezezezezezeze*, which usually gradually increases somewhat in strength and often fades a little at the end; sometimes the song sounds rather undulating due to variation in strength and frequency within a strophe. The strophes are separated by pauses of a few to many seconds, depending on the bird's level of excitement. One or more sharp *zrit* calls (see Calls below) are often interspersed between the song strophes. At a finer scale, a strophe consists of 7–44 (mean 18.8 ± 6.5) similar syllables (referred to as syllable type A; cf. Fig. 2). Ocasionally, strophes can have two series of different syllable types, so that a strophe changes character after some time (Fig. S1b, second strophe). Each syllable consists of one to three (mean 2.1 ± 0.4) elements (not counting thin
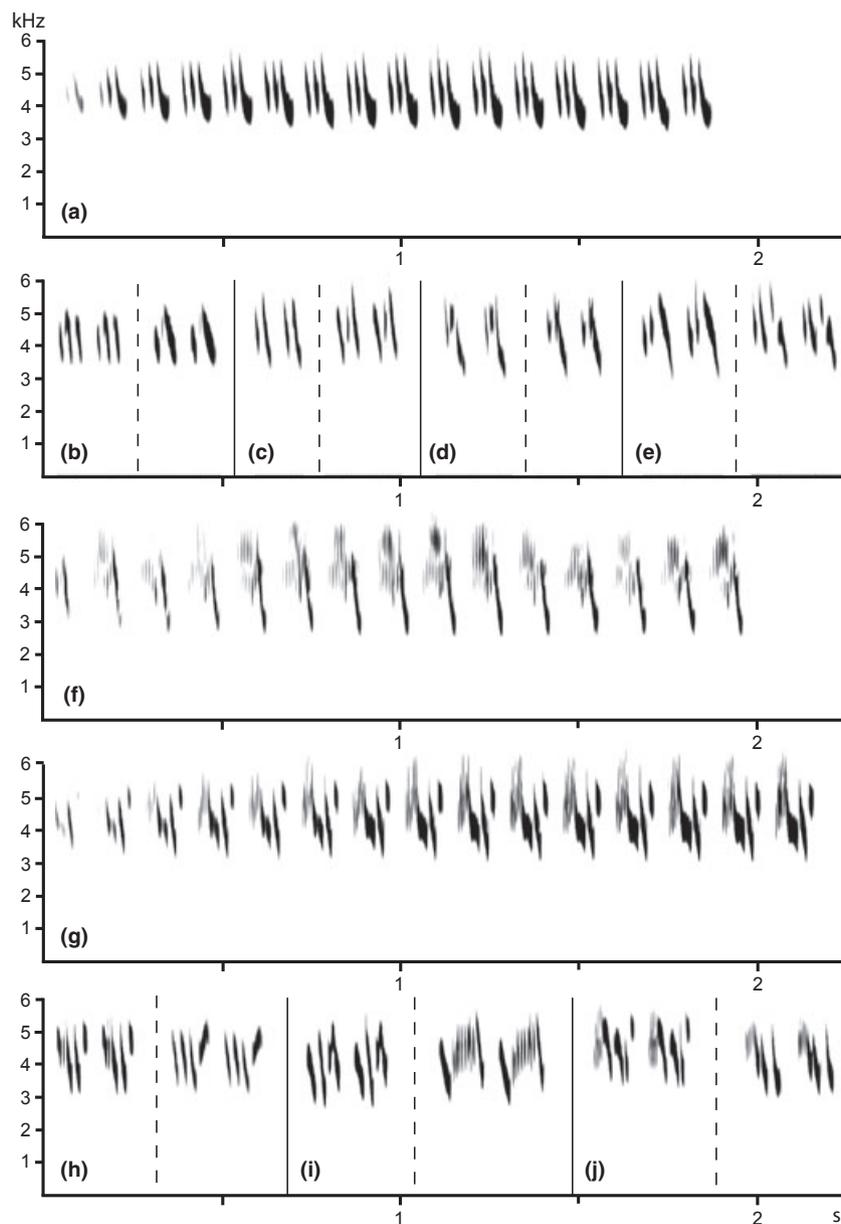
Figure 3. Song of *borealis*: (a) Abisko[1], Sweden, June (Krister Mild); (b) northern Norway[1], July (Ivan Hills∕The British Library Sound Archive (BL) 06673); (c) Ivalo[1], Finland, June (Hannu Jännes); (d) Kuusamo[1], Finland, July (Per Schiermacher Hansen∕BL 43066); (e) Norilsk[4], Russia, July (Christoph Zöckler); (f) Huzhong[14], Heilongjiang province, China, June (Per Alström∕BL WA 1994∕82). Song of *kennicotti*, Alaska: (g) E of Nome[17], June (G.A. Keller∕ML 105866); (h) Mt. McKinley[18] (L.J. Peyton∕ML 49580); (i) W of Paxson[18], July (L.J. Peyton∕ML 49585); (j) NE of Nome[18], June (L.J. Peyton∕ML 49979). Long sonograms represent complete strophes, whereas short ones show two syllables per strophe. Superscript numbers represent the localities referenced in Figure 1 (details in Appendix S1).

elements at the beginning of the syllables in eastern populations; see below). There is considerable individual variation in the number and appearance of the elements. In our sample, each male had a repertoire of up to 21 different strophes consisting of different syllable types, which he alternated between. It seems likely that all males can sing at least a few different strophes, although one bird from Norway sang only one strophe type in a recording of 105 consecutive strophes.

The song is very consistent throughout the range of *borealis*. However, eastern birds, from Olonyek (Russia) and Huzong (China) eastward, i.e. east of *c.* 120°E, usually have syllables that begin with several thin elements (Fig. 3f and Supporting Information Fig. S2g–k and Table S1). In addition, songs of birds from Respublika Tyva (Russia) eastwards tended to be slower (fewer syllables per time unit), with a drier quality and more elements per syllable than songs from Fennoscandian birds.

The song of *kennicotti* (Fig. 3g–j, Supporting Information Fig. S3 and Table S1) resembled that of *borealis*, although the strophes were on average longer and more slow-paced (fewer syllables per time unit) and tended to sound slightly sharper. At a fine scale, the syllables were on average more complex than in *borealis*. As in eastern *borealis*, most syllables contained several thin elements, which were usually at the very beginning of the syllable, but which could also in rare cases be positioned 'inside' the syllable, and sometimes the same syllable contained thin elements both at the beginning and internally. The final element is usually higher-pitched than the others, unlike in most *borealis*.

The song of *examinandus* (Fig. 4, Supporting Information Fig. S4, Tables S1, S2 and Audio S7–S9) is a slightly harsh, fast, rather short series of notes with a regular pulsating rhythm. It was easily distinguishable from the songs of *borealis* and *kennicotti* by the pumping rhythm, which resulted from the presence of usually two different syllable types (A and B) arranged in phrases (usually AAB) that are given three to eight times in succession (the first and last phrases are usually incomplete). The strophes are also on average shorter than in *borealis/kennicotti*. The A syllable begins with a few thin elements, as in most eastern *borealis* and *kennicotti*, which contribute to the somewhat harsh quality of the song. The A syllable consisted of one to four (mean 2.8 ± 0.65) elements (excluding the thin introductory elements), whereas the B syllable usually consisted of a single element (none to three, mean 1.2 ± 0.44). There is considerable individual variation in the number and appearance of the elements, whereas the syntax did not vary much. In our sample, each male had a repertoire of up to 15 different strophe types. One individual from Hokkaido once gave a *borealis/kennicotti*-like song with repetition of a single syllable, *treetreetreetreetreetreetreetreetreetree*, in addition to typical strophes (Supporting Information Fig. S4d, second strophe). This strophe type has not been recorded in any other *examinandus*. There are no consistent differences between songs from Kamchatka (Fig. 4a and Supporting Information Fig. S4a and Audio S9), Sakhalin (Fig. 4b–d, Fig. S4b), Hokkaido (Fig. 4e,f, Fig. S4c,d and Audio S7, S8) or the Kurile Islands (not shown). As in *borealis* and *kennicotti*, the song strophes generally began rather faintly and then increased in strength, and calls (see below) were often interspersed between song strophes.

The song of *xanthodryas* (Fig. 5, Supporting Information Fig. S5, Tables S1, S2 and Audio S12–S15) was more variable, both individually and geographically, than the songs of the other taxa, and especially birds from northern Honshu (Mt Hachimantai, Iwate) deviated in syntax from the others (Fig. 5e and Supporting Information Fig. S5c). The song resembled that of *examinandus*, but generally sounded slower, lower-pitched and less sharp and harsh, and the rhythm was clearly different as a result of additional A syllables (e.g. AAAB), or the presence of more than two syllable types in the phrases (see below). In central Honshu the commonest (*c.* 86%) strophe type consists of two different syllable types (A and B) arranged in phrases that are given three to five times (first and last phrases are often incomplete); the most common phrase was AAAB. More rarely, one or two other syllable types (C and D) were given in a strophe in addition to the A and B types (Fig. 5e). Also in Kyushu and Shikoku, most strophes consisted of repetitions of phrases of two syllable types (e.g. AAAB), but three rare strophe types also contained C syllables in addition to the A and B syllables, and one strophe type (given once) included five different syllable types. Moreover, in Shikoku, five of six individuals (*c.* 29% of strophe types) had, in addition to the commoner types, a *borealis/kennicotti*-like single-syllable *treetreetreetreetreetreetreetreetreetree*, although with more 'pumping' rhythm than in *borealis/kennicotti* (Fig. 5g). In northern Honshu (Iwate), *c.* 70% of the unique strophe types included phrases consisting of three syllable types (A, B, C; Fig. 5e), whereas *c.* 26% had only two syllable types (incuding the phrase AAB), and *c.* 4% had just a single syllable (AAAA…). In all strophe types of *xanthodryas*, except those from northern Honshu with repetitions of the phrase AAB and the single-syllable strophes (AAAA…), the syntax differed from that of *examinandus*.

In *xanthodryas* the A syllable consisted of two to six (mean 3.6 ± 0.63) elements, with slight variation between the main geographical areas.
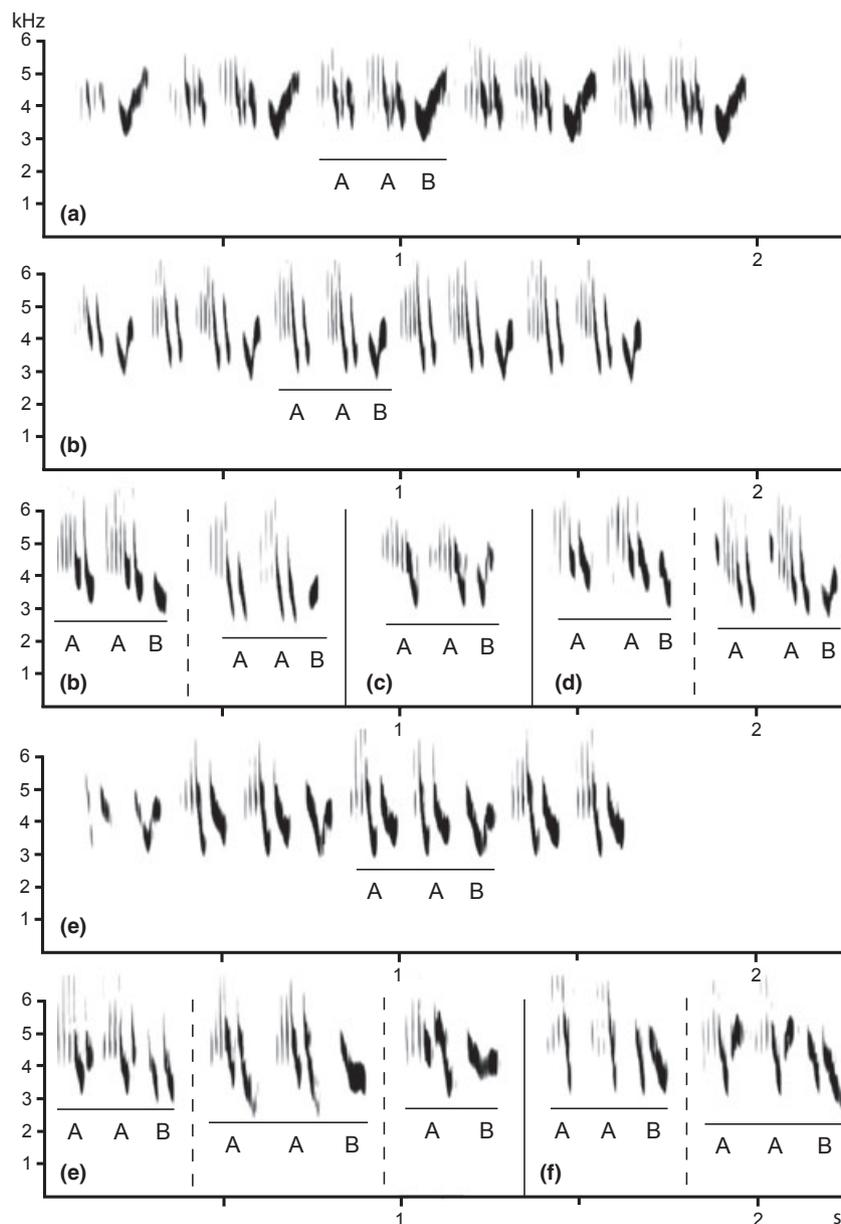
Figure 4. Song of *examinandus*: (a) Kamchatka[19], Russia, July (Veprintsev 1982); (b) Sakhalin[20], Russia, July (Oda 2005); (c) Sakhalin[20], July (Oda 2005); (d) Sakhalin[20], July (Oda 2005); (e) Mt Rausu[23], Hokkaido, Japan, July (Takema Saitoh); (f) Mt Rausu[23], July (Takema Saitoh). Long sonograms represent complete strophes, whereas short ones represent one phrase per strophe. Superscript numbers represent the localities referenced in Figure 1 (details in Appendix S1).

The B syllable was either missing (in AAAA… strophes) or consisted of one to five (mean 1.9 ± 1.10) elements, with a considerably higher number of elements in northern Honshu than at the other localities. On average, the number of elements in the A syllable was higher than in *examinandus*. Importantly, *xanthodryas* never had the thin elements at the beginning of the A syllable that *examinandus* invariably had.

Other, minor, differences between *xanthodryas* and *examinandus* were that the strophes of the former had on average a narrower frequency band, lower mean frequency and fewer syllables per time unit (i.e. slower tempo).
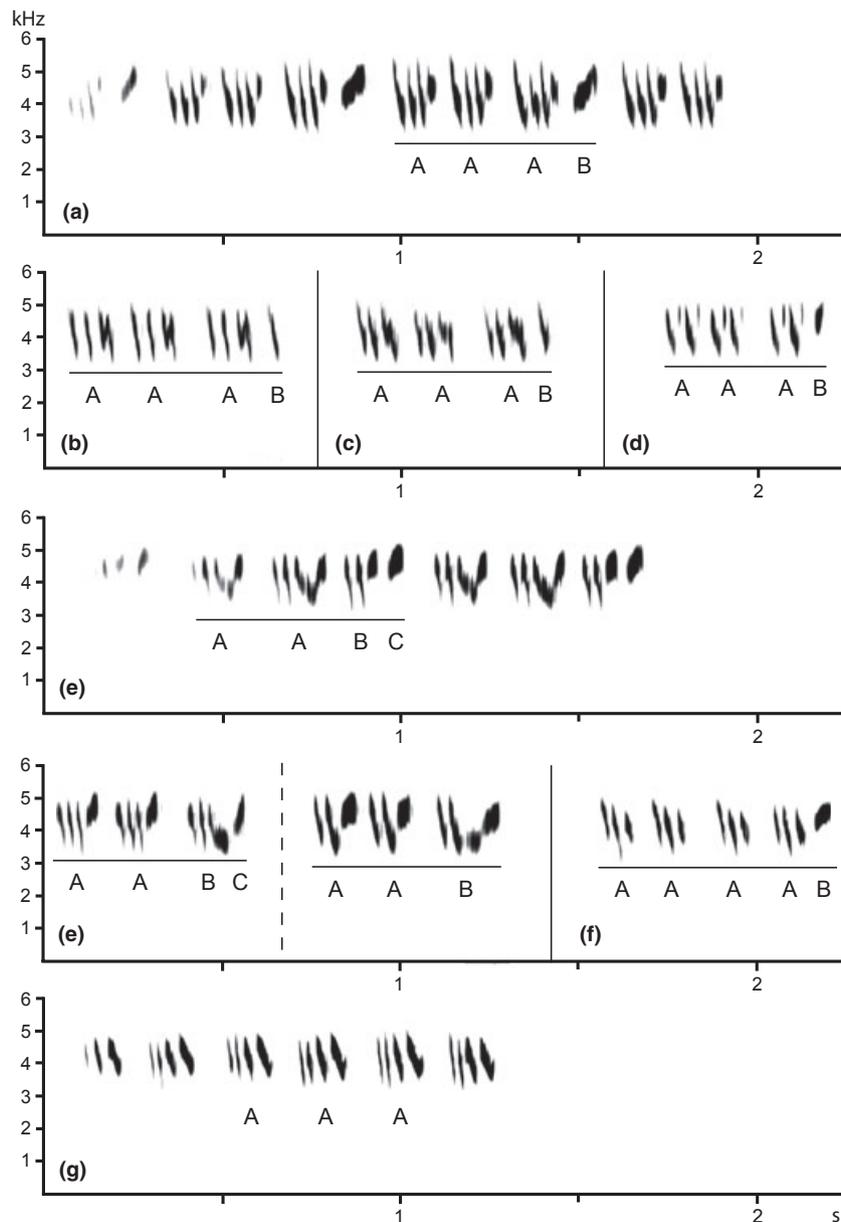
Figure 5. Song of *xanthodryas*: Honshu, Japan. (a) Karuizawa[25], May (Urban Olsson); (b) Mt Fuji[25], July (Takema Saitoh); (c) Mt Fuji[25], July (Takema Saitoh); (d) Nikko, Tochigi[25] (Michio Matsuda); (e) Mt Hachimantai, Iwate[24], July (Takema Saitoh); (f) Mt Ishizuchi[26], Shikoku, August (Haruo Kuroda); (g) Mt Ishizuchi[26], Shikoku, August (Haruo Kuroda). Long sonograms represent complete strophes, whereas short ones represent one phrase per strophe. Superscript numbers represent the localities referenced in Figure 1 (details in Appendix S1).

Also in *xanthodryas* there was much individual variation in the number and appearance of the elements. In our sample, each male had a repertoire of up to 18 different strophe types. As in the other taxa, calls (see below) were often interspersed between song strophes, and the strophes usually began more quietly.

Calls

In agreement with the song data, three geographical groups were distinguishable, with all individuals being unambiguously attributable to one of these groups. The call of continental Eurasian birds (*borealis*) can be described as a sharp, harsh
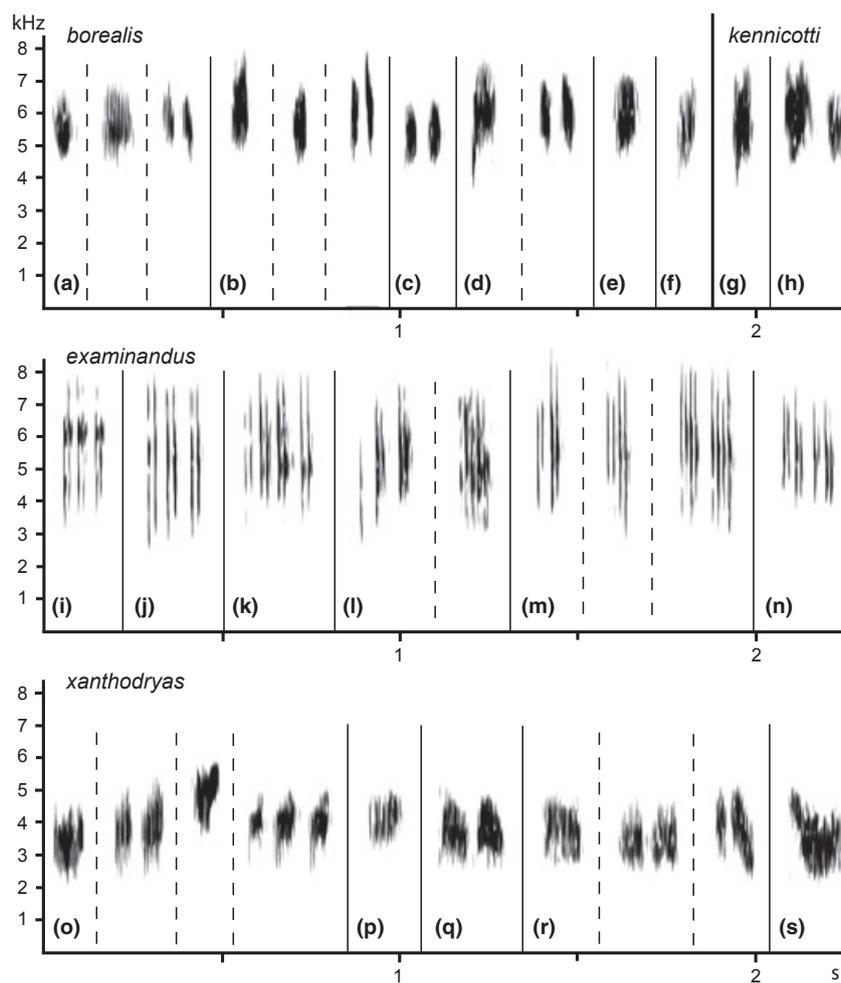
Figure 6. Calls. *borealis*: (a) Abisko[1], Sweden (Krister Mild; same individual as in Fig. 3a); (b) Ivalo[1], Finland (Hannu Jännes; same individual as in Fig. 3c); (c) Kuusamo[1], Finland (Per Schiermacher Hansen/British Library Sound Archive (BL) 43066; same individual as in Fig. 3d); (d) Khovsgol lake[8], Mongolia (Geoff J. Carey; same individual as in Fig. S2b); (e) Huzong[14], Heilongjiang province, China (Per Alström/BL WA 1994/82; same individual as in Fig. 3f); (f) Magadan[12], Russia (Ulf Hassel); *kennicotti*: (g) Mt McKinley[18], Alaska (L.J. Peyton/ML 49582; same individual as Fig. 3h); (h) Nome[17], June (C.D. Duncan/ML 81854); *examinandus*: (i) Kamchatka[19], Russia (Boris Veprintsev; same individual as Fig. 4a); (j) Mt Rausu[23], Hokkaido, Japan (Takema Saitoh; same individual as Fig. 4e); (k) Mt Rausu, Hokkaido, Japan[23] (Takema Saitoh; same individual as in Fig. 4f); (l) Mt Shari[23], Hokkaido, Japan (Takema Saitoh; same individual as Fig. S4d); (m) Sakhalin[20], Russia (Oda 2005, same individual as in Fig. 4d); (n) Sakhalin[20], Russia, May (Veprintsev 1982); (o) Karuizawa[25], Honshu, Japan, May (Urban Olsson); (p) Mt Fuji[25], Honshu, Japan, (Takema Saitoh; same individual as Fig. 5c); (q) Mt Sobo[27], Kyushu, Japan (Keisuke Ueda); (r, s) Mt Hachimantai, Iwate[24], Honshu, Japan, July (Takema Saitoh). Superscript numbers represent the localities referenced in Fig. 1 (details in Appendix S1).

dzrit, sometimes doubled *dze-zet* or *tze-ret* (Fig. 6a–f, Supporting Information Table S3 and Audio S9). At a finer scale, it consisted of a number of very thin elements that were so tightly spaced that they formed a single note or, when the call is doubled, two clearly separated notes. Birds from Alaska (*kennicotti*) had calls that were indistinguishable from continental Eurasian birds (Fig. 6g–h, Supporting Information Table S3). The call of birds from Hokkaido, Kuriles, Kamchatka and

Sakhalin (*examinandus*) was less sharp, more slowly rattling and more drawn-out than the calls of *borealis/kennicotti*: a dry, crackling *trrrt*, sometimes faster *trrt*, or doubled *trr-trrt* (Fig. 6i–n, Table S3 and Audio S4–S6). At a finer scale, the elements were more clearly separated than in *borealis/kennicotti* and frequently appeared in a series of pairs, and the frequency range was considerably wider. The call of birds from Honshu, Shikoku and Kyushu (*xanthodryas*) was clearly lower-

pitched and less sharp and rasping than in the other taxa: *dzyrt* or, less often, *dzirt* or doubled *dzyr-dzyr* or even tripled *dzyr-dzyr-dzyr*; or *dzjy* or doubled *bzee-bzjy* (Fig. 6o–s, Table S3 and Audio S10, S11). Unlike *examinandus*, but in common with *borealis/kennicotti*, the elements were very closely spaced, and the frequency range was narrow.

Morphology

Plots of the discriminant scores (Supporting Information Fig. S7) placed the syntypes of *xanthodryas* with the Honshu population and the syntype of *flavescens* with the Kamchatka/Sakhalin/Hokkaido and Alaska/East Siberia groups along the first canonical axis (CAN1).

DISCUSSION

Main groups – three species

The differences in mitochondrial DNA, song, call and morphology among the three groups representing *borealis/kennicotti*, *examinandus* and *xanthodryas sensu* Ticehurst (1938) were concordant, and all support long-standing separation between them. Based on mostly the same cytochrome-*b* data as used in the present study, Saitoh *et al.* (2010) estimated the mean age of the split between *xanthodryas* and the two others at 2.5 or 3.0 million years ago, i.e. in the late Pliocene or early Pleistocene, respectively, and between *borealis/kennicotti* and *examinandus* at 1.9 or 2.3 million years ago, in the early Pleistocene. The sister relationship between *borealis/kennicotti* and *examinandus* was strongly supported by Saitoh *et al.* (2010) in an analysis based on several mitochondrial loci.

The mean cytochrome-*b* divergences among these three main clades are more than an order of magnitude greater than the differences within them. The values are in agreement with differences between other closely related, mostly allopatric *Phylloscopus* and *Seicercus* taxa that are currently classified as separate species, but exceed those between presently recognized subspecies (Helbig *et al.* 1995, 1996, Hansson *et al.* 2000, Martens *et al.* 2004, Olsson *et al.* 2004, 2005, Päckert *et al.* 2004, 2009), even though these studies are not directly comparable, as different sequence lengths, correction methods, etc., were used in the different studies.

The songs of the three groups *borealis/kennicotti*, *examinandus* and *xanthodryas* were distinctly and consistently different, and much more divergent than the differences within these groups. For example, although there is some geographical variation within *xanthodryas*, this is slight in comparison with the differences between the three main groups. Also the differences between western *borealis*, on the one hand, and eastern *borealis* and *kennicotti*, on the other, are considerably less pronounced than the differences between the three main groups. The reduced discrimination in the factor analysis when the variable 'number of thin elements/unique multi-element A syllable' is included reflects the fact that eastern *borealis/kennicotti* resemble *examinandus* in having thin elements at the beginning of the syllables, whereas western *borealis* resembles *xanthodryas* in lacking thin elements. Subjectively, the differences in song between *borealis/kennicotti*, *examinandus* and *xanthodryas* are at least as pronounced as between some sympatric species of *Phylloscopus* and *Seicercus* warblers (e.g. Western Crowned Warbler *Phylloscopus occipitalis* vs. Blyth's Leaf Warbler *Phylloscopus reguloides*; Blyth's Leaf Warbler vs. Davison's Leaf Warbler *Phylloscopus davisoni*; Martens's Warbler *Seicercus omeiensis* vs. Grey-crowned Warbler *Seicercus tephrocephalus*; Alström & Olsson 1999, Päckert *et al.* 2004, 2009, Rasmussen & Anderton 2005; P. Alström & U. Olsson pers. experience). Finally, the differences in calls among the three groups *borealis/kennicotti*, *examinandus* and *xanthodryas* are also marked and consistent.

Saitoh *et al.* (2008) reported differences in morphometrics between *borealis/kennicotti*, *examinandus* and *xanthodryas*, with canonical discriminant analysis accurately identifying 94.6% of the individuals to one of these three main groups (only adult males analysed). The taxon *xanthodryas* was the most distinctive taxon, whereas there was some overlap between *borealis/kennicotti* and *examinandus* (names *sensu* Ticehurst 1938). The reanalysis of these data including type specimens of *flavescens* and *xanthodryas* agrees with the DNA data in the placement of these types, although the types of *xanthodryas* deviate somewhat from previously measured Japanese breeding birds, notably in having an even longer P10. The long wing and P10 of *xanthodryas* in relation to the other taxa contributes most to its distinctness. Ticehurst (1938) noted that in fresh plumage, *xanthodryas* is brighter green, less greyish above and more yellow-tinged below than the other taxa, and this was confirmed in our comparison of museum specimens.

The pronounced and concordant differences in mitochondrial DNA, song and call, along with differences (albeit less marked) in morphology, between *borealis/kennicotti*, *examinandus* and *xanthodryas* suggest that these are appropriately treated as three separate species. However, as is evident from Table 1, there is some uncertainty concerning the names of these species. The name *borealis* can be applied unambiguously to the most widely and most northerly distributed species. The application of the names *xanthodryas* and *examinandus* is unclear, as the type specimens of both these taxa were collected away from the breeding grounds, the former on migration in China and the latter in winter quarters in Indonesia (Table 1). However, our cytochrome-*b* sequences from the name-bearing types of these taxa show that Ticehurst's (1938) application of these names to their respective breeding populations in Kamchatka, the Commander Islands, the northern Kuriles and perhaps Sakhalin and in Honshu and Hokkaido, respectively, was largely correct. The morphometrics of two of the syntypes of *xanthodryas* (including the one that was not sequenced) further support this (lectotype of *examinandus* not measured). However, issues have just arisen concerning the type status of the three presumed *xanthodryas* syntypes that will require further investigation (R. Prŷs-Jones and E. Dickinson pers. comm.), and lectotypification using one of these specimens or another one might be required. At any rate, the original description of *xanthodryas* (Swinhoe 1863) matches Japanese breeding birds better than any of the other taxa, so it seems clear that the name *xanthodryas* should apply to that population.

Another issue concerns the name *hylebata* Swinhoe, 1861. We have not examined the type of *hylebata*, which was collected on migration at the same locality as *xanthodryas* but described 2 years earlier (Table 1). Its location, if it still exists, is unknown to us; there is a specimen in the Netherlands Centre for Biodiversity, Naturalis, Leiden, which might be the type, although it is not registered as such (S. van der Mije pers. comm.). Accordingly, the name *hylebata* might in fact apply to either the Kamchatka/Sakhalin/Hokkaido or the Honshu/Kyushu/Shikoku populations. The same applies to the taxon *sylvicultrix* Swinhoe, 1860, which was also collected at the same place as *xanthodryas* and *hylebata*. We have not been able to trace any type specimens of this taxon. Despite the fact that Swinhoe had nearly 200 specimens in his possession (Swinhoe 1863), none of his specimens currently in The Natural History Museum, Tring, is definitely pre-1860 (R. Prŷs-Jones pers. comm.) and there is no reference to any type specimen in the original description or in subsequent publications (Swinhoe 1860, 1863, 1871).

Despite the nomenclatural uncertainties, we use the name *examinandus* for the Kamchatka/Sakhalin/Hokkaido population and the name *xanthodryas* for the Honshu/Kyushu/Shikoku population. We thus differ from Ticehurst (1938) only in assigning the populations from Hokkaido and all of the Kuriles to *examinandus*, and in confirming that Sakhalin birds are indeed *examinandus* (and in noting that *xanthodryas* also breeds on Kyushu and Shikoku, which was unknown to Ticehurst).

It is uncertain whether the breeding distributions of *borealis/kennicotti*, *examinandus* and *xanthodryas* overlap. Presumably, *xanthodryas* is geographically isolated from the others. It is possible that *borealis* and *examinandus* meet somewhere in central or northern Kamchatka, but this is unknown. One of us (P.A.) identified '*xanthodryas*' (i.e. most likely *examinandus*, but no sound recordings available) by song at Milkovo (*c.* 54.40°N, 158.32°E) and on Ostrov Beringa (*c.* 55.4°N, 166.16°E) in June 1992, and we have received one recording of *examinandus* (by Christoph Zöckler) from near Ust-Kamchatsk (*c.* 56.1°N, 162.4°E). The only recordings that we have come across from northern Kamchatka are from Ossora (*c.* 59.15°N, 163.05°E) in mid-June (songs and calls of four individuals, and call of one additional individual; Alexander Hellquist), and these are classic eastern *borealis*. We have no recordings of any 'Arctic Warbler' from Kamchatka in between these localities.

We have recently come across a sound recording of *examinandus* from the mainland immediately adjacent to the northern tip of Sakhalin (Vlas'evo: 53.25°N, 140.53°E) on 17 June (Xeno-canto XC40211; http://xeno-canto.org), which indicates that *examinandus* might also breed on the mainland. However, the statement by Watson *et al.* (1986) that *xanthodryas* (*examinandus*) breeds along the northern shores of the Sea of Okhotsk is probably incorrect. More research is needed to establish the detailed breeding distributions of the three species, and to find out whether there is any contact among them and, if there is, to study their interactions.

Furthermore, the migration routes and winter distributions of the three species are uncertain, and need to be studied. The easiest approach would probably be to analyse recordings of calls. We have confirmed the presence of *borealis* from the Thai–Malay Peninsula, the Philippines and Borneo, but our sample of recordings is small. The lectotype of *examinandus* is from Bali, Indonesia.

The breeding habitats differ at least between *xanthodryas* and the other taxa. Both *borealis/kennicotti* and *examinandus* prefer broadleaved forest at low elevation (Dement'ev & Gladkov 1968, Chrabryj *et al.* 1991, Cramp 1992, Lowther 2001), although the latter is said to reach 1000 m or higher on Sakhalin (Dement'ev & Gladkov 1968, called *hylebata*) and to be common also in the mountains in Kamchatka (below 'the upper limit of the Alder scrub'; Bergman 1935). In contrast, *xanthodryas* breeds exclusively in the subalpine zone in mountains (mainly above *c.* 1500 m, up to *c.* 2500 m), chiefly in coniferous forest with Birch *Betula* spp. admixed, but also in pure Birch forest where that forest type is present at the upper tree limit (Jahn 1942, pers. experience, *contra* Brazil 1991 with respect to preferred forest type).

Subspecies

Most authors recognize *borealis* as the only subspecies in continental Eurasia (Ticehurst 1938, Williamson 1967, Cramp 1992, Dickinson 2003, Bairlein *et al.* 2006, Table 1). In contrast, Vaurie (1959) and Watson *et al.* (1986), following Portenko (1938), divide the continental populations into *borealis*, *talovka*, *transbaicalicus* and *hylebata* (Table 1). Dement'ev and Gladkov (1968) synonymize *talovka* with *borealis* and *transbaicalicus* with *hylebata* (Table 1). The sequence data in the present study and in the studies by Reeves *et al.* (2008) and Saitoh *et al.* (2010) represent all of these taxa, and none of them is differentiated with cytochrome-*b*. Accordingly, the mitochondrial data do not support recognition of any of these taxa, including the widely accepted *kennicotti* (although they do not reject them either, as morphologically distinct taxa can be undifferentiated in mitochondrial markers; cf. Zink 2004, Phillimore & Owens 2006). As *kennicotti* seems to also be poorly differentiated morphologically (Ticehurst 1938, Vaurie 1954, Williamson 1967, Cramp 1992, Saitoh *et al.* 2008), it seems to be best synonymized with *borealis*.

It is worth noting that the mitochondrial haplotypes of *borealis* (as used here) from northeast Siberia (Magadan, Anadyr) and *kennicotti* form a clade (Reeves *et al.* 2008, Saitoh *et al.* 2010), suggesting that it might be appropriate to recognize these birds taxonomically. However, the geographical distribution of this clade apparently does not correlate perfectly with the differences in song between different populations of *borealis/kennicotti*, as birds with the eastern song type (thin elements at beginning of syllables) breed south (Khabarovsk, number 16 in Fig. 1; *c.* 48°N, 135°E) and west (Huzhong, number 14 in Fig. 1; *c.* 52°N, 123°E) of a breeding season *borealis* haplotype from 50.77°N, 134.75°E, which was reported by Reeves *et al.* (2008) to belong outside of the northeastern clade. Moreover, the distribution of the eastern song type does not coincide with the distribution of any of the subspecies recognized by Portenko (1938) or Dement'ev and Gladkov (1968), as it encompasses both *borealis* (*sensu* these authors) and *hylebata*. More research is warranted on the detailed phylogeography and distribution of song types within the eastern part of the range of *borealis*.

The Sakhalin population has been treated either as *hylebata* (Dement'ev & Gladkov 1968) or as *xanthodryas* (Stepanyan 1978, Cramp 1992, Dickinson 2003), whereas Ticehurst (1938) thought that it probably belonged to *examinandus*. The molecular results of Saitoh *et al.* (2010) confirm that it belongs to *examinandus*. The Hokkaido population was discovered recently (Nakagawa & Fujimaki 1985), and its affinities were uncertain until it was shown to belong to *examinandus* by Saitoh *et al.* (2010). Although no molecular data are available from the Kurile Islands, the vocalization data suggest that all of the Kurile Islands belong to *examinandus*, *contra* Ticehurst (1938) and Dement'ev and Gladkov (1968), who treated northern and southern Kuril populations as different taxa (Table 1).

TAXONOMIC RECOMMENDATION

To conclude, we suggest that *P. borealis* is better treated as three species: (1) *P. borealis* Blasius, 1858, on mainland Eurasia (except southern Kamchatka) and Alaska; (2) *P. examinandus* Stresemann, 1913, in southern Kamchatka (north to at least 56°N), Sakhalin, the Kuril Islands and Hokkaido; and (3) *P. xanthodryas* Swinhoe, 1863

in Japan except Hokkaido. The taxon *kennicotti* appears to be best synonymized with *borealis*. The taxon *flavescens* is confirmed to be a junior synonym of *borealis*. We propose the following English names: Arctic Warbler for *P. borealis sensu stricto*, Kamchatka Leaf Warbler for *P. examinandus* and Japanese Leaf Warbler for *P. xanthodryas*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Detailed comparison of songs of different taxa in the Arctic Warbler complex.

Table S2. Syllable order (syntax) in *examinandus* and *xanthodryas*.

Table S3. Detailed comparison of calls of different taxa in the Arctic Warbler complex.

Appendix S1. Information on sound recordings and sequences analysed.

Figure S1. Mitochondrial cytochrome-*b* tree estimated by Bayesian inference using the GTR + I model.

Figure S2. Song of *borealis*: (a) Abisko[1], Sweden, June (Krister Mild; same individual as in Fig. 3a); (b) Khovsgol lake[8], Mongolia, June (Geoff J. Carey); (c) Respublika Tyva[7], Russia, July (Magnus Robb); (d) Respublika Tyva[7], Russia, May (Nicolai Formosov/BL 46264); (e) Respublika Tyva[7], Russia, June (Veprintsev 1982); (f) Ulan Bator[10], Mongolia, June (Dieter Wallschläger/BL 14496); (g) Huzhong[14], Heilongjiang province, China, June (Per Alström/BL WA 1994/82; same individual as in Fig. 3f); (h) Magadan[12], Russia, June (Ulf Hassel); (i) Magadan[12], Russia, June (Ulf Hassel); (j) Magadan[12], Russia, June (Ulf Hassel); Magadan[12], Russia, June (Trevor Price); (k) Khabarovsk[16], Russia, May (Anvar B. Kerimov/BL 46280). Superscript numbers represent localities referenced in Fig. 1 (details in Appendix S1).

Figure S3. Song of *kennicotti*: Alaska. (a) Matanuska Susitna[18], June (C.A. Marantz/Macaulay Library of Natural Sounds [ML] 77051); (b) NW of Nome[17], June (G.A Keller/BL 105867); (c) N of Nome[17], June (G.A. Keller/ML 105870). Complete strophes. Susperscript numbers represent

localities referenced in Fig. 1 (details in Appendix S1).

Figure S4. Song of *examinandus*: (a) Kamchatka[19], Russia, July (Veprintsev 1982, same individual as in Fig. 4a); (b) Sakhalin[20], Russia, July (Toshio Oda/Oda 2005, same individual as in Fig. 4b); (c) Mt Rausu[23], Hokkaido, Japan, July (Takema Saitoh; same individual as in Fig. 4e); (d) Mt Shari[23], Hokkaido, Japan, August (Takema Saitoh). Superscript numbers represent localities (details in Appendix S1).

Figure S5. Song of *xanthodryas*: Honshu, Japan. (a) Karuizawa[25], May (Urban Olsson; same individual as in Fig. 5a); (b) Mt Fuji[25], July (Takema Saitoh); (c) Mt Hachimantai, Iwate[24], July (Takema Saitoh); (d) Mt Ishizuchi, Shikoku[26], August (Haruo Kuroda). Complete strophes. Superscript numbers represent localities referenced in Fig. 1 (details in Appendix S1).

Figure S6. Factor analysis of song variables. In (a) nine variables are included, and in (b) the variable 'number of thin elements/unique multi-element A syllable' is excluded.

Figure S7. Canonical discriminant analysis of four measurements of 58 adult Arctic Warblers, including three type specimens.

Audio S1. *Phylloscopus borealis* call, Huzhong, Heilongjiang, China. Per Alström.

Audio S2. *Phylloscopus borealis* song, Huzhong, Heilongjiang, China. Per Alström.

Audio S3. *Phylloscopus borealis* song, Khovsgol lake, Mongolia. Geoff J. Carey.

Audio S4. *Phylloscopus examinandus* call, Japan (migration). Per Alström.

Audio S5. *Phylloscopus examinandus* call, Japan (migration). Per Alström.

Audio S6. *Phylloscopus examinandus* call, Mt Rausu, Hokkaido ind1-PG5. Takema Saitoh.

Audio S7. *Phylloscopus examinandus* song, Mt Rausu, Hokkaido ind4-PG3. Takema Saitoh.

Audio S8. *Phylloscopus examinandus*, song Mt Shari, Hokkaido ind3-PG9. Takema Saitoh.

Audio S9. *Phylloscopus examinandus* song, Opala river, Kamchatka ind2-PG4-2. Takema Saitoh.

Audio S10. *Phylloscopus xanthodryas* call, Karuizawa, Honshu. Urban Olsson.

Audio S11. *Phylloscopus xanthodryas* call, Karuizawa, Honshu. Urban Olsson.

Audio S12. *Phylloscopus xanthodryas* song, Iwate, Honshu ind6-PG1. Takema Saitoh.

Audio S13. *Phylloscopus xanthodryas* song, Iwate, Honshu ind12-PG1. Takema Saitoh.

Audio S14. *Phylloscopus xanthodryas* song, Karuizawa, Honshu. Urban Olsson.

Audio S15. *Phylloscopus xanthodryas* song Shikoku, Japan ind2-PG2. Takema Saitoh.

Audio S16. *Phylloscopus borealis* song, Ivalo, Finland. Hannu Jännes.

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