On the taxonomy of Yellow-browed Warbler, *Phylloscopus inornatus* sensu lato, based on the analysis of collection specimens (Aves: Sylviidae)

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Red'kin, Ya.A. & Konovalova, M.V. 2004. On the taxonomy of Yellow-browed Warbler, *Phylloscopus inornatus* sensu lato, based on the analysis of collection specimens (Aves: Sylviidae). *Zoosystematica Rossica*, **13**(1): 137-150.

The comparative analysis was performed on 749 specimens of Yellow-browed Warbler forms (*Phylloscopus inornatus inornatus, Ph. i. humei, Ph. i. mandellii*). Morphometrical parameters as well as the patterns of plumage coloration have been estimated. All three forms steadily differ from each other in the coloration patterns, while the dimensional parameters are greatly overlapping. The birds with intermediate features of *inornatus* Ч *humei* were found out to be rather numerous in their spatial contact zone. Their total number turned to be less than the number of phenotypically "pure" *humei,* but more than that of *inornatus,* while according to literature the individuals with intermediate type of song have never been recorded so far. Hence, we suppose that the hybrid birds inherit the song of either one or another form. Therefore the conclusion about species status of *inornatus* and *humei* appears to be rather ungrounded because it was based only on the results of vocalization analysis without examining of collection. We suppose that the most correct way is to consider this monophyletic group (*inornaus – humei – mandellii*) as a single polytypic species having originally a circular range.

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Introduction

Recently, taxonomy of closely related forms of the genus *Phylloscopus* has attracted attention of both Russian and foreign researchers. Many representatives of this group tend to have geographic variation, which is caused by spatial isolation of populations. The study of the secondary contact zones of leaf-warblers is rather difficult because of significant morphological similarity within the group. But many close forms of this group have acoustic repertoires that differ greatly from one another, which in many cases allows the researchers to point out their taxonomic independence. For the last decade, over ten taxa, which were treated as geographical races, have been elevated to the status of species (Irwin et al., 2001). In the majority of cases, such conclusions were based on field observations and analysis of acoustic signals (Helb et al., 1982; Formozov & Marova, 1986; Mild, 1987; Martens, 1988; Salomon, 1989; Salomon & Hemim, 1992; Lisovsky & Rubtzov, 2001), and in some cases on molecular analysis (Helbig et al., 1993, 1995, 1996). The collected specimens were examined only in few cases, primarily by Russian ornithologists (Stepanyan, 1983; Veprintsev et al., 1990; Salomon et al., 1997, etc.).

Phylogenetic and taxonomic relations of *inornatus*, *humei* and *mandellii* are one of the difficult taxonomic problems of the Palaearctic avifauna. Originally all three forms of Yellow-browed Warbler were described from the territory of India as three separate species: *Regulus inornatus* Blyth, 1842, *Reguloides humei* Brooks, 1878, and *Reguloides mandellii* Brooks, 1879. Hartert (1910) was the first to consider these three taxa as subspecies of the polytypic species. This solution was based on the significant morphological similarity of three forms, two of which (*inornatus* and *humei*) were distributed in the vast area from high mountain forests of Middle Asia to the zone of forest tundra in the north of Siberia, and one form occupied an isolated area in the high mountain forests of Central China (Fig. 1). For 50 years, this point of view was not changed (Dementiev, 1937; Ticehurst, 1938; Ptushenko, 1954; Vaurie, 1959; Portenko, 1960, etc.).

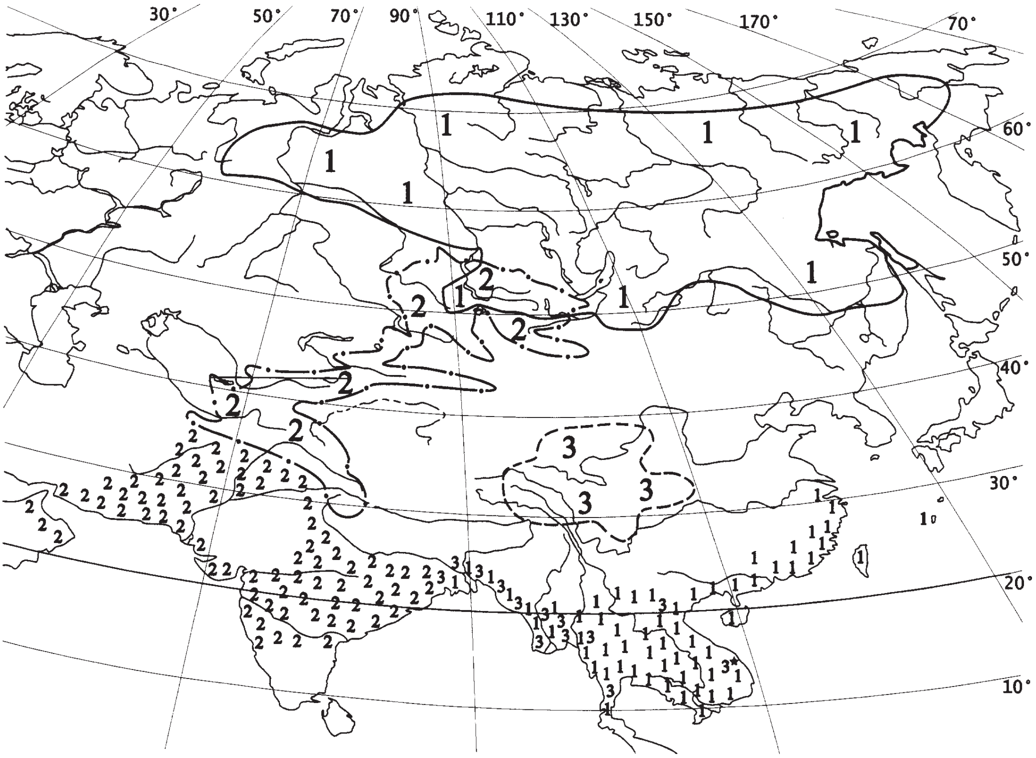

Fig. 1. Distribution of *Phylloscopus inornatus* s. l. Breeding areas: **1** – *Ph. i. inornatus*; **2** – *Ph. i. humei*; **3** – *Ph. i. mandelii*. Winter areas: $1_1{}^1$ – *Ph. i. inornatus*; $2_2{}^2$ – *Ph. i. humei*; $3_3{}^3$ – *Ph. i. mandelii* (3*, new record: Vietnam, Kon Tum Prov., western slope of Mount Ngoc Linh (15є04’N; 107є59’E), 1700 m, April 2004, M. Kaliakin leg.).

In particular, there was an opinion about spatial disconnection of nesting areas of *Ph. i. inornatus* and *Ph. i. humei* (Sushkin, 1938; Ticehurst, 1938). However some authors pointed out that the form *humei* “is strongly different, does not have smooth transitions, is also different in vocalization, nesting habitats, etc.” (Portenko, 1960). Later, there was a continuous increase of information concerning the existence of sympatry zones of Yellow-browed Warbler (*Ph. i. inornatus*) and Hume’s Yellow-browed Warbler (*Ph. i. humei*). Maursberger (1983) recorded combined nesting of these two forms in the north of Mongolia and marked noticeable differences in their vocalization, which had been distinguished by Schubert (1982). Durnev et al. (1984) reported about the nesting of Hume’s Yellow-browed Warbler at the upper border of forest in the Khamar-Daban Mountains, in that very region where Yellow-browed Warbler nests. These authors also discovered reliable distinctions in the songs of two mentioned forms. Formozov & Marova (1986) found the zone of sympatry of *inornatus* and *humei* in the territory of Tuva (Tannu-Ola Mountains) based on the records of sound signals. These authors supposed that the habitat disconnection of two forms of Yellow-browed Warbler as well as the records in the narrow zone of intergradations of habitats and the absence of birds with intermediate song type or having both types may be considered as a reason for upgrading of these forms to the species status. The last article should be treated as a start point of the development of opinions about the existence of species status barrier between these taxa. Mild (1987) also came to conclusion that these forms should be regarded as separate species according to the results of playback experiments with mutual presentation of song records to territorial males of *inornatus* and *humei*. Later, Marova (1993) noted that the findings of combined settlements of *inornatus* and *humei* as well as the absence of information about individuals with intermediate morphological and acoustic features confirm that these forms had reached the level of megasubspecies or semispecies. The viewpoint about *inornatus* and *humei* being separate species has been expressed many times in the studies devoted to the analysis of particular taxonomic features of morphologically close forms of European Passeriformes and in the reviews of Palaearctic avifauna as a whole (Svensson, 1987, 1992; Cramp, 1992). The latest stage in this investigation are the field studies by Lisovsky & Rubtzov (2001) and Irwin et al. (2001). These researches were carried out in the Western Sayan and nearby regions of spatial contacts of *humei* and *inornatus*. In these cases, the researchers repeated the playback experiments within combined and "pure" settlements of both forms. In both cases, only the responses to the playbacks of their own form's song were observed and the signals of the other form were ignored. The structure of the *mandellii* song was found to be more similar to that of *humei*. When the records of two other forms were presented to *mandellii* males, only the song of Hume's Yellow-browed Warbler was responded (Irwin et al., 2001). Besides, the results obtained during the mitochondrial DNA control region sequences are analysed in that article. The analysis revealed much more similarity between *mandellii* and *humei* than between these forms and *inornatus*. At the same time the analysis of 8 specimens of *humei* and 3 specimens of *inornatus* did not revealed gene flow between these forms. This fact together with the results of playback experiments allowed the authors to consider the form *inornatu*s as a separate species. The form *mandellii* was included into the second polytypic species *Phylloscopus humei* despite the fact that it is intermediate between *humei* and *inornatus* in its morphological characteristics. This standpoint was reflected in the latest checklist of the birds of the world (Dickinson, 2003) as well.

The results gained during the field work in 1999 and 2000 in the Republic of Tuva allowed us to complete the range of opinions about spatial and reproductive relationships of these forms. Our own observations and few collected specimens of warblers made us deal with the problem of real relationships of *humei* and *inornatus* forms. This was the purpose of the analysis conducted with the use of extensive material of several ornithological collections.

Material and methods

Our own field observations and collecting were carried out during the expedition of Moscow State University Zoological Museum to the Kyzyl, Erzin, Tes-Khem, Ovyur and Mongun-Tayga Districts of the Republic of Tuva in 1999 and 2000. In addition we have examined extensive collections of Zoological Institute, Russian Academy of Sciences, St.Petersburg (ZISP), Moscow State University Zoological Museum (ZMMU), Department of Zoology and Ecology of the Moscow Pedagogical State University, Department of Vertebrate Zoology, Biological Faculty, Moscow State University, State Darwinianum Museum, Moscow (SDM), and Vladimir N. Sotnikov's private collection. We also examined the collections made by the joint expeditions of State Darwinianum Museum and Burke Museum of Washington, Seattle (UWBM) during the field work in the Republic of Tuva in 2000. Type specimens of *Ph. i. humei* and *Ph. i. mandellii* were examined in the Ornithological Department of National History Museum, Tring. In total, we have analysed 749 bird specimens.

Such morphological characteristics as wing length, tail length, tarsus length and bill length were analysed. The wing length was measured when it was straightened to the maximum on the plate. The tail length was measured from the root of the middle pair of rectrices to the end of the longest rectrices. The tarsus length was measured from intertarsal joint to the lower edge of the last complete scale before the toes diverge. The bill length was estimated from the distal edge of the nostril to the end of the bill (the length of a bill from a nostril) as well as along the culmen from the back edge of upper mandible (bill length from the forehead edge).

We estimated other plastic features, such as the length ratio of the second primary to the 7th and 8th primaries.

The material for comparative analysis and description of coloration was chosen with account of feather condition. The specimens in fresh plumage (collected after finishing of post breeding or post juvenile moult), as well as ones in worn breeding plumage (April – early June) and specimens in strongly worn plumage (late June – July) were analysed separately. The scale of colours (Smithe, 1975) was used for the description of coloration.

The abbreviations used in the description of plumages: P – primaries; GC – Greater coverts; MC – Median coverts.

Results

Plumage coloration

The characteristic colour patterns of three forms of Yellow-browed Warbler were described in many articles (Dement'ev, 1937; Ticehurt, 1938; Vaurie, 1959; Portenko, 1960, etc.). However, it seems rather important to give our own description of their plumage coloration for the further discussion of reproductive and phylogenetic relationships of the examined forms.

The plumage coloration of leaf-warblers is provided by the presence and combination of three groups of pigments (eumelanin, feumelanin, and lypochrome). Eumelanin provides all range of shades from light gray to black. "Pure" feumelanin provides the shades from pale sulfur-yellow to bright chestnut. Lypochrome determines yellow coloration. Greenish colour common to the most part of the genus *Phylloscopus* is provided by the combination of feumelanin and lypochrome while olive-brown shades, by the combination of lypochrome and eumelanin.

Fresh plumage

Ph. i. inornatus. Upperparts olive-green; cap slightly darker. Underparts whitish. Breast tinged with light smoke gray. Sulfur yellow longitudinal streaks spread over the whole underparts. Flanks slightly olive yellow. Supercilium and the wing bars formed by light tips of GC and MC sulfur yellow.

Ph. i. humei. Upperparts olive-green but a bit paler than those of *inornatus*. Cap noticeably different from the upperparts by its dark grayish horn colour. Underparts pale horn. Yellowish streaks widely spread over the whole underparts, less expressed than those of *inornatus*. Throat whitish, without grey tinge. Central part of breast pale horn. Sides of breast and belly straw yellow. Wing bars sulfur yellow, brighter than those of *inornatus*. Colour of supercilium varies from sulfur yellow to trogon yellow.

Ph. i. mandellii. Upperparts olive grey; cap darker olive. Underparts whitish. Yellow longitudinal streaks on the underparts narrower and sparser than those of *humei* and *inornatus*. Throat and breast smoke grey. Sides of breast also smoke grey without sulfur yellow shade. Sides of belly tinged with grayish olive shade. Supercilium pale sulfur yellow (slightly paler than that of *humei* and *inornatus*). Wing bars straw yellow.

Worn plumage (April – early June)

Ph. i. inornatus. Upperparts olive green; cap dark brownish olive. Underparts whitish. Breast slightly smoke gray. Sulfur yellow longitudinal streaks are spread over the whole underparts, they are a bit paler than in fresh plumage. Olive yellow shade on the sides of the belly practically unnoticeable. Supercilium yellowish, but paler than that in fresh plumage. Wing bars whitish.

Ph. i. humei. Upperparts grayish olive; cap intermediate between greyish horn and dark brownish olive. Sulfur yellow shade of lower part paler. Throat and central part of the belly, whitish. On the belly, pale sulfur yellow streaks are noticeable. Breast and belly sides slightly greyish olive. Yellow streaks less developed than those of *inornatus*. Supercilium in average less sulfur yellow. Wing bars whitish, sometimes with faint yellow shade.

Ph. i. mandellii. General coloration of upperparts darker than that of *inornatus*. Back olive green. Cap dark brownish olive. Underparts whitish. Throat and breast smoke grey. Sulfur yellow streaks on the underparts less noticeable than those in fresh feather. Breast sides smoke gray. Sides of belly slightly greyish olive. Supercilium paler than that of birds in fresh feather and more whitish. The dark colour of ear-coverts more contrasting than that of *inornatus*. Wing bar whitish with faint yellow shade.

Strongly worn plumage (late June – July)

Ph. i. inornatus. Upperparts and head olive. Underparts whitish. Yellow shade of streaks is the least noticeable and almost absent in July. Breast tinged light smoke grey. Coloration of supercilium varies from pale yellow to white. Wing bars whitish.

Ph. i. humei. Upperparts greyish olive; cap olive. Underparts whitish. Yellowish shade expressed as very weak tinge on the sides of the belly or absent. There is a smoke grey shade on breast and belly sides. Coloration of supercilium varies from cream to pale horn. Wing bar, whitish.

Ph. i. mandellii. Upperparts olive green. Cap dark brownish olive, but paler than that of specimens collected in May. Underparts whitish. Throat and breast smoke grey. On breast sides, this shade is darker. Sides of belly slightly greyish olive. Yellowish shade on the lower part virtually unnoticeable. In general, the underparts coloration darker than that of *inornatus*. Supercilium paler than that of the birds in fresh feather, and more whitish. Ear coverts coloration darker than that of *inornatus*. Wing bar whitish.

As evidenced by the above descriptions, there is some regularity of pigment distribution which determines the leaf-warbler plumage coloration. *Ph. i. inornatus* and *Ph. i. humei* plumage, coloration of which is the most different, demonstrate two opposite ways of melanin pigmentation. *Ph. i. inornatus* presents almost only eumelanin plumage pigmentation reflected in full absence of brown and sulfur shades. On the contrary, in *Ph. i. humei* olive-brown colours predominate as well as sulfur shades determined by almost complete substitution of feumelanin for eumelanin. The *Ph. i. mandellii* plumage coloration is more similar to that of *Ph. i. inornatus*, has a number of features (sulfur yellow shade of supercilium, etc.) typical of *Ph. i. humei* as well. Thus it is intermediate between them. As a whole, the three discussed forms of yellow-browed warblers are characterized by rather distinctive colour patterns that allow identification of most specimens in any feather condition.

Plastic features

The dimension parameters of three forms of Yellow-browed Warblers are presented in the tables. Wing length and tail length are significantly smaller in females of all forms than in males ($p<0.001$); tarsus length and body weight in females is found to be smaller than those in males on average though the difference is not significant ($p>0.05$). There are no significant differences of the wing and tail length in both fresh and worn plumage as well as of all other parameters between the samplings from different parts of the range in each examined taxon.

The differences of wing length between *Ph. i. inornatus*, *Ph. i. humei* and *Ph. i. mandellii* are not great (Table 1) and greatly overlap, but the difference of this feature in the first two forms is rather noticeable. On average, *Ph. i. humei* has the longest wing, while *Ph. i. inornatus* has the shortest wing. We found significant differences between these forms comparing worn plumage of adult males ($p<0.05$), and females ($p<0.01$), as well as birds of both sexes in fresh feather ($p<0.001$). The average parameter of wing length of *Ph. i. mandellii* is definitely intermediate between two previous forms, but has no significant difference from each of them.

Table 1. *Phylloscopus inornatus* sensu lato, wing length, mm

Subspecies	Sex	Plumage	n	M	σ	m	min	max
Ph. i. inornatus	m	fresh	121	57.11	1.774	0.237	51.0	61.0
Ph. i. humei	m		92	57.98	2.030	0.269	51.1	61.6
Ph. i. mandellii	m		12	57.45	2.528	0.350	53.0	61.3
Ph. i. inornatus	f		30	54.04	2.282	0.313	51.0	59.6
Ph. i. humei	f		36	55.21	1.895	0.257	52.0	60.0
Ph. i. mandellii	f		6	54.95	3.153	0.429	51.8	59.7
Ph. i. inornatus	m	worn	36	56.35	1.373	0.185	52.4	58.7
Ph. i. humei	m		72	57.49	1.954	0.260	52.1	60.7
Ph. i. inornatus	f		10	54.40	1.499	0.205	52.7	57.0
Ph. i. humei	f		33	56.15	1.975	0.266	52.4	59.7

Table 2. *Phylloscopus inornatus* sensu lato, tail length, mm

Subspecies	Sex	Plumage	n	M	σ	m	min	max
Ph. i. inornatus	m	fresh	121	41.48	1.821	0.286	37.0	45.8
Ph. i. humei	m		92	42.08	2.118	0.330	36.1	45.9
Ph. i. mandellii	m		12	43.50	2.696	0.414	38.7	47.4
Ph. i. inornatus	f		30	38.91	2.027	0.329	35.1	43.2
Ph. i. humei	f		34	40.15	2.139	0.342	36.3	45.3
Ph. i. mandellii	f		6	39.20	2.829	0.458	36.5	44.0
Ph. i. inornatus	m	worn	36	41.15	2.394	0.378	34.3	45.8
Ph. i. humei	m		72	42.01	1.832	0.286	37.3	45.7
Ph. i. inornatus	f		10	39.54	1.693	0.273	37.0	42.1
Ph. i. humei	f		32	40.78	2.291	0.363	36.2	46.0

Table 3. *Phylloscopus inornatus* sensu lato, length of tarsus, mm

Subspecies	Sex	n	M	σ	m	min	max
Ph. i. inornatus	m	153	17.36	0.714	0.177	15.0	19.3
Ph. i. humei	m	158	18.14	0.627	0.152	16.7	19.7
Ph. i. mandellii	m	12	17.99	0.558	0.135	17.1	18.9
Ph. i. inornatus	f	40	16.95	0.756	0.189	15.7	18.7
Ph. i. humei	f	67	17.89	0.612	0.149	15.5	19.4
Ph. i. mandellii	f	6	17.30	1.092	0.270	15.8	19.0

Table 4. *Phylloscopus inornatus* sensu lato, length of bill from nostril, mm

Subspecies	Sex	n	M	σ	m	min	max
Ph. i. inornatus	m	144	5.54	0.301	0.141	4.9	6.9
Ph. i. humei	m	153	5.29	0.288	0.139	4.5	6.2
Ph. i. mandellii	m	11	5.37	0.211	0.101	5.0	5.7
Ph. i. inornatus	f	39	5.48	0.251	0.118	5.0	6.0
Ph. i. humei	f	68	5.25	0.462	0.224	4.7	8.5
Ph. i. mandellii	f	6	5.33	0.273	0.131	4.9	5.6

Table 5. *Phylloscopus inornatus* sensu lato, length of bill, mm

Subspecies	Sex	n	M	σ	m	min	max
Ph. i. inomatus	m	143	8.47	0.518	0.190	7.0	9.8
Ph. i. humei	m	153	7.90	0.543	0.207	6.7	9.5
Ph. i. mandellii	m	11	8.28	0.519	0.192	7.7	9.2
Ph. i. inomatus	f	39	8.49	0.542	0.198	7.3	9.4
Ph. i. humei	f	66	7.75	0.478	0.184	6.9	9.6
Ph. i. mandellii	f	6	8.05	0.362	0.136	7.6	8.7

Table 6. *Phylloscopus inornatus* sensu lato, weight, g

Subspecies	Sex	n	M	σ	m	min	max
Ph. i. inornatus	m	26	6.53	0.979	0.417	5.0	9.2
Ph. i. humei	m	7	6.43	0.834	0.358	5.3	7.7
Ph. i. inornatus	f	8	7.13	1.160	0.4.69	5.0	8.5
Ph. i. humei	f	3	6.05	0.983	0.438	5.0	7.0

The differences of tail length between these forms (Table 2) are rather great. *Ph. i. inornatus* has the least average parameter of this feature, *Ph. i. humei* and *Ph. i. mandellii* having longer rectrices. Males of *Ph. i. mandellii* appeared to have significantly longer tail than both *Ph. i. inornatus* ($p<0.001$) and *Ph. i. humei* ($p<0.01$). Females of *Ph. i. humei* surpass those of two other forms by this parameter, but differ significantly only in *Ph. i. inornatus* ($p<0.01$).

Ph. i. inornatus has the shortest tarsus (Table 3), it is significantly different from the tarsus length of *Ph. i. humei* ($p<0.001$) and *Ph. i. mandellii* ($p<0.01$). *Ph. i. humei* has the greatest average value of this parameter although it does not significantly differ from that of *Ph. i. mandellii* ($p>0.05$).

The differences of bill length between these forms can be noticed only while measuring from the edge of upper mandible (Tables 4, 5). In average, *Ph. i. inornatus* appears to have the longest bill, *Ph. i. humei* has the shortest bill, *Ph. i. mandellii* is intermediate between them. Only the bill lengths of *Ph. i. inornatus* and *Ph. i. humei* are significantly different ($p<0.05$ for males, $p<0.01$ for females).

The body weight of *Ph. i. inornatus* is a bit greater than that of *Ph. i. humei* (Table 6). We do not have our own information on body weight of *Ph. i. mandellii*.

The most reliable feature to distinguish the forms of yellow-browed warblers is considered the relative length of 2P (Vaurie, 1959; Portenko, 1960; Stepanyan, 2003, etc.). 2P of *Ph. i. inor-*

Table 7. Wing formula variability in subspecies of *Phylloscopus inornatus* sensu lato

Subspecies	Region		Wing formula							Source
			6>2>7	6>2=7	7>2>8		8>2>9		9>2	
Ph. i. inornatus	Far East (from basin of the Anadyr' River to Primorsk Terr.)		67.3% (n=33)	4.1% (n=2)	28.6% (n=14)		–		–	Our data
	South of Krasnoyarsk Terr., Irkutsk Prov., Transbaikalia, Eastern Mongolia		78.3% (n=18)	8.7% (n=2)	8.7% (n=2)		4.3% (n=1)		–	Our data
	North Siberia (including Yakutia)		66.6% (n=38)	8.8% (n=5)	24.6% (n=14)		–		–	Our data
	All breeding area (including autumn-migration birds)		67.9% (n=167)	9.3% (n=23)	21.2% (n=56)		1.6% (n=4)		–	Our data
	All breeding area	Males	40%	40%	20%		–		–	Ticehurst, 1938
		Females	20%	38%	42%		very rare		–	
Ph. i. humei	Altay, Tarbagatay, Saur, South-Western Mongolia		–	2.2% (n=1)	80.4% (n=37)		15.2% (n=7)		2.2% (n=1)	Our data
	Western Tien Shan (South Kazakhstan, Kirgizia)		12.9% (n=8)	–	70.9% (n=44)		16.2% (n=10)		-	Our data
	North-Western China (Dzhungaria, Kashgaria)		–	–	43.6% (n=17)		56.4% (n=22)		–	Our data
	Pamiro-Alai, Western Himalayas		–	–	33.3% (n=2)		50.0% (n=3)		16.7% (n=1)	Our data
	All breeding area (including autumn-migration birds)		3.9% (n=13)	2.7% (n=9)	68.8% (n=229)		21.6% (n=72)		3.0% (n=10)	
	All breeding area	Males	–	–	53%	2=8: 25%	20%	2=9: 2%	–	Ticehurst, 1938
		Females	–	–	24%	28.5%	36%	8%	3.5%	
Ph. i. mandellii	All breeding area		–	–	35.3% (n=6)		35.3% (n=6)		29.4% (n=5)	Our data
			–	–		2=8: 4%	21%	2=9: 40%	32%	Ticehurst, 1938

Table 8. Measurements of the specimens with intermediate features *Phylloscopus inornatus inornatus* x *Ph. i.humei* (mm)

# specimens	Sex	Wing length	Tail length	Length of tarsus	Length of bill from nostril	Length of bill
1	m	56.8	40.8	18.1	5.5	8.5
2	m	59.0	44.4	18.4	5.4	7.9
3	?	55.3	40.3	17.1	5.5	7.6
4	m	56.0	40.6	16.7	5.6	8.0
5	?	59.3	43.0	18.4	5.5	8.4
6	m	56.9	44.2	18.2	5.5	8.9
7	m	56.1	42.2	19.2	5.2	8.4
8	m	56.2	41.0	19.1	5.5	9.4
9	f	55.6	40.6	17.0	4.9	8.5
10	m	57.0	41.5	17.0	5.4	8.0
11	m	54.4	38.2	17.0	5.4	8.1
12	m	57.6	41.9	18.2	5.9	8.4
13	m	56.8	41.5	17.4	6.1	8.4
14	m	56.9	39.7	18.2	5.6	7.3

natus is longer than 2P of other forms and usually exceeds the length of 7P, while 2P of *Ph. i. mandellii* and *Ph. i. humei* is shorter than 7P. However, Ticehurst (1938) showed that this parameter widely overlaps within three forms of yellow-browed warblers; in addition, the females of *Ph. i. inornatus* and *Ph. i. humei* differ from the males in shorter 2P on average. We conducted comparative analysis of wing formula (Table 7) of both general samples for each taxon discussed and separate samplings of breeding birds from different parts of *Ph. i. humei* and *Ph. i. inornatus* breeding areas. Since the sex of only half of examined specimens had been determined in collections, we left this feature out of account while performing the analysis. The study revealed great individual variation in every form of *Ph. inornatus*. It makes wing formula rather doubtful criterion for determination of a specimen. This confirms the data previously obtained by Ticehurst (1938). For example, more than 20% of *Ph. i. inornatus* individuals have wing formula 7>2 which is characteristic for *Ph. i. humei*, and not more than 9% have intermediate variant 7=2. One can distinguish specimens with wing formula 2>7 among *Ph. i. humei*, which is more common to *Ph. i. inornatus*.

Ph. i. inornatus has the longest 2P (2>7 for up to 65% of birds) and therefore its wing is the sharpest. *Ph. i. mandellii* differs in the shortest 2P in average (for more than 60% of specimens 2<8) and therefore in the most rounded wing. *Ph. i. humei* occupies intermediate position according to this feature (7>2>8 for more than 65% of examined birds), and the southernmost populations are close to *Ph. i. mandellii* (2<8 for over 50% of birds from South-Western China, Pamir-Alai and the Western Himalayas). The given differences correspond with the conception about the correlation between the wing shape and the season migration distance (Rensch, 1938), because the breeding area of *Ph. i. inornatus* (having sharper wing) is the most remote from winter territories, whereas the distance covered by migrating *Ph. i. mandellii* and *Ph. i. humei* of southern breeding populations turns out to be the least remote.

Spatial contact zone of *Ph. i. inornatus* and *Ph. i. humei*

Spatial contact zone of *Ph. i. inornatus* and *Ph. i. humei* is rather extensive (Fig. 2), it stretches from the west to the east from the Western spurs of the Sayan Mountains (Khakass Autonomous Province of Russia) and the Monguntayga Mountains (Western Tuva) to the mountain regions near Hubsugul Lake (Mongolia) and at least to the western parts of the Khamar-Daban Mountains (Buryatia and Irkutsk Prov.). This zone seems to stretch to the northern spurs of the Eastern Sayans (Krasnoyarsk Terr. and Irkutsk Prov.). Within the outlined zone, one can reveal habitat and altitude separation of two forms of Yellow-browed Warbler. In Tuva Depression, the birds belonging to *Ph. i. inornatus* were recorded in

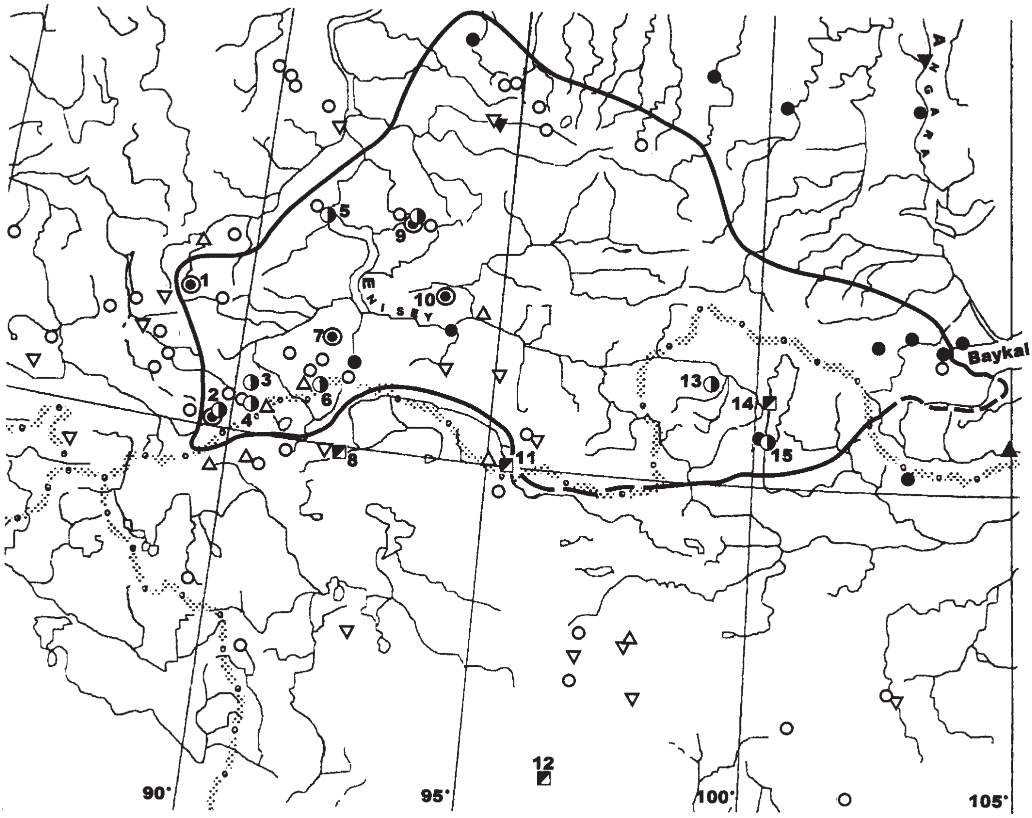

Fig. 2. Distribution of *Phylloscopus inornatus inornatus* and *Ph. i. humei* in their spatial contact zone (**—**, border of the spatial contact zone; ——, parts of the border requiring further specification). *Ph. i. inornatus*: - , records during breeding period; - , records during autumn migration; - , records during spring migration. *Ph. i. humei*: - , records during breeding period; - , records during autumn migration; - , records during spring migration. Both subspecies: - , records during breeding period. Specimens with intermediate features: - , records during breeding period; - , records during autumn migration. **1**, Khakassia, National park "Malyi Abakan" (Irwin et al., 2001); **2**, Tuva, Dund-Jigertein-Gol River Valley (Ortaa-Shetti) (UWBM); **3**, Tuva, southern slope of Tsagan-Shibetu Range (ZMMU); **4**, Tuva, Mugur-Aksy village; **5**, Krasnoyarsk Terr., Borus Range (ZISP); **6**, Tuva, Bora-Shay River (UWBM); **7**, Tuva, 30 km from Chadan town (Irwin et al., 2001); **8**, Mongolia, Ulaangom town; **9**, Krasnoyarsk Terr., Western Sayan, Buyba River (ZISP, ZMMU, SDM; Lisovsky & Rubtsov, 2001; Irwin et al., 2001); **10**, Tuva, Uyukskiy Range (Irwin et al., 2001); **11**, Tuva, Tsagan-Tolgoy River (ZISP); **12**, Mongolia, Yusun-Bulak village (ZISP); **13**, Mongolia, Tsagan-Sair River (ZISP); **14**, Mongolia, western bank of Hubsugul Lake (ZISP); **15**, Mongolia, southern extremity of Hubsugul Lake (ZMMU).

flood plain willow-beds and larch forests. In the Tannu-Ola Mountains, *Ph. i. inornatus* rises almost to the upper forest border along these habitats. Open Siberian cedar woodlands and larch forests on the northern macroslope of the Tannu-Ola Mountains are inhabited by *Ph. i. humei* (Formozov & Marova, 1986). In the Western Sayans, *Ph. i. humei* inhabits open woodlands above boreal coniferous zone, mountain tundra with dwarf (Arctic) birch thickets and rare trees as well as open places of slopes below the forest border. Birds of *Ph. i. inornatus* are recorded there in flood plain alder-willow thickets and in the open places of boreal coniferous zone on the altitudes of 1300-1600 m above sea level (Lisovsky & Rubtzov, 2001). In the Eastern Sayans, *Ph. i. humei* nests at the upper border of the Siberian cedar open woodlands and in the bushes of mountain tundra, while *Ph. i. inornatus* were recorded only in the middle mountain zone (Yudin, 1952). In the Khamar-Daban Mountains, *Ph. i. humei* inhabit only the Siberian cedar forests at the upper border and, above it, cedar elfin and dwarf birch thickets, whereas the birds of *Ph. i. inornatus* usually settle a bit lower (Durnev et al., 1984). However, in some regions these two forms of Yellow-browed warbler are known to inhabit similar habitats. For example, on the southern macroslope of the Tannu-Ola Mountains, *Ph. i. humei* inhabit wet larch and spruce-larch forests along the streams down to the bottom of the mountains (Formozov & Marova, 1986), whereas in the Northern Transbaikalia *Ph. i. inornatus* are quite common in the zone of elfin and dwarf birch above the upper forest border (Red'kin, 2000).

Both forms of Yellow-browed warbler were recorded together in the same habitats in the following localities: National park "Maliy Abakan", Adardash (about 30 km from the town of Chadan, Tuva), the Uyukskiy Mountain Range (Tuva), many times in the Western Sayans on the Buiba River and adjacent areas (Aradanskiy Pass, the Olen'ya River) as well as in the south-west of Tuva in the Dund-Jigerteyn-Gol River Valley in the Monguntayga Mountains (ZISP, ZMMU, SDM, UWBM; Lisovsky & Rubtzov, 2001; Irwin et al., 2001). In these localities, combined settlements of Yellow-browed warbler were situated in willow-birch thickets in river valleys (National park "Maliy Abakan", the Monguntayga Mountains), in fir forests (region of the Olen'ya River in the Sayans) and in larch forests (the Uyukskiy Mountain Range). In addition, the findings of *inornatus* and *humei* were made near each other in the upper reaches of the Torgalyk River (Tannu-Ola) and in Tuva Depression (Formozov & Marova, 1986), northern part of the Eastern Sayans (Yudin, 1952) and in the western part of the Khamar-Daban Mountains (Durnev et al., 1984).

Specimens with intermediate features (*Ph. i. inornatus* Ч *Ph. i. humei*)

Among the examined collected specimens we have managed to find at least 14 ones with intermediate features *inornatus* Ч *humei* from the Western Sayans, the Mongun-Tayga Mountains, the Tsagan-Shibetu Mountains, Western Tannu-Ola, regions adjacent to Northern Mongolia and region of Hubsugul (Hцvsgцl) Lake. Eleven specimens constitute 22% of the total number of birds (n = 50) collected within the outlined zone of spatial contact during the breeding period.

1 (ZISP). Male (ad). July 5, 1913, Western Sayan, Borus Range (breeding). Coloration of upperparts (back) close to that of *humei*, paler than that in *inornatus*. Cap as pale as that of *humei*, but without brownish tinge, pure grey (much paler than in *inornatus*). Light sites on sides of head and supercilium whitish and a bit yellowish, but without sulfur yellow. Breast sides without sulfur yellow tint. Belly coloration as in *inornatus*. Wing formula 7>2>8.

2 (ZISP). Male (ad). June 23, 1912, Mongolia, region of Hubsugul Lake, Tsagan-Sair River (breeding). Coloration of upperparts (back) close to that of *humei* but a bit more greenish. Head coloration close to that of *humei* (brownish tint) but with darker general shade. No sulfur yellow tinge on light sites of plumage; supercilium and sides of head whitish with slight yellowish tint. Belly coloration as in *inornatus*. Wing formula 7>2>8.

3 (ZISP). Sex – ? (ad). June 22, 1912, Mongolia, region of Hubsugul Lake, Tsagan-Sair River (breeding). Plumage coloration of upperparts close to that of *inornatus* but paler as a whole. Lower parts and head flanks as in *inornatus*. Wing formula 2=7.

4 (ZISP). Male (subad). July 27, 1910, Tuva, Tes-Khem River Valley, Tsagan-Tolgoi (this individual was finishing post-juvenal moult, and appears to be a bird on local movements). Head coloration as in *humei*. Back a bit more greenish than in *humei*, but much paler than in *inornatus*. Head sides, underparts and wing bar as those of *inornatus*. Supercilium coloration without sulfur yellow tinge. Wing formula 7>2>8.

5 (ZMMU). Sex – ? (ad). July 17, 1960, Western Sayans, Buiba River (breeding). Coloration of the back like that of *humei*. Head coloration intermediate, less brownish and darker than that of *inornatus*. Head flanks generally whitish with yellowish tint. Very pale sulfur yellow tint present in the central part of ear covering and on neck flanks. Coloration of lower parts as that of *inornatus*. Wing formula 8>2.

6 (ZMMU). Male (ad). July 3, 1981, Mongolia, southern shore of Hubsugul Lake (breeding). Head and back coloration strictly intermediate: greyer and darker than that of *humei*, but a bit paler and more brownish than that of *inornatus*. Light coloration of head and neck flanks with sulfur yellow tint, which is less intensive than in *humei*. Coloration of lower parts as in *inornatus*. Wing formula 7>2>8.

7 (ZMMU). Male (ad). June 14, 2000, Tuva, southern macroslope of Tsagan-Shibetu Mountains (nesting). Upperparts coloration strictly intermediate. Back more grey-green and less brownish olive than that of *humei*. Cap darker and less brownish than that of *humei* and as dark and a bit more brownish (less greenish) than that of *inornatus*. Light coloration on head sides whitish without yellow tint but with weak sulfur yellow tint (paler than that of *humei*). Very weak sulfur yellow tint present on breast sides. The rest of underparts coloration as in *inornatus*. Wing formula 2>7.

8 (ZMMU). Male (ad). June 14, 2000, Tuva, southern macroslope of Tsagan-Shibetu Mountains (nesting). Upperparts coloration as pale as that of *humei*, but brownish tinge less developed (more greenish grey, less olive). Light coloration on head flanks whitish without yellow tint, but with weak sulfur yellow tint (paler than that of *humei*). Breast and belly coloration as that of *humei*. Wing formula 2=7.

9 (ZMMU). Female (subad). September 14, 1977, Mongolia, Ulaangom town (migrating). Upperparts greyish olive, paler and less olive-green than those of *inornatus* but much less olive than those of *humei*. Head darker than back, greenish grey, almost without brownish tint which is common in *humei*, but noticeably paler than head of *inornatus*. Head and neck sides as well as supercilium sulfur yellow, but this tint is much weaker than that of typical *humei* in the same feather condition. Breast and belly coloration like that of *inornatus* and much paler than that of *humei*, sulfur yellow tint practically absent, some longitudinal strokes more distinct than those of *humei*. Wing bar whitish yellow, without any sulfur yellow tint and a bit less bright yellow than that of *inornatus*. Wing formula 2=7.

10 (ZISP). Male (ad?). September 8, 1957, Mongolia, Yusun-Bulak village (migrating). Underparts, head sides and light sites of wings of the same colour as those

of *inornatus*. Upper part of head brownish olive. Back paler than that of *inornatus*. Wing formula 2=7.

11 (ZISP). Male (subad?). September 7, 1871, Mongolia, western shore of Hubsugul Lake (migrating). Underparts, head and light sites of plumage of the same colour as those of *inornatus*. Back coloration almost the same as that of *humei* and it much paler than upper part of head. Wing formula 2>7.

12 (UWBM). Male (ad). June 18, 2000, Tuva, Mugur-Aksy village (breeding). Basic tinges of head similar to those of *inornatus*. At the same time the general shade of coloration is noticeably pale and therefore closer to that of *humei*. Wing formula 7>2>8.

13 (UWBM). Male (ad). June 14, 2000, Tuva, Bora-Shay River (breeding). Coloration intermediate, similar to that of specimens # 6 and # 7. Wing formula 7>2>8.

14 (UWBM). Male (ad). June 14, 2000, Tuva, Dund-Jigerteyn-Gol River Valley (Ortaa-Shetti) (nesting). Coloration the same as that of the latter specimen. Wing formula 7>2>8.

Discussion

Thus, the gene flow between *Ph. i. inornatus* and *Ph. i. humei* in their spatial contact zone is actually taking place. Relatively small number of phenotypically intermediate specimens (22%) can be considered as evidence that rather reliable mechanisms of reproductive isolation do exist for these forms. From the other hand, this figure exceeds the conditional 10% barrier of gene in itrogression (Mayr, 1944) common for closely related forms. However, it is rather difficult to estimate the concentration of hybrid individuals because the significant amount of them cannot be phenotypically distinguished from the parent forms as it was shown for example in the articles dealing with analysis of hybridization zones of *Corvus* (*corone*) *cornix* with neighbouring forms of *Corvus corone corone* (Picozzi, 1976) and *Corvus* (*corone*) *orientalis* (Blinov et al., 1993).

The main argument of the supporters of the opinion about species status of *Ph. i. inornatus* and *Ph. i. humei* is strong differences in their songs and signals. Besides, the absence of individuals with intermediate type of song was noted many times. However, one must pay attention to quite paradoxical fact. In different regions of Tuva (flood-lands of the Yenisey near the settlement Kaa-Khem, Lake Tore-Khol', flood-lands of the Kargy River), we recorded early birds with typical song of Yellow-browed warbler during the spring migration (May – June). All 40 specimens of birds (collected and live birds examined), captured by nets in those days were of *humei* phenotype, whereas individuals of *inornatus* were not collected in that region. Birds with songs characteristic of *humei* were recorded only from Western Tannu-Ola, from the Tsagan-Shibetu Mountains and from the regions adjacent to the mountain part of Altai near Lake Khindictik-Hol'. At the same time, specimens of Yellow-browed warbler are extremely rare both in our collection and in other ones from Tuva territory (among 21 phenotypically pure specimens, 19 belonged to *humei*). The latter data allows us to suggest that the significant part of the population with morphological features of *humei* have the song of Yellow-browed Warbler. This explains the data of Formozov & Marova (1986) about the great number of birds with the song of Yellow-browed warbler in Tuva, which was not confirmed by the collected specimens.

The ratio of the examined specimens (total 50) from the outlined spatial contact zone is 31 individuals (62%) with *humei* phenotype and 8 (16%) with *inornatus* phenotype, while 11 warblers (22%) had intermediate features. Thus, birds with intermediate features predominate in number upon phenotypically "pure" individuals of Yellow-browed warbler. This phenotype ratio can be explained by rarity of the *inornatus* form in the most part of this territory. This situation seems to be corresponding with the fact that in the most part of the outlined zone (at least in Tuva and Western Sayans) the Yellow-browed warblers (which are on the boundaries of their distribution here) settle in solitary groups among Hume's Yellow-browed warblers. Gene flow between these forms may be sufficient enough, but it does not have significant influence on the of phenotypical structure of *humei* population due to the little number of the nominotypical form.

The data obtained in the playback experiments (Lisovsky & Rubtzov, 2001; Irwin et al., 2001), seem to prove undoubtedly the existence of stable reproductive isolation. However, the phenotype of the birds under analysis in majority of cases remained unknown when recorded by song. At the same time the results gained by Mild (1987), who was the first to make such experiments, were rather uneven because he, at least once, recorded the *inornatus* respond to the Hume's Yellow-browed warbler song being played.

The mitochondrial DNA control site DNA sequence analysis did not prove the existence of specimens with phenotype and voice not corresponding to genotype. However, such results were obtained in the analysis of 11 specimens only, from that only 4 *Ph. i. humei* and 2 *Ph. i. inornatus* specimens being known from the spatial contact zone. Thus, the use of so small sample was unlikely to give really significant results. The gene distance between *Ph. i. mandellii* and *Ph. i. humei* was turned out to be noticeably less than that between *Ph. i. inornatus* and these forms, which may by considered as analogous to the situation in the genus *Motacilla* (Odeen & Bjorklund, 2003; Pavlova et al., 2003). These studies, also based on the mitochondrial DNA analysis of the distance between separate *Motacil-*

la citreola subspecies, which are morphologically similar, turned out to be much more considerable. However this fact must not be the final argument to consider them as separate species.

Possible ways of taxonomic interpretation

The suggested by Irwin et al. (2001) separation of the form *inornatus* as a monotypic species from the *mandellii – humei* group based on two criteria only, vocalization and DNA-analysis, seems to be rather unjustified for a number of reasons.

Judging from the morphological features, the form *mandellii* has an intermediate position between *inornatus* and *humei*, being closer to the first one. Songs and communicative signals of *mandellii* also are intermediate, but close to those of *humei*. In the zone of spatial contact, the forms *humei* and *inornatus* occupy quite wide range of habitats, which are frequently overlapping. Finally, in the zone of spatial contact, as it was shown in the paper, permanent gene flow is taking place between *inornatus* and *humei*, the rate of the exchange may be too large to be permissible for the forms with species status.

Taking into account all mentioned facts, it seems to be more correct to consider all three forms as geographical races (subspecies) of a single polytypic species. The distribution pattern of these forms is similar to the distribution of breeding areas of *Phylloscopus trochiloides* subspecies, two of which, *Ph. t. viridanus* and *Ph. t. plumbeitarsus,* also form the spatial contact zone in the Sayans and Tannu-Ola Mountains (Formozov & Marova, 1986). The taxonomic status of the last two forms seems to be rather disputable for the reason of the different types of vocalization (Schubert, 1982). The case with *Phylloscopus* subspecies (*viridanus – ludlowi – trochiloides – obscuratus – plumbeitarsus*), distribution areas of which cover forestless territories of Dzhungaria, Gobi, Takla-Makan desert and Tibet, can be considered as an example of ring area. The terminal links (*Ph. t. viridanus* and *Ph. t. plumbeitarsus*) form the secondary contact zone with some rate of reproductive isolation (Knox et al., 2002). On our opinion, the situation with distribution of *Phylloscopus inornatus* subspecies is to a great extent analogous one. Formerly, the ranges of these forms must have occupied a similar continuous ring, which divided afterwards into three isolated sites. The terminal links (*Ph. i. inornatus* and *Ph. i. humei*) formed the secondary contact zone relatively recently. Perhaps it occurred because Yellow-browed warbler (more ecologically plastic form) moved westwards. This form moved into the South Siberia mountains, that had been occupied by Hume's Yellow-browed warbler, which is more adopted to the Central Asia high mountain conditions. *Ph. i. mandellii* should be considered a relic mountain-forest form, keeping the features characteristic of the ancestor of the group being discussed.

Conclusion

In the vast region of the area of spatial contact zone of Hume's Yellow-browed Warbler and Yellow-browed Warbler, one can record individuals with transitional features, but the birds with transitional song have not been recorded so far. So, we can suppose that the great amount of those individuals of hybrid origin inherit the song of either the Hume's Yellow-browed warbler or the Yellow-browed warbler. However, the general opinion that these forms do not produce hybrids is based only on the results of field observations and vocalization analysis without performing morphological analysis and thus it seems rather incorrect.

Determination of real reproductive relations of *Ph. i. inornatus* and *Ph. i. humei* is possible only as a result of special investigation combining a vocalization analysis, morphological research and biochemical analysis of as great number of specimens from the spatial contact zone as possible, as well as study of pair structure in mixed settlements.

The taxonomic interpretation of the *Phylloscopus inornatus* (sensu lato) group is rather disputable. The most correct one seems to be considering this group as a single polytypic species, which originally had a ring range.

Many recent publications concerning the taxonomy of the forms of infraspecific level contain hasty conclusions about taxonomic position of particular forms phylogenetic closeness of which seems quite evident. The conclusions about the status must be supported by the morphological analysis of the examined objects and not only by results obtained during field observations and vocalization study (ecological criteria).

Acknowledgements

We thank V.M. Loskot (Chairman of Ornithological Department of Zoological Institute RAS), I.V. Fadeev and E.V. Nesterov (Moscow State Darwinian Museum), V.T. But'ev and D.A. Shitikov (Zoology and Ecology Chair of Moscow State Pedagogical University), M.N. Dement'ev (Department of Vertebrate Zoology of Moscow State University), P. Prys-Jones and M. Adams, (Ornithological Department of the Natural History Museum, U.K.), S.V. Drovetsky and R. Fausset (Burk Museum, Washington University, Seattle) for the permission to study the collections. We are grateful to V.N. Sotnikov (town of Kirov), who gave us the specimens of his private collection and helped us greatly in collecting in Tuva in 1999 and 2000, as well as to the other participants of these expeditions to Tuva: E.A. Koblik, A.B. Tsvetkov, A.A. Manylov, A.A. Mosalov and A.V. Mikulin. We are also grateful to L.V. Stepanova for her help in translating this paper into English.

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Received 3 March 2004