

On the taxonomic status and denomination of the Iberian Chiffchaffs

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We carried out a Principal Component Analysis on 196 Iberian and Common Chiffchaffs of both sexes (live and collection specimens), characterized by seven variables derived from wing, tarsus and bill measures. This method, complemented by colour comparison of the taxa, led us to the following conclusions. (1) *Phyllopneuste brehmii*, Homeyer, 1871, is a junior synonym of *Sylvia collybita*, Vieillot, 1817. The correct name for the Iberian Chiffchaff is *Phylloscopus ibericus* (Ticehurst 1937). (2) *P. ibericus* is itself represented by two subspecies: the southern form *P. i. ibericus* (Ticehurst 1937), and the northern form, for which we propose the name *P. i. biscayensis* ssp. nov. (3) The Common and Iberian Chiffchaffs are very distinct in the contact zone. But an overall geographical variation following Bergmann's and Allen's rules within both taxa generates an ecomorphological convergence, i.e. *P. i. ibericus* and the populations of *P. c. collybita* from northern central Europe have similar sizes. This may explain why previous authors were unable to diagnose the two taxa on morphological criteria alone.

The Iberian Chiffchaff, currently named *Phylloscopus [collybita] brehmii* (Homeyer 1871), lives in southern and north-western Iberia, and in a very small adjacent area of south-western France. The Common Chiffchaff *Phylloscopus [collybita] collybita* (Vieillot 1817) breeds in southern, central and north-western Europe. The two taxa coexist along a narrow secondary contact belt located in the foothills of the western Pyrenees. They differ considerably in their songs (Lynes 1914, Ingram 1926, Ticehurst & Whistler 1928, Mayaud 1943, Niethammer 1963, Thielcke & Linsenmair 1963, Becker *et al.* 1980, Salomon 1987) and calls (Bernis 1945, Salomon 1987) but their morphometric diagnosis was difficult to ascertain until recently (Salomon *et al.* 1997). Studies based on vocalizations (songs and calls), behaviour, reproductive ecology, morphology and molecular markers (Salomon 1987, 1989a, 1989b; Erard & Salomon 1989, Salomon 1990, Salomon & Hemim 1992, Helbig *et al.* 1993, 1996, Salomon *et al.* 1997, Helbig *et al.* 2001, Salomon 2001) showed that

they behave like two speciating taxa, at the semi-species level *sensu* Haffer (1986). The main arguments for this conclusion were parapatry, partial pre- and post-mating reproductive isolation, a tendency toward different habitat preferences, diagnostic morphological differences within the contact zone and results from molecular analyses. The two taxa were recently proposed paraspecies rank on molecular and descriptive acoustic considerations (Helbig *et al.* 1996).

Homeyer (1871) was the first author to advocate that chiffchaffs from Iberia constituted a specific form, distinct from the other chiffchaffs (at his time known as *Phyllopneuste rufa* or *Sylvia rufa* according to authors). He described this 'Iberian taxon' on one specimen from Portugal under the name *Phyllopneuste Brehmii*, hence considering it as a distinct species. He argued this on the grounds that the Iberian specimen displayed (1) darker, more brown olive upperparts, (2) a bill of the same length but more slender, (3) a different wing-formula with shorter second primary and secondaries, and (4) smaller ulna, tarsus and total sizes. Homeyer made no mention of any vocal specificity, and deposited the holotype in his private

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collection in Brunswick, which at present belongs to Brunswick's Natural History Museum. Homeyer did not collect this specimen himself, but purchased it from the natural history dealer W. Schlütter, who in turn had bought it from a certain Rey. The latter was a German traveller who had shot the bird in April 1869 (no mention of day) in Portugal (no mention of locality). A chiffchaff captured in Portugal during this month may be either a breeder or a migrant. Schlütter's label on the specimen mentions its sex as male, without stating on what criteria the collector sexed the bird.

Soon after Homeyer's work, birds fitting the description of *P. brehmii* were discovered in Turkey (Dresser 1872), southern Spain (Irby 1875) and the Netherlands (Seebohm 1877). Seebohm carefully examined specimens of *P. collybita* and *brehmii* and came to the conclusion that the two forms did not differ substantially. Therefore he considered them to be synonyms (Seebohm 1877, 1881). This position was upheld by most systematists (e.g. Kleinschmidt 1903, Hartert 1910, Trouessart 1912) until the end of the 1920s, even by the authors who first mentioned the song specificity of the Chiffchaff in Iberia (Lynes 1914, Stenhouse 1921, Tait 1924, Ingram 1926, Ticehurst & Whistler 1928).

Based on a sample of eight Iberian Chiffchaffs, characterized by the specific song just mentioned, Ticehurst and Whistler (1928) concluded that there were enough specific morphological traits to assign these birds to a separate taxon. They gave it subspecific rank, under the name *Phylloscopus collybita brehmii* (Homeyer 1871). Ten years later, Ticehurst (1937, 1938) revised his judgement about this subspecific designation on the basis that Iberian chiffchaffs did not fit Homeyer's data at all, but tended to be bigger and have brighter colours. Therefore, Ticehurst described the Iberian Chiffchaff as a new subspecies under the name *Phylloscopus collybita ibericus* Ticehurst, 1937. Ticehurst chose one of Witherby's specimens, mentioned in Witherby (1922) and deposited in the British Museum, as the holotype of this new taxon. Subsequently, until the beginning of the 1960s, the Iberian Chiffchaff was generally considered as a subspecies and both names, *brehmii* or *ibericus*, were used (Mayaud 1943, 1953, Bernis 1945, 1962, Williamson 1962). Vaurie (1954) hesitated to consider the Iberian Chiffchaff as a taxon separate from the nominate subspecies, for he was not convinced that it was possible to distinguish it morphologically; which for him was the only acceptable criterion in systematics. Vaurie

also thought that, in case the Iberian Chiffchaff was to be considered as a taxon of its own, it should be given the name *brehmii* since there was for him no convincing statistical evidence allowing the exclusion of Homeyer's specimen from the Iberian singers. Hence, most modern authors have continued to use the name *brehmii* for the Iberian birds. For more details on this historical account, see Salomon (1997).

None of the studies mentioned above took geographical variation into account. Only recently has it been shown that in their contact zone, the Iberian Chiffchaff tends to be larger than the Common Chiffchaff, with more pointed wings and proportionally shorter tarsus and bill (Salomon *et al.* 1997), a result which confirms Ticehurst's observations (Ticehurst 1937, 1938). In this paper, we provide a new insight into the taxonomy of the Iberian Chiffchaff through the analysis of morphological and coloration geographical variation.

MATERIALS AND METHODS

The measurements

Five measurements were taken on each of 196 *Phylloscopus (collybita)*, among which 117 were live birds and 79 museum specimens. Table 1 gives the number of birds per taxon (Iberian Chiffchaffs, mixed singers, *collybita* and the category '*brehmii*' as defined by Homeyer, e.g. specimens described by Homeyer himself), sex and region. The five measurements taken were wing length (WL), third primary length (P3 ascendant), 10th primary length (P10), tarsus length (T) and culmen length (BL). Wing measurements were taken according to the « maximum chord » method, wing flattened. Three variables were derived from the above measurements: wing pointedness ($WP = [P3 - P10 \times 100/WL]$), proportional, or relative, tarsus length ($PTL = T \times 100/WL$) and proportional, or relative, culmen length ($PBL = BL \times 100/WL$), as already defined in Salomon *et al.* (1997).

The 117 live birds were captured, measured and released during fieldwork in their breeding season (Fig. 1). Identification as Iberian or Common Chiffchaff was based on songs (males) or calls (males and females). Sex was determined by the presence of incubation patches in females or of specific behaviour patterns (Salomon 1989a); 10 of these birds were mixed singers, i.e. birds emitting mixed songs, with structures pertaining to both taxa (Thielcke &

Table 1. Number of birds examined per region, sex and category (only live and museum specimens unambiguously sexed and taxonomically identified). MS = Mixed singers.

	Live birds					Museum specimens					
	Iberian		MS	<i>collybita</i>		Iberian		'brehmii'		<i>collybita</i>	
	M	F	M	M	F	M	F	M	F	M	F
Morocco	0	0	0	0	0	0	0	0	1	0	0
S Andalusia	11	1	0	0	0	6	4	0	0	0	0
C & S Portugal	0	0	0	0	0	7	2	1	0	0	0
Galicia/N Portugal	7	0	1	0	0	6	1	0	0	0	0
Cantabrian zone	7	1	1	1	0	1	1	0	0	0	0
W Pyrenees	16	1	8	23	2	0	0	0	0	0	0
Poitou	0	0	0	13	1	0	0	0	0	0	0
Picardy	0	0	0	21	2	0	0	0	0	1	0
W France	0	0	0	0	0	0	0	0	0	9	6
British Isles	0	0	0	0	0	0	0	0	0	11	8
NE France	0	0	0	0	0	0	0	0	0	1	1
Benelux	0	0	0	0	0	0	0	0	0	1	0
N Germany & Poland	0	0	0	0	0	0	0	0	0	9	2

Linsenmair 1963, Salomon 1987) (cf. Table 1). The 79 museum specimens encompass skins from the collections of the National Museum of Natural History of Paris, the National Museum of Natural Sciences of Madrid, the Natural History Museum of Brunswick, the British Natural History Museum in Tring and the Doñana Institute of Seville.

The statistical and coloration analyses on morphological patterns

We first verified that live birds and museum skins were morphologically sufficiently comparable to be analysed together. (Indeed, one frequently observes *post mortem* body shrinkage in museum specimens, especially of the tarsus and bill.) For this verification, we compared the regression lines of BL vs. T, and of WL vs. T (see Table 2) for the southern Iberian, northern Iberian and nominate male chiffchaffs. (The samples of females are too small to be analysed statistically in a convincing way, but, for allometric reasons, the results for this sex would certainly be similar to those analysed on the males.) If the regression line of live birds is $y^{(1)} = s_1x^{(1)} + b_1$ and that of museum specimens is $y^{(2)} = s_2x^{(2)} + b_2$, the Student tests (1) comparing the slopes is $|s_1 - s_2|/\sqrt{(\text{Var } s_1 + \text{Var } s_2)}$ where $\text{Var } s_i = 2 \times \text{Var } y^{(i)}/(\text{Max } x^{(i)} - \text{Min } x^{(i)})^2$, and (2) comparing the origin ordinates is $|b_1 - b_2|/\sqrt{(\text{Var } b_1 + \text{Var } b_2)}$ where $\text{Var } b_i = \text{Var } y^{(i)} + (\text{Mean } x^{(i)})^2 \times \text{Var } s_i$.

Afterwards, we applied Principal Component Analyses (PCA), first on a sample containing 196

warblers, which could be accurately sexed, taxonomically identified and geographically located (PCA1), secondly on the 64 male Iberian Chiffchaffs of the sample mentioned above (PCA2). PCA1 aimed to contribute to the definitive status of the *brehmii* specimens as defined by Homeyer, and PCA2 aimed to analyse the taxonomy of the two geographical components of the Iberian Chiffchaff. Our entire data set consisted of a matrix, whose rows were the 196 birds treated in PCA1 and whose columns were the eight variables WL, P3, P10, T, BL, WP, PTL and PBL. The analysed individuals belonged to four regions SI, NI, EC and WC we define just below:

- 1 SI (zone of the southern Iberian chiffchaffs) = Andalusia and central and southern Portugal;
- 2 NI (zone of the northern Iberian chiffchaffs) = an area stretching from extreme northern Portugal and Galicia to western Pyrenees;
- 3 EC (zone of the eastern or continental *collybita* chiffchaffs) = France except Brittany, southern Belgium, Holland, Germany and Poland;
- 4 WC (zone of the western or Atlantic arch *collybita* chiffchaffs) = Brittany and Great Britain.

The analysis of plumage coloration added information to interpretation ambiguities stemming from the component analyses, in particular concerning the *brehmii* specimen still considered as the type of the Iberian taxon. Here, a precise typology and multivariate description of the Iberian chiffchaffs is revealed for the first time, with taxonomic consequences.

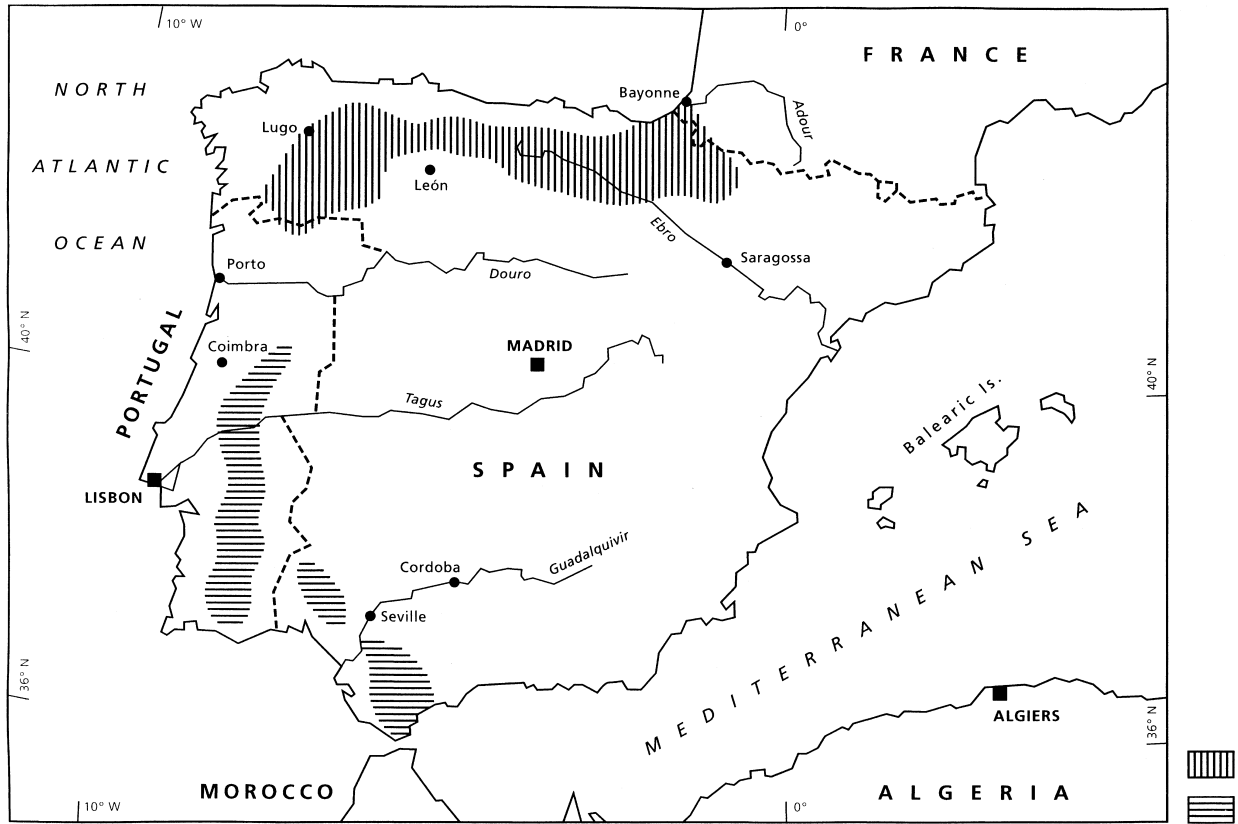


Figure 1. Distribution map of the Iberian Chiffchaff (during the breeding season). Horizontal hatching = SI area; vertical hatching = NI area.

Table 2. Regression tests between live birds and museum specimens in order to verify their comparability, prior to the statistical analysis pooling them.

Pairs of variables	Parameters	S Iberian chiffchaff		N Iberian chiffchaff		Nominate chiffchaff	
		Live birds	Museum spec.	Live birds	Museum spec.	Live birds	Museum spec.
	Number of the individuals of the sample	11	13	31	7	57	32
T-BL	Regression lines	$y = 0.321x + 2.59$	$y = -0.156x + 12.75$	$y = -0.207x + 13.21$	$y = -0.03x + 9.85$	$y = 0.288x + 3.5$	$y = 0.12x + 6.95$
	Slope test		0.942		0.47		0.514
	t significance		$P > 0.05$		$P > 0.05$		$P > 0.05$
	Origin ordinate test		0.989		0.434		0.555
	t significance		$P > 0.05$		$P > 0.05$		$P > 0.05$
T-WL	Regression lines	$y = 0.302x + 54.33$	$y = 0.733x + 45.82$	$y = 0.865x + 45.33$	$y = 1497x + 31.75$	$y = 0.43x + 52.11$	$y = 0.76x + 43.94$
	Slope test		1.25		0.528		0.109
	t significance		$P > 0.05$		$P > 0.05$		$P > 0.05$
	Origin ordinate test		1.196		0.726		0.133
	t significance		$P > 0.05$		$P > 0.05$		$P > 0.05$

RESULTS

Comparison between live birds and museum specimens

The regression lines from live birds did not differ significantly in either slope or origin ordinate from those of museum specimens (Table 2). Hence, we can assume that measurements from these two groups can be compared without undue concern for *post mortem* shrinkage effects. Thus, we have pooled data from live birds and museum specimens in the PCAs.

Principal Component Analyses

For a detailed description of Principal Components Analysis see Legendre and Legendre (1984). The PCAs and associated cluster analyses were performed using the SPAD 3 (1998) computer software (CISIA, Saint-Mandé, France).

In PCA1 and PCA2, all the individuals and variables of the data matrix were processed, except P3 as this was highly correlated with WL. These individuals and variables are represented by their projections on plane P12 generated by the most

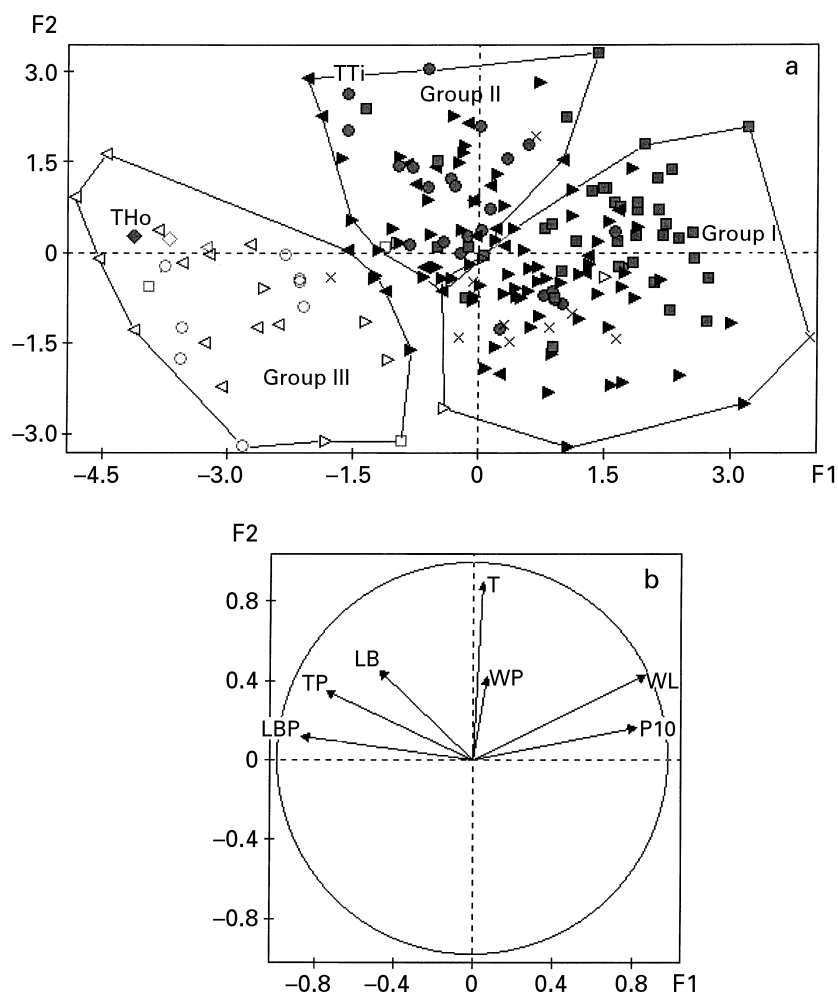


Figure 2. PCA1 scatter diagrams projecting the Common and Iberian Chiffchaffs of the two sexes and the mixed singers, on plane P12. (a) Scatter plot with the projections surrounded by the three Venn curves (groups I, II and III), established by the associated cluster analysis. (b) Scatter plot of the correlation circle of PCA1 and the variables, once centred and reduced, correlated to the axes F1 and F2. Identification symbols; each symbol of (a) represents an individual and depicts its taxon, region and sex. The full symbols represent the males; and the open ones, the females. (1) Iberian chiffchaffs are represented by grey symbols: circles = the SI Iberian chiffchaffs; squares, the NI Iberian chiffchaffs; (2) Mixed singers, all males, are symbolized by diagonal crosses; (3) Homeyer's *brehmii* specimens are symbolized by grey rhombuses; (4) Nominate chiffchaffs are symbolized by black triangles. Triangles pointed to the right = EC nominate chiffchaffs; triangles turned to the left = WC nominate chiffchaffs.

Table 3. Number of chiffchaffs per category (taxon × sex) and group – I, II, III, IV, V and VI (as defined in Figs 2 and 3).

Groups Categories	I	II (All samples: 196 birds)	III	IV	V (Male Iberian Chiffchaffs: 64 birds)	VI
NI-m	33	6	0	28	2	6
SI-m	7	17	0	2	13	13
EC-m	45	23	3	–	–	–
WC-m	5	12	2	–	–	–
mixed singer-m	8	1	1	–	–	–
<i>brehmii</i> -m	0	0	1	–	–	–
<i>brehmii</i> -f	0	0	1	–	–	–
NI-f	0	1	2	–	–	–
SI-f	0	0	8	–	–	–
EC-f	2	1	4	–	–	–
WC-f	0	0	13	–	–	–

Abbreviations: NI = North Iberian chiffchaffs, SI = South Iberian chiffchaffs, EC = Eastern *collybita* chiffchaffs, WC = Western *collybita* chiffchaffs, m = males, f = females.

explanatory factorial axes F1 and F2. In PCA1 and PCA2, the associated cluster analyses were performed on the 196 and 64 individuals, respectively. In both cases, the optimal result of this method is the selection of one partition of N classes constructed in such a way that the respective numbers of elements of the classes are as equal as possible. The classes gather the individuals which are closest. SPAD 3 calculated the optimal solution for both analyses as a partition containing three classes. In Fig. 2, we grouped the projections on P12 in three Venn curves – I, II and III for PCA1; and IV, V and VI for PCA2. Each Venn curve gathers the projections of the individuals belonging to the same class of the partition. We shall call these Venn curves groups and interpret the points and groups in the diagram. As usual for such analyses, we shall identify the projections and the individuals.

PCA1

According to Table 3, groups I and II almost exclusively comprise male chiffchaffs (98%). Group I mainly contains NI or continental nominate chiffchaffs (87%), and relatively few SI or Atlantic nominate chiffchaffs (less than 13%); 80% of the mixed singers belong to this group.

In group II, among the Iberian chiffchaffs, most are SI birds (74%) including ‘Ticehurst’s type’; and among the nominate chiffchaffs, continental as well as Atlantic individuals are represented. Group III contains 90% of all the females, and only a tiny proportion of males, all belonging to the nominate taxon (c. 14%).

Hence, NI chiffchaffs (mostly represented in group I) are well differentiated from SI chiffchaffs (mostly represented in group II). Among nominate

chiffchaffs, Atlantic individuals display stronger sexual dimorphism than continental chiffchaffs.

Two important points are shown by the composition of group III:

- 1 no male Iberian chiffchaffs belong to group III;
- 2 both *brehmii* specimens, defined as such by Homeyer, belong to group III.

Although most of the individuals near ‘Homeyer’s type’ in Fig. 2(a) consist of Atlantic nominate females, a substantial number of SI females also lie in its neighbourhood. Hence, Homeyer’s specimen, previously taken as the Type for the Iberian Chiffchaffs, is probably a migratory Atlantic nominate female, although its membership of the SI female group cannot be excluded totally. What is certain is that it cannot be a male Iberian Chiffchaff. Since this bird was sexed as male and has been considered until now as the holotype of the Iberian Chiffchaff, we face a contradiction between the results of our analysis and the recognized position of Homeyer’s type.

The analysis of the correlation circle reveals that P10, WL, T, TP and LBP are represented by vectors nearly reaching the circle of radius 1 (Fig. 2b). Consequently, they are the only variables explaining F1 and/or F2. The sense of a variable vector indicates the increasing value of this variable. In addition, the smaller the angle between a variable and an axis F_i the stronger it is correlated with this axis. Hence, P10, WL, TP and LBP are strongly correlated with F1, and T with F2. The large positive abscissa (F1 direction) corresponds to large values of P10 and WL and small values of LBP and TP; and the large ordinates (F2 direction) to the large value of T. Consequently, NI chiffchaffs tend to have (1) larger 10th

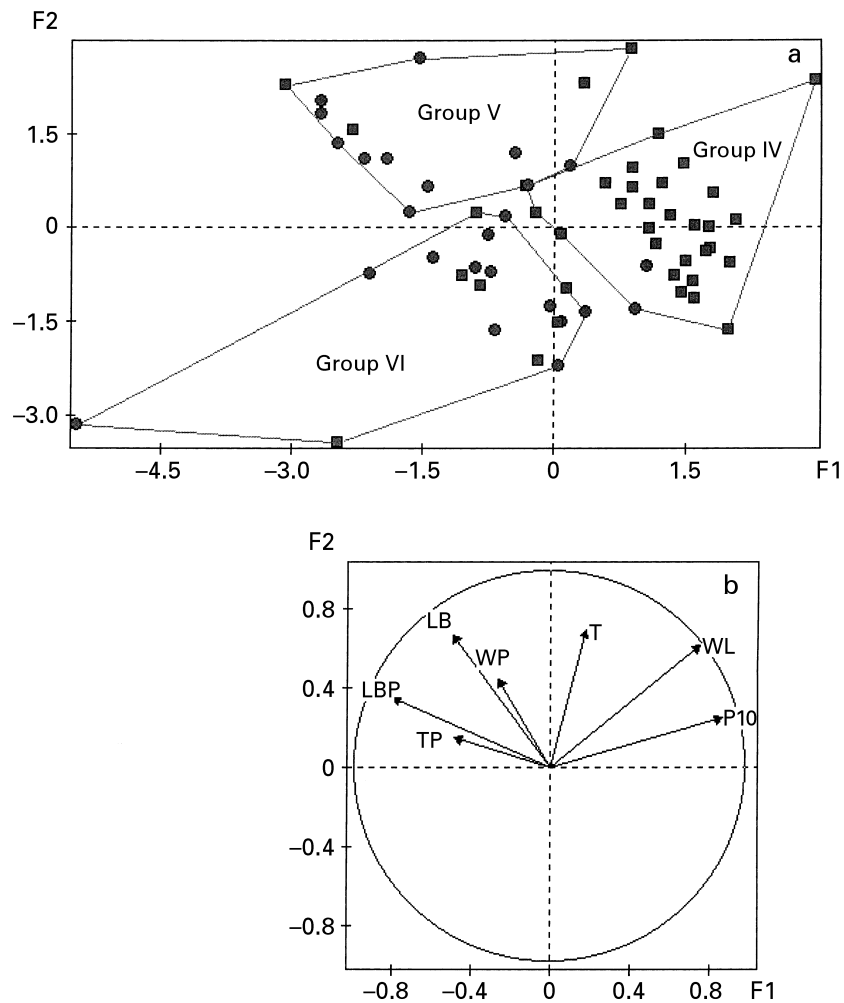


Figure 3. PCA2 scatter diagrams projecting the male Iberian Chiffchaffs; the identification symbols of these birds are identical to those defined in Fig. 2(a). (a) Scatter plot with the projections surrounded by the three Venn curves (groups IV, V and VI), established by the associated cluster analysis. (b) Scatter plot of the correlation circle of PCA2 and the variables, once centred and reduced, correlated to the axes F1 and F2.

primaries and wing lengths, (2) proportionally shorter tarsi and bills, and (3) shorter absolute tarsus lengths than SI chiffchaffs. The females have the shortest wing lengths and 10th primaries, and proportionally the longest tarsus and bill lengths.

PCA2

Figure 3(a) shows that among male Iberian chiffchaffs, the southern and northern populations segregate well. Table 3 shows that most members of group IV are NI chiffchaffs (93%) and that, consequently, SI chiffchaffs are rare (7%). In the two other groups, i.e. V and VI, the prevailing warblers are the SI chiffchaffs (76%). Hence, group IV can be identified as the NI male chiffchaffs and groups V and VI as the SI male chiffchaffs.

According to Fig. 3(b), NI male chiffchaffs are characterized by longer wings and tenth primaries, and proportionally shorter bills and tarsi, than SI male chiffchaffs.

Coloration analysis of museum specimens

We compared the mantle and breast colours of Common Chiffchaffs, Iberian Chiffchaffs and the *brehmii* holotype. Colours of these parts are known to differ empirically (Erard & Salomon 1989, M. Salomon & J. Bried pers. obs.). This analysis has been performed on 34 museum skin specimens, 10 Common Chiffchaffs, 23 Iberian Chiffchaffs and the *brehmii* specimen (Table 4). The colour designation

Table 4. Coloration analysis of the mantle and chest of Iberian and Common Chiffchaffs.

Body parts Colours	Mantle bistre green	old moss green holly green	Chest Uniform white yellow, mostly light	Whitish soaked with buff or greyish tinges
Chiffchaff Taxa				
Common	0	10	1	8
Iberian	22	1	20	2

stems from the 'Code Universel des Couleurs' of Séguy (1936) containing 720 colours represented in monochromic rectangles. These colours are the most frequently encountered among living organisms, and each is coded by a number (between 1 and 720). These code numbers are translated into accepted vernacular expressions like 'turquoise blue' or 'vermillion red', etc.

The Iberian Chiffchaff definitely displays a 'bistre green' (261 or 262) mantle and a uniformly coloured breast – its coloration spanning from pure white to buffish yellow, but mainly lemon yellow (white, 234, 250, 258, 260, 265, 320). However, in the Common Chiffchaff, the mantle has an 'old moss green' (276) or 'holly green' (301) colour; and the breast is a less pure hue – whitish either soaked with buff, or with various greyish tinges (259–336; 260–522; 260–524). The mantle of the *brehmii* holotype is holly green (301), and its breast, whitish heavily buff-tinged, like that of Common Chiffchaff specimens and unlike Iberian Chiffchaffs.

DISCUSSION

Inferences from the PCA

Males of the northern and southern populations of the Iberian Chiffchaff are different, the former showing longer wings and 10th primaries than the latter. On the other hand, the northern Iberian Chiffchaffs show the smallest relative and absolute bill and tarsus lengths. This may be consistent with Bergmann's and Allen's rules. Females would tend to segregate between the northern and southern populations but more subtly; which means that sexual dimorphism is significantly more pronounced in the northern than in the southern populations of the Iberian Chiffchaff. Most of the mixed singers are biometrically similar to the northern Iberian Chiffchaffs and to the continental male nominate chiffchaffs. Rather than analyse the variation within the nominate chiffchaffs, we now focus on the Iberian Chiffchaffs and the *brehmii* individuals.

PCA has already revealed that the specimen, called *Phyllopede brehmii* by Homeyer (1871), cannot be a male Iberian Chiffchaff, in the sense of a chiffchaff breeding in the Iberian Peninsula and emitting the specific Iberian vocalization. The bird is positioned by the analyses among the females of western France and the British Isles, although female SI chiffchaffs may resemble *P. brehmii* biometrically. Our analysis showed that *brehmii* displays colours identical to those of *collybita*, and not to those of the Iberian Chiffchaff. All these results confirm Ticehurst's arguments (Ticehurst 1937) that the sizes and coloration would place this bird near to female nominate chiffchaffs. We agree with his rejection of *brehmii*'s membership of the Iberian Chiffchaff. We cannot be sure that this bird, identified as a male, was sexed correctly, since it was captured during migration. For all these reasons, Homeyer's Portuguese specimen was very probably a female *collybita* captured during migration, which would have bred either in western France, or in the British Isles. Hence, *P. c. brehmii* is not the correct name for the Iberian Chiffchaff. Independently of us, Lars Svensson (pers. comm.) came to the same conclusion with another dataset.

Ticehurst's *P. c. ibericus* falls within the group identified as the southern populations of the Iberian Chiffchaff, as do the type-series (for their identification, see below).

Conclusion and taxonomic implications

The results of the multivariate and coloration analyses clearly show that the holotype of *Phyllopede brehmii* Homeyer, 1871, does not belong to the Iberian Chiffchaff. On the contrary, this specimen is revealed, probably, to be an incorrectly sexed female *Phylloscopus collybita* (Vieillot 1817) belonging to one of the breeding populations of Great Britain or Brittany, and captured during migration. Its coloration is typical of *collybita*, which adds further confirmation of the findings inferred from the PCA (Ticehurst 1937, 1938, our analyses in this paper).

Table 5. Morphological comparison between *Phylloscopus ibericus ibericus* and *P. i. biscayensis*.

Variable	Categories	<i>ibericus</i>	No.	sd	<i>biscayensis</i>	No.	sd	Comparison <i>t</i> -test results
Wing Length (V1)	Males	<i>60.76</i>	23	1.95	<i>62.04</i>	50	1.43	**
	Females	<i>55.3</i>	5	1.6	<i>57.3</i>	6	1.48	*
	Types	<u>60.5</u>			<u>63</u>			
10th Primary (V2)	Males	<i>48.74</i>	23	1.16	<i>49.98</i>	38	1.23	***
	Females	<i>44.3</i>	5	1.04	<i>47.75</i>	6	1.47	*
	Types	<u>47.5</u>			<u>51</u>			
Tarsus Length (V3)	Males	<i>20.78</i>	23	0.57	<i>20.33</i>	39	0.8	*
	Females	<i>19.3</i>	5	0.56	<i>19.07</i>	6	0.32	NS
	Types	<u>21.4</u>			<u>20.7</u>			
Bill Width (V4)	Males	<i>3.66</i>	23	0.29	<i>3.86</i>	26	0.36	*
	Females	<i>3.8</i>	5	0.31	<i>3.96</i>	6	0.45	NS
	Types	<u>3.8</u>			<u>3.7</u>			
Relative Tarsus Length (V5)	Males	<i>33.53</i>	23	0.93	<i>32.33</i>	39	1.06	**
	Females	<i>34.05</i>	5	1.18	<i>32.8</i>	6	1.53	*
	Types	<u>35.37</u>			<u>32.64</u>			
Relative Bill Length (V6)	Males	<i>15.29</i>	23	1.02	<i>14.74</i>	39	1.01	*
	Females	<i>16.38</i>	5	1.6	<i>16.91</i>	6	0.94	NS
	Types	<u>16.36</u>			<u>13.44</u>			

The mean values are given in italics. The values for the types underlined (both types have been sexed as males). Each variable V_k corresponds to a confidence interval I_k encompassing the mean value of a sample of n_k *biscayensis* chiffchaffs. Within the test results column, NS = non-significant difference, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Therefore, *Phyllopneuste brehmii* Homeyer, 1871, is a junior synonym of *Sylvia collybita* Vieillot, 1817, as already noticed by Ticehurst (1938); and the correct name for the Iberian Chiffchaff is *ibericus*, Ticehurst, 1938. A thorough description is given below.

The results of the analyses also show clear-cut biometric differences between the southern and the northern populations of the Iberian Chiffchaff (cf. Table 5), which moreover breed allopatrically in two separated areas.

Relative to the SI Iberian Chiffchaff, the NI Iberian Chiffchaff has significantly longer wings, longer 10th primaries and, relative to body size, shorter tarsi (both sexes) and shorter and wider bills (males only).

The northern form inhabits a region spreading between the extreme north of Portugal and Galicia to the French basque country across the Cantabrian Cordillera (northern and southern slopes), the Spanish Basque provinces and Navarra (Fig. 1). This area is characterized by a wet Atlantic climate, moist and mild throughout the year. In contrast, the southern form breeds in an area composed of relatively wet Mediterranean habitats, mainly cork-oak formations sparsely spreading from central Portugal (Coimbra region) to southern Andalusia, wherever eucalyptus and pines have not been planted (Fig. 1). These are

important ecological differences, far greater than that prevailing between areas inhabited by the NI Iberian Chiffchaffs and the neighbouring Common Chiffchaffs living parapatrically. In addition, NI and SI are allopatric regions, separated by a wide gap where chiffchaffs are very rare or absent as breeders. Therefore, the NI and SI Iberian chiffchaffs may be considered as distinct taxonomic units, although at a low level of differentiation. These categories, studied in botany as well as zoology, have received various denominations, e.g. Functional Biologic Units *sensu* Sastre (1994), 'weak' subspecies *sensu* Deuve (1994) or, to some extent, races *sensu* Verity (1929, 1951).

As we pointed out in the introduction, the taxa *collybita* and *ibericus* behave mutually like semi-species or paraspecies, which means that gene flow between them is extremely limited. As the International Code of Zoological Nomenclature only allows one infraspecific category, the best way to deal with this problem is, in our opinion, to give the Iberian Chiffchaff species rank, and its northern and southern forms subspecies rank.

The name of the Iberian Chiffchaff is *Phylloscopus ibericus*, Ticehurst, 1938, the holotype of which is a bird collected by Sir H.F. Witherby at Paul d'Argila (Province of Coimbra, Portugal) on 23 May 1920, and

Table 6. The paratypes of *Phylloscopus ibericus biscayensis*.

Collection	Registration no.	Sex	Capture localities	Collector and year of capture
NHM, Tring (UK)	1934.1.5047	male	Vizela (Braga, Portugal)	Witherby (1920)
	1941.5.30.4798	male	Bom Jesus (Braga, Portugal)	Ticehurst (1937)
	1949.Whi.1.12246	male	Bom Jesus (Braga, Portugal)	Whistler (1934)
MNCN, Madrid (Spain)	13818	male	Lugo (Lugo, Spain)	Bernis (1944)
	13819	male	Lugo (Lugo, Spain)	Bernis (1945)
	13820	male	Lugo (Lugo, Spain)	Bernis (1944)
EBD, Seville (Spain)	20508 A	male	Villarcayo (Burgos, Spain)	C. Valverde (1970)
	20509 A	male	Villarcayo (Burgos, Spain)	C. Valverde (1970)
	20510 A	female	Villarcayo (Burgos, Spain)	C. Valverde (1970)

NHM = Natural History Museum (British Museum), MNCN = Museo Nacional de Ciencias Naturales, EBD = Estación Biológica de Doñana.

kept in the British Natural History Museum (Tring, Herts., UK) under registration number 1934.1.1.5045. As Ticehurst's holotype belongs to the southern population, the latter is to be considered as the nominate subspecies *Phylloscopus ibericus ibericus* Ticehurst, 1938. In addition, five other specimens that had bred in southern Portugal were designated by the same author as paratypes of *ibericus* (register numbers: 1934.1.1.5048; 1949.Whi.1.12243, 1949.Whi.1.12244; 1949.Whi.1.12245; 1949.Whi.1.12247). The last four specimens belonged to Witherby's private collection when described, and were registered in 1949 by the British Museum (Natural History), when Witherby donated them to the latter.

A new name is needed for the northern form. We propose

Phylloscopus ibericus biscayensis ssp. nov.

HOLOTYPE [white label] *Phylloscopus (collybita)/brehmii*/male. Loc.: Aya (Guipuzcoa)/20 May 1995/3398///Muséum National d'Histoire Naturelle, Paris/coll. Marc Salomon Pays Espagne CG1999 no.664.

[red label] *Phylloscopus ibericus biscayensis*, Salomon, Voisin & Bried HOLOTYPE.

PARATYPES

The nine paratypes of the subspecies *Phylloscopus ibericus biscayensis* are deposited in the British Natural History Museum (Tring), the National Museum of Natural Sciences (Madrid) and the Doñana Biological Station (Seville), and are listed in Table 6.

Coloration (numbers referring to Séguy's colour guide [Séguy 1936]): Crown, mantle and rump,

bistre green (paratypes and holotype: 261); inner and outer tail-feathers, primaries and secondaries, yew green (paratypes and holotype: 315); chin, throat and breast, yolk yellow from 265 to white soaked with 250 (holotype: 259, 260); belly and vent, cream (white soaked with 250, white soaked with 260, 260); (holotype: 260); flank, a mixture of pure white, greyish (521, 522), bistre green (262) and buttercup yellow (257). Undertail- and underwing-coverts, cream 258 and 260 (holotype: 260); axillaries, white to cream 260 to white (holotype: 260). Wing bend, yolk yellow [admixture of 258 and 259 (holotype: 258, 259)].

Measurements (cf. Table 5).

Table 5 shows the dimensions of *Phylloscopus ibericus biscayensis* for which a significant difference has been shown with *P. i. ibericus*. Hence, *Phylloscopus ibericus biscayensis* differs from *P. ibericus ibericus* by its dimensions, its geographical distribution and habitat. As far as we could see, the vocalizations of these two forms do not differ appreciably.

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REFERENCES

- Becker, P.H., Thielcke, G. & Wüstenberg, K.** 1980. Der Tonhöhenverlauf ist entscheidend für das Gesangserkennen beim Mitteleuropäischen Zilpzalp (*Phylloscopus collybita*). *J. Ornithol.* **121**: 229–244.
- Bernis, F.** 1945. Datos sobre el *Phylloscopus collybita brehmii*. *Bol. Soc. Española Historia Natural* **43**: 339–348.
- Bernis, F.** 1962. Mas sobre el *Phylloscopus collybita ibericus*. *Ardeola* **8**: 286–287.
- Deuve, T.** 1994. *Une Classification du Genre Carabus*. Venette, France: Sciences Nat.
- Dresser, H.E.** 1872. Mr H. E. Dresser, F. Z. S., exhibited some skins and eggs of various species of *Reguloides* and *Phylloscopus*, and made the following remarks. *Proc. Zool. Soc. Lond.* 24–26.
- Erard, C. & Salomon, M.** 1989. Essai de caractérisation morphologique du Pouillot véloce *Phylloscopus collybita brehmii* (Homeyer). *Oiseau Rev. Fr. Ornithol.* **59**: 26–44.
- Haffer, J.** 1986. Superspecies and species limits in Vertebrates. *Z. Zool. Syst. Evolutionsforschung* **24**: 169–190.
- Hartert, E.** 1910–32. *Die Vögel der Paläarktischen Fauna*. Berlin: Friedländer & Sohn.
- Helbig, A.J., Martens, J., Henning, F., Schottler, B., Seibold, I. & Wink, M.** 1996. Phylogeny and species limits in the palearctic Chiffchaff (*Phylloscopus collybita*) complex: mitochondrial genetic differentiation and bioacoustic evidence. *Ibis* **138**: 650–666.
- Helbig, A.J., Salomon, M., Bensch, S. & Seibold, I.** 2001. Male-biased gene flow across an avian hybrid zone: evidence from mitochondrial and microsatellite DNA. *J. Evol. Biol.* **14**: 277–297.
- Helbig, A.J., Salomon, M., Wink, M. & Bried, J.** 1993. Absence de flux mitochondrial entre les Pouillots 'véloces' méditerranéen et ibérique (Aves: *Phylloscopus collybita collybita*, *P. (c.) brehmii*); implications taxonomiques. Résultats tirés de la PCR et du séquençage d'ADN. *CR Acad. Sci. Paris Série III (Sci. la Vie)* **316** (III): 205–210.
- Homeyer, E.F. (v)** 1871. Über portugiesische Vögel. In Von Homeyer, E.F. (ed.) *Erinnerungsschrift an die Versammlung der Deutschen Ornithologen in Görlitz im Mai*: 46–48. Anlage C. Frankfurt an der Oder: Stolp.
- Ingram, C.** 1926. Ouessant ornithology and other notes on French birds. *Ibis* **12**: 247–269.
- Irby, H.** 1875. *Ornithology of the Straits of Gibraltar*. London: Porter.
- Kleinschmidt, O.** 1903. Ornis von Marburg an der Lahn. *J. Ornithol.* **51**: 440–505.
- Legendre, L. & Legendre, P.** 1984. *Ecologie Numérique. 1. Le Traitement Multiple des Données Écologiques*. Paris: Masson.
- Lynes, H.** 1914. Remarks on geographical distribution of Chiffchaff and Willow Warbler. *Ibis* **10**: 304–314.
- Mayaud, N.** 1943. L'avifaune des Landes. *Phylloscopus collybita*. *Oiseau Rev. Fr. Ornithol.* **13**: 71–72.
- Mayaud, N.** 1953. Liste des oiseaux de France. *Alauda* **21**: 1–63.
- Niethammer, G.** 1963. Zur Kennzeichnung des Zilpzalps des iberischen Halbinsel. *J. Ornithol.* **104**: 403–411.
- Salomon, M.** 1987. Analyse d'une zone de contact entre deux formes parapatriques: le cas des Pouillots véloces *Phylloscopus c. collybita* et *P. c. brehmii*. *Rev. d'Ecologie (Terre Vie)* **42**: 377–420.
- Salomon, M.** 1989a. *Recherches sur la spéciation allopatrique. Le cas des Pouillots véloces européen Phylloscopus c. collybita et ibérique P. c. brehmii dans leur zone de contact des Pyrénées Occidentales*. PhD Dissertation. Paris: Paris 7 University.
- Salomon, M.** 1989b. Song as a reproductive isolating mechanism. The case of the Chiffchaffs *Phylloscopus c. collybita* and *P. c. brehmii*. *Behaviour* **111**: 270–290.
- Salomon, M.** 1990. Interprétation taxonomique de la distribution parapatrique de deux groupes de populations: les Pouillots véloces (*Phylloscopus collybita*) des formes *collybita* et *brehmii*. *CR Séances Soc. Biogéogr.* **66**: 75–84.
- Salomon, M.** 1997. Quel statut taxonomique donner au Pouillot véloce ibérique? *Alauda* **65**: 63–81.
- Salomon, M.** 2001. Guest editorial: evolutionary biogeography and speciation: essay on a synthesis. *J. Biogeogr.* **28**: 13–28.
- Salomon, M., Bried, J., Helbig, A.J. & Riofrio, J.** 1997. Morphometric differentiation between male Common Chiffchaffs *Phylloscopus [c.] collybita* Vieillot, 1817, and Iberian Chiffchaffs *P. [c.] brehmii* Homeyer, 1871, in a secondary contact zone (Aves: Sylviidae). *Zool. Anzeiger* **236**: 25–36.
- Salomon, M. & Hemim, Y.** 1992. Song variation in the chiffchaffs (*Phylloscopus collybita*) of the western Pyrenees – the contact zone between the *collybita* and the *brehmii* forms. *Ethology* **92**: 265–272.
- Sastre, C.** 1994. Paléoclimats, spéciation et taxonomie. Quelques exemples chez les Ochnacés tropicaux. *Mém. Soc. Biogéogr.* 3^{ème} Série **4**: 3–10.
- Seebohm, H.** 1877. On the *Phylloscopi* or Willow-Warblers. *Ibis* **4**: 66–108.
- Seebohm, H.** 1881. *Catalogue of Birds in the British Museum*. London: Order of the Trustees.
- Séguy, E.** 1936. *Code Universel des Couleurs*. Paris: Paul Lechevalier.
- Stenhouse, J.M.** 1921. Bird-notes from southern Spain. *Ibis* **11**: 573–594.
- Tait, W.** 1924. *The Birds of Portugal*. London: Witherby.
- Thielcke, G. & Linsenmair, K.E.** 1963. Zur geographischen Variation des Gesanges des Zilpzalps, *Phylloscopus collybita*, in Mittel- und Südwesteuropa mit einem Vergleich des Gesanges des Fitis, *Phylloscopus trochilus*. *J. Ornithol.* **104**: 372–402.
- Ticehurst, C.B.** 1937. *Phylloscopus collybita ibericus*, subsp. nov. *Bull. Brit. Orn. Club* **57**: 63–64.
- Ticehurst, C.B.** 1938. *A Systematic Review of the Genus Phylloscopus*. London: British Museum.
- Ticehurst, C.B. & Whistler, H.** 1928. On the avifauna of Galicia. *Ibis* **12**: 663–683.
- Trouessart, E.L.** 1912. *Catalogue Des Oiseaux d'Europe Pour Servir de Compléments et de Suppléments À L'Ornithologie Européenne de Degland et Gerbe (1867)*. Paris: Lhomme.
- Vaurie, C.** 1954. *The Birds of Palearctic Fauna. A Systematic Reference*. London: Witherby.
- Verity, R.** 1929. Essai sur les origines des Rhopalocères européens et méditerranéens et particulièrement des Anthocaridi et des Lycaenidi du groupe d'*Agestis* Schiff. *Ann. Soc. Entomol. France* **48**: 322–360.
- Verity, R.** 1951. *Les Variations Géographiques et Saisonnières des Papillons Diurnes en France*. Paris: Sciences Nat.
- Williamson, K.** 1962. *Identification for Ringers. The Genus Phylloscopus*. Oxford: B.T.O.
- Witherby, H.F.** 1922. Results of a collecting trip in the Cantabrian mountains, northern Spain. *Ibis* **11**: 323–345.

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