



**HYBRIDIZATION BETWEEN THE MEGASUBSPECIES *CAILLIAUTII*
AND *PERMISTA* OF THE GREEN-BACKED WOODPECKER,
*CAMPETHERA CAILLIAUTII***

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The two woodpeckers, *Campethera cailliautii* (with races *nyansae*, "fuelborni", *loveridgei*) and *C. permista* (with races *togoensis*, *kaffensis*) were long regarded as distinct species (Sclater, 1924 ; Chapin 1939). They are quite dissimilar : *permista* has a plain green mantle and barred underparts, while *cailliautii* is characterized by clear spots on the upper side and black spots on the underpart. The possibility that they would be conspecific was however considered by van Someren in 1944. Later, van Someren and van Someren (1949) found that specimens of *C. permista* collected in the Bwamba Forest tended strongly towards *C. cailliautii nyansae* and suggested again that *permista* and *cailliautii* may be conspecific. Chapin (1952) formally treated *permista* as a subspecies of *C. cailliautii*, noting two intermediates from the region of Kasongo and Katombe, Zaire, and referring to a correspondence of Schouteden who confirmed the presence of other intermediates from Kasai in the collection of the MRAC (see Annex 2). Hall (1960) reported two intermediates from the Luau River and from near Vila Luso, Angola. Traylor (1963) noted intermediates from eastern Lunda. Pinto (1983) mentioned seven intermediates from Dundo, Mwaoka, Lake Carumbo and Cafunfo (Luango). Thus the contact zone between *permista* and *nyansae* extends from the region north-west of Lake Tanganika to Angola, crossing Kasai, in Zaire.

A second, shorter, contact zone may exist near the eastern border of Zaire, not far from the Equator. The map published by Short and Tarbaton (*in* Snow, 1978) shows *cailliautii* from the Semliki Valley, on the Equator but I know of no specimens of this woodpecker from this region. The IRSNB has a long series of *permista* from the Semliki Valley, collected north of the Equator, but they don't show any approach to *nyansae*, except that for some of them the bars on the chest form a half-moon (see Fig. 2). I have not seen the specimens collected in the Bwamba Forest by van Someren and van Someren (1949) ; three specimens from the same forest in LACM show no trend to *cailliautii*. Sassi (1912) mentions a male of *per-*

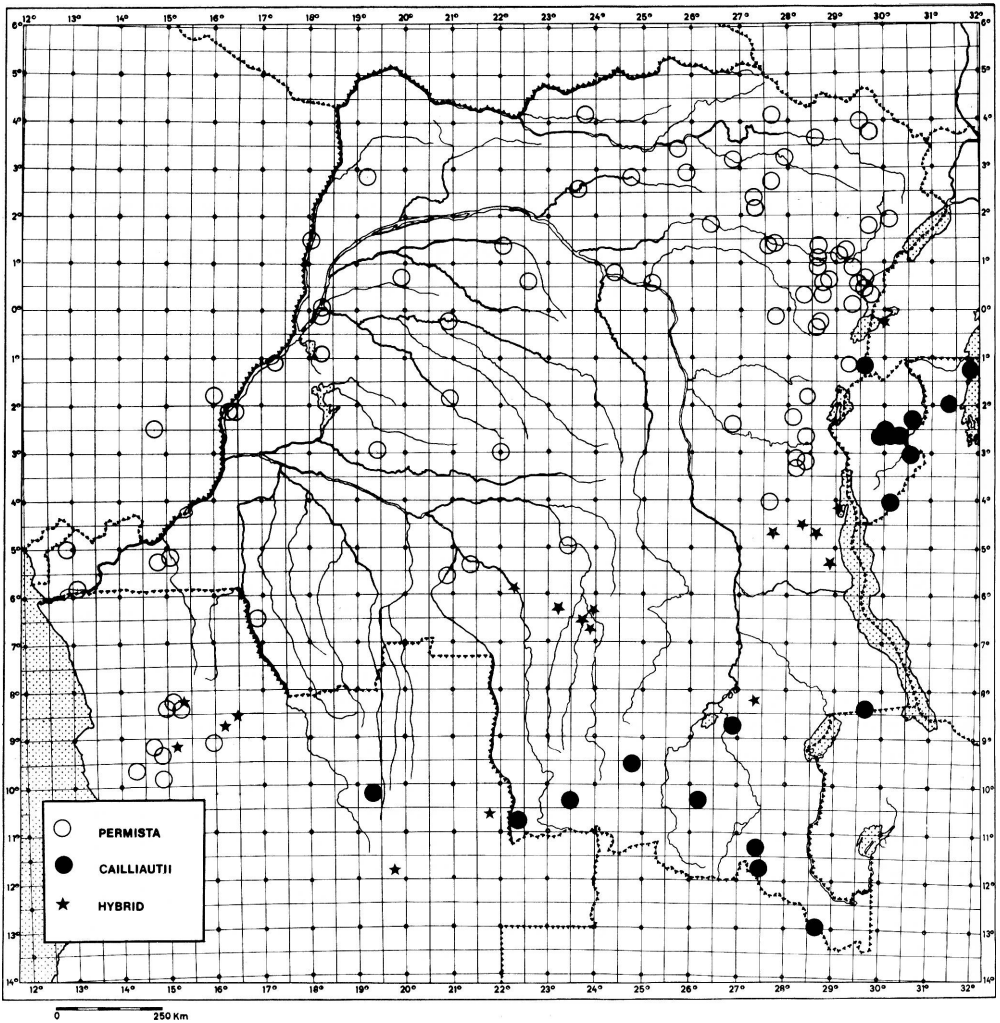


Fig. 1. Collecting localities of *permista*, *cailliautii* and hybrids in Zaire, Rwanda, Burundi and Angola.

mista from Ukaika, near Beni, with green yellowish spots on the top of the mantle ; except for this particularity, the specimen (NHMW 24588) is a pure *permista*. I have examined three specimens collected in the Rutshuru Plain, south of Lake Edward (MRAC, NHMW, NHRM), two of them pure *nyansae*, the third (NHRM 234), an immature female obtained by Arrhenius, a pure *permista*. A female from Rutanda, Queen Elizabeth National Park (NMK B6123) seems to be intermediate : the mantle has a small amount of clear spots.

Continuing my studies of the hybridization phenomena in Central Africa, I have examined about 460 specimens of the megasubspecies *cailliautii* and *permista* to clarify their interaction at the contact. Fig. 1 shows the localities of origine of the specimens examined. *C. permista* is confined to low altitude forests and avoids montane forests ; my native collectors have repeatedly found it in the transition forest of Kakanda, at 1350 m, but never at higher altitudes ; it seems to prefer second growth, forest clearing edges and forest galleries ; it has been collected in Angola in coffee wood plantations. *C. cailliautii* prefers more open habitats and has been found in various types of wooded savanna up to 1560 m (Kigamba, Burundi). The contact between the two megasubspecies is principally limited to the southern edge of the Zaire forest, where it desintegrates in a multitude of forest blocs and smaller or larger gallery forest.

Table 1. Measurements (in mm) of *Campethera* ssp. males belonging to *permista*, *nyansae* and their intermediates

	Wing				Tail				100 T/W				Total culmen			
	N	m	M	\bar{X}	N	m	M	\bar{X}	N	m	M	\bar{X}	N	m	M	\bar{X}
<i>permista</i>																
West Africa (1)	8	95	99.5	97.3	8	54.5	59	57.1	8	55.6	61.5	58.7	8	16	19	17.6
Zaire	25	96	103	99.9	24	53	61	56.9	24	53.0	59.8	57.0	22	16	20	18.3
Shaba (HI 1.5-4) (3)	1			98	1			62	1			63.3				
Kasai (HI < 1.5)	11	97.5	106	102.0	11	55	65	59.3	11	54.5	61.3	58.1				
Kasai (HI 1.5-4)	7	94.5	105	99.4	7	51	63	58.0	7	52.8	62.1	58.3				
Angola (HI < 1.5)	17	98	107	102.0	16	52	65	59.6	16	52.3	61.7	58.5	16	16	19	17.8
Angola (HI 1.5-4)	6	96	105	101.2	6	53	65	59.3	6	55.2	61.9	58.6	6	15.5	20	18.0
<i>nyansae</i>																
Angola (HI > 4)	3	101	111	105.3	3	57	62	59.3	3	55.9	56.7	56.3	3	17	20	18.2
Shaba (HI > 6.5)	15	97	104	100.1	15	53	65	59.9	15	52.0	63.7	59.8				
Shaba (HI 6.5 > 4)	15	94.5	106	100.1	15	53.5	63.5	59.3	15	55.4	62.9	59.2				
Kasai (HI 6.5 > 4)	1			101.5	1			58.5	1			57.6				
Burundi	2	97.5	100	98.8	2	58		58.0	2	58.0	59.5	58.8	2	17.5	19	18.3
Rwanda	2	97	100	98.5	2	59	60	59.5	2	59.0	61.9	60.5	2	17		17.0
Kivu (HI > 6.5) (4)	1			97	1			59	1			60.8	1			18.5
Kivu (HI > 6.5) (4)	2	99	102	100.5	2	57.5	58.5	58.0	2	56.4	59.1	57.8	2	18.5	19	18.8
Kivu (HI > 6.5) (5)	1			96	1			59	1			61.5				

(1) Cameroon, Congo (2)

(2) Far from the contact zone, including 1 specimen from Bwamba

(3) Lulimba

(4) Baraka

(5) Rutshuru

Table 2. Measurements (in mm) of *Campethera* ssp.females belonging to *permista*, *nyansae* and their intermediates

	Wing				Tail				100 T/W			Total culmen				
	N	m	M	\bar{X}	N	m	M	\bar{X}	N	m	M	\bar{X}	N	m	M	\bar{X}
<i>permista</i>																
West Africa (1)	8	96	107	99.1	7	54.5	63	57.6	7	52.8	63.0	58.0	6	17	18	17.3
Zaire (2)	24	95	106	99.2	21	53	66	57.8	21	54.1	63.3	58.1	19	16	18.5	17.2
Kivu (HI < 1.5) (3)	1			101.5	1			63	1			62.1				
Kivu (HI 1.5-4) (4)	2	96	101	98.5	2	53	59	56.0	2	55.2	58.4	56.8				
Shaba (1.5-4) (5)	1			102	1			59.5	1			58.3				
Kasai (HI < 1.5)	11	95	107	101.3	11	56	71	61.0	11	55.4	66.4	60.2				
Kasai (HI 1.5-4)	10	96	104.5	99.5	10	53	63	58.6	10	52.6	61.6	58.8				
Angola (HI < 1.5)	13	97	105	101.3	12	55	62	58.9	12	56.3	61.2	58.3	13	14.5	19.5	17.3
Angola (HI 1.5-4)	4	98	101	100.0	4	57.5	61.5	58.2	4	57.5	60.9	58.9	4	15.5	18	16.9
<i>nyansae</i>																
Angola (HI > 4)	1			104	1			62	1			59.6				
Shaba (HI > 6.5)	8	97	102	99.9	8	53.5	62	57.7	8	53.5	62.0	57.8				
Shaba (HI 6.5 > 4)	9	99.5	106	103.4	9	55	66	60.1	9	51.9	62.9	57.6				
Kasai (HI 6.5 > 4)	2	101.5	102	101.8	2	55	59	57.0	2	53.9	58.1	56.0	2	17.5	18	17.8
Kivu (HI > 6.5) (6)	1			104	1			61	1			58.7	1			17
Burundi	5	95	98	96.9	5	53	59	56.2	5	54.4	60.2	58.2	5	16.5	18	17.5
Tanzania (7)	2	98	101	99.5	8	56	58	57.0	2	57.1	57.4	57.3	2	17		17.0

- (1) Cameroon (4), Gabon (2), Congo (2)
 (2) Far from the contact zone, including 2 specimens from
 Bwamba
 (3) Namoya

- (4) Kasongo, Kabambare
 (5) Mahila
 (6) Baraka
 (7) W of Lake Victoria

Tables 1 and 2 show that *permista* and *cailliautii* are of about the same size (at least in the region of Africa considered: *loveridgei*, of Tanzania, is smaller). Thus measurements are of no help in separating the two taxa and analysing their hybridization.

I have constructed an index of hybridization (H.I.) based on four characters:

Upperparts: *permista* is characterized by plain green yellowish upperparts (nape, scapulars, mantle, rump, uppertail-coverts); *nyansae* is heavily spotted on the nape, scapulars, mantle and rump, while the uppertail-coverts are narrowly barred; for many specimens examined the individual yellow whitish spots are round, for others, they are also numerous, but a little elongated.

Wing coverts and secondaries: *permista* has plain green yellowish lesser coverts, primary coverts, secondary coverts and secondaries (wing closed, the barring of

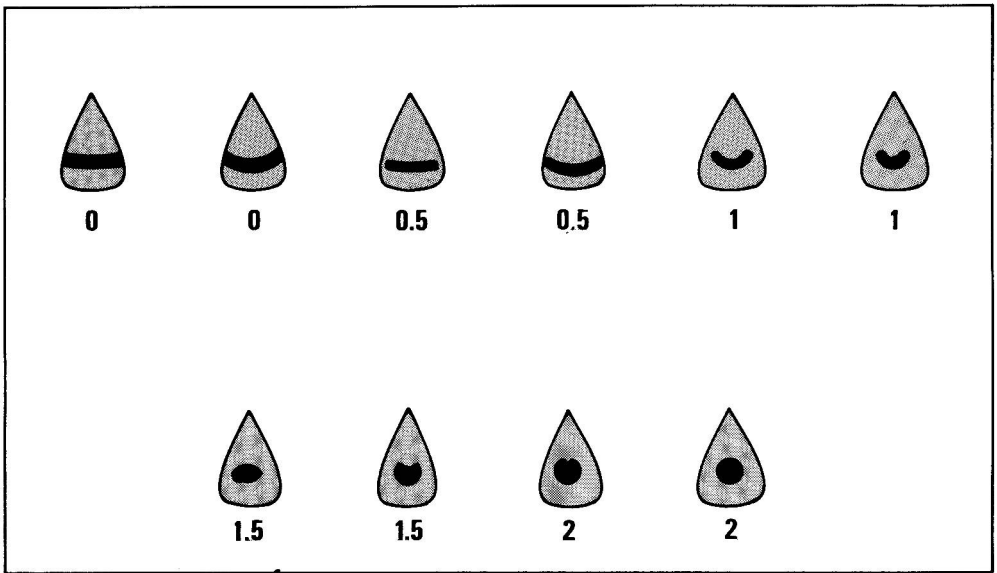


Fig. 2. Variation of the markings of the underpart of *permista* and *cailliautii* (*nyansae*).

the interior part of the secondaries being concealed); the same coverts and the secondaries are spotted or even barred with yellow whitish in *nyansae* (wing closed).

Rectrices : the shafts of the median rectrices are blackish or dark brown in *permista*. Their colour is golden yellowish in *nyansae* ; the colour of the tips cannot be used because they are often soiled ; I considered also the colour of the external rectrices : plain dark green in *permista*, barred with yellowish in *nyansae*. However, this character, very constant in pure *permista* and pure *nyansae*, proved difficult to use because of wear in some specimens ; moreover, I saw a specimen from Abokobi, Goldcoast (= Ghana) (ZMB), labeled as a juvenile male, resembling *permista*, but with all rectrices heavily barred ; for these reasons, I did not use this character.

Underparts : in *permista* the chest and the flanks are barred with black ; the width of the bars varies from 1.6 to 2.4 mm (mean 2.0 mm ; N = 20) ; *nyansae* is heavily marked on the underparts with round black spots, especially numerous on the breast and flanks ; the diameter of these spots varies from 2.2 to 3.1 mm (mean 2.8 mm ; N = 20) ; these round spots have a tendency to change progressively into bars as shown in Fig. 2.

Table 3 shows the establishment of the hybrid index. Pure *permista* is characterized by a H.I. of 0, pure *nyansae* by 8. It is impossible to give here the value of the

Table 3. Establishment of the hybridization index between *permista* and *cailliautii*

Upperparts	without spots	feebly spotted	moderately marked by round or elongated spots	strongly marked with elongated spots	strongly marked with round spots
	0	0.5	1	1.5	2
Wing coverts, secondaries	non spotted	feebly spotted	moderately spotted or barred	less strongly spotted or barred	strongly spotted and barred
	0	0.5	1	1.5	2
Shaft of median rectrices	blackish or dark brownish	brownish	pale brown	soiled yellow	golden yellowish
	0	0.5	1	1.5	2
Underparts	straight bars	barred with half moons	marks quite elongated	spots elongated	round spots
	0	0.5	1	1.5	2

permista pure : H.I. = 0

cailliautii pure : H.I. = 8

H.I. for all specimens examined. To decide which values of the H.I. can be taken to indicate hybridization. I have examined a large number of specimens of *permista* collected far from the expected hybridization zone (in Zaire and even in West Africa), and of *nyansae* from Burundi and of *loveridgei* from East Africa. The great majority of specimens examined have a H.I. of respectively 0-0.5 and 8-7.5. A small percentage (2.8 %) is characterized by a H.I. of respectively 1 and 7, only few (1.2 %) by respectively 1.5 and 6.5. I conclude that a H.I. of more than 1.5 and less than 6.5 indicates hybridization. I have assembled, in Table 3, all specimens with a H.I. varying from 2 to 6, collected in Zaire, which are considered as hybrids. Moreover specimens that probably show slight signs of hybridization have been collected at Meroide (6 x 1.5), Kabambare (1 x 1.5), Dilolo (1 x 6.5), Kasaji (3 x 6.5) and Kasapa (2 x 6.5).

This part of the contact zone is represented in Fig. 3. For each collecting locality I give the number of specimens belonging to different degrees of interbreeding. To facilitate the discussion I admit that the middle of the hybridization zone can be represented by a straight line beginning in the region north-west of Lake Tanganika and crossing the Kasai. This line starts approximatively from Lulimba and passes between Katombe and Gandajika. Lusambo, in the north, is already situated in the tropical lowland forest. It can be noted that the region west of Baraka is already included in woodlands with *Brachystegia* and is separated from the forest-savanna mosaic where *nyansae* meets *permista* by the southern prolongation of the Itombwe Highland and the Mt. Kabobo range, where the altitudes are too high

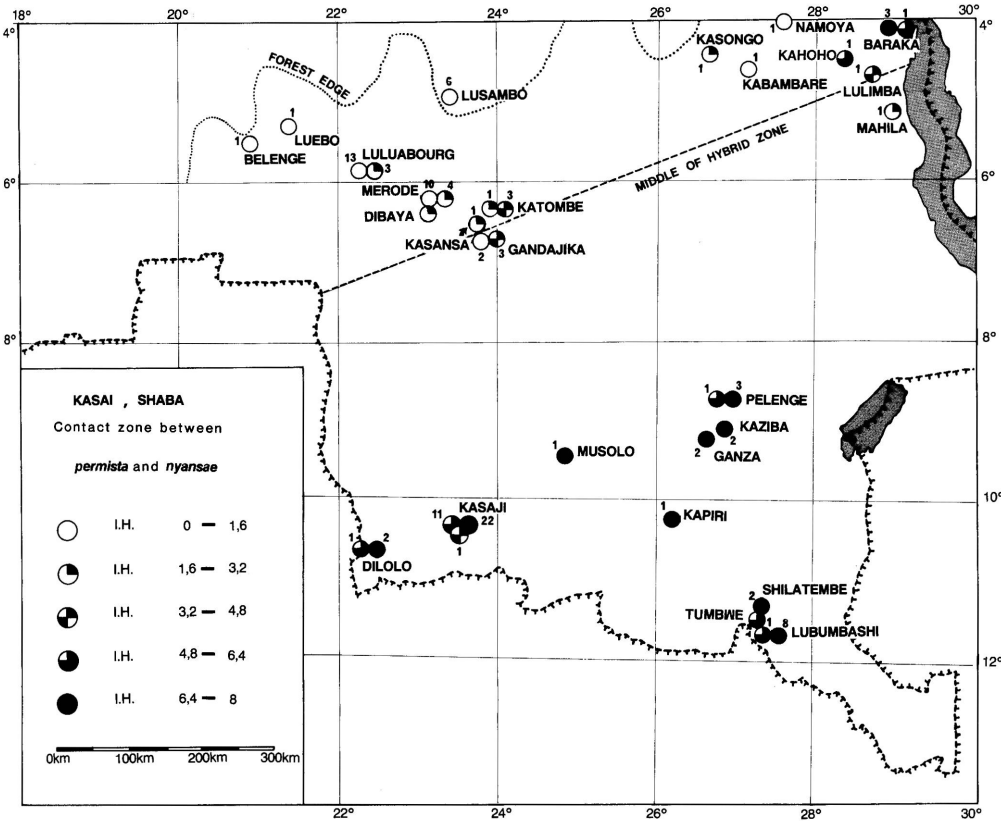


Fig. 3. Contact zone between *permista* and *nysae* in Kasai and Shaba.

for *permista*. For this reason, the Baraka population of *nysae* has little contact with *permista*. However, the separation is not complete, as one specimen out of four shows a H.I. of 5 (see Table 4).

Most of the specimens coming from the hybridization zone have been collected between 1940 and 1960. It is probable that, since this period, the cutting of the forest patches has continued. The present situation is not known, but it is probable that *permista* is confined to the forest islands which still remain.

The greatest number of real intermediates, with an H.I. 3 to 5, have been collected in localities near the contact line of Fig. 3, as in Katombe (4), Gandajika (3), Mahila (1), Lulimba (1), Kaholo (1) and Baraka (1). Introgression is much pronounced to the south of this line. Hybrids can be found as far as Kasaji, at a distance of 380 km, and, even as far as Lubumbashi (650 km). On the other hand, in

the north, the phenomenon of introgression is much less pronounced. Hybrids are present at a maximum distance of 140 km, as in Merode (3), Luluabourg (3), Kasansa (1) and near Kasongo. Unfortunately, no collecting has taken place at a distance 40 to 360 km to the south of the middle of the hybridization zone (line of Fig. 3).

Contrary to Zaire, where the contact between *permista* and *nyansae* takes place in a continuous mosaic of forest and savanna, the situation in Angola is complex. An extensive bloc, called « escarpment forest », exists at low altitudes in the

Table 4. Hybrids between *permista* and *nyansae* collected in Zaire

Museum	number	Locality	H.I.
AMNH	258168	Luluabourg	2
MRAC	44443	Merode	2
MRAC	44835	Merode	2
MRAC	13412	Luluabourg	2
MRAC	9341	Luluabourg	2
AMNH	549856	Nr. Kasongo	2
MRAC	44444	Merode	2.5
MRAC	76832	Kasansa	2.5
MRAC	40564	Merode-Dibaya	2.5
IRSNB	AP 420	Mahila	3
AMNH	703750	Katombe	3
MRAC	68630	Lulimba	3.5
MRAC	57553	Gandajika	3.5
MRAC	76566	Gandajika	4
MRAC	52852	Katombe	4
MRAC	61479	Gandajika	4.5
AMNH	388212	Katombe	4.5
AMNH	703749	Katombe	4.5
MRAC	66604	Kasaji	4.5
AMNH	549853	Baraka	5
AMNH	764284	Kahoho	5
MRAC	55718	Kasaji	5
MRAC	62224	Kasaji	5.5
MRAC	66633	Kasaji	5.5
MRAC	67395	Kasaji	5.5
MRAC	74077	Kasaji	5.5
IRSNS	25959	Pelenge	5.5
MRAC	23190	Dilolo	5.5
MRAC	15686	Lubumbashi	6
MRAC	54551	Kasaji	6
MRAC	55493	Kasaji	6
MRAC	56773	Kasaji	6
MRAC	71419	Kasaji	6
MRAC	99665	Kasaji	6
MRAC	106595	Kasaji	6
IRSNS	25963	Munoi	6
IRSNS	25958	Pelenge	6
MRAC	112571	Tumbwe	6

Cuanza Norte (District), continuing to the north, in the Congo (now Zaire District). This forested area has a length of about 360 km and a width of about 130 km. It is surrounded in the north and east by forested savannas of moist types followed more to the east by savannas with *Brachysregia*. A large gallery exists also along the Kwango River, at the border with Zaire. Traylor (1963) noted already that « representative subspecies of the escarpment zone frequently differ strikingly from their relatives in the adjoining zones » ; *permista* is found in Cuanza Norte, south to the Cuanza River, and in Malanje (Traylor, *loc. cit.*). *Nyansae* exists in north eastern Moxico, intergrading with *permista* in Luanda (Traylor, *loc. cit.*). In general, *permista* is confined to the forest bloc and the gallery forest, while *nyansae* is found in the savannas. An eventual hybridization can exist in a belt where the two populations meet.

Most of the specimens examined have been collected in 1903 by Ansorge and, from 1950 to 1960, by Heinrich (1958). It can be supposed that, at this time, the forest was intact, but the present situation is not known.

Among the examined specimens (50) only eight can be considered as hybrids ($H. I. \geq 2 \leq 6$). They are listed in Table 5.

Table 5. Hybrids between *permista* and *nyansae* collected in Angola

Museum	number	Locality	H.I.
AMNH	549511	Canhoca	2
AMNH	549512	Girri	2
YPM	78470	Quitondo	2.5
FMNH	250611	Lucala River	3.5
AMNH	549503	Katole	4
YPM	78473	Bolengongo	4.5
BMNH	1957.35.91	Luau River	5
BMNH	1957.36.90	Vila Luiso	6

Probably four more specimens (H.I. 1.5) are hybrids, close to *permista* : Canhoca (2), Dondo, Golungo Alto, Ndala Tando, Quitondo/Calulo ; another from Cacolo is near *nyansae* (H.I. 6.5). A specimen from Lucano, not examined, is a pure *nyansae* (Pinto, 1983).

Fig. 4 shows that pure or almost pure *permista* can be found south of the forest bloc, as at Dondo and between Quitondo and Calulo, and in the east at Duque de Bragança. However, a true hybrid has been collected inside the escarpment forest, at Bolongongo. The hybridization zone seems to be situated around the forest bloc, but introgression is conspicuous even at great distances at Katole (about 120 km).

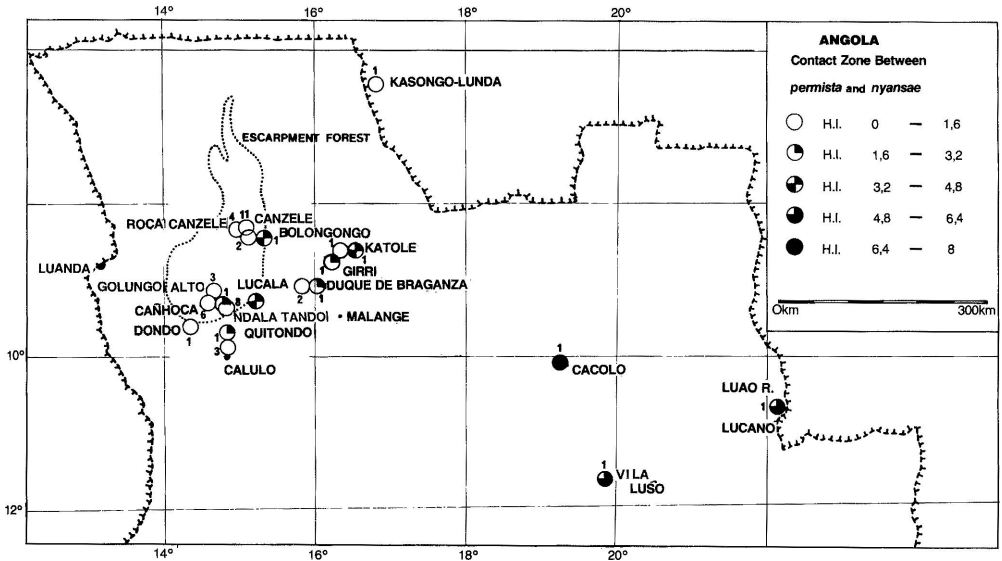


Fig. 4. Contact zone between *permista* and *nyansae* in Angola.

In most cases, the type of habitat is not noted on the label. Only Heinrich, when collecting in Angola, gave indications about the biotope where the woodpeckers had been collected (FMNH, YPM) : 1, primary tropical wood ; 2, secondary tropical wood ; 3, gallery wood ; 4, coffee plantations (coffee wood, lower trees of coffee plantations) ; 5, savanna wood. The 19 specimens collected by Heinrich can be distributed as follows between these five habitats :

Type 1 and type 2 : Canzele (Inside the forest bloc) : H.I. 0(3), 0,5 ;

Type 2 : Quitondo (south of forest bloc) : H.I. 0,5.

Type 3 : Duque de Bragança (east of forest bloc) : H.I. 1 ; Dondo (south of forest bloc) : H.I. 1,5, Bolongongo (inside the forest bloc) : H.I. 5 ; Cacolo (Lunda) : H.I. 6,5.

Type 4 : Bolongongo, Canzele, Roça Canzele (inside the forest bloc) : H.I. 0(4), 0,5 (2) ; Quitondo/Calulo : H.I. 0,5, 1,5 ;

Type 5 : Duque de Bragança : H.I. 0, 0,5.

Fifteen specimens are *permista* (or near) (H.I. 0-1), two are hybrids near *permista* (H.I. 1,5), one a true hybrid (H.I. 1,5) and one a hybrid near *nyansae* (H.I. 6,5). No correlation can be found from this small sample between hybridization and habitat. The presence of *permista* in coffee plantations seems normal for plantations established in forest clearings. It appears also that *permista* is found outside the forest bloc, if sufficient wood is present. On the other hand, the presence of a specimen with a H.I. of 5, at Bolongongo, inside the forest bloc, seems due to introgression.

DISCUSSION

Campethera cailliautii is a member of the *C. maculosa* superspecies (Short and Tarbaton *in* Snow, 1978 ; Short, 1980). The two paraspecies meet in Ghana, but only one hybrid is known from the contact zone (Short and Tarbaton, *loc. cit.*). As *permista* and *cailliautii* are morphologically very different, but interbreed freely, the two taxa are considered as megasubspecies (Short, 1980). The zone of allopatric hybridization (Woodruff, 1973) starts from the region north-east of Lake Tanganika, crosses Shaba and Kasai, and reaches Angola. These two woodpeckers are ecologically separated : the first is confined to equatorial forest, while the second prefers more open habitats, like humid wooded savannas. The hybrid zone corresponds to the presence of an ecotone. Gene flow appears very pronounced in the southern part of this zone, in wooded savannas. On the other hand, it is less strong in the Afrotropical forest, north of the hybrid zone where, probably, natural selection is acting against some genes, those giving to *cailliautii* a brighter general appearance (clear spotting on the back, blackish spots on the underside, golden median rectrices). To explain the non symmetric introgression at the two sides of the hybrid zone, I suppose that in the south, far from the contact zone, the existence of intermediates is in relation with the presence of wooded patches.

Inside the hybrid zone, the distribution of intermediates corresponds to a cline. The contact zone is not a zone of overlap and hybridization, in conformity with Short's (1969, 1972) definition : in Zaire, pure or almost pure *permista* has been collected in the hybrid zone, situated at the two sides of the line of Fig. 3, while no pure *cailliautii* exists in this zone. Likewise, in Angola, several pure *permista* have been found inside the hybrid zone, which includes the escarpment forest bloc, but no pure *cailliautii*.

Short (1980) has discussed the speciation in African woodpeckers in relation with past climatic changes. A succession of interglacial and glacial periods during the Pleistocene produced an extension, a reduction, with eventual isolations, of the forest biome. Short (*loc. cit.*) supposes that the ancestor of *Campethera maculosa* originated in mid-Pleistocene, but the evolutionary history of the taxa belonging to this superspecies finished only in late Pleistocene.

In the beginning prior to c. 25 000 B.P., the ancestor of the *C. maculosa* superspecies occupied the whole forest bloc of central Africa (Fig. 5). Then, in a second stage, during an arid period, an extension of the Sahara about 500 km southwards produced the Dahomey gap. This break of the forest took place around 18 000 B.P. (Livingstone, 1975 ; Van Zinderen Bakker, 1982), while, prior to this event, the Upper and Lower Guinea forests were united. Thus, the western part of the forest bloc became isolated and, during an especially arid period, the width of the Dahomey Gap reached 1 100 km (Moreau, 1969). The speciation of *C. maculosa* took place in the isolated western bloc, when no gene flow was possible between the Upper Guinea and Lower Guinea forests. Later, when the aridity in this part of Africa diminished, the two forest blocs started to advance from either

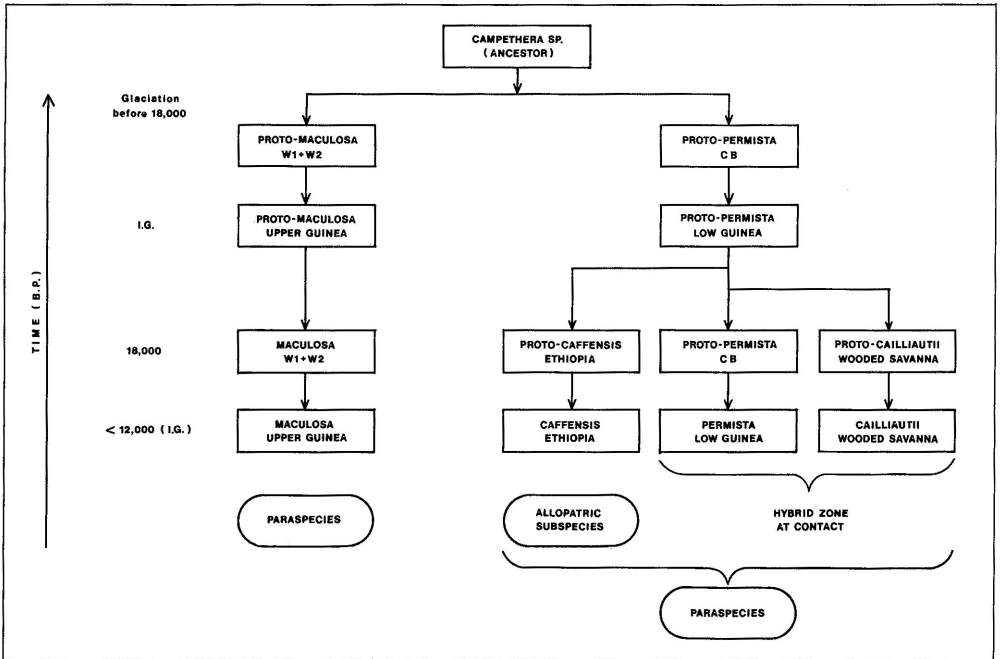


Fig. 5. Hypothetical differentiation of *Campethera* spp. during the end of the Pleistocene. (W1 and W2 : West African forest refugia ; CB : Congo basin forest refugium)

side and the present situation of the Dahomey Gap was reached c. 10 000 years B.P. (Livingstone, *loc. cit.* ; Van Zinderen Bakker, *loc. cit.*). Half of the Dahomey Gap is occupied by a forest-savanna mosaic with forest patches. As *permista* is not a real primary forest bird, this woodpecker crossed the Dahomey Gap, coming from the east, as it is shown by several collecting localities (Short and Tarbaton *in* Snow, 1978). The secondary contact with *maculosa* is situated a little west of the Dahomey Gap. But there is no overlap between the two paraspecies which, probably, are in competition.

The interglaciation period, c. 10 000 B.P., produced a great extension of the central African forest bloc which even reached the Ethiopian highlands. This north-eastern part of Africa was occupied by a population, which adapted itself to higher altitudes. Later, during a more arid oscillation, possibly between 7 000 and 5 000 B.P. (Livingstone, 1975), the population of Ethiopia became detached from the central population. After its isolation, the woodpeckers inhabiting Ethiopia, started a differentiation process which led finally to *kaffensis*, morphologically near to *permista*. It is possible that *kaffensis* is a close relative of *permista*, though, for allopatric taxa, close phenotypical characters are not necessarily a proof of their conspecificity (Prigogine, 1984).

The question arises whether the contact between *permista* and *cailiautii* is a secondary one. These taxa correspond exactly to the definition of a mega-subspecies (Amadon and Short, 1976) : they show sufficient phenetic differences to be considered previously as distinct species and each of them includes several (at least two) subspecies. Yet, they interbreed in a relatively broad contact zone. Amadon and Short (*loc. cit.*) suggest a secondary contact for taxa which warrant treatment as megasubspecies.

I will try to establish the various steps of their evolutionary history based, however, on several hypothesis difficult to prove. I suppose that in a period of the Pleistocene, during more humid climatic conditions, the central African's rainforest refuge extended its range in the direction of the south-east. Probably, this expansion took place about the same time, when the forest expanded also in the direction of the north-east. During this stage I, the ancestor of present *permista* increased its range following the progression of the forest. Surely, the forest did not advance continuously but patchily, as more and more places become suitable for its implantation. As *permista* is a woodpecker preferring secondary forest, forest edges, clearings and even (now) coffee plantations, the formation of real primary forest was not necessary to explain the colonization of the new forest patches by *permista*. To have an idea of the extension reached by the forest and that by the birds associated with it, I have examined the present distribution of a certain number of species associated principally with the central African's rainforest, confined however to second growth, forest edges and clearings, which still are distributed especially in south-eastern Africa. The following species can be considered : *Baepogon indicator* (up to c. 11° S, 27° E), *Chlorocichla flavicollis* (up to c. 14° S, 32° E), *Bias musicus* (found in East Africa and south of Lake Malawi), *Andropadus virens* (with a population in East Africa and another south of the central Africa's forest bloc, on the two sides of Lake Malawi, reaching even the Indian Ocean, south-east of this lake), *Ceuthmochares aereus* (a population in Ethiopia, another in East Africa near the Indian Ocean and a third population west of Lake Malawi continuing south to the evergreen forests along the seaside of southern Africa - a distribution quite similar of the present distribution of the Green-backed Woodpecker). I suppose that, during the stage I, the ancestor of the present *permista* reached about the same regions, where the habitat was, at this time, favorable to this woodpecker.

Later, during stage II, which corresponds to a shrinking of the forest during an arid period, this south-eastern population of *permista* became isolated from the parental population in central Africa. The progressive formation of the distribution gap acted finally as a barrier preventing gene flow between the two populations.

As the climate changed into a drier one, in the south-eastern part of Africa, the vegetation was progressively modified in a more open habitat. The new habitat differed by climatic and biotopic conditions from the environment occupied by the parental population and an adaptive evolution of the isolated population took place. The colour pattern especially was adjusted to match the background of the

new environment, that of a moist wooded savanna. Thus, the adaptation was influenced by the lighter biotope : the woodpecker acquired a distinct pattern (white yellow spots on back, clear-barred secondaries, round dark spots on under-side) giving the bird a general lighter colour. In other words, during stage III, this woodpecker population got phenotypical characters very near to the present *cailliautii*.

After having completed its eco-geographic adaptation, the isolated population started the distribution in the new bloc of habitat and finally, during the last stage IV, *cailliautii* increased its distribution area taking the direction of central Africa, the ecological conditions in the gap being now satisfactory to the adapted requirements of *cailliautii*. Thus, this form managed to cross the same region like, during stage I, its ancestor passed, but in the opposite direction, during other climatic conditions. Coming in contact with the *permista* population of the rainforest of central Africa, an intensive interbreeding took place showing that the mechanisms of reproductive isolation had not been developed during the isolation stage III which, probably, was too short. This schema supposes that the contact between *permista* and *cailliautii* is a secondary one.

On the other hand, *caffensis* remained isolated in Ethiopia and never succeeded to cross the gap between Ethiopia and central Africa.

It can be concluded that the isolation of *cailliautii* has occurred in late Pleistocene. But all these suggestions suppose that the speciation process of these taxa occurred in the same rate in the various regions of Africa. This is not proven, but it may be accepted as a working hypothesis.

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SUMMARY



The two taxa *permista* and *cailliautii*, belonging to the genus *Campethera*, have been considered first at distinct species, but later as subspecies. In fact they are in contact in a zone which starts from the region north-west of Lake Tanganika, crosses Shaba and Kasai, and reaches Angola. A detailed study of all museum specimens collected in or near this zone has been achieved. *Permista* and *cailliautii* are morphologically different, but they interbreed freely in a zone which corresponds to a zone of allopatric hybridization. This hybridization occurring on a large scale demonstrates that these two taxa are conspecific. They are ecologically separated: *permista* is confined to equatorial forest, while *cailliautii* prefers more open habitats. The hybrid zone corresponds to an ecotone.

A hypothesis is discussed to explain the evolutionary history of the paraspecies *Campethera maculosa* and *C. cailliautii* (including *permista* and *kaffensis*).

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ANNEX 1

Nominate *Campethera cailliautii* Malherbe, 1849, has been described from coastal Kenya. The races *nyansae* Neumann, 1900, and *fuelleborni* Neumann, 1900, have respectively Mwanza and Tukuyu as locality of the type. White (1965) puts *nyansae* in synonymy with nominate *cailliautii* and this is surely wrong, but he admits *fuelleborni*. Hartert, 1920, described moreover *loveridgei*, with Morongoro, eastern Tanzania, for the locality of the type. In reality it is of little importance to admit *nyansae* or *fuelleborni* as Neumann described both in the same paper and there is no priority for the two names. Following Chapin (1939) I admit *nyansae*. Clancey (1971) showed that only three subspecies of *Campethera cailliautii* are present in eastern and south-eastern Africa, nominate *cailliautii* from coastal Kenya, *nyansae* in north-eastern Angola, Zambia, southern Zaire, northern Malawi, south-eastern Tanzania to south of Lake Victoria, and *loveridgei* in East Africa, from eastern Tanzania to Moçambique. *Fuelleborni* is placed in synonymy with *nyansae*. Later, Clancey (1980) confirmed the validity of *loveridgei* and these three subspecies have been accepted by Short (1982).

For the megasubspecies *permista* (Reichenow, 1876), Short (1982) does not recognize *kaffensis* (Neumann, 1902) and *togoensis* (Neumann, 1904). I follow Short in accepting that *togoensis* seems to depend on individual variable characters. But I have seen several specimens of *kaffensis* which appear quite different from nominate *permista* : back dark green, more greyish, shafts of central rectrices more clear, not blackish or dark brown. Thus I think that *kaffensis* is valid. Moreover, the ecological requirements of this race are different from that of *permista*, as *kaffensis* inhabits in Etiopia subtropical humid forest, from 1200 to 1800 m, and Olive-*Podocarpus*-Juniper forest, from 1800 to 2400 m (Urban and Brown, 1971).

There is no contact between nominate *cailliautii* and *loveridgei* and *permista*. Thus the hybridization zone is formed by *C.cailliautii nyansae* and by *C.c.permista*.

ANNEX 2

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), Tring
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
IRSNB	Institut royal des Sciences naturelles de Belgique, Bruxelles
LACM	Natural History Museum of Los Angeles County, Los Angeles
MHNG	Muséum d'Histoire Naturelle de Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Musée royal de l'Afrique Centrale, Tervueren
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
NMNH	National Museum of Natural History, Washington
NMK	National Museums of Kenya, Nairobi
RNH	Rijksmuseum van Natuurlijke Historie, Leiden
YPM	Peabody Museum of Natural History, Yale University, New Haven
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZIMH	Zoologisches Institut und Zoologisches Museum, Universität Hamburg
ZMB	Zoologisches Museum, Berlin
ZMK	Zoologisk Museum, København

SAMENVATTING

De twee taxa *permista* en *cailliautii*, die beide behoren tot het genus *Campethera*, werden aanvankelijk beschouwd als afzonderlijke soorten maar later als ondersoorten. In feite zijn ze in contact met mekaar in een gebied dat begint in de streek ten noordwesten van het Tanganika meer en verder doorheen Shaba en Kasai naar Angola loopt. Een gedetailleerde studie van alle museummateriaal, dat in of nabij deze zone werd verzameld, werd uitgevoerd. *Permista* en *cailliautii* vertonen morfologische verschillen die toelaten een hybridiseringsindex te berekenen voor elk onderzocht exemplaar (*permista* 0, *cailliautii* : 10). De hybridiseringszone heeft een breedte van ongeveer 250 km. Buiten deze zone treft men slechts zuivere fenotypes aan, terwijl men erbinnen vooral intermediaire vormen vindt met verschillende hybridiseringsindices, naast enkele zuivere *permista*. Rekening gehouden met de toestand in de contactzone, komt de auteur tot het besluit dat de twee taxa, *cailliautii* en *permista*, nog geen reproductieve isolatiemechanismen ontwikkeld hebben en dat ze als conspecifiek dienen beschouwd te worden. Er wordt tevens een hypothese naar voor gebracht om de evolutieve geschiedenis van beide taxa te verklaren en om aan te tonen dat het om een secundair contact gaat.

RESUME

Les mégasous-espèces *cailliautii* et *permista*, appartenant au Pic à dos vert, *Campethera cailliautii*, sont en contact dans une zone qui s'étend du nord-ouest du lac Tanganika jusqu'à l'Angola, en traversant le Kasai. Poursuivant mes études des phénomènes d'hybridation, j'ai examiné un grand nombre de spécimens de ces deux taxons pour connaître les interactions dans la zone de contact et ses environs. Les caractères morphologiques de ces deux oiseaux m'ont permis de calculer un indice d'hybridation (*permista* : 0, *cailliautii* : 10) pour chaque spécimen examiné. La zone d'hybridation a une largeur qui atteint, à certains endroits, environ 250 km. A l'extérieur de cette zone, on ne rencontre que des phénotypes purs, tandis qu'à son intérieur on trouve surtout des intermédiaires caractérisés par des indices d'hybridation variables et quelques *permista* purs. En tenant compte de la situation trouvée dans la zone de contact j'arrive à la conclusion que les deux taxons, *cailliautii* et *permista*, n'ont pas encore développé des mécanismes d'isolement de reproduction et qu'il faut les considérer comme conspécifiques. Une hypothèse est émise pour expliquer l'histoire évolutive de ces deux taxa et pour montrer qu'il s'agit d'un contact secondaire.

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