Myotis | Vol. 40 | 95 - 126 | Bonn, December 2002

A revision of the *Rhinolophus maclaudi* species group with the description of a new species from West Africa (Chiroptera: Rhinolophidae)

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Abstract. *Rhinolophus ziama* n. sp. from the Upper Guinea highlands in Guinea and Liberia is described. This new taxon differs from *R. maclaudi* in being significantly smaller in size, and from *R. ruwenzorii* and *R. hilli* by skull shape and noseleaf morphology. These four related species are allocated to the formally established *R. maclaudi* group. A published record of *R. maclaudi* from Nigeria is here re-identified as *R. hildebrandtii* and represents the first record for West Africa. *R. ruwenzorii* is reported for the first time from Rwanda. We discuss the biogeography of the species group and propose that its members might represent an ancient radiation now restricted to two disjunct refuges in the Upper Guinea highlands and the mountain range along the Albertine Rift. This pattern strikingly resembles that of *Micropotamogale lamottei* and *M. ruwenzorii* (Tenrecidae). The conservation status of the four species is discussed and updated IUCN Red List categories are proposed. It seems likely that these species are seriously threatened both by habitat degradation within their small distribution ranges and direct exploitation in their day roosts.

Key words. Africa, biogeography, Chiroptera, conservation, distribution, first records, Ethiopian Region, evolution, new species, Rhinolophidae, taxonomy.

Introduction

The West African *Rhinolophus maclaudi* Pousargues, 1897 has its noseleaf characteristically structured: a broad and forward-inclined sella with large basal lobes forming a heart-shaped cup, almost completely covering the nostrils, the connecting process only weakly developed and low, leaving a deep emargination between the sella and the lancet, and the nostrils bordered on each side by a more or less straight rim. The skull is characterized by its slenderness and a heavy rostrum. The interpterygoid pit is barrel-shaped and unusually deep.

Two closely related taxa were discovered in the region of the Albertine Rift, i.e. *R. ruwenzorii* J. Eric Hill, 1942 and *R. hilli* Aellen, 1973. These three species were reviewed by Smith & Hood (1980). They considered all described character differences in morphology and size of these taxa as being of no particular significance. Therefore, they classified *R. ruwenzorii* - including *hilli* as a synonym - as a subspecies of *R. maclaudi*. This view was accepted by most subsequent authors.

In 1992, one of the authors (HV) and Wilfried Bützler captured three specimens (one collected) near Sérédou, SE-Guinea that were initially identified as *R. maclaudi*. However, they were significantly smaller than the known specimens from SW-Guinea.

In Liberia, *R. maclaudi* was first recorded by a single specimen (Koopman 1993, Koopman et al. 1995). In the latter publication the authors briefly commented on the "somewhat smaller" size of this specimen in comparison to other than West African specimens referred to the same taxon by Smith & Hood (1980).

However, the size differences between *R. maclaudi* from southwestern Guinea on one hand, and specimens from southeastern Guinea and Liberia on the other hand, are definitely not within the range of a documented variation or cline within West Africa but appeared step-like. Furthermore, the presence of two different forms in close vicinity seemed comparable to *R. ruwenzorii* and *hilli* far to the East. This would be contradicting the currently held subspecies concept. Considering size class as an indicator separating congeneric, (near-) sympatric species, we studied the specimens from SE-Guinea and Liberia more closely and found them to represent an undescribed species.

Material and methods

Standard body measurements and mass were taken from specimen labels or in the field. Preserved specimens were measured with digital callipers under a dissecting microscope; body measurements (20 variables) to the nearest 0.1 mm, craniodental measurements (28 variables) to the nearest 0.01 mm.

Measurements (in mm, body mass in g), abbreviations and museum acronyms:

Body measurements

Total	total length: head & body length + tail length (from tip of snout to tip of tail)
Tail	length of tail from posterior margin of anus to tip of tail
Ear	length of ear from lower margin of conch to tip of ear
Forearm	length of forearm, including carpals
3rd Meta	length of metacarpal of third digit, excluding carpals (ditto 4th & 5th digit)
3rd Pha1	length of first phalanx of third digit (ditto 4th & 5th digit)
3rd Pha2	length of second phalanx of third digit (ditto 4th & 5th digit)
Tibia	length of tibia
HF (su); HF (cu)	length of hind foot excluding or including claws, respectively

Craniodental measurements

Crn	greatest length of skull from posteriormost point to front of praemaxillae
CrnC	length of skull from posteriormost point to front of canine crown
Cbs	length of skull from posteriormost point of condyles to front of praemaxillae
CbsC	length of skull from posteriormost point of condyles to front of canine crown
MastoidW	mastoid width
BraincaseB	breadth of braincase at broadest point
BraincaseH	height of braincase between bullae including sagittal crest

ZygomaticW	zygomatic width
C-C	width across crowns of upper canines
M^3-M^3	width across crowns of posterior upper molars
C-M^3	length of upper (maxillary) toothrow from front of canine to back of posterior molar
C-PM^4	length from front of upper canine to back of posterior premolar
PostorbConstr	least breadth at postorbital constriction
InflationB	greatest breadth of nasal inflations
RostrumB (infl)	breadth of rostrum at nasal inflations
PalateL	length of palatal bridge
PalateB	breadth of palatal bridge between talons of anterior molars
Mandible	length of mandible from condyle to anteriormost point, excluding incisors
C-M_3	length of lower toothrow from front of canine to back of posterior molar

x ± sd.	mean ± 1 standard deviation
min-max	minimum and maximum of measurements
n	sample size
F-N°	field number
N.P.	National Park
P.N.	Parc National
Congo (K.)	Congo (Kinshasa) = Democratic Republic of Congo, formerly Zaïre

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
IFAN	Institut Fondamental d'Afrique Noire, Dakar
IRSNB	Institut royal des Sciences naturelles de Belgique, Bruxelles
LACM	Los Angeles County Museum of Natural History
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Centrale, Tervuren
SMNS	Staatliches Museum für Naturkunde Stuttgart
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZMA	Zoölogisch Museum Universiteit van Amsterdam
ZMUZ	Zoologisches Museum der Universität Zürich

Results are based on 36 specimens: *Rhinolophus* n. sp.: n=4, three ♂♂ and one ♀ examined (ZFMK 99.934, AMNH 265708, two released); *R. maclaudi*: n=9, three ♂♂ and three ♀♀ examined (SMNS 6117 – 119, ZFMK 59.171 – 173); *R. ruwenzorii*: n=21, four ♂♂ and three ♀♀ examined (FMNH 144312, MRAC RG 35170, -208, -217, -218, MRAC 85006 M 447, -448); *R. hilli*: n=2, both ♀♀ examined (ZMUZ 126639, holotype, MRAC 82006 M 1). Additionally, we included published measurements (Pousargues 1897, Laurent 1940, Hill 1942, Aellen 1956, 1973, Hayman 1957, 1960, Smith & Hood 1980, Baeten et al. 1984, Claessen 1987) and measurements obtained by Wiesław Bogdanowicz (pers. comm. 18.V.2001) for a total of three specimens of *R. maclaudi*, 18 specimens of *R. ruwenzorii* and one specimen of *R. hilli*. Only adult specimens with fully ossified epiphyses were used in the final analysis, excluding the juvenile specimen SMNS 6119 (F-N° 119 of Eisentraut & Knorr 1957). Neither *R. maclaudi* nor *R. ruwenzorii* showed sexual dimorphism and sexes were subsequently pooled.

Available geographic co-ordinates were taken from the literature or museum catalogues and verified with maps and the GEOnet Names Server (http://164.214.2.59/gns/html) or the Global Gazetteer (www.calle.com/world). Co-ordinates of all localities are listed in Appendix 1. Distribution ranges were plotted with ESRI's ArcView GIS 3.2a and range sizes calculated as the minimum convex polygon. Habitat associations were determined by superimposing point localities onto the latest version of WWF ecoregions (Olson et al. 2001; www.worldwildlife.org/ecoregions) with the function "assign data by location (spatial join)".

Results

Rhinolophus maclaudi species group

Very large rhinolophid bats with an Afrotropical paramontane distribution. Head with large ears. Central noseleaf (sella and basal lobes) large in relation to the entire complex of nasal appendages. Skull large, slender, and with a heavy rostrum, interpterygoid pit very deep. Includes *R. maclaudi*, *R. ruwenzorii*, *R. hilli* and *Rhinolophus* n. sp.

Rhinolophus maclaudi Pousargues, 1897

1897 *Rhinolophus maclaudi* Pousargues, Bull. Mus. natn. Hist. nat. 3: 358; Conakry Island, Guinea.
1905 *Rhinolophus maclaudi* – Andersen, Ann. Mag. nat. Hist. (7) 16: 254; 660 – *philippinensis*-group.
1939 *Rhinolophus maclaudi* – Allen, Bull. Mus. Comp. Zool. 83: 76 – *philippinensis*-group (of Andersen 1905) or *luctus*-group (of Andersen 1918).
1940 *Rhinolophus maclaudi* – Laurent, Bull. Mus. natn. Hist. nat. (2) 12(6): 231 – nec *philippinensis*-group.
1941 *Rhinolophus maclaudi* – Laurent, Bull. Soc. zool. France 66: 68 – nec *philippinensis*-group.
1942 *Rhinolophus maclaudi* – J. Eric Hill, Am. Mus. Novit. (1180): 1 – *philippinensis*-group.
1956 *Rhinolophus maclaudi* – Aellen, Bull. Inst. franç. Afr. Noire (A) 18(3): 885.
1965 *Rhinolophus maclaudi* – Rosevear, The Bats of West Africa: 200, 212.
1971 *Rhinolophus maclaudi* – Hayman & Hill, Order Chiroptera, in: The Mammals of Africa: 20, 21.
1973 *Rhinolophus maclaudi* – Aellen, Period. biol. 75(1): 104 – *philippinensis*-group.
1980 *Rhinolophus maclaudi maclaudi* – Smith & Hood, Proc. 5th Int. Bat Res. Conf.: 170 – new name combination.
1982 *Rhinolophus maclaudi* – Koopman, Rhinolophidae, in: Mammal Species of the World: 145 – partim: Guinea.
1991 *R[hinolophus]. maclaudi* – Nowak, Walker's Mammals of the World, Vol. 1, 5th ed.: 254.
1993 *Rhinolophus maclaudi* – Koopman, Order Chiroptera, in: Mammal Species of the World, 2nd ed.: 167 – partim: Guinea.
1994 *R[hinolophus]. m[aclaudi]. maclaudi* – Koopman, Chiroptera: Systematics, in: Handbuch der Zoologie VIII(60): 57 – *luctus*-group.
1995 *Rhinolophus maclaudi* – Koopman, Kofron & Chapman, Am. Mus. Novitates (3148): 6; partim: Guinea.
1999 *Rhinolophus maclaudi* – Nowak, Walker's Mammals of the World, Vol. 1, 6th ed.: 330 – partim: Guinea – *trifoliatus*-group.

Differential characters (Tab. 2).
R. maclaudi is the largest taxon in the species group and absolutely larger in all measurements except three wing elements (3rdPha2, 4thPha1, 5thPha2) and two cranial variables (BraincaseB, PostorbConstr; see Tab. 1). It differs from the other species in having the apex of the braincase at height of the glenoid process (vs. clearly posterior to the glenoid process). In lateral view, the braincase is conspicuously deflected against the anterior skull axis. The infraorbital bridge is long and moderately thick (Figs. 1-3, 6).

Measurements. See Tab. 1.

Distribution (Figs. 8, 9).
GUINEA: **Ile de Conakry** (Pousargues 1897; Andersen 1905b; Maclaud 1906; Laurent 1940, 1941; Rode 1941; Hill 1942; Aellen 1956, 1973; Hayman 1957; Rosevear 1965; Smith & Hood 1980; Koopman et al. 1995; MNHN 1897-281, holotype, ♀, alc. & skull, leg. C. Maclaud, 1896); **Grotte Garrigues** (4 km NE Souguéta) (Hiernaux & Villiers 1955; Aellen 1956; Hayman 1957; Rosevear 1965: as from "Sougeta"; Smith & Hood 1980: as from "Souqueta"; IFAN 54-1-25, ♂, alc. & skull, leg. A. Villiers, 14.IV.1954); near **Nyembaro** (12 km W Kolenté, 400 m, Salung-Plateau) (Eisentraut & Knorr 1957; SMNS 6117 – 119, ZFMK 59.171 – 173, 3 ♂♂, 3 ♀♀, leg. H. Knorr, 15.&19.XI.1956); **btw. Kankasili & Souguéta** (Aellen 1973; ZMA 11.885, ♂, alc., leg. J. van Orshoven, 14.XI.1968); **no spec. loc.** (Andersen 1905a; Hayman 1960, 1967; Hayman & Hill 1971; Villiers 1971: Fouta-Djallon; Koopman 1982, 1989, 1993, 1994; Nowak 1991, 1999).

Note.
The specimens (ROM 86054, -56, leg. M. E. Gartshore) on which a record of *R. maclaudi* from Kagoro, central Nigeria, was based (Happold 1987: p. 60; Koopman et al. 1995: p. 6, 19) have been re-identified as *R. hildebrandtii* Peters, 1878 (J. Eger pers. comm. 2.XI.1998). They represent the first record of *R. hildebrandtii* for West Africa, with the nearest records being those documented for eastern Congo (K.).

Rhinolophus ruwenzorii J. Eric Hill, 1942

1942 *Rhinolophus ruwenzorii* J. Eric Hill, Am. Mus. Novit. (1180): 1; S-side of Butahu Valley, 2286 m, W-slope Rwenzori Mts., Congo (K.) – *philippinensis*-group.
1956 *R[hinolophus]. ruwenzonii* – Aellen, Bull, Inst. franç, Afr. Noire (A) 18(3): 886.
1966 *Rhinolophus ruwenzorii* – Hayman, Misonne & Verheyen, Ann. Mus. Roy. Afr. Centr. (Sci. Zool.) 154: 14, 40.
1971 *Rhinolophus ruwenzorii* – Hayman & Hill, Order Chiroptera, in: The Mammals of Africa: 20, 22.
1973 *Rhinolophus ruwenzorii* – Aellen, Period. biol. 75(1): 104 – *philippinensis*-group.
1980 *Rhinolophus maclaudi ruwenzorii* – Smith & Hood, Proc. 5th Int. Bat Res. Conf.: 170 – stat. nov.
1982 *Rhinolophus maclaudi* – Koopman, Rhinolophidae, in: Mammal Species of the World: 145 – partim: Congo (K.) & Uganda.
1991 *R[hinolophus]. ruwenzorii* – Nowak, Walker's Mammals of the World, Vol. 1, 5th ed.: 254.
1992 *R[hinolophus]. maclaudi* – Bogdanowicz, Acta theriol. 37(3): 227; Bogdanowicz & Owen, Z. zool. Syst. Evolut.-forsch. 30: 151 – incertae sedis.
1993 *Rhinolophus maclaudi* – Koopman, Order Chiroptera, in: Mammal Species of the World, 2nd ed.: 167 – partim: Congo (K.) & Uganda.
1994 *R[hinolophus]. m[aclaudi]. ruwenzorii (=hilli)* – Koopman, Chiroptera: Systematics, in: Handbuch der Zoologie VIII(60): 57 – partim: Congo (K.) & Uganda – *luctus*-group.
1994 *Rhinolophus maclaudi* – Kityo, Gathua & Howell, Checklist of the Mammals of East Africa: 8 – Uganda.
1995 *Rhinolophus maclaudi* – Koopman, Kofron & Chapman, Am. Mus. Novitates (3148): 19; partim: Congo (K.) & Uganda.
1996 *Rhinolophus ruwenzorii* – Kityo & Kerbis, J. East Afr. nat. Hist. 85: 52.
1999 *Rhinolophus maclaudi* – Nowak, Walker's Mammals of the World, Vol. 1, 6th ed.: 330 – partim: Congo (K.) & Uganda – *trifoliatus*-group.

Tab. 1. Body and craniodental measurements of *Rhinolophus maclaudi*, *R. ziama* n. sp., *R. ruwenzorii*, and *R. hilli*.

	R. maclaudi		*R. ziama* n. sp.		*R. ruwenzorii*		*R. hilli*	
	x ± sd. (min-max)	n	§	#	x ± sd. (min-max)	n	¥	‡
Sex	4 ♂♂, 4 ♀♀		1 ♂	1 ♂	14 ♂♂, 7 ♀♀		1 ♀	1 ♀
Mass	31.8 ± 1.2 (30.0-33.0)	6	20.5	(24)	17.6 ± 1.3 (16.0-19.5)	5		16.5
Total	117.7 ± 9.8 (111.0-137.0)	6	[100]	[110.8]	93.6 ± 5.8 (83.0-104.0)	18	92.0	
Tail	40.6 ± 1.5 (38.0-43.0)	7	34.5	36.7	29.8 ± 2.2 (25.0-34.0)	18	29.3	
Ear	41.4 ± 2.5 (40.0-46.0)	7	36.3	35.3	34.4 ± 2.2 (28.0-38.0)	20	28.5	
FA	65.8 ± 1.9 (63.6-68.7)	7	59.9	60.0	57.6 ± 2.0 (55.0-61.7)	21	54.3	54.2
3rd Meta	46.3 ± 0.9 (45.0-47.5)	7	42.2	42.2	39.8 ± 1.9 (37.4-43.6)	19	37.1	36.6
3rd Pha1	22.0 ± 1.0 (20.0-23.0)	7	19.5	17.7	18.5 ± 1.2 (16.5-21.1)	18	17.2	17.3
3rd Pha2	35.4 ± 1.2 (33.7-37.0)	7	34.0	34.8	30.4 ± 1.5 (27.8-32.6)	19	29.3	28.5
4th Meta	48.8 ± 1.4 (47.0-50.8)	7	43.6	44.7	42.6 ± 2.4 (39.2-46.9)	19	40.9	40.6
4th Pha1	12.8 ± 0.6 (12.0-13.5)	6	12.6	11.5	11.6 ± 0.7 (10.3-12.8)	18	10.9	10.6
4th Pha2	22.1 ± 0.5 (21.5-22.7)	6	19.9	18.9	19.2 ± 0.8 (17.7-20.9)	19	19.1	17.9
5th Meta	48.3 ± 0.8 (47.6-50.0)	7	43.9	42.7	43.5 ± 2.3 (39.6-46.8)	19	41.0	41.7
5th Pha1	16.3 ± 0.5 (15.6-17.0)	7	14.7	14.0	13.0 ± 0.8 (11.3-14.1)	18	12.7	13.0
5th Pha2	21.2 ± 0.9 (19.7-22.0)	7	19.8	18.2	17.3 ± 1.1 (14.1-18.9)	18	18.5	16.8
Tibia	29.0 ± 1.1 (28.0-31.0)	7	26.9	26.2	23.6 ± 1.3 (21.7-26.0)	19	23.8	
HF (su)	12.7 ± 0.6 (12.0-13.3)	6	12.6	12.6	11.1 ± 0.5 (10.0-12.2)	12	11.1	
HF (cu)	14.7 (14.5-14.8)	2	14.4	13.6	12.5 ± 1.0 (11.0-14.5)	11	12.2	
Crn	30.55 ± 0.35 (30.25-31.14)	7	27.09	26.90	25.41 ± 0.73 (24.20-26.37)	9	23.89	23.3
CrnC	29.32 ± 0.37 (28.99-30.11)	7	26.13	26.18	24.47 ± 0.71 (23.65-25.55)	12	23.02	
Cbs	27.30 ± 0.34 (26.95-27.84)	6	24.07	23.96	22.90 ± 0.50 (22.00-23.62)	9	21.22	20.7

Tab. 1 (continued).

	R. maclaudi		*R. ziama* n. sp.		*R. ruwenzorii*		*R. hilli*	
	x ± sd. (min-max)	n	§	#	x ± sd. (min-max)	n	¥	‡
CbsC	25.98 ± 0.35 (25.69-26.65)	6	22.97	22.97	21.65 ± 0.68 (20.70-22.70)	12	20.19	
Mastoid	13.56 ± 0.23 (13.29-13.93)	7	12.31	12.38	11.97 ± 0.26 (11.20-12.30)	18	10.90	11.2
BraincaseB	11.36 ± 0.34 (11.00-11.70)	5	11.08	10.84	10.06 ± 0.26 (9.85-10.81)	12	9.96	10.1
BraincaseH	8.43 ± 0.21 (8.07-8.57)	5	7.69	7.83	7.28 ± 0.27 (6.85-7.67)	12	6.92	
Zygomatic	13.56 ± 0.22 (13.20-13.80)	7	12.31	12.49	11.07 ± 0.23 (10.50-11.40)	18	10.60	10.9
C-C	7.67 ± 0.14 (7.40-7.80)	7	6.33	6.29	5.60 ± 0.16 (5.30-5.90)	14	5.67	5.6
M^3-M^3	9.71 ± 0.10 (9.57-9.80)	7	8.23	8.56	7.72 ± 0.23 (7.30-8.20)	19	7.81	8.0
C-M^3	10.63 ± 0.11 (10.52-10.80)	6	8.95	8.90	8.41 ± 0.23 (8.15-8.90)	14	8.08	7.9
C-PM^4	4.62 ± 0.09 (4.47-4.68)	5	3.92	4.01	3.67 ± 0.08 (3.59-3.74)	3	3.55	
PostorbConstr	3.01 ± 0.18 (2.70-3.27)	7	2.89	3.01	2.83 ± 0.21 (2.50-3.30)	19	2.82	2.5
InflationB	5.80 ± 0.25 (5.48-6.08)	5	4.73	5.08	4.41 ± 0.01 (4.40-4.42)	3	4.55	
RostrumB (infl)	7.28 ± 0.09 (7.18-7.39)	6	6.17	6.45	6.73 ± 0.11 (6.60-6.97)	13	6.41	
PalateL	4.99 ± 0.18 (4.74-5.24)	6	3.78	3.94	3.62 ± 0.17 (3.25-3.91)	18	3.58	
PalateB	4.40 ± 0.18 (4.22-4.58)	3	3.77	4.06	3.67 ± 0.17 (3.53-3.86)	3	3.90	
Mandible	20.00 ± 0.20 (19.84-20.37)	6	17.38	17.15	15.83 ± 0.45 (15.10-16.45)	13	14.96	15.4
C-M_3	11.22 ± 0.08 (11.09-11.32)	6	9.44	9.57	8.78 ± 0.18 (8.45-9.10)	14	8.50	8.5

R. maclaudi: **Guinea** (MNHN 1897-281 (holotype), IFAN 54-1-25, SMNS 6117–18, ZFMK 59.171–73, ZMA 11.885).

R. ziama n. sp.: §: **Guinea** (ZFMK 99.934, holotype); #: **Liberia** (AMNH 265708, paratype).

R. ruwenzorii: **Congo (K.)** (AMNH 82394 (holotype), BMNH 60.99–101, IRSNB 7047, MRAC RG35170, -173, -206, -208, -211, -217, -218), **Uganda** (BMNH 55.1187, FMNH 144309, -10, -12, LACM 51751, 57774, -76), **Rwanda** (MRAC 85006 M 447, -48).

R. hilli: ¥: **Rwanda** (ZMUZ 126639, holotype); ‡: **Rwanda** (MRAC 82006 M 1).

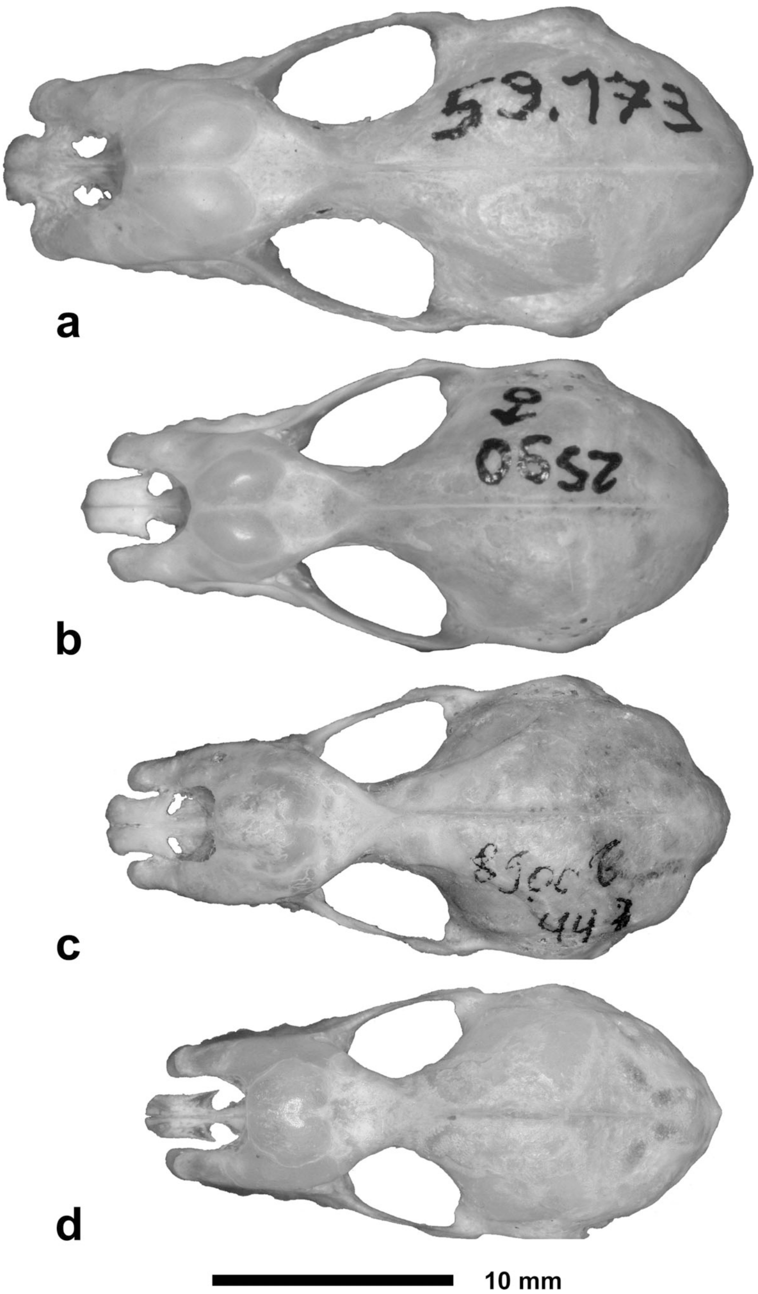

Fig. 1. Skulls in dorsal view. (a) *Rhinolophus maclaudi*, ZFMK 59.173; (b) *R. ziama* n. sp., holotype, ZFMK 99.934; (c) *R. ruwenzorii*, MRAC 85006 M447; (d) *R. hilli*, holotype, ZMUZ 126639.

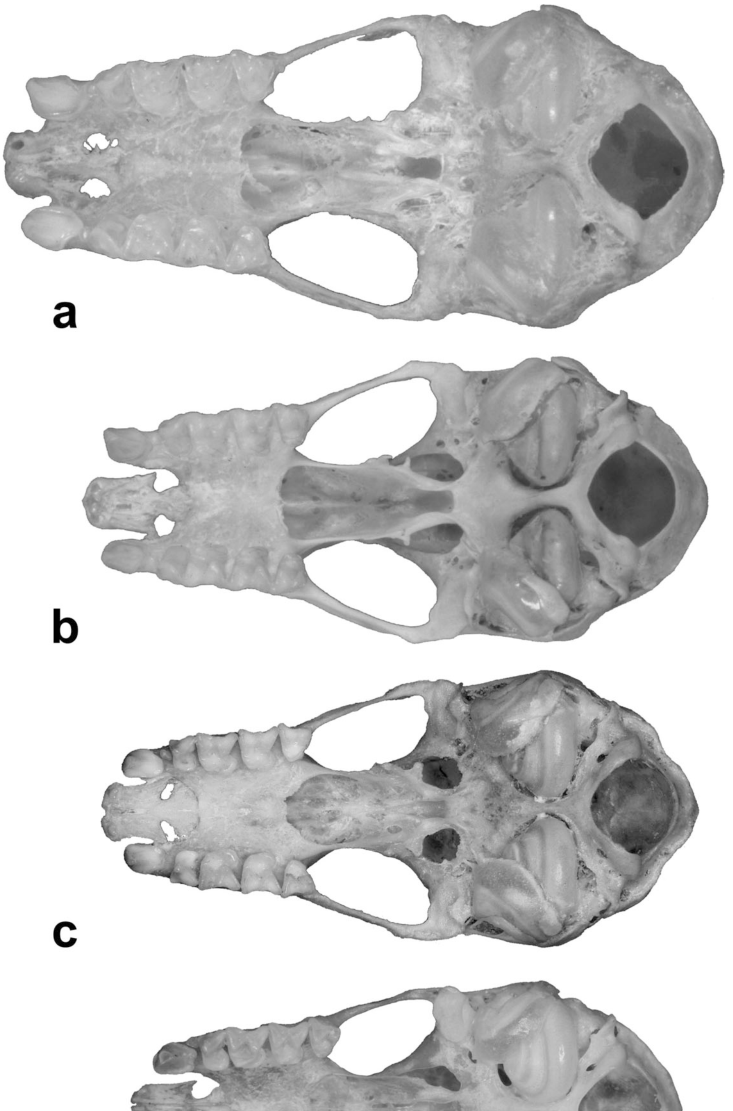

Fig. 2. Skulls in ventral view. (a) *Rhinolophus maclaudi*; (b) *R. ziama* n. sp.; (c) *R. ruwenzorii*; (d) *R. hilli* (same specimens as in Fig. 1).

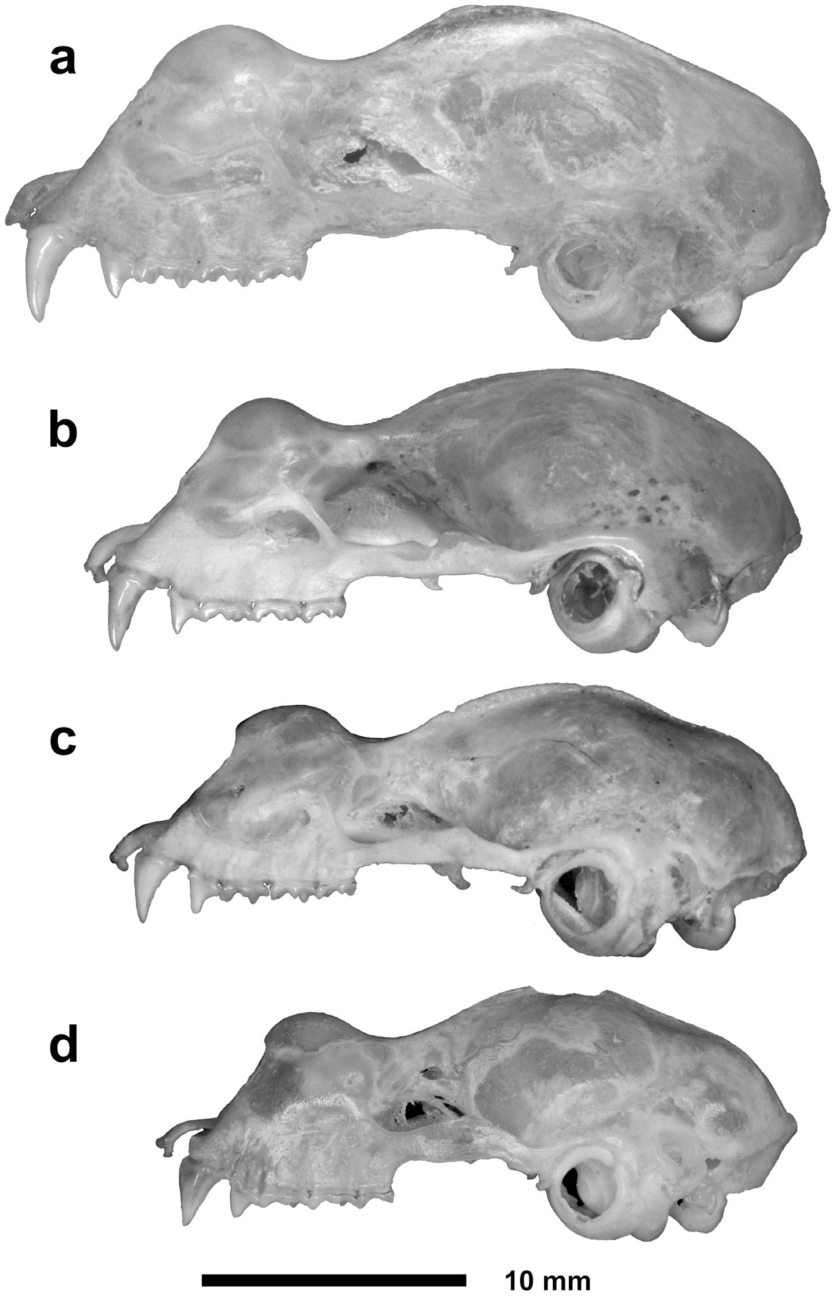

Fig. 3. Skulls in lateral view. (a) *Rhinolophus maclaudi*; (b) *R. ziama* n. sp.; (c) *R. ruwenzorii*; (d) *R. hilli* (same specimens as in Fig. 1).

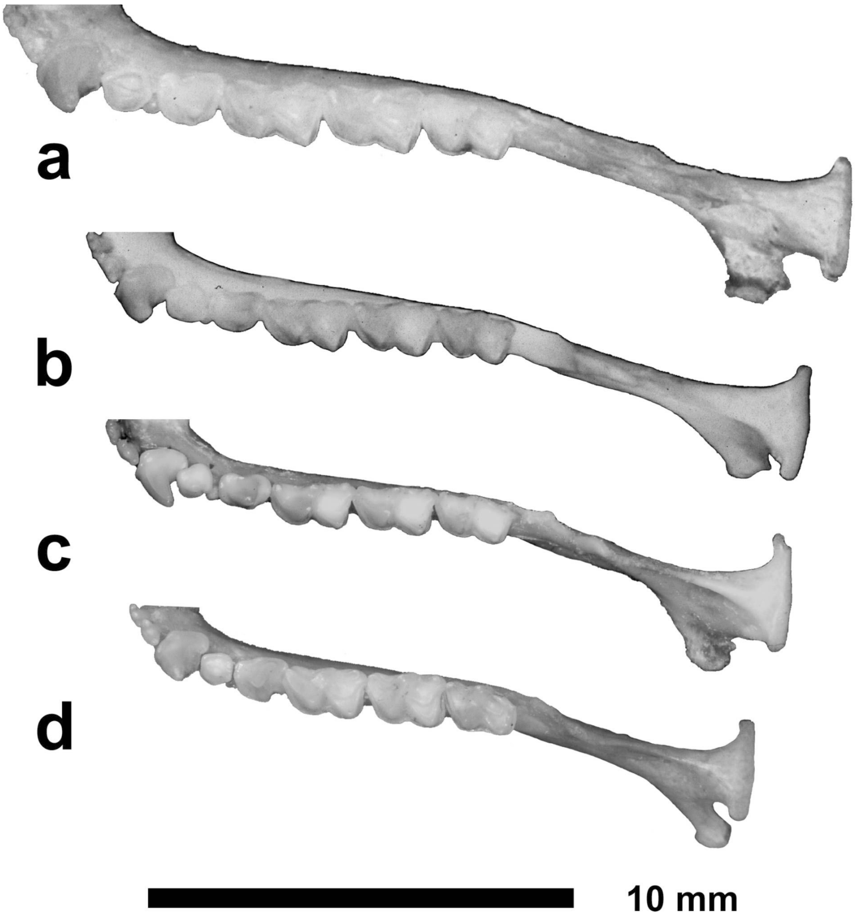

Fig. 4. Left mandibular ramus in occlusal view. (a) *Rhinolophus maclaudi*; (b) *R. ziama* n. sp.; (c) *R. ruwenzorii*; (d) *R. hilli* (same specimens as in Fig. 1).

Differential characters (Tab. 2).
In lateral view, the anterior margin of the rostrum rises shallowly from the canine and the nasal swellings are displaced from the rostral sinus. In dorsal view, the rostrum is laterally conspicuously inflated and the maxillary bone concealed (Figs. 1-3). The infraorbital bridge is short and stout (Fig. 6). The lower molars are comparatively weak (Fig. 4). The height of the lancet is low in relation to the sella and the breadth of the connecting process in lateral view very narrow (Fig. 5).

Differential characters shared between *R. ruwenzorii* and *R. hilli* (Tab. 2).
In dorsal view, the chambers of the rostral swellings are subcircular in outline and the postero-median indentation is weak. The rostral emargination is squarish with rounded

corners. The zygomatic is narrower than the mastoid width (Figs. 1-3). The top of the sella is erect and parallel to the lancet; the lateral margins of the sella are concave and the tip is distinctly broadened (spoon-shaped). The anterior margin of the horseshoe has a conspicuous median emargination; the inner margin of the horseshoe around nostrils is semicircular and parallel to the inner cup, not reaching the anterior margin of horseshoe (Fig. 5). Secondary leaflets present; number of ear folds 8-9.

Measurements. See Tab. 1.

Distribution (Figs. 8, 10).
CONGO (K.): S-side of **Butahu Valley** (cave, 7500 ft., W-slope Rwenzori Mts.) (Hill 1942; Hayman 1957, 1960; Koopman 1965; Hayman et al. 1966; Aellen 1973; Smith & Hood 1980; AMNH 82394, holotype, ♀, alc. & skull, leg. 24.XII.1926); **Butembo** (1760 m, Kivu) (Hayman et al. 1966; Aellen 1973; Smith & Hood 1980; Bogdanowicz 1992, Bogdanowicz & Owen 1992 as "IRSNB 15966"; IRSNB 7047, ♂, skin & skull, leg. J. Hiernaux, 16.VIII.1947); **Kasuo-Kibwe Cave** (1500 m, Lya-Mikako, Lubero Distr.) (Bogdanowicz 1992, Bogdanowicz & Owen 1992; MRAC RG 35170, -173, -174, -206, -208, -211, RG 35216 – 219, 3 ♂♂, 4 ♀♀, 3 unsexed, leg. Celis & Lejeune, 28.XII.1966); **Matata Cave** (1160 m, Kibali-Ituri) (Hayman et al. 1966; Aellen 1973; Smith & Hood 1980; IRSNB 7048, ♂, skull only, leg. J. Hiernaux, 10.VIII.1947); **Matupi Cave** (3500 ft., Mt. Hoyo, S of Irumu, Ituri Forest) (Hayman 1960; Hayman et al. 1966; Smith & Hood 1980; Bogdanowicz 1992, Bogdanowicz & Owen 1992; BMNH 60.99 – 101, 3 ♂♂, 2 skin & skull, 1 alc., leg. A. E. Wright, 14.&16.IX.1959); **Mt. Hoyo** (1200 m, Ituri Forest) (Hayman et al. 1966; Aellen 1973; Smith & Hood 1980; IRSNB 7049, ♀, skull only, leg. J. Hiernaux, 10.VIII.1947); **no spec. loc.** (Rosevear 1965: Mt. Ruwenzori; Ituri Forest; Hayman 1967, Hayman & Hill 1971: W-Ruwenzori; E-Ituri Forest; Kingdon 1974, 1989: Ruwenzori Mts.; Koopman 1982, 1993, 1994, Koopman et al. 1995: E-Zaïre; Nowak 1991: Ruwenzori region).

RWANDA: **Mutura** (2200 m) (this study; MRAC 85006 M 447, -448, 2 ♂♂, alc. & skull, leg. Baeten & Janssens, 16.XII.1982).

UGANDA: **Itama Mine** (1615 m, Bwindi-Impenetrable-N.P., Kigezi) (Smith & Hood 1980; LACM 51750, 57772 – 777, 3 ♂♂, 4 ♀♀, 1 skin & skull, 3 alc. & skull, 3 alc., leg. A. L. Archer, 31.III.1967); **Luhizha Mine** (2286 m, Bwindi-Impenetrable-N.P., Kigezi) (Smith & Hood 1980; Bogdanowicz 1992, Bogdanowicz & Owen 1992; LACM 51747 – 749, 2 ♂♂, 1 ♀, 3 skin & skull, leg. R. Glen & A. Williams, 27.III.1967); near **Mahoma River** (cave, 6700 ft., above Ibanda, E-slope Rwenzori Mts.) (Hayman 1957, 1960; Aellen 1973; Smith & Hood 1980; Bogdanowicz 1992, Bogdanowicz & Owen 1992; BMNH 55.1187, ♀, alc. & skull, leg. G. O. Evans, 22.VIII.1952); right bank of **Mubuku River** (6900 ft., above confluence with Mahoma River, Rwenzori Mts.) (Kityo & Kerbis 1996; FMNH 144309 (at Makerere Univ.), ♂, skin, skel. & skull, leg. W. T. Stanley, 25.XI.1990); **Nteko Parish** (1600 m, edge of Bwindi-Impenetrable-N.P., Bufumbira) (FMNH 160357 (exchanged), ♂, skin, skull & skel., leg. R. M. Kityo, 19.V.1997); **Nyabitaba** (2591 m, Mubuku Valley, E-slope Rwenzori Mts.) (Smith & Hood 1980; LACM 51751, ♂, leg. R. Glen & A. Williams, 5.VI.1967); **Nyabitaba Hut**

(8750 ft., right bank of Mubuku River, below confluence with Bujuku River, Rwenzori Mts.) (Kityo & Kerbis 1996; FMNH 144310, ♂, alc., leg. W. T. Stanley, 11.XII.1990; FMNH 144311, -312, 2 ♂♂, 1 alc., 1 skin, skull & skel., leg. J. C. Kerbis, 19&20.IV.1991); **no spec. loc.** (Hayman 1967, Hayman & Hill 1971: E-Ruwenzori; Kingdon 1974, 1989: Ruwenzori Mts.; Koopman 1982, 1993, 1994: W-Uganda; Nowak 1991: Ruwenzori region; Kityo et al. 1994).

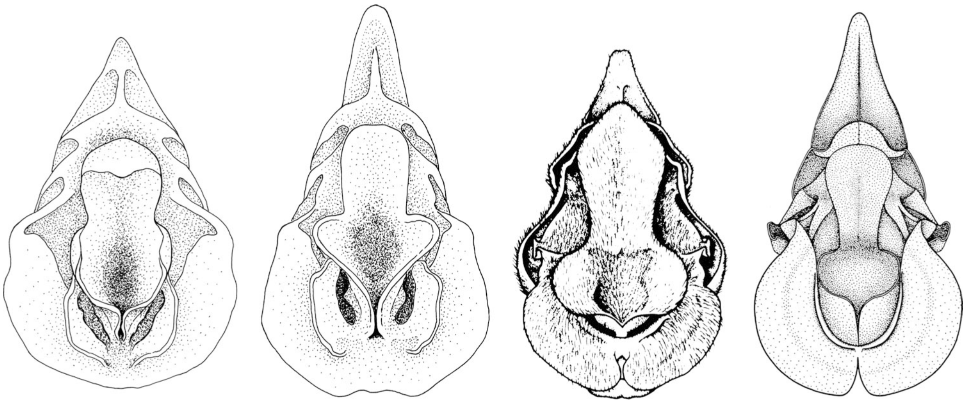

Fig. 5. Sketches of the noseleaf of *Rhinolophus maclaudi* ZFMK 59.173, *R. ziama* n. sp., holotype, *R. ruwenzorii* (modified from fig. 2c in Smith & Hood 1980), and *R. hilli*, holotype (modified from fig. 2 in Aellen 1973) (from left to right; not to scale).

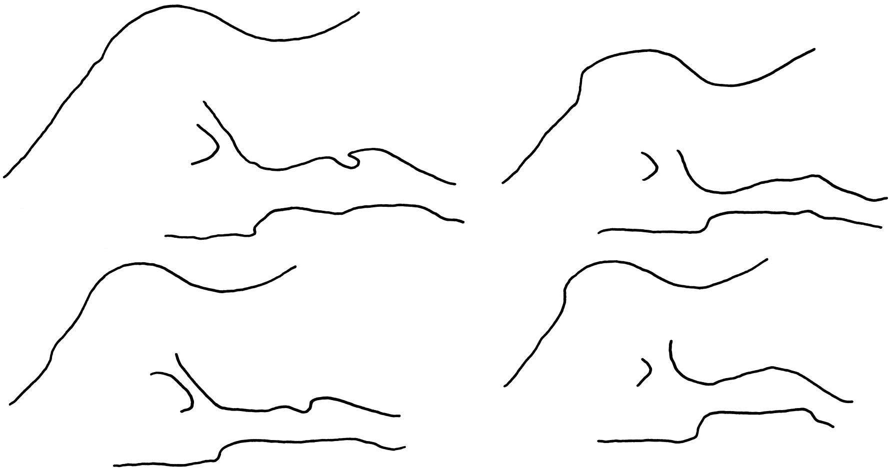

Fig. 6. Comparison of the rostral sinus, infraorbital bridge and zygomatic bone. Upper left: *Rhinolophus maclaudi*, lower left :.*R. ziama* n. sp., upper right: *R. ruwenzorii*, lower right: *R. hilli* (same specimens as in Fig. 1).

Rhinolophus hilli Aellen, 1973

1973	*Rhinolophus hilli* Aellen, Period. biol. 75(1): 101; Uwinka, 2300 m, Préf. de Cyangugu, Rwanda – *philippinensis*-group.
1980	*Rhinolophus maclaudi ruwenzorii* – Smith & Hood, Proc. 5th Int. Bat Res. Conf.: 170 – partim: Rwanda – syn. nov.
1982	*Rhinolophus maclaudi* – Koopman, Rhinolophidae, in: Mammal Species of the World: 145 – partim: Rwanda.
1984	*Rhinolophus hilli* – Baeten, Van Cakenberghe & De Vree, Rev. Zool. afr. 98(1): 186.
1990	*Rhinolophus maclaudi* – Dowsett & Dowsett-Lemaire, Tauraco Res. Rep. 3: 113.
1991	*R[hinolophus]. hilli* – Nowak, Walker's Mammals of the World, Vol. 1, 5th ed.: 254.
1992	*Rhinolophus maclaudi* (*hilli*) – Monford, J. Afr. Zool. 106(2): 143.
1993	*Rhinolophus maclaudi* – Koopman, Order Chiroptera, in: Mammal Species of the World, 2nd ed.: 167 – partim: Rwanda.
1994	*R[hinolophus]. m[aclaudi]. ruwenzorii* (= *hilli*) – Koopman, Chiroptera: Systematics, in: Handbuch der Zoologie VIII(60): 57 – partim: Rwanda – *luctus*-group.
1995	*Rhinolophus maclaudi* – Koopman, Kofron & Chapman, Am. Mus. Novitates (3148): 19; partim: Rwanda.
1999	*Rhinolophus maclaudi* – Nowak, Walker's Mammals of the World, Vol. 1, 6th ed.: 330 – partim: Rwanda – *trifoliatus*-group.

Differential characters (Tab. 2).
In dorsal view, the braincase is not constricted behind the mastoid process and is more or less evenly rounded. In lateral view, the occiput is rather high and the posteriormost point of the lambdoid crest is raised above the height of the auditory bulla. The infraorbital bridge is very short and stout. The premaxillae are very narrow. The canine and the last upper premolar (PM^4) are almost in contact and the first upper premolar (PM^2) is extruded from the toothrow. In occlusal view, the last upper premolar (PM^4) attains almost the breadth of the anterior upper molar (M^1). The last lower premolar (PM_4) and the lower molars (M_{1-3}) are comparatively powerful and broad. The angular process is directed backwards and reaches the height of the condyle. The connecting process of the noseleaf is comparatively broad in lateral view.

Differential characters shared between *R. ruwenzorii* and *R. hilli.*
See under *R. ruwenzorii*.

Measurements. See Tab. 1.

Distribution (Figs. 8, 10).
RWANDA: **Uwinka** (2512 m, P.N. de Nyungwe, Préfecture de Cyangugu) (Aellen 1973; Anciaux de Faveaux 1978; Smith & Hood 1980; Baeten et al. 1984; Claessen 1987; Dowsett & Dowsett-Lemaire 1990; Monford 1992: as from “Nyungwe Forest”; ZMUZ 126639, holotype, ♀, alc. & skull, leg. U. Goepel, 25.VIII.1964, F-N° 481); **Ruta Bansugera** (near Uwinka, P.N. de Nyungwe, 1750 m) (Baeten et al. 1984; Claessen 1987; Dowsett & Dowsett-Lemaire 1990: as from “Rutabanzogera”; MRAC 82006 M 1, ♀, leg. F. De Vree et al. 19.X.1981); **no spec. loc.** (Kingdon 1989: S of Lake Kivu; Nowak 1991: Ruwenzori region of E-Zaïre [lapsus], W-Uganda [lapsus], W-Rwanda; Koopman 1982, 1993, 1994, Koopman et al. 1995).

Rhinolophus ziama n. sp.

1993 *Rhinolophus maclaudi* – Koopman, Order Chiroptera, in: Mammal Species of the World, 2nd ed.: 167; partim: Liberia.

1995 *Rhinolophus maclaudi* – Koopman, Kofron & Chapman, Am. Mus. Novitates (3148): 6; near Ziggida, Wonegizi Mts., Liberia.

1999 *Rhinolophus maclaudi* – Nowak, Walker's Mammals of the World, Vol. 1, 6th ed.: 330 – partim: Liberia – *trifoliatus*-group.

Holotype.

ZFMK 99.934, western edge of **Sérédou** near park station, border of "Réserve de la Biosphère du Massif du Ziama", Guinée Forestière, Guinea, ad. ♂, alc., skull & skeleton, leg. H. Vierhaus, 12.VIII.1992, F-N° HV 2590.

Paratype.

AMNH 265708, 7 mi N, 1 mi E **Ziggida**, Lofa County, Wonegizi Mts., Liberia, ad. ♂, alc. & skull, leg. R. W. Dickerman, 4.III.1990, F-N° 21440.

Additional specimens.

Two specimens were captured near the same place as the holotype on 20.VIII. (♀) and 3.IX.1992 (♂). They were examined (field measurement of FA for both specimens: 58 mm), photographed and subsequently released.

Diagnosis.

Essentially similar to *R. maclaudi*, but of considerably smaller size externally and craniodentally. Noseleaf narrower. Braincase not deflected against skull axis; infraorbital bridge very long and slender (Figs. 1-6).

Description.

Head, noseleaf & ears (Figs. 5, 7): Horseshoe without secondary leaflets, no median emargination anteriorly, its outer margin of nearly even width, narrowing only slightly proximally. Nasal apertures laterally bordered by conspicuously raised and almost parallel rims ("chalice" of Pousargues), reaching anterior margin of horseshoe. Lobes at base of sella greatly enlarged, forming a roughly heart-shaped corolla-like cup. Top of sella inclined forward, lateral margins almost parallel-sided. Ears large and pointed, length ca. 1.5 times width; anterior margin convex (clad with pale hairs along the basal three-quarters of the inner side), posterior margin concave. Conch with 11-12 inner folds. Chin with well developed median groove.

Body: Pelage long, soft and woolly. Hairs thin, dorsally 9 mm long, bicoloured: bases pale buff, tips pale brown; ventrally 8 mm long, somewhat paler, unicoloured dirty buff with a light brown sheen.

Skull (Figs. 1-6): Braincase in dorsal view constricted behind mastoid process; in lateral view evenly rounded, highest point at height of anterior third of auditory bullae; sagittal crest not prominent. Anterior margin of rostrum in lateral view steeply rising from canine, nasal swellings included in rostral sinus. Chambers of rostral swellings in dorsal view with conspicuous postero-median indentation, roughly heart-shaped in outline; rostral emargination U-shaped; premaxillae broad. Infraorbital bridge very long and slender. Zygomatic arches broad, dorsally notched, flaring as wide as mastoid width. Interpterygoid pit (i.e., depression in basisphenoid) deep, broad and barrel-shaped, laterally rimmed. Angular process of mandible chiefly directed backwards and almost reaching height of condyle.

Teeth (Figs. 2, 4): Incisors bicuspid. Anterior upper premolar PM^2 reduced, but not extruded from toothrow, maintaining a short diastema between upper canine and posterior premolar PM^4. Anterior and middle upper molars M^{1-2} with well developed postero-lingual talons. Lower second premolar PM_3 slightly to clearly extruded from toothrow, distance between PM_2 and PM_4 variable (holotype: in contact; paratype: not in contact).

Etymology.
In reference to the protected area near the type locality, the "*Réserve de la Biosphère du Massif du Ziama*", and as a noun in apposition.

Measurements. See Tab. 1.

Comparison.
R. ziama n. sp. is absolutely smaller than *R. maclaudi* in all body dimensions except some wing elements (3rdPha2, 4thPha1, 5thPha2; see Tab. 1). The new taxon differs from *R. maclaudi* in having the braincase not deflected against the anterior skull axis (vs. clearly deflected); by the apex of the braincase at height of bullae (vs. at height of glenoid process); by a longer and more slender infraorbital bridge; and by better-developed talons of M^{1-2}. *R. ziama* n. sp. is smaller in all craniodental measurements except BraincaseB and PostorbConstr. The noseleaf is narrower.

R. ziama n. sp. differs from both *R. ruwenzorii* and *hilli* in being on average slightly larger in most and absolutely larger in some body dimensions (e.g., Total, Tail, 3rdPha2, Tibia; see Tab. 1); by a larger number of ear folds (11-12 vs. 8-9); by absence of secondary leaflets (vs. present); by absence of an anterior emargination of the horseshoe; and by the broad width of the horseshoe posteriorly (vs. narrowing conspicuously). The top of the sella is inclined forward (vs. parallel to lancet), its lateral margins are parallel-sided (vs. clearly concave and with a broadened top); cup at base of sella heart-shaped (vs. subcircular); rims of inner horseshoe margin straight, (almost) reaching anterior margin of horseshoe (vs. semicircular, not reaching margin).

R. ziama n. sp. is larger than both *R. ruwenzorii* and *hilli* in most skull measurements (except PostorbConstrict, RostrumB, PalateL, PalateB; see Tab. 1). Mastoid width about equal to zygomatic width (vs. zygomatic narrower than mastoid width). Nasal swellings included in rostral sinus (vs. displaced from sinus); heart-shaped in outline (vs. subcircular). Infraorbital bridge very long and slender (vs. short and broad); rostral emargination U-shaped (vs. squarish).

Distribution (Figs. 8, 9).
Only known from two localities in the Guinea Highlands of SE-Guinea (Ziama Forest) and NW-Liberia (Wonegizi Mts.).

Fig. 7. Details of the head and noseleaf of *Rhinolophus ziama* n. sp. Top and lower left: ♂ holotype, photographed 12 August 1992; lower right: ♀ photographed 20 August 1992 and released; both at type locality by H. Vierhaus.

Habitat.

The specimens in Guinea were captured in degraded forest (ca. 600 m) near montane rain forest (holotype and additional ♀), and in a valley with rice fields (additional ♂). The bats were captured around 21:00 hours in the lowest shelves of mist nets placed along a path in bamboo undergrowth, and across a small river in the rice fields nearby. Together with these specimens, we caught the following bat species: *Rousettus aegyptiacus unicolor* (E. Geoffroy, 1810), *Lissonycteris angolensis smithii* (Thomas, 1908), *Scotonycteris zenkeri* Matschie, 1894, *Megaloglossus woermanni* Pagenstecher, 1885, *Hipposideros jonesi*, Hayman, 1947, *Pipistrellus nanulus* Thomas, 1904, *Miniopterus* cf. *schreibersii* (Kuhl, 1817). The annual precipitation at Sérédou was 2170 mm in 1991 and 2650 mm in 1992 (J.-P. Labouisse pers. comm.). The specimen from Liberia was caught in "undisturbed High Forest" (fide Koopman et al. 1995).

Close to the type locality in Guinea, fairly undisturbed forest can be found in the Massif du Ziama. Three major vegetation types have been described (Schnell 1952, S. Porembski pers. comm.):

The semideciduous lowland forests are characterized by tree species such as *Triplochiton scleroxylon*, *Sterculia tragacantha* (both Sterculiaceae), *Chrysophyllum perpulchrum* (Sapotaceae), *Morus mesozygia*, *Chlorophora excelsa* (both Moraceae), *Terminalia superba* (Combretaceae), and *Parkia bicolor* (Mimosaceae). The wetter evergreen lowland forests are distinguished, among other tree species, by *Lophira alata* (Ochnaceae), *Tarrieta utilis* (Sterculiaceae), *Combretodendron africanum* (Lecythidaceae), and *Uapaca guineensis* (Euphorbiaceae). The montane forests (above 800 - 1000 m elevation) are characterized by *Parinari excelsa* (Rosaceae), *Syzygium staudtii* (Myrtaceae), *Bersama abyssinica* (Melianthaceae), *Trichilia heudelotii* (Meliaceae), and *Polyscias fulva* (Araliaceae).

Key to the species of the *Rhinolophus maclaudi* group

1a Horseshoe without secondary leaflets; no or very inconspicuous median emargination; rims around nostrils ± straight and parallel; sella inclined forward. FA: 60 - 69, Cbs: 24.0 - 27.8, MastoidW: 12.3 - 13.9, ZygomaticW: 12.3 - 13.8 2

1b Horseshoe with one pair of secondary leaflets; with conspicuous median emargination; rims around nostrils semicircular; sella erect and ± parallel to lancet. FA: 54 - 62, Cbs: 20.7 - 23.6, MastoidW: 10.9 - 12.3, ZygomaticW: 10.5 - 11.4 3

2a FA: 63.6 - 68.7, Cbs: 27.0 - 27.8, MastoidW: 13.3 - 13.9, ZygomaticW: 13.2 - 13.8, C-M^3: 10.5 - 10.8 *maclaudi*

2b FA: 59.9 - 60.5, Cbs: 24.0 - 24.1, MastoidW: 12.3 - 12.4, ZygomaticW: 12.3 - 12.5, C-M^3: 8.9 - 9.0 *ziama* n. sp.

3a Lancet moderately exceeding height of sella. FA: 55.0 - 61.7, Cbs: 22.0 - 23.6, MastoidW: 11.2-12.3, ZygomaticW: 10.5 - 11.4, M^3-M^3: 7.3 - 8.2, C-M^3: 8.2 - 8.9 *ruwenzorii*

3b Lancet conspicuously exceeding height of sella. FA: 54.2 - 54.3, Cbs: 20.7 - 21.2, MastoidW: 10.9 - 11.2, ZygomaticW: 10.6 - 10.9, M^3-M^3: 7.8 - 8.0, C-M^3: 7.9 - 8.1 *hilli*

Fig. 8. Distribution map of the *Rhinolophus maclaudi* species group in Africa. *Rhinolophus maclaudi* (diamonds), *R. ziama* n. sp. (triangles), *R. ruwenzorii* (circles), *R. hilli* (squares).

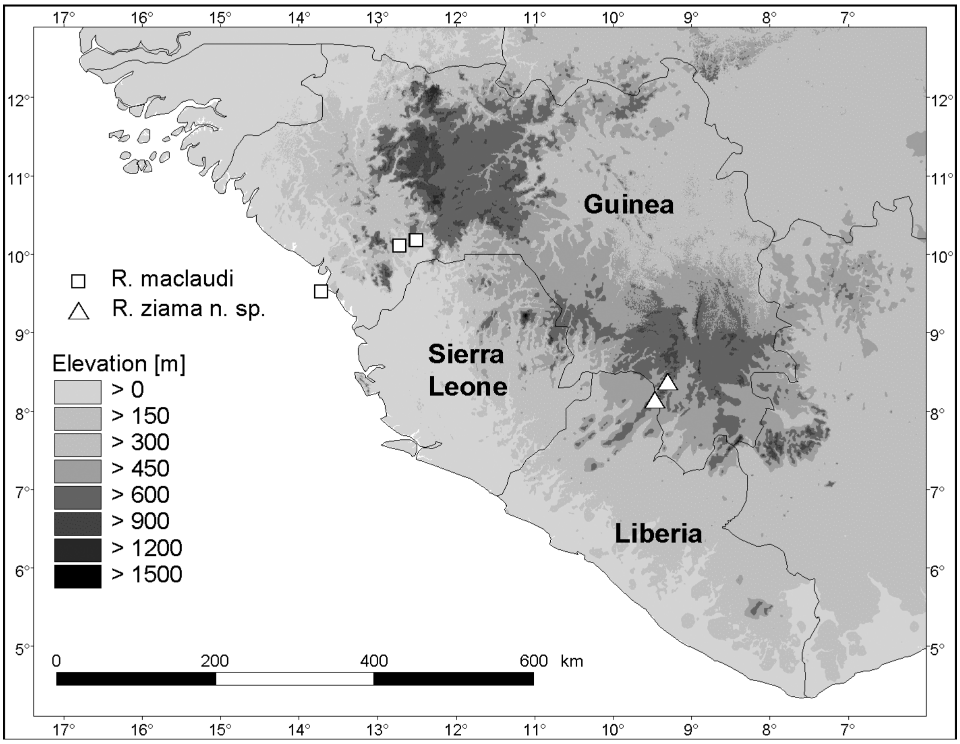

Fig. 9. Distribution map of *Rhinolophus maclaudi* (squares) and *R. ziama* n. sp. (triangles) in West Africa.

Tab. 2. Comparison of craniodental and body characters of the four species studied.

	R. maclaudi	*R. ziama* n. sp.
Skull & Teeth		
shape of braincase, dorsal view	constricted behind mastoid process	constricted behind mastoid process
highest point of braincase, lateral view	at height of glenoid process	clearly behind glenoid process
skull axis, lateral view	braincase deflected posteriorly	straight
posterior point of lambdoid-crista, lateral view	very low	low
anterior margin of rostrum, lateral view	steeply rising from canine, nasal swellings included in rostral sinus	steeply rising from canine, nasal swellings included in rostral sinus
saddle btw. rostrum and frontal	shallow	shallow
rostral emargination, dorsal view	U-shaped	U-shaped
position of anterior margin of rostral swellings in profile	at height of center of M^1	at height of centre of M^1
chambers of rostral swellings, dorsal view	heart-shaped (conspicuous postero-median indentation)	heart-shaped (conspicuous postero-median indentation)
infraorbital bridge	long	very long, slender
ratio ZygomaticW : MastoidW	1.01±0.02, (0.96 - 1.03), n = 7	1.00 - 1.01, n = 2
premaxillae, dorsal view	broad	broad
maxillary bone, dorsal view	visible along 2/3 of its posterior length	visible along 3/4 of its posterior length
ratio RostrumB : M^3-M^3	0.75±0.01, (0.73 - 0.77), n = 5	0.75, n = 2
ratio C-C : RostrumB	1.06±0.02, (1.04 - 1.07), n = 5	0.98 - 1.03, n = 2
C-PM^4	diastema, PM^2 in toothrow	diastema, PM^2 in toothrow
breadth of PM^4	about 3/4 of breadth of M^1	about 3/4 of breadth of M^1
relative size of lower molars	medium	medium
angular process of mandible	clearly anterior to condyle, outward oriented	just anterior to condyle
Noseleaf & Ear		
orientation of sella	inclined forward	inclined forward
horseshoe, median emargination	none (or only slight)	none
corolla-like cup formed by basal lobes of sella	heart-shaped	heart-shaped
inner margin of horseshoe around nostrils	± parallel, straight, slightly raised above horseshoe, (almost) reaching anterior margin of horseshoe	± parallel, straight, strongly raised above horseshoe, (almost) reaching anterior margin of horseshoe
breadth of connecting process, lateral view	narrow	narrow
lateral margins of sella, frontal view	± parallel (slightly concave)	± parallel (slightly concave)
height of lancet in relation to sella	large	large
secondary leaflets	absent	absent
number of ear folds	10-12	11-12

Tab. 2. continued

	R. ruwenzorii	*R. hilli*
Skull & Teeth		
shape of braincase, dorsal view	constricted behind mastoid process	hind margin rounded
highest point of braincase, lateral view	clearly behind glenoid process	clearly behind glenoid process
skull axis, lateral view	straight	straight
posterior point of lambdoid-crista, lateral view	low	high (raised)
anterior margin of rostrum, lateral view	shallowly rising from canine, nasal swellings displaced from rostral sinus	steeply rising from canine, nasal swellings displaced from rostral sinus
saddle btw. rostrum and frontal	deep	moderately deep
rostral emargination, dorsal view	squarish with rounded corners	squarish with rounded corners
position of anterior margin of rostral swellings in profile	at height of centre of M^1	at height of front of M^1
chambers of rostral swellings, dorsal view	subcircular (only slight postero-median indentation)	subcircular (only slight postero-median indentation)
infraorbital bridge	short, stout	very short, stout
ratio ZygomaticW : MastoidW	0.93±0.02, (0.88 - 0.96), n = 18	0.97, n = 2
premaxillae, dorsal view	broad	narrow
maxillary bone, dorsal view	not visible (concealed by rostrum)	visible along the entire length
ratio RostrumB : M^3-M^3	0.87±0.03, (0.83 - 0.91), n = 13	0.82, n = 1
ratio C-C : RostrumB	0.83±0.02, (0.80 - 0.86), n = 13	0.88, n = 1
C-PM^4	diastema, PM^2 in toothrow	almost in contact, PM^2 extruded
breadth of PM^4	about ¾ of breadth of M^1	almost as broad as M^1
relative size of lower molars	small	large
angular process of mandible	clearly anterior to condyle, outward oriented	at height of condyle
Noseleaf & Ear		
orientation of sella	erect, parallel to lancet	erect, parallel to lancet
horseshoe, median emargination	present	present
corolla-like cup formed by basal lobes of sella	subcircular	subcircular
inner margin of horseshoe around nostrils	semicircular and parallel to the inner cup, low, not reaching anterior margin of horseshoe	semicircular and parallel to the inner cup, low, not reaching anterior margin of horseshoe
breadth of connecting process, lateral view	very narrow	broad
lateral margins of sella, frontal view	concave, tip of sella strongly broadened (spoon-shaped)	concave, tip of sella strongly broadened (spoon-shaped)
height of lancet in relation to sella	small	large
secondary leaflets	present	present
number of ear folds	8	9

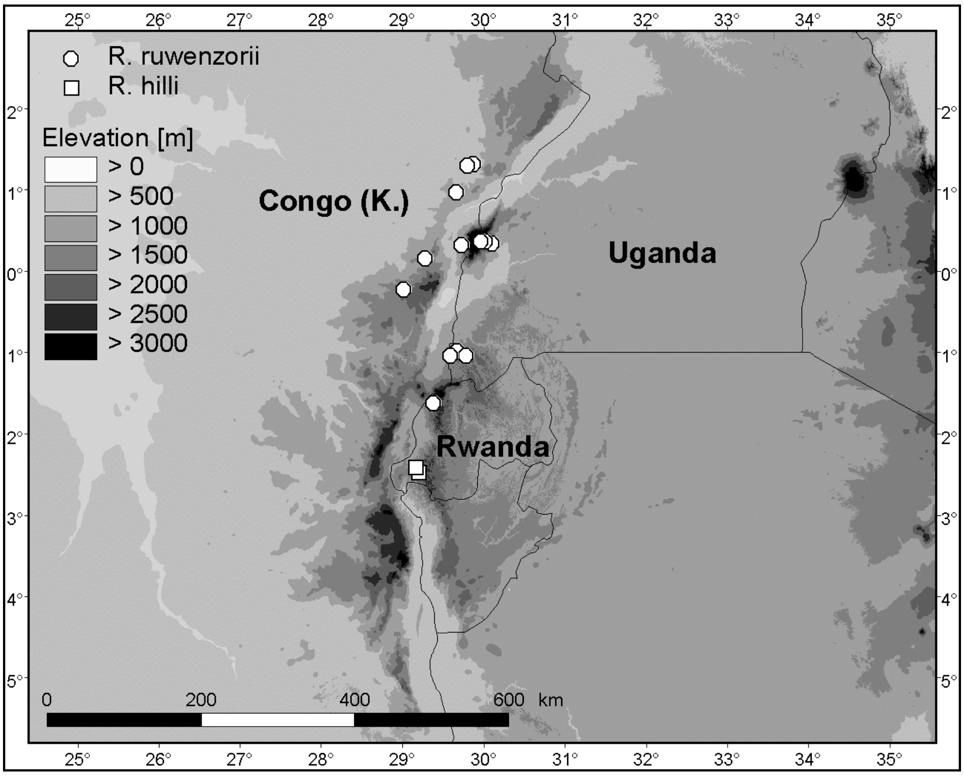

Fig. 10. Distribution map of *Rhinolophus ruwenzorii* (circles) and *R. hilli* (squares) in the Albertine Rift.

Discussion

Andersen (1905a, b) related *R. maclaudi* to the otherwise Australasian *philippinensis*-group (later named *luctus*-group, Andersen 1918; = *trifoliatus*-group of Hill 1992) but not to any African species of the genus *Rhinolophus* Lacépède, 1799. This would imply that *maclaudi* is an ancient relic dating back to an early colonisation of Africa (assuming an Oriental origin of the genus, see Bogdanowicz & Owen 1992). The relationship of *maclaudi*, *ruwenzorii* and *hilli* within the *philippensis* / *luctus*-group was accepted by Hill (1942), Aellen (1973) and Koopman (1994). However, Laurent (1940, 1941) who studied in detail the skull of *maclaudi* and compared it with *R. luctus* Temminck, 1834, disagreed with Andersen's grouping and concluded that *maclaudi* is in no way closely related to any Australasian form but instead represents an archaic African species. Recently, Bogdanowicz (1992) and Bogdanowicz & Owen (1992) studied phenetic and phylogenetic relationships of a large set of *Rhinolophus* taxa. Due to the high intrageneric similarity of *Rhinolophus* species, some of their results were rather equivocal, among them the position of *maclaudi*. It should be noted that the *R. maclaudi* sample used by these authors in fact consisted of *R. ruwenzorii*.

In the phenetic analysis (Bogdanowicz 1992), a minimum-spanning tree connecting the 50 taxa data set placed *maclaudi* closer to African rhinolophids than to Australasian species but other ordination analyses considerably changed the position of *maclaudi* within *Rhinolophus*. Bogdanowicz (1992) could not allocate "*maclaudi*" [= *ruwenzorii*] to any recognisable group and left it as *incertae sedis*. In the phylogenetic analysis of the common-part-removed data (Bogdanowicz & Owen 1992), "*maclaudi*" grouped as a derived clade together with the African taxa *capensis* Lichtenstein, 1823, *denti* Thomas, 1904 and *simulator* Andersen, 1904, again contradicting any relationship with Oriental or Australian forms. Although the alternative analyses of the size-free data and the consensus tree placed *maclaudi* near Australasian taxa or in a geographically mixed clade, Bogdanowicz & Owen (1992) concluded that the common-part-removed cladogram provided a better agreement with complementary data sets and as such a better working hypothesis regarding the phylogenetic relationships within the genus *Rhinolophus* (see also supporting evidence in Maree & Grant 1997).

Following Laurent (1940, 1941), Bogdanowicz (1992) and Bogdanowicz & Owen (1992), we remove *R. maclaudi* from the Australasian *luctus*-group and formally establish a new *R. maclaudi* group to comprise *R. maclaudi*, *R. ziama* n. sp., *R. ruwenzorii*, and *R. hilli*. The precise phylogenetic position of this new group is outside the scope of our paper but of special interest in the light of the striking disjunct distribution pattern of the group. Whether this represents an ancient and basal isolate or rather an unusually disjunct pattern of a derived clade remains to be tested. It should also be noted that the group morphologically falls into two distinct subgroups comprising *R. maclaudi* and *R. ziama* n. sp. on one side, and *R. ruwenzorii* and *R. hilli* on the other side (Tab. 2, Key).

Biogeography

When viewed at large, the species of the *R. maclaudi*-group show a very particular distribution pattern: *R. maclaudi* and *R. ziama* n. sp. are restricted to small regions in the Upper Guinea highlands while both *R. ruwenzorii* and *R. hilli* are confined to the mountainous region along the Albertine Rift (Figs. 8-10). Apparently all species show a paramontane distribution (sensu Koopman 1983), i.e. their distribution is restricted to mountainous regions although their altitudinal range covers both lower and higher elevations. Interestingly, to date no member of this species group has been found in the mountainous regions between the Upper Guinea highlands and the Albertine Rift, e.g. Jos Plateau, Mt. Cameroon, Bioko Isl., or the Cameroon highlands. This lack of occurrence might be due to insufficient sampling but at least the Cameroon Mountains are comparatively well studied (e.g., Eisentraut 1973, Hutterer et al. 1992). Moreover, at least *R. maclaudi* and *R. ruwenzorii* seem to roost preferably if not exclusively in caves or artificial substitutes. These kinds of roosts are fairly easy to survey, thus cave-dwelling species are rather well represented in species inventories and collections (unpubl. data). The large disjunction of the species group therefore seems to reflect reality and stands in marked contrast to a wide range of animal and plant species, superspecies or species groups that occur both in the Upper Guinea Highlands and on mountains along the Albertine Rift but which are also found on the Cameroon Mountains.

Within mammals, the only example of an established monophyletic group with a strikingly similar distribution pattern is that of the aquatic Dwarf Otter Shrews, *Micropotamogale* spp. (Afrotheria: Tenrecidae; Van Dijk et al. 2001). The Nimba Otter Shrew *M. lamottei* Heim de Balsac, 1954 occurs only in the Mt. Nimba area and its surroundings of Guinea, Liberia, and Ivory Coast (Vogel 1983). The Rwenzori Otter Shrew *M. ruwenzorii* (De Witte & Frechkop, 1955) is distributed along the Albertine Rift in the Rwenzori Mts. of eastern Congo (K.) and western Uganda, west of Lake Edward and Lake Kivu (Congo (K.) (Rahm 1960). The latter species has been found between 1000 and 2500 m altitude, similar to the elevational range covered by *Rhinolophus ruwenzorii*.

In birds, two examples were drawn to our attention that seem to exhibit a fairly similar distribution pattern (Mary Gartshore pers. comm. 11.I.2001). The nominate form of Lagden's Bush Shrike, *Malaconotus l. lagdeni* (Sharpe, 1884), is confined to Upper Guinea and occurs both at low and high elevations. The eastern subspecies, *M. l. centralis* Neumann, 1920, inhabits montane forest along the Albertine Rift between 1390 and 2800 m (Fry & Keith 1997). The Nimba Flycatcher, *Melaenornis annamarulae* Forbes-Watson, 1970, is restricted to Upper Guinea while the Yellow-eyed Flycatcher, *Melaenornis ardesiacus* Berlioz, 1936, is endemic to the Albertine Rift and found between 1300 and 2450 m altitude (Urban et al. 2000).

According to the pluvial hypothesis, Africa faced a both wetter and cooler climate during the late Pleistocene / early Holocene. In this scenario, montane forest would have covered wide areas at much lower altitudes than today, thereby connecting mountains and acting as a corridor for the exchange of species between distant mountains. When climate became warmer, montane forest would have retreated to higher elevations and species associated with this habitat would have been “trapped” on the mountains. The patchy and disjunct distribution pattern of Afromontane species would be the result of larger distribution ranges that subsequently shrunk to isolated fragments.

However, there is little evidence in support of the pluvial theory. A growing body of data is showing that Africa faced not a wetter but much drier climate during the late Pleistocene (Livingstone 1993, Elenga et al. 2000). This probably resulted in a fragmentation and reduction of both lowland and montane forests. A forest corridor between mountainous regions seems little supported. Instead, most of tropical Africa that today is forested was covered with xerophytic woods and scrubs or grassland / steppe (Elenga et al. 2000). This scenario is also confirmed by the analysis of subfossil mammal remains from Matupi Cave, a locality where *R. ruwenzorii* has been found in recent times. The composition of mammals from deposits between 22000 and 12000 B.P. is indicative of a savanna fauna with gallery forest nearby, while a shift to rain forest communities was found in deposits between 12000 and 3000 B.P. (Van Neer 1989).

A central question concerns the age of these Afromontane species. It is commonly assumed that populations of formerly widespread ancestral taxa became fragmented during the Late Pleistocene, eventually leading to genetically isolated and differentiated species. Later range expansions would have brought these newly evolved species into secondary contact. However, some studies have shown that many taxa diversified much earlier than the Pleistocene (e.g., Klicka & Zink 1997). Fjeldså & Lovett (1997) and Roy et al. (1997) found peak concentrations of neoendemic bird and plant species that were congruent with the distribution of phylogenetically older relict species. They suggested that specific montane regions might offer paleoecological stability in small pockets due to the heterogeneity of vegetation, climate and topography. They likened this scenario to the stabilising influence of orographic rainfall and mist precipitation in climatically favoured regions.

This hypothesis might be expanded: mountains offer a stable environment in the sense that species are provided with a wide range of habitat types between which they can switch when climatic conditions and accordingly biomes change. Mountain systems might therefore be seen as buffered small-scale refuges where specialised organisms are more likely to survive than in lowland regions. We think that this scenario applies to the *Rhinolophus maclaudi*-group and possibly also to the Dwarf Otter Shrews, *Micropotamogale* spp. In our opinion this hypothesis is supported by the fact that these taxa are not confined to purely montane habitats but instead range through a broad altitudinal gradient.

Interestingly, the distribution pattern of the *R. maclaudi*-group can be seen as both relict and recent. The species group as such is very disjunct with relict populations in Upper Guinea and along the Albertine Rift that are separated by more than 4300 km. However, within each of these regions a species pair has evolved. In the Upper Guinea highlands, *R. maclaudi* has been found in the savanna habitat of the Fouta Djallon Range. In contrast, *R. ziama* n. sp. is known from (montane) forest of the Ziama-Wonegizi Range. Apparently both species evolved in rather close proximity (closest known occurrence ca. 400 km distant) but developed different habitat preferences. The Central African species *R. ruwenzorii* and *R. hilli* evolved likewise in close proximity (known occurrence ca. 90 km distant). However, both species seem to prefer similar habitat types. In conclusion, we propose a phylogenetic relationship of the species group as follows: ((*R. maclaudi, R. ziama* n. sp.)(*R. ruwenzorii, R. hilli*)).

Habitat and conservation

R. maclaudi is listed in the latest IUCN Red List as “Low Risk: near threatened” (Hutson et al. 2001). This assessment was based on the taxonomy of Smith & Hood (1980), who treated *R. ruwenzorii* as a subspecies of *R. maclaudi* and *R. hilli* as a synonym of *R. ruwenzorii* (see Introduction). In the present study we show that all three taxa are distinct species and describe an additional species, *R. ziama* n. sp. We therefore re-assess the IUCN Red List status of all four taxa of the *R. maclaudi*-group and propose to raise their threat status for the following reasons.

R. maclaudi is known from only nine specimens and four localities since its description. The holotype was collected in 1896, additional eight specimens came to science between 1954 and 1968. The known distribution range of *R. maclaudi* covers only 360 km^2, stretching from Conakry on the coast roughly in a straight line about 150 km to the east-northeast. Except for the type locality, supposedly Conakry Island, all records are located along the lower, southern slope of the Fouta Djallon region between Kindia and Mamou near the border with Sierra Leone. Predominant vegetation of this region is bush-tree savanna, intersected by gallery forest along the rivers and in protected pockets (Guinean Forest-Savanna Mosaic ecoregion). Most of the specimens were taken from their day roosts in caves (Aellen 1956, Eisentraut & Knorr 1957), one specimen was caught in a house (Aellen 1973). Bats were found in their day roosts either singly or in a colony of six individuals. *R. maclaudi* shared its day roost with *Lissonycteris angolensis smithii*, *Nycteris macrotis* Dobson, 1876, *Rhinolophus guineensis* Eisentraut, 1960, *R. fumigatus foxi* Thomas, 1913, *R. denti knorri* Eisentraut, 1960, *Hipposideros jonesi* and *H. ruber* (Noack, 1893) (Eisentraut & Knorr 1957; identifications here updated).

R. ziama n. sp. is known from only four specimens (two collected), mistnetted in 1990 and 1992. The two known localities (Guinea: Ziama Forest; Liberia: Wonegizi Mts.), about 32 km distant from each other, are situated in the Guinean Montane Forests ecoregion. The specimens from Guinea were captured in secondary forest not far from primary forest, the single Liberian specimen was caught in fairly undisturbed upland forest. The day roosts are unknown.

R. ruwenzorii is known from 13 localities and 36 specimens. The holotype was collected in 1926, a further 28 specimens between 1947 and 1967, and seven specimens between 1982 and 1997. The known distribution range covers about 20740 km^2 and is apparently confined to the ecoregions of the Albertine Rift Montane Forest (n = 7) and the Rwenzori-Virunga Montane Moorlands (n = 2). *R. ruwenzorii* extends marginally along these ecoregions into the Northeastern Congolian Lowland Forests (n = 3) and the Victoria Basin Forest-Savanna Mosaic (n =1). The distribution range includes the Rwenzori Mts. (Congo (K.), Uganda), Kivu Region and Kibali-Ituri-Forest (Congo (K.)), Bwindi-Impenetrable Forest (Uganda) and Mutura in northwestern Rwanda. The majority of specimens was captured either in natural caves (5 out of 13 collecting localities) or disused mine shafts (2 out of 13), and one was a mist-net record. For five localities we could not obtain information concerning the collection circumstances. Colony sizes ranged from one to ten individuals (median: 3, n = 7). This bat has been reported to share its day roost with *Rousettus lanosus* Thomas, 1906, *Rhinolophus clivosus* Cretzschmar, 1828, and *Hipposideros caffer* (Sundevall, 1846) (Hill 1942, Smith & Hood 1980), the latter population probably representing *H. ruber*. The known altitudinal range covers 1066 - 2667 m (median 1760 m, n = 13).

Smith & Hood (1980) characterised the vegetation of the known localities as “Montane Evergreen / Bamboo forest”. One specimen was mistnetted in heavy undergrowth near a dense bamboo forest (Smith & Hood 1980).

R. hilli is known from two specimens collected between 1964 and 1981. The two localities are situated in the Albertine Rift Montane Forest ecoregion about 8 km distant from each other and located between 1750 and 2512 m altitude. The holotype was mistnetted (Aellen 1973). The day roosts are unknown.

In conclusion, all species show very restricted range sizes and are known from very few localities in a narrow range of habitat types (Tab. 3). Most specimens of *R. maclaudi* and *R. ruwenzorii* were captured between 1947 and 1968 and only the latter species was recorded as recently as 1997. Both, *R. maclaudi* and *R. ruwenzorii* seem to be dependent on caves or artificial substitutes such as mine shafts as day roosts and colony sizes are small. Equivalent data are lacking for *R. ziama* n. sp. and *R. hilli*. However, it seems likely that both species will turn out to have similar roosting requirements and colony sizes.

We propose to classify *R. maclaudi* as Endangered A2cd + B1, *R. ruwenzorii* as Vulnerable A2cd, and *R. ziama* n. sp. and *R. hilli* as Data Deficient.

Tab. 3: Number of specimens in collections, recorded localities, range size, occupied ecoregions and historical coverage for species of the *maclaudi*-group.

	No. of specimens	No. of localities	Range size	No. of ecoregions	Records from
R. maclaudi	9	4	360 km^2	2	1896 - 1968
R. ziama n. sp.	2	2	[32 km]	1	1990 - 1992
R. ruwenzorii	36	13	20740 km^2	4	1926 - 1997
R. hilli	2	2	[8 km]	1	1964 - 1981

Justification

R. maclaudi is known from an area much smaller than 5000 km^2, roosts apparently exclusively in caves that are increasingly exploited as bush meat supply in Upper Guinea (JF unpubl.) and is known from a densely populated area in which the remaining forest patches are continuously degraded.

R. ruwenzorii is known from an area slightly larger than 20000 km^2, roosts in caves or artificial substitutes that are vulnerable to direct exploitation and disturbance. Additionally, the recent wars in the region of occurrence have seriously affected several of the protected areas and remaining forests by uncontrolled settlement, small-scale farming, and logging. The rural human population density is amongst the highest in Africa

The data for *R. hilli* and *R. ziama* n. sp. are insufficient for a sound classification according to the IUCN Red List criteria. However, both species are likely to be threatened due to habitat destruction and direct exploitation in their day roosts. We consider their status as critical and surveys should be immediately carried out to evaluate their threat status. Additionally, *R. ziama* n. sp. is only known from an area that has been and still is heavily affected by the civil war in Liberia and the adjacent region of Guinea.

Acknowledgements

We gratefully thank Wilfried Bützler (Fachhochschule Hildesheim/Holzminden/Göttingen), the *Direction Nationale des Forêts et Chasse* (Ministère de l'Agriculture et des Ressources Animales) and the staff of *Projet de Gestion des Ressources Forestières* (PROGERFOR; both Republique de Guineé) who invited and supported HV to survey small mammals in the *Réserve de la Biosphère du Massif du Ziama* where the holotype of the new species was found. We express our gratitude to Elisabeth Kalko (Univ. of Ulm) and the late Charles Handley, jr. (USNM) who examined the AMNH-specimen of the new species. We thank Nancy B. Simmons (AMNH) who first sent this specimen on loan to the USNM and subsequently to the SMF. Judith Eger (ROM) kindly examined and re-identified horseshoe bats from Nigeria previously published as *R. maclaudi*. We thank Wiesław Bogdanowicz (Institute of Zoology, Warsaw) who provided measurements of *R. ruwenzorii*. We are most grateful to the curators Cäsar Claude (ZMUZ) for the loan of the type of *R. hilli* and Wim van Neer (MRAC) for the loan of *R. ruwenzorii* from Rwanda and additional collection data. Fritz Dieterlen (SMNS), Bill Stanley & Julian Kerbis (FMNH) and Bea DeCupere (MRAC) permitted access to specimens while JF, RH and HV were visiting the respective collections. Additionally, we received collection data from A. G. Rol (ZMA), David Janiger (LACM) and Georges Lenglet (IRSNB). Victor van Cakenberghe (Univ. of Antwerpen) provided a copy of Claessen's Masters-thesis that contained additional data on the second known specimen of *R. hilli*. We thank Stefan Porembski (Univ. of Rostock) for valuable information on the vegetation of Ziama Forest. We appreciate the suggestions of Mary Gartshore who pointed out several examples of bird distribution. Meredith Happold and Wiesław Bogdanowicz commented on earlier versions of the manuscript.

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Appendix 1. Gazetteer

GUINEA:

Nyembaro	10°06'N, 12°43'W	12 km W Kolenté, Salung-Plateau, 400 m [= Grotte D & E in Eisentraut & Knorr (1957)]
Grotte Garrigues	10°10'N, 12°31'W	4 km NE Souguéta
Conakry Island	09°31'N, 13°43'W	
Kankasili	10°11'N, 12°29'W	near Bandi River, 500 m
Sérédou	08°23'N, 09°18'W	Réserve de la biosphère du Massif du Ziama
Souguéta	10°09'N, 12°32'W	

LIBERIA:

Ziggida	08°09'N, 09°28'W	7 mi N, 1 mi E; 25 mi N Zorzor, Lofa County, Wonegizi Mts.

CONGO (K.):

Butahu Valley	00°19'N, 29°44'E	W-slope Rwenzori Mts., 7500 ft. [2286 m]
Butembo	00°09'N, 29°17'E	Kivu Province, 1760 m
Kasuo-Kibwe Cave	00°14'S, 29°01'E	Lya-Mikako, Lubero Distr., 1500 m
Matata Cave	00°58'N, 29°40'E	Kibali-Ituri, 1160 m
Matupi Cave	01°19'N, 29°52'E	Mt. Hoyo, S of Irumu, Ituri Forest, 3500 ft. [1066 m]
Mt. Hoyo	01°18'N, 29°48'E	Ituri Forest, 1200 m

UGANDA:

Itama Mine	00°59'S, 29°41'E	Bwindi-Impenetrable-National Park, Kigezi Highlands, 1615 m
Luhizha Mine	01°02'S, 29°47'E	Bwindi-Impenetrable-National Park, Kigezi Highlands, 2286 m
Mahoma River	00°20'N, 30°06'E	above Ibanda, E-slope Rwenzori Mts., 6700 ft [2042 m]
Mubuku River	00°22'N, 30°01'E	above confluence with Mahoma River, Rwenzori Mts., 6900 ft. [2103 m]
Nteko Parish	01°02'S, 29°36'E	edge of Bwindi-Impenetrable-National Park, Bufumbira, 1600 m
Nyabitaba (Hut)	00°22'N, 29°58'E	right bank of Mubuku River, below confluence with Bujuku River, E-slope Rwenzori Mts., 8750 ft. [2667 m]

RWANDA:

Ruta Bansugera	02°25'S, 29°10'E	Parc National de Nyungwe, 1750 m
Uwinka	02°29'S, 29°12'E	Parc National de Nyungwe, Préfecture de Cyangugu [= Shangugu], 2512 m
Mutura	01°37'S, 29°23'E	2200 m