THE GENUS MAIZANIA BGT. (GASTROPODA, MAIZANIIDAE) IN EASTERN AFRICA

By

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Introduction

The genus Maizania was erected by Bourguignat in 1889; Thiele (1929) considered it to be a subgenus of Ostodes Gould but Bequaert and Clench (1936), who discussed the genus more fully than anyone else up to that time, quite correctly refuted this idea. They divided the genus into three subgenera, Maizania s.s., Maizaniella Bequaert and Clench, and Thomeomaizania Bequaert and Clench, but only the former occurs in Eastern Africa. They list nine species in this subgenus and describe one new species (M. zanzibarica) but also omit a previously described species, M. lugubris Preston, which is closely similar to their new one. Pilsbry (1919, fig. 162) gives a map showing the distribution of the genus as a whole. Tierlecke (1940) considered that the genus should be placed in a separate family. Taylor and Sohl (1962) have accepted this view and I have followed them here.

I have examined the radulae of a number of species and races and since certain radula characteristics are associated with shell size I have divided the subgenus Maizania into two sections.

Section Maizania
Shell large, exceeding 8 mm. in width; central tooth of the radula with three cusps.

Section Micromaizania new section
Shell small, not exceeding 8 mm. in width; central tooth of the radula with five cusps.

Thiele (1929) figures the radula of M. preussi and shows the central tooth with three cusps.

The following list gives, so far as I am aware, all the names associated with the subgenus.
Maizania Bourguignat, Moll. Afr. Equat. 148 (1889) (genotype M. olivacea Bourguignat)
Synonyms: Cyclophorus subg. Aferulus von Martens (1897) (subgenotype chosen by Bequaert and Clench as M. olivacea Bourguignat)
Cyclophorus subg. Natalia Godwin Austen (1897) (subgenotype Cyclostoma wahlbergi Benson)
Hijabia Godwin Austen (1898) (new name for Natalia)
Austrocyclus Ancey (1898) (genotype chosen by Bequaert and Clench as Cyclostoma wahlbergi Benson)
Cyclophorus section Cyclophoropsis Dautzenberg (1908) (type of section Cyclophorus hildebrandti von Martens)
Specific and varietal names: Cyclophorus wahlbergi Benson (1852), Cyclophorus angolensis Dohrn (1878), Cyclophorus hildebrandti von Martens (1878), Cyclophorus magilensis Craven (1880), Maizania olivacea Bourguignat (1889), Cyclophorus elatior von Martens (1892), Cyclophorus volkensi von Martens (1895), Cyclophorus intermedius

von Martens (1897), Cyclophorus rugosus Putzeys (1899), Cyclophorus intermedius var. cingulatus Dupuis and Putzeys (1901), Cyclophorus kibonotoensis D'Ailly (1910), Aferulus lugubris Preston (1910), Aferulus intermedius var. angolensis Preston (1910), Maizania zanzibarica Bequaert and Clench (1936), Maizania marsabitensis Verdcourt (1963).

Three fossil species have also been described (Verdcourt, 1963a) and these will be discussed later.

It is unfortunate that amongst the fairly extensive collections of the genus which I have gathered together at the Coryndon Museum, there is nothing which matches the figure given by Bourguignat of his M. olivacea, the genotype. The nearest match is a small juvenile collected by myself on Kilimanjaro. I therefore wrote to Paris and Prof. Fischer kindly arranged for a photograph of the type to be sent to me; with his permission I have reproduced it here (fig. 1).

The species are difficult to separate, chiefly because the populations are separated and each population differs slightly in dimensions; there are few definite characters apart from the ratios of dimensions and colour. Whilst searching for characters by going over the material many times, uninfluenced by labels, a constant character was found in the striation which is correlated with geographical distribution. M. wahlbergi and M. zanzibarica have close, rather regular, raised striae, whereas M. hildebrandti has distinctive, spaced, dark costae with faint striae between. This is, I consider, an important character which has helped solve the relationship of the Natal forms to those occurring in East Africa. It is extremely difficult to decide whether M. hildebrandti and its relatives represent distinct species or only races. If extremes are compared e.g. M. hildebrandti hildebrandti and M. hildebrandti thikensis, one would doubtless decide that they could not possibly be considered conspecific, but other areas produce intermediate forms which are, however, constant for a given area. Mere size appears to be a poor character because, although it is probably constant in any one locality, juveniles of a large race may exactly resemble adults of a small race. One cannot help but think that arrested development of the shell has been involved in evolution and in some way fixed.

Key to the East African Species of Maizania

1. Shell always minute, never more than 8 mm wide (Micromaizania) 2
1. Shell larger (Maizania sensu stricto)..... 3

2. Shell conical, umbilicus narrow; 3.7-6 x 3.3-4.7 mm. ..... 1. volkensi
2. Shell depressed, umbilicus wide, 6.75 x 4-4.5 mm ..... 2. marsabitensis

(Note: juveniles of larger species will key here and they can only be recognised by experience - the apical whorl is larger and there is usually one whorl less for shells of the same size; also with experience the non-adult state can be recognised by the appearance of the aperture)

3. Shell conical, not very depressed, dark brown, almost always with traces of pale bands but very vague in Western Tanganyika forms ..... 7. elatior
3. Shell conical or depressed, usually a pale chestnut brown, never banded 4

4. Spire angle about 80°..... 6. olivacea
4. Spire angle much more obtuse 5

5. Shell sculptured with very close costulae developed into faint lamellae; umbilicus always widely open and shell depressed; coastal species 6
5. Shell sculptured with spaced costulae which are frequently developed into lamellae; umbilicus open or narrow; upland species 7

6. Shell with spire almost flat ..... 3. zanzibarica
6. Shell with spire distinctly raised ..... 4. wahlbergi

7. Shell attaining 25-30 mm in breadth 8
7. Shell usually under 20 mm wide, rarely attaining 22 mm 9

8. Shell higher, apical angle about 100°... 5b. hildebrandti elevata
8. Shell more depressed, apical angle about 120°..... 5a. hildebrandti hildebrandti

9. Shell small, under 15 mm wide; apical angle about 120°..... 5d. hildebrandti thikensis
9. Shell larger, up to 22 mm wide; apical angle 100 - 120°..... 5c. hildebrandti kibonotoensis

The West African species are clearly quite distinct and Bequaert and Clench have erected the subgenus Maizaniella for them. M. leonensis (Morelet) (Sierra Leone, Liberia) is similar in shape to M. marsabitensis Verdcourt but is strongly ribbed; M. lilliputianus (Morelet) (Gaboon) is also sublamellate; M. preussi (von Martens) (Cameroons) of which M. costulatus Boettger (? MS) may be a synonym, is closely allied to M. leonensis but larger - it does not belong to Maizania proper as Bequaert and Clench thought possible, but they had seen no material. Two Congo species, M. lukolelensis Bequaert and Clench (and its var. chapini Bequaert and Clench) and M. chondrocycloides Bequaert and Clench also belong to Maizaniella, the former being close to M. lilliputianus. The S. Tome species M. vandellii (Nobre) is placed by Bequaert and Clench in their subgenus Thomeomaizania which is justified since the spiral rows of tubercles are very distinctive. The other species from S. Tome, formerly referred to Cyclophorus, they place in their genus Afroditropis.

Enumeration of the Species

The following abbreviations are employed:

CM - Coryndon Memorial Museum, Nairobi.

B - Zoological Museum of the Humboldt University, Berlin.

BM - British Museum (Nat.Hist.), London.

S - Natural History Museum, Stockholm.

ANSP - Academy of Natural Sciences, Philadelphia.

P - Laboratory of Malacology, National Museum of Natural History, Paris.

1. M. volkensi (von Martens, 1895)
Cyclophorus volkensi von Martens, Sitzb. Ges. Naturf. Fr. Berlin 121 (1895) and Deutsch Ost-Afr. 4, Beschalte Weichth. 9, pl.2, fig. 6 (1897)

2. M. marsabitensis Verdcourt, Archiv. Mollusk. 92: 16, figs. 1,2a,b (1963)

These two species are adequately dealt with in a previous reference (Verdcourt, 1963b)

3. M. zanzibarica Bequaert and Clench, Rev. Zool. Bot. Afric. 29: 100, pl.1, figs. 5-7 (1936)

This species is characterised by its very depressed shape; it is obviously closely related to M. wahlbergi (Benson) and abundant material might indicate that it deserves only subspecific rank. Only a very small amount of material has been seen.

		Height	Breadth	Aperture diameter
ZANZIBAR.	Chuaca (Chwaka) (BM, paratype)	9	15.5	7
	Jembiani, 5m. S of Paje (Ostheimer in ANSP 213082)	13.1	20.1	9.4
	Chwaka (Ostheimer in ANSP 214525)	9.2	14.6	7.2

A specimen in the Berlin Museum from the Paetel collection labelled Zanzibar is M. wahlbergi and is probably wrongly localised. It doubtless was collected on the nearby mainland which was often called Zanzibar in the last century.

4. M. wahlbergi (Benson, 1852)
Cyclophorus wahlbergi Benson, Ann. Mag. Nat. Hist. (2) 10: 271 (1852); Smith, Proc. Zool. Soc. Lond. 277 (1881); von Martens, Deutsh Ost-Afr. 4, Beschalte Weichth. 9 (1897)
Aferulus lugubris Preston, Ann. Mag. Nat. Hist.(8) 6: 536, pl.9, fig. 27

This species is characterised by its low form, wide umbilicus and close, rather regular striae which are sometimes developed into very close lamellae. Kenya material does not merit even a racial name although it seems to attain a slightly larger size.

KENYA.	Shimba Hills (BM, paratype)			
	Vipingo	19.5	28.5	13.0
	(B. Verdcourt, CM)	16.5	24.0	10.5
	Sokoke Forest	15.0	21.0	10.0
	(J.G. Williams, CM)			
	Diani Beach, San Diego	20.0	29.0	14.0
	(H. Copley, CM 1040-1044)	17.0	24.5	12.0
		16.0	23.5	11.0
		16.0	24.0	11.0
		15.0	21.5	10.5
	Kikambala			
	(H. Copley, CM 2591)	15.5	24.0	11.2
TANGANYIKA	East Usambaras	7.0	11.5	5.0
	(B. Verdcourt, CM)			
	Between L. Nyasa and the coast	11.0	16.5	7.5
	(Thomson, BM)			
	Tanga (Karasek, B)	no data recorded		
	Kitohaui (Lieder, B)	no data recorded		

(Note: the two last were determined by von Martens as wahlbergi but I saw the specimens before I realised the true characters of this species).

ZANZIBAR.	Locality dubious, almost certainly from East African mainland	18.0	24.0	12.0
	(ex Paetel collection, B)			
NATAL.	Zulu country (BM)	11.0	17.5	--
		12.0	17.5	9.0
	Port Natal (BM)	12.5	16.5	8.0
		12.0	15.5	8.5
		11.0	15.5	8.0
	Port Natal	19.5	19.5	9.0
	(W. Jardine, BM)	to	to	to
		12.0	17.5	8.0
	Port Natal	12.0	15.5	8.5
	(57.1.16.16 BM)	9.5	11.5	5.5
	Port Shepstone	17.0	24.5	11.5
	(H.C. Burnup, BM)	17.5	23.5	11.5

	Cape Natal	15.5	21.0	10.0
	(Dr. Strangie? ex Mus.Cum., BM)	15.0	20.5	9.5
	Durban (W.T. Blanford ex coll. Godwin Austen, BM) (Note says animal drawn & dissected, Nov. 1896)	15.0	18.5	9.5
CAPE PROVINCE	Port St. Johns (Power - cited by Connolly)	18.8	23.5	11.5

5a. M. hildebrandti hildebrandti (von Martens, 1878)
Cyclophorus hildebrandti von Martens, Monatsb. Akad. Wiss. Berlin 289, pl.1, figs. 1-3 (1878) and Deutsch Ost-Afr. 4, Beschalte Weichth. 8 (1897)

This is undoubtedly specifically distinct from M. wahlbergi although superficially very similar in appearance, more so in fact than it is to other races of hildebrandti. The shell attains a large size and there are spaced dark ribs; the umbilicus is much narrower than it is in M. wahlbergi but wider than it is in M. hildebrandti elevata. M. hildebrandti and its races are of a much paler colour than M. elatior. In a footnote to Pilsbry's account (1919, p. 326) J. Bequaert suggests that M. elatior, M. hildebrandti, M. intermedius and M. rugosus are merely variations of a single specific type and that nothing in the distribution of these forms allows one to consider them as geographical races, but this is definitely not true so far as M. hildebrandti is concerned.

KENYA	Kibwesi	25.0	30.0	16.0
	(B. Verdcourt, CM)	24.0	28.0	15.0
		16.0	20.5	10.0
	Kitui	20.0	28.0	13.5
	(Hildebrandt, holotype, B).			
	Ditto from description	19.5	28.3	14.0
	Kibwesi	17.0	23.0	13.0
	(C. Harries, CM)	6.5	12.0	5.5
		5.5	10.5	5.0
	Kibwesi	22.5	27.5	14.0
	(R.M. Polhill &	21.0	26.0	13.0
	B. Verdcourt 17, CM)	18.0	25.0	13.0
		14.0	18.0	8.5
		8.5	12.5	6.0
	Kibwesi, Chai Dam	24.5	29.5	14.5
	(S. Coryndon, CM)	21.0	25.0	13.0
		20.5	25.5	12.5
	Makindu	17.5	22.0	11.5
	(S. Coryndon, CM)	17.0	22.0	11.2
		16.0	21.0	10.5
		7.2	11.0	5.2

The following material is too poor to place but is certainly a form of M. hildebrandti.

KENYA.	Chyulu Hills (H.F. Allen Turner, CM F 324)	9.5	11.5	6.0

5b. M. hildebrandti elevata Verdcourt new subspecies

This subspecies is characterised by having a more lamellate periostracum than any of the others; it also attains a larger size and has a narrow umbilicus. The lamellae are most evident in younger snails and tend to become rubbed off with age but they are always obvious. It is restricted to the ancient mountain blocks in the north east and eastern parts of Tanganyika, and is most closely related to M. hildebrandti kibonotoensis.

TANGANYIKA.	Uluguru Mountains, Bunduki (J. Bond, holotype & paratypes BM; paratypes CM)	25.0 HT 22.0 14.0 12.0 9.5	30.0 25.0 19.0 14.0 12.5	16.5 13.5 10.0 7.5 7.0
	East Usambaras (Rolle, B)	17.0 16.0	20.5 21.0	11.5 10.0
	East Usambaras, Amani (Vosseler, B)	no data recorded		
	East Usambaras, Nderema (L. Conradt, B)	no data recorded		
	East Usambaras, Amani, Bomole (B. Verdcourt, CM)	18.5 14.0 8.0	21.5 15.5 12.0	11.0 9.0 6.0
	East Usambaras, Ngua (B. Verdcourt, CM)	15.0	19.5	10.5
	West Usambaras, Magamba, Mkusi (B. Verdcourt, CM)	5.5	9.0	4.2
	Without locality (Methner, B)	no data recorded		

A shell from Ukami (BM, ex Sykes collection), i.e. the area immediately north-east of the Uluguru Mountains has the last whorl very lamellate and is taller than shells from the Usambaras but probably belongs to this subspecies; it measures 22.0 x 21.5 x 11.5-13 mm. There is also a juvenile shell from Ukami in the Berlin Museum.

Cyclophorus magilensis Craven, Proc. Zool. Soc. Lond. 218, pl.22, fig. 1 (1880) has long been a puzzle and a number of shells from varying localities have been referred to this name in the past. The name is, however, best dismissed as being based on unidentifiable material. In the collections of the British Museum (Nat. Hist.) there are the holotype and two paratypes, all very worn, white,

juvenile shells. The largest shell measures 8.5 x 12.0 x 5.0 mm and the sculpture is not preserved. The type locality, Magila, in the foothills of the East Usambaras near Mt. Mlinga suggests that it might be referable to M. hildebrandti elevata but one lot of two juveniles I collected at Amani, actually in the East Usambaras, has proved to be a mixture of M. wahlbergi and M. hildebrandti elevata, thus showing that the two occur together. I have not therefore used Craven's name.

5c. M. hildebrandti kibonotoensis (D'Ailly, 1910)
Cyclophorus kibonotoensis D'Ailly, Wiss. Ergebn. Schwed. Zool. Exp. Kilimandjaro 1 (6): 3 (1910)

The types have a rather elevated shell with the apex roseate; the umbilicus is narrow and the costae dark and well-spaced. Although undoubtedly close to M. hildebrandti hildebrandti, it never attains such a large size. The Masuku Plateau specimens were referred to M. intermedius by Smith (1899) but there is no doubt that they belong to M. hildebrandti; there are some slight differences e.g. the apices are not roseate but the costae are dark, spaced and have faint striae between them. Material from Mt. Kulal bears some resemblance to M. elatior von Martens but is more depressed and the periostracum more lamellate. Specimens from Marsabit are distinctly more elevated than those from Kulal but otherwise very similar. There is no good reason why these populations, though isolated and perhaps statistically separable, should be treated as separate races - the differences are too slight.

KENYA.	Mt. Kulal, 5-7000 ft. (B. Verdcourt, CM)	14.0	20.0	9.5
		13.0	18.5	9.0
		13.0	19.0	9.0
		12.5	17.5	8.5
		12.0	17.0	8.0
		12.0	17.0	8.5
		12.0	16.0	7.8
		11.5	17.0	8.0
		11.0	17.0	8.5
		11.0	16.5	8.0
		11.0	16.0	8.0
		10.5	16.0	7.7
		6.5	10.0	5.0
	Mt. Kulal (J. Alexander, CM)	17.0	22.0	11.0
		14.5	18.5	9.0
		14.5	18.5	8.5
		14.5	18.5	9.0
		14.5	19.5	9.5
		14.5	19.0	9.0
		14.0	19.0	9.0
		14.0	18.5	9.0
		14.0	18.0	8.8
		14.0	18.0	9.0
		14.0	18.0	9.5
		13.5	18.0	8.8
		13.0	19.0	9.0
		13.0	18.0	8.5
		13.0	16.5	8.5
		13.0	17.5	9.0
		12.5	17.0	8.5
		12.5	16.5	8.0

		12.0	15.5	7.5
		12.0	17.0	8.0
		12.0	18.0	8.8
		12.0	17.0	8.0
		12.0	16.5	8.0
		11.5	15.5	7.0
		11.0	16.5	8.0
		8.8	11.5	6.2
	Mt. Marsabit	12.5	16.0	8.0
	(J. Adamson &	12.5	16.5	8.0
	J.G. Williams, CM)	12.5	16.5	8.0
		11.0	14.0	7.0
		9.5	12.5	6.0
		9.0	12.5	6.0
		8.5	11.5	6.0
		8.0	11.5	5.5
		6.5	9.5	4.5
	Mt. Marsabit	13.0	17.0	7.5
	(B. Verdcourt, CM)	13.0	17.0	8.0
		13.0	16.0	8.0
		12.5	15.0	8.0
		12.0	16.0	7.5
		12.0	15.0	7.5
		11.5	14.0	6.8
		11.5	14.5	7.0
		11.0	15.5	7.5
		11.0	14.5	7.5
		10.5	14.0	6.5
		10.5	14.0	6.5
		10.5	14.0	7.0
		9.5	13.5	6.3
		9.5	14.0	7.0

Mathews Range material is slightly wider than Kulal material.

	Mathews Range, Wamba	17.0	22.0	10.5
	(Opiko, CM)	15.0	20.0	10.0
		14.5	20.5	10.0
		10.5	15.5	7.5
TANGANYIKA.	Kilimaniaro, Kibonoto (Y. Sjöstedt, holotype, S, three paratypes, BM)	14.5	18.0	9.0
	Ngurdoto Crater	16.0	19.0	9.0
	(L.D. Verdcourt, CM, BM)	15.0	19.0	9.0
		12.0	16.5	8.0
		11.0	4.5	7.0
NYASALAND.	Masuku Plateau,* 6000-7000 ft. (H.H. Johnston)	no data recorded		

* i.e. Misuku Hills, 33° 32' E., 9°42' S.

5d. M. hildebrandti thikensis Verdcourt new subspecies

This subspecies has the spaced dark ribs of M. hildebrandti but is depressed and uniformly small in size; the apex is roseate as in M. hildebrandti kibonotoensis. The worn types of Cyclophorus magilensis Craven are very similar to this subspecies but they are distinctly juveniles of a much larger form. It is interesting to note that an Euonyma from the same locality also shows 'arrested' juvenile characteristics.

KENYA.	Thika, Chania Gorge	9.5	14.0	6.2
	(B. Verdcourt, CM)	9.5	14.5	6.5
		9.0	13.0	6.0
		9.0	14.5	6.5
		8.5	12.5	6.0
		8.5	13.2	6.0
		8.5	13.0	6.0
		8.2	13.0	6.2
		8.0	14.0	6.5
		7.5	12.5	6.0
		7.5	12.5	6.0
		7.5	13.0	5.5
		7.0	12.0	5.5
		7.0	12.0	5.5
		7.0	11.0	5.5
	Same locality	10.0 HT	14.5	6.7
	(R.M. Polhill 113,	10.0	14.5	6.7
	holotype & paratypes,	10.0	14.5	6.7
	BM; paratypes CM)	9.5	15.0	6.7
		8.5	13.0	6.2
		8.0	13.5	6.0
		5.0	8.5	4.2
		4.5	7.5	3.7
		4.5	7.5	3.7

6. M. olivacea Bourguignat, Moll. Afr. Equat. 148, pl.7, figs. 14-18 (1889)
Cyclophorus olivaceus Bourguignat; von Martens, Deutsch. Ost-Afr. 4, Beschalte Weichth. 9 (1897)

Bourguignat's species is apparently quite distinct from the forms occurring in the Ulugurus and Usambaras. Lamellae are not mentioned in his description nor are they visible in the figure or in the photograph of the type. This photograph shows a shell much more acute than that of any of the subspecies of M. hildebrandti. Topotypic material is however required to elucidate the true position of this form, since the type is not adult. A small juvenile shell I collected at 9000 ft. on the Marangu track, Kilimanjaro might belong here but has an apical angle of over 90°; it measures 6.5 x 5.2 mm.

TANGANYIKA.	Summit of Nguru Mts. 2,000 m. (holotype, P)	12.0	12.0	6.5

7. M. elatior (von Martens, 1892)
Cyclophorus elatior von Martens, Sitzb. Ges. Naturf. Fr. Berlin 180 (1892) and Deutsch Ost-Afr. 4, Beschalte Weichth. 8, pl.1, fig. 1 & pl.2, fig. 4 (1897); Smith, Trans. Zool. Soc. Lond. 19: 47 (1909); Thiele, Wiss. Ergebn. Deutsch Zentr. Afr. Exp. (1907-8) 3: 210 (1911)

C. intermedius von Martens, Deutsch Ost-Afr. 4, Beschalte Weichth. 8, pl.2, fig. 3 (1897); Thiele, loc. cit. 210 (1911); Dautzenberg and Germain, Rev. Zool. Afric. 4: 48 (1914); Pilsbry, Bull. Am. Mus. Nat. Hist. 40: 325 (1919)

Cyclophorus rugosus Putzeys, Ann. Soc. Malacol. Belg., Bull. Séances 34, 55, fig. 1 (1899)

C. intermedius var. cinqulatus Dupuis and Putzeys, Ann. Soc. Malacol. Belg. Bull. Séances 36, 41, figs. 17-18 (1901)

Aferulus intermedius var. angolensis Preston, Proc. Malac. Soc. 9: 55 (1910)

? Cyclophorus angolensis Dohrn, Jahrb. Deutsch. Mal. Ges. 5: 151 (1878)

It will be seen from the synonymy that there may be an older name for this species than the one I have used. Dohrn's type has not been traced but the description is of a dark shell measuring 16 x 21 x 11 with the aperture bluish within; there is no mention of pale bands. The type locality is extremely vague - "in provincia Angolensi" and no figure is given. It is very likely identical with the Kungwe material but practically no material has been seen from Angola. Since Dohrn's species may be a distinct form never recollected I am not using the name. Kenya and Tanganyika material shows rather more widely spaced ribs and the bands are obscure or practically non-existent. This material shows some approach to forms of M. hildebrandti, e.g. Kenya elatior is very similar to M. hildebrandti kibonotoensis from Marsabit but the darker colour separates them.

Pilsbry (1919) gives a good account of the Congo material he examined. He particularly notes the variation in spacing of the ribs. I have not seen any of the unbanded material he mentions but some, e.g. that from Penge must be very similar to Kungwe material. I had intended to treat the material from western Tanganyika as a separate race but insufficient material has been seen; other single specimens from throughout the range of the species seem equally distinctive. Racial distinctions will, however, be necessary and there is for example a wide difference between the very small specimens from the Sudan and the large specimens from Tschibinda.

Typical elatior is readily recognised by its elevated form, very narrow umbilicus and dark colour with pale spiral bands; the periostracum is not so lamellate as in other species.

Mr. M.R. Block has communicated some details of a specimen collected by Mrs. D.P. Irwin in Kakamega Forest on old leaves in damp undergrowth. He managed to keep the snail alive in England for a month or so. "The animal was very shy but would emerge and crawl about at any time of day or night provided it had a moist atmosphere of about 60°F. The most striking feature was its colour, a bright shrimp-pink shaded to a deeper colour about the snout and with orange-red tentacles, which folded back along the sides when the creature withdrew its head. The body was finely rugose, the oval rugae difficult to see save in certain lights. The foot was not divided longitudinally as in Cyclostoma. I never saw this snail eat though I gave it a wide variety of foods e.g. fungi, leaf-mould, rolled oats and algae and moss. Microscopical examination of the faeces (the remains

of its last meal in Africa) showed tiny fragments of leaf epidermis, plant hairs, short lengths of fungal hyphae, round green algal cells and various spores. I therefore concluded that it was a detritus-feeder. The faeces were tiny oval pellets quite unlike the coiled masses produced by the Helicidae".

SUDAN.	Nagichot, Didinga Mts. (G.D. Hale Carpenter, BM, CM)	11.0	12.5	6.7
		10.2	11.5	6.2
		10.0	11.5	6.2
		9.8	11.0	5.7
		9.7	11.5	6.2
CONGO.	Tschibinda (F. Hendrickx, CM)	18.5	23.0	13.0
	Nsendwe (paratype of var. cinqulata, Dupuis & Putzeys, BM)	12.2	14.3	7.0
UGANDA.	Mabira Forest (R.L. Harger, BM)			
	Bugoma Forest, 4000 ft. (C.R.S. Pitman, BM)			
	Ruwenzori (1907. 12.11.64-6, BM)			
	sine locality (Capt. Powell Cotton, BM)			
	Ruwenzori, Mobuku Valley (G.H. Yeoman, CM)	15.0	24.0	10.0
	Ruwenzori, Byuku Valley, Nyamleja (G.H. Yeoman, CM)	12.0	15.5	8.7
	Ruwenzori (G.D. Hale Carpenter, BM)			
	Entebbe (E. Degen?, BM)			
	Entebbe (G.D. Hale Carpenter, CM)	14.5	17.0	9.5
	Toro (G.D. Hale Carpenter, CM)	13.5	15.2	8.2
		13.5	15.2	8.2
		13.0	16.0	8.5
		11.0	13.2	7.2
		10.5	12.5	7.0
KENYA.	Kapsabet, Nandi Forest (M. Powell, CM)	20.0	22.5	11.5
		20.0	21.8	11.5
		18.0	21.0	11.0
		16.8	19.5	10.5
		16.5	18.5	10.0

KENYA (Contd.)	Kakamega Forest (E. Pinhey, CM)	12.5	14.0	8.0
	Kakamega Forest	17.0	19.0	10.3
	Yala River	15.0	17.0	9.5
	(M. Powell, CM)	13.5	16.5	9.0
		12.5	13.5	7.5
	Kakamega Forest	14.5	18.0	9.5
	(B. Verdcourt, CM)	14.0	17.5	8.8
	Kakamega Forest	16.5	18.0	9.5
	(S. Cary, CM)	13.0	15.5	8.3
	Kakamega Forest	18.0	20.5	11.0
	(J. Morris-Goodall,	16.5	18.5	10.0
	CM)	15.0	17.5	9.5
		15.0	17.0	9.2
		14.0	17.0	9.0
		14.0	16.2	8.0
		12.5	15.5	9.0
		12.5	14.5	8.5
		10.5	13.0	7.2
TANGANYIKA	Kungwe Mt. south	12.5	17.0	8.5
	ridge, 6000 ft.	11.0	16.0	7.5
	(D.H. Eccles, CM)			
	Kungwe Mt., 5000 ft.	13.0	17.8	8.5
	(J. Newbould, CM)	12.5	16.5	8.2
	Kungwe Mt.	12.0	17.5	8.5
	(J.A.L. Cooke, CM)	11.0	16.0	7.8
	Lukandamila, 5000 ft.	19.0	23.0	12.5
	(D.H. Eccles, CM)			
	Buha District,	14.0	18.5	10.0
	Gombe stream chimp-	14.0	18.5	9.0
	anzee reserve,	13.5	17.5	8.5
	Kasakela 16 miles N.	13.5	16.0	8.0
	of Kigoma	13.5	17.0	8.5
	(B. Verdcourt CM)	13.0	16.0	8.0
		12.5	16.0	8.0
		12.0	15.5	8.0
		12.0	14.0	7.0
		11.5	14.5	7.5
		10.5	14.5	7.0
		9.5	13.0	7.5
ANGOLA.	200 miles E. of Loanda (paratypes of A. intermedia var. angolensis Preston, BM)	15.0	17.0	9.0

Discussion of the Distribution of the Species

From wherever Maizania was first derived it is undoubtedly an evergreen forest group in origin. It has affinities with groups both in Tropical America and in Asia. In the past Maizania has been considered as a subgenus of Cyclophorus, an eastern genus, but its present treatment as a separate family suggests that it is an isolated genus of ancient origin. It seems likely also that the basic subdivisions of the genus diverged long ago, but until anatomical studies of a fair proportion of the species are available it is not possible to decide how closely related to each other they are. Thomeomaizania and Maizaniella are purely S. Tome and Guinean groups respectively.

The Congo forest is undoubtedly a very old vegetation type and, as is well known, this type of forest extends down into western Tanganyika and across to Kenya, but it has not existed with its boundaries static any longer than other vegetation types in eastern Africa. There was for instance a large lake in the Congo basin during the Pliocene. From Angola to the southern Sudan and ranging throughout the eastern part of this vegetation type, Maizania elatior is found, usually on the swampy banks of streams subject to periodical inundation. Bequaert (in Pilsbry, 1919) gives an account of the favoured habitats and I found the species near Kigoma under identical conditions. In Kakamega Forest, however, the species lives under slightly drier conditions under leaf litter. One is tempted to consider this species as probably an old one but it is an extremely variable and plastic taxon. M. wahlbergi appears to exist in two disjunct areas since it seems unlikely that this rather large species has been entirely overlooked in Mozambique, although it must be admitted that there is little published literature about that area and I have seen no local collections in that country. A large number of species of plants and animals extend from Port Elizabeth and Natal up to East Africa and were probably well distributed inland as well. A considerable number are now left as relicts in scattered areas or are compressed into the coastal strip by inland tectonic and climatic changes. A typical example of a plant still widely distributed is Xymalos monospora (Harv.) Baill. ex Warb., an ancient species which occurs in evergreen forest throughout much of East Africa including forest on isolated mountain tops from 900 - 2700 m; it also extends to the Cameroons, Fernando Po and South Africa. Maizania has a more or less parallel distribution. Pseudobersama mossambicensis (Sim) Verdcourt is a species of the coastal strip alone from Natal to Kenya and its distribution parallels that of M. wahlbergi. Heywoodia lucens Sim has a remarkably disjunct distribution, occurring in Uganda (Ankole), Kenya (Thika and Kitui areas), Tanganyika (Minziro Forest, Bukoba) and the coastal evergreen forests of South Africa. This distribution indicates that there were evergreen forest links probably during the Miocene or before, all over the areas inhabited by Maizania. M. zanzibarica is very closely related to M. wahlbergi and probably is only a depressed subspecies. It may of course be older in the sense that the ancestor of both was a depressed form. M. hildebrandti is in part confirmed to Tertiary and Recent volcanic areas but one subspecies, ulugurensis, is found in forest areas on ancient basement complex rocks which have had connections with the rain forest to the west of the continent in the past. M. olivacea is confined to a similar but less ancient forest area. M. volkensi occurs in both old and recent volcanically disturbed areas but is so small that racial differences are not apparent, although on Marsabit the related depressed M. marsabitensis and a third undescribed race

or species have been found. The larger M. marsabitensis might be looked on as a step on the way to M. volkensi but if so it is strange that similar forms have not been found elsewhere. The Marsabit forest seems to be very similar in content to the Kenya highlands and must have been part of the extensive similar forests which stretched to the Ethiopian highlands. It does not appear to be an ancient relict area but may of course be on the site of an ancient highland area rising above the Miocene peneplain, subsequently much altered but not destroyed entirely during later volcanic activity. So little of Africa has been adequately explored that negative distribution evidence can be of little or no value. The racial segregates found in M. hildebrandti can be attributed to the isolation of habitats caused by the extensive Pliocene and Pleistocene geological upheavals and the race kibonotoensis is characteristic of isolated evergreen forest areas on volcanic rocks.

There is very little fossil record of Maizania. I have described several from the Miocene of Rusinga (Verdcourt, 1963b) and similar material has also been found in the Leopard Caves, Mt. Elgon in beds probably younger than the Miocene. All this material has the surface sculpture poorly preserved but it is certain that at least the majority and perhaps even all of it is close to M. hildebrandti hildebrandti, since traces of widely spaced ribbing are apparent. They are big forms similar to M. hildebrandti hildebrandti but some are very depressed and widely umbilicated, more so than any existing species. Depressed and elevated species occur in exactly the same beds and were thus contemporaneous as they are today. It does not appear that degree of elevation, which is due to tightness of coiling, can be looked upon as a primitive or advanced character, but that the physiological cause is a delicately balanced one and variation occurs readily. It would not appear to be due to environment (humidity and temperature, etc.) since depressed and elevated forms occur together at Marsabit. Depressed, widely umbilicated forms are today mostly confined to the coastal areas. In Miocene times it is evident that large forms closely resembling M. hildebrandti hildebrandti were widely spread and that the smaller races evolved during the extensive Tertiary climatic and associated vegetational changes. There were undoubtedly extensive forest links across much of East Africa, in fact very large acreages have only very recently been destroyed by man. Some forest areas were isolated by extensions of the desert areas quite early on. The true Somali desert area is an ancient wedge which I feel must date back to probably before the Miocene and at least well before the Tertiary volcanic activity and, in fact, is part of desert conditions which may formerly have extended at a pre-Miocene date (?) from Sind to South West Africa. This wedge may not have been uniformly continuous and has now been obscured by vegetational changes in Central Africa. The flora of this dry belt is impressively characteristic, particularly that area which extends from the Ogaden and Somaliland through Eastern Kenya to the Pare Mountains in Tanganyika. The idea of a continuous dry link between Sind and South West Africa is not easy to envisage since at an early enough date there was no link with India to the north east and the flora of the fire-swept savannah in Rhodesia, with its curious subshrubby pyrophytes in otherwise large, woody genera, and its endemic annuals is undoubtedly very old. It is unlikely that any of these floras was formed suddenly. All may be old but their extent and thus possibilities as barrier formers did vary enormously. A constant struggle between evergreen forest areas and desert and savannah areas must have occurred during alternating dry and wet periods, both before and after the

Tertiary upheavals, the relative areas shrinking and enlarging, with bridges linking similar areas being destroyed and restored. This dry Somali wedge separates M. wahlbergi, M. zanzibarica and, to a certain extent, M. hildebrandti elevata from other taxa of Maizania. If this dry area is as old as I believe, the coastal forest vegetation may have gained many of its components from the west via loops through southern Tanganyika. There are certainly floristic components that extend from Chirinda in Southern Rhodesia up the Tanganyika coast to Kenya, and others of western origin which are quite alien to the evergreen forest in the centre of Kenya.

M. wahlbergi, M. zanzibarica, M. volkensi, M. marsabitensis and most M. elatior have close striae but M. elatior shows considerable variation in this respect and wide costae are present in material, particularly from eastern localities. In fact M. elatior from Kenya and Kungwe closely resemble M. hildebrandti kibonotoensis, but some Kungwe material almost equally resembles M. wahlbergi. There is little doubt that each isolated locality has a population that is slightly different, but for practical purposes it is not reasonable to give them all names. Without more fossil evidence it is not possible to even guess at a phylogenetic arrangement. Despite the occurrence of large species with wide costae in Miocene beds (assuming that these are correctly dated) it is difficult to look on the closely striated species as newer, rather, I believe, they are older. Species similar to M. volkensi and M. wahlbergi were already evolved at the beginning of the Miocene and widespread through much of the forest according to their ecological requirements. Present M. wahlbergi and its ally M. zanzibarica are the product of long isolation from parent stock, as presumably are the strongly ribbed species of West Africa. M. elatior may well be close to the original type and it still appears to be very plastic. Larger species (wahlbergi, hildebrandti hildebrandti, hildebrandti elevata, and presumably the Miocene species) live in rather hotter places and may have been forced into the eastern areas during colder periods. That M. hildebrandti evolved before the volcanic upheavals seems evident from its occurrence in the East Usambaras and the Ulugurus as a large elevated race. The races of hildebrandti on volcanic ground have been modified by the severe climatic and tectonic changes from a previously widely distributed larger form. M. volkensi which has survived through much of the area may well be the result of an adaptation to colder climates but is still capable of living in some hotter, lower areas. A possibility with much evidence in its favour is a cold spell that extended alpine conditions in fairly old elevated areas. The Aberdares, Cherangani Hills and Ethiopian Highlands have all had alpine conditions on their summits for three to five times as long as Mount Kenya has existed. Some such area is necessary to explain the origin of the Afroalpine flora now found also on quite recently formed mountain tops which have been isolated since their origin. This peculiar Afroalpine flora is scarcely of very recent origin and non alpine relatives of the Giant Lobelias are to be found from Ethiopia and the Cameroons to the Usambaras, and even in Southern Rhodesia in forest areas. It is difficult to believe that this flora reached the individual mountains by long distance dispersal, but no other explanation seems to fit. A cold spell which put the alpine zones in contact with each other, or which did the same for hypothetical prevolcanic elevated alpine areas, would have destroyed a vast amount of the lowland flora and this did not happen. The long distance dispersal could have been helped considerably by a less violent cold spell and some of the volcanos now mere remnants (e.g. Suswa, Longonot, Crater Highlands, etc.) may have been tall enough to support afroalpines if they had quiescent periods before they erupted violently.

THE GENUS MAIZANIA IN EASTERN AFRICA

Explanation of Plates

Fig.

1. M. olivacea Bgt.
Tanganyika, Nguru Mountains, holotype

2,5. M. hildebrandti elevata Verdc.
Tanganyika, Uluguru Mountains, holotype (J. Bond)

3. M. wahlbergi (Benson)
Kenya, Vipingo (B. Verdcourt)

4. M. hildebrandti elevata Verdc.
Tanganyika, E. Usambaras, Amani, Mt. Bomole, cotype (B. Verdcourt)

6. M. elatior (von Martens)
Kenya, Nandi Forest (M. Powell)

7,10. M. elatior (von Martens)
Tanganyika, Buha District, Kasakela - north of Kigoma (B. Verdcourt)

8. M. elatior (von Martens)
Tanganyika, Kungwe, Lukandamila (D.H. Eccles)

9. M. elatior (von Martens)
Sudan, Didinga Mountains (G.D. Hale Carpenter)

11,19. M. elatior (von Martens)
Tanganyika, Kungwe, Mahari Mountains (J. Cooke)

12. M

12. M. elatior (von Martens)
Uganda, Toro (G.D. Hale Carpenter)

13. M. hildebrandti hildebrandti (von Martens)
Kenya, Kibwezi (S. Coryndon)

14. M. elatior (von Martens)
Congo, Tschibinda (F. Hendrickx)

15,16. M. hildebrandti kibonotoensis (D'Ailly)
Tanganyika, Ngurdoto Crater (L.D. Verdcourt)

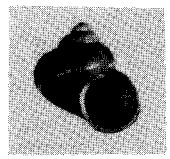
17,20. M. hildebrandti kibonotoensis (D'Ailly)
Kenya, Mathews Range, Wamba (Opiko)

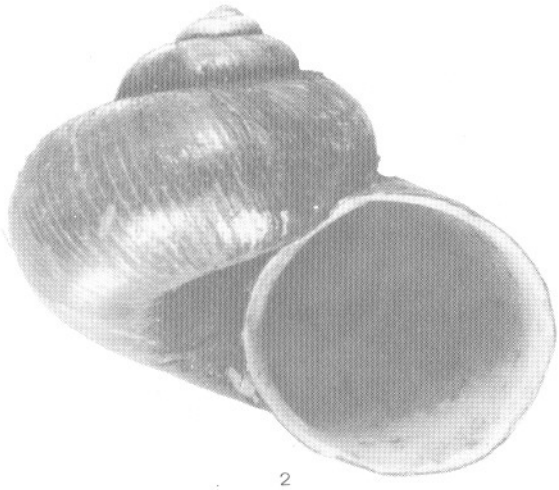
21,22. M. hildebrandti thikensis Verdcourt
Kenya, Thika, Chania Gorge, cotype (B. Verdcourt)

18,23. M. hildebrandti kibonotoensis (D'Ailly)
Kenya, Mt. Marsabit (B. Verdcourt)

24,25. M. hildebrandti kibonotoensis (D'Ailly)
Kenya, Mt. Kulal (B. Verdcourt)

The scale represents millimetres and refers to all figures save Fig. 1 which is x 1.50.

Fig. 1 



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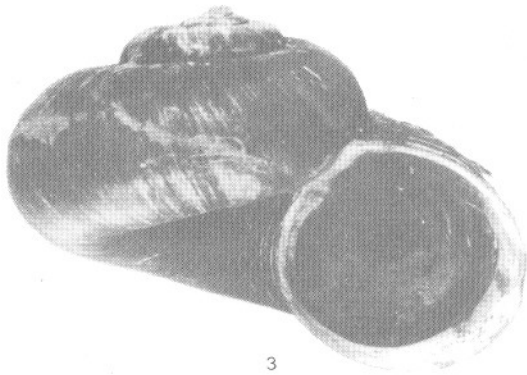

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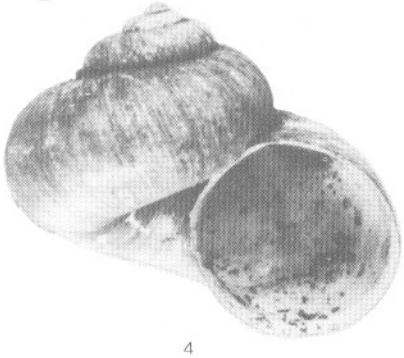

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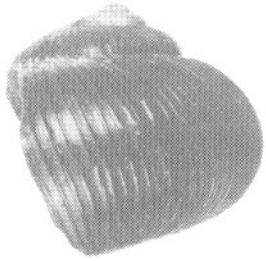

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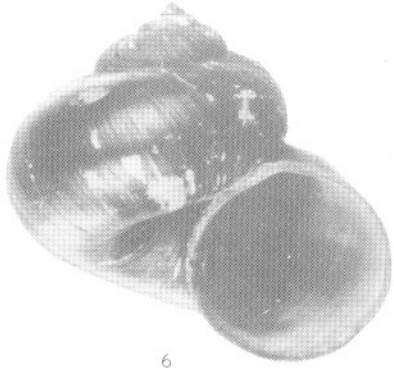

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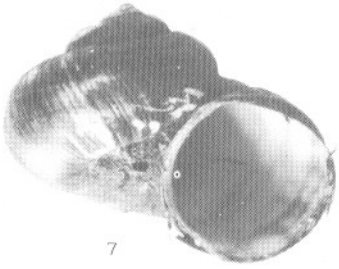

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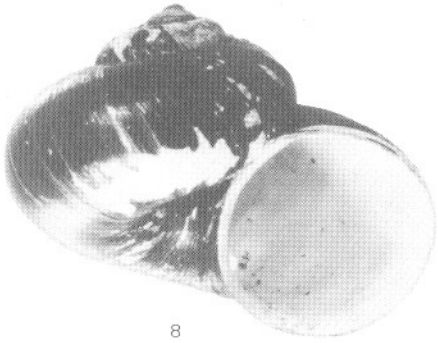

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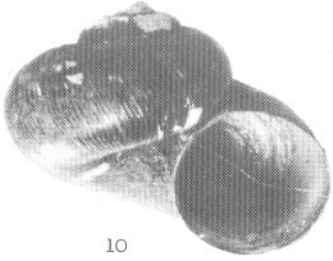

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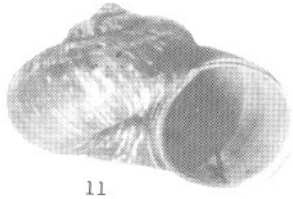

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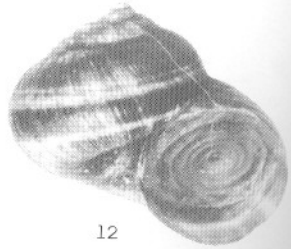

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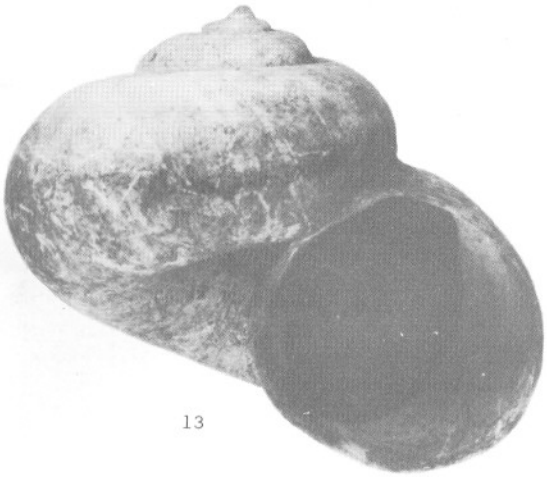

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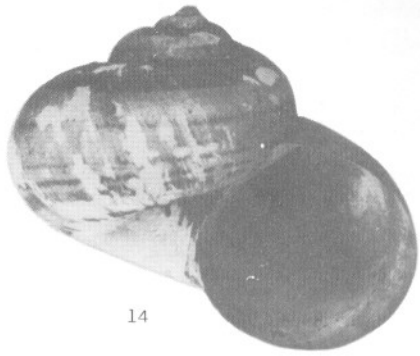

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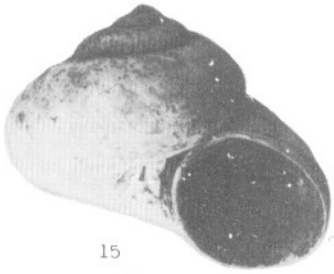

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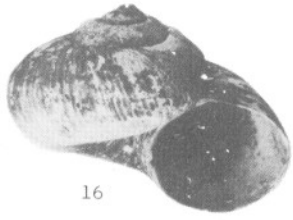

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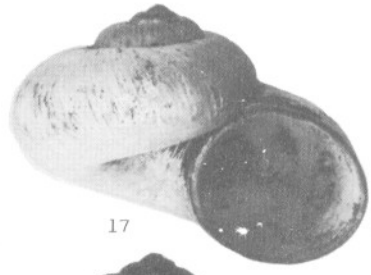

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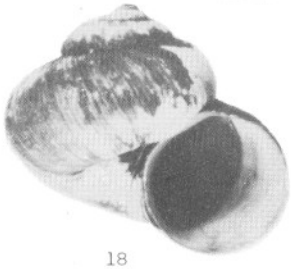

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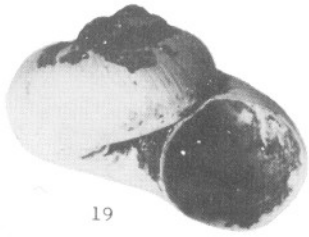

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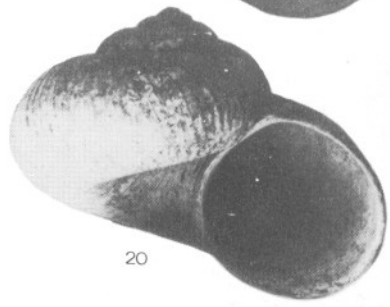

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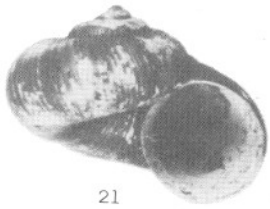

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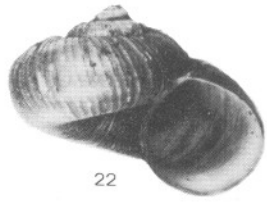

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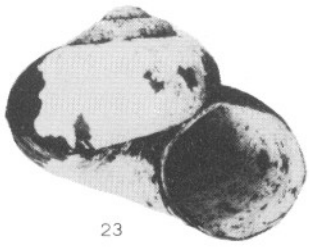

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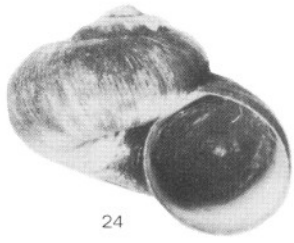

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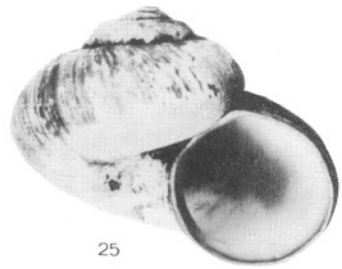

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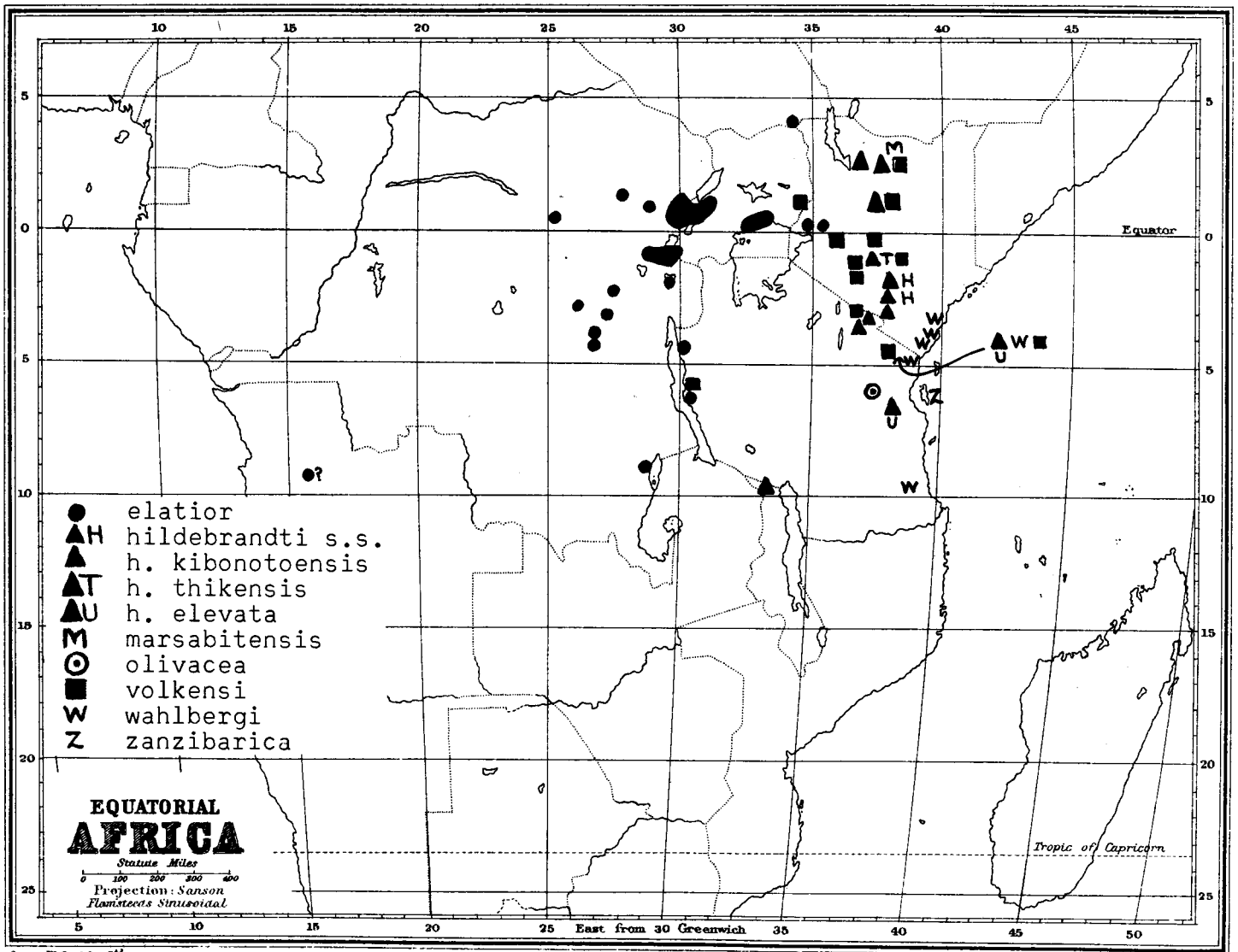
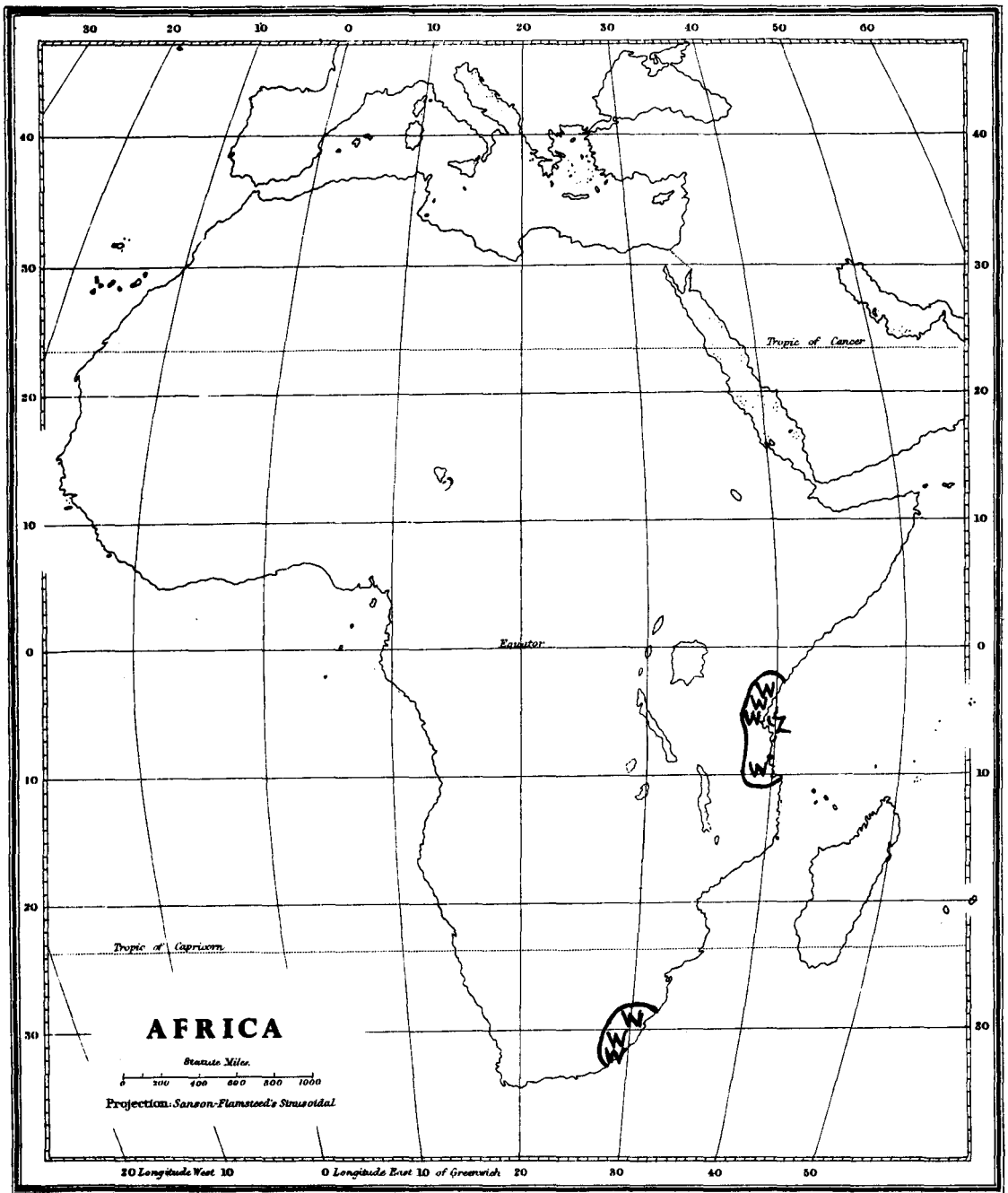
The genus Maizania in tropical Africa



Distribution of Maizania zanzibarica and M.wahlbergi



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