# Description of four new species of *Monodora* and *Isolona* (Annonaceae) from Tanzania and an overview of Tanzanian Annonaceae diversity

**Thomas L. P. COUVREUR**
Nationaal Herbarium Nederland, Wageningen University Branch,
Biosystematics Group, Wageningen UR,
Generaal Foulkesweg 37, NL-6703 BL Wageningen (The Netherlands)
Thomas.Couvreur@wur.nl

**Roy E. GEREAU**
Missouri Botanical Garden, PO Box 299, St. Louis, MO, 63166-0299 (USA)
Roy.Gereau@mobot.org

**Jan J. WIERINGA**
Nationaal Herbarium Nederland, Wageningen University Branch,
Biosystematics Group, Wageningen UR,
Generaal Foulkesweg 37, NL-6703 BL Wageningen (The Netherlands)
Jan.Wieringa@wur.nl

**James E. RICHARDSON**
Nationaal Herbarium Nederland, Wageningen University Branch,
Biosystematics Group, Wageningen UR,
Generaal Foulkesweg 37, NL-6703 BL Wageningen (The Netherlands)
Present address: Royal Botanic Garden,
20A Inverleith Row, Edinburgh EH3 5LR (United Kingdom)
J.Richardson@rbge.ac.uk

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**ABSTRACT**
Four new species of Annonaceae from Tanzania are described and illustrated: *Monodora carolinae*, from coastal Tanzania and northern Mozambique, with reflexed outer petals and inner petals connivent by their tips; *M. globiflora*, endemic to the montane forests of the Udzungwa Mountains, with inner petals fully connivent as a globe over the receptacle; *M. hastipetala*, endemic to the Kiwengoma Forest (Matumbi Hills), with hastate inner petals acuminate at apices; and *Isolona linearis*, endemic to Iringa region, with linear corolla lobes. Keys are provided to all species of both genera for East Africa. Pollen

**KEY WORDS**
Annonaceae,
*Monodora*,
*Isolona*,
diversity,
pollen,
tectum structure,
Tanzania,
new species.

morphology and tectum structure are indicated for every new species, and evolutionary trends are discussed for *Isolona*. Finally, an overview of Tanzanian Annonaceae is given, with a species checklist and distributional maps of species and genera, based on data gathered from literature and the MO and WAG herbarium databases. Most Annonaceae biodiversity is confined to the Eastern Arc and Coastal Forests, underlining once again the importance of these endangered regions.

**RÉSUMÉ**
*Description de quatre nouvelles espèces de* Monodora *et* Isolona *(Annonaceae) de Tanzanie, et aperçu de la diversité des Annonaceae tanzaniennes.*
Quatre nouvelles espèces d'Annonaceae sont décrites et illustrées : *Monodora carolinae*, distribuée dans les forêts côtières de la Tanzanie et au nord du Mozambique, avec les pétales externes réfléchis et les internes connivents par leurs extrémités ; *M. globiflora*, endémique des forêts montagneuses du Udzungwa, à pétales internes totalement connivents et formant un globe au-dessus du réceptacle ; *M. hastipetala*, endémique de la forêt de Kiwengoma (Matumbi Hills), à pétales internes hastés et acuminés au sommet ; et enfin *Isolona linearis*, endémique de la région d'Iringa, avec les lobes de la corolle linéaires. Des clés de détermination sont données pour toutes les espèces de *Monodora* et *Isolona* croissant en Afrique orientale. Une étude palynologique de ces nouvelles espèces est présentée avec une discussion sur l'évolution d'*Isolona*. Un aperçu des Annonaceae de Tanzanie est donné ainsi qu'une liste exhaustive des espèces reconnues pour le pays. Des cartes de distribution aux niveaux spécifique et générique ont été générées grâce à des données rassemblées dans la littérature et des bases de données des herbiers MO et WAG. Les « Eastern Arc » et « Coastal Forests » de la Tanzanie présentent la plus grande concentration d'espèces d'Annonaceae, ce qui souligne une fois encore l'importance de ces régions grandement menacées.

**MOTS CLÉS**
Annonaceae,
*Monodora*,
*Isolona*,
diversité,
pollen,
structure du tectum,
Tanzanie,
espèces nouvelles.

## INTRODUCTION

### The African Annonaceae

Annonaceae is a pantropical family of trees, shrubs, and lianas belonging to the order Magnoliales (APGII 2003). It is the most diverse family of the order, comprising some 130 genera and *c.* 2500 species (Chatrou *et al.* 2004). The combined area of South-East Asia, Australia, and the Pacific islands is the richest in genera and species with *c.* 60 and *c.* 1100 (Kessler 1993), respectively. In terms of genera, tropical Africa and the Neotropics are equivalent (*c.* 40), but the latter holds more species, *c.* 900 compared to *c.* 500 (Mols *et al.* 2004). Similar differences occur within continents, and the reasons for these differences at both the inter- and intra-continental scales are of great interest. However, African Annonaceae are largely understudied, like most of the African flora, which could partly explain the observed lower diversity. Little is known about the diversity of species, the ecology or the pollination of Annonaceae in Africa. In 2003, the Nationaal Herbarium Nederland, Wageningen branch (WAG), initiated a long term project focusing on the systematics of African Annonaceae. African Annonaceae as a whole were treated for the last time over 100 years ago by Engler & Diels (1901). Since then regional accounts have been published in the latter part of the last century such as those of *Flore du Gabon* (Le Thomas 1969) and *Flora of Tropical East Africa* (Verdcourt 1971), or small proportions of African

species have been part of monographic research (e.g., Maas *et al.* 2003).

Because of their pantropical distribution, great diversity, and key ecological role in tropical forests, Annonaceae will provide important insights into the evolution of tropical floras.

### The Eastern Arc Mountains and the Coastal Forests of East Africa

The Eastern Arc Mountains and the Coastal Forests of Kenya and Tanzania are one of the most diverse regions on the planet in terms of both their flora (1500 known endemic species and rising with new discoveries) and fauna (Newmark 2002). Previously considered together as a single biodiversity hotspot (Myers *et al.* 2000; Critical Ecosystem Partnership Fund 2003), they are now part of two distinct hotspots: the Eastern Afromontane Hotspot and the Coastal Forests of Eastern Africa Hotspot (Mittermeier *et al.* 2004).

The Eastern Arc Mountains are a disjunct chain of ancient mountain ranges (*c.* 100 Ma old) situated 40-450 km from the Indian Ocean. They are situated from Southern Kenya (Taita Hills) to south central Tanzania (Udzungwa Mountains) and rise to slightly over 2000 m a.s.l. Rainfall is on average 1000-1500 mm/year with usually two rainy seasons at the northern end and one at the southern end (Lovett 1993b). The Coastal Forests of East Africa are small patches of fragmentary forests not bigger than 370 km$^2$, running down the east coast from southern Somalia to southern Mozambique.

Historically, these forests used to belong to the large pan-African forest (Axelrod & Raven 1978) before the uplifting of the central Tanganyikan plateau at the end of the Oligocene (30 Ma, Clarke & Burgess 2000), which biogeographically separated West and Central Africa from East Africa. This uplift brought a drier and cooler climate to East Africa. However, the Eastern Arc Mountains and the Coastal Forests of East Africa enjoyed a stable humid climate (Lovett 1993a) because of the influence of the Indian Ocean even during Pleistocene climatic oscillations (Lovett 1990).

Annonaceae form an important part of the flora of the Eastern Arc Mountains and Coastal Forests, with 13 species on the 2004 IUCN Red List of Threatened Species (http://www.iucnredlist.org) and 35 described species currently undergoing conservation assessment for possible Red Listing (Gereau & Luke 2003). The description of these four new species in this paper, all considered as potentially threatened by Gereau & Luke (2003), provides a good context for a review of Tanzanian Annonaceae, knowing that the last overview was published 35 years ago (Verdcourt 1971).

### *Monodora* and *Isolona*

The African genus *Monodora* Dunal and the Afro-Malagasy genus *Isolona* Engl. are exceptional within the family because of their truly syncarpous gynoecium, which has in the past resulted in their assignment to their own subfamily (Monodoroideae Kostel.). Recent morphological (Doyle & Le Thomas 1996), palynological (Doyle & Le Thomas 1994, 1997), and molecular phylogenies (Richardson *et al.* 2004) indicated that both genera form a well supported clade nested within the family.

These genera are easily distinguishable with *Isolona* having one whorl of fused petals that are reflexed, spreading horizontally or recurved over the receptacle and the flower colour varying from bright yellow to bronzy red. In contrast, *Monodora* has two whorls each of three conspicuous petals slightly fused at their bases. The outer three petals are usually crisped or undulate and are white to yellow with purple-red streaks. The inner three petals are unguiculate and are sometimes connivent by a network of intricate trichomes or just pressed together over the receptacle to form a pollination chamber.

## MATERIALS AND METHODS

### Specimen data

Since the publication of the *Flora of Tropical East Africa* (FTEA) account (Verdcourt 1971) many new species have been described or collected for Tanzania. In order to account for all the species present in Tanzania, bibliographic sources, as well as the WAG and MO herbarium databases, were used.

Analysis of distribution data of Tanzanian Annonaceae from Verdcourt (1971), the TROPICOS database of the Missouri Botanical Garden

(http://tropicos.org), and the database of Wageningen branch of the National Herbarium of the Netherlands, was undertaken using BRAHMS. The Wageningen database shows some bias, having additional specimens of *Isolona* and *Monodora* entered from additional herbaria (C, COI, EA, FHO, G, P, US, Z), while the Verdcourt (1971) data will introduce a small bias towards older specimens and specimens from different regions (FTEA does not cite all known specimens). These pooled datasets resulted in 797 different Annonaceae collections, of which 785 were georeferenced. Distributional maps were generated using the ArcView 3.3 software (ESRI 2000).

### Pollen material

Pollen material from herbarium specimens was available for all four new species. Pollen samples were prepared in the following way: anthers collected from herbarium material were soaked in three consecutive baths of an organic solvent (Hexane) to clean the surface of the pollen grains of all external structures (lipids and orbicules). They were then gold-coated and examined under a Scanning Electron Microscope (SEM). These palynological results will contribute to the overall revision of both genera. A description of the pollen of *Isolona hexaloba* Engl. & Diels was included in order to compare its tectum structure with that of the Tanzanian specimen.

Pollen has proven very useful for higher level systematics in Annonaceae (Walker 1971; Le Thomas 1980, 1981; Doyle & Le Thomas 1994, 1997). At the infrageneric level few studies have been undertaken, but these few studies have shown that there is variability within genera and that pollen characters have some taxonomic value (Su & Saunders 2003).

## SYSTEMATICS

### Genus *Monodora* Dunal

### *Monodora* in East Africa

At present, *Monodora* comprises 14 species that occur from Sierra Leone to Angola in West and Central Africa, and from southern Somalia to northern South Africa in East Africa. Verdcourt (1971) recognised five species of *Monodora* for East Africa, plus two unnamed species from Tanzania that he called *Monodora* sp. A. and *Monodora* sp. B. More material is now available that permits the description of these two species as new, and one additional one.

The three new species of *Monodora* are all quite characteristic and unique, and are rather difficult to relate to other members of the genus, except maybe by the disposition of the inner petals. The position of the clawed inner petals of *Monodora* seems to play an important role in pollination, allowing or not direct access to the receptacle for the pollinator. Within the genus, three different types can be recognized:

– type 1: blades of inner petals fully connivent by margins (e.g., *M. myristica* (Gaertn.) Dunal; *M. brevipes* Benth.), access limited;

– type 2: blades of inner petals connivent at apex only (e.g., *M. angolensis* Welw.; *M. crispata* Engl. & Diels), access easy by the sides;

– type 3: blades non-connivent but recurved and pressed over the receptacle at the central part (e.g., *M. junodii* Engl. & Diels; *M. zenkeri* Engl.), access by the sides and the top.

In this clasification *M. globiflora* would fit into type 1, *M. carolinae* into type 2 and *M. hastipetala* into type 3. More morphological and molecular studies are in course to see if this character has any phylogenetic significance.

### Key to East African species of *Monodora*

1. Flowers several in an inflorescence ..... *M. minor*
— Flowers solitary ..... 2

2. Pedicel < 5 cm long ..... *M. myristica*
— Pedicel ≥ 5 cm long ..... 3

3. Outer petals straight, not undulate ..... 4
— Outer petals clearly undulate or crisped ..... 5

4. Outer petals less than 2 times as long as wide, obovate to elliptic, shortly pubescent ..... ..... *M. junodii*
— Outer petals at least 5 times as long as wide, linear to lanceolate, glabrous ... *M. stenopetala*

5. Inner petals broadly clawed, the claw at least 2 times as wide as long ..... 6
— Inner petals narrowly clawed, the claw at least 3 times as long as wide ..... 7

6. Leaves with percurrent (parallel) tertiary venation; pedicel pubescent; inner petals pubescent on both surfaces ..... *M. globiflora*
— Leaves with intermediate tertiary venation; pedicel glabrous; inner petals glabrous on outside ..... *M. carolinae*

7. Leaves usually pubescent, cordate at base; outer petals spatulate ..... *M. grandidieri*
— Leaves glabrous, rounded to cuneate at base; outer petals lanceolate to ovate ..... 8

8. Inner petals with lamina long-acuminate at apex, densely pubescent on the inside; outer petals patent ..... *M. hastipetala*
— Inner petals with lamina rounded to acute at apex, glabrous on the inside; outer petals recurved ..... *M. angolensis*

*Fruiting specimens*

1. Peduncle 8 to 25 cm, woody and > 1 cm thick ..... *M. myristica*
— Peduncle short, < 8 cm long and < 0.6 mm thick ..... 2

2. Leaves pubescent ..... 3
— Leaves glabrous ..... 4

3. Leaves with cordate base, tertiary venation intermediate between percurrent (parallel) and reticulate ..... *M. grandidieri*
— Leaves with rounded to cuneate base, tertiary venation percurrent (parallel) ... *M. globiflora*

4. Fruits globose ..... 5
— Fruits conical or ellipsoid ..... 7

5. Peduncle from 6 to 7 cm long ..... *M. minor*
— Peduncle < 6 cm ..... 6

6. Mature fruits ≥ 30 mm, dark blue-black ..... *M. junodii*
— Mature fruits < 30 mm, light brown ..... *M. hastipetala*

7. Fruits ellipsoid, finely rugose ..... *M. stenopetala*
— Fruits conical, irregularly longitudinally ribbed ..... *M. angolensis*

***Monodora carolinae*** Couvreur, sp. nov.
(Fig. 1)

Verdcourt, *Flora of Tropical East Africa*: 122 (1971) as *Monodora* sp. A.

*Haec species inter congeneros quoad flores solitarios, petala externa margine undulata etiam interna unguiculata ad apicem conniventia ad* Monodoram angolensem Welw. *maxime accedit, sed ab ea petalis externis reflexis rectis atque bracteis cupuliformibus distinguitur.*

TYPUS. — **Tanzania.** Pwani Region, Rufiji Distr., Matumbi Hills, Kiwengoma Forest, 08°08'34"S, 38°59'56"E, 18.X.1997, fl., *Phillipson 4940* (holo-, C!; iso-, P!, MO!).

OTHER MATERIAL EXAMINED. — **Tanzania.** Lindi Region, Lindi Rural Distr., Mchinjiri, Rondo Plateau, 10°10'S, 39°15'E, alt. 82 m, XI.1951, fl., *Eggeling 6406* (FHO!, K!, S!).
Pwani (Coast) Region, Rufiji Distr., Kiwengoma Forest, 8°19'06"S, 38°56'54"E, alt. 375 m, 19.X.1997, fl., *Phillipson 4946* (C!, MO!).
**Mozambique.** Cabo Delgado Province, Mueda Plateau, Pt 509, 11°23'S, 39°22'E, alt. 790 m, 12.XII. 2003, fl., *Luke 10054* (EA!, K!, LMA, MO!, NHT).

HABITAT. — Coastal thicket, at 50-800 m altitude, on deep leached sandy soils.

DISTRIBUTION. — Known in coastal Tanzania and northern Mozambique (Fig. 5).

DESCRIPTION
Tree or shrub *c.* 6 m tall; bark grey, striated with white lenticels; young branchlets drying black, glabrous or sometimes sparsely pubescent all over but soon glabrescent. Petiole *c.* 4 mm long, glabrous, with a groove above; leaf blade coriaceous, oblanceolate, 8-10 × 4-6 cm, acuminate at apex, cuneate at base, usually glabrous, sometimes pubescent in younger leaves; midrib prominent below, sunken above; 9 to 11 pairs of secondary veins, anastomosing *c.* 5 mm from the margin; tertiary venation intermediate between percurrent and reticulate.

Flowers solitary and axillary, pendulous, flowering before or during leaf flush; pedicel slender, 15-35 mm long, glabrous; bract inserted in upper half of pedicel, 4-6 × 6-9 mm, auriculate-clasping, acute at apex, cup-shaped, green, glabrous, the margins non-undulate and densely white-ciliate. Sepals triangular, 6-12 × 4-8 mm, rounded at apex, red-brown, the margins entire and densely white-ciliate; outer petals narrowly ovate, reflexed when fully opened, 15-25 × 6-12 mm, acute at apex, undulate, creamy with red spots on both sides, glabrous, sometimes very sparsely ciliate along margins; inner petals clawed, the claw widening into lamina, 3-5 × 2-4 mm at base, cream, the lamina transversely elliptic, 6-15 × 6-14 mm, slightly acuminate at apex, creamy streaked with red and yellow, densely ciliate-manicate around upper margins, the apices connivent over receptacle; stamens *c.* 0.8 mm long, glabrous, the connective appendages *c.* 0.1 mm long; ovary 1-2 mm long with a glabrous stigma.

Fruit unknown.

Pollen: tetrad acalymmate, tetragonal sub-square shaped, monads coherent. Size at longest axis: tetrad, 58-64 µm; monad, 32-48 µm. Tectum structure: psilate, coarsely fossulate-perforate; perforations round to oval, > 0.5 µm in diam. (Fig. 7A, B).

ETYMOLOGY
*Monodora carolinae* Couvreur is named after Carolina, wife of the first author.

## ***Monodora globiflora*** Couvreur, sp. nov. (Fig. 2)

Verdcourt, *Flora of Tropical East Africa*: 123 (1971) as *Monodora* sp. B.

*Haec species inter congeneros quoad flores solitarios, petala externa margine undulata etiam interna unguiculata supra receptaculum omnino conniventia ad* Monodoram brevipedem Benth. *maxime accedit, sed ab ea foliis venatione tertiaria percurrente, pedicello pubescente atque petalis internis utrinque pubescentibus distinguitur.*

TYPUS. — **Tanzania.** Iringa Region, Kilolo Distr., Udzungwa Mountains, 07°42'S, 36°37'E, 13.X.2002, fl., *Luke 9136* (holo-, MO!; iso-, EA!, K!, NHT).

OTHER MATERIAL EXAMINED. — **Tanzania.** Iringa Region, Kilolo Distr., Uhimbila, 7°31'S, 36°10'E, alt. 1850 m, XI.1953, fl., *Carmichael 274* (EA!, K!). — Udzungwa Mountains NP, Mt. Luhomero Pt 131, 7°47'S, 36°33'E, alt. 1440 m, 27.IX.2000, fl., *Luke 6724* (EA!, K!, NHT). — Udzungwa Mountains, Pt 362, 7°40'S, 36°39'E, alt. 1800 m, 15.X.2002, fl., *Luke 9178* (EA!, K!, MO!, NHT). — Ndundulu, Udzungwa Mountains, West of Kilombero F. R., 7°46'46"S, 36°28'26"E, alt. 1700 m, 10.II.2000, fr., *Price WK354* (MO!). — Image Mt., 7°30'S, 36°10'E, alt. 2000 m, XI.1959, fl., *Procter 1541* (EA!, K!).

HABITAT. — Sparse high montane forest, at 1700-2000 m altitude, on well drained brown sandy loams with extensive areas of rock faces.

DISTRIBUTION. — Only known from montane forests of the Udzungwa Mountains, Tanzania (Fig. 5).

DESCRIPTION
Tree *c.* 4 m tall; bark grey with white lenticels; young branchlets drying black, densely pubescent. Petiole *c.* 8 mm long, pubescent, with a groove above; leaf

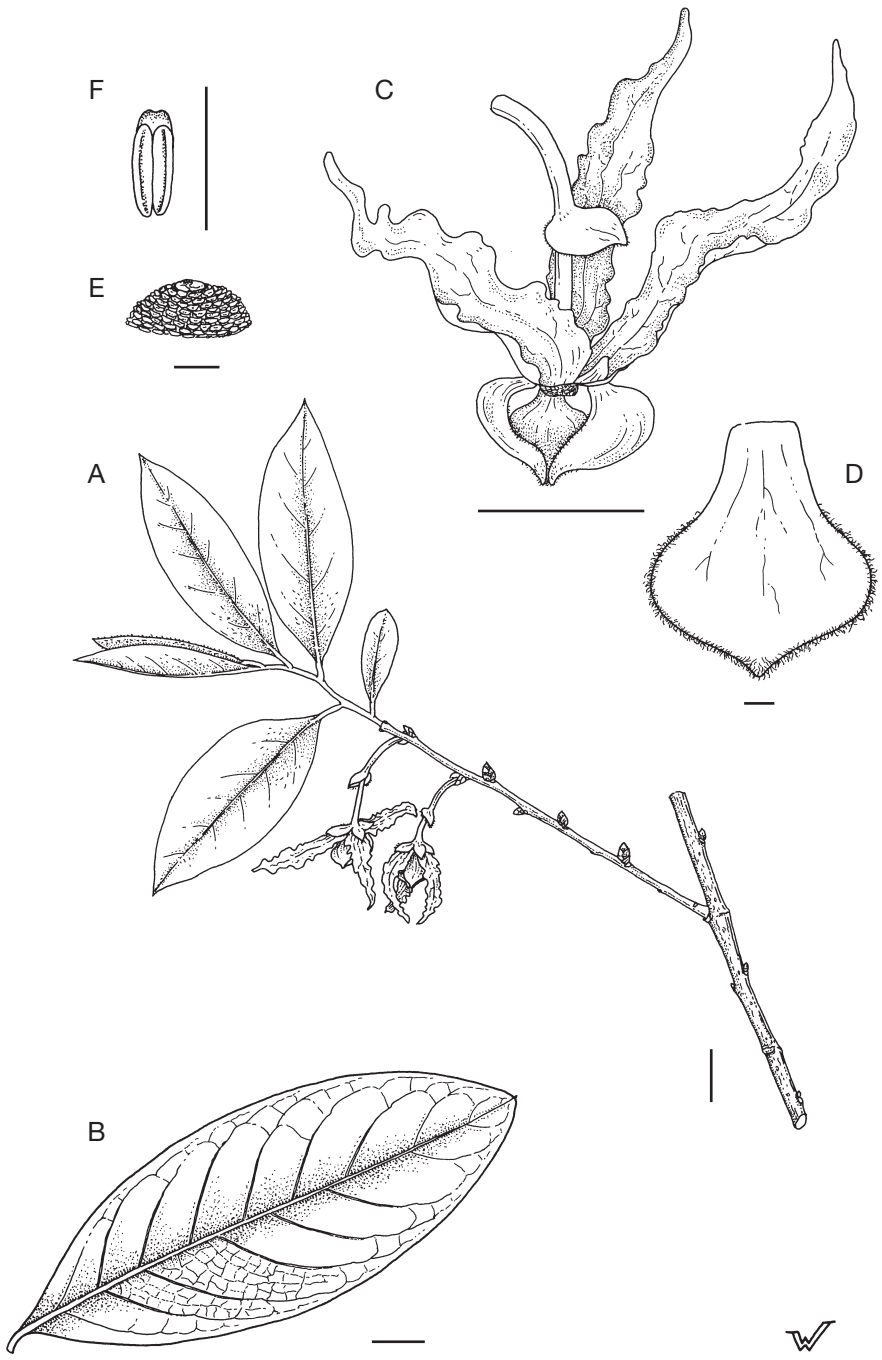


FIG. 1. — *Monodora carolinae* Couvreur: **A**, flowering branch; **B**, leaf; **C**, mature flower; **D**, detail of inner petal (inside view); **E**, androecium and gynoecium (stigma missing); **F**, stamen. Drawing by Wil Wessel-Brand. Scale bars: A-C, 1 cm; D-F, 1 mm.

blade elliptic, sometimes obovate, papyraceous, 12-13 × 4-5 cm, acute to cuspidate at apex, cuneate to rounded at base, pubescent below, glabrous above; younger leaves more densely pubescent than older ones; midrib densely pubescent on both sides with pubescence disappearing in older leaves, prominent below, raised above; secondary veins 14 to 16 pairs, strongly curved and regularly parallel, anastomosing 3-4 mm from the margin; tertiary nerves percurrent.

Flowers solitary and axillary, pendulous, flowering on previous year's branches; pedicel slender, in flower 40-45 mm long, pubescent; in fruit woody, black with white lenticels *c.* 40 mm long, 3-4 mm in diam., glabrous; bract inserted in lower half of pedicel, rounded, cup-shaped, *c.* 8 × *c.* 7 mm, auriculate-clasping, green, the margins non-undulate and very densely white-ciliate. Sepals broadly elliptic, 8-10 mm long, 6-8 mm wide, rounded at apex, the margins entire and densely white-ciliate; outer petals slightly reflexed and curved inwards at apex when fully opened, elliptic, 28-32 × 18-23 mm, cuneate apex, creamy yellow streaked with red slashes and spots or sometimes light green streaked with darkish green, undulate, glabrous; inner petals clawed, same colour as outer petals, the claw widening gradually into lamina, 3-5 × 2-4 mm at base, the lamina broadly transversely elliptic, 7-8 × 10-12 mm, slightly acuminate at apex, pubescent with trichomes *c.* 1 mm long in center, manicate along the margins, the whole lamina connivent over receptacle like a globe; stamens *c.* 0.8 mm long, glabrous, the connective appendages *c.* 0.1 mm long; ovary *c.* 1 mm long with a glabrous stigma.

Fruit irregularly globose, 4-5 cm in diam., glabrous, irregularly ribbed, the pericarp thin, white, green-reticulate; seeds *c.* 15 mm long, *c.* 7 mm wide, oval, embedded in white pulp.

Pollen: tetrad acalymmate, tetragonal sub-square shaped monads coherent. Size at longest axis: tetrad, 63-76 µm; monad, 39-45 µm. Tectum structure: reticulate-perforate (Fig. 7C, D).

VERNACULAR NAME

Mkimi (Kihehe).

NOTES

The species has been photographed by Mr Quentin Luke. The specimen *Luke 9178* has green to yellow flowers with white streaks, while *Luke 9136* has yellow petals with red streaks. This indicates some variation in colour that needs further investigation in the field.

***Monodora hastipetala*** Couvreur, sp. nov.
(Fig. 3)

*Haec species inter congeneros quoad folia glabra ad basin rotundata cuneatave, flores solitarios, petala externa elliptica usque ovata margine undulata etiam interna ungue longiore quam latiore ad* Monodoram angolensem Welw. *maxime accedit, sed ab ea petalis internis hastatis lamina longiacuminata intus ad basin dense pubescente trichomatibus c. 1 mm longis distinguitur.*

TYPUS. — **Tanzania.** Pwani Region, Rufiji Distr., Matumbi Hills, Kiwengoma Forest, 19.X.1997, fl., 08°19'01"S, 38°57'07"E, *Phillipson 4958* (holo-, MO!).

OTHER MATERIAL EXAMINED. — **Tanzania.** Pwani (Coast) Region, Rufiji Distr., northern edge of the Matumbi Highlands, Kiwengoma Forest, 8°21'S, 38°51'E, alt. 365 m, 20.XI.1989, fl., *Frontier-Tanzania 22* (C!, MO!). — Matumbi Hills, Kiwengoma Forest, 8°19.0'S, 38°57.1'E, 8.VI.1997, fr., *P. B. Phillipson 4803* (MO!).

HABITAT. — Dry scrub and riverine coastal forest, at 225-365 m altitude.

DISTRIBUTION. — Only known from the Kiwengoma forest (Matumbi Hills) in Tanzania (Fig. 5).

DESCRIPTION

Tree to 8 m tall; bark grey with white lenticels; young branchlets drying black, glabrous. Petiole *c.* 2 mm long, glabrous, with a groove above; leaf blade spatulate to narrowly obovate, sometimes narrowly elliptic, papyraceous, 10-12 × 3-4 cm, acuminate at apex, cuneate to rounded at base, glabrous; midrib prominent below, raised above; secondary veins 10 to 14 pairs, strongly curved, anastomosing *c.* 4 mm from margin; tertiary veins intermediate between percurrent and reticulate.

Flowers solitary and axillary, pendulous, flowering on new branches; pedicel slender, in flower 17-20 mm long, in fruit *c.* 20 mm long, robust, glabrous; bract inserted in upper half of pedicel, rounded, cup-shaped, 5-9 × 3-5 mm, auriculate-clasping, pale green, glabrous, the margins non-undulate. Sepals elliptic, 6-7 × 3-4 mm, rounded at apex, glabrous,

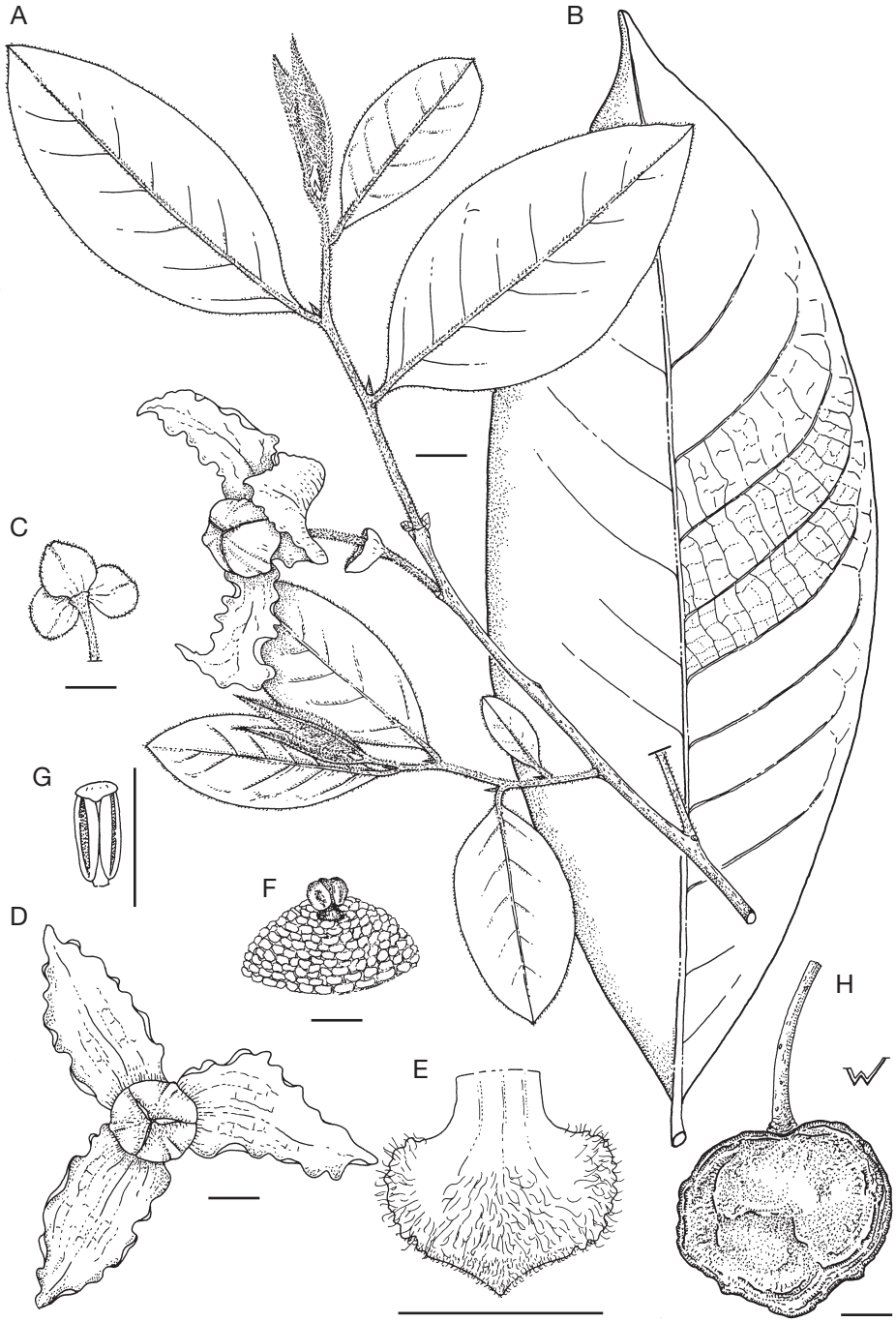


FIG. 2. — *Monodora globiflora* Couvreur: **A**, flowering branch; **B**, leaf; **C**, pedicel with sepals; **D**, mature flower (top view); **E**, detail of inner petal (inside view); **F**, androecium and gynoecium; **G**, stamen; **H**, fruiting pedicel and fruit. Drawing by Wil Wessel-Brand. Scale bars: A, C-E, H, 1 cm; F, G, 1 mm.

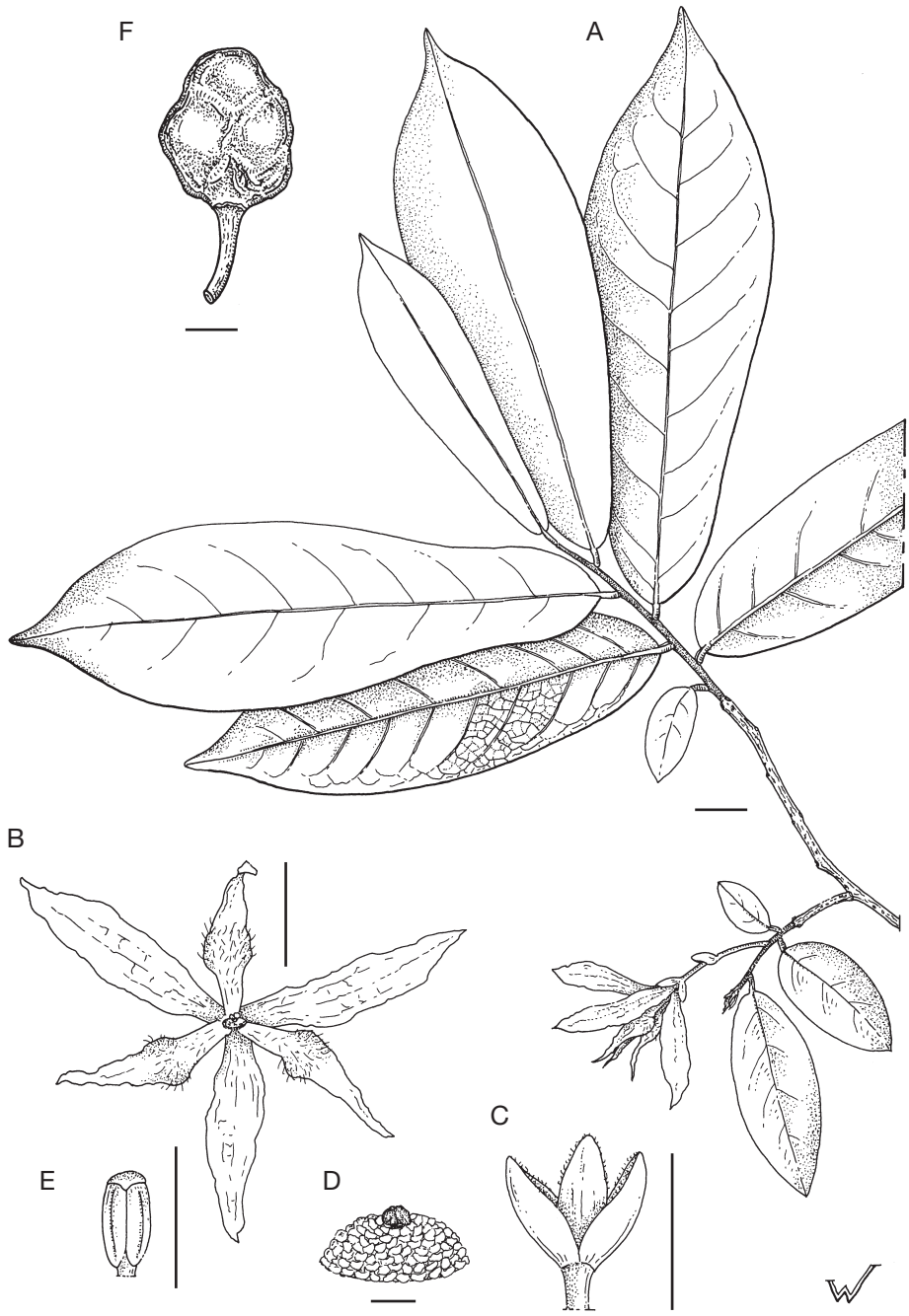


FIG. 3. — *Monodora hastipetala* Couvreur: **A**, flowering branch; **B**, mature flower (top view), outer petals opened; **C**, pedicel with sepals; **D**, androecium and gynoecium; **E**, stamen; **F**, fruiting pedicel and fruit. Drawing by Wil Wessel-Brand. Scale bars: A-C, F, 1 cm; D, E, 1 mm.

the margins entire; outer petals held horizontally when fully opened, narrowly elliptic, 20-26 × 6-8 mm, cuneate at apex, undulate, glabrous, white; inner petals clawed, white to pale green, tinged purple, the claw 4-5 mm long, *c.* 1 mm wide, the lamina narrowly ovate, 10-17 × 4-7 mm, connivent by the center over receptacle, long-cuneate at apex, densely pubescent with trichomes *c.* 1 mm long inside at base, less pubescent on outer side; stamens 40 to 50, *c.* 0.6 mm long, glabrous, the connective appendages *c.* 0.1 mm long; ovary *c.* 1 mm long with a glabrous stigma.

Fruit nearly ovoid, 30 mm long, *c.* 20 mm in diam., bumpy and irregularly ribbed when dried; seeds *c.* 10 mm long, *c.* 7 mm wide, smooth, light brown.

Pollen: tetrad acalymmate, tetragonal sub-square shaped, monads coherent. Size at longest axis: Tetrad: 50-57 µm; monad: 21-33 µm. Tectum structure: smooth, rugulate-perforate. Perforations rounded to oval > 0.2 µm. More coarsely rugulate than in *M. carolinae* (Fig. 7E, F).

VERNACULAR NAME

Nnjende (Kimatumbi).

NOTES

This species has a very restricted distribution and has characteristic flowers.

## Genus *Isolona* Engl.

*ISOLONA* IN EAST AFRICA

*Isolona* comprises 21 species occurring from Sierra Leone to northern Angola, and from Kenya to northern Mozambique. Five species are endemic to the eastern and northern coast of Madagascar. In East Africa, Verdcourt (1971) recognized three species, plus one unidentified specimen: *Schlieben 1539* referred to as *Isolona* sp. A. He indicated that it could be a glabrous variant of *Isolona heinsenii* Engl. & Diels. Based on more collections by Polhill and Lovett, Verdcourt (1986) identified the specimens as *Isolona hexaloba*, a very polymorphic West African species (Le Thomas 1969). Verdcourt specified however that fruiting material must be found in order to confirm its status. More collections have been made since, with fruiting material and photographs now available. On the basis of floral morphology, fruits, tectum structure, and ecology, we are now able to describe these collections as a new species. However, *Schlieben 1539* from the Mahenge Mountains is excluded from it and identified as a glabrous variant of *I. heinsenii* as speculated by Verdcourt (1971), a species already known from that area.

*Isolona* species are always confined to humid regions across Africa and Madagascar, and are mainly present in the moist montane forests of Tanzania.

KEY TO THE EAST AFRICAN SPECIES OF *ISOLONA*

1. Flowers growing on *c.* 2 m long shoots running from base of trunk; fruits conical and warty, to 6 cm long ..... *I. cauliflora*
— Flowers on branches and axillary ..... 2

2. Leaves narrowly elliptic; densely red-tomentose ..... *I. congolana*
— Leaves elliptic to ovate; glabrous or pubescent ..... 3

3. Sepals lanceolate, 5-6 mm long; corolla lobes recurved over receptacle; fruits fusiform, clearly 6-ribbed in fresh material ..... *I. heinsenii*
— Sepals triangular, 2-3 mm long; corolla lobes spreading horizontally; fruits irregularly elliptic, with caudate apex ..... *I. linearis*

***Isolona linearis*** Couvreur, sp. nov.
(Fig. 4)

*Haec species inter congeneros quoad folia glabra, flores axillares etiam lobulos corollinos horizontaliter patentes ad* Isolonam hexalobam (Pierre) Engl. & Diels *maxime accedit, sed ab ea sepalis triangularibus 2-3 mm longis atque lobulis corollinis anguste lanceolatis usque linearibus distinguitur.*

TYPUS. — **Tanzania.** Iringa Region, Mufindi Distr., Luhega Forest Reserve, 08°21'S, 35°58'E, 20.I.1997, fl., *Frimodt-Møller TZ 59* (holo-, C!; iso-, K!).

HABITAT. — Moist montane forest, at 1100-1700 m altitude.

DISTRIBUTION. — Only known from Iringa Region in Tanzania (Fig. 6).

OTHER MATERIAL EXAMINED. — **Tanzania.** Iringa Region, Mufindi Distr., Lulanda Forest, 8°30'S, 35°30'E, alt. 1450 m, 6.XII.1987, fl., *Congdon s.n.* (P!). — Mufindi Distr., Lulanda Forest Reserve, 8°36'S, 35°37'E, alt. 1650 m, 16.II.1979, fl., *Cribb 11470* (K!). — Luhega Forest Reserve, Mufindi Distr., 8°21'S, 35°58'E, alt. 1650 m, 18.II.1996, fl., *Frimodt-Møller 5* (C!, K!). — *Idem*, 8.II.1996, fl., *Frimodt-Møller 12* (C!). — *Idem*, 21.II.1996, ster., *Frimodt-Møller 64* (C!). — *Idem*, 21.II.1996, ster., *Frimodt-Møller 66* (C!). — Udzungwa Scarp Forest Reserve, Mufindi Distr., 8°23'S, 35°25'E, alt. 1550-1700 m, 18.XII.1997, fr., *Frimodt-Møller 679* (C!). — Udzungwa Scarp Forest Reserve, Mufindi Distr., 8°23'S, 35°25'E, alt. 1550-1700 m, 18.II.1997, fl., *Horlyck 325* (C!, K!). — *Idem*, 20.II.1997, fl., *Horlyck 359* (C!). — Kilolo Distr., Ridge above Sanje Falls, 7°46'S, 36°54'E, alt. 1150 m, 24.VII.1983, fl., *Polhill 5143* (EA!, K!, MO!). — Mufindi Distr., Lulanda, 8°36'S, 35°37'E, alt. 1500 m, 24.XI.1998, fl., *Gereau 2552* (MO!, NY!). — *Idem*, 25.I.1989, ster., *Gereau 2882* (MO!, P!). — Mufindi Distr., Lulanda Forest, isolated patch of closed high forest on Uzungwa escarpment, 8°40'S, 35°35'E, alt. 1430 m, 6.IX.1986, fl., *Lovett 592* (MO!). — Kilolo Distr., Mwanihana F. R. above Sanje Village, moist forest on edge of Gologolo Mountains overlooking the Kilombero flood plain, 7°45'S, 36°55'E, alt. 1250 m, 17.VI.1986, fl., *Lovett 861* (MO!). — Kilolo Distr., Udzungwa Mountains National Park, Mt. Luhomero, 7°47'S, 36°49'E, alt. 1200 m, 23.IX.2001, fl., *Luke 7732* (EA!). — Kilolo Distr., Mwanihana Forest Reserve above Sanje Village, 7°50'S, 36°55'E, alt. 1400-1700 m, 10.X.1984, ster., *Thomas 3899* (MO!).
No location indicated, alt. 1650 m, 23.II.1996, fl., *Mikkelsen 384* (K!).

DESCRIPTION

Tree to 15 m tall; bark dark brown to black, smooth; young branchlets glabrous, smooth. Petiole 4-5 mm long, 1.0-1.5 mm in diam., glabrous, verrucose; leaf blade obovate to elliptic, 14-18(-25) × 5-7(-9) cm, coriaceous, short- to long-acuminate at apex, rounded to cuneate at base, glabrous; midrib prominent below; secondary veins 11 to 13 pairs, anastomosing 2-3 mm from margin; tertiary venation intermediate between percurrent and reticulate.

Flowers axillary and pendulous, solitary; pedicel in flower (3-)5-10 mm long, in fruit 10-15 mm long, glabrous; bracts 3, inserted at base of pedicel, *c.* 1 mm, the margins ciliate. Sepals triangular, 2-3 × *c.* 3 mm, acute at apex, usually persistent in fruit, the margins white-ciliate; corolla cupulate, glabrous, pale red, verrucose when dried, with tube 4-5 mm long, the lobes patent, 10-30 × 3-4(-8) mm, lanceolate to linear, sometimes elliptic, rounded at apex, narrowed at base, fleshy, greenish, sparsely ciliate when very young, glabrous and bronzy-red when mature; stamens flat, glabrous, *c.* 1.1 mm long, the connective appendages *c.* 0.1 mm long; gynoecium 0.2 mm long topped by glabrous stigma.

Fruit *c.* 5 cm long, 2-3 cm in diam., irregularly elliptic, with caudate apex *c.* 1 cm long, furrowed, green tinged with white; seeds 10-15 mm long, smooth, light brown.

Pollen: monad, apolar, globose. Size at longest axis: monad, 35-40 µm. Tectum structure: rugulate, coarse (Fig. 7G, H).

VERNACULAR NAMES

Mulinditi (Kihehe).

NOTES

*Isolona* is very variable in floral characters. Flowers seem to continue growth after anthesis and before abscission, resulting in considerable polymorphism. *Isolona linearis* and *I. hexaloba* are both very polymorphic. The shape and size of the corolla lobes in *I. linearis* vary, with the predominant shape being linear. One other striking feature is that some flowers of various specimens of *I. linearis* have five corolla lobes instead of six, which could indicate a tendency towards pentamery. This tendency is also observed in *I. campanulata* Engl. & Diels (Adam 1971).

## DISCUSSION

### *MONODORA* AND *ISOLONA* IN TANZANIA

*Monodora* is the fourth most diverse genus of Annonaceae in Tanzania (eight species, Table 1) and

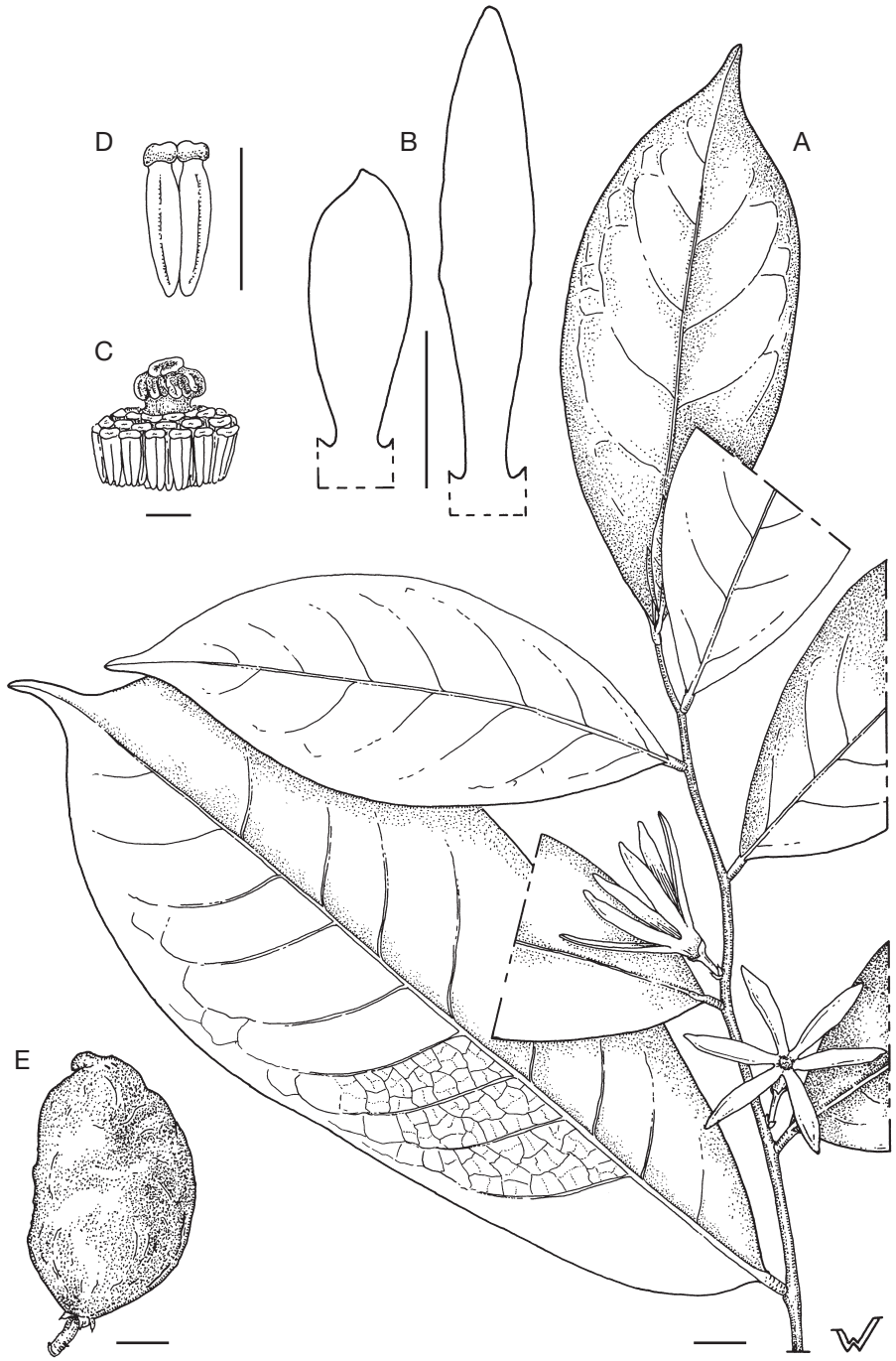


FIG. 4. — *Isolona linearis* Couvreur: **A**, flowering branch; **B**, lobe variation within *I. linearis*; **C**, androecium and gynoecium; **D**, stamen; **E**, fruit. Drawing by Wil Wessel-Brand. Scale bars: A, B, E, 1 cm; C, D, 1 mm.

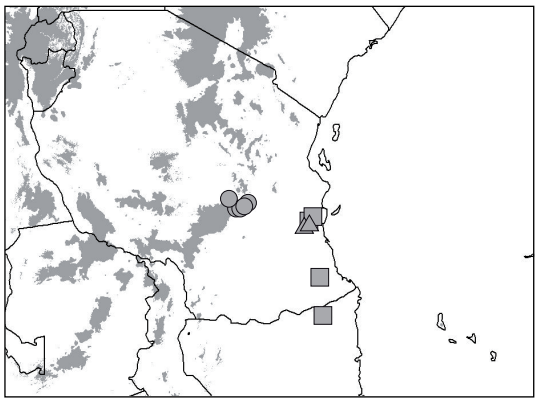

FIG. 5. — Distribution of the new species of *Monodora* in Tanzania and Mozambique. Symbols: grey patches, land above 1400 m; ■, *M. carolinae* Couvreur; ●, *M. globiflora* Couvreur; ▲, *M. hastipetala* Couvreur.

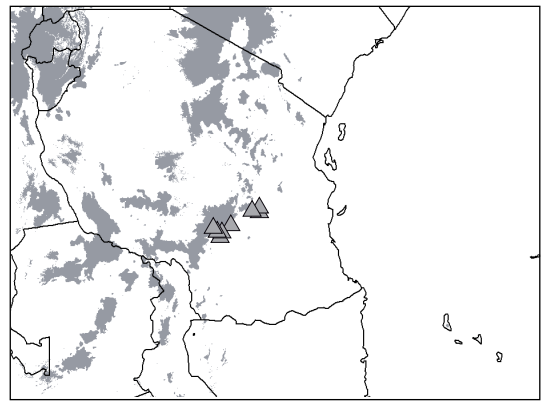

FIG. 6. — Distribution of *Isolona linearis* Couvreur (▲). Grey patches, land above 1400 m.

has a widespread distribution in eastern Africa, from southern Somalia to northern South Africa, as well as in Malawi, Zambia and Zimbabwe. On the other hand, *Isolona* is less well represented in Tanzania (three species, Table 1) and presents a more restricted distribution in East Africa, present in Uganda (one species), Kenya and Tanzania. However, *Isolona* has five endemic species in Madagascar (Cavaco & Keraudren 1958), where *Monodora* is absent.

The only species of either genus shared between the Guineo-Congolian block and East Africa are *Monodora angolensis* and *M. myristica.* These species are widely distributed in western central Africa, extending east into Uganda and were recorded for the extreme western part of Tanzania in Kigoma Rural District (*M. angolensis*, *c.* 150 km SE of Kigoma, *Y.S. Abeid 1419, 1427*, *J. Kahurananga 2623*) and Bukoba Regional District (*M. myristica*, Kiamawa, *Gillman 408*). Brenan (1978) considered the forests of Uganda as an impoverished extension of the rain forest of the Democratic Republic of Congo. The presence of *M. angolensis* and *M. myristica* in Tanzania may likewise be considered an extension of their ranges from the Congolian forest. Therefore, there seems to be a clear distinction between the Guineo-Congolian forest bloc and the eastern mountains and coastal forest fragments of East Africa in terms of species composition of these two genera.

All three species of *Isolona* present in Tanzania are endemic or near-endemic to the country, as are three of the eight species of *Monodora*. All six occur in the Eastern Arcs and/or in the Coastal Forests as listed below:

– *Isolona cauliflora* Verdc., present in the lowlands adjacent to the East Usambara Mountains (north-eastern Tanzania) and the Shimba Hills of south-eastern Kenya;

– *Isolona heinsenii* Engl., present from the East Usambara Mountains (north-eastern Tanzania) south to the Mahenge Mountains in south central Tanzania and Kiwengoma Forest of the Matumbi Hills, and has an IUCN status of "endangered";

– *Isolona linearis* (described here), restricted to the Udzungwa Mountains in south-central Tanzania;

– *Monodora hastipetala* (described here), only found in Kiwengoma Forest of the Matumbi hills;

– *Monodora globiflora* (described here), only found in the Udzungwa Mountains and Image Mountain, both in south-central Tanzania;

– *Monodora carolinae* (described here), a near-endemic to Tanzania and found in Kiwengoma Forest, the Rondo Plateau and with one record from the Mueda Plateau in north-eastern Mozambique.

The cited localities are well known to contain high numbers of endemics from different families (e.g., Rondo Forest has 60 endemic species and two endemic genera; East Usambaras with 17 endemic

TABLE 1. — List of genera and species of Annonaceae recorded for Tanzania. Symbols: *, endemic to Tanzania; **, near-endemic to Tanzania; ***, naturalised; #, monotypic genus; **WA**, West and Central Africa; **M**, Madagascar; **AA**, Australasia; **N**, Neotropics. Notes: **1**, *Flora of Tropical East Africa*; **2**, *Xylopia latipetala* Verdc. is considered as a taxonomic synonym of *X. collina* Diels (D. M. Johnson pers. comm.); **3**, *X. parviflora* Spruce (1861) is a validly published name for a South American species and causes *X. parviflora* (A.Rich.) Benth. (1862) to be an illegitimate later homonym. As indicated in Lebrun & Stork 1991, *X. longipetala* De Wild. & T. Durand (1899) is probably the oldest legitimate name for the African species long known as *X. parviflora* (A.Rich.) Benth.

| Genus | no. of species | Species | Source | Distribution |
|---|---|---|---|---|
| *Annickia* | 1 | | | WA |
| | | *A. kummerae* (Engl. & Diels) Setten & Maas | Setten & Maas 1990 | |
| *Annona* | 2 | | | WA, N |
| | | *A. stenophylla* Engl. & Diels subspp. *stenophylla* and *longipetiolata* (R.E.Fr.) N.Robson | Verdcourt 1971[1] | |
| | | *A. senegalensis* Pers. subspp. *oulotricha* Le Thomas and *senegalensis* | *Lovett & Thomas 2870* (MO); Verdcourt 1971[1] | |
| *Anonidium* | 1 | | | WA |
| | | *A. usambarense* R.E.Fr. | Verdcourt 1971[1] | |
| *Artabotrys* | 7 | | | WA, M, AA |
| | | *A. brachypetalus* Benth. | Verdcourt 1971[1] | |
| | | *A. collinus* Hutch. | Verdcourt 1971[1] | |
| | | *A. modestus* Diels var. *modestus* and *macranthus* Verdc. | Verdcourt 1971[1] | |
| | | *A. monteiroae* Oliv. | Verdcourt 1971[1] | |
| | | *A. rupestris* Diels | Verdcourt 1971[1] | |
| | | *A. stolzii* Diels | Verdcourt 1971[1] | |
| | | *A. velutinus* Scott-Elliot | Verdcourt 1971[1] | |
| *Asteranthe*** | 2 | | | |
| | | *A. asterias* (S.Moore) Engl. & Diels subspp. *asterias* and *triangularis* Verdc. | Verdcourt 1971[1] | |
| | | *A. lutea* Vollesen | Vollesen 1980 | |
| *Cananga**** | 1 | | | AA |
| | | *C. odorata* (Lam.) Hook.f. & Thomson | Verdcourt 1971[1] | |
| *Cleistochlamys*# | 1 | | | |
| | | *C. kirkii* (Benth.) Oliv. | Verdcourt 1971[1] | |
| *Dielsiothamnus*# | 1 | | | |
| | | *D. divaricatus* (Diels) R.E.Fr. | Verdcourt 1971[1] | |
| *Friesodielsia* | 1 | | | WA, AA |
| | | *F. obovata* (Benth.) Verdc. | Verdcourt 1971[1] | |
| *Greenwayodendron* | 1 | | | WA |
| | | *G. suaveolens* (Engl. & Diels) Verdc. subsp. *usambaricum* Verdc. | Verdcourt 1971[1] | |
| *Hexalobus* | 1 | | | WA, M |
| | | *H. monopetalus* (A.Rich.) Engl. & Diels var. *obovatus* Brenan | Verdcourt 1971[1] | |
| *Isolona* | 3 | | | WA, M |
| | | *I. cauliflora* Verdc. | Verdcourt 1971[1] | |
| | | *I. heinsenii* Engl. & Diels | Verdcourt 1971[1] | |
| | | *I. linearis* Couvreur | described here | |
| *Lettowianthus*** # | 1 | | | |
| | | *L. stellatus* Diels | Verdcourt 1971[1] | |
| *Mkilua*** # | 1 | | | |
| | | *M. fragrans* Verdc. | Verdcourt 1971[1] | |
| *Monanthotaxis* | 13 | | | WA, M |
| | | *M. buchananii* (Engl.) Verdc. | Verdcourt 1971[1] | |
| | | *M. dictyoneura* (Diels) Verdc. | Verdcourt 1971[1] | |

| Genus | no. of species | Species | Source | Distribution |
|---|---|---|---|---|
| | | *M. discolor* (Diels) Verdc. | Verdcourt 1971[1] | |
| | | *M. discrepantinervia* Verdc. | Verdcourt 1986 | |
| | | *M. faulknerae* Verdc. | Verdcourt 1971[1] | |
| | | *M. ferruginea* (Oliv.) Verdc. | Verdcourt 1971[1] | |
| | | *M. fornicata* (Baill.) Verdc. | Verdcourt 1971[1] | |
| | | *M. littoralis* (Bagsh. & Baker f.) Verdc. | *Kayombo 3118* (MO) | |
| | | *M. parvifolia* (Oliv.) Verdc. subsp. *parvifolia* | Vollesen pers. comm. | |
| | | *M. poggei* Engl. & Diels | Verdcourt 1971[1] | |
| | | *M. schweinfurthii* (Engl. & Diels) Verdc. var. *schweinfurthii* | Verdcourt 1971[1] | |
| | | *M. trichantha* (Diels) Verdc. | Verdcourt 1971[1] | |
| | | *M. trichocarpa* (Engl. & Diels) Verdc. | Verdcourt 1971[1] | |
| *Monodora* | 8 | | | WA |
| | | *M. angolensis* Welw. | Verdcourt 1971[1] | |
| | | *M. carolinae* Couvreur | described here | |
| | | *M. globiflora* Couvreur | described here | |
| | | *M. grandidieri* Baill. | Verdcourt 1971[1] | |
| | | *M. junodii* Engl. & Diels | Verdcourt 1971[1] | |
| | | *M. hastipetala* Couvreur | described here | |
| | | *M. minor* Engl. & Diels | Verdcourt 1971[1] | |
| | | *M. myristica* (Gaertn.) Dunal | Verdcourt 1971[1] | |
| *Ophrypetalum*** # | 1 | | | |
| | | *O. odoratum* Diels subspp. *odoratum* and *longipedicellatum* Verdc. | Verdcourt 1971[1] | |
| *Polyalthia* | 3 | | | AA, M |
| | | *P. stuhlmannii* (Engl.) Verdc. | Verdcourt 1971[1] | |
| | | *P. tanganyikensis* Vollesen | Vollesen 1980 | |
| | | *P. verdcourtii* Vollesen | Vollesen 1980 | |
| *Polyceratocarpus* | 1 | | | WA |
| | | *P. scheffleri* Engl. & Diels | Verdcourt 1971[1] | |
| *Sanrafaelia** # | 1 | | | |
| | | *S. ruffonammari* Verdc. | Verdcourt 1996 | |
| *Sphaerocoryne* | 1 | | | AA |
| | | *S. gracilis* (Engl. & Diels) Verdc. subsp. *gracilis* | Verdcourt 1986 | |
| *Toussaintia* | 2 | | | WA |
| | | *T. orientalis* Verdc. | Verdcourt 1971[1] | |
| | | *T. patriciae* Q.Luke & Deroin | Deroin & Luke 2005 | |
| *Uvaria* | 15 | | | WA, M, AA |
| | | *U. acuminata* Oliv. | Verdcourt 1971[1] | |
| | | *U. angolensis* Welw. ex Oliv. | Verdcourt 1971[1] | |
| | | *U. decidua* Diels | Verdcourt 1971[1] | |
| | | *U. dependens* Engl. & Diels | Verdcourt 1971[1] | |
| | | *U. faulknerae* Verdc. | Verdcourt 1971[1] | |
| | | *U. kirkii* Oliv. ex Hook.f. | Verdcourt 1971[1] | |
| | | *U. leptocladon* Oliv. subsp. *leptocladon* | Verdcourt 1984 | |
| | | *U. lucida* Bojer ex Benth. subspp. *lucida* and *virens* (N.E.Br.) Verdc. | Verdcourt 1971[1] | |
| | | *U. lungonyana* Vollesen | Vollesen 1980 | |
| | | *U. pandensis* Verdc. | Verdcourt & Mwasumbi 1988 | |
| | | *U. puguensis* D.M.Johnson | Johnson *et al.* 1999 | |
| | | *U. scheffleri* Diels | Verdcourt 1971[1] | |
| | | *U. schweinfurthii* Engl. & Diels | *Mbago 1373* (MO) | |
| | | *U. tanzaniae* Verdc. | Verdcourt 1986 | |
| | | *U. welwitschii* (Hiern) Engl. & Diels | Verdcourt 1971[1] | |
| *Uvariastrum* | 1 | | | WA |
| | | *U. hexaloboides* (R.E.Fr.) R.E.Fr. | Verdcourt 1971[1] | |

| Genus | no. of species | Species | Source | Distribution |
|---|---|---|---|---|
| *Uvariodendron* | 5 | | | WA |
| | | *U. gorgonis* Verdc. | Verdcourt 1971[1] | |
| | | *U. kirkii* Verdc. | Verdcourt 1971[1] | |
| | | *U. oligocarpum* Verdc. | Verdcourt 1986 | |
| | | *U. pycnophyllum* (Diels) R.E.Fr. | Verdcourt 1971[1] | |
| | | *U. usambarense* R.E.Fr. | Verdcourt 1971[1] | |
| *Uvariopsis* | 1 | | | WA |
| | | *U. bisexualis* Verdc. | Verdcourt 1986 | |
| *Xylopia* | 7 | | | WA, M, AA, N |
| | | *X. aethiopica* (Dunal) A.Rich. | Verdcourt 1971[1] | |
| | | *X. arenaria* Engl. | Verdcourt 1971[1] | |
| | | *X. collina* Diels[2] | Verdcourt 1971[1] | |
| | | *X. longipetala* De Wild. & T.Durand[3] | Lebrun & Stork 1991 | |
| | | *X. mwasumbii* D.M.Johnson | Johnson *et al.* 1999 | |
| | | *X. odoratissima* Welw. ex Oliv. | Verdcourt 1971[1] | |
| | | *X. rubescens* Oliv. | Verdcourt 1971[1] | |

species and one endemic genus; Clarke *et al.* 2000). It is clear that these endemics have small distributional ranges in Tanzania, often restricted to a single forest or mountain range (e.g., *Monodora hastipetala* and *Isolona linearis*). This is in agreement with Brenan (1978), who indicated that eastern African endemics have smaller distributions than western ones. The presence of *M. carolinae* in northern Mozambique follows the prediction of Clarke *et al.* (2000) that endemics from Tanzania and Kenya "will be found to extend into northern Mozambique".

## Pollen

In Annonaceae, the exine is composed of three different layers: the tectum, the infratectum, and the basal layer. Within Annonaceae three different types of infratectum structure are recognized: granular, columellar, and intermediate (Le Thomas 1980, 1981). In *Isolona*, *Monodora* and some other African genera, the intermediate type exists, with granules radially elongated and sometimes resembling the shape of columellae. Although we have not examined the infratectum of *I. linearis* by Transmission Electronic Microscopy (TEM), we can however speculate on the evolutionary tendency within *Isolona* knowing that "exine ornamentation is a function of infratectal structure" (Le Thomas 1980: 308) and that Le Thomas (1980, 1981) defines the columellar structure as derived within Annonaceae compared to the granular structure.

Adding to the different morphological characters observed, the differences between *I. hexaloba* and *I. linearis* are also visible in the tectum layer. *I. hexaloba* presents a verrucose tectum with many perforations (Fig. 7I, J), which is in accordance with the studies by Le Thomas & Lugardon (1976: 553). They also noted that the infratectum layer of *I. hexaloba* is composed of large granules, with the outer ones fusing and binding into a mass constituting a thin tectum. The inner layer is quite disorganised but there is a clear tendency of granules to aggregate forming columellae-like structures. *Isolona linearis* on the other hand (Fig. 7G, H) presents a rugulate tectum structure more uniform than that of *I. hexaloba*, with very small perforations (microperforations). This tectum structure indicates that the infratectum is likely composed of granules aggregating into more or less clear columellar structures. Le Thomas & Lugardon (1976) analysed one more species of *Isolona*: *I. thonneri* (De Wild. & T. Durand) Engl. & Diels. The infratectum of this species is composed of large granules situated with no apparent order, showing a very verruculose surface with hardly any tectum. We thus go from a disorganised granular structure with hardly any tectum (*I. thonneri*) passing through an intermediate structure (*I. hexaloba*) to an organisation of the granules into columellae-like structures with the presence of a tectum (*I. linearis*). It would therefore seem that there is a tendency within *Isolona* for

granules to aggregate into some kind of "columellar" derived form leading to the reconstitution of the tectum, strengthening the conclusion reached by Le Thomas & Lugardon (1976). *Isolona linearis* thus appears more derived than either *I. hexaloba* or *I. thonneri*. This would however have to be confirmed with more palynological data of the other species and with molecular data too.

More palynological data and a molecular phylogeny are necessary in order to elucidate the evolutionary trends within *Monodora*.

### Annonaceae diversity in Tanzania

The known species of Annonaceae in Tanzania are given in Table 1. In total 83 species in 27 genera are recognized. Since the *Flora of Tropical East Africa* publication in 1971, 15 species (17%) were added, and one genus was discovered that was new to the region (*Uvariopsis bisexualis* Verdc.). Three genera (*Uvaria* L., *Monanthotaxis* Baill., *Xylopia* L.) make up just over 43% of the total species diversity.

*Sanrafaelia* Verdc. (Verdcourt 1996) is endemic to the lowland forests adjacent to the East Usambara Mountains in north-eastern Tanzania. Moreover, there are five near-endemic genera occurring in Tanzania: *Asteranthe* Engl. & Diels (two species), *Dielsiothamnus* R.E.Fr., *Lettowianthus* Diels, *Mkilua* Verdc., and *Ophrypetalum* Diels, found in coastal Tanzania (including the islands of Zanzibar and Pemba) and in southern Kenya. However, the coastal flora of Kenya is regarded merely as an extension of the coastal element extending to southern Tanzania (Brenan 1978). It is interesting to note that at family level, the Annonaceae contain the highest number of endemic genera in the Coastal Forests. Rubiaceae, for example, a much more diverse family at the species level, has only four endemic genera in the Coastal Forests (Clarke *et al.* 2000: table 4.1.1). In Tanzania five genera are monotypic (Table 1), with four of them endemic or near-endemic to the Coastal Forests and the Eastern Arc. *Dielsiothamnus* is the only monotypic genus with a more southern distribution, just reaching into Tanzania.

The distributional analysis reveals that Annonaceae are found in most parts of Tanzania (Figs 8; 9), but are apparently absent or extremely rare in the driest parts of the country (e.g., Shinyanga Region in the North and Ruvuma Region in the South). In Tanzania, high Annonaceae species diversity is also usually correlated with high generic diversity, as shown by the similarity between Figures 8 and 9. Species are more abundant and diverse in the lowland evergreen forests of approximately the eastern third of the country, although they extend into moist montane forest and relatively dry deciduous woodlands. By far the greatest diversity of genera and species occurs at elevations from sea level to just under 1000 m throughout the Eastern Arc Mountains and the Coastal Forests. However, species of the genus *Artabotrys* R.Br. ex Ker Gawl. occur at elevations of over 2000 m in both the Rubeho Mountains of the Eastern Arc (*A. rupestris* Diels) and in drier montane forests near Lake Tanganyika (*A. monteiroae* Oliv.). Species of *Artabotrys*, *Isolona*, *Monanthotaxis*, *Monodora*, *Polyceratocarpus* Engl. & Diels, *Uvaria*, and *Uvariodendron* (Engl. & Diels) R.E.Fr. occur sporadically at elevations of 1500-2000 m in montane forests in the Eastern Arc, the Southern Highlands, and the Lake Tanganyika forests. The lowland forests adjacent to the Usambara Mountains are very rich at both genus and species levels. *Sanrafaelia* can only be found in that zone. The relatively dry woodlands of the southern Coastal Forests in Lindi Region have significant species-level diversity (Figs 8; 9) and some endemic species: e.g., *Polyalthia tanganyikensis* Vollesen, *Uvaria decidua* Diels, and *Uvaria lunyongana* Vollesen. In the driest Annonaceae habitats of central Tanzania (e.g., Singida and Tabora Regions) diversity is very low and is confined to a very few widespread species (e.g., *Friesodielsia obovata* (Benth.) Verdc., *Annona senegalensis* Pers., and *Xylopia odoratissima* Oliv.).

### Affinities of Tanzanian Annonaceae with other regions

At the generic level, Tanzanian Annonaceae present strong links with the Guineo-Congolian region, with 17 genera (63%) shared between the two (Table 1). However, very few species are shared between the two regions, suggesting that Tanzanian Annonaceae genera are relictual lineages from a formerly pan-African distribution that were isolated in Eastern Arc or Coastal Forests during the Miocene as a result of climate change. This link was also suggested by

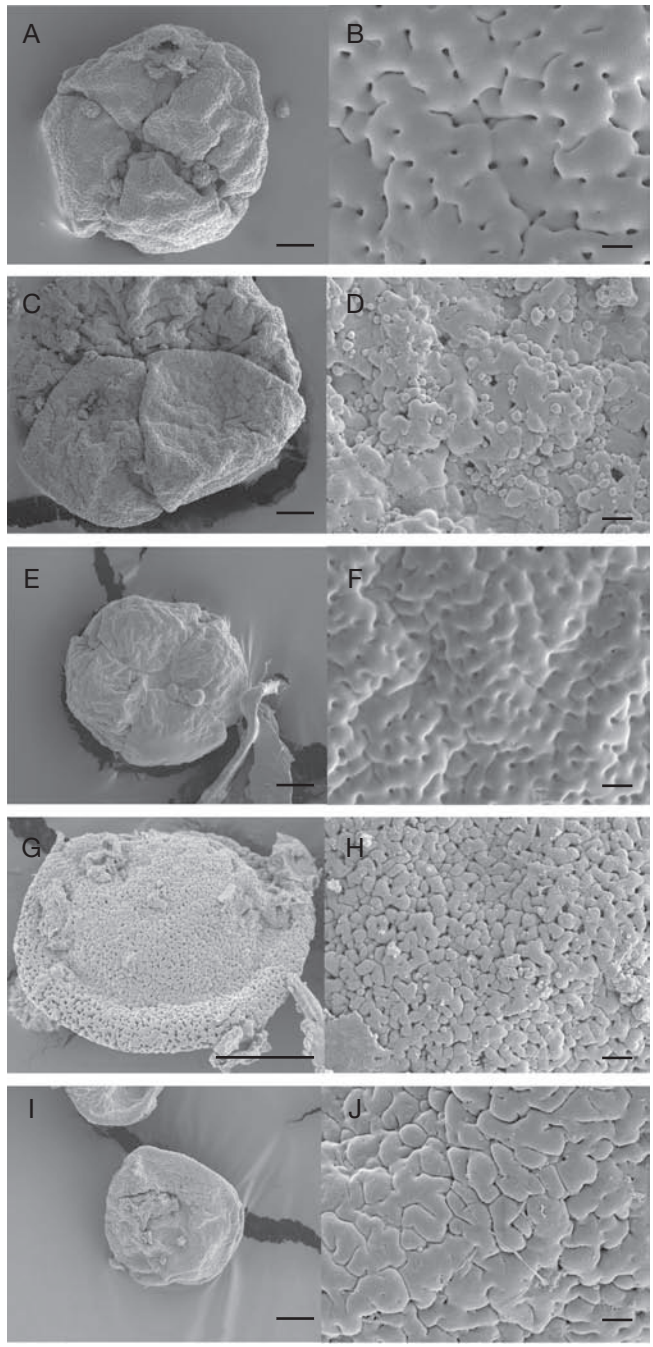


FIG. 7. — SEM of pollen grains and tectum structure: **A**, **B**, *Monodora carolinae* Couvreur; **C**, **D**, *M. globiflora* Couvreur; **E**, **F**, *M. hastipetala* Couvreur; **G**, **H**, *Isolona hexaloba* Engl. & Diels from Ivory Coast; **I**, **J**, *Isolona linearis* Couvreur. A, B, *Phillipson 4940* (C); C, D, *Luke 3136* (MO); E, F, *Phillipson 4958* (MO); G, H, *de Wilde et al. 839* (WALKB, WAG); I, J, *Frimodt-Møller et al. TZ59* (C). Scale bars: A, C, E, G, I, 10 µm; B, D, F, H, J, 1 µm.

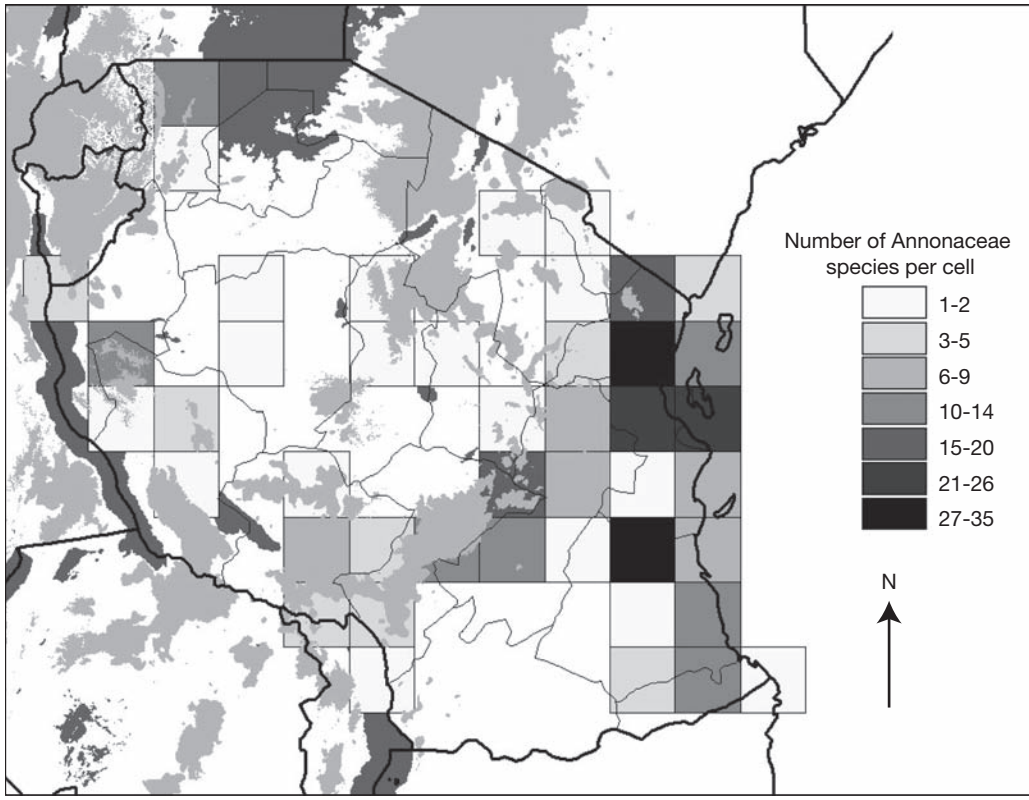


FIG. 8. — Map of diversity of Annonaceae species in Tanzania. Regional administrative boundaries are indicated. Symbols: light grey patches, land above 1400 m; dark grey patches, water.

Lovett (2000) and Clarke *et al.* (2000) based on distributional analyses of tree genera.

All genera found in Madagascar are also present in Eastern Africa (26% of the Tanzanian genera), except for the single genus endemic to Madagascar: *Ambavia* Le Thomas (Le Thomas 1972). However, no species are shared between the two regions (Leroy 1978). Disjunct distributions of genera between East Africa and Madagascar could be due to vicariance after the breakup of Gondwana (Leroy 1978) or long-range dispersal (Clarke *et al.* 2000; Lovett 1993b). The recent fossil-dated molecular phylogeny of Annonaceae (Richardson *et al.* 2004) estimated that the family diverged from its closest relatives in the mid Cretaceous (*c.* 82-91 Ma), after the split between Africa and Madagascar (165 to 121 Ma; Griffiths 1993), which would eliminate the vicariance hypothesis. Long-range dispersal in plants (Givnish & Renner 2004; Renner 2004) was suspected in some taxa based on the fact that they either shared species or had easily dispersed fruits (e.g., via birds or wind). Little research has been carried out on fruit dispersal in Annonaceae but it is likely that none of these taxa have propagules suitable for dispersal over great expanses of ocean. For example, fruits in *Isolona* are large and seeds are embedded in pulp, and it is likely that they would be dispersed by mammals (e.g., monkeys or elephants). This kind of dispersal is unlikely to explain the presence of *Isolona* in Madagascar via long-range dispersal. Although long distance dispersal is unlikely and its mechanism is unknown, it seems that it has occurred at least once in Annonaceae between Africa and Madagascar.

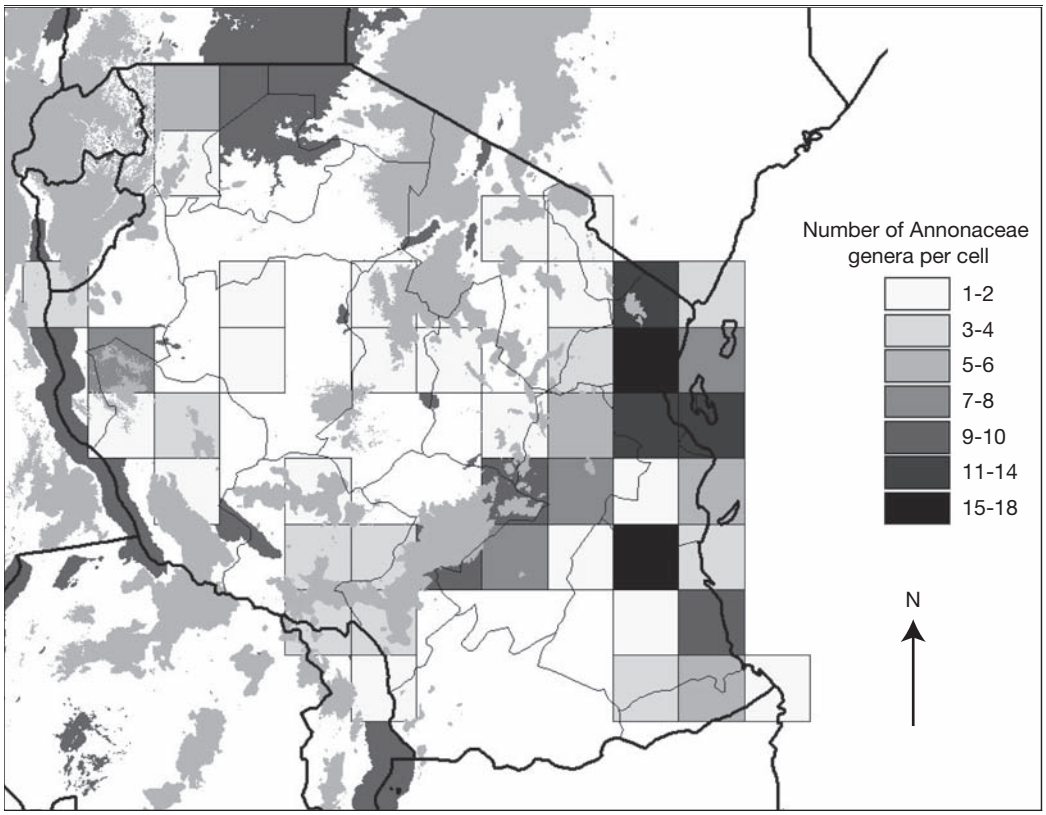


FIG. 9. — Map of diversity of Annonaceae genera in Tanzania. Regional administrative boundaries are indicated. Symbols: light grey patches, land above 1400 m; dark grey patches, water.

Tanzanian Annonaceae also show a slight affinity with South East Asia with five genera occurring in both regions (Table 1): *Xylopia* which is a pantropical genus; *Uvaria* and *Artabotrys* R.Br. also present in West-Central Africa; and two genera with a strict East African/South-East Asian affinity: *Sphaerocoryne* (Boerl.) Scheff. ex Ridl. with *c.* 10 species (five in South-East Asia; four in Madagascar and one in Africa) and *Polyalthia* Blume with *c.* 150 species. *Sphaerocoryne gracilis* (Engl. & Diels) Verdc. is represented by *S. gracilis* subsp. *engleriana* (Exell & Mendonça) Verdc. in central and south-central Africa, and by subsp. *gracilis* in East Africa. *Polyalthia* is much in need of a revision as it is highly polyphyletic in the molecular phylogeny of Mols *et al.* (2004). The relationship between the East African *Polyalthia* taxa with the South-East Asian ones is not clear as only one East African species (*P. stuhlmannii* (Engl.) Verdc.) out of three was sampled. However, *P. stuhlmannii* does form a monophyletic group with one species sampled from Madagascar (*P. pendula* Capuron ex G.E.Schatz & Le Thomas).

## CONCLUSION

Most of the Annonaceae biodiversity of Tanzania is confined to the Eastern Arcs and Coastal forests, stressing once again the importance of the biodiversity of these regions. Many endemics can be found at the species level (e.g., in *Monodora* and *Isolona*) as well as at the genus level in those two regions. It is however uncertain whether these endemics

are neoendemics or paleoendemics, i.e. whether these two regions act as centers for generating new species or sustaining old species that have disappeared elsewhere. One hypothesis speculates that the Eastern Arc mountains would have acted as centers of diversification while the lowland Coastal Forests acted as centers of accumulation of old species (Fjeldsa & Lovett 1997; Burgess *et al.* 1998). A better understanding of these processes for the Eastern Arc Mountains and the Coastal Forests is vital for the better conservation management of these extremely important regions.

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