

# Passion and combat on a floral stage: a new species of *Uvariopsis* (Annonaceae) from Monts de Cristal, Gabon, with notes on its unique pollination ecology

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## Abstract

**Background and aims** – Gabon is a major centre of biodiversity. We describe a new species from the tropical plant family Annonaceae: *Uvariopsis niangadoumae* sp. nov., known from a single population in the Monts de Cristal National Park.

**Material and methods** – Field work was conducted to collect plant specimens and observe floral visitors. Pollen samples were collected and prepared for microscopic analysis. The phylogenetic tree of *Uvariopsis* was reconstructed using a maximum likelihood method and based on hundreds of nuclear markers. Pollination biology was studied using a DIY camera trap (PICT) placed near a female flower to record floral visitors and their behaviour for one full day. Several flower visitors were collected and identified using DNA barcoding.

**Key results** – *Uvariopsis niangadoumae* is a tree reaching five metres tall, characterized by strong-scented leaves, few-flowered cauliflorous foul-smelling flowers, and large pollen grains shed in tetrads. The species is endemic to a small area within the Monts de Cristal National Park. Phylogenetic analysis places *U. niangadoumae* within the “large-leaved clade” species complex with now five taxa. Pollination is diurnal, and the primary pollinator is a rove beetle (Staphylinidae), which uses the female flowers as a mating site, with males fighting for control of the flower. The rove beetles might be attracted by a chemical cue, the foul scent of the flowers, and visual cues, with the inner part of the petals resembling mushrooms.

**Conclusion** – These results emphasize once again the importance of the Monts de Cristal National Park for biodiversity and highlight conservation concerns for the newly described species. The new species is monitored regularly, especially for fruiting individuals, to support ex situ propagation. The Kinguéle Aval project maintains a conservation nursery with 56 species, including 20 individuals of this new species.

## Keywords

camera trap, hydrological dam, IUCN conservation, plant-insect interactions, saprocanthrophily, Staphylinidae

## INTRODUCTION

Gabon is a centre of plant diversity across Africa (Sosef et al. 2006, 2017; Texier et al. 2022). Lowland rain forests are the main biome covering over 85% of the country. Botanical exploration has been ongoing for several decades, and a major feat is the near complete (end 2025) treatment of all plant families within the Flore du Gabon series (Marc Sosef pers. comm.). The Monts de Cristal National Park in north west Gabon is a major hotspot of plant diversity. New species are regularly discovered even today, making this region one of the most in need of continued exploration (Lachenaud et al. 2018; Mogue Kamga et al. 2018). Annonaceae is a cosmopolitan tropical family of trees and lianas typical of lowland rain forests represented to date by 108 genera and 2,500 species worldwide (Nge et al. 2024). In Gabon, the family as a whole was revised by Le Thomas (1969) and since then a number of taxonomic revisions have been undertaken on African Annonaceae. For example, a new genus of Annonaceae, *Sirdavidia* Couvreur & Sauquet, was described from Monts de Cristal (Couvreur et al. 2015). Gabon is also an important centre of endemism for Annonaceae, with 36 species only known from Gabon and which represented an excess of diversity when compared to other Central African countries rich in plant biodiversity (Texier et al. 2022). In comparison, Cameroon is reported to have 22 endemic species of Annonaceae (Couvreur et al. 2022).

The tree genus *Uvariopsis* Engl. (tribe Monodoreae, subtribe Uvariopsidinae, Nge et al. 2024) is unusual in African Annonaceae in having flowers with two sepals (vs three normally) and one whorl of four petals (vs two whorls of three petals) (Dagallier et al. 2023). The plants are also monoecious with separate male and female flowers occurring on the same individuals, except for the Tanzanian species *U. bisexualis* Verdc. which has flowers containing both male and female parts (Verdcourt 1986). In Monts de Cristal, a new species was recently described (Couvreur and Niangadouma 2016): *Uvariopsis citrata* Couvreur & Niang., which has lemon scented leaves, a rare characteristic for Annonaceae (Dagallier et al. 2023). The genus *Uvariopsis* was subsequently revised resulting in 17 currently accepted species (Dagallier et al. 2023). The pollination ecology of three *Uvariopsis* species has been studied (Gottsberger et al. 2011; Mertens et al. 2018), as briefly reviewed in Dagallier et al. (2023). The flowers, mainly cauliflorous, generally have thick, dark red petals and release pungent (rotten) scents. Several studies and photographs document flies visiting the flowers in *U. bakeriana* (Hutch. & Dalziel) Robyns & Ghesq. and *U. pedunculosa* (Diels) Robyns & Ghesq. (Gottsberger et al. 2011; Mertens et al. 2018).

Here, we describe another new species of *Uvariopsis* and preliminary document the unique pollination biology of this species using camera trap surveys.

## MATERIAL AND METHODS

### Study site

A field trip was undertaken to the Monts de Cristal National Park in Gabon during the first two weeks of November 2023. We visited the rain forests near the Kinguéle hydraulic station, a highly visited spot in the region for botanists.

### Pollen

We sampled pollen from male flowers at full anthesis and conserved them in 70% alcohol in the field. Pollen was prepared following the Couvreur et al. (2024) protocol using a hexane washing method. Individual pollen grains were viewed, photographed, and measured using a Zeiss Axio light microscope.

### Phylogenomic analysis

We inferred the phylogenetic position of the new species by reconstructing the phylogenomic relationships within the genus *Uvariopsis*. We extracted the DNA of the new species following the protocol of Soulé et al. (2023). A hybrid sequence capture approach was used to sequence nuclear markers: the Annonaceae specific baiting kit (Couvreur et al. 2019), which targets 469 Annonaceae specific exonic regions, and the universal Angiosperms 353 bait kit (Johnson et al. 2018). Libraries and hybridization protocols followed Soulé et al. (2024). We downloaded already available paired fastq sequence data (Dagallier et al. 2023) of all other *Uvariopsis* species except one (*U. dicaprio* Cheek & Gosline) from GenBank SRA under Bioproject number PRJNA508895 (<https://dataview.ncbi.nlm.nih.gov/object/PRJNA508895>). *Xylopia hypolampra* Mildbr., *Monodora myristica* (Gaertn.) Dunal, *Dennettia tripetala* Baker f., *Monocylanthus vignei* Keay, and three species of the genus *Uvariodendron* (Engl. & Diels) R.E.Fr. were selected as outgroups based on prior results (Dagallier et al. 2023; Nge et al. 2024) and were also downloaded from Bioproject number PRJNA508895.

Using the newly generated data and the downloaded sequences, we used Hybpiper v.2 (Johnson et al. 2016) to process paired reads and retrieve cleaned alignments. Paralogs identified by Hybpiper were discarded from downstream analyses. We filtered remaining supercontigs to select only those that were present in 75% of specimens for over 75% of their length (Couvreur et al. 2019; Helmstetter et al. 2024). Based on the concatenated alignments, we reconstructed the phylogenetic tree of *Uvariopsis* under a maximum likelihood method using RAxML “HPC-PTHREADS” (Stamatakis 2014) under a GTRGAMMA model and 100 bootstrap replicates to estimate branch support.

## Pollination biology

Preliminary information about the pollination biology of the new species was summarised from observations recorded using one PIC camera (Droissart et al. 2021). The camera was placed at ca 5 cm from one female flower at anthesis (emitting a scent) growing on the main trunk, about 50 cm from the ground. We filmed continuously for 30 hours: from 10 am (day 1) to 4 pm the next day (day 2). Recordings were reviewed and all animals that touched the flower were documented. We noted two types of behaviour: 1) touching: animals touching the reproductive organs (carpels); 2) visiting: animals only moving along the non-reproductive parts of the flower (petals) but never touching the reproductive parts. We also recorded the behaviour of the large Staphylinidae (see results) when they visited, fought, and mated. We were not able to film a male flower, but surveyed and photographed one flower at anthesis.

After video recordings, flower visitors were collected, stored in 96% ethanol, and sent to the Centre de Biologie pour la Gestion des Populations (CBGP, Montpellier, France) for identification. Each sample was pre-sorted to morphospecies and a leg of one specimen per morphospecies was taken for molecular identification (DNA barcoding). For details on DNA extraction, amplification, sequencing, and post-sequencing treatment, see protocol used in Nève de Mévergnies et al. (2024).

## RESULTS

### Taxonomic treatment

*Uvariopsis niangadoumae* Couvreur & Dagallier, **sp. nov.**

urn:lsid:ipni.org:names:77367847-1

WFO: wfo-1000077776

Figs 1–3

**Type.** GABON – Estuaire • Monts de Cristal National Park, ca 6 km before Kingué, in forest located ca 500 m after concrete sign indicating the entrance to the park towards Kingué, then 500 m along the Sobéa river after passing clearing for high tension cables on the west of the road; 00°25.297'N, 10°15.447'E; 90 m; 12 Nov. 2023; fl., fr.; Couvreur T.L.P. & Niangadouma R. 1803; holotype: WAG!; isotypes: LBV!, MPU!, P!.

**Diagnosis.** *Uvariopsis niangadoumae* resembles *U. korupensis* in the shape and dimensions of its leaves and the overall size of the flowers. It differs by having strong scented leaves versus no clear scent in *U. korupensis*. Furthermore, *U. niangadoumae* bears no more than two, few-flowered inflorescences on small protrusions at the base of the trunk, whereas in *U. korupensis* the base of the trunk is densely covered with inflorescences. Flowers of *U. niangadoumae* have free petals with a length:width ratio between 1.3 and 1.7 vs fused at base and a l:w

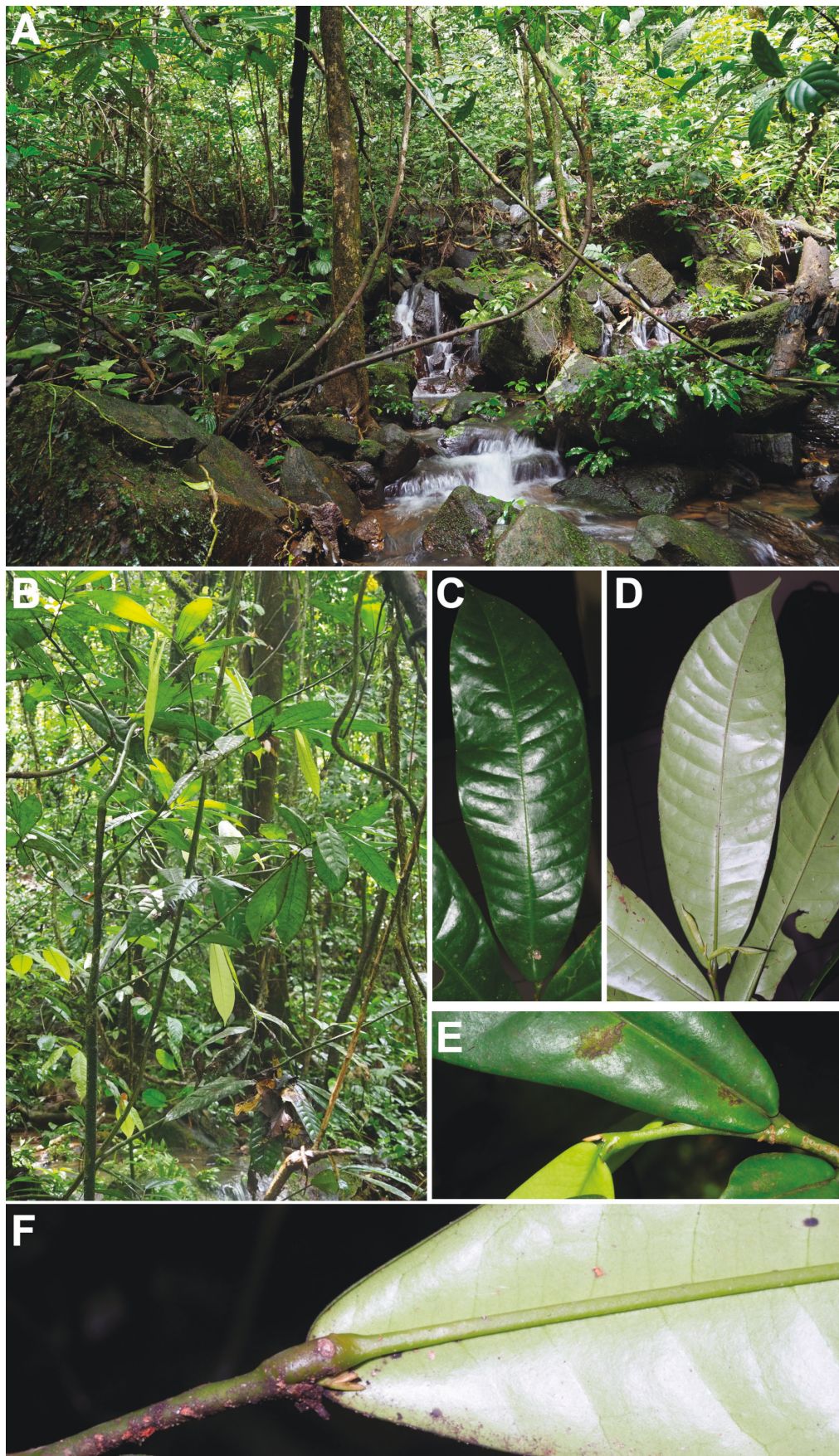
ratio between 2.2 and 7 in *U. korupensis*. *Uvariopsis niangadoumae* also has fewer carpels than *U. korupensis* (20–25 vs 25–120).

**Description.** Tree up to 5 m tall, up to 9 cm in diameter at breast height, multi-branched, old branches grey, striate, glabrous; very young branches light green, pubescent; slash light cream with a black ring. Leaves alternate; petiole 3–4 mm long, 4 mm in diameter, glabrous, leaf blade inserted on top; lamina 33–36 cm × 9–10 cm wide, length/width ratio 3.6 to 3.8, elliptic, acuminate, acumen ca 2 cm long, base narrowly cordate, glabrous on both sides, emitting a strong scent with similarities to both mint and thyme, young laminae light green pending; secondary veins 17 to 19, brochidodromous, arching 0.5 to 1 cm from margin, tertiary veins reticulate, slightly visible above and below. Inflorescences cauliflorous at the base up to 1 m high on the main trunk, on small protuberances. Flowers functionally unisexual, monoecious, but with more female flowers than male per individual stem; flower buds conical; male and female flowers similar, but female flowers larger and more robust; female flowering pedicels up to 4 cm long, ca 4 mm in diameter, sparsely covered with hairs less than 1 mm long, one bract present at base of pedicel, 0.5 mm long and wide, soon falling; male flowering pedicel 2 cm long, 2 mm in diameter, glabrous or with sparse hairs less than 1 mm long, bracts not seen, probably soon falling. Female flowers sepals 2, ca 1 × 4 mm wide, orbicular, acuminate, glabrous, green to dark green, slightly reflexed; petals 4, in the same whorl, ca 2 × 1.5 cm wide, ca 5 mm thick, triangular, apex acute, base truncate, outer surface with raised central vein and a network of smaller veins, glabrous with ciliate margins, hairs less than 0.5 mm, pink reddish in vivo, inside surface heavily warty, glabrous, cream to pink in vivo. Floral receptacle ca 1 cm wide, slightly convex. Carpels 20 to 25, 5 mm long, 3 mm in diameter, cream, covered in hairs less than 0.5 mm long, cream; stigma sessile less than 0.5 mm long, glabrous, cream; ovules biseriate. Some female flowers with sterile stamens at the base forming 2 to 10 whorls. Male flowers sepals 2, minute, glabrous; petals 4, sometimes flowers with three petals but rare, ca 1.5 × 0.9 cm wide, ca 3 mm thick, triangular, apex acute, base truncate, free, outer and inner surfaces like female flowers, pink reddish outside in vivo, cream to pink inside in vivo. Receptacle 5 mm in diameter, strongly concave; stamens ca 400, less than 0.5 mm long, cream to light yellow in vivo. Fruiting pedicel ca 3–4 cm long, 2 mm in diameter, sparsely pubescent, green. Young monocarps light green, older monocarps darker green, monocarps 1 to 3, ca 4 cm long (3 cm when dried), 2 cm in diameter (1.5 cm when dried), surface smooth, glabrous; immature seeds biseriate, 5 per side. Hilum and raphe not seen.

**Distribution.** Endemic to Gabon, Monts de Cristal National Park.

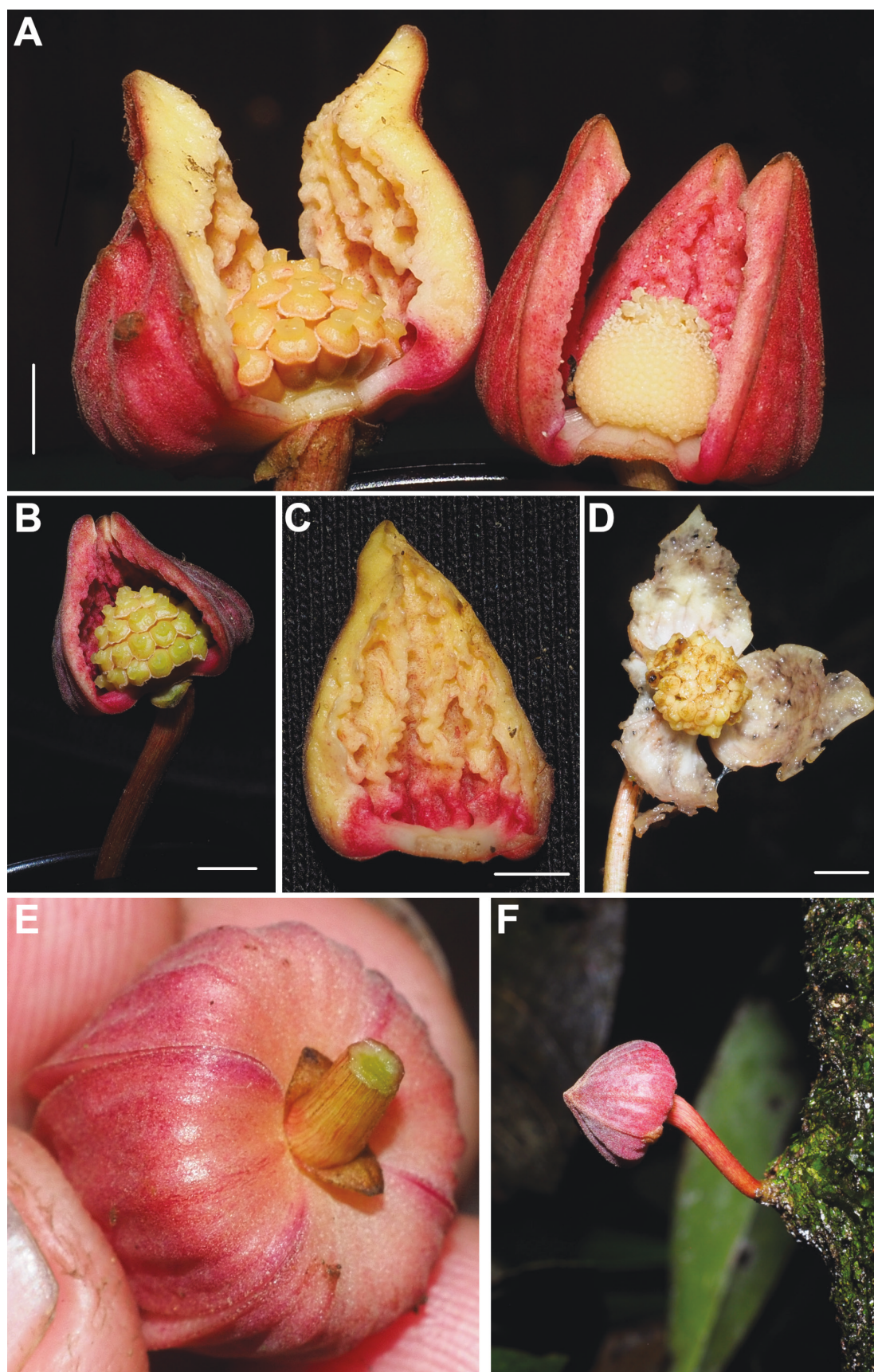
**Habitat and ecology.** *Uvariopsis niangadoumae* occurs on rocky soil on a slope at the base of a hill and along a stream, leading to a larger river. To date, it is only known from a single locality. We prospected the area extensively over





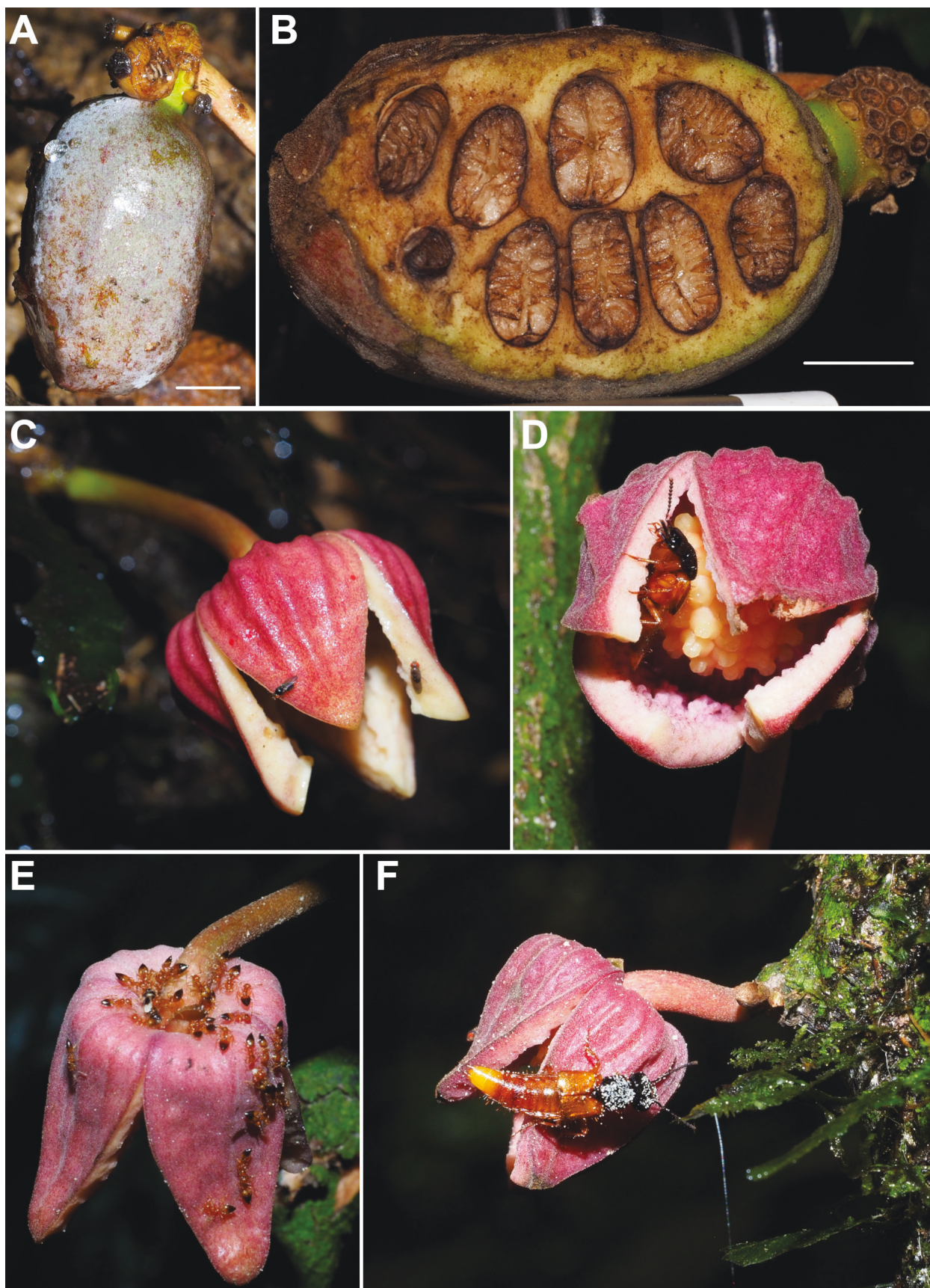
**Figure 1.** *Uvariopsis niangadoumae*, natural habit and vegetative characters. A. Habitat along a small stream. B. General view. C. Young leaves, light green, dropping. D. Detail of adaxial side of leaf base. E. Detail of abaxial side of leaf base. From Couvreur 1803. Photos by Thomas L.P. Couvreur.





**Figure 2.** *Uvariopsis niangadoumae*, detail of male and female flowers. A. Detail of inner side of female (left) and male (right) flowers, one petal removed. B. Detail of female flower, one petal removed. C. Detail of inner side of one female petal. D. Old female flower. E. Detail of sepals on male flower. F. Young male flower, not at anthesis yet. From *Couvreur 1803*. Photos by Thomas L.P. Couvreur. Scale bars: A–D = 0.5 cm.





**Figure 3.** *Uvariopsis niangadoumae*, detail of fruits and flower visitors. **A.** One monocarp. **B.** Longitudinal section of a single monocarp showing the seeds. **C.** Male flower with small Diptera visitors. **D.** Female flower with one large Staphylinidae beetle. **F.** Upper side of male flower covered with *Crematogaster* sp. ants. **F.** Male flower with large Staphylinidae beetle emerging covered in pollen. From *Couvreur 1803*. Photos by Thomas L.P. Couvreur. Scale bars: A, B = 1 cm.



three visits. It appears to occur within an area of about 40 × 20 m (ca 800 m<sup>2</sup>). We saw about 100 individuals, most of them in flower or fruit at the time of the survey. The taller individuals were generally located towards the base of the hill near the Sobéa river (an affluent of the larger Mbé river).

**Phenology.** Flowering in October and November. Fruits seen in November.

**Etymology.** This species is dedicated to the Gabonese botanist Raoul Niangadouma who participated in the (long and arduous) botanical inventories that led to the official recognition of the Monts de Cristal National Park. Raoul Niangadouma is also one of the collectors of the type specimen of this species.

**Preliminary IUCN conservation assessment.** *Uvariopsis niangadoumae* is a rare species, currently known from a single population located in the Monts de Cristal massif in Gabon, within the Monts de Cristal National Park. As such, the AOO is 4 km<sup>2</sup> and the EOO cannot be calculated. This unique population is threatened by the flooding expected to result from the Kinguéle Aval dam project. The population is located along a small stream adjacent to the Sobéa River, an affluent of the larger Mbé River. According to the IUCN guidelines (IUCN 2012), the species is known from two distinct locations: one of around 60 individuals within the projected flood zone, which will be lost if the dam is built, and another of around 40 individuals at higher elevation outside the immediate flood risk area. Although the second location will not be directly submerged, it remains exposed to habitat alteration or degradation, as local environmental conditions are likely to be disrupted.

Despite extensive searches conducted during complementary inventories for the Kinguéle Aval project, no additional populations were located within the immediate project area. While the Kinguéle region represents one of the most thoroughly surveyed areas within the Monts de Cristal massif, vast portions of this massif remain unexplored. This is evidenced by the discovery of numerous species described or currently under description in recent years, such as *Hunteria maasiorum* Jongkind & E. Bidault, described in 2022 as part of this same project (Jongkind and Lachenaud 2022). Only a limited stretch of the Sobéa River, where *Uvariopsis niangadoumae* is located, has been surveyed. Further targeted efforts should focus on exploring upstream areas of the Sobéa where habitats remain unaffected, as well as other tributaries of the Mbé River, to locate additional populations of this species.

Although there is no doubt that *Uvariopsis niangadoumae* is rare, similar cases of recently described species initially believed to be highly localized have demonstrated that additional populations can be discovered through targeted fieldwork. For instance, *Sirdavidia solannona* Couvreur & Sauquet and *Trichoscypha nyangensis* Pellegr. were both found in new localities after additional surveys.

In the meantime, conservation efforts for *Uvariopsis niangadoumae* are underway. Its population is being monitored, particularly for fruiting individuals, to support ex situ propagation efforts. The Kinguéle Aval project has also established a conservation nursery where seeds and seedlings of species of concern are maintained, currently encompassing 56 species. Twenty individuals of this new species are now growing in the nursery.

Based on current knowledge, if *Uvariopsis niangadoumae* were to be assessed under the IUCN Red List Categories and Criteria, it would qualify as Endangered (EN) under criterion B, due to its restriction to a single population spread across two locations and the imminent threat posed by the dam project. We recommend ongoing botanical surveys in the region to search for potential new populations of *Uvariopsis niangadoumae* and the continuation of ex situ conservation efforts.

**Additional specimens examined.** GABON – Estuaire • Parc National des Monts de Cristal, rive gauche de la Sobéa (à l'ouest de la route Kinguéle–Andok Foula); 00°25'20"N, 10°15'25"E; 115 m; 23 Oct. 2020; fl.; Lachenaud O. et al. 3111; BRLU, LBV, MO • Parc National des Monts de Cristal, au NW de la route Kinguéle–Andok Foula, rive gauche de la Sobéa; 00°25'13"N, 10°15'26"E; 99 m; 22 Oct. 2023; fl.; Paradis A.-H. et al. 1049; BR, BRLU, LBV, MO, P, WAG.

### Pollen morphology

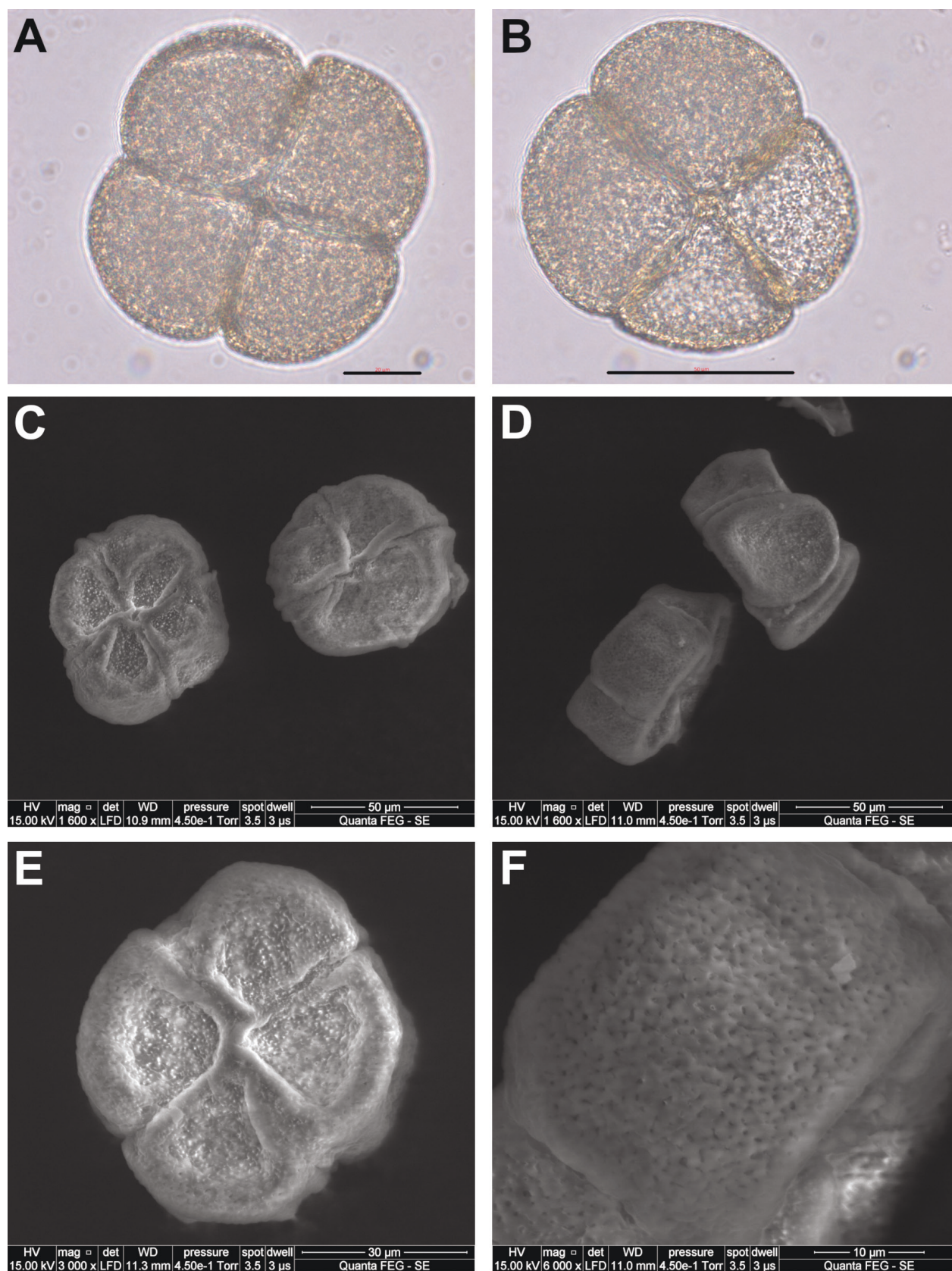
*Uvariopsis niangadoumae* has tetragonal tetrad pollen grains (Fig. 4), 66–73 µm (± 6 µm) in diameter, with constitutive monads measuring ca 46 µm. The exine had a rugulate ornamentation.

### Phylogenomic tree of *Uvariopsis*

Sequence data of the new species is available on GenBank SRA under Bioproject number PRJNA508895 (<https://dataview.ncbi.nlm.nih.gov/object/PRJNA508895>). A total of 319 supercontigs were selected after sequencing (75/75, no paralogs) leading to a concatenated alignment of 802,870 bp. Overall, the phylogenetic relationships were supported by 100% bootstrap values (Fig. 5). A few nodes within *Uvariopsis* were weakly supported, in particular the relationship of *U. korupensis* (TC-S0735) as sister to the *U. bakeriana* and *U. citrata* clade (BS 38). The new species *U. niangadoumae* clusters within the “large-leaved clade” of *Uvariopsis*. It is inferred as sister with maximal support to one specimen of *U. korupensis* (TC-S1630) sampled from Gabon (Louis 1863).

### Flower scent and visitors

We detected a strong unpleasant/putrid scent emitted by the flowers during the day. The scent resembled “old mushrooms”. We were able to sample four visitors collected on the female flower and identified them using DNA barcoding and morphology as: one fly (Diptera, family Phoridae), one ant (Formicidae, genus *Crematogaster*



**Figure 4.** *Uvariopsis niangadoumae*, tetrad pollen morphology. A, B. Tetrad pollen under a light microscope (scale bar A = 20 µm, B = 40 µm). C–F. Pollen grains under a scanning electron microscope. C. Apical view of two tetrads. D. Side view of two tetrads. E. Close up of a single tetrad. F. Close up of side view of tetrad showing exine structure. From *Couvreur 1803*.

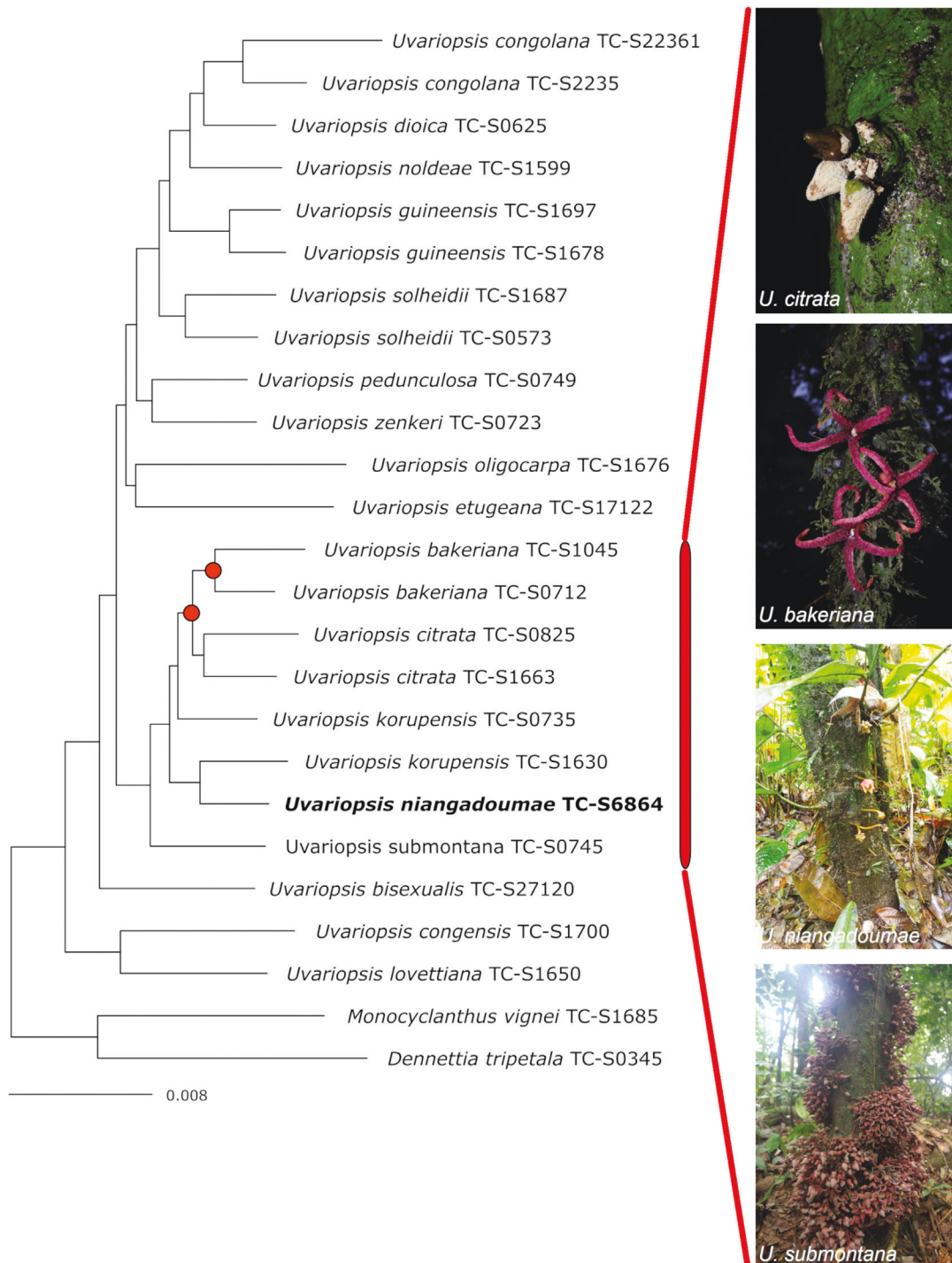


Lund, 1831), one leaf beetle (Chrysomelidae, subfamily Galerucinae), and one rove beetle (Staphylinidae, subfamily Staphylininae). We were not able to identify any of the samples to species level with available literature and barcode reference databases. Sequences are provided in Supplementary material 1 as a baseline for future

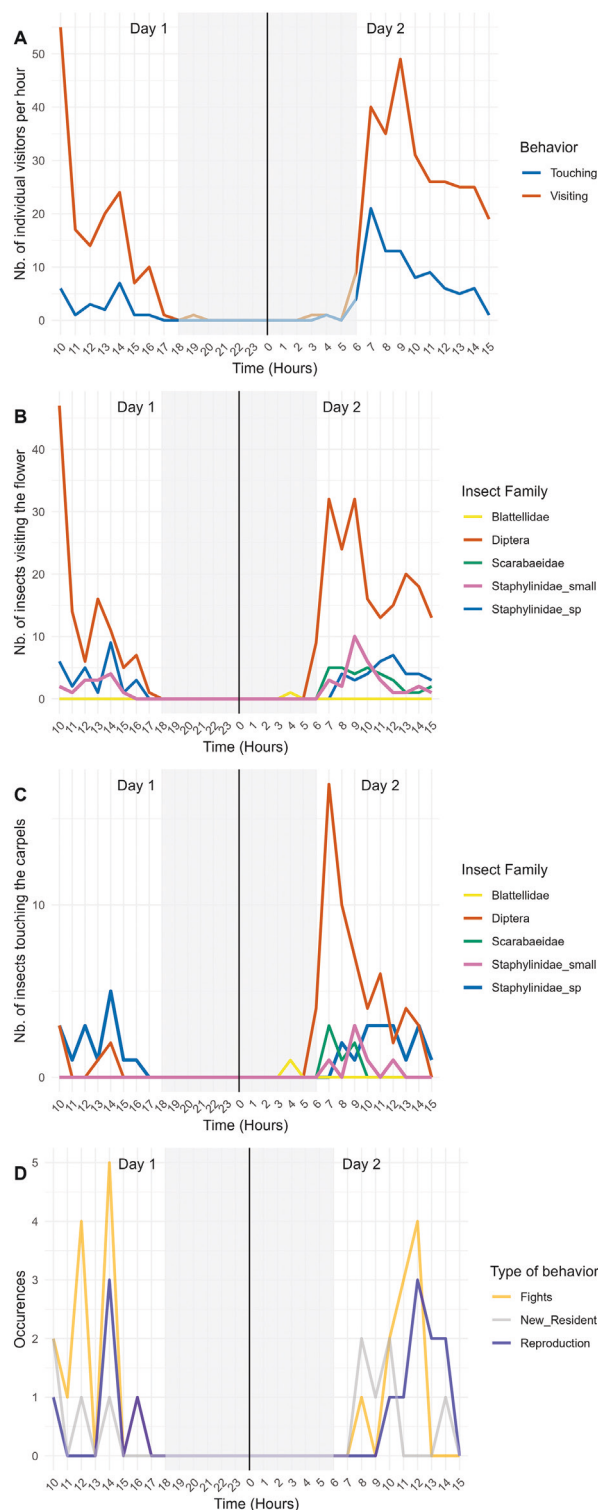
improvement of knowledge of the identity of species visiting flowers of *Uvariopsis*.

### Pollination biology

The video recording (Couvreur 2025: <https://youtu.be/wANN0FYkIzw>) revealed a very active life around the



**Figure 5.** *Uvariopsis niangadoumae*, phylogenetic relationships within *Uvariopsis*. Maximum likelihood tree inferred by RAxML from 319 nuclear markers. Red circles indicate nodes with bootstrap values below 100. Outgroups *Xylopia hypolampra* and *Monodora myristica* removed for better visualization. The large-leaved clade is highlighted in red. *Uvariopsis korupensis* is not illustrated. TC-S numbers are the DNA accession numbers available in the SRA database.



**Figure 6.** *Uvariopsis niangadoumae*, pollination activity. Insect activity recorded around one female flower from 10 am to 4 pm the next day. Scripts for the graphs can be found here: [https://forge.ird.fr/diade/global\\_erc/pollination\\_annonaceae](https://forge.ird.fr/diade/global_erc/pollination_annonaceae).

female flower during the day (Fig. 6, Suppl. materials 2, 3). During the night (6 pm to 6 am) no activity was recorded (Fig. 6), except for one grasshopper that seemed to be licking the petals around 4 am (Suppl. material 3F). The main visitor was the large rove beetle identified as belonging to subfamily Staphylininae (Fig. 3, Suppl. materials 2, 3). An individual entered the female flower and waited (for several minutes) until another individual arrived. If it was a male, the two rove beetles fought until one of the individuals was ejected from the flower. In one case, two individuals entered the flower and waited, but after a few minutes they fought after which only one remained. If a female beetle arrived, the male resident would initiate mating (Suppl. material 3D). They would first meet face to face. The female would then turn and the male would grab the female's abdomen with his hind legs. The male would then proceed to caress the abdomen of the female. This would last anywhere between 7 and 18 minutes, after which both would detach and pause for a while. The female then normally moved away from the inner part of the flower, eventually flying away. For the two days of observation, the mating phase was observed at midday and was generally preceded by a peak in fighting between males (Fig. 6D). Observation of the male flowers showed that the large rove beetles also visited the male flowers and emerged covered in pollen (Fig. 3F, Suppl. material 2).

Besides the behaviour of the large rove beetle, a number of other insects were observed during the day and less so during the night (Fig. 6). Small Diptera (probably several species, but just one sampled) were seen mainly just after sunrise resting on the petals (Suppl. material 3C), but sometimes moving towards the inner side of the petals and even touching the carpels (Fig. 6A). The presence of flies attracted a spider (not identified) that preyed on them (Suppl. material 3C, D). In addition, we observed another smaller Staphylininae rove beetle species (we did not sample this species, but see Suppl. material 3A, C) that visited the flower without showing the behaviour described above, although it did spend time touching the carpels. Finally, at night the flower is deserted, and only a single curious grasshopper was seen (Suppl. material 3F).

The male flower also emits a strong mushroom-like scent. Male flowers are slightly smaller than female ones (Fig. 2A), with a highly convex receptacle (torus). At anthesis, the male flower accommodates only one of these larger Staphylinidae at a time (Suppl. material 2). We observed them moving within the flower and emerging covered in pollen (Fig. 3F). We did not investigate whether flower scents vary throughout the day.

## DISCUSSION

This discovery represents the second new species of *Uvariopsis*, and a third new species for Annonaceae in general, described from this same area over the last decade. *Uvariopsis citrata* was described as new to science in 2016 (Couvreur and Niangadouma 2016) and the new genus



*Sirdavidia solannona* was described in 2015 (Couvreur et al. 2015), both occurring just 5 km from the type locality of *Uvariopsis niangadoumae*. This once again underlines the remarkable diversity of this region of Gabon, and even though it is regularly visited by botanists, it remains an area with a lot of new species yet to be described.

The morphology of the leaves of *Uvariopsis niangadoumae* suggests this species belongs to the informal “large-leaved clade” identified with *Uvariopsis* using sequence capture data (Dagallier et al. 2023). This was confirmed by our phylogenetic analyses, with the new species clustering in the large-leaved clade, that now comprises five species: *U. bakeriana* (Cameroon, Nigeria); *U. citrata* (south Cameroon and Gabon); *U. korupensis* (Cameroon, Gabon, but see below), *U. submontana* Kenfack, Gosline & Gereau (Cameroon), and *U. niangadoumae* (Gabon). These species have quite different flower morphologies (see Table 1), but are characterized by large leaves (16–50 cm long) with narrowly cordate leaf bases (Dagallier et al. 2023). Moreover, these species occur along parts of the Cameroon Volcanic line and the Central African Atlantic Swell from north-western Cameroon to western Republic of the Congo (Mayumbe massif), generally occurring between 50 and 800 m, and between 900 and 1300 m for *U. submontana*. These generally low-lying mountain ranges harbor an important and unique flora (Gonmadje et al. 2012). *Uvariopsis niangadoumae* is recovered as sister to a specimen identified as *U. korupensis* from Gabon (BS 100). This latter species was already recovered as polyphyletic in the study of Dagallier et al. (2023). Our results cast further doubt on the identification of the *U. korupensis* specimen from Gabon (Louis 1863, WAG.1540069). After careful examination, we excluded the possibility that Louis 1863 is a specimen of *U. niangadoumae* (Table 1) because the latter has broader petals (w:l ratio 1.5 vs 7) and fewer carpels (20–25 vs 40) fitting more with *U. korupensis* than *U. niangadoumae*. There is also no mention of scent from the leaves on the label of Louis 1863. It is thus possible that Louis 1863 might represent yet another undescribed species of *Uvariopsis* for Gabon, and more field work is needed to confirm this hypothesis.

The crushed leaves of *U. niangadoumae* have a strong scent of African basilic (*Ocimum gratissimum* Forssk.), a scent that is close to thyme and mint. Interestingly, the other *Uvariopsis* species in the region, *U. citrata*, also has strongly scented leaves, but in these the scent tends toward citrus. Finally, another species from the genus *Uvariadendron* also emits a strong citrus scent, *U. citriodorum* (Le Thomas) Dagallier & Couvreur, known from the Belinga region in Gabon (Dagallier et al. 2023), also a mountainous region known for its iron-rich bedrock. The drivers of these differences remain unclear, but possible explanations could involve microadaptations to specific soils or plant herbivore interactions.

## Pollination ecology

Pollination ecology has been well studied across Annonaceae, and Staphylinid beetles are generally cited as frequent flower visitors (Gottsberger 2012; Saunders 2012). However, none of the studies report the type of interactions and very specific diurnal pollination mode observed here. Indeed, thanks to the use of a PICT camera (Droissart et al. 2021), we were not only able to continuously observe what insects visited the flowers but also to document the behaviour of these visitors. Given recent technical developments and the increasing availability of new cameras capable of filming tiny and/or furtive plant-insect interactions (i.e. Darras et al. 2024; Sittinger et al. 2024), it is likely that other pollination mechanisms and/or animal behaviour will be documented in the near future.

*Uvariopsis* species generally lack a pollination chamber (Saunders 2010; Mertens et al. 2018), leaving the carpels fully exposed at all times, which makes the videos exceptionally clear and revealing. We show that the female flowers of *Uvariopsis niangadoumae* act as a “nuptial bed” for a species of rove beetle (Staphylinidae, subfamily Staphylininae), but also as a “battle arena”, where males fight for control over the flower and thus mating privileges. Flowers attract the rove beetles via a strong unpleasant fungi-like scent during the day (7 am–4 pm, Fig. 6B), and visual cues on the inner side of the four petals mimicking what resembles fungal fruiting bodies (Fig. 2C). Overall, this pollination mode is linked to saprocanthrophily, a specialized form of pollination involving beetles that are attracted to decaying organic matter and mushroom-like visual cues for feeding and/or reproduction (Teichert et al. 2012). Such a pollination mode was described in Annonaceae for the first time in the Neotropical species *Duguetia cadaverica* Huber (Teichert et al. 2012). Annonaceae have a wide variety of flower scents ranging from sweet to rotten, and play a major role in pollination especially deceptive strategies (Goodrich 2012). More detailed studies of the floral scent should be undertaken in order to characterize the chemical composition and better understand how these rove beetles are attracted.

Our results add to the diversity of pollination strategies described for *Uvariopsis*. To date, sapromyophily (pollination by flies) has been reported in *U. congolana* (De Wild.) R.E.Fr. and *U. bakeriana* (Gottsberger et al. 2011), while species of *Orthoptera* and *Blattodea* Wattenwyl, 1882 were suggested as the main pollinators in *U. dioica* (Diels) Robyns & Ghesq. (Mertens et al. 2018). In this latter species, visitors were frequent during the night and the day, while in the former, visitors were only reported during the day, similar to *U. niangadoumae*.

Besides the main rove beetle pollinator, the female flowers of *U. niangadoumae* were also visited by several other species (a second smaller species of rove beetle, flies, Chrysomelidae, one spider, ants) that appear to play little or no role in pollination (Suppl. material 3A).

**Table 1.** Morphological comparison between the species of the large-leaved clade: *U. bakeriana*, *U. citrata*, *U. korupensis*, *U. niangadoumae*, *U. submontana*, and specimen *Louis 1863*, identified as *U. korupensis* to date. l:w = length:width ratio.

	Leaf lamina length (cm)	Scent	Inflorescences	Pedicel length (mm)	Sepals	Petals	Carpel number	Altitudinal range (m a.s.l.)
<i>Uvariopsis bakeriana</i>	15–34	None reported	Borne on trunk, spaced	2–8	Male and female flowers: 1–3.5 mm long, 1.5–3 mm wide, free	Male and female flowers: l:w ratio 4–10, bright pink to dark pinkish red	15–40	50–800
<i>Uvariopsis citrata</i>	31–50	Crushed leaves emit a strong lemon scent	Borne on trunk, sparsely spaced, mostly towards the lower half of the trunk	0–2	Male and female flowers: 9–15 mm long, 4–6 mm wide, basely fused	Male and female flowers: l:w ratio ca 3.5, greenish yellow	ca 60	60–300
<i>Uvariopsis korupensis</i> (excl. specimen <i>Louis 1863</i> )	28–62	None reported	Borne on thickenings of the trunk, mainly at the base of the trunk	6–70	Male flowers: 1–5(–7.5) mm long, 2–6.5 mm wide, basely fused  Female flowers: 3–5 mm long, 4–5 mm wide, basely fused	Male flowers: l:w ratio 2.3–5, free to fused at base  Female flowers: petals more than 3 times longer than the sepals, l:w ratio 2.2–3, free to fused at base, cream to pinkish	25–120	90–160
Specimen <i>Louis 1863</i>	31–35	None reported	Borne at base of trunk (10 cm)	35–50	Male flowers: ca 3 mm long, ca 3.5 mm wide, basely fused Female flowers: ca 4 mm long, ca 4 mm wide, basely fused	Male flowers: l:w ratio ca 7, free  Female flowers: l:w ratio ca 5, free, cream to pinkish	ca 40	ca 100
<i>Uvariopsis niangadoumae</i>	Up to 36	Leaves emit a strong scent between mint and thyme	Borne at base of trunk, on small and sparse lumps, up to 1 m maximum	Up to 40	Male flowers: minute  Female flowers: ca 1 mm long, ca 4 mm wide, free	Male flowers: l:w ratio ca 1.7, free, cream to pink-reddish Female flowers: l:w ratio ca 1.3, free, cream to pink-reddish	20–25	ca 350
<i>Uvariopsis submontana</i>	16–38	None reported	Borne in dense clumps on thickenings at base of the trunk (sparse above 2 m)	24–60	Male flowers: 5–11 mm long, 6–12 mm wide, basely fused  Female flowers: 6–8 mm long, 6–9 mm wide, basely fused	Male flowers: l:w ratio 1.8–4.7, free to fused at base over 30% of their length Female flowers: petals less than 3 times longer than the sepals, l:w ratio 5–9, free to fused at base over 30% of their length, cream to pinkish	50–100	900–1300



This is common in Annonaceae where scented flowers can attract a large non-specialized cohort of insects (Gottsberger 1999). At night, the flower is deserted, and we only observed a visiting grasshopper. The flower also acted as a “food court” for an opportunistic spider (indet.) that spent significant time catching the flies that were attracted by the putrid scent. The flies (Diptera, family Phoridae; plus, potentially several other species) regularly touched the carpels, especially before the arrival of the rove beetles (Fig. 6C). They were also observed on the male flowers (Fig. 3C). However, *Uvariopsis* pollen forms large tetrads (Couvreur et al. 2008: fig. 3), which are generally adapted for beetle pollination (Fig. 4). These flies are unlikely pollinators, as we did not observe any with pollen on their bodies. Ants, identified as a species of the genus *Crematogaster*, were seen forming small colonies around the sepals of male flowers (Fig. 3E), but not always, and were never seen within the flower or touching the reproductive structures. Ants have been reported to be frequent visitors of *Uvariopsis dioica*, but never showed much interest (Mertens et al. 2018), similar to our observations here.

The mating system of the rove beetles reported here appears to follow one already known from other Staphylinidae (Jepson née Walker 1984), who suggested eight stages of copulation: (1) examination of the female by the male, (2) examination of the male by the female, (3) prolonged examination between male and female (Suppl. material 3B), (4) male mounting, (5) extrusion of male genitalia, (6) intromission (that is the insertion of the male copulatory organ into the female during mating), (7–8) aggression of female and/or male (separation). Overall, we did observe these different stages, but based on our video it is hard to precisely see the transition between phases 5 and 6. The copulation time, interpreted from the start of abdomen caresses till separation, is quite variable in length, ranging between 7 to 18 min. This phase has been reported to last different lengths and might be species specific (Jepson née Walker 1984). In parallel, the female flower is also an area where two males will fight to retain control of the nuptial bed. Fights happen often, in many cases with the newly arrived Staphylinid winning and becoming the new resident (Fig. 6D).

In addition to re-emphasizing the importance of Monts de Cristal National Park as a centre of African biodiversity, this study also underlines a potential hotspot for pollination mode diversity with Annonaceae. Indeed, another recently discovered species is *Sirdavidia solannona*, the floral morphology of which suggests buzz pollination by bees (Couvreur et al. 2015). Other species known to the area such as *Uvarioidendron molundense* (Diels) R.E.Fr. or *Xylopia aethiopica* (Dunal) A.Rich. (Haran et al. submitted) are likely pollinated by specialized weevils of the genus *Endaeus* Schoenherr, 1826 acting as brood-site pollinators, the larvae developing in the large petals (Dao et al. 2023). More research could be undertaken to document other species pollination syndromes such as *Uvariopsis citrata* or *Piptostigma macranthum* Mildbr.

& Diels which probably also differ. Finally, with five species described to date, the large-leaved clade could serve as a model to understand diversification of plants along the Central African Atlantic Swell mountain range. Indeed, the combination of unique traits such as strong scented leaves, diverse petal morphology, and specialized pollination systems could be suggested as potential drivers of diversity in this heterogeneous rain forest region.

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## SUPPLEMENTARY MATERIALS

### Supplementary material 1

DNA sequences of the four insect species sampled on the flowers of *Uvariopsis niangadoumae*. <https://doi.org/10.5091/plecevo.152843.suppl1>

### Supplementary material 2

*Uvariopsis niangadoumae*, detail of male flower with a rove beetle in it. Photos by Rémi Allio. <https://doi.org/10.5091/plecevo.152843.suppl2>

### Supplementary material 3

*Uvariopsis niangadoumae*, pollinator visitors. **A.** Two large Staphylinidae rove beetles resting, note presence of flies, a smaller (black) Staphylinidae, and a Chrysomelidae (subfamily Galerucinae) beetle. **B.** Male and female Staphylinidae reproducing, abdomen stroking phase. **C.** Spider preying on flower, with one large Staphylinidae (left) and a small Staphylinidae (right), also presence of flies. **D.** Spider preying on flower, with large Staphylinidae beetle. **E.** Night view of flower, note the absence of insects. **F.** A grasshopper visiting the flower (but not touching the carpels) at 8 pm. All photos taken as screenshots from the PICT camera. <https://doi.org/10.5091/plecevo.152843.suppl3>