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RESEARCH ARTICLE

Vivipary, a rare phenomenon in Afrotropical Melastomataceae: first report in *Amphiblemma ciliatum* (Sonerileae)

Marie Claire Veranso-Libalah[1], Chen Luo[1], Ehoarn Bidault[2,3]

1 Prinzessin Therese von Bayern-Lehrstuhl für Systematik, Biodiversität & Evolution der Pflanzen, Ludwig-Maximilians-Universität München, München, Germany
2 Missouri Botanical Garden, Africa & Madagascar Department, St. Louis, Missouri, USA
3 Institut de Systématique, Évolution, et Biodiversité (ISYEB), Unité Mixte de Recherche 7205, Centre National de la Recherche Scientifique/Muséum national d'histoire naturelle/École Pratique des Hautes Études, Université Pierre et Marie Curie, Sorbonne Université, Paris, France

Corresponding author: Marie Claire Veranso-Libalah (mario_clario@yahoo.ca)

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Abstract

Background and aims – Within angiosperms, vivipary has been reported in less than 0.1% of all species. We herein report the first occurrence of vivipary in an Afrotropical Melastomataceae and discuss its phylogenetic position, habit, habitat, and fruit attributes.
Material and methods – Observational data were gathered from a field expedition to Gabon, and from herbarium specimens from BR, BRLU, P, and WAG. A phylogeny was generated to map all the eight species exhibiting vivipary in Melastomataceae.
Key results – *Amphiblemma ciliatum* is currently the only known melastome species in the Afrotropics exhibiting vivipary. It is likely that its angular capsules depend on rainwater for seed dispersal.
Conclusion – The combination of a herbaceous habit and angular fruits with the occurrence on shaded humid tropical rainforest floor during periods of incessant rainfall and high humidity might be responsible for vivipary in most Melastomataceae.

Keywords

Amphiblemma, capsular fruits, Melastomataceae, raindrop dispersal, seed dispersal, Sonerileae, vivipary

INTRODUCTION

Vivipary is a rare phenomenon among angiosperms (Elmqvist and Cox 1996; Cota-Sánchez and Abreu 2007) and is only reported in less than 0.1 % of flowering plant species (Farnsworth 2000). In viviparous species, seeds germinate within the fruit while still on the parent plant (i.e. precocious germination). Vivipary is well known in mangroves (Rhizophoraceae: *Bruguiera* Lam., *Rhizophora* L.; Acanthaceae: *Avicennia* L.), Cactaceae, and Gesneriaceae (Tomlinson and Cox 2000; Cota-Sánchez et al. 2007; Cota-Sánchez 2022). In these families, vivipary has been suggested as an adaptive mechanism for protecting the embryo from high saline concentrations, a specialized character providing new avenues for survival, rapid rooting, and seedling establishment; and a dispersal attribute conferring habitat specialization (Elmqvist and Cox 1996; Farnsworth 2000; Cota-Sánchez 2022).

In Melastomataceae, vivipary is a rare convergent attribute that has evolved multiple times. It has been reported in three neotropical tribes (Bertolonieae: *Bertolonia acuminata* Gardner, *B. carmoi* Baumgratz, *B. mosenii* Cogn.; Merianieae: *Macrocentrum minus* Gleason, *M. vestitum* Sandwith; and Trioleneae: *Triolena*

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amazonica (Pilg.) Wurdack), as well as in the Southeast Asian endemic *Memecylon umbellatum* Burm.f. (Thite et al. 2016; Bacci et al. 2021). So far, there are no reports on vivipary in African Melastomataceae.

In this paper, we report the first occurrence of viviparous seeds in Afrotropical Melastomataceae in the tribe Sonerileae (*Amphiblemma ciliatum* Cogn.) based on field observation. We also discuss its phylogenetic position, habit, habitat, and fruit attributes in comparison to other viviparous melastome species.

MATERIAL AND METHODS

A natural population of *A. ciliatum* with viviparous seeds was observed by the last author and colleagues during a field collection trip in Gabon in November 2017. The observation was made along the Louétsi River, at Dibwangui, in the Ngounié province, ca 20 km north-east of Lébamba, at an elevation of 422 m. A collection (*Bidault et al. 3811*) was made, and duplicates are stored at BR, BRLU, LBV, and MO. Silica-gel samples and photographs were also taken. To assess the presence or mention of vivipary among other Sonerileae genera, and particularly in the genus *Amphiblemma*, fruiting herbarium specimens and labels from BR, BRLU, P, and WAG were inspected.

Sequences of two nuclear (nrETS and nrITS) and two plastid markers (*ndhF* and *psbK-psbL*) were downloaded from GenBank (Supplementary material 1). In total, the dataset consisted of 249 terminals. Instead of using the well-sampled phylogeny of Melastomataceae published by Reginato et al. (2020), we generated a new phylogenetic tree to include all the melastome species that exhibit vivipary. The phylogenetic tree was generated using maximum likelihood (ML) analysis with RAxML v.8 (Stamatakis 2014) using the GTRGAMMA model of sequence evolution and it was run on CIPRES Science Gateway (Miller et al. 2010).

RESULTS

In a natural population of *Amphiblemma ciliatum* (Sonerileae, Melastomataceae), many seedlings were observed to have germinated within the brownish ripened fruits while still being attached to the mother plant (Fig. 1). Some seedlings were observed slightly below the fruit or on the pedicel (Fig. 1A, E). Inspection of herbarium specimens did not unearth the presence of viviparous seeds in other Sonerileae or *Amphiblemma*. The phylogenetic results suggest that vivipary in Melastomataceae has evolved independently several times (Fig. 2).

DISCUSSION

In *A. ciliatum*, the specimen *Bidault et al. 3811*, wherein viviparous seeds were seen, makes no mention of this phenomenon on the label and neither can it be seen on the dried herbarium specimens. This therefore suggests that there might be more viviparous seeds but collectors need to mention this rare phenomenon on labels since observing them later on herbarium specimens is difficult. Bacci et al. (2021) also reported that it is very hard to see viviparous seeds on herbarium specimens, even on collections they themselves collected.

In Melastomataceae, vivipary has evolved independently several times (Fig. 2). In *M. umbellatum*, the fruits are berries and quite distinct from the viviparous species with capsular fruits. Generally, the members of the tribe Sonerileae share similar overall morphology with the Neotropical Bertolonieae sensu Triana (1866) with many species now in Trioleneae, Bertolonieae, or Merianieae (Bacci et al. 2019, 2020). Vivipary has been reported in the latter three tribes (Bacci et al. 2021). Except for its geographic distribution, the convergence of morphological characters such as habit, fruit type, and capsule morphology makes it almost impossible to separate the mostly Paleotropical endemic Sonerileae from these other tribes.

Sonerileae are a pantropical tribe composed of 1080 species in 44 genera, typically occupying humid habitats under primary/secondary forest canopies or along forest margins, often on slopes, near streams, on riverbanks, or epiphytic on trees, from sea level to about 3200 m in elevation in the tropics (Liu et al. 2022). They are mostly herbs, with a few shrubs and epiphytes. Inflorescences are racemose, dichasial or scorpioid cymose, umbellate, sometimes reduced to a single flower, or form thyrses and panicles. Capsules are terete to angular, uncrowned or with a persistent crown enlarged to various extent, and dehiscence apical, loculicidal, and valvate (Liu et al. 2022). Seeds are dispersed by raindrops and wind in capsule-fruited species, and by monkeys, civet cats, squirrels, bats, birds, and ants in berry-fruited species (Clausing 2000; Kadereit 2005; Quakenbush 2016).

Unlike the Afrotropical members in the tribe Melastomateae where most genera and species occur in dry open habitats, the members of the tribes Sonerileae and Dinophoreae are restricted to humid shaded habitats. In most African Melastomateae, the fruits are dry loculicidal or apical dehiscent capsules, and rarely baccate or indehiscent capsules (e.g. *Tristemma* Juss. with an irregular bursting of the fruit). In Dinophoreae, on the other hand, the fruit is a berry (*Dinophora* Benth.) or a dry dehiscent globose capsule (*Ochthocharis* Blume). In Sonerileae, the fruits are ellipsoid, angular (tetra- or pentagonal), dehiscence can be loculicidal, apical, or septicidal, but occasionally the entire wall of the hypanthium breaks up and exposes the ovary. These capsules or berries usually have numerous small seeds, ca 1 mm long.

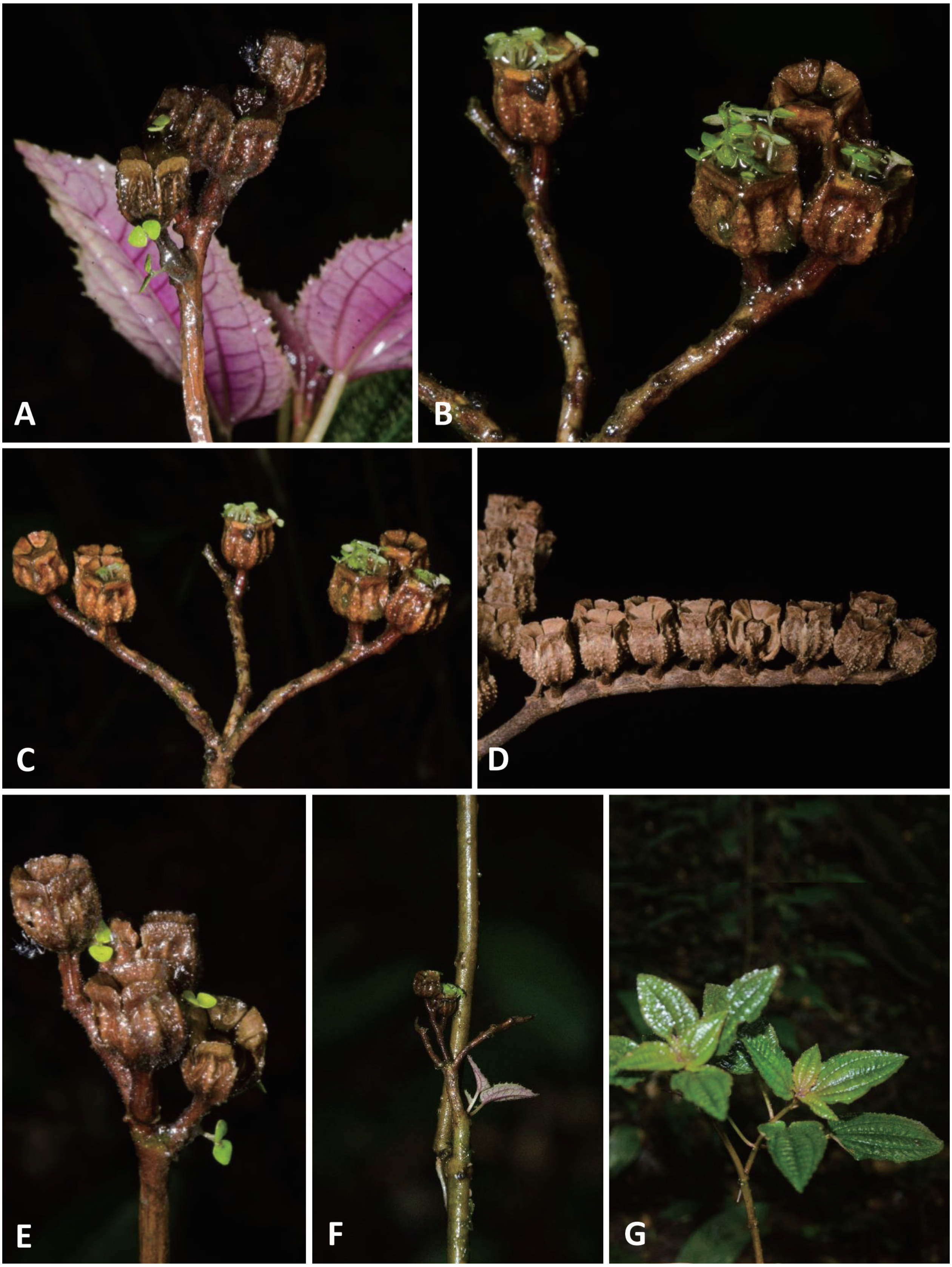

Figure 1. Developing viviparous offspring with chlorophyllic cotyledons still attached to the capsules. **A**–**C**, **E**–**F**. Infructescence of *Amphiblemma ciliatum*, showing the seedlings. **D**. Infructescence of *A. ciliatum*, with no seedlings. **G**. Habit of *A. ciliatum*. A–C, E–G from *Bidault et al. 3811* (BR, BRLU, LBV, MO); D from *Bidault et al. 4264* (BR, BRLU, LBV, MO, P).

So far, nothing is known or mentioned about seed dispersal in Afrotropical Sonerileae, except for *Medinilla* Gaudich., which might be bird-dispersed because of its berry fruits. In melastomes, angular capsules have been associated with shaded and moist understory under rainforest canopy and their dependence on seed dispersal by rainwater in the Neotropics and Southeast Asia (Stone and Weber 1987; Weber 1987; Bacci et al. 2019). In *Bertolonia* Raddi and *Triolena* Naudin, seed dispersal is through the "squirt-corner" mechanism wherein the capsules are filled with water from raindrops and the seeds are expelled through the corners (Pizo and Morellato 2002; Bacci et al. 2019). Contrarily, in *Macrocentrum* Hook.f., *Salpinga* Mart. ex DC. (Bacci et al. 2019), and *Phyllagathis maxwellii* Stone & Weber (Weber 1987), the capsules are trumpet- or cup-shaped, and seed dispersal is performed by the splash-cup mechanism, which is also associated with raindrops (Nakanishi 2002). Like in Bertolonieae, Trioleneae, and Merianieae, raindrops might be a very important dispersal syndrome among Afrotropical Sonerileae and in particular in *Amphiblemma*, but this needs to be investigated for other Afrotropical melastomes with angular fruits.

Amphiblemma is a shade tolerant genus and consists of 14 species restricted to Central Africa with only one species, *A. cymosum* Naudin extending to West Africa (Veranso-Libalah et al. 2023). *Amphiblemma* species are mostly terrestrial caulescent perennial herbs and shrubs with glandular hairs very frequent on the floral organs, and often showing interpetiolar lenticels. The inflorescences are cymes with two to five digitate branches forming a corymb, panicle, contracted umbel or sometimes axillary cymes. The flowers are pentamerous with the sepals lacking linear appendages, the stamens are dimorphic,

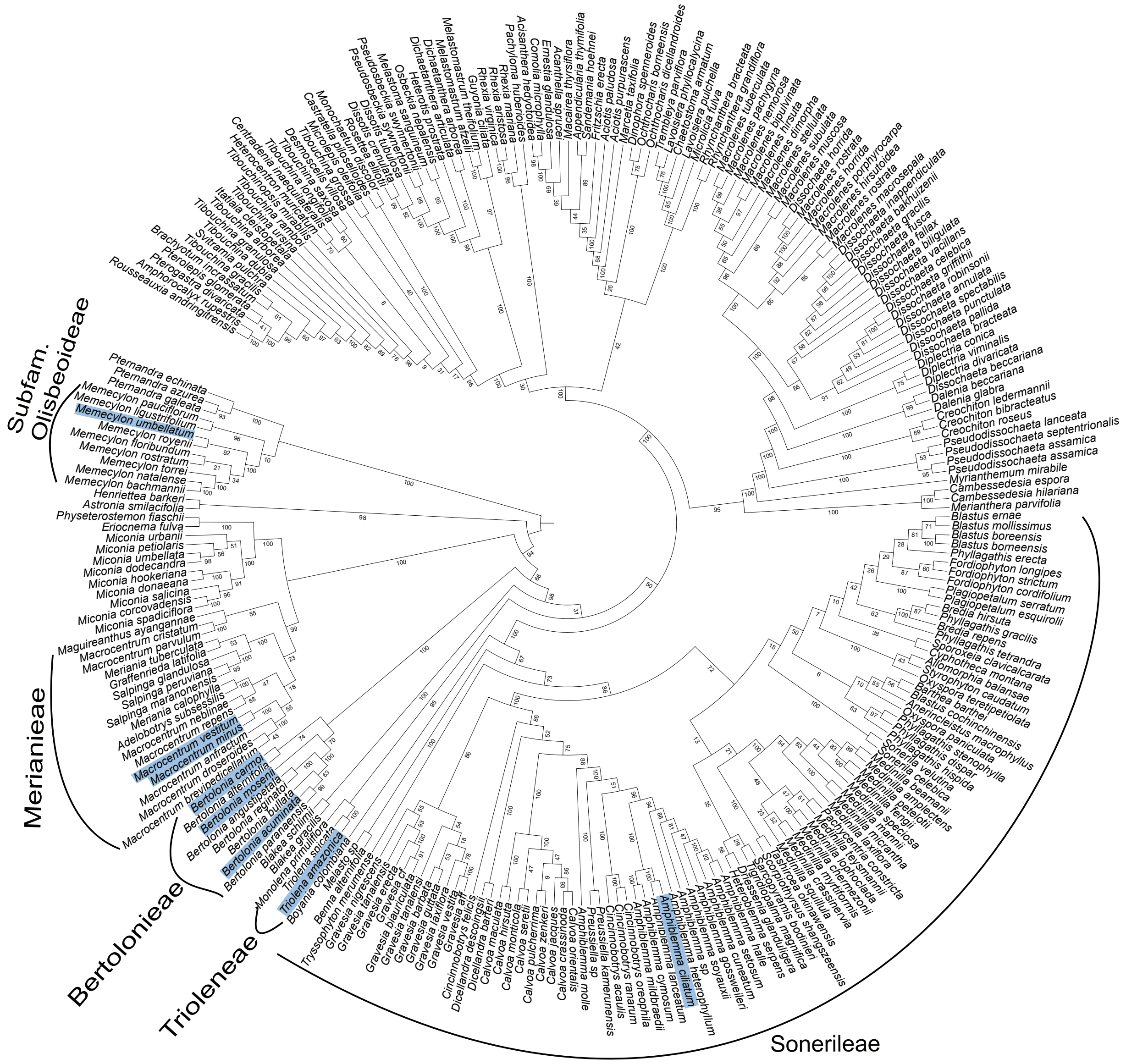

Figure 2. Maximum likelihood tree of Melastomataceae based on a concatenated data matrix (nrETS, nrITS, *ndhF*, and *psbK-psbL*). Values on branches refer to bootstrap values. The taxa highlighted in blue indicate the species for which vivipary has been reported.

the ovary is inferior to semi-inferior, with an included epigynous crown having five lobes, and fruit dehiscence is valvate (Veranso-Libalah et al. 2023).

In *A. ciliatum*, the fruits are short, 5–7 mm long, pentagonal, with warty traces of deciduous hairs on the surface. The locules are short with accrescent perigynous scales, reaching the margin of the hypanthium. The seeds are ellipsoid, ca 1 mm long, the lateral membrane is progressively dilated into an apical-frontal vesicle. The scorpioid inflorescence in *A. ciliatum* ensures that the flowers are arranged at different positions preventing any overlap and subsequently on the infructescence. Even on horizontal infructescences, the cup-shape capsules are usually uprightly positioned since the pedicels are always in a vertical position (Fig. 1). This upright position of the capsules and the arrangement of the capsules on the infructescence ensure reception of raindrops. Like the other neotropical Bertolonieae s.l., it is quite possible that seed dispersal is ensured through rainwater. Nevertheless, there are no field observations or literature on dispersal syndromes among Afrotropical melastomes. Whether vivipary in *A. ciliatum* is a secondary consequence of seed dispersal or an inefficient dispersal syndrome in *A. ciliatum* is still unknown.

Based on precipitation data from the collection locality (02°05’53”S, 11°35’36”E), there was incessant rainfall (except for 29 Oct. 2017, which still had 89% humidity), with thunderstorms for more than a month before the collection date (see Supplementary material 2). Even more interesting, the collection was made near an important waterfall that creates a particularly humid micro-habitat (even more humid than “regular” forests along rivers). For vivipary to occur, intrinsic and extrinsic factors such as physiology, soil condition, temperature, and dry spell followed by high humidity induced by heavy rainfall is very important (Deore and Johnson 2008). In *M. umbellatum* (Thite et al. 2016) and *Grindelia squarrosa* (Pursh) Dunal (Pliszko and Górecki 2021), it has been suggested that incessant rainfall and high humidity are the promoters of vivipary. It is likely that since October and November 2017 were extremely wet, with heavy and incessant rainfall for long durations and the resulting in high humidity, plus the humid micro-habitat from the nearby waterfall, might have promoted vivipary in *A. ciliatum*. For viviparous seedlings to establish in nature, they need to overcome extreme environmental conditions such as extreme temperatures, desiccation, exposure to direct sunlight, wind, and rain (Cota-Sánchez and Abreu 2007). However, whether these seedlings would fall off and establish is still uncertain and needs to be tested.

CONCLUSION

In most Melastomataceae, the convergence of herbaceous habit and capsular-angular fruits, in shaded tropical rain forest floor during periods of incessant rainfall and high humidity might be responsible for vivipary. During periods of continuous rainfall and high humidity, field studies are encouraged to observe if there are more species exhibiting vivipary and if these seedlings establish. More vivipary observations like the one discussed in this paper need to be reported to boost the knowledge of this rare phenomenon among flowering plants.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

GenBank accession numbers.
https://doi.org/10.5091/plecevo.106696.suppl1

Supplementary material 2

Climate data of Gabon from 16 Oct. 2017 to 22 Nov. 2017 (from https://www.visualcrossing.com).
https://doi.org/10.5091/plecevo.106696.suppl2