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RESEARCH ARTICLE

A new *Ypsilopus* (Orchidaceae, Angraecinae) from Zimbabwe and notes on the parallel evolution of extreme column exsertion in African angraecoids

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Abstract

Background and aims – A preliminary review of hawkmoth-pollinated angraecoids from Africa unveiled a remarkable case of parallel evolution of extreme column exsertion between the two species formerly classified in in the defunct genus *Barombia*. These belong to one clade of *Aerangis*, including *A. gracillima* and *A. stelligera*, and *Ypsilopus* sect. *Barombiella*, including *Y. amaniensis* and *Y. schliebenii*. The exploration of the geographical distribution of these two clades, followed by an examination of morphological variation within *Y.* sect. *Barombiella*, revealed that the disjunct population identified as *Y. amaniensis* from Zimbabwe represents an undescribed species.
Material and methods – Occurrence records of *Ypsilopus amaniensis*, *Y. schliebenii*, *Aerangis gracillima,* and *A. stelligera* were comprehensively mapped and distribution patterns were visually analysed. Pollination syndromes and pollinaria attachment sites were inferred based on a review of floral and hawkmoth morphology. Standard herbarium practices and mining of photographs of wild and cultivated plants in social media allowed the description of the novelty.
Key results – *Ypsilopus zimbabweensis* sp. nov. (*Y.* sect. *Barombiella*) is a narrow endemic of significant horticultural interest and it is preliminarily assessed as Endangered. The evolution of a *Barombia*-type column presents a parallel geographical pattern in the *Aerangis gracillima*–*A. stelligera* clade and *Ypsilopus* sect. *Barombiella* and probably induced a shift of pollen placement sites in these sphingophilous species.

Keywords

Great Zimbabwe National Monument, iNaturalist, lithophytic orchids, sphingophily, taxonomy, Tropical Africa

INTRODUCTION

The evolution of mechanical barriers leading to pollen placement shifts (i.e. changes of the position of pollen loads on pollinators) are exclusively reported in plants with high floral integration (i.e. coordinated covariance of floral traits) and accuracy (Armbruster and Muchhala 2009), notably in Orchidaceae (e.g. Dressler 1968; Nilsson et al. 1987). Column exsertion is one of the characters associated with the evolution of these shifts, as observed in Stylidiaceae (Armbruster et al. 1994) and Campanulaceae (Muchhala and Potts 2007; Muchhala 2008), but its importance in orchids remains undocumented.

A preliminary review of hawkmoth pollination in angraecoid orchids (Farminhão 2021), identified two clades of African species that possibly illustrate how column exsertion leads to shifts of pollen attachment sites in species sharing large hawkmoths as pollinators. In the Guineo-Congolian region, *Aerangis gracillima* (Kraenzl.) J.C.Arends & J.Stewart presents a column attaining more

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than double the length of those of closely-allied *Aerangis stelligera* Summerh. and *A. bouarensis* Chiron. Similarly, in eastern and southeastern Africa, and with a more sizeable difference, *Ypsilopus schliebenii* (Mansf.) D'haijère & Stévart bears a column four to approximately five times longer than sister *Y. amaniensis* (Kraenzl.) D'haijère & Stévart. The striking resemblance in column elongation of *A. gracillima* and *Y. schliebenii* led taxonomists to class both species in the now defunct genus *Barombia* Schltr. (Schlechter 1914; Cribb 1980), which was revealed to be polyphyletic by molecular phylogenetics (Simo-Droissart et al. 2018; D'haijère et al. 2019; Farminhão et al. 2020).

To better understand this parallelism, we explored the geographical distribution of *A. stelligera*, *A. gracillima*, *Y. amaniensis*, and *Y. schliebenii* and examined in further detail morphological variation within these taxa, with a focus on the two species of *Ypsilopus* Summerh.

Ypsilopus is an angraecoid genus (from the cyrtridactyloid clade) confined to eastern and southern Africa, which encompasses 12 species arranged in two sections, comprising species formerly included in *Tridactyle* Schltr and *Rangaeris* (Schltr.) Summerh. (D'haijère et al. 2019, 2021; Farminhão et al. 2021). *Ypsilopus schliebenii* and *Y. amaniensis* are the only representatives of *Ypsilopus* sect. *Barombiella* (Szlach.) D'haijère & Stévart, which were formerly classified within polyphyletic *Rangaeris* (Farminhão et al. 2020). The well-known *Y. amaniensis* is widespread in East Africa from Eritrea and Ethiopia south to Tanzania (Cribb 1989; Demissew et al. 2004). It is also reported from Zimbabwe, amongst others, by Ball (1978) and la Croix and Cribb (1998). However, the three collections (viz. *Ball 1394*, *Jackson 56814*, *Mullin* in *GHS 25198*) we have examined from there differ significantly from the East African ones, enough to consider them to belong to a distinct, albeit closely allied species which we describe here.

MATERIAL AND METHODS

We mapped all occurrences of *A. gracillima*, *A. stelligera*, *Y. amaniensis*, and *Y. schliebenii* vouchered by specimens deposited in BR, BRLU, P, K, and SRGH using QGIS v.3.4.15.

We compiled spur length and column measurements for the same angraecoid species based on a comprehensive literature survey (Cribb 1989; Geerinck 1992; la Croix and Cribb 1998; Szlachetko and Olsweski 2001). Body measurements of *Xanthopan morganii* (Walker, 1856), the largest hawkmoth from Tropical Africa, were estimated using ImageJ v.1.52d (Schneider et al. 2012) based on forewing length and iconography provided by Minet et al. (2021).

We applied standard herbarium practices to investigate the variability of plants identified as *Y. amaniensis* kept at BR, K, and SRGH, including reproductions of specimens kept at FI, and all type material (acronyms following Thiers 2023). Based on newly collected data, we update the key to the sections of *Ypsilopus*, with a focus on *Ypsilopus* sect *Barombiella*, presented by D'haijère et al. (2019, 2021). Distribution records and photographs of species in *Y.* sect. *Barombiella* were mined from social media, namely iNaturalist, Facebook, and Flickr, and used to complete the description, phenology, and range of the species.

IUCN Red List categories and criteria (IUCN 2022) were applied to evaluate the conservation status of the new species. The number of "locations" (sensu IUCN 2022) was calculated considering the type of threats, such that a single "location" may include more than one adjacent occurrence. The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCAT (Bachman et al. 2011) on georeferenced specimen data. The AOO was calculated based on a 2 × 2 km grid cell size.

RESULTS

In *Aerangis* Rchb.f. and *Ypsilopus*, the *Barombia*-type column that has evolved in parallel occurs in the species with the narrowest distribution, which is marginal to the range of the most widespread taxa with shorter columns (Fig. 1). There is at least one contact zone between *A. gracillima* and *A. stelligera* in southern Cameroon, while species in *Y.* sect. *Barombiella* are separated by large geographical gaps: ca 200 km and 800 km separate *Y. schliebenii* from the closest populations of *Y. amaniensis* to the north and south of its range, respectively. The population of *Y. zimbabweensis*, newly described here, is separated by a gap of more than 1,200 km from the southernmost occurrence of *Y. amaniensis* in the Rubeho and Uluguru Mountains in Tanzania.

The range of spur and column length in the studied angraecoids is summarised in Table 1.

Ypsilopus zimbabweensis can be morphometrically separated from *Y. amaniensis* namely according to leaf length, flower number, and peduncle length. Differences are summarised in the taxonomic treatment.

DISCUSSION

Distribution of *A. gracillima*, *A. stelligera*, *Y. amaniensis*, and *Y. schliebenii* is consistent with different floristic bioregions of the Afrotropics (Droissart et al. 2018): in the Guineo-Congolian region, *A. gracillima* is confined to Lower Guinea, while sister *A. stelligera* is more widespread in Lower Guinea and Congolia; in Eastern Africa, the range of *Y. schliebenii* is centred in the Southern Rift montane region, whereas *Y. amaniensis* is more widespread in Central Tanzania and East African montane regions, with the isolated population of *Y. zimbabweensis* included in the South Zambesian. The geographical pattern of column length distribution suggests that column exsertion may have been reinforced after secondary contact in a scenario

Table 1. Spur and column lengths in the *Aerangis gracillima–A. stelligera* clade and *Ypsilopus* sect. *Barombiella*.

	Spur length (cm)	Column length (cm)
Aerangis gracillima	18–25	3–4
Aerangis stelligera	14–25	1–1.5
Ypsilopus amaniensis	8–16	0.5
Ypsilopus schliebenii	16–17.5	2–2.7
Ypsilopus zimbabweensis	11–14	0.5

of allopatric/peripatric speciation in both angraecoid clades (Farminhão 2021).

Considering spur length (see Johnson et al. 2017) and field observations (Martins and Johnson 2013; Balducci et al. 2019), it is likely that the *Aerangis gracillima–A. stelligera* clade and *Ypsilopus* sect. *Barombiella* share some large sphingid species as their exclusive pollinators, namely *Agrius convolvuli* (Linnaeus, 1758), *Coelonia fulvinotata* (Butler, 1875), and/or *Xanthopan morganii*. It is hypothesised that the pollinia attachment site shifted from the head to the dorsal region of the thorax (Fig. 1), based on the head-thorax length of 1.9 cm in *Xanthopan morganii*, mirroring the gap in column exsertion (see Table 1). The use of camera traps optimised for studying plant-insect interactions (e.g. Droissart et al. 2021) will be instrumental to test these hypotheses, notably near the contact zones between sister species.

Populations previously identified as *Y. amaniensis* in Zimbabwe are here recognised as *Ypsilopus zimbabweensis* sp. nov. The novelty is apparently endemic to the Central Watershed biogeographical area (Mapaura 2002), and it is one of the five angiosperms restricted to the inselbergs of Zimbabwe (Seine et al. 1998; Mapaura 2002), the others being *Craterostigma syncerus* (Seine, Eb.Fisch. & Barthlott) Eb.Fisch., Schäferh. & Kai Müll., *Delosperma steytlerae* L.Bolus, *Kalanchoe wildii* Raym.-Hamet ex R.Fern., and *Portulaca rhodesiana* R.A.Dyer. The number of species in *Y.* sect. *Barombiella*, thus, rises to three, all presenting non-overlapping latitudinal distributions in Tropical Africa.

TAXONOMIC TREATMENT

Key to *Ypsilopus*

1. Leaves spread along the stem; lip spur at least 7.5 cm long; column glandular, at least 5 mm long .... **2 sect. *Barombiella***
– Leaves arranged in a fan; lip spur less than 5 cm long; column eglandular, less than 2 mm .... **sect. *Ypsilopus*** (see D'haijère et al. 2021)
2. Column longer than 2 cm .... ***Y. schliebenii***
– Column up to 2 cm long **3**
3. Inflorescence 5–8-flowered; peduncle 1–1.5 cm .... ***Y. amaniensis***
– Inflorescence 10–13-flowered; peduncle 4.5–7 cm .... ***Y. zimbabweensis* sp. nov.**

Ypsilopus zimbabweensis Farminhão & P.J.Cribb, **sp. nov.**
urn:lsid:ipni.org:names:77328944-1
Figs 1–4

Type. ZIMBABWE • Masvingo [Victoria District], ± 3 km from Zimbabwe turn-off on Morgenster road; 12 Jan. 1976; *J.S. Ball 1394*; holotype: K; isotype: SRGH.

Diagnosis. Closely allied to *Ypsilopus amaniensis* (Kraenzl.) D'haijère & Stévart from eastern Africa but differs in having longer leaves (80–130 mm vs 35–115 mm in *Y. amaniensis*), inflorescences that greatly exceed the leaves, bearing 10–13 flowers (vs 5–8 in *Y. amaniensis*), and having a longer peduncle (45–70 mm vs 10–15 mm) and rachis (120–170 mm vs 50–80 mm).

Description. Robust, erect or rarely pendent, lithophytic or epiphytic herb, often forming clumps. Roots emerging through the leaf bases opposite the leaves, stout, 8–9 mm in diameter, branching distally, silvery grey. Stems 20–30 or more cm long, 7–9 mm in diameter, covered with sheathing leaf bases. Leaves rigidly coriaceous, 12–16, distichous, twisted just above the basal articulation to lie in one plane, linear-oblong, unequally roundly lobed at the apex, conduplicate at base just above the leaf sheath, 80–130 × 12–19 mm, deep olive-green, articulated to 10–17 mm long leaf sheath. Inflorescences longer than the leaves, arching to pendent, secund in two ranks, 1-several, from leaf sheaths 30–50 mm below the stem apex, 17–23 cm long, 10–13-flowered; peduncle cylindrical, 45–70 mm long, bearing 2–4 sheathing sterile bracts, 5–8 mm long; rachis slenderly cylindrical, slightly zigzag, 12–17 cm long; floral bracts cucullate, ovate, subacute, 6–8 × 4–8 mm. Flowers 22 × 28 mm, showy, white with a buff-tinged spur, the basal flower opening last, diurnally and nocturnally scented of vanilla; pedicel and ovary 22–25 mm long, the ovary scabrid. Sepals and petals reflexed at anthesis. Dorsal sepal linear-elliptic, acuminate, 15–20 × 1.5–2 mm. Lateral sepals similar. Petals narrowly linear-tapering, acuminate, 14–15 × 1–1.5 mm. Lip 3-lobed in the middle, 15–16 × 5–6 mm; side lobes obliquely oblong, truncate, 8–9 × 2–3 mm; midlobe linear-tapering, acuminate, 7–8 mm long; spur pendent, narrowly cylindrical from a narrow mouth, 110–140 mm long. Column 5 mm long, glandular; anther cap giving the tip of the column a hooked appearance; pollinia 2, stipes bifid with linear lobes; viscidium oblong.

Distribution. Endemic to the Central Watershed of Zimbabwe, in the inselbergs of the southern middleveld margin of the Zimbabwe Craton, west of the Save River, in Masvingo Province (Fig. 1).

Habitat. Epiphyte or lithophyte on inselberg partly-shaded bare rock surfaces; 1000–1300 m.

Phenology. Flowers in the rainy season, from December to February.

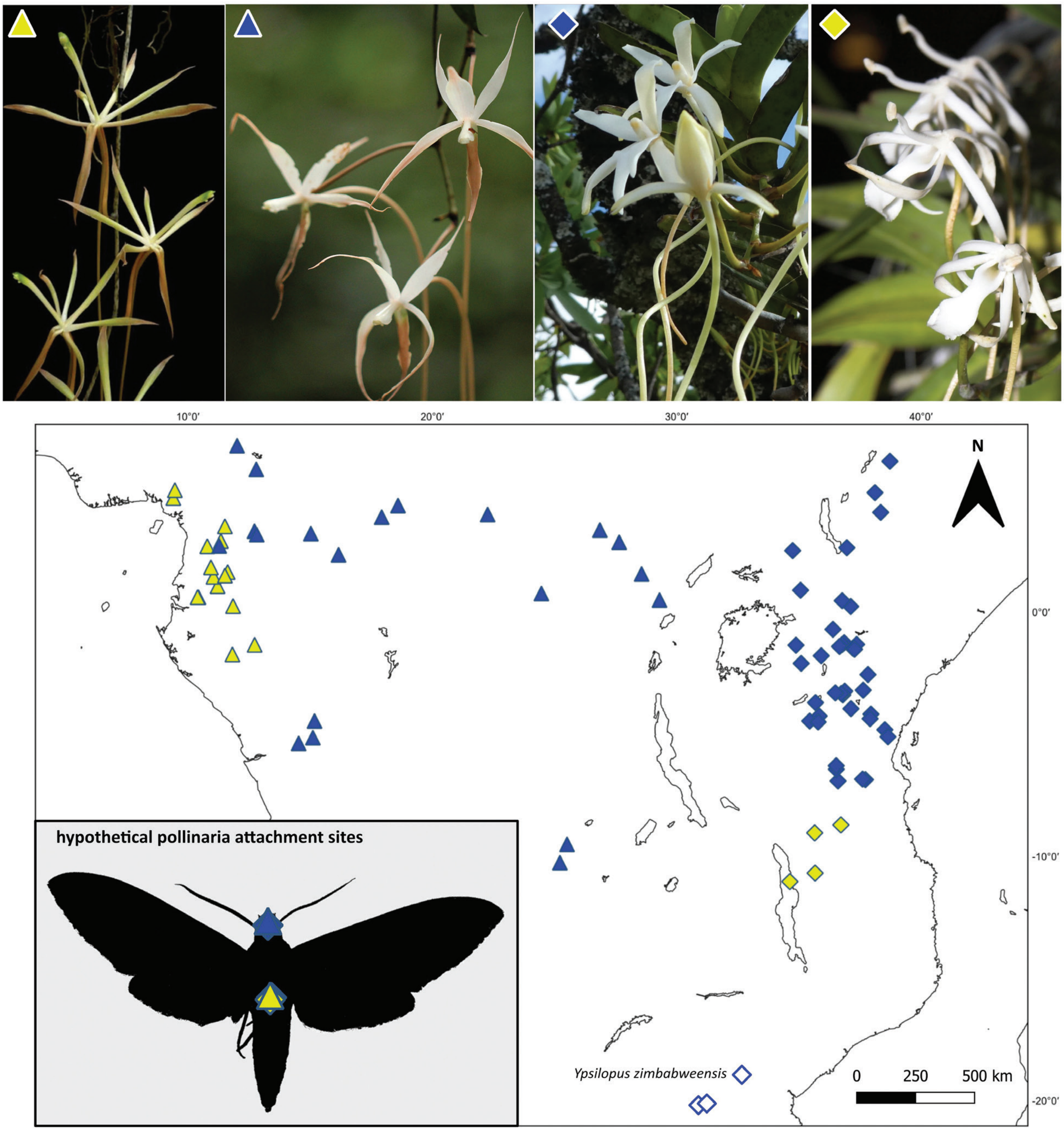

Figure 1. Possible evidence for reinforcement in the geographical distribution and hypothetical pollinaria attachment sites (on a large sphingid hawkmoth) of two angraecoid clades with divergent column exsertion lengths in tropical Africa. *Aerangis gracillima* (yellow triangles) is closely allied to *A. stelligera* (blue triangles), while *Ypsilopus amaniensis* (blue diamonds) is closely related to *Y. schliebenii* (yellow diamonds). An extremely elongated *Barombia*-type column is present in *A. gracillima* and *Y. schliebenii*. The three isolated collections of *Y. amaniensis* in Zimbabwe are here assigned to *Ypsilopus zimbabweensis* (white diamonds). Photos by Murielle Simo-Droissart (*A. gracillima*), Bart Wursten (*A. stelligera*), Guido van Asten (*Y. amaniensis*), and Russell Hutton (*Y. schliebenii*).

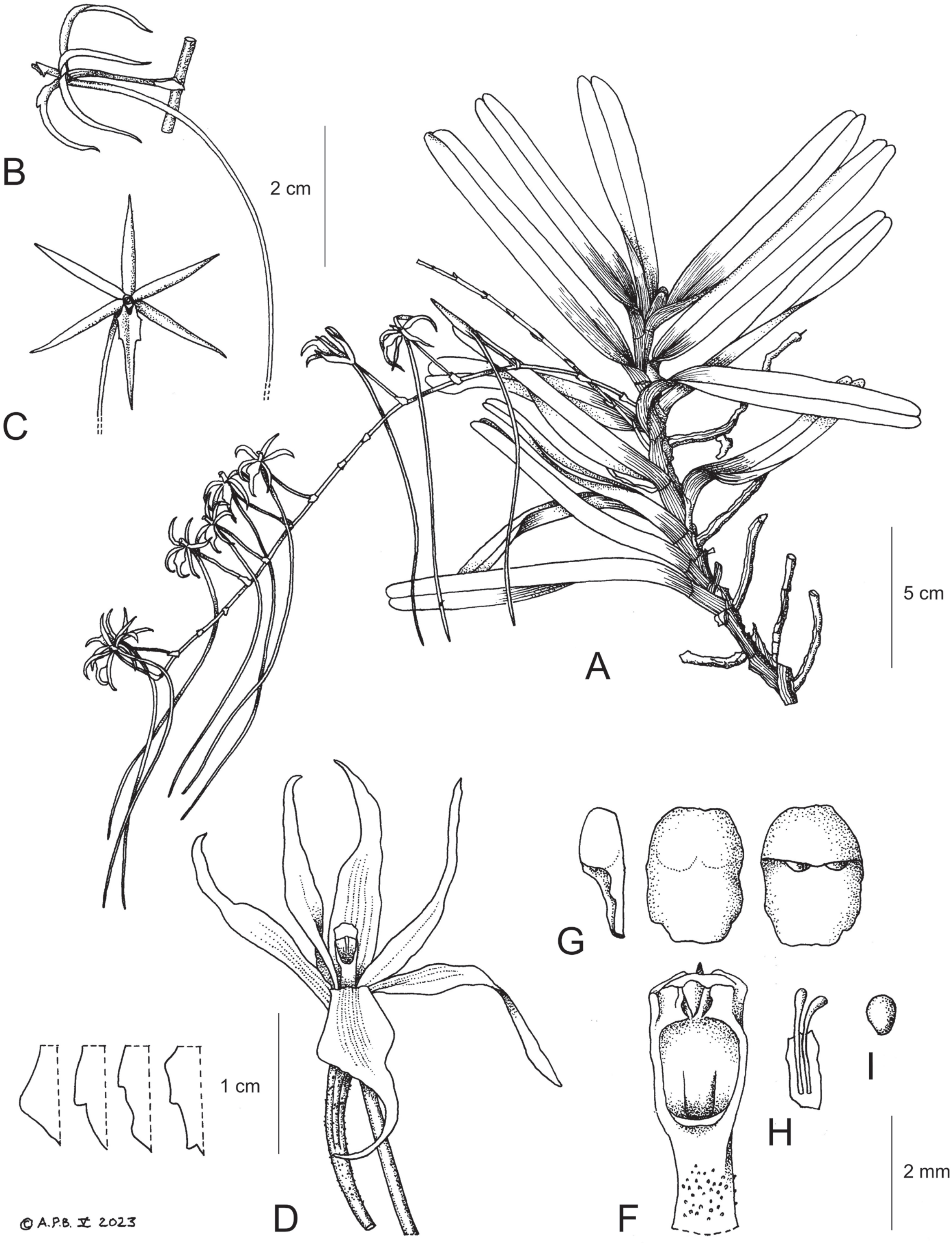

Figure 2. *Ypsilopus zimbabweensis*. **A**. Habit. **B**. Flower, side view. **C**, **D**. Flower, front view. **E**. Lip margin variability. **F**. Column, ventral view, with glandular trichomes visible. **G**. Anther cap, side, dorsal, and ventral views. **H**. Viscidium and stipes. **I**. Pollinium (one of two). A (in part), E (in part), F–I drawn from the type collection; A, E (both in part) and I from *Jackson 56814*; B, C after watercolour by Patricia van de Ruit. All drawn by Andrew Brown.

Figure 3. Watercolour of *Ypsilopus zimbabweensis*, originally identified as *Rangaeris amaniensis*, by Patricia van de Ruit, published in Ball (1978: 1394). Reproduced with permission.

Etymology. The species is only recorded from Zimbabwe, namely from the area around the Great Zimbabwe National Monument, which gives the country its name.

Additional material (paratypes). ZIMBABWE • **Masvingo** [Victoria District], Mt Morgenster; 1000 m (3500 ft); fl. in cult. Harare [Salisbury]; 24 Jan. 1956; *R.W. Jackson 56814*; K!, SRGH • Masvingo, 16 km NW of Ndanga; 29 Dec. 1976; *L.J. Mullin* in *GHS 25198*; SRGH!.

Preliminary IUCN conservation assessment. The species is given a Red List status of Endangered: EN B1ab(v)+B2ab(v). *Ypsilopus zimbabweensis* is known from three collections and one observation (https://www.inaturalist.org/observations/143791156) made between 1956 and 2012, representing four occurrences and three locations, including one within the Great Zimbabwe National Monument, a Cultural World Heritage Site. The extent of occurrence (EOO) is 132.1 km^2 and the area of occupancy (AOO) is 16 km^2. The EOO and AOO fall within the limits of the Endangered (CR) category under subcriteria B1 and B2. Since this species occurs only in three locations and a decline of mature individuals is projected because of illegal collection for the orchid trade, it meets condition b(v) for the EN category.

Notes. *Ypsilopus amaniensis* is to be excluded from Flora Zambesiaca, since all regional occurrences correspond to *Y. zimbabweensis*, namely the recent records illustrated on the Flora of Zimbabwe website (Hyde et al. 2023). Specimens identified as *Angraecum* sp. in the inselbergs of Zimbabwe (Seine et al. 1998) are also possibly ascribable to *Y. zimbabweensis*. Patricia van de Ruit's fine watercolour illustration of this species (as *Rangaeris amaniensis*) is reproduced here (Fig. 3). Iconography produced by the same artist, for the same book, was instrumental to the description of another new orchid from Zimbabwe (Farminhão and Cribb 2020). The new species is also illustrated here with a line drawing by Andrew Brown (Fig. 2) and a photograph in la Croix and la Croix (1997), reproduced here (Fig. 3). The novelty has been widely cultivated and misidentified as *Rangaeris amaniensis* by hobbyists in Zimbabwe, South Africa, Australia, and Europe.

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Figure 4. *Ypsilopus zimbabweensis*. **A**. Plants growing as lithophytes in situ. **B**. Inflorescence, side view, of plant cultivated in Harare. Photos by Bart Wursten (A) and Isobyl la Croix (B).

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