



***Gastrodia madagascariensis* (Gastrodieae, Orchidaceae): from an historical designation to a description of a new species from Madagascar**

FLORENT MARTOS, STEVEN D. JOHNSON & BENNY BYTEBIER

School of Life Sciences, University of KwaZulu-Natal Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa;
e-mail: florentmartos@gmail.com

Abstract

Gastrodia madagascariensis, a leafless achlorophyllous orchid, is described and illustrated here. The epithet was originally coined by Perrier de la Bâthie in 1939 for fruiting material found on the eastern coastal plain of Madagascar more than a century ago, but the name was never validly published. This new species is closely related to *G. similis* from Reunion Island, from which it can be distinguished by the perianth tube spreading towards the apex, the shape of the column and stigma, and the flower colour. The achlorophyllous genus *Gastrodia* currently comprises five species in the tropical parts of the Afro-Madagascan region, one of which, *G. africana*, is possibly extinct. We provide an artificial key to distinguish them. In addition, there is also an extratropical species in continental Africa, the introduced *G. sesamoides* (very local near Cape Town, South Africa).

Keywords: *Didymoplexis*; Flora of Madagascar; myco-heterotrophy; Perrier de la Bâthie

Résumé

Gastrodia madagascariensis, une orchidée aphyllé non-chlorophyllienne, est décrite et illustrée ici. L'épithète fut initialement proposé par Perrier de la Bâthie en 1939 pour décrire une plante en fruit trouvée dans la même région côtière de Madagascar il y a plus d'un siècle, mais sa publication était alors invalide. Cette nouvelle espèce est proche de l'espèce *G. similis* endémique de l'Île de la Réunion, mais s'en distingue toutefois par un calice campanulé, la forme de la colonne et du stigmate, ainsi que la couleur de la fleur. Le genre non-chlorophyllien *Gastrodia* comprend aujourd'hui cinq espèces en Afrique tropicale et à Madagascar; l'une d'entre elles, *G. africana*, étant probablement éteinte. Une clé d'identification de ces espèces est proposée ici. De plus, on recense une sixième espèce sur le continent africain, c'est-à-dire l'espèce introduite *G. sesamoides* (près de la ville du Cap, Afrique du Sud).

Mots-clés: *Didymoplexis*; Flore de Madagascar; myco-hétérotrophie; Perrier de la Bâthie

Introduction

Just before his untimely death on 16 November 1925, Rudolf Schlechter (1925) published “Orchidaceae Perrierianae”, in which he enumerated all the orchids from Madagascar known until then. Out of the 446 taxa mentioned, 332 were described by Schlechter himself, all based on material collected by H. Perrier de la Bâthie (hereinafter referred to as Perrier) and sent to Schlechter in Berlin for naming. Amongst the specimens studied by Schlechter was a leafless orchid lacking chlorophyll collected in September 1912 and numbered *Perrier de la Bâthie 11349*. Schlechter assigned it to the genus *Gastrodia* Brown (1810: 330) and was convinced that it was a new species, but refrained from describing it, because only fruiting and no flowering material was sent to him.

After the death of Schlechter, Perrier took it upon himself to continue documenting the orchid flora of Madagascar. This eventually resulted in a 2-volume treatment of the orchid family for “Flore de Madagascar”, published in 1939 and in 1941 respectively. In the first volume of this work, he proposed the name *Gastrodia madagascariensis* (Perrier de la Bâthie 1939: 212) based on the above-mentioned specimen. However, he only provided a description in French and therefore the name was not validly published according to Art. 39.1 of the International Code of Nomenclature (McNeill *et al.* 2012), which at the time required a description or diagnosis in Latin.

Summerhayes must not have realised that the name was not validly published when he proposed to transfer it to the genus *Didymoplexis* Griffith (1844: 383), as *D. madagascariensis* (H.Perrier) Summerhayes (1953: 131). He was of the opinion that it was better placed in this genus on the basis of the “appreciable elongation of the fruiting pedicels”, a characteristic he had also observed in his recently described *D. africana* Summerhayes (1951: 465), but not in any of the other 13 species of *Gastrodia* then at his disposition in the Kew Herbarium. Our understanding of the Gastrodieae has since improved considerably and we know now that the lengthening of the pedicel also occurs in *Gastrodia* (Kores *et al.* 2006). Indeed, Cribb *et al.* (2013) pointed out that it is extremely difficult to distinguish between the genera *Gastrodia* and *Didymoplexis* on the basis of fruiting material only, since both produce oblong capsules borne on slender pedicels that elongate during fruit maturation. The distinction can only be made from the observation of flowers. *Didymoplexis* has a short floral tube (if present) and four granular pollinia, whereas *Gastrodia* has sepals adnate for more than half their length forming a long perianth tube and two sectile pollinia (Kores *et al.* 2006). According to Kores *et al.* (2006) the stigma in *Gastrodia* is borne on a raised projection at the base of the column, whereas in *Didymoplexis* the stigma is situated directly below the rostellum.

No flowering plants referable to either *Didymoplexis* or *Gastrodia* were seen in Madagascar for almost a century, until Louis Nusbaumer with Patrick Ranirison, Mark Clements with Anne Mackenzie, Jean-Michel Hervouet, and Jean-Philippe Castillon, collected or photographed flowering specimens of *Didymoplexis* in 2005, 2006, 2007 and 2010 respectively (Cribb *et al.* 2011, 2013). At first these were assumed to represent the long lost *Gastrodia/Didymoplexis madagascariensis* of Perrier (Cribb & Hermans 2009, Bosser & Lecoufle 2011) until it became clear that at least three taxa of *Didymoplexis* occur in Madagascar. Cribb *et al.* (2011) first identified Castillon’s photograph as *D. verrucosa* Stewart & Hennessy (1980: 841), previously only known from the KwaZulu-Natal Coast of South Africa. Two new species were then described, *D. avaratraensis* P.J.Cribb, Nusb. & L.Gaut. in Cribb *et al.* (2013: 43), and *D. recurvata* P.J.Cribb, Nusb. & L.Gaut. in Cribb *et al.* (2013: 44), based on herbarium collections of Nusbaumer and Ranirison. The photographs of Clements and Mackenzie, and Hervouet, illustrate the former species. Cribb *et al.* (2013) also discussed the confusion around the application of the name *D. madagascariensis*. Since none of the above-mentioned taxa could be directly linked to the material collected by Perrier in 1912, the epithet *madagascariensis* was not used and was left associated with the *Perrier de la Bâthie 11349* specimen.

In August 2013, one of us (FM) found several flowering plants of a taxon clearly belonging to *Gastrodia*. We here describe it as a new species, and as we have good arguments to link it to the original Perrier material, we propose to use Perrier’s original designation. In addition, we provide an artificial key to identify the species of *Gastrodia* found in the tropical Afro-Madagascan region.

Taxonomy

Gastrodia madagascariensis H.Perrier ex Martos & Bytebier, *sp. nov.* (Figs 1–2)

TYPE:—MADAGASCAR. Toamasina: Manompana village, Ambodiriana Forest, elev. 145 m, 16°40′21.30″S, 49°42′8.52″E, 16 August 2013, *Martos 906* (holotype NU (spirit)!, isotype TAN!).

Diagnosis:—Similar to *Gastrodia similis* Bosser (2006: 52), from which it can be distinguished by the perianth tube spreading towards the apex, the cordate stigma, and the emerald green lip colour.

Slender, leafless, achlorophyllous herb. Rhizome subterranean, fleshy, fusiform, villose to tomentose, 20–50 × 3–7 mm, densely noded; adventitious roots up to 300 × 1 mm. Peduncle erect, 100–300 mm tall, glabrous, dark brown to blackish, with 3–4 tubular sheaths in the lower half; sheaths 3–6 mm long, truncate and with an abrupt acumen 3–4 mm long. Inflorescence racemose, with (1–)3–12 flowers, rachis 10–40 mm long; bracts lanceolate to ovate, acute, 6 × 3 mm. Pedicel slender, twisted, 5–8 mm long. Flowers resupinate, campanulate, spreading; sepals and petals dull brown adaxially, light brown or reddish brown abaxially, blackish brown at apex; lip yellow-orange, tinged with emerald green at apex; two tubercular processes borne on the column-foot emerald green. Sepals fleshy, ovate, obtuse, 12–14 × 7–9 mm, connate for about two thirds of their length except between the lateral sepals where the fusion only reaches halfway, verrucose adaxially, wrinkled abaxially. Petals slightly fleshy, broadly ovate, obtuse, 5–6 × 3–4 mm, adnate to the sepals and forming a floral tube together with them. Lip inserted at the apex of the column-foot, free from other perianth parts, completely enclosed within perianth tube, fleshy, broadly ovate, 7–8 × 3–4 mm, broadly acuminate, papillose; base shortly clawed; margin ascending on the sides; adaxial side transversely wrinkled and bearing two

apical incurved ridges which are somewhat V-shaped, the tip of the V lengthening towards the front; abaxial side canalliculate. Column elongate, 6–7 mm tall, narrowed at base, winged distally, with a tooth-like appendage on either side of the column at apex; foot incurved, with a pair of cephaloid tubercular processes at apex; anther subcircular, $\pm 1.2 \times 0.4$ mm, broadly rounded at the front; pollinia 2, granular, composed of friable massulae, attached to a shared viscidium; stigma borne on a raised projection at base, cordate. Ovary trigonous, obconical, ± 5 mm long. Capsule erect, ovoid, $\pm 25 \times 5$ mm, borne on a pedicel elongating up to 40 cm during fruit maturation.

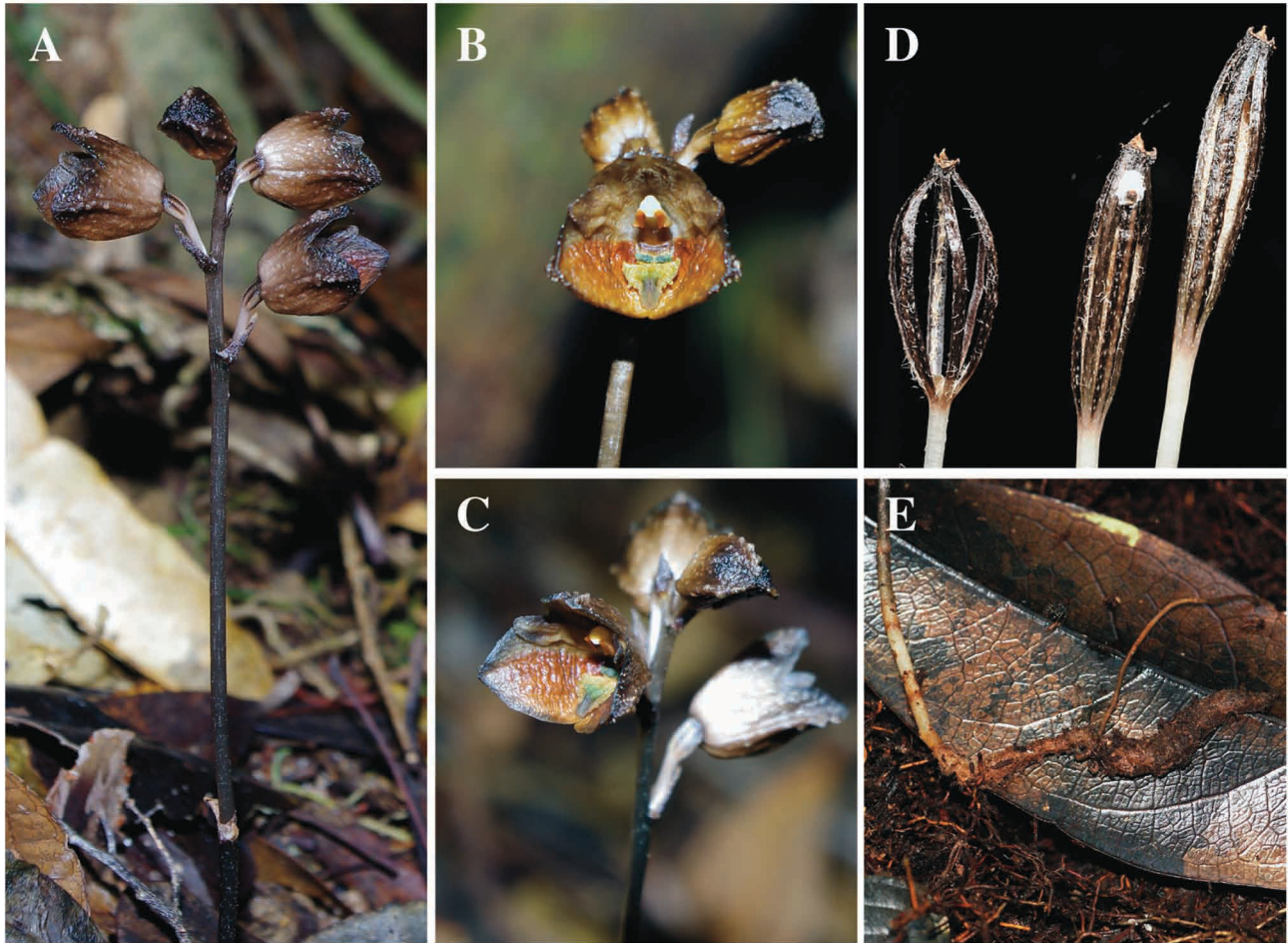


FIGURE 1. *Gastrodia madagascariensis*. **A.** Habit; note the dark color of the peduncle contrasting with the whitish pedicels, and the dark colour of the perianth tube at the apex. **B.** Open flower, front view; note the perianth tube spreading towards the apex, and the reddish brown (bottom half) and light brown (top half) colour of the perianth tube on the inner surface. **C.** Open flower, three quarter view; note the emerald green colour of the lip tip and of two tubercular calli borne on the column-foot (also seen on **B**). **D.** Dehiscent capsules borne on elongated fruiting pedicels. **E.** Fusiform rhizome with fine adventitious roots. Photographs: A.Charbouillot (**A–C**) and J.-M.Hervouet (**D**).

Distribution and habitat:—*Gastrodia madagascariensis* is only known from Ambodiriana Forest near Manompana (Fig. 3). Here, it grows in evergreen, humid forest below 200 m and is more commonly found in the vicinity of the river Manompana and its tributaries.

Conservation:—Since 1996, Ambodiriana Forest is protected by a non-governmental organisation, namely the *Association de Défense de la Forêt d’Ambodiriana* (ADEFA). However, slash-and-burn deforestation is common along this part of the coast of Madagascar, and Ambodiriana Forest is situated less than two km away from the nearest rice fields and seven km from Manompana village. In addition, the fact that the *Gastrodia* orchids require specific mycorrhizal associations for carbon uptake throughout their life cycle (Martos *et al.* 2009, Selosse *et al.* 2010, Selosse & Martos 2014) renders them extremely vulnerable to habitat disturbance. In August 2013, less than 50 flowering plants were seen throughout Ambodiriana Forest, covering an area of approximately 2.25 km² and we are at present not aware of any other locality where this species persists. Therefore, *G. madagascariensis* is considered “Critically Endangered” according to the IUCN Red List Categories and Criteria (IUCN 2014).

Etymology:—The epithet *madagascariensis* refers to Madagascar, where this species is endemic.

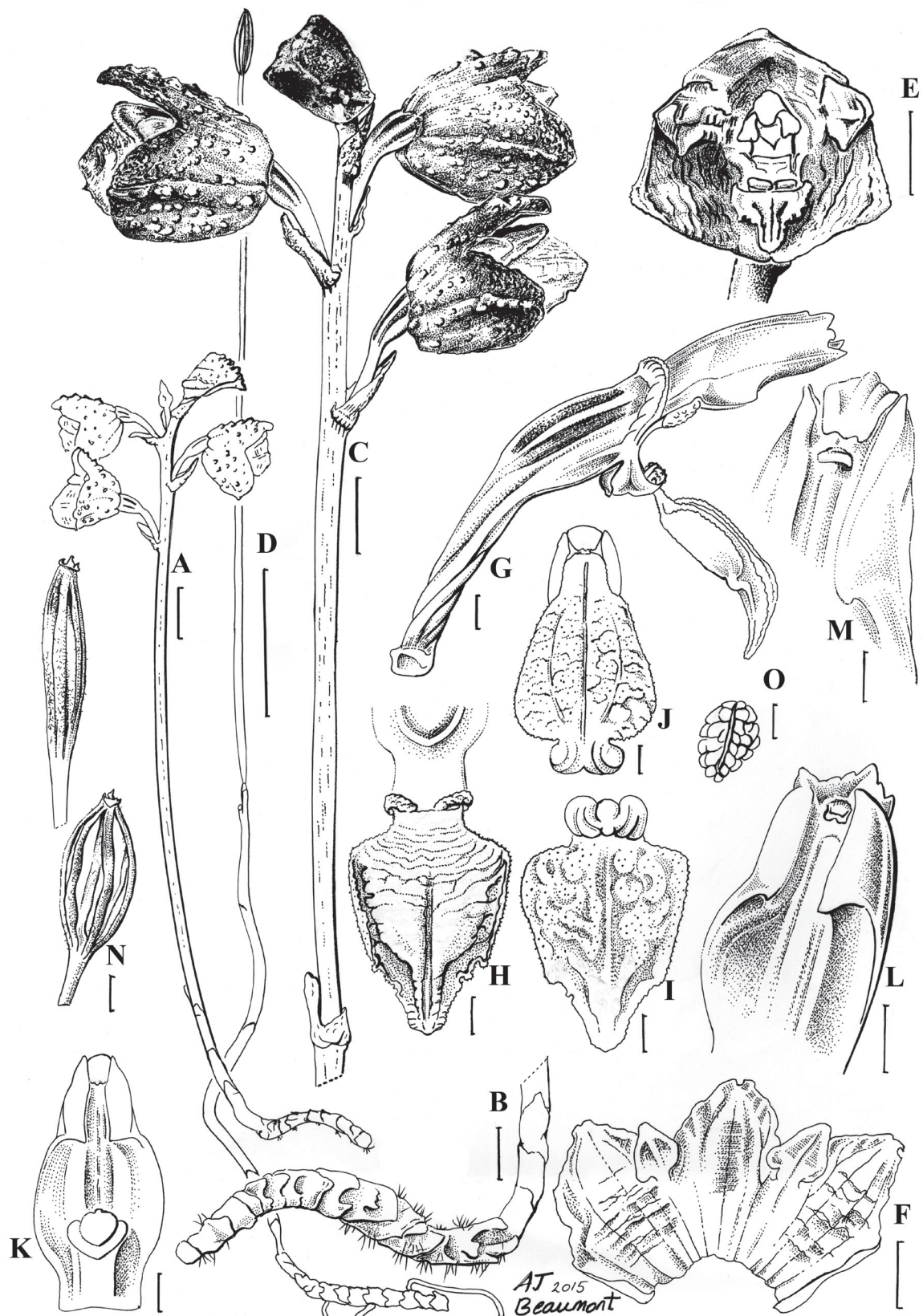


FIGURE 2. *Gastrodia madagascariensis*. **A.** Habit (inflorescence with rhizome). **B** Detail of rhizome. **C.** Detail of inflorescence. **D.** Elongating pedicel. **E.** Open flower, front view. **F.** Sepals and petals flattened. **G.** Pedicel, ovary, column and lip, side view. **H.** Lip (adaxial) and base of column. **I.** Lip (abaxial). **J.** Lip (abaxial) appressed to column. **K.** Column (adaxial). **L.** Detail of column apex without anther cap. **M.** Detail of column apex with anther cap. **N.** Fruits. **O.** Pollinia. **A–C, E–M** from *Martos 906*; **D, N, O** from photographs. Scale bars: **A,** 10 mm; **B–C, E–F, N,** 5 mm; **D,** 50 mm; **G–L,** 1 mm; **M, O,** 0.5 mm. Drawn by A.J.Beaumont.

Phenology:—*Gastrodia madagascariensis* flowers during the cooler, drier season between July and August. Fruiting occurs from August and throughout September.

Other specimens examined:—MADAGASCAR. Toamasina: Fandrarazana River basin (N. E.), elev. 200 m, September 1912, *Perrier de la Bâthie 11349* (P [barcode P00540570] digital image!) (in fruit stage).

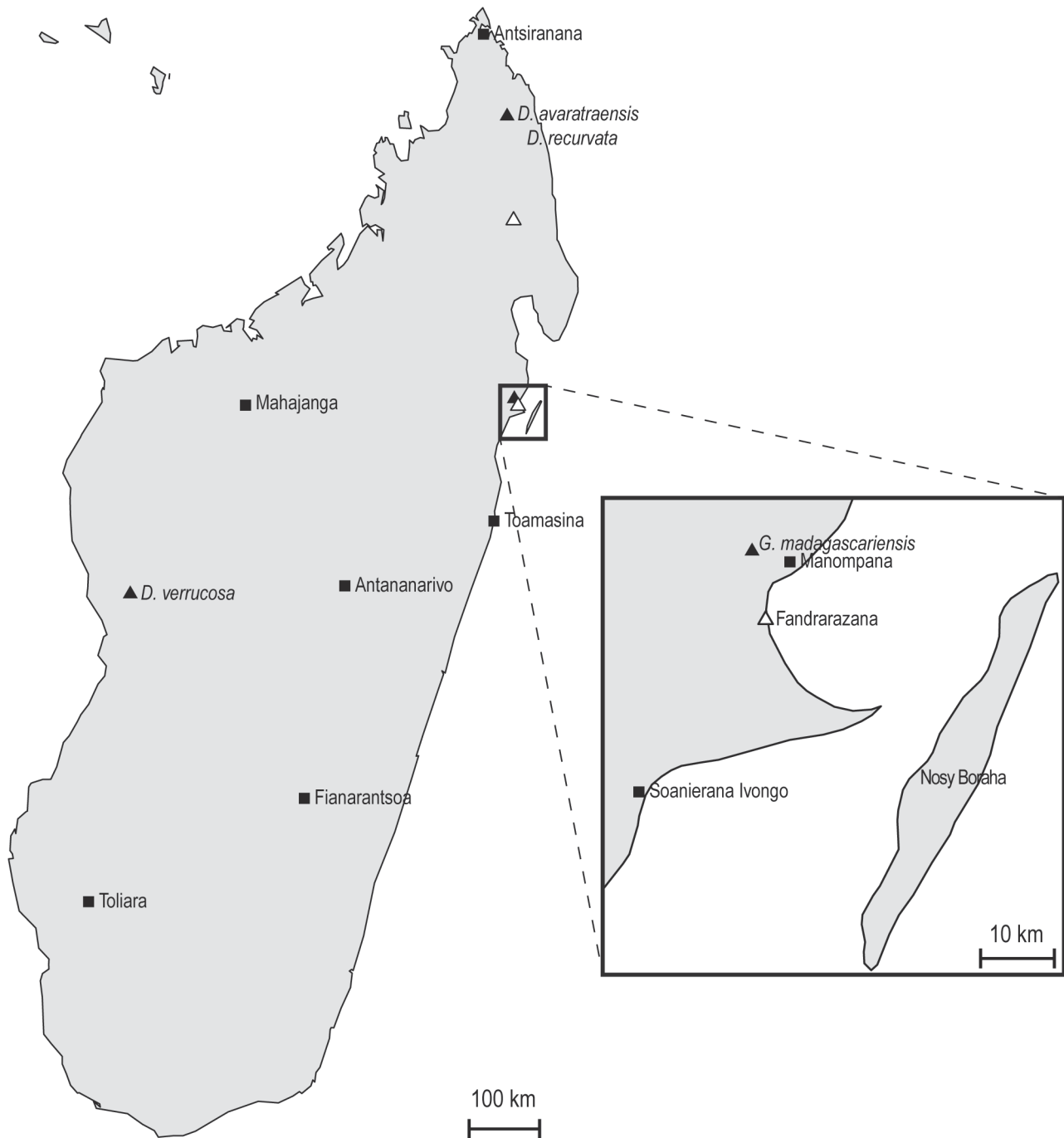


FIGURE 3. Map of Madagascar showing the distribution of the various observations of Gastrodieae on the island. *Didymoplexis avaratraensis* and *D. recurvata*, both endemic to Madagascar, co-occur in the northern province of Antsiranana, in evergreen wet forest at mid elevation (Cribb *et al.* 2013). *Didymoplexis verrucosa*, also known from South Africa, was recently photographed in the western province of Mahajanga, in deciduous seasonally dry forest (Cribb *et al.* 2011). *Gastrodia madagascariensis* occurs in the eastern province of Toamasina opposite the island Nosy Boraha, in evergreen wet forest at low elevation. Filled triangles: flowers observed. Open triangle: only fruits observed.

Keys to the species of *Gastrodia* R.Br. in the tropical Afro-Madagascan region (modified from Cribb *et al.* 2010)

1. Flowers greenish; sepals free for half their length; dorsal sepal markedly shorter than the lateral sepals; petals spatulate; lip with two rugulose calli at base of midlobe *G. africana*
- Flowers brownish to rarely white; sepals free in apical third only; sepals of equal length; petals ovate or broadly ovate; lip lacking two rugulose calli at base of lip midlobe 2.
2. Callus on lip of three ridges, the middle one highest; column foot with two brownish calli at apex *G. rwandensis*
- Callus on lip V-shaped, the tip of the V at base of lip midlobe; column foot with two cephaloid tubercular processes at apex 3.
3. Perianth tube uniformly brown; lip yellow-green with an apricot tip *G. ballii*
- Perianth tube not uniformly brown; lip yellow-emerald green or orange-green with an emerald green or whitish tip 4.
4. Perianth tube brownish to blackish brown towards the tips; lip yellow-emerald green with a darker tip; cephaloid tubercular processes emerald green *G. madagascariensis*
4. Perianth tube brownish to translucent white towards the tips or uniformly white; lip orange-green with a whitish-yellowish tip; cephaloid tubercular processes white *G. similis*

Discussion

The discovery of a flower of *Gastrodia* on the eastern coastal plain of Madagascar raises the question of its relation to Perrier's fruiting specimen found more than a century ago. From a geographical perspective, the type locality of *G. madagascariensis* is less than 10 km in a straight line from Perrier's presumed locality in the basin of the river Fandrarazana (Fig. 3). The vegetation in both places is dense evergreen forest with a canopy not exceeding 30 m and an understory only allowing for the growth of shade-tolerant plants such as *G. madagascariensis*. After one of us (FM) observed flowering plants of *G. madagascariensis* for the first time in August 2013, fruiting plants of what may well be the same species of *Gastrodia* were seen and photographed in August and September 2014 (J.M.Hervouet, pers. comm.), in a palm forest in the vicinity of the mouth of the river Fandrarazana i.e. Perrier's presumed locality (16°45'32.8"S; 49°43'26.9"E; elev. 20 m) (Fig. 3).

Besides the geographical proximity between our type and Perrier's locality, the phenology of *G. madagascariensis* is consistent with Perrier's observation of plants being already in fruit by September. Indeed, with the help of C.Misandeau and A.Kaloloha (*ADEFA*), we have been monitoring the orchid population at the type locality between 2008 and 2014, and *G. madagascariensis* consistently appears above ground during the austral winter between July and September. Although flowering shoots can sometimes already be seen in July, the flowering peak is usually during the first two weeks of August, after which plants will be fruiting throughout September, the month in which Perrier collected his specimen. As for any of the taxa of *Didymoplexis* occurring in Madagascar (Fig. 3), the current understanding of their reproductive phenology indicates that they are seen above ground only during the austral summer between November and December (Cribb *et al.* 2013). Thus it is unlikely that the fruiting plant that Perrier found in September 1912 belongs to any of the Madagascan taxa of *Didymoplexis*.

On the basis of the above two considerations, we argue here that Perrier's specimen is conspecific with ours. The suggestion by Cribb *et al.* (2013) that only molecular comparison could settle the matter is fraught with several difficulties. As far as we are aware, there is only one extant duplicate of *Perrier de la Bâthie 11349*, preserved in Paris (P), as the material sent to Schlechter in Berlin for naming was destroyed during the bombing of the Berlin Herbarium during the night of 1–2 March 1943. Furthermore, the little material that is available is more than 100 years old, and the chloroplast loci used for DNA barcoding such as *rbcL* and *matK* do not amplify in this achlorophyllous orchid tribe (but see Smidt *et al.* 2015 for amplification of nuclear ITS in the closely allied genus *Uleiorchis* Hoehne 1944: 129), so that any attempt to retrieve DNA sequences from that specimen may prove to be fruitless.

Gastrodia madagascariensis is undoubtedly closely related to *G. similis*, endemic to Reunion Island in the Mascarene Archipelago (Bossert 2006, Martos *et al.* 2009, 2015). Except perhaps for the darker (often blackish) peduncle observed in *G. madagascariensis* (Fig. 1A), these two species are almost indistinguishable before anthesis. At anthesis, the two species can be easily distinguished by the shape of the perianth tube which is almost campanulate in *G. madagascariensis* (Fig. 4A), whereas it is urceolate in *G. similis* (Fig. 4B). The stigma, borne on a raised projection at the base of the column in both species, is clearly cordate in *G. madagascariensis* (Figs 2K, 4E), whereas it is broadly ovate in *G. similis* (Bossert 2006). Flower colour is also a distinguishing feature between the Afro-Madagascan species of *Gastrodia* (Cribb *et al.* 2010). The cephaloid tubercular processes at the apex of the column-foot are emerald green in *G. madagascariensis* (Figs 1B, 4C) but whitish in *G. similis* (Fig. 4D), and the two apical incurved ridges forming a V at the tip of the lip are darker in *G. madagascariensis* (Fig. 4C).

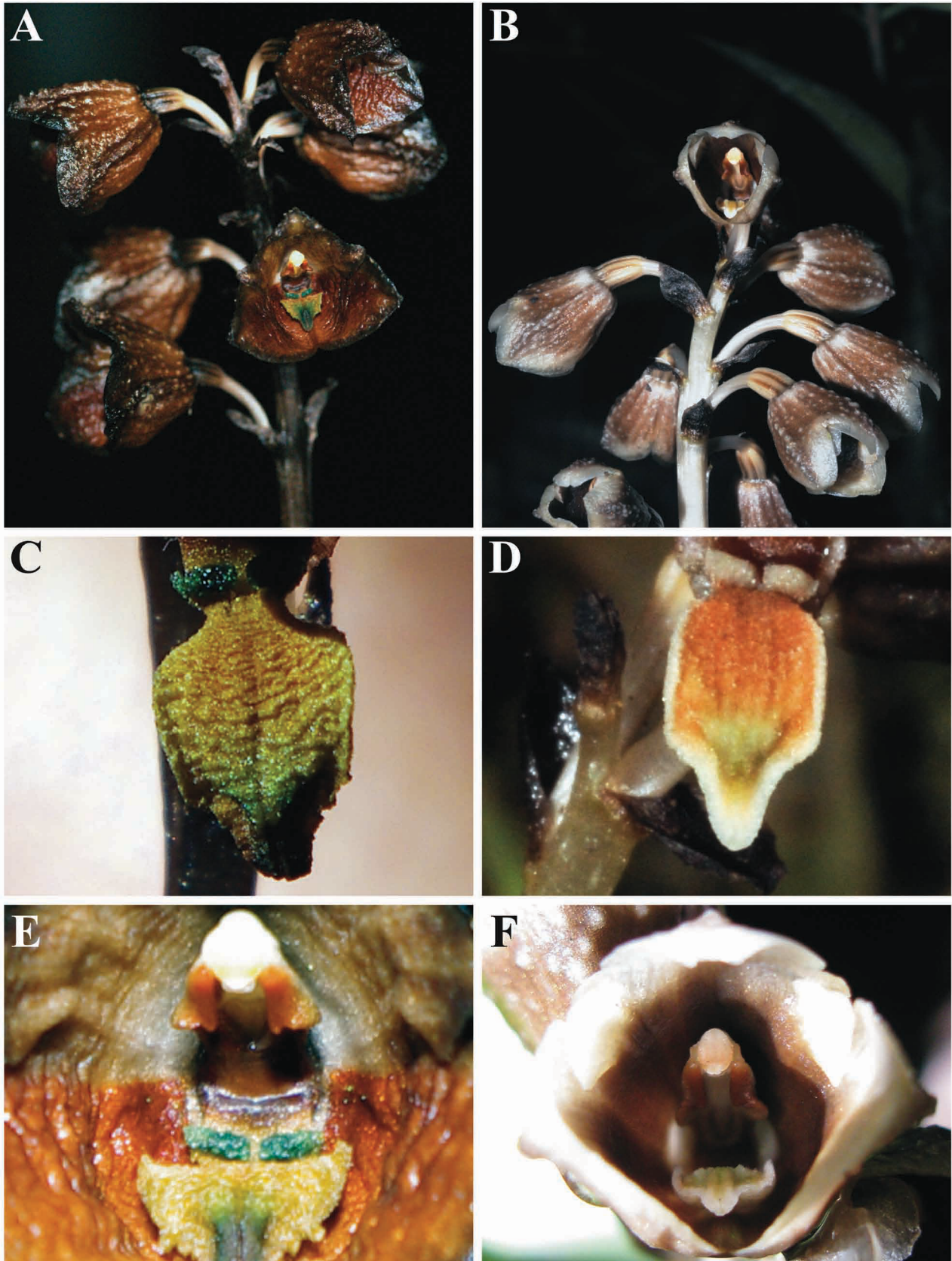


FIGURE 4. Morphological comparison between the Madagascan species *Gastrodia madagascariensis* (A, C & E) and a closely related species from Reunion Island, *G. similis* (B, D & F). A–B. Inflorescence; note the difference between the perianth tube spreading at the apex in A or urceolate in B. C–D. Lip and pair of tubercular processes at the apex of the column-foot; note the difference between the emerald green and whitish coloration in C and D, respectively. E–F. Column with lip attached to its foot; note the difference between the cordate and ovate stigma in E and F, respectively. Photographs: A.Charbouillot (C & E), D.Caron (F).

In continental Africa, *Gastrodia africana* Kraenzlin (1900: 179), endemic to Mount Cameroon where it is possibly extinct (Cable & Cheek 1998), was the only known species in this genus until recently. However, two mainland species of *Gastrodia* were recently described: *G. ballii* P.J.Cribb & Browning in Cribb *et al.* (2010: 317) known to occur in a small area on the Mozambique/Zimbabwe border and also in southern Malawi; and *G. rwandensis* Fischer & Killmann in Cribb *et al.* (2010: 317) that is only known from the type locality in Rwanda. With *G. madagascariensis* the new species endemic to Madagascar, there are now five species of *Gastrodia* in the tropical Afro-Madagascan region. Although the two island species, *G. similis* and *G. madagascariensis*, are distinguished from the mainland species in several respects (see character descriptions in Cribb *et al.* 2010), they share a distinctive character with the southern African species *G. ballii*; that is, a pair of cephaloid tubercular processes borne on the apex of the column foot (Figs 4C, 4D).

Conclusion

Since the recent treatment of *Gastrodia* in Genera Orchidacearum (Kores *et al.* 2006), the number of species has increased considerably from approximately 20 to 50 species (Hsu & Kuo 2010, 2011, Yeh *et al.* 2011, Hsu *et al.* 2012, Tan *et al.* 2012, Suetsugu 2013, 2014, Hu *et al.* 2014), making it the most diverse genus in the orchid tribe Gastrodieae. In view of that, investigations into nuclear and mitochondrial markers that would suitably resolve the phylogenetic relationships between the *Gastrodia* species found in the Asia-Pacific and the Afro-Madagascan region are now needed.

Acknowledgements

We thank C.Misandeau (President of ADEFA) for authorizing this study in Ambodiriana Forest; A.Kaloloha and J.E.Lemarina (ADEFA) for monitoring the orchid population since 2008 and for valuable field assistance in Ambodiriana Forest; S.Rapanarivo and J.Andriantiana (*Parc de Tsimbazaza*; TAN) for hospitality and assistance in their herbarium; J.-M.Hervouet (*Société Française d'Orchidophilie*) for sharing with us localities and photographs; A.Beaumont for preparing the illustration of *G. madagascariensis*; C.van den Berg who edited this paper, as well as two anonymous reviewers, for their useful comments. FM was funded by the Claude Leon Foundation as part as a postdoctoral fellowship in South Africa. BB and SDJ acknowledge financial support from the National Research Foundation (NRF).

References

- Bosser, J. (2006) Contribution à l'étude des Orchidaceae de Madagascar, des Comores et des Mascareignes — XXXV Description d'un *Oeceoclades* nouveau de Madagascar, et notes sur trois genres nouveaux pour les Mascareignes. *Adansonia*, sér. 3 28: 52–53.
- Bosser, J. & Lecoufle, M. (2011) *Les Orchidées de Madagascar*. Biotope (collection Parthénope), Mèze, France, 496 pp.
- Brown, R. (1810) *Prodomus Florae Novae Hollandiae, et insulae van Diemen*. Johnson, London, 446 pp.
- Cable, S. & Cheek, M. (1998) *The plants of Mount Cameroun. A conservation checklist*. Royal Botanic Gardens, Kew, 277 pp.
- Cribb, P.J., Fischer, E. & Killmann, D. (2010) A revision of *Gastrodia* (Orchidaceae: Epidendroideae; Gastrodieae) in tropical Africa. *Kew Bulletin* 65: 315–321.
<http://dx.doi.org/10.1007/s12225-010-9193-4>
- Cribb, P.J., Gautier, L. & Nusbaumer, L. (2013) How many species are there in the holomycotrophic genus *Didymoplexis* Griff. (Orchidaceae) in Madagascar? *Candollea* 68: 41–49.
<http://dx.doi.org/10.15553/c2013v681a3>
- Cribb, P.J., Gautier, L., Trigui, S. & Nusbaumer, L. (2011) Two new records of Orchidaceae from Madagascar, with an updated list of species shared with continental Africa. *Candollea* 66: 413–416.
<http://dx.doi.org/10.15553/c2011v662a22>
- Cribb, P.J. & Hermans, J. (2009) *Field guide to the orchids of Madagascar*. Royal Botanic Gardens, Kew, 456 pp.
- Griffith, W. (1844) On some plants, mostly undescribed, in the H. C. Botanic Gardens, Calcutta. *Calcutta Journal of Natural History, and Miscellany of the Arts and Sciences in India* 4: 375–390.
- Hoehne, F.C. (1944) Orchidaceae novas para a flora do Brasil, dos herbários do Inst. de Botânica, Jardim Botânico, Rio de Janeiro, e comissão das linhas telegráficas, estratégicas de Mato-Grosso ao Amazonas. *Arquivos de Botânica do Estado de São Paulo* 1:

129–134.

- Hsu, T.C. & Kuo, C.M. (2010) Supplements to the orchid flora of Taiwan (IV): four additions to the genus *Gastrodia*. *Taiwania* 55: 243–248.
- Hsu, T.C. & Kuo, C.M. (2011) *Gastrodia albida* (Orchidaceae), a new species from Taiwan. *Annales Botanici Fennici* 48: 272–275.
<http://dx.doi.org/10.5735/085.048.0308>
- Hsu, T.C., Chung, S.W. & Kuo, C.M. (2012) Supplements to the orchid flora of Taiwan (VI). *Taiwania* 57: 271–277.
- Hu, A.Q., Hsu, T.C. & Liu, Y. (2014) *Gastrodia damingshanensis* (Orchidaceae: Epidendroideae): a new mycoheterotrophic orchid from China. *Phytotaxa* 175 (5): 256–262.
<http://dx.doi.org/10.11646/phytotaxa.175.5.3>
- IUCN (2014) *The IUCN red list of threatened species*, version 2014.3. IUCN Red List Unit, Cambridge U.K. Available from: <http://www.iucnredlist.org/> (accessed: 4 May 2015)
- Kores, P., Molvray, M., Pridgeon, A.M., Veitch, N.C. & Grayer, R.J. (2006) E. Tribe Gastrodieae. In: Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen, F.N. (Eds.) *Genera Orchidacearum, volume 4, Epidendroideae (Part 1)*. Oxford University, Oxford, pp. 435–452.
- Kraenzlin, F. (1900) Orchidaceae Africanae. *Botanische Jahrbücher für Systematik* 28: 162–179.
- Martos, F., Cariou, M.-L., Pailler, T., Fournel, J., Bytebier, B. & Johnson, S.D. (2015) Chemical and morphological filters in a specialized floral mimicry system. *New Phytologist* 207: 225–234.
<http://dx.doi.org/10.1111/nph.13350>
- Martos, F., Dulormne, M., Pailler, T., Bonfante, P., Faccio, A., Fournel, J., Dubois, M.-P. & Selosse, M.-A. (2009) Independent recruitment of saprotrophic fungi as mycorrhizal partners by tropical achlorophyllous orchids. *New Phytologist* 184: 668–681.
<http://dx.doi.org/10.1111/j.1469-8137.2009.02987.x>
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N. (2012) *International Code of Nomenclature for algae, fungi and plants (Melbourne Code)*. Regnum Vegetabile 154. Koeltz Scientific Books, Koenigstein, 240 pp.
- Perrier de la Bâthie, H. (1939) 49^e Famille, Orchidées, Tome I. In: Humbert, H. (Ed.) *Flore de Madagascar*. Imprimerie Officielle, Tananarive, 477 pp.
- Schlechter, R. (1925) Orchidaceae Perrieriana. *Repertorium specierum novarum regni vegetabilis. Beihefte* 33: 122–123.
- Selosse, M.-A. & Martos, F. (2014) Do chlorophyllous orchids heterotrophically use mycorrhizal fungal carbon? *Trends in Plant Science* 19: 683–685.
<http://dx.doi.org/10.1016/j.tplants.2014.09.005>
- Selosse, M.-A., Martos, F., Perry, B., Padamsee, M., Roy, M. & Pailler, T. (2010) Saprotrophic fungal symbionts in tropical achlorophyllous orchids: finding treasures among the ‘molecular scraps’? *Plant Signaling & Behavior* 5: 349–353.
<http://dx.doi.org/10.4161/psb.5.4.10791>
- Smidt, E.C., Engels, M.E., Bolson, M. & van den Berg, C. (2015) A new species of *Uleiorchis* (Orchidaceae, Gastrodieae) from the Atlantic Forest of Brazil. *Phytotaxa* 197 (4): 257–266.
<http://dx.doi.org/10.11646/phytotaxa.197.4.3>
- Stewart, J. & Hennessy, E.F. (1980) Orchids of Africa: *Didymoplexis verrucosa* — a new saprophytic orchid from South Africa. *American Orchid Society Bulletin* 49: 841–847.
- Suetsugu, K. (2013) *Gastrodia takeshimensis* (Orchidaceae), a new mycoheterotrophic species from Japan. *Annales Botanici Fennici* 50: 375–378.
<http://dx.doi.org/10.5735/085.050.0613>
- Suetsugu, K. (2014) *Gastrodia flexistyloides* (Orchidaceae), a new mycoheterotrophic plant with complete cleistogamy from Japan. *Phytotaxa* 175 (5): 270–274.
<http://dx.doi.org/10.11646/phytotaxa.175.5.5>
- Summerhayes, V.S. (1951). African orchids XX. *Kew Bulletin* 6: 461–475.
<http://dx.doi.org/10.2307/4118030>
- Summerhayes, V.S. (1953) African orchids XXI. *Kew Bulletin* 8: 129–162.
<http://dx.doi.org/10.2307/4117167>
- Tan, Y.H., Hsu, T.C., Pan, B., Li, J.W. & Liu, Q. (2012) *Gastrodia albidoides* (Orchidaceae: Epidendroideae), a new species from Yunnan, China. *Phytotaxa* 66: 38–42.
- Yeh, C.L., Leou, C.S., Hsu, T.C. & Yeh, C.R. (2011) *Gastrodia sui sp. nov.* (Orchidaceae) from Taiwan. *Nordic Journal of Botany* 29: 417–419.
<http://dx.doi.org/10.1111/j.1756-1051.2011.01147.x>