Brazilian Journal of Botany
https://doi.org/10.1007/s40415-021-00761-5

STRUCTURAL BOTANY - ORIGINAL ARTICLE

Underground system of geoxylic species of *Homalolepis* Turcz. (Simaroubaceae, Sapindales) from the Brazilian Cerrado

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Received: 9 June 2021 / Revised: 20 October 2021 / Accepted: 21 October 2021
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Abstract

In the prevailing savanna formations of the Cerrado biome, several plants show special morphological and anatomical features, such as cork bark, a thickened underground system and bud-forming underground structure. These traits have been considered to have evolved in distinct lineages as adaptations to drought, fire, or nutrient-deficient soils. Among the 28 recognized species of *Homalolepis* Turcz. (Simaroubaceae), 20 species occur in drier habitats, as semiarid Caatinga, Cerrado and Restinga. Due to different habitats, a variety of either small geophytic shrubs or large trees can be found in this family. The geoxylic species are characterized by a woody underground perennial axis and a less persistent aerial system that can regrow. However, studies including its morphology and anatomy are lacking in the literature. In the present study, morphology and anatomy of the underground system of five geoxylic species of *Homalolepis* occurring in the Brazilian Cerrado were investigated. Our results show that all species have xylopodia (upper region) associated with tuberous roots (lower region), and possibly have a sympodial branching from the news shoots, originating from the axillary buds, which were covered by cataphylls. The gemmiferous potential of the xylopodia associated to its tissue parenchyma, with nutrient reserve (starch), and tuberous roots, with wide storage xylematic parenchyma tissue, are important features in the regeneration of aerial organs after drought and fire occurrence. This study then evaluates the possible relation between characteristics of the underground systems found within two taxonomic sections of *Homalolepis,* as well to the evolution of the geoxylic life-form in the Cerrado lineages of the genus.

Keywords Cataphylls · Gemmiferous potential · Geophytes · Tuberous roots · Xylopodium

1 Introduction

The savanna biome covers approximately 20% of the Earth's land surface (Scholes and Archer 1997). Furthermore, 45% of the land area of South America and Brazil are known as Cerrado, which constitutes the second largest biome of the country, extending for about 2 million km^2, approximately 23.92% of the national territory (Costa and Olszevski 2008). The Cerrado is characterized by a mosaic of different phytophysiognomies. This biome is considered the richest tropical savanna in biodiversity in the world, standing out in number of endemic species and being recognized as one global biodiversity hotspot (Mittermeier et al. 2004; Falero et al. 2008). A recent survey revealed 12,338 angiosperm species in the Brazilian Cerrado, of which 7258 are endemic to the country (Flora do Brasil 2020).

The Cerrado biome is related to tropical seasonally dry climate, and to soil that is usually deep and acid latosol, meso- to oligotrophic, with high aluminum content, sometimes rocky, and usually subjected to natural fires (Coutinho 1982; Souza et al. 2018). Several traits, which were found in distinct plant lineages of this biome, have been considered to have evolved as adaptations to drought, fire, or nutrient-deficient soils: trees and shrubs with tortuous stems and thick, corky bark; shrubs, subshrubs or herbs with thickened, often bud-forming underground organs, like rhizomes and xylopodia (e.g., Ratter et al. 1977; Coutinho 1982, 1990;

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Published online: 12 January 2022

Gottsberger and Silberbauer-Gottsberger 2006; Alonso and Machado 2007; Appezzato-da-Gloria et al. 2008; Appezzato-da-Gloria and Cury 2011; Fidelis and Pivello 2011; Simon and Pennington 2012). Most of these features are also present in plants from other savannas around the globe, the remarkable congruence of New and Old World savanna vegetation ecology and origins have been previously pointed out (e.g., Pennington and Hughes 2014), while detailed studies indicate that savanna vegetation-fire-climate relationships differ across Africa, Australia and South America (Lehmann et al. 2014).

The ability of some plants to resprout after disturbance, which is widespread in Cerrado lineages, depends on the number and location of the dormant buds (Pausas et al. 2018). Plants have buds protected under the soil surface, due to their geophytic habit, are especially adaptive in fire-prone ecosystems with highly seasonal climates, since soil is an efficient insulator (Pausas et al. 2018). Underground organs play an important role in dry season, as they store water, carbohydrates and nutrients. This is a fundamental mechanism deployed by plants which aids in promoting organ resprouting in savanna species. Furthermore, this is a strategy that can be widespread in the Cerrado system (Silva and Rossatto 2019).

The underground system can be either, or both, root or caulinar in nature. However, characterization and identification based exclusively on morphological features have shown to be insufficient in defining this structure in different species (Vilhalva and Appezzato-da-Gloria 2006; Santos et al. 2016). Therefore, it would be prudent to evaluate the anatomical features of opposing species.

Additionally, it is noteworthy that the classical description of the different types of underground structures include anatomical features. According to Simon and Pennington (2012), there is evidence for a repeated independent origin of those features as adaptations to drought and fire in diverse Cerrado lineages related to groups inhabiting neighboring fire-free biomes, as the Atlantic Forest and the Amazonian rainforests. Current evidence from several sources suggests “tropical forests have existed in the Neotropics since the Paleocene, whereas most plant lineages present in South American savannas are recently derived from clades of the called forested biomes” (Azevedo et al. 2020). In Bombacoideae (Malvaceae), numerous morphological transitions were found from evergreen rain forest to seasonally dry biomes, including the Cerrado, and fewer in the opposite direction (Zizka et al. 2020).

Numerous evolutionary transitions into the savanna biome have also been documented in Africa (Maurin et al. 2014), and hence it has been suggested that the evolution of adaptations to fire in woody plants may be a relatively simple process, either in developmental and genetic terms (Simon et al. 2009; Simon and Pennington 2012). Also, it is important to highlight that plant traits, which are commonly characterized as fire adaptations in habitats prone to fires, may have complex origins and that selective factors other than frequent fire are likely to have driven their evolution (e.g., Bradshaw et al. 2011; Simon and Pennington 2012).

Further studies focusing on the nature of the morphological structures related to geophytic life forms in the Cerrado are fundamental to properly address this line of research, as these studies may help the understanding of the evolutionary switch from one major biome to another.

Among the tropical groups mostly represented in forests but with several Cerrado species, including geophytes, is Simaroubaceae, a small family of Sapindales, Eudicots and Rosids. The largest genus of this family, *Homalolepis* Turcz., is an ecologically diverse genera that have most members in the extra-Amazonian part of Brazil (Devecchi et al. 2018b). According to the authors, among its 28 recognized species, 20 occur in drier habitats as semiarid Caatinga, Cerrado and the eastern coastal Restinga, with different habits, varying from shrubs or subshrubs, commonly geoxylic to tall trees, reaching 30 m.

Devecchi et al. (2018c) the geoxilic *Homalolepis* species present a woody underground perennial axis, with a less persistent aerial system that can regrow, such as described for geophytes of several plant families inhabiting other savannas of the globe (e.g., White 1976). Approximately eight species of *Homalolepis* (e.g., *H. salubris* and *H. pumila*) composed of geoxylic structures have been described (Devecchi et al. 2018b). This dwarf, geophytic life-form seems to have evolved at least three times among the members of the genus. Additionally, the multiple origins of the geophytic life-form seem to have been acquired through distinct evolutionary pathways: either from shrubby ancestors, or from arboreal ancestors (palmlike or not) (Devecchi et al. 2018a).

However, the nature of these geoxylic structures in *Homalolepis* is not known. Hence, this study aimed to investigate the nature of the subterranean structure of geoxylic *Homalolepis* inhabiting the Brazilian Cerrado, applying a terminology based on morphological and anatomical features. In addition, this study aimed to enlighten the discussion of the evolutionary pathways related to the transitions to the geophytic life-form during the likely shift to the Cerrado of those lineages.

2 Material and methods

For this study, we sampled five *Homalolepis* species including representatives of the two taxonomic sections proposed by Devecchi et al. (2018a). All species were analyzed from populations occurring in the vegetation of Cerrado at different localities of central Brazil (Table 1). They all inhabit the locally called *campo sujo,* which is a savannic

Table 1 Species of geophytes studied, with habitat and voucher data

Studied taxa	Localities	Phytophysiognomies	Voucher/Herbarium acronym
Homalolepis sect. Grandiflorae			
H. intermedia (Mansf.) Devecchi & Pirani	Goiás, Serranópolis	*campo sujo*	Devecchi et al. 482 (SPF)
H. planaltina Devecchi & Pirani	Minas Gerais, Córrego Danta	*campo sujo*	Devecchi et al.445 (SPF)
H. salubris (Engl.) Devecchi & Pirani	Minas Gerais, Ituiutaba	*campo sujo*	Devecchi et al.472 (SPF)
Homalolepis sect. Homalolepis			
H. pumila Devecchi & Pirani	Goiás, Mineiros, Parque Nacional das Emas	*campo sujo*	Devecchi et al. 467 (SPF)
H. suffruticosa (Engl.) Devecchi & Pirani	Minas Gerais, Uberlândia	*campo sujo*	Devecchi et al.450 (SPF)

phytophysiognomy characterized by a mostly grassy landscape with scattered shrubs or seldom treelets.

For the anatomical study, the underground systems of three adult plants/species were collected and fresh samples were fixed in formalin-acetic acid-alcohol (FAA 50) (Johansen 1940). Samples of different regions of the underground structure were dehydrated in ethanol series and embedded in paraffin (Johansen 1940). Transverse sections were cut (5–12 µm), using a Reichertt-Jung AutoCut 2040 microtome, and stained with astra blue and safranin (Bukatsch 1972). Additionally, samples of *Homalolepis intermedia* (Mansf.) Devecchi and Pirani, *H. pumila* Devecchi and Pirani and *H. planaltina* Devecchi and Pirani were embedded in polyethylene glycol-PEG 1500 from increasing the concentrations, with final step 100% PEG (Barbosa et al. 2010). Transverse Sects. (15–20 µm) were supported with Styrofoam resin and sectioned with sliding microtome (Barbosa et al. 2010). Thereafter, samples were stained with astra blue and safranin (Bukatsch 1972). Samples of roots and shoots were subjected to a histochemical test using Lugol (Johansen 1940), for starch, and polarized optics, detecting crystals.

Anatomic analyses of sections were made using a light microscope (DMLB, Leica, Germany) equipped with a digital camera (DFC310 FX, Leica, Germany) and images were recorded using a Leica IM50 scanning system. The anatomical features of the secondary xylem and bark of each species were aided by the IAWA List of Features for Hardwood Identification (IAWA Committee 1989) and IAWA List of Microscopic Bark Features (IAWA Committee 2016), respectively.

3 Results

Morphology of the underground system – All studied species are dwarf geophytic subshrubs (Fig. 1), with a thickened underground system and leaves clustered on top of short aerial shoots (Fig. 2). The thickened underground system has a tuberous lower region with a radicular structure, vertically oriented in the soil (Fig. 3a–d), and an upper region which exhibits a caulinar structure with high bud-forming potential and new shoots arise from it, as seen in *H. pumila* (Fig. 3e) and *H. salubris* (Fig. 3f), which have buds covered by cataphylls in the underground region (Fig. 3g). There were no suckers, i.e., underground horizontal runners which grow and form a new leafy aerial shoot far away from the main shoot.

Anatomy of the underground system – The tuberous roots of all analyzed species were pentarchy with centripetal development of the primary xylem occupying the central region (Fig. 4a). The roots show a periderm (Fig. 4b), followed internally by reduced parenchyma (Fig. 4a, b). The secondary vascular tissues consist of secondary phloem with large amounts of parenchyma cells (Fig. 4a), and secondary xylem with lignified cells organized in narrow fiber bands interrupted by broad rays (Fig. 4c–e).

The upper regions of the underground systems (Fig. 5) have a stem anatomy with a medullary region (Fig. 5a) and centrifugal development of the primary xylem. In all analyzed species, the subterranean and aerial shoots were covered by a periderm, followed internally by the parenchyma tissue (Fig. 5b). The pericycle is multiseriate, which may have some lignified cells as in *H. salubris* (Fig. 5c, d). At the vascular secondary growth, the cambium produces early secondary xylem highly lignified (Fig. 5a–c) and later starts producing large amounts of parenchyma cells on the rays and axial system (Fig. 5a, b). Parenchyma bands are observed in the secondary xylem of *H. intermedia* and *H. pumila* (Fig. 5a, b). The phloem shows higher proportion of thin-walled parenchyma cell during both early and late stages of the secondary growth (Fig. 5a–e).

The histochemical test (Fig. 6) shows that all species accumulate starch in both secondary xylem and phloem of the tuberous roots (Fig. 6a–c). In the subterranean stem, starch deposits are observed in the vascular secondary tissues and the medullary region (Fig. 6e–g). Prismatic crystals were observed in the secondary phloem of the tuberous roots

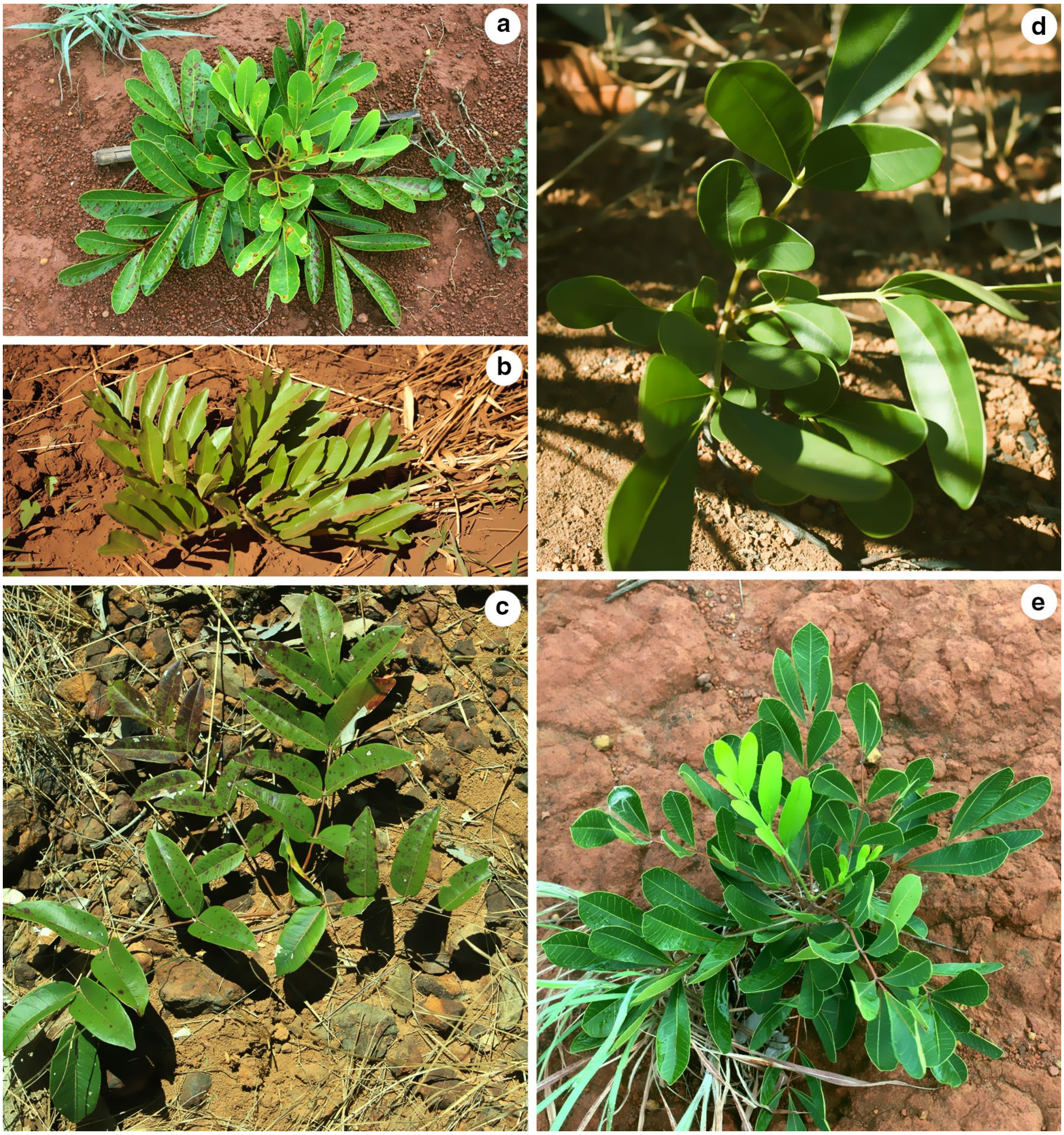

Fig. 1 Aerial parts (mostly pinnately compound leaves) of adult plants of geoxylic species of *Homalolepis* Turcz. in their natural habitats. **a** *Homalolepis suffruticosa* in *campo sujo*—an open, mostly herbaceous to shrubby savana of wide occurrence throughout the Brazilian cerrado, on sandy latosol. **b** *H. salubris* in disturbed cerrado, on latosol. **c** *H. planaltina* in low cerrado vegetation on top of a flat plateau ("chapada") with a ferrugineous rocky latosol, locally called "canga". **d** *H. pumila* in *campo sujo*, on sandy latosol, cerrado. **e** *H. intermedia* in open cerrado, on sandy, rocky latosol

and subterranean stem of *H. intermedia*, *H. pumila* (Fig. 6a) and *H. suffruticosa* (Fig. 6d), especially on the dilated portion of the rays.

4 Discussion

The geoxylic species of *Homalolepis* studied herein inhabit the Cerrado biome, have underground systems, bear leaves on reduced aerial branches near to the soil surface, and which sprout at their distal parts after drought or fire. The Cerrado is a biome conditioned to tropical climates, with a marked dry season and prone to natural fires (Eiten 1978). It is precisely this phenomenon that hinders Cerrado colonization by forest species (Bond and Keeley 2005; Simon et al. 2009), since, unlike native species, they do not have attributes that allow survival in the occurrence of fire. This biome burn up during the dry season has been a phenomenon enhanced by human activities in recent decades (Alho and Martins 1995).

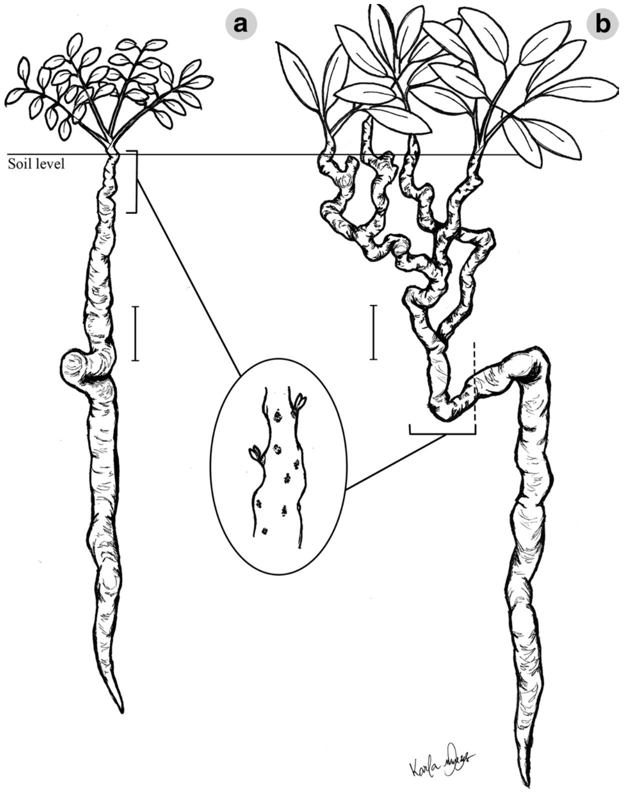

Fig. 2 Schematic representation of the underground system of *Homalolepis* geophyte species. **a** Unbranched underground system, as in *H. suffruticosa*. **b** Branched underground system, as in *H. pumila*. Note that in both cases, the underground system is formed by a lower tuberous region and an upper one containing axillary buds (circled region). Bars: 10 cm (**a**), 12.5 cm (**b**)

It is well known that in the Cerrado natural fires control vegetative growth of some species, trigger flowering, and dormancy break in seeds of others, and promote enrichment of soils with nutrients from the deposition of ashes (Coutinho 1982; Pausas et al. 2004; Simon et al. 2009). Hence, the natural occurrence of fires is important for the maintenance of biodiversity, especially in the herbaceous strata, altering the landscape and favoring nongraminoid species, which possess underground gemmiferous structures that allow rapid regrowth (Fidelis et al. 2014; Appezzato-da-Glória 2015).

The high regrowth capacity, found in *Homalolepis*, is common in many Cerrado species and is associated with underground geoxylic systems (Appezzato-da-Glória 2015; Pausas et al. 2018), to such an extent that the shorter the interval between fires, the greater the diversity of nongraminoid herbs and plants with underground structures such as rhizomes, xylopodia, bulbs and tuberous roots (Fidelis et al. 2014). According to Raunkiaer (1934), geophytes have their shoot apical meristem (SAM) below ground level, often being one of the more complex plant systems to understand, as there may be root- and stem-related structures linked to different bud protection strategies. According to Appezzato-da-Glória (2015), among the subterranean stems with gemmiferous potential present in Cerrado species, the lignotuber and xylopodium stand out, which can be differentiated by the nature of their buds, with accessory buds in lignotubers and axillary buds in xylopodia.

Another characteristic of xylopodia is described by Rizzini and Heringer (1961), as structures usually constituted by primary root and hypocotyl, or originating solely from the primary root. Although developmental analysis of the underground system of *Homalolepis* species has not been carried out in this study, the presence of a continuous structure which has a cauline nature in its upper part, with the presence of axillary buds protected by cataphylls, along with a tuberous taproot in the lower region, allow us to infer that the xylopodium in *Homalolepis* has a mixed origin, that is, from the hypocotyl and the primary root.

Well-developed underground systems are present in the following Cerrado species, *Andira humilis* Mart. ex Benth. (Fabaceae), *Anacardium humile* A.St-Hil. (referred as *A. pumilum*—Anacardiaceae), *Jacaranda decurrens* Cham. (Bignoniaceae) (Rawitscher 1948), *Stryphnodendron platyspicum* Rizz. & Her. (Leguminosae), *Annona warmingiana* Mello-Silva and Pirani (referred to as *A. pygmaea* Warm., Annonaceae), and *Esenbeckia pumila* Pohl (Rutaceae) (Rizzini and Heringer 1966). These species have a thick main root and a branched underground stem system, being described by some authors as subterranean trees (e.g., Lopez-Naranjo 1977; Lopez-Naranjo and Pernía 1990). According to Lopez-Naranjo (1977) and Lopez-Naranjo and Pernía (1990), the underground system of *Anacardium humile* has sympodial growth, with plagiotropic branches and axillary buds protected by cataphylls. These characteristics were also observed in the *Homalolepis* species analyzed herein, although the organisms themselves still had underdeveloped underground systems when compared to the ones described by the authors for the species mentioned above.

Based on field observations of *Homalolepis* during the present study, it was possible to observed that the species may present individuals with either branched or nonbranched xylopodia. The three studied species of *Homalolepis* sect. *Grandiflorae* (*H. intermedia*, *H. planaltina*, *H. salubris*) exhibit branched xylopodia. In *H.* sect. *Homalolepis*, *H. suffruticosa* has an unbranched xylopodium, while *H. pumila* exhibits both states. The intense branching observed in some individuals of the latter species may have been stimulated by local external factors such as intense droughts and frequent fires. It is not common to find branched xylopodia and there are few reports of this feature for Cerrado species, as in Rubiaceae (Cabral et al. 2007), Verbenaceae (Salimena and Múlgura 2015) and Aristolochiaceae (Freitas and Alves-Araújo 2017).

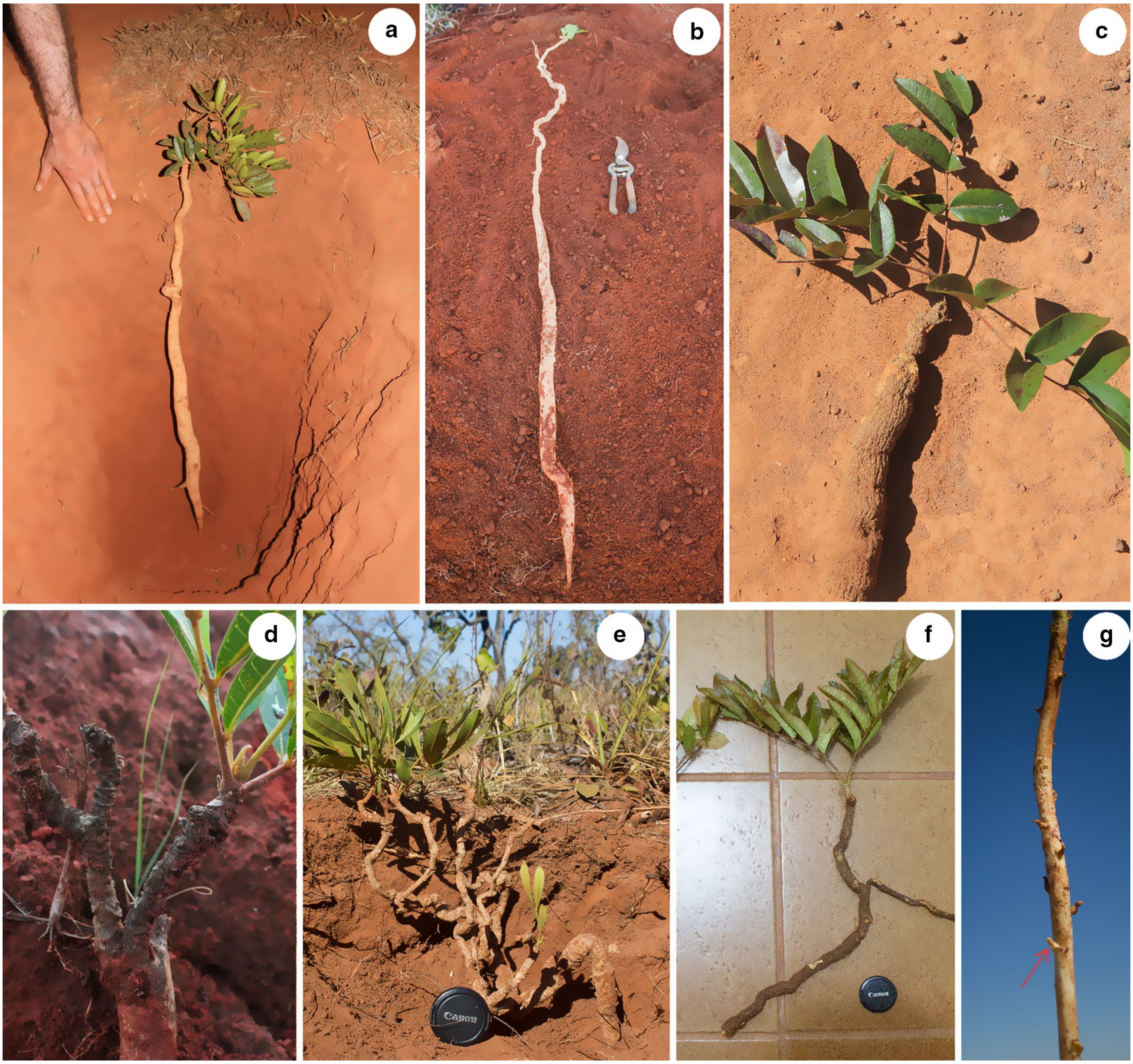

Fig. 3 General view of the underground system of the geoxylic species of *Homalolepis*. **a** *Homalolepis suffruticosa*. **b** *H. pumila*. **c** *H. planaltina*. **d** *H. intermedia.* **e** *H. pumila*. **f, g** *H. salubris*. Note examples of an unbranched underground system at **a–c**; a branched system at **d–f**. A detail of the new underground branch with axillary buds protected by cataphylls at **g** (arrows)

The distinct branching patterns documented herein in different sections of *Homalolepis* deserve further investigation, because they could be related to the multiple independent origins of the subshrubby life-form in the genus, as suggested by Devecchi et al. (2018a). According to these authors, the geophytic habit may have been acquired through distinct evolutionary pathways: (1) In *H.* sect. *Floribundae* it probably evolved either from shrubby ancestors (as in the case of *H. pumila*) or from non-palmlike arboreal ancestors (as in *H. suffruticosa*); (2) the transition more likely occurred from palmlike trees in *H.* sect. *Grandiflorae*, where "the geophytic subshrubs strongly resemble the palmlike plants, but with a shortened trunk that is sunken into the ground".

The transition from an arborescent habit to a geophytic subshrubby life-form in distinct lineages of *Homalolepis* seems to have been accompanied by the selection of features other than the underground system, including xeromorphic characters as rigid coriaceous leaflet blades, deciduousness, and blooming triggers—e.g., after fires or at the beginning of the rainy season, sometimes even before the new leaves have sprouted (Devecchi et al. 2018a). Such transitions seem to be

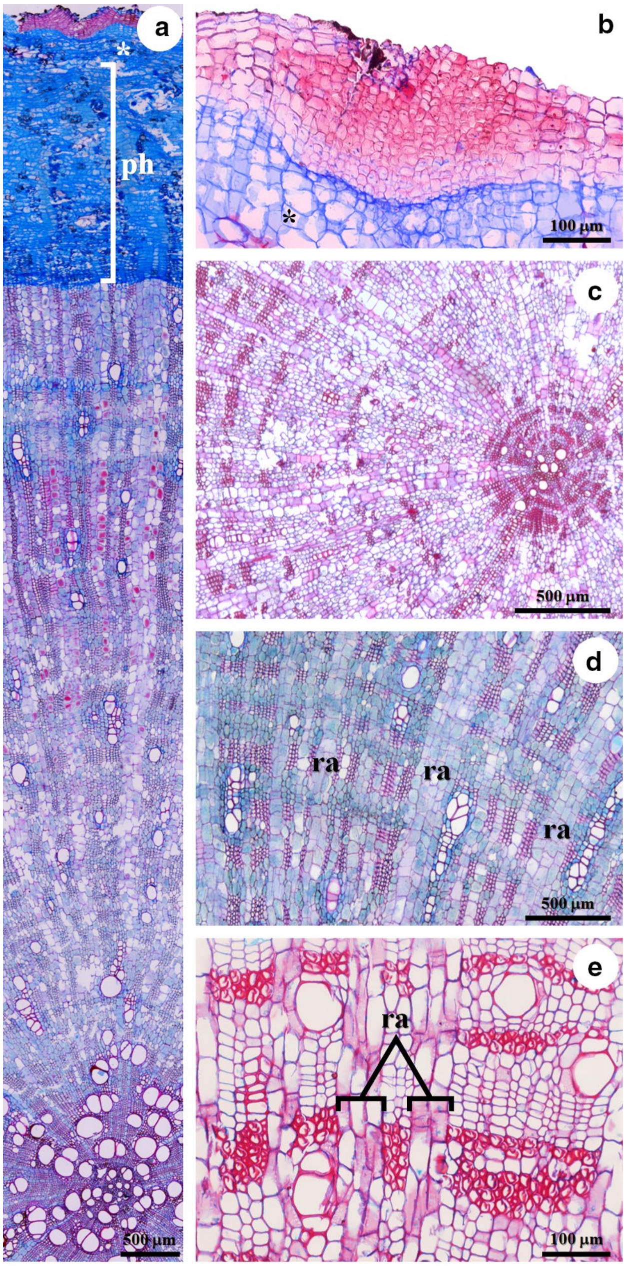

Fig. 4 Transverse sections of the tuberous roots of *Homalolepis* species. **a** General view showing wide secondary phloem and xylem in *H. pumila*. **b** Detail of the periderm in *H. salubris*. **c** Secondary xylem in *H. salubris*, showing wide storage parenchyma and fibrous early phase of the secondary xylem. **d** Secondary xylem with abundant storage parenchyma in *H. intermedia*. **e** Detail of the secondary xylem showing narrow fiber bands interrupted by broad rays in *H. salubris*. Asterisks: parenchyma tissue internally to periderm. *ph* phloem, *ra* ray

associated with colonization of the Cerrado habitat by members derived from moist forest ancestors of *Homalolepis*, as have been indicated also in Fabaceae (*Mimosa, Andira, Lupinus*), Melastomataceae (*Microlicia*) (Simon et al. 2009; Simon and Pennington 2012), and Bombacoideae (Malvaceae) (Zizka et al. 2020).

As some of these studies indicate, many Cerrado lineages switched to a savanna habitat within the last 2 million years, suggesting that ecological transitions from fire-free into fire-prone environments are an ongoing process (Simon and Pennington 2012). Likewise, colonization of dryer open habitats from ancestral forests has been suggested to have occurred in several lineages of Lychnophorinae (Asteraceae) (Loeuille et al. 2015), and *Chamaecrista* (Fabaceae) (Rando et al. 2016), but in these cases they moved into *campo rupestre* (montane rocky formations from Eastern and Central Brazil), rather than Cerrado.

Hence, as the dwarf geophytic life-form described in *Homalolepis* is commonly found in several species from other unrelated families that inhabit the Cerrado biome, it is usually assumed that it likely enables these Cerrado species to cope with drought, fire disturbance, and nutrient-deficient soils (Rachid 1947; Rizzini and Heringer 1961; Gottsberger and Silberbauer-Gottsberger 2006; Simon et al. 2009; Simon and Pennington 2012).

Several Cerrado plants have underground systems swollen with an ample carbohydrate storage tissue, which enables the production of new shoots (Vieira and Figueiredo-Ribeiro 1993; Appezzato-da-Glória and Estelita 2000; Milanez and Moraes-Dallaqua 2003; Hayashi and Appezzato- da-Glória 2007; Palhares et al. 2007; Appezzato-da-Glória et al. 2011). As soil can act as a thermal insulator, it can maintain temperature within a smaller range of variation (Tromp 1983; Miranda et al. 1993). In lieu, plants that undergo sudden temperature changes, use the roots as a potentially better storage place for carbohydrates (Tromp 1983). Also, the accumulation of different types of carbohydrates in the roots may be related to a need for vegetative reproduction after the loss of buds above the ground (Palhares et al. 2007).

Tuberous roots are commonly reported in Cerrado plants (Appezzato-da-Gloria and Estelita 2000; Milanez and Moraes-Dallaqua 2003; Hayashi 2005; Hayashi and Appezzato-da-Gloria 2007; Duputié et al. 2011; Pausas et al. 2018). However, the association of xylopodia, as a structure of gemmiferous potential, along with tuberous roots containing large amounts of storage parenchyma (Appezzato-da-Glória and Estelita 2000; Milanez and Moraes-Dallaqua 2003; Hayashi and Appezzato-da-Glória 2007; Palhares et al. 2007; Appezzato-da-Glória et al. 2011, 2008), provides an important ability for survival in typical Cerrado weather, since accumulated reserves in tuberous roots can be readily reallocated to the xylopodium.

In the present analyses, the xylopodia of the five examined species of *Homalolepis* are provided with a starch storage tissue in their secondary phloem and xylem, and in their medulla, while also exhibiting considerable starch storage tissue in tuberous roots. The xylopodia found in

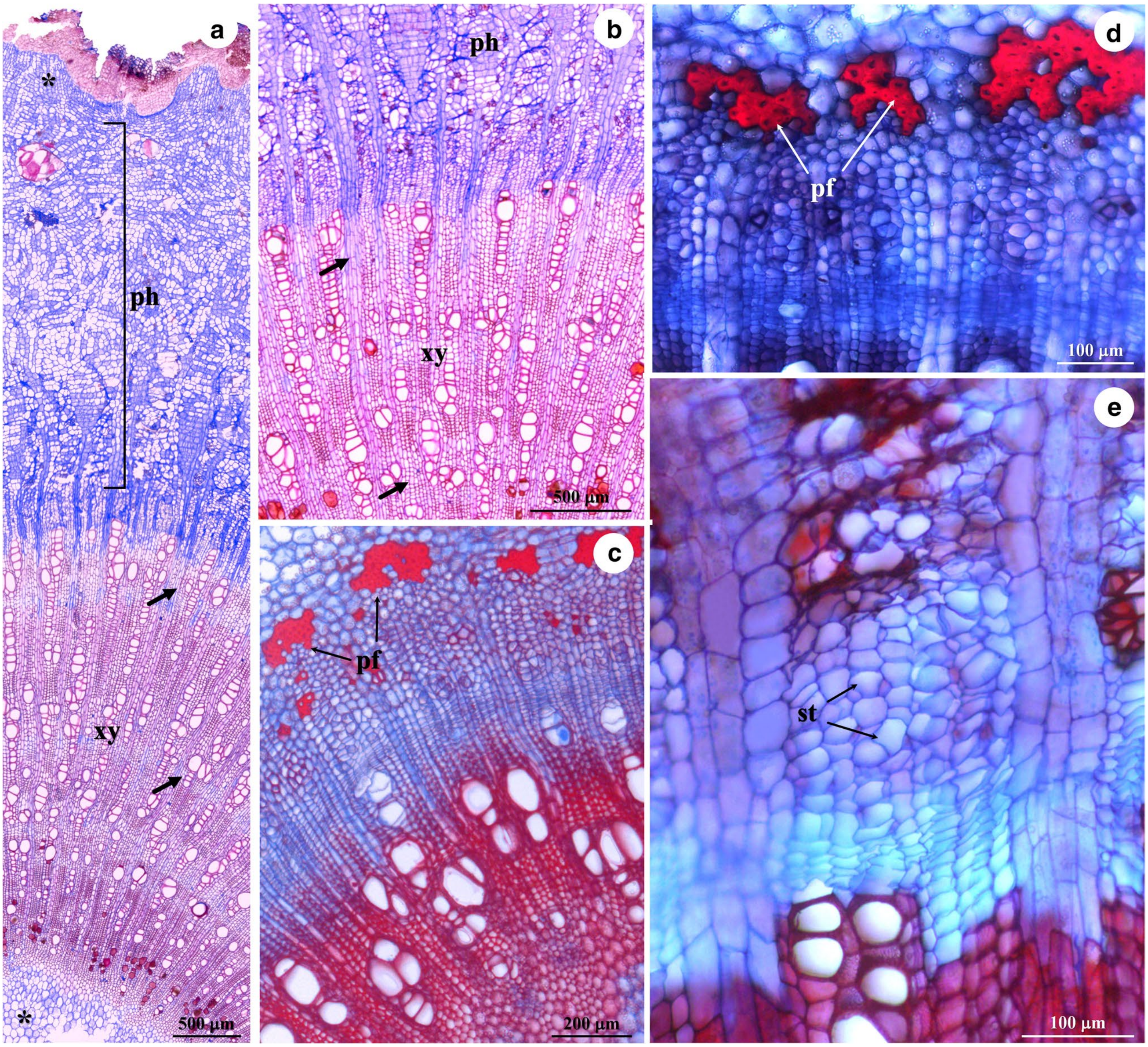

Fig. 5 Transverse sections of the xylopodium of *Homalolepis* species. **a** General view showing secondary phloem and xylem, periderm and medullary region (asterisk) in *H. intermedia*. **b** Detail of the secondary vascular system in *H. pumila*, with abundant parenchyma tissue in phloem and xylem. **c, d** Vascular system showing pericyclic fibers in *H. salubris*. **e** Detail of the functional secondary phloem in *H. planaltina*. Arrows: parenchyma bands in secondary xylem. *ph* phloem, *xy* xylem, *pf* pericyclic fibers, *st* sieve tube

Homalolepsis are soft, contrasting to the usual description of those systems in the literature, which report a hard consistency (Rizzini and Heringer 1961; Appezzato-da-Glória 2015). This may be because the wood of Simaroubaceae is pithy or fistulous making it lightweight compared to other Sapindales families (Cronquist 1944; Chave et al. 2006).

Although xylopodia, in general, do not have a storage parenchyma (Appezzato-da-Gloria 2015), some studies report the occurrence of a storage tissue in xylopodia of Apocynaceae, Asteraceae and Fabaceae species (Appezzato-da-Gloria and Estelita 2000, Milanez and Moraes-Dallaqua 2003, Appezzato-da-Gloria et al. 2008, Silva et al. 2015). Although Groppo et al. (2005) have not defined the subterranean stem system of *Hortia oreadica* Groppo, Kallunki and Pirani (Rutaceae) as a xylopodium, it is interesting to note that the authors describe it as an underground plagiotropic stem system forming several clones and provided with a starch reserve, features that could constitute adaptations of the species to fires that destroy their entire aerial part, that is, favoring their regrowth capability.

In conclusion, the five geoxylic species belonging to the *Homalolepis* genus have a tuberous root associated with a

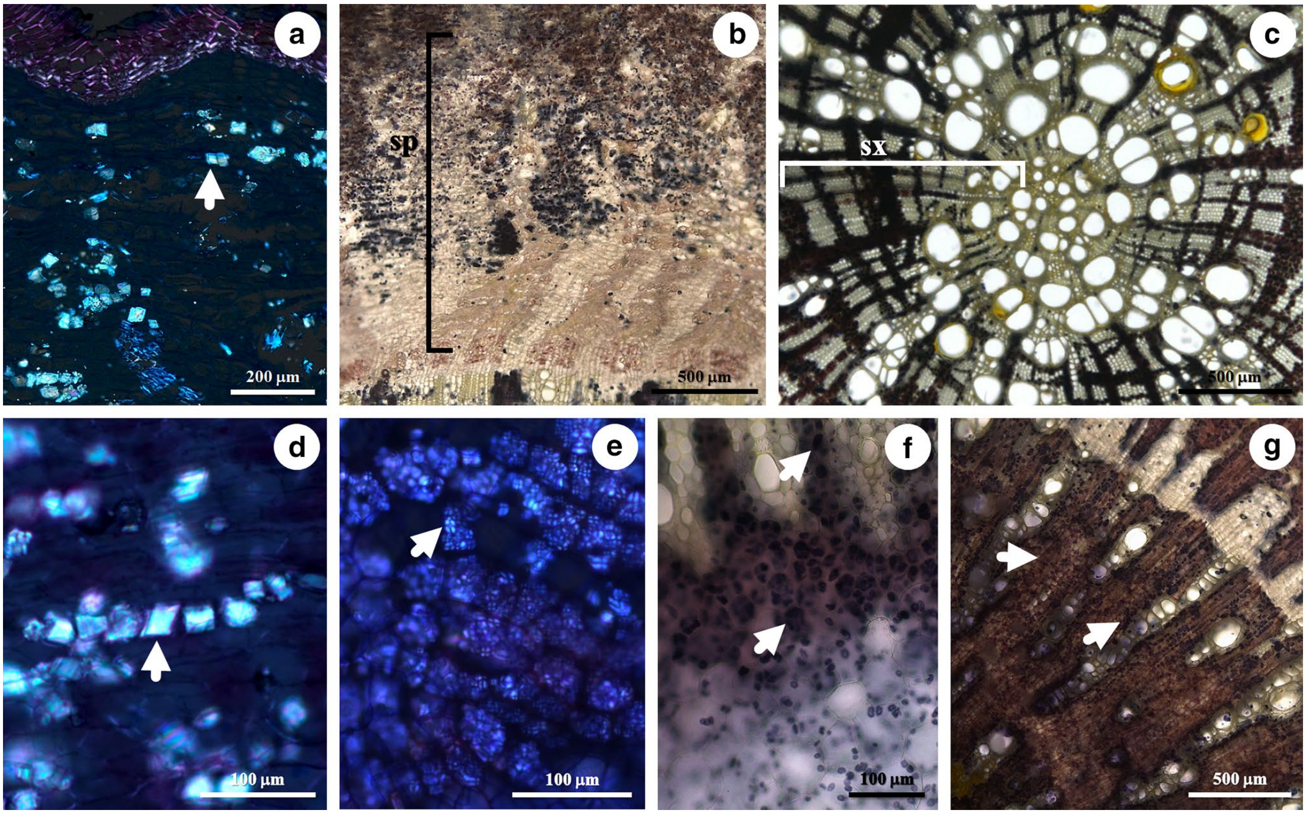

Fig. 6 Transverse sections of the tuberous roots of *Homalolepis* species (**a–c**). **a** *H. pumila*, crystals scattered throughout the secondary phloem (arrow). **b** *H. suffruticosa*, starch on the secondary phloem. **c** *H. pumila*, starch on the secondary xylem. **d–h** Transverse sections of the xylopodium of *Homalolepis* species. **d** *H. suffruticosa*, crystals on secondary phloem (arrow). **e** *H. planaltina*, starch on the secondary phloem (arrow). **f** *H. salubris*, starch on the pith and xylem parenchyma (arrows). **g** *H. salubris*, starch on the secondary xylem (arrows). Polarized light: **a, d–h** Iodine-potassium iodide histochemical test: **b, c, f, g**. *sp* secondary phloem, *sx* secondary xylem

xylopodium of soft consistency, with a gemmiferous potential, and can be branched. Some important anatomical and potentially adaptive attributes were observed, such as crystals in nonconducting phloem elements, which may be associated with characteristics of the Cerrado soil; an occurrence of starch reserves in secondary xylem and phloem; and the medullary region of the xylopodium as a potential storage of carbohydrates, which can allow a rapid regrowth after loss of the aerial system, often caused by the frequent occurrence of fires in the Brazilian Cerrado.

Considering the controversy whether plant traits that are commonly assumed to be fire adaptations in habitats prone to fires originally evolved in response to selective factors other than fire (e.g., Bradshaw et al. 2011; Simon and Pennington 2012), future investigations under an evolutive framework may help understand what were the ecological factors that had major selective pressure in the establishment of those peculiar structural characters of the *Homalolepis* lineages, and hence which among them could properly be interpreted as adaptations or exaptations.

Acknowledgements This study was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Process 2014/18002-2; 2019/15195-8). GFMP and JRP thank to CNPq (Productivity Grant Process 303962/2019-4 and 307655/2015-6, respectively) for financial support.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by GFAMP and BSC. The first draft of the manuscript was written by GFAMP, BSC, BEC, KMV and RCCL, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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