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A living bridge between two enemies: haustorium structure and evolution across parasitic flowering plants

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Abstract

Parasitic flowering plants are characterized by the development of an organ known as *haustorium*, which has evolved in multiple independent angiosperms clades. The haustorium has also been deemed "the most plastic of organs" due to its ability to accommodate physiological and anatomical differences between the parasite itself and its host plants. This is achieved through the development of vascular connections, which involve the differentiation of various specialized cell types by the parasite. The development, structure, and evolution of the haustorium and the connections it fosters are reviewed here considering all 12 parasitic plant lineages. A multi-level comparison between "model" parasitic plants, such as Orobanchaceae and *Cuscuta* species, with members of often neglected groups, such as Lennoaceae, Mitrastemonaceae, and Santalales yields the idea of a shared general body plan of the mature haustorium. This proposed haustorium bauplan is composed of an upper part, including structures associated with mechanical attachment to the host body, and a lower part, including all parasitic tissues and cell types within the host body. The analysis of multi-level convergence is also applied here to the comparison between haustoria and other plant organs. Considering the structure, molecular development, and functionality of this organ under the framework of continuum and process plant morphology, I propose the interpretation of haustoria as morphological misfits.

Keywords Body plan · Continuum morphology · Morphological evolution · Orobanchaceae · Rafflesiaceae · Santalales

1 Introduction

Parasitism is a widespread ecological interaction, observed in all domains of life (Combes 2001). In the Archaeplastida, the clade that harbors red algae, glaycophytes, multiple green algae lineages, and land plants (Baldauf 2008), parasitic interactions are often established by both green and red algae, as well as by land plants (Oborník 2019). Within the later, parasitic lifestyle is manifested in two different nutritional modes. On the one hand, mycoheterotrophism is observed in nearly all main lineages, including liverworts, ferns, conifers, and angiosperms, which exploit fungal hosts to fulfill their nutritional needs (Feild and Brodribb 2005; Merckx et al. 2009; Merckx 2013). On the other hand, plant parasitism is currently observed in 12 independent clades, exclusively among angiosperms (Fig. 1a; Nickrent 2020). These species are unique in their capacity of obtaining water and nutrients directly from other plants, without the aid of a fungal partner or host.

In terms of their diversity, parasitic flowering plants add up to ca. 1% of extant angiosperm species (Westwood et al. 2010). Such taxonomic diversity is matched by a broad variation of plant habits and functional attributes (Těšitel 2016). Most parasitic species, ranging from trees and shrubs, to small herbs and tuberous plants, germinate on the ground and attack the root system of their hosts (Fig. 1b–d; Bell and Adams 2011). Twining vines, i.e., *Cassytha* (Lauraceae) and *Cuscuta* (Convolvulaceae), germinate on the ground but develop no functional root system, attaching instead to the stems and branches of a wide variety of host plants (Fig. 1e; Kuijt 1969). Aerial shrubs, *i.e.*, mistletoes, also parasitize host branches (Fig. 1f; Aukema 2003). However, their seeds, which are mostly transported by animal dispersers, germinate directly upon the aerial organs of their hosts (Lamont 1983). A final habit, known as endoparasitism, is observed in a few species that exhibit extreme vegetative body reduction and grow exclusively within the host roots/stems during most of their life cycle (Fig. 1g; Mauseth and Rezaei 2013; Nikolov et al. 2014).

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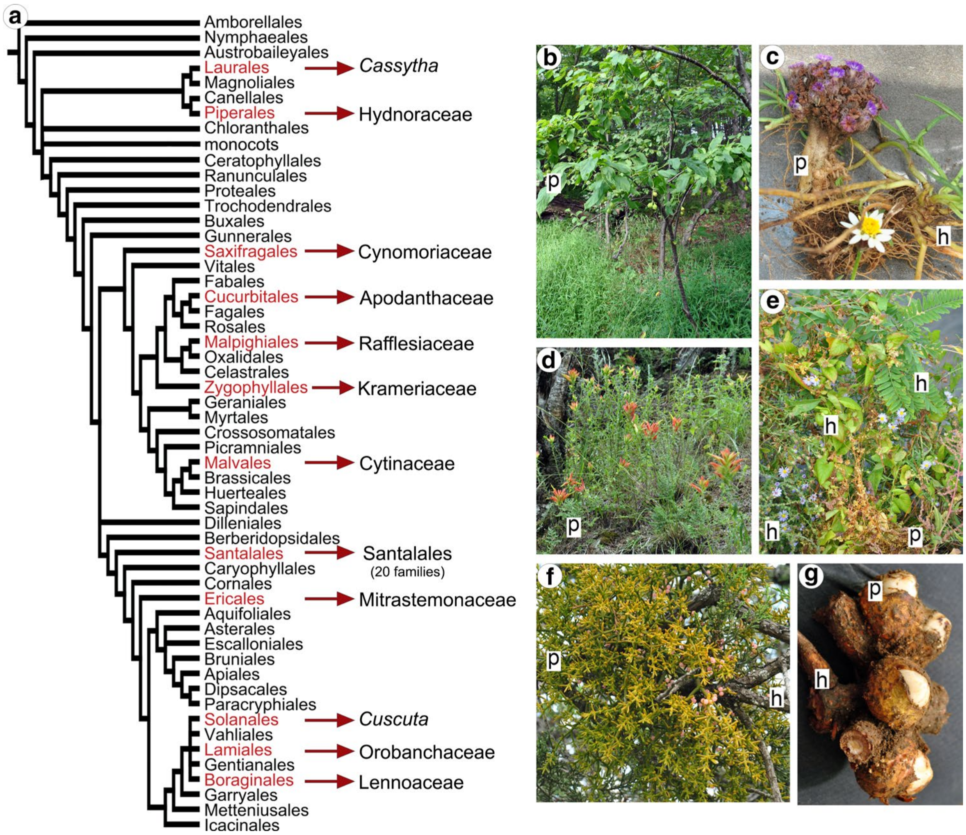

Fig. 1 Diversity of parasitic flowering plants. **a** Angiosperm phylogeny (modified from Nickrent 2020) indicating 12 independent origins of the parasitic lifestyle (in red). **b** *Pyrularia pubera* Michx. (Santalaceae, Santalales), a root hemiparasitic tree. **c** *Lennoa madreporoides* Lex. (Lennoaceae), a root holoparasite. **d** *Castilleja mexicana* (Hemsl.) A. Gray (Orobanchaceae), a root hemiparasitic herb. **e** *Cuscuta campestris* Yunck. (Convolvulaceae), a parasitic vine. **f** *Phoradendron juniperinum* Engelm. ex A. Gray (Santalaceae), a mistletoe. **g** *Mitrastemon matudae* Yamam. (Mitrastemonaceae), an endoparasite. *p* parasite, *h* host

Among the species exhibiting each of these growth habits, photosynthetic ability also varies widely, ranging from fully and partially photosynthetic plants, to species completely devoid of chlorophyll or chloroplast genome (Bromham et al. 2013; Molina et al. 2014). These non-green species are usually termed holoparasites (Fig. 1c, g), while species that are at least partially photosynthetic are termed hemiparasites (Fig. 1b, d, e, f) (Musselman and Press 1995). Parasitic plants also show great diversity in terms of geographical distribution, having colonized the most different environments, from arctic to tropical regions (Irving and Cameron 2009; Heide-Jørgensen 2013). This widespread occurrence is frequently associated with a wide host range, from ferns to cacti, from trees to crops, and from shrubs to lianas (Heide-Jørgensen 2008).

The unifying feature of this broad diversity of species is their capacity to develop an organ known as a haustorium, which represents the "very essence of plant parasitism" (Kuijt 1969). The haustorium acts in the initial attachment of a parasite to a suitable host, in the penetration of host tissues, and in the establishment of vascular connections between the two plants, enabling the exchange of water, nutrients, and genetic information (Joel 2013; Yoshida et al. 2016). Given the importance of this organ for the parasitic nutritional mode, a wealth of information is available in the literature regarding haustorium morphology, anatomy, and ultrastructure.

However, most of the research attention to date has been dedicated to parasitic plants considered as either forest pathogens, or weeds to horticultural and agricultural crops, including *Cuscuta*, Orobanchaceae, and a few mistletoe species (Hawksworth 1983; Clarke et al. 2019; Watson et al. 2020). Indeed, much of the available information on haustorium structure, development, functionality, and evolution is based on the study of these parasites. This reflects both the considerable focus of current research on these economically important parasites and the need for more work on other parasitic plant species (Riopel and Timko 1995). The need for increased work dealing with non-pathogenic and non-weedy parasitic plants becomes even more relevant when one considers that the interest in parasitic plants has increased over the past three decades (Nickrent 2020).

In this context, this review discusses the development, structure, and functionality of the parasitic plant haustorium, with a special focus on the vascular connections between parasite and host. The broad diversity of parasitic plant clades is considered here, including "model lineages," such as Orobanchaceae and *Cuscuta* (Cesarino et al. 2020), as well as groups that are often neglected in literature reviews, such as Santalales, Lennoaceae, and Mitrastemonaceae. The goal is to provide a comparison across the different angiosperm groups that include parasitic plants. Furthermore, based on insights from evolutionary developmental biology and continuum morphology, an approach that acknowledges gradations between typical plant structures (Sattler 1996), a new perspective and interpretation of haustorium identity and development is discussed here.

2 Haustorium development

The continuum process of haustorium development can be divided into three phases, namely initiation, intrusion, and conduction (Kokla and Melnyk 2018), each of which involves the formation of a different set of structures. Upon initiation, which is often triggered by chemical and/or physical stimuli provided by the host (Thoday 1951; Goyet et al. 2019; Shimizu and Aoki 2019), appendages associated with mechanical anchorage to the host surface are formed. These include the modified root hairs of some Balanophoraceae and most Orobanchaceae species (Holzapfel 2001; Cui et al. 2016), as well as expansions of the haustorium upper part, such as the attaching folds of Santalales and Krameriaceae root parasites (Kusano 1902; Musselman 1977) and the holdfast of mistletoes (Sallé 1983). Adhesion to the host surface is also attained through the release of cementing substances by structures such as the papillae of *Orobanche* spp. (Joel and Losner-Goshen 1994), the secretory trichomes of *Cuscuta* (Vaughn 2002), and the adhesive disc, which corresponds to the external, flattened part of the young haustorium of *Cassytha* and mistletoe species (Sallé 1983; Heide-Jørgensen 1991).

Attachment to the host surface allows the parasite to mechanically penetrate host dermal tissues. Cell-wall-degrading enzymes are also considered to play an important role in loosening the middle lamellae of host cells, thus facilitating penetration (Nagar et al. 1984; Losner-Goshen et al. 1998; Ouyang et al. 2016). Invasion of the host body leads to the development of a penetration peg, also known as intrusive organ, which develops either endogenously, from the pericycle, or exogenously, from the epidermis and outer cortex of the parasitic haustorium (Lee 2007; Pérez-de-Luque 2013; Kuijt 2015; Kokla and Melnyk 2018; Wakatake et al. 2018). Irrespective of its origin, the general anatomy of the penetration peg is similar across most parasitic plants, being composed of multiple parenchyma cells. The main exception is the searching hyphae formed by *Cuscuta*, which are formed by single parenchyma cells that grow via cell tip elongation (Vaughn 2003). It is noteworthy that regular root hairs, which differentiate from epidermal cells, also grow via tip elongation (Miller et al. 1997). The searching hyphae of *Cuscuta*, however, originate from cortical cells and later differentiates into vascular cells (Shimizu and Aoki 2019).

The final stage of haustorium development involves the expansion and differentiation of penetrating structures into specialized tissues and cell types that promote connection between the vascular systems of parasite and host. In addition to the contact hyphae described above, such tissues also include cortical strands and haustorium flanges, which expand the parasite–host interface by spreading through the host bark and wood, respectively (Kuijt 1977; Condon and Kuijt 1994). Cell types other than tracheary elements are also common at the host–parasite interface, including transfer cells and flange cells (Fineran 1985; Fineran and Calvin 2000). This set of parasitic tissues embedded within the host body is then termed the endophyte (Teixeira-Costa and Ceccantini 2018). These and other peculiar structures of parasitic plants will be discussed in more detail in the following sections.

It is noteworthy that the three phases of haustorium development summarized above have not been observed for all parasitic plant lineages. Early haustorium development, including the phases of initiation and penetration, has yet to be described for seven of the 12 currently recognized parasitic plant lineages. This includes Apodanthaceae, Cynomoriaceae, Cytinaceae, Hydnoraceae, Lennoaceae, Mitrastamonaceae, and Rafflesiacae (Kuijt 1966; Heide-Jørgensen 2008). Among these groups, scanty information is available regarding seed germination (Heinricher 1917; Bolin et al. 2009; Wicaksono et al. 2020); still, no reports of how the parasite first penetrates the host are available. Nevertheless, the structure of the mature haustorium, including establishment of parasite–host phloem and xylem connections, has been described for species in all of these families. The following section discusses the structure and origin of these connections.

3 Structure of haustorium vascular connections

Haustorium vascular connections to the host xylem and eventually to the host phloem are classified as either direct, or indirect. Direct connections (Fig. 2a–d) occur when uninterrupted luminal/symplastic continuity is observed between tracheary/sieve elements of both plants (Hibberd and Jeschke 2001). Connections are classified as indirect (Fig. 2e–h) when mediated by parenchymatic tissue, often including specialized cells, such as flange and transfer cells (Pate et al. 1990; Fineran and Calvin 2000). A combination of both direct and indirect connections is also observed in many species (Fig. 2b, f) (Cameron and Seel 2007).

Phloem and symplast connections – Phloem differentiation in the haustorium of parasitic plants and the development of parasite–host phloem connections have been points

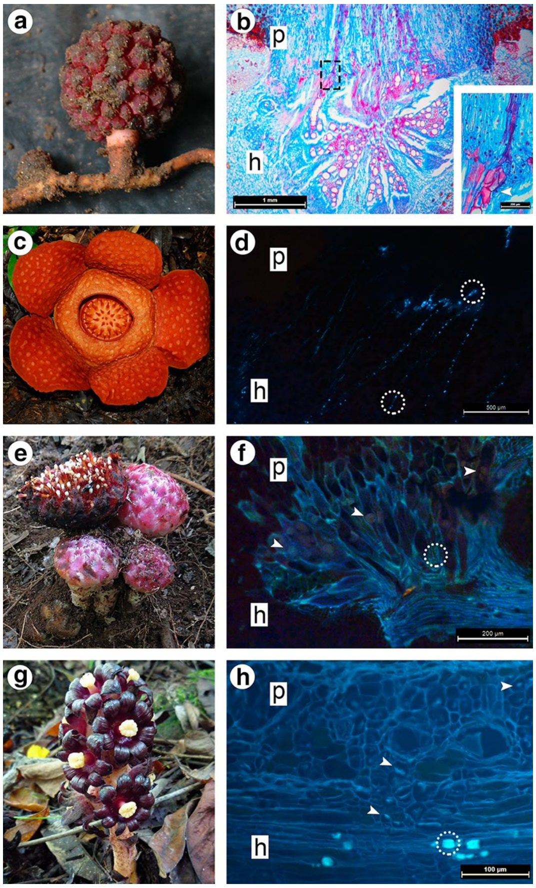

Fig. 2 Examples of parasitic plant species and the types of vascular connections formed with host plants. **a**, **b** *Helosis cayanensis* (Sw.) Spreng. (Balanophoraceae, Santalales). **a** External morphology. **b** Light microscopy of the parasite-host interface showing direct xylem connection (dashed square) between vessel elements of parasite and host; notice parasite parenchyma cell abutting a host vessel (arrowhead). **c**, **d** *Rafflesia cantleyi* Solms (Rafflesiaceae). **c** External morphology (photograph by Charles C. Davis). **d** Fluorescence microscopy of the parasite-host interface showing direct phloem connection between parasite and host sieve elements (callose marked with aniline blue dye; dashed circles). **e**, **f** *Scybalium fungiforme* Schott & Endl. (Balanophoraceae, Santalales). **e** External morphology. **f** Fluorescence microscopy (autofluorescence) of the parasite-host interface showing indirect xylem connection between parenchyma cells of the parasite and vessel elements of the host; notice large nuclei of parasite parenchyma cells (arrowheads). **g**, **h** *Bdallophytum americanum* (R. Br.) Eichler ex Solms (Cytinaceae). **g** External morphology (photograph by Cyril H. Nelson). **h**. Fluorescence microscopy of the parasite-host interface showing indirect phloem connection between parasite parenchyma cells and host sieve elements (callose marked with aniline blue dye); notice large nuclei of parasite parenchyma cells (arrowheads). *p* parasite, *h*: host

of controversy in the parasitic plant literature for decades. The use of inadequate methods for the detection of phloem sieve elements might have contributed to this debate (Esau 1969; Dörr 1990). To date, direct phloem connections have been confirmed in few parasitic species. Sieve connections between certain species of *Cuscuta* (Israel et al. 1980) and *Orobanche* (Dörr and Kollmann 1995; Krupp et al. 2019) were revealed through the analysis of haustorium ultrastructure. More recently, phloem-mobile fluorescent dyes and in situ hybridization have also been used to detect the presence of sieve elements and the occurrence of direct phloem connections between *Cuscuta* species and their hosts (Birschwilks et al. 2006; Shimizu et al. 2018; Shimizu and Aoki 2019). Uninterrupted parasite–host phloem connections can also be detected by labeling the callose of sieve plates with specific fluorescent dyes (Angyalossy et al. 2016). Following this method, sieve elements of Apodanthaceae and Rafflesiaceae species were observed to connect directly to the sieve elements of host plants (Teixeira-Costa et al. in press).

It is crucial to note that the presence of sieve elements in the haustorium is not necessarily an indication of direct parasite–host phloem connections (Dörr 1990). Indeed, sieve elements and companion cells have been observed in the haustorium of hemiparasites with no connection to the host phloem (Calvin 1967; Kuijt and Dobbins 1971). At the same time, the endophytic tissue of holoparasites can also contain sieve elements that do not connect directly to the host phloem. This has been shown to be the case in Balanophoraceae, Cytinaceae, Hydnoraceae, and, more recently, Cynomoriaeae species (Hsiao et al. 1995; De Vega et al. 2007; Tennakoon et al. 2007; Fahmy and Hassan 2020). Furthermore, although transfer cells are observed at the interface between *Balanophora* species (Balanophoraceae) and their hosts, connections to host sieve elements were not detected (Gedalovich-Shedletzky and Kuijt 1990). Similarly, electron microscopy revealed no phloem connections between *Boschniakia hookeri* Walp. (Orobanchaceae) and its host (Kuijt and Toth 1985).

These observations suggest that direct phloem connections are either ephemeral or absent in several holoparasites, which would imply that these parasites obtain most (or all) of their nutrition by tapping into the host xylem. Considering holoparasites usually have low transpiration rates (Seel et al. 1992; Fahmy 1993), species without direct access to the host phloem would be expected to grow slow as a response to consequent low rates of resource uptake. This is observed in Balanophoraceae species, in which transpiration is also reduced to a minimum due to the absence of stomata (Moore 1940; Kuijt and Dong 1990). A similar situation could occur for Cytinaceae and Mitrastemonaceae species, which have been anecdotally reported to take several years to bloom for the first time (Watanabe 1933; Forstmeier et al. 1983). To a certain degree, the relation between slow growth and absence of direct sieve connections can be extended to *Striga* (Orobanhaceae). These annual hemiparasites remain underground for most of their life cycle, being fully dependent on the host for their carbon supply during this period (Spallek et al. 2013; Lambers and Oliveira 2019). The lack of parasite–host phloem connections (Dörr 1997) could then be an explanation to the delayed emergence of the above-ground stems of most *Striga* species.

Xylem connections – As with many aspects of haustorium development and functionality, the growth of parasitic penetration structures and subsequent differentiation of haustorium vasculature depend, to a certain extent, on the anatomy of host stems/roots. When infesting herbaceous species or other plants that do not undergo pronounced secondary growth, parasite penetration structures are able to continue growing and elongating until they have reached the host primary xylem. This has been illustrated and reviewed for both aerial (McLuckie 1924; MacLeod 1962) and root parasites (Pérez-de-Luque 2013). Conversely, contact with the host secondary xylem is usually achieved by a coordinated proliferation between the endophyte and the host cambium. When infesting woody roots/stems, centripetal growth of the penetration peg is halted once it reaches the host cambial zone (Fig. 3a) (Fineran 1965). At this point, the meristematic tip of the peg usually becomes flattened and promotes further circumferential growth against the surface of the host secondary xylem (Pate et al. 1990). Then, as the host cambium produces new xylem tissue, the parasitic endophyte becomes passively embedded within the host wood (Kuijt 1965).

Alternatively, a few species can actively penetrate the host secondary xylem by growing in between radial cells (Fig. 3b) (Heil 1926; Dell et al. 1982; Kuijt et al. 1985; De Vega et al. 2007). Detection of this penetration strategy requires detailed examination of the transition between intrusion and conduction phases of haustorium development. For this reason, such strategy may still be underestimated

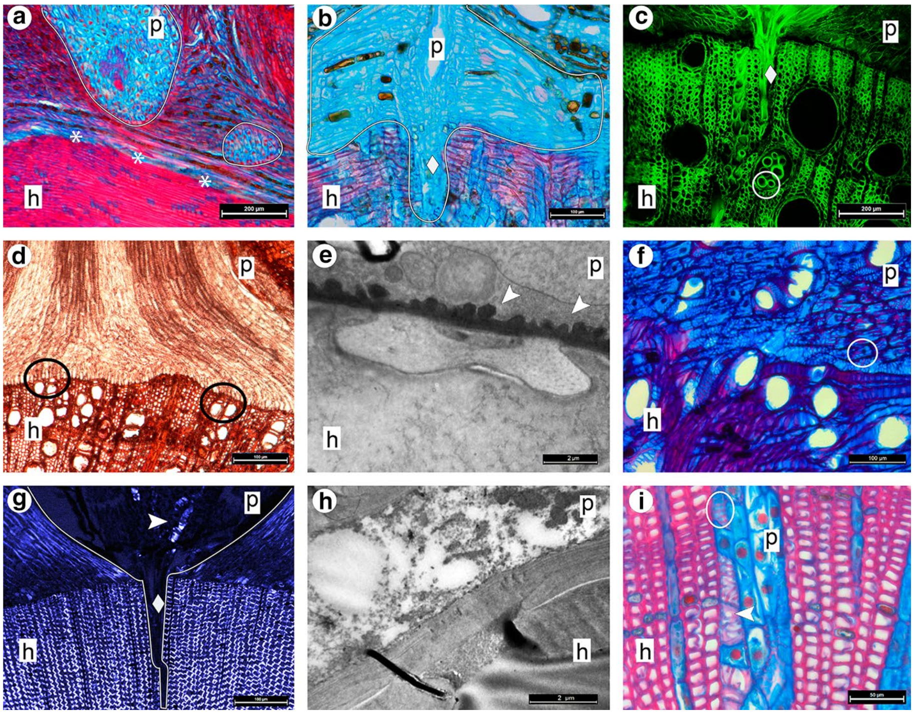

Fig. 3 Details of parasite–host xylem connections. Light (**a**, **b**, **d**, **f**, **i**), autofluorescence (**c**), and polarized light (**g**) microscopy shows longitudinal and cross sections through the host stem/root. **a** Penetration peg (white outline) of *Phoradendron juniperinum* (Santalaceae) halted at the host cambial zone (asterisks). **b** Endophyte (white outline) and sinker (diamond) of *Bdallophytum americanum* (Cytinaceae) penetrating through the host wood rays. **c** Parasite sinker (diamond) of *Struthanthus martianus* Dettke & Waechter (Loranthaceae, Santalales) branching to form vessel elements (white circle) within a host vessel. **d** Predominance of parenchymatic tissue at the interface between *Pyrularia pubera* (Santalaceae, Santalales) and its host; notice two areas of direct xylem connection (black circles). **e** Transmission electron microscopy showing transfer cell at the interface between *Phoradendron perrottetii* (DC.) Eichler (Santalaceae, Santalales) and its host; notice invaginations of the parasite cell wall (arrowheads). **f** Flange cells (white circle) at the interface between *Phoradendron perrottetii* (Santalaceae, Santalales) and its host. **g** Interface between *Struthanthus flexicaulis* (Mart. ex Schult. f.) Mart. (Loranthaceae, Santalales) and a conifer host indicating parenchymatic composition of the sinker (diamond) and endophyte (white outlines); notice parasite vessel elements (arrowhead) are absent in the sinker. **h** Transmission electron microscopy showing parenchymatic cell of the sinker formed by *Struthanthus flexicaulis* (Loranthaceae, Santalales) at the interface with a conifer host. **i** Direct vascular connection (white ellipse) at the interface formed by *Arceuthobium americanum* Nutt. ex Engelm. (Santalaceae, Santalales) and its conifer host; notice perforation plate (arrowhead). *p* parasite, *h* host

among parasitic species. This is especially relevant in the case of root holoparasites, due to difficulties in sampling these plants during early developmental stages. The portion of the endophyte that extends radially into the host xylem is termed "sinker," alluding to the sinking of parasitic cells deeper within the host (Kuijt 1977; Teixeira-Costa and Ceccantini 2018).

Sinkers are initially composed of parenchymatic cells (Fig. 3b), part of which later differentiate into tracheary elements (Fig. 3c, d) and other specialized conductive cells, such as transfer cells (Fig. 3e) and flange cells (Fig. 3f) (Fineran 1996; Hibberd and Jeschke 2001; Vaughn 2006). Oftentimes, parenchymatic cells of the sinker invade host vessels trough lateral pit apertures, in a process similar to what is observed in the formation of tyloses (Esau 1965; Kuijt 1977). Once within the host vessel, the process of programmed cell death leads to the formation parasitic vessels elements inside and in continuity with host vessels (Fig. 3c) (Toth and Kuijt 1977; Venturelli 1980; Heide-Jørgensen and Kuijt 1995; Cameron et al. 2006). In Orobanchaceae species, this type of parasitic vessel element is usually referred as "oscula" (Dörr 1997). Another peculiar cell type frequently observed in the haustorium of Orobanchaceae, Santalales, and *Cassytha* hemiparasites is known as graniferous tracheary element (Musselman and Dickison 1975; Fineran 1985; Calvin and Wilson 1996; Rajanna and Shivamurthy 2001). This is a xylem conduit that contains amylaceous or proteinaceous granules attached to its inner cell walls, which have been hypothesized to help regulate sap flow from host to parasite (Fineran and Bullock 1979; Joel 2013).

In several cases, however, direct connections between parasite and host tracheary elements can be extremely rare (Lambers and Oliveira 2019). This is especially observed in Santalalean root hemiparasites and a few mistletoes, in which direct xylem connections account for less than 10% of the parasite–host interface area (Fig. 3d) (Pate et al. 1990; Calvin and Wilson 1995). In that event, indirect parasite–host xylem connections often involve transfer cells (Fig. 3e), characterized by intricate wall labyrinths that amplify the surface area of the plasma membrane (Offler and Patrick 2020), and flange-type parenchyma cells (Fig. 3f), which show wall thickenings in the form of flanges (Fineran 1996). Both cell types are associated with intense transport of nutrients (Fineran 1996; Fineran and Calvin 2000; Offler and Patrick 2020).

Parenchyma cells can also play a crucial role in xylem connections of species with a broad host range, known as host–generalist parasites, that attack tracheid-bearing hosts, such as conifers and most ferns. In the sinker of the mistletoe *Struthanthus flexicaulis* (Loranthaceae), for instance, parenchyma cells usually differentiated into vessel elements. However, when infesting conifer hosts, the sinker remains parenchymatic, leading to the formation of indirect xylem connections only (Fig. 3g, h) (Ceccantini et al. 2019). On the other hand, in mistletoes that exclusively infest conifer species, such as *Arceuthobium* spp. (Santalaceae), although most of the parasite–host interface is comprised of parenchyma cells, direct xylem connections are achieved via tracheary pits (Fig. 3i). This comparison suggests that parasitic species with broad host ranges can recognize the surrounding cells of the host xylem and accommodate the structure of their sinkers accordingly. Furthermore, this comparison highlights haustorium plasticity and its ability to accommodate physiological and anatomical differences between the parasite itself and its host plants. Future investigation of this topic should focus on the molecular mechanisms behind this form of host recognition, which could provide insights into why some parasitic plants display a virtually unlimited host range. At the same time, understanding how a parasite can differentiate between distinct types of tracheary elements could broaden the general understanding molecular xylem development.

4 Proposal for a general haustorium bauplan

As the parasitic habit evolved multiple times independently, so did the haustorium. Considered as a homoplastic character, there would be no a priori reason to imagine all haustoria to be similar in their developmental origin or structural organization (Kuijt 1969). Indeed, haustorium morphology and anatomy may vary greatly when comparing species from distantly related lineages and different functional groups, such as endoparasites and the root hemiparasites. Differences are less pronounced when comparing species with similar life histories. Similarities in development and structure of the haustorium among and within root hemiparasitic clades, including Krameriaceae (Fig. 4a), Orobanchaceae (Fig. 4b), and Santalaceae, have been long recognized (Barber 1907; Musselman and Dickison 1975; Musselman 1977). Likewise, the convergence between *Cassytha* (Fig. 4c) and *Cuscuta* (Fig. 4d) has long been observed, and it extends from their lianescent form and rudimentary roots, to the general aspect of their haustorium (Kuijt 1969; Heide-Jørgensen 2008).

Among mistletoes, the remarkable diversity in haustorium morphology has been recently shown to have a common developmental trajectory, one that is also partially shared with Santalalean root hemiparasites (Teixeira-Costa et al. 2020). Striking developmental similarities have also been observed among endoparasitic species of the families Apodanthaceae, Cytinaceae, Mitrastemonaceae (Fig. 4e), and Rafflesiaceae (Fig. 4F) (Teixeira-Costa et al. in press). On the other hand, root holoparasites are more diverse, forming haustorial systems with different origins and morphologies.

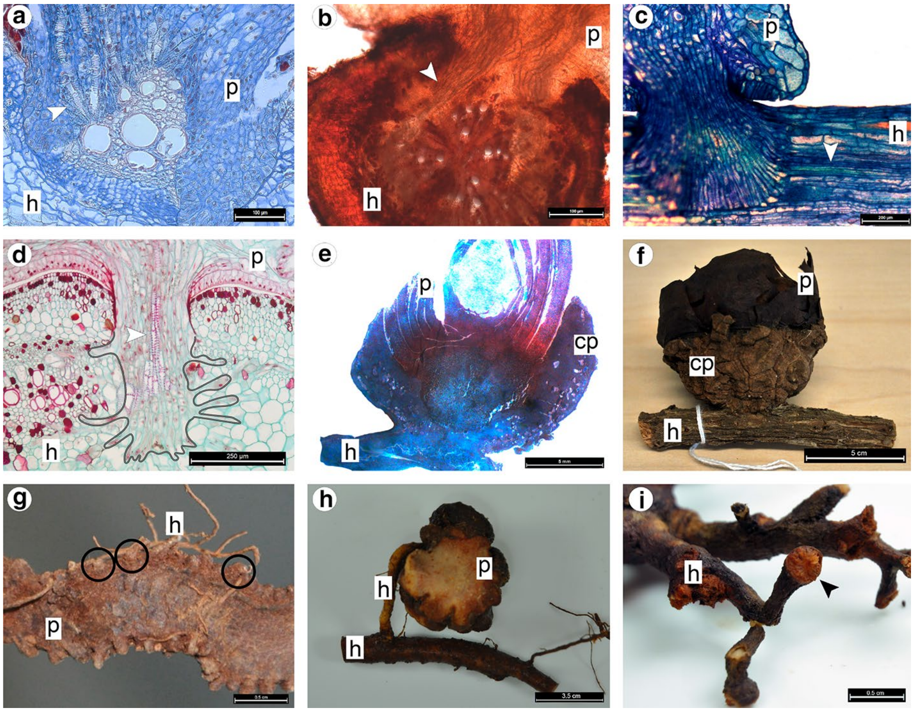

Fig. 4 Similarities and differences in the haustorium of multiple parasitic plant lineages. **a**, **b** Cross section through host roots showing a similar form of penetration by the parasites **a** *Krameria lappacea* (Dombey) Burdet & B.B. Simpson (Krameriaceae; image provided by G. Brokamp and M. Weigend) and **b** *Aureolaria pedicularia* (L.) Raf. ex Pennell (Orobanchaceae). **c**, **d** Longitudinal and cross sections through host stems showing the general aspects of the haustorium in **c** *Cassytha filiformis* L. (Lauraceae) and **d** *Cuscuta* sp (Convolvulaceae); note searching hypha (black outline). **e**, **f** Longitudinal section through the host root and macroscopical image showing similarities of the interface formed by **e** *Mitrastemon matudade* Yamam. (Mitrastemonaceae) and **f** *Rafflesia cantleyi* Solms (Rafflesiaceae); note the presence of a cupule (cp) in both species. **g** Habit of the parasite *Prosopanche caatingicola* (Hydnoraceae) bearing lateral haustoria (black circles). **h** Habit of the parasite *Scybalium fungiforme* (Balanophoraceae) bearing a terminal haustorium (tuber). **i**. Habit of the parasite *Scybalium glaziovii* Eichler (removed) causing the formation of a placenta-like structure (black arrowhead) in the host root. *p* parasite, *h* host; white arrowheads: parasite xylem

For instance, *Prosopanche caatingicola* Machado & L.P. Queiroz (Hydnoraceae, Fig. 4g) forms multiple haustoria, which emerge laterally along the root system, while *Scybalium fungiforme* (Balanophoraceae, Fig. 4h) forms a single haustorium, which emerges at a terminal position. As expected, similarities have been more often recognized between root holoparasites with the same type of haustorium, such as in the case of the endophyte tissue of Hydnoraceae and Lennoaceae, both of which have lateral haustoria (Tennakoon et al. 2007). A similar endophyte is also observed in Cynomoriaceae (Fahmy and Hassan 2020). Among root holoparasites with a terminal haustorium, the same form of parasite-induced alteration to the host xylem, forming a "placenta-like" structure that accommodates parasite tissues (Fig. 4i), is observed in Orobanchaceae (Kuijt and Toth 1985; Baird and Riopel 1986) and Balanophoraceae (Holzapfel 2001). Curiously, this feature is also developed in the association of many mistletoe species and their hosts, being called a woodrose (Kuijt and Lye 2005).

The examples discussed above highlight the value of examining convergence, and more specifically, phenotypic convergence at multiple levels of biological organization. Similarity/difference at one hierarchical level not necessarily implies similarity/difference at another level (Rosenblum et al. 2014). Indeed, conservation or divergence in morphology can be influenced by developmental, genetic or structural constrains (Lau and Oakley 2020). Because haustorium development is a dynamic process that involves shifts in structure and functionality (Yoshida et al. 2016), tissues and cell types that are readily identified during one phase may not be distinguishable later in development. For instance, in Loranthaceae mistletoes such as *Psittacanthus* and *Loranthus* species, few sinkers can be observed at young stages of haustorium development, but become indistinguishable at a later, mature stage (Dzerefos and Witkowski 1997; Teixeira-Costa et al. 2020).

Based on a comparative analysis across parasitic plant lineages, a convergence in the topology of haustorium tissues emerges, suggesting a convergent haustorium bauplan. This shared body plan can be artificially divided in two parts: the upper haustorium and lower haustorium. The first lies external to the host body and, in most cases, originates from the appendages that aid in mechanical anchorage, which are formed during haustorium initiation. The lower haustorium comprises the endophyte and its diverse set of tissues and cell types, all of which derive from the penetration peg formed during haustorium intrusion. This includes tissues that establish vascular connections with the host phloem and/or xylem. The proposed haustorium bauplan is represented in Fig. 5, indicating the similar topology observed in both aerial (Fig. 5a) and root (Fig. 5b, c) parasites.

This schematic representation also illustrates the topology observed in the haustorium of Balanophoraceae species (Fig. 5d). It has been suggested that plants in this family have a unique type of haustorium in which the host vascular system is stimulated to differentiate new conductive cells toward the parasite (Mangenot 1947; Kuijt 1969). While this is indeed the case, stimulation and rearrangement of host phloem and/or xylem is not an exclusive feature of the Balanophoraceae haustorium. The extreme phenotype observed in Balanophoraceae is similar to what has been reported in other root holoparasites (Tate 1925), mistletoes (Aloni 2015), and endoparasites (García-Franco et al. 2007; do Amaral and Ceccantini 2011; Teixeira-Costa et al. in press). The frequent occurrence of host vascular cells converging toward the haustorium highlights another level of convergence among different parasitic plants. At a physiological level, these changes caused to host vascular development appear to be mediated by the same hormones released by the parasite at the interface with the host (Zhang et al. 2012; Hu et al. 2017; Spallek et al. 2017).

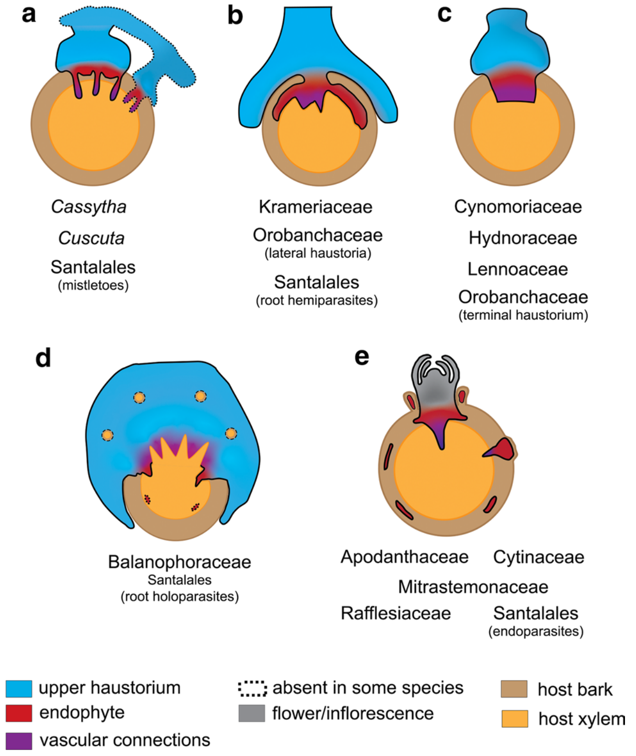

Fig. 5 Schematic representation of different morpho-anatomical types of haustoria according to the interpretation of a shared body plan. Transition zones between different parts of the haustorium are represented with color gradients

Another feature of the Balanophoraceae haustorium that deserves special mention is the highly modified chimeric structure that many of them develop with their hosts. The tuberous organ of *Balanophora*, *Langsdorffia*, and *Thonningia* species is traversed by chimeric vascular strands composed of both parasite and host cells (Fig. 5d) (Holzapfel 2001). In addition to xylem, phloem, and transfer cells, these chimeric strands contain both parasitic and host-derived meristematic cells at the apical region (Gedalovich-Shedletzky and Kuijt 1990; Hsiao et al. 1995). This close integration of meristematic cells is also observed in endoparasites such as *Pilostyles thurberi* A. Gray (Apodanthaceae; Rutherford 1970), *Arceuthobium douglasii* Engelm. (Santalaceae; Lye 2006), and at least temporarily in *Tristerix aphyllus* (DC.) Barlow (Loranthaceae; Mauseth et al. 1985). Moreover, endoparasites such as Rafflesiaceae and Mitrastemonaceae species develop another type chimeric structure known as cupule, which is part of the parasite haustorium (Fig. 4e, f, cp) and partially produced by the host as a response to the burst of parasite flower buds (Kuijt 1969; Nikolov et al. 2014).

It is noteworthy that, at their mature developmental stage, endoparasites lack a recognizable upper haustorium (Fig. 5e). In other parasites, the upper haustorium provides a link between the exterior parasite body (i.e., the exophyte) and the vascular connections formed with host tissues via the lower haustorium. Through the course of evolution, the increased specialization of the endophytic system, which acquired the function of giving rise to the main exophyte (Kuijt 1969; Těšitel 2016), could have coincided with a reduction of the upper haustorium, rendering it ultimately superfluous. In endoparasites with remnant photosynthesis, such as *Tristerix aphyllus* (Loranthaceae) and *Viscum minimum* Harv. (Santalaceae), a distinct upper haustorium is formed upon germination (Mauseth et al. 1985; Kuijt 1986). As development progresses, the shoot apex is aborted and the upper haustorium disintegrates (Mauseth et al. 1985; Kuijt 1986). A similar form of germination and initial development could also occur for other endoparasites.

5 New interpretation of haustorium organ identity

Questions of homology between parasitic plant structures, especially the haustorium, and other plant organs have long puzzled researchers and divided opinions. For instance, structures that foster the development of additional lateral haustoria, such as the epicortical roots of certain mistletoes, the pilot roots of Lennoaceae and Hydnoraceae species, and the runners of Balanophoraceae have all been initially identified as modified roots (Kuijt 1964, 1966, 1969). However, more recent publications have reopened the question of homology in all of these structures (Mauseth et al. 1992; Tennakoon et al. 2007; Kuijt 2015).

The most debated issue, however, is the question to whether haustoria are modified roots, stems, or an entirely different type of structure. Based on the evolutionary plasticity of plants, leading to a diverse array of morphologies, Kuijt (1969) claims that the haustorium "represents a root in function and evolutionary origin." Considering haustorium anatomy is highly modified, showing no clear parallels with other organs, Goebel (1905) and Forstreuter (1988) have interpreted the haustorium as an organ *sui generis*, that is, a structure of its own kind. Finally, Weber (1987) avoided the "*sui generis* debate" by suggesting that a terminal haustorium could be interpreted as a type of lateral haustoria formed directly at the root apex due to extreme root reduction.

The analysis of multi-level convergence is an interesting approach that can also be helpful in the discussion of organ identity of parasitic plant haustoria. At the functional level, all different types of haustorium exert the same basic functions of a root system. In fact, parasitic plants depend upon their hosts in a similar way that non-parasitic plants depend on the soil (Calvin and Wilson 1998). Haustoria provide mechanical anchorage to the host and act in the uptake of water and mineral nutrients (Joel 2013). In some cases, haustoria might also be involved in mycorrhizal interactions (Baird and Riopel 1986; de Vega et al. 2010). At the molecular level, albeit data are still restricted to a few *Cuscuta* and Orobanchaceae species (Yang et al. 2015; Vogel et al. 2018; Yoshida et al. 2019), evidence suggests genes that control lateral root formation in non-parasitic plants have been coopted for haustorium development in parasite species (Yoshida et al. 2019). Similarities between hormonal control of haustorium formation and root development have also been described (Zhang et al. 2015, 2016). Nevertheless, at the developmental and anatomical levels, the message is not quite clear.

Four key features are used in comparative morphology and anatomy of seed plants to differentiate roots from shoots: (1) the organization of xylem and phloem tissues in alternating sectors (roots, Fig. 6a) versus same axial sectors (shoots, Fig. 6b); (2) endogenous (root, Fig. 6c) versus exogenous (shoot, Fig. 6d) origin of daughter axes; (3) presence (roots, Fig. 6e) versus absence (shoots, Fig. 6f) of a root cap; (4) absence (roots, Fig. 6g) versus presence (shoots, Fig. 6h) of exogenously formed leaves (Rutishauser and Isler 2001). Internal haustorium anatomy in the different lineages of parasitic plants is not organized in sectors and cannot be classified as either root-like, or stem-like (Fig. 6i; Bhandari and Mukerji 1993). In terms of their ontogenesis, terminal haustoria develop from the embryo root apex soon after germination, while lateral haustoria have an exogenous origin (Fig. 6j), developing from cells in the cortical region of roots or stems (Kuijt 1969; Heide-Jørgensen 2008). Despite their root-like origin, the root apical meristem of most parasites with a terminal haustorium lacks a root cap (Calvin 1966; Musselman and Dickison 1975; Lamont 1983). In parasites with lateral haustoria, a cap-like tissue can be present (Brokamp et al. 2012), however, with a different appearance, more similar to bark tissues (Fig. 6k). The underground structures of Balanophoraceae are regarded as not having a root (nor a shoot) organization (Hansen 2015).

Considering the exogenous development of lateral haustoria, a similar origin is mostly common for bud formation (Fig. 6d), developing from either pre-existing shoots (stem ramification or branching) or roots (root–shoots or root buds) (Esau 1965). On the other hand, lateral and adventitious root formation in angiosperms are both associated exclusively with an endogenous origin (Fig. 6c), i.e., developing from cells in the vascular system (Esau 1965). Development of structures that emerge directly from a haustorium occurs in few parasitic clades. In root holoparasites with a terminal haustorium, such as some Orobanchaceae and all Balanophoraceae, inflorescences develop from the tuberous haustorium, originating from parenchyma cells among the many vascular bundles (Schrenk 1894; Shivamurthy et al. 1981). In the haustorial roots of Lennoaceae species, stem apical meristems also develop from parenchyma cells among vascular bundles (Fig. 6l). In Loranthaceae mistletoes, basal epicortical roots develop at the base of the hypocotyl, in close proximity to the upper haustorium, but separate from it (Calvin and Wilson 2006). Finally, in the case of most endoparasites, such as Apodanthaceae, Cytinaceae, Mitrastemonaceae, and Rafflesiaceae species, flower/inflorescence axes also develop endogenously, from a secondary morphological surface formed internally to the reproductive meristem apex (Kuijt 1969; Nikolov et al. 2014).

In face of these multiple interpretations, all of which based on somehow conflicting evidence, the haustorium appears as a "misfit" in the sense of the classical morphology discipline (Bell 1991). Often used in reference to plants such as river-weeds (Podostemaceae) and bladderworts (Lentibulariaceae), the term "morphological misfit" has been applied to label a variety of natural deviations to the norm of a root–shoot axis with independent, non-overlapping structures (Rutishauser 2016). Using these peculiar plants as subjects and examples, several plant morphologists, philosophers, and developmental geneticists (e.g., Arber 1950; Sattler 1996; Sinha 1999; Rutishauser and Isler 2001) have argued in favor of a complementary approach to the classical morphology framework. Known as Continuum Morphology,

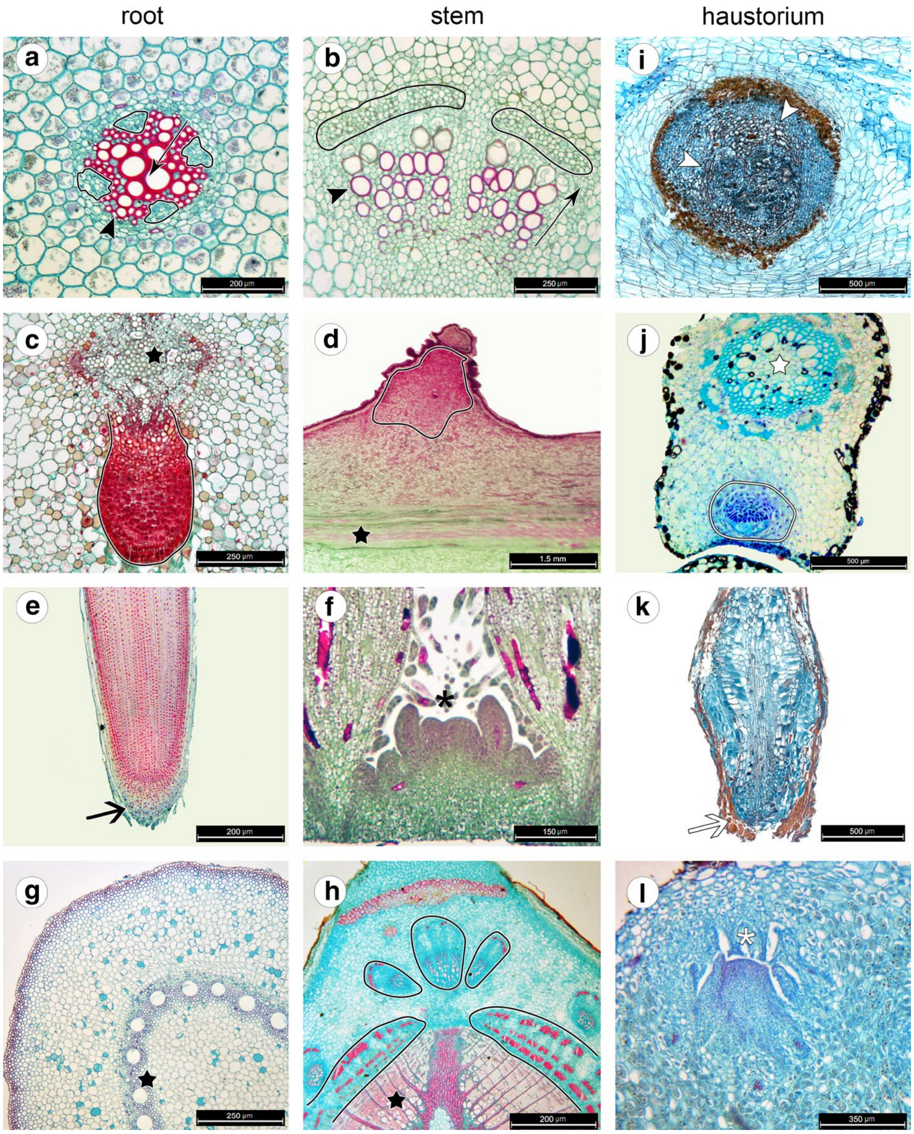

Fig. 6 Diagnostic anatomical features of roots (**a**, **c**, **e**, **g**) and stems (**b**, **d**, **f**, **h**) compared with aspects of haustorium (**i**–**l**) anatomy. **a**, **b** Organization of xylem (black arrowheads) and phloem (black outlines) tissues in alternating sectors (roots, **a**) versus same axial sectors (shoots, **b**); note the opposite direction of vessel element differentiation (curvy black arrows) in each organ. **c**, **d** Daughter axes (black outlines) with an endogenous (root, **c**) versus exogenous (shoot, **d**) origin; note the position of the vascular system in each organ (black star). **e**, **f** Apical meristem (black asterisks) showing presence (root, **e**) versus absence (shoot, **f**) of a root cap. **g**, **h** Absence (roots, **g**) versus presence (shoots, **h**) of exogenously formed leaves; note the position of the vascular system in each organ (black star) and the shape of the leaf gap in the stem (black outline). **i** Cross section through the haustorium of *Krameria lappacea* (Krameriaceae; image provided by G. Brokamp and M. Weigend); note the absence of phloem and presence of xylem (white arrowhead) tissues. **j** Haustorium initiation (white outline) in the cortex of *Cuscuta americana* L. (Convolvulaceae); note the position of the vascular system (white star). **k** Pre-haustorium of *Krameria lappacea* (Krameriaceae; image provided by G. Brokamp and M. Weigend); note the presence of a bark-like dermal tissue (white arrow) covering part of the structure. **l** Shoot apical meristem (white asterisk) developed from parenchyma cells in the haustorial root of *Lennoa madreporoides* (Lennoaceae)

or Fuzzy Arberian Morphology, in homage to the pioneer work of Agnes Arber (1950), this complementary approach understands plant structures as processes, highlighting that drastic evolutionary changes to the basic root–shoot program may require *fuzzy,* rather than clear-cut concepts of organ identity (Rutishauser 2020).

Under this framework, the haustorium of parasitic flowering plants would be better interpreted as a root–shoot mosaic, as it has been suggested for the underground structures of *Utricularia* and *Pinguicula* (Lentibulariaceae) (Rutishauser and Isler 2001). Using the mosaic as a metaphor, a terminal haustorium could then be interpreted as composed mostly of "root-like tiles," while lateral haustoria would be composed of roughly equal parts of "root-like tiles" and "stem-like tiles." This interpretation provides more than a resolution to the conflict of haustorium homology and organ identity, opening up new research avenues for the comparison between parasitic plants and other morphological misfits, especially in terms of their evolutionary development. The continuum morphology approach complements the interpretations based on classical morphology, providing a more comprehensive framework for the comparison and investigation of the haustorium across the multiple angiosperm lineages. Finally, this mosaic interpretation reinforces that, despite being a homoplastic character, the haustoria of the different functional and taxonomic groups of parasitic plants are more similar to each other, than they are similar to other plant organs. The shared developmental trajectory of the different types of haustoria could then be due to homologous regulatory genes expressed in a similar manner in all different lineages of parasitic flowering plants.

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Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

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