Parasitic flowering plants on postal stamps: vehicles for learning

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It is proposed that philately and the study of parasitic plants can be conflated for educational purposes. Of the 12 lineages of parasitic flowering plants, eight are currently represented on postal stamps. The most frequent genus seen on stamps is Rafflesia, closely followed by Viscum. These stamps convey messages about the history and importance of parasitic plants such as witchweed (Striga), sandalwood and mistletoes. Some of the parasitic plants are beautiful wildflowers such as Castilleja, Euphrasia and Pedicularis, whereas many mistletoes in Loranthaceae have flowers that rival orchids. Countries with rich parasite floras that currently do not have stamps featuring these plants should consider them as worthy subjects.

Keywords: Botanical diversity, educational purpose, parasitic angiosperm, philately, plant blindness.

ACCORDING to Raven[1], 'we need to find ways to pay more attention to plants'. To combat 'plant blindness' and increase the connections that humans feel for plants, activities such as gardening, participation in outdoor activities and anthropomorphization have been recommended[2]. One way to promote appreciation of plants that has not been widely discussed is the seemingly unlikely conflation of botany with another popular human endeavour: the collection and study of postage stamps (philately). It is proposed here that collecting stamps is an activity that can provide a gateway for both young and old to explore botanical diversity.

Images of stamps featuring parasitic flowering plants (angiosperms) were first posted on the Parasitic Plant Connection website decades ago[3]. Since then, it has become increasingly evident that philately can be used as an educational tool. Philatelic organizations are international in nature with thousands of members who often specialize in particular themes. For the biological world, a rich inventory of stamps exists depicting animals[4,5] and fungi[6] as well many botanical themes. Indeed the journal *Biophilately* represents an international cooperative society dedicated to the study of biological postal stamps. Although the study of parasitic plants is a specialized botanical sub-discipline, research in this area spans a myriad of fields, including agriculture, forestry, ecology, physiology, anatomy, phytopathology, biotechnology, molecular biology, biochemistry, taxonomy and phylogenetics.

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Parasitic plants are referred to as heterotrophic, i.e. 'different feeding' because they obtain at least some of their water and nutrients from another vascular plant. The parasite attaches to the host plant through a structure called the haustorium that connects to the xylem and, in some cases, the phloem of the host. Parasites that obtain water and minerals from the host, but are green and retain photosynthetic activity are called hemiparasites. They attach to the xylem but not the phloem. In contrast, parasitic angiosperms that attach to both xylem and phloem and have lost the ability to photosynthesize are called holoparasites. They also have highly altered morphologies, often with leaves reduced to scales, or in some cases, where stems and leaves are missing altogether. Mycoheterotrophs are another type of heterotrophic angiosperms that rely on mycorrhizal fungi to obtain nutrients, but do not attach directly to tree roots.

The question 'how many angiosperm parasite lineages exist?' was recently reviewed[7] and it appears that this nutritional mode has evolved independently 12 times. Holoparasites exist in 10 of the 12 lineages, and seven of these are composed entirely of holoparasites. In 11 of the 12 orders, the parasitic members are present in one family, whereas in the sandalwood order (Santalales) about 20 families can be recognized. Finding the closest photosynthetic, non-parasitic relatives of the holoparasites has proven to be challenging, but molecular analyses have provided definitive answers.

The purpose of this study is to highlight the parasitic angiosperms that occur on stamps and discuss their importance to human endeavours as well as their role in natural ecosystems. We also want to promote future production of additional parasitic plant stamps that are scientifically relevant, of economic or humanistic importance or simply beautiful.

Parasitic plants: the good, bad and ugly

The term 'parasite' often provokes a negative first impression, leading to the idea that these plants kill their hosts. That this is not true is supported by the fact that only about 25 of the 280 genera of parasitic angiosperms are pathogens that negatively impact plants cultivated by humans[8]. Two genera are particularly damaging to crops: *Striga* (witchweed) and *Orobanche* (broomrape). Witchweed derives its name from the observation that it 'bewitches' its host. Even before the parasite emerges from the soil, the host shows physical symptoms of parasitism, such as stunted growth and loss of reproduction. *S. asiatica* and *S. hermonthica* cause major crop damage in Subsaharan Africa, and have thus been the focus of intense research to mitigate these losses[9]. The broomrapes are problematic in the Middle East, Europe and Asia[10]. Some stem parasites (mistletoes) in Santalales can cause damage to fruit trees. The dwarf mistletoes (*Arceuthobium* spp.) are major pathogens of coniferous trees grown in agroforestry settings[11]. Human alteration of the forest ecosystem, such as planting monocultures, encourages the spread and damage caused by these native components of the flora.

The above examples highlight some of the 'bad' players, but what about the 'good' parasitic plants? That expression may sound like a non-sequitur, but indeed the vast majority of parasitic angiosperms are benign and even integral components of their ecosystems[12]. Work in Australia showed that removal of mistletoes negatively affected the nesting behaviour of several bird species; thus they are keystone resources in these woodland habitats[13]. Similarly, root parasites such as *Rhinanthus* may lower host plant biomass, thus allowing increased diversity. At high density they enhance the number of invertebrates and affect herbivores, predators and detritivores[14]. Parasitic plants can even alter the physical environment around them, such as soil water and nutrients, atmospheric carbon dioxide and temperature[15]. Many parasitic plant species are rare and, being dependent upon their hosts, are particularly susceptible to population decline; thus they merit conservation and restoration efforts[16]. These organisms represent a large proportion of biodiversity and therefore their importance should be recognized[17]. Finally, what about 'ugly' parasites? Like troll dolls, whether any parasite species is ugly or beautiful is probably in the eye of the beholder. As shown below, some parasitic angiosperms are as beautiful as orchids and thus fully deserve showcasing on postal stamps.

Parasitic plants on stamps

Of the 12 lineages (orders) containing parasitic angiosperms, eight have been represented on postal stamps. Table 1 shows these groups and the full taxonomic names of the species included. At least 95 different stamps show parasitic angiosperms representing 52 species in 29 genera. Indonesia has the highest number of parasitic plant stamps (seven) followed by Malaysia (six). These two countries achieved high numbers because *Rafflesia* is a popular plant to be represented on stamps. Like the rhinoceros and panda, *Rafflesia* is a 'charismatic mega *flora*' because its members have the largest flowers in existence. The next most popular subject is *Viscum* owing to its symbolism during the Christmas season (see below).

Although this study focused on haustorial angiosperm parasites, we would be remiss to not mention the New Caledonian endemic *Parasitaxus usta* (Podocarpaceae), the only parasitic gymnosperm. *Parasitaxus* is a physiological chimera mixing haustorial parasitism with mycoheterotrophy[18]. This amazing plant was featured on a commemorative postal stamp by New Caledonia in 1989.

Lamiales – Orobanchaceae

One-third of all stamps bearing images of parasitic plants (10 genera, 23 species) show members of the broomrape family, Orobanchaceae (Figure 1). This is the largest family among parasitic angiosperms with 101 genera and over 2100 species[8]. *S. asiatica* is a major pathogen on maize, sorghum, rice and sugarcane[19]. In response to its accidental introduction into the United States in the 1950s, the US Department of Agriculture initiated a control programme. This species is shown on stamps from British Indian Ocean Territory (Figure 1 *k*) and Saudi Arabia. *Striga elegans*, a close relative of *S. asiatica*, was depicted on two stamps, one from Lesotho and another from Togo (Figure 1 *l*). Given their morphological similarity, it has been suggested that these species share a recent common ancestor. *S. asiatica* is agrestal, that is, it is only known from agricultural fields, whereas *S. elegans* is only known from native grasslands[20]. Thus human activities may have provided the conditions necessary for the evolution of this crop pathogen. Another major crop pest in Africa is *S. hermonthica*, which is shown parasitizing maize on a stamp issued in 1989 from Burkina Faso.

In recent years the genus *Orobanche* has undergone taxonomic revision owing to DNA sequence data analysis. *Orobanche* contains 117 species, whereas its segregates are *Phelipanche* (62 species) and the New World *Aphyllon* (20 species). Two of these holoparasites are feature on stamps, *Orobanche rapum-genistae* (Figure 1 *h*) and *Phelipanche purpurea* (Figure 1 *j*). In contrast to the stamps with *Striga*, none of the ex-*Orobanche* crop pests such as *Phelipanche aegyptiaca*, *P. cernua* and *P. ramosa* is featured on stamps. A stamp showing *Cistanche* was issued in 1959 from French West Africa (eight former French colonies, dissolved in 1960), possibly the first parasitic flowering plant stamp. This species was also featured on a stamp from Bahrain in 1993 (Figure 1 *d*) as

Table 1. Haustorial parasitic flowering plants shown on stamps

Taxon	Parasite type	Political entity	Year	Comments
Lamiales, Orobanchaceae				
Alectra sessiliflora (Vahl) Kuntze	hemi-, root	South Africa	1991	From Transkei (formerly independent)
Alectra vogelii Benth.	hemi-, root	Burkina Faso	1989	In group of four stamps with Orobanchaceae
Bellardia viscosa (L.) Fisch. and C.A. Mey	hemi-, root	Baliwick of Jersey	2006	On stamp as *Parentucellia viscosa* Caruel (a synonym)
Castilleja linariifolia Benth.	hemi-, root	USA (Wyoming)	1982	
Castilleja sp.	hemi-, root	USA	1992	Stylized painting of paintbrush. Wildflower issue
Castilleja sp.	hemi-, root	USA	1992	With Rufous Humming bird. In a series of five stamps with humming birds
Cistanche phelypaea (L.) Cout.	holo-, root	Bahrain	1993	
Cistanche phelypaea (L.) Cout.	holo-, root	Jordan	2003	On stamp as *Cistanche tubulosa* (Schenk) Wight (a synonym)
Cistanche phelypaea (L.) Cout.	holo-, root	Oman	2013	On stamp as *Cistanche tubulosa* (Schenk) Wight (a synonym)
Cistanche phelypaea (L.) Cout.	holo-, root	Saudi Arabia	1990	
Cistanche sp.	holo-, root	French West Africa	1959	A former French administrative unit now comprising several African countries. Species may also have been on a stamp in 1943
Cycnium tubulosum (L.f.) Engl.	hemi-, root	Kenya	1983	On stamp as *Rhamphicarpa montana* N.E.Br. (a synonym)
Euphrasia transmorrisonensis Hayata	hemi-, root	Taiwan	2011	
Harveya huttonii Harm.	holo-, root	South Africa	1991	On stamp as *Harveya pulchra* Hilliard and B. L. Burtt (a synonym). From Transkei (formerly independent)
Harveya speciosa Bernh.	holo-, root	South Africa	1991	From Transkei (formerly independent)
Orobanche rapum genistae Thuill.	holo-, root	Balliwick of Guernsey (Alderney)	1994	Parasitic on *Cytisus scoparius* ssp. *maritimus* (Rouy) Heywood with *Bombus lucorum* L.
Pedicularis apodochila Maxim.	hemi-, root	Japan	1986	An ambiguous name
Pedicularis hirsuta L.	hemi-, root	Greenland	1992	Highest latitude of any parasitic plant
Pedicularis hoermanniana K. Malý	hemi-, root	Yugoslavia	1997	Former Yugoslavia now six republics. Known also from Italy, quite rare
Pedicularis oederi Vahl	hemi-, root	Norway	2000	Endangered. See Kobiv & Nesteruk. (2001, *Polish Bot. J.*, **46**, 241–250)
Pedicularis sceptrum-carolinum L.	hemi-, root	Germany	1981	Endangered bog, marsh meadows and water plants
Pedicularis siamensis Tsoong	hemi-, root	Thailand	2001	Name ambiguous. Known only from Chiang Mai Province
Pedicularis sudetica Willd.	hemi-, root	Poland	2006	Endangered
Phelipanche purpurea (Jacq.) Soják	holo-, root	Balliwick of Guernsey (Alderney)	2016	Shown as Yarrow Broomrape; formerly *Orobanche purpurea* Jacq.
Striga asiatica (L.) Kuntze	hemi-, root	British Indian Ocean Territory	2001	
Striga asiatica (L.) Kuntze	hemi-, root	Saudi Arabia	1990	
Striga aspera (Willd.) Benth.	hemi-, root	Burkina Faso	1989	
Striga elegans Benth.	hemi-, root	Lesotho	1985	
Striga elegans Benth.	hemi-, root	Togo	2000	
Striga gesnerioides (Willd.) Vatke	hemi-, root	Burkina Faso	1989	In group of four Orobanchaceae stamps
Striga hermonthica (Delile) Benth.	hemi-, root	Burkina Faso	1989	In group of four Orobanchaceae stamps
Striga hermonthica (Delile) Benth.	hemi-, root	Burkina Faso	1963	On stamp as *S. senegalensis* Benth. (a synonym); as Republique de Haute-Volta
Santalales, Balanophoraceae				
Thonningia sanguinea Vahl	holo-, root	Democratic Republic of Congo	1960	On stamp as Belgisch (Belge) Congo
Thonningia sanguinea Vahl	holo-, root	Ivory Coast	2013	A group of three stamps, with the mistletoe *Tapinanthus belvisii* (DC) Danser and the aquatic plant *Ottelia ulvifolia* (R.Br.) Rich
Santalales, Loranthaceae				
Agelanthus brunneus Tiegh.	hemi-, stem	Rwanda	1981	On stamp as *Tapinanthus brunneus* (Engl.) Danser (a synonym)
Agelanthus cf. *musozensis* (Rendle) Polhill and Wiens	hemi-, stem	Rwanda	1975	On stamp as *Tapinanthus prunifolius* (E. Mey ex Harv.) Tiegh. (a synonym), now *Agelanthus prunifolius* (E. Mey. ex Harv.) Polhill and Wiens, but this species not reported from Rwanda

(*Contd*)

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Taxon	Parasite type	Political entity	Year	Comments
Amyema incarnatiflora (Elmer) Danser	hemi-, stem	Philippines	2007	In group with *Rafflesia lagascae* Blanco (as *R. manillana* Teschem.)
Amyema scandens (Tiegh.) Danser	hemi-, stem	New Caledonia	1978	Showing flowers emerging from epicortical runners.
Decaisnina forsterianum (Schult) Barlow	hemi-, stem	Fiji	1983	On stamp as *Amylotheca insularum* Danser (a synonym). Widely distributed in the south Pacific (see Barlow and Schodde 1993).
Macrosolen melintangensis Miq.	hemi-, stem	Federated States of Micronesia	2015	On stamp as 'Loranthaceae'. Photo is of *Macrosolen melintangensis* Miq. taken by Arthit Buarapa in the Phu Luang Wildlife Sanctuary in Thailand. No *Macrosolen* species occur in Micronesia
Tapinanthus belvisii (DC) Danser	hemi-, stem	Ivory Coast	2013	Accurately representing this species that occur in the Ivory Coast. Fake versions of these stamps were made.
Tapinanthus globiferus (A. Rich.) Tiegh.	hemi-, stem	Chad	1975	The only species of *Tapinanthus* from Chad (Polhill and Wiens 1998). Also looks like *T. dependens* (Engl.) Danser (S of Chad)
Santalales, Opiliaceae				
Opilia amentacea Roxb.	hemi-, root	Burkina Faso	1977	On stamp as *Opilia celtidifolia* Endl. exWalp. (a synonym); as Republic of Upper Volta
Santalales, Santalaceae				
Santalum album L.	hemi-, root	Portugal	2015	East Timor (= Timor-Leste) gained independence from Portugal in 1975, later invaded by Indonesia, independent again in 1999
Santalum album L.	hemi-, root	India	2006	Stylized tree representing sandalwood, with elephant
Santalum album L.	hemi-, root	India	2019	Two stamps, one showing Sandalwood and jasmine perfumes
Santalum album L.	hemi-, root	Indonesia	1995	Stamp shows trunk of sandalwood tree
Santalum album L.	hemi-, root	New Caledonia	1991	
Santalum album L.	hemi-, root	New Caledonia	2004	
Santalum insulare var. *hendersonense* (F.Br.) Fosberg and Sachet	hemi-, root	Pitcairn Islands	1992	On stamp as *S. hendersonense* F. Br. P. Scott Commemorative expedition
Santalum yasi Seem.	hemi-, root	Fiji	1990	Trees series
Santalales, Viscaceae				
Phoradendron leucarpum (Raf.) Reveal and M. C. Johnst.	hemi-, stem	USA	1964	Christmas stamp; group of four, also showing poinsettia, holly and spruce
Phoradendron leucarpum (Raf.) Reveal and M. C. Johnst.	hemi-, stem	USA (Oklahoma)	1982	Oklahoma, USA with a Scissor-tailed Flycatcher, the state bird of OK
Viscum album L.	hemi-, stem	Hungary	1963	New Year stamp showing mistletoe and calendar
Viscum album L.	hemi-, stem	Hungary	1963	New Year stamp
Viscum album L.	hemi-, stem	Yugoslavia	1973	Former Yugoslavia now six republics
Viscum album L.	hemi-, stem	Switzerland	1974	Pro Juventute: Poisonous plants of the forest
Viscum album L.	hemi-, stem	Baliwick of Guernsey	1978	Christmas flowers series
Viscum album L.	hemi-, stem	England	1980	13.5 Pence Christmas stamp
Viscum album L.	hemi-, stem	Canada	1987	*Viscum album* L. or *Phoradendron leucarpum* (Raf.) Reveal and M. C. Johnst.? The berries are shown as both white and red
Viscum album L.	hemi-, stem	Switzerland	1997	Pro Juventute: Mistletoe, animals on and in the water
Viscum album L.	hemi-, stem	Sweden	1998	Christmas 1998. Julpost
Viscum album L.	hemi-, stem	Baliwick of Jersey	1999	Christmas 1999
Viscum album L.	hemi-, stem	Baliwick of Guernsey	2008	Photograph of plant in fruit. Christmas 2008 – Festive Foliage
Viscum album L.	hemi-, stem	Baliwick of Jersey	2013	Frosts and nature
Viscum album L.	hemi-, stem	England	2014	Post and go winter greenery
Viscum album L.	hemi-, stem	Netherlands	2014	Kissing under the mistletoe
Santalales, Ximeniaceae				
Ximenia caffra Sond.	hemi-, root	Botswana	1979	Painting of plant with flowers and fruit
Ximenia caffra Sond.	hemi-, root	Malawi	1993	Painting of plant in fruit
Ximenia caffra Sond.	hemi-, root	Malawi	2016	Photograph of the plant in fruit
Ximenia caffra Sond.	hemi-, root	Mozambique	1998	A stylized painting of the plant in fruit
Malpighiales, Rafflesiaceae				
Rafflesia arnoldii R.Br.	holo-, root	Indonesia	1992	The 'rare flower' (Puspa Langka in Indonesian)

(*Contd*)

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Taxon	Parasite type	Political entity	Year	Comments
Rafflesia arnoldii R.Br.	holo-, root	Indonesia	1993	The 'rare flower' (Puspa Langka). The common name in Indonesian is Padma Raksasa meaning 'Giant Rafflesia'
Rafflesia arnoldii R.Br.	holo-, root	Indonesia	2008	Stamp shows a photograph of the species. Indonesia-Japan Joint Issue
Rafflesia arnoldii R.Br.	holo-, root	Malaysia	1979	Misidentified as *R. hasseltii* Suring. Possibly *R. arnoldii* R.Br. or *R. gadutensis* Meijer
Rafflesia arnoldii R.Br.	holo-, root	Malaysia	1979	Misidentified as *R. hasseltii* Suring. Possibly *R. arnoldii* R.Br. or *R. gadutensis* Meijer
Rafflesia arnoldii R.Br.	holo-, root	Malaysia	2007	Unidentified but likely *Rafflesia arnoldii* R.Br., with hornbill
Rafflesia azlanii Latiff and M. Wong	holo-, root	Malaysia	2013	Wonders of Malaysian Forests
Rafflesia kerrii Meijer	holo-, root	Thailand	2006	Group of 4 stamps, with *Sapriapoilanei* Gagnep. and two carnivorous plants, *Nepenthes* and *Drosera*
Rafflesia lagascae Blanco	holo-, root	Philippines	2007	Identified as *R. manillana* Teschem., this *Rafflesia* from Mt Makiling is now known as *R. lagascae* Blanco
Rafflesia micropylora Meijer	holo-, root	Indonesia	1989	Identified only as *Rafflesia* on the stamp, but the morphology indicates *R. micropylora* Meijer
Rafflesia micropylora Meijer	holo-, root	Indonesia	2002	Issued with another stamp showing *Trimeresurus hageni* (Lidth de Jeude) – a snake
Rafflesia pricei Meijer	holo-, root	Brunei Darussalam	2000	Flower series
Rafflesia pricei Meijer	holo-, root	Indonesia, Jakarta, St Maarten	2012	Misidentified as *Rafflesia arnoldii* R.Br.
Rafflesia sp.	holo-, root	Caribbean Netherlands	2012	*Rafflesia* does not occur in the Caribbean Netherlands
Rafflesia sp.	holo-, root	Malaysia	2004	Unidentified species of *Rafflesia*, with elephant
Rafflesia sp.	holo-, root	Malaysia	2014	World Youth Stamp Exhibition 2014
Rafflesia sp.	holo-, root	Philippines	2019	Painting is vague, resembles *R. arnoldii* R.Br. which does not occur in the Philippines
Rhizanthes lowii (Becc.) Harms	holo-, root	Brunei Darussalam	2000	Specific epithet misspelled 'lowi'
Sapria poilanei Gagnep.	holo-, root	Thailand	2006	International Letter Writing Week stamp
Laurales, Lauraceae				
Cassytha filiformis L.	hemi-, stem	Marshall Islands	1985	Under the medicinal plants series
Piperales, Hydnoraceae				
Hydnora africana Thunb.	holo-, root	South Africa	1991	From Transkei (formerly independent)
Saxifragales, Cynomoriaceae				
Cynomorium coccineum L.	holo-, root	Bahrain	1993	As the 'Maltese Fungus', under mushroom theme
Zygophyllales, Krameriaceae				
Krameria lappacea (Dombey) Burdet and B.B. Simpson	hemi-, root	Federated States of Micronesia	?	On stamp as *K. triandra* Ruiz and Pav. (a synonym)
Solanales, Convolvulaceae				
Cuscuta epithymum (L.) L.	hemi-, stem	Balliwick of Guernsey (Alderney)	1994	Parasitic on *Ulex europaeus* L. with the Dartford Warbler – *Sylvia undata* (Boddaert)

well as stamps from Jordan, Oman and Saudi Arabia (Table 1).

Except for *Alectra*, the remaining hemiparasitic plants shown on stamps are non-pathogenic species. Indeed, some of these are beautiful wildflowers that are admired and cherished, at least by a few. Wyoming adopted *Castilleja linariifolia* as its state wildflower in 1917, but not without objection by botanist Aven Nelson. He argued that only experts could distinguish among the more than 200 species of Indian paintbrush (the common name for *Castilleja*). He also asked, 'who would want to plant a parasitic plant in a garden?' Despite these objections, Wyoming retained paintbrush as its state flower and it was featured on a stamp in 1982 along with the western meadowlark (Figure 1 *c*). With about 600 species, *Pedicularis* (lousewort) is the most speciose genus in Orobanchaceae followed by *Euphrasia* (eyebright, Figure 1 *f*) with 246 species[8]. *Pedicularis* has been chosen as a subject for stamps by seven different political entities. Greenland chose *P. hirsuta* which notably occurs at the highest latitude on earth for any parasitic flowering plant. Except for *P. apodochila* of Japan (Figure 1 *i*), the remaining five *Pedicularis* species are rare and/or endangered and require conservation efforts for their preservation.

Santalales – six families

Sandalwood (Santalales) has 179 genera and 2428 species[8], of which 11 genera and 16 species are represented

Figure 1. Stamps of parasites in Orobanchaceae. ***a***, *Alectra vogelii*; ***b***, *Bellardia viscose*; ***c***, *Castilleja linariifolia*; ***d***, *Cistanche phelypaea*; ***e***, *Cycnium tubulosum*; ***f***, *Euphrasia transmorrisonensis*; ***g***, *Harveya speciosa*; ***h***, *Orobanche rapum-genistae*; ***i***, *Pedicularis apodochila*; ***j***, *Phelipanche purpurea*; ***k***, *Striga asiatica*; ***l***, *Striga elegans*.

on stamps. Six stamps commemorate the sandalwood of commerce, *Santalum album*. This root parasitic tree has been utilized for centuries because of its aromatic heartwood that contains the essential oil santalol, the source of odour in incense[21]. Various themes are depicted on these stamps, such as the woody trunk of this tree (Indonesia), an elephant harvesting sandalwood trees (India 2006), and perfume (India 2019; Figure 2 *f*). Indeed, the Indian sandalwood stamps were infused with the fragrance of the plant, possibly the first and only time this has been done. The 150th anniversary of the arrival of Captain Robert Clark Morgan and his 'santaliers' in New Caledonia in 1841 has been commemorated on a 1991 stamp. The 'boom and bust' history of exploiting sandalwood in Hawaii is well documented; however, such commercial operations were also taking place in other regions as early as the 16th century. The stamp from 2015 showing a woman bearing baskets with sandalwood commemorates the 500th anniversary since Portugal colonized East Timor. Other sandalwood species besides *S. album* were also harvested and two of these are shown on stamps: *Santalum insulare* var. *hendersonense* from Pitcairn Islands in 1992 and *Santalum yasi* from Fiji in 1990 (Figure 2 *g*).

Three African countries (Botswana, Malawi and Mozambique) have all issued stamps with images of the root parasite *Ximenia caffra* (Figure 2 *l*) commonly known as sour plum for its edible fruits. In Africa, the leaves and roots are used medicinally to treat several diseases and ailments[22]. In a wild fruit series of stamps issued by Upper Volta (now Burkina Faso) in 1977, *Opilia amentacea*

Figure 2. Stamps of parasites in Santalales. Loranthaceae: ***a***, *Agelanthus brunneus*; ***b***, *Agelanthus* cf. *musozensis*; ***c***, *Amyema scandens*; ***d***, *Amyema incarnatiflora*; ***e***, *Tapinanthus belvisii*. Santalaceae: ***f***, *Santalum album*; ***g***, *Santalum yasi*. Opiliaceae: ***h***, *Opilia amentacea*. Balanophoraceae: ***i***, *Thonningia sanguinea*. Viscaceae: ***j***, *Phoradendron leucarpum*; ***k***, *Viscum album*. Ximeniaceae: ***l***, *Ximenia caffra*.

was shown (as *Opilia celtidifolia*, a synonym; Figure 2 *h*). This root parasite is a woody vine that is widely distributed from tropical Africa to Australia.

One holoparasite in Santalales has been illustrated on stamps: *Thonningia sanguinea* (Balanophoraceae), a plant utilized in traditional medicine. This family, with 14 genera and 42 species, contains some of the most unusual holoparasites in the angiosperms. The plants are highly modified to the point that some of them resemble fungi. The Democratic Republic of Congo (Kinshasa) issued its stamp with *Thonningia* in 1960 (Figure 2 *i*) followed by the Ivory Coast in 2013 that also showed a mistletoe (*Tapinanthus belvisii*).

The mistletoe family Loranthaceae includes members with large, showy flowers. Thus they have often been chosen as subjects for stamps. Eight species are listed in Table 1; however, in some cases, the species were misidentified or the taxonomy has changed since the stamp was issued. A stamp from Rwanda shows *Agelanthus brunneus* (Figure 2 *a*) or possibly *A. krausii* that also occurs in that country. Another stamp from Rwanda shows a brush fire juxtaposed with a painting of a mistletoe labelled *Tapinanthus prunifolius* (Figure 2 *b*). According to Polhill and Wiens[23], that species (now in *Agelanthus*) does not occur in Rwanda; thus the painting may depict *A. muzozensis* which is native to that country. A stamp issued in 1983 from Fiji shows the mistletoe *Decaisnina forsteriana* (as *Amylotheca insularum*), which is widely distributed in the South Pacific. Although not specifically identified, the stamp from the Federated States of Micronesia shows *Macrosolen melintangensis*, a species that occurs in Southeast Asia but not Micronesia. Stamps with correctly identified Loranthaceae include *Amyema scandens* from New Caledonia (Figure 2 *c*), *A. incarnatiflora* from the Philippines (Figure 2 *d*), *Tapinanthus belvisii* from Ivory Coast (Figure 2 *e*) and *T. globiferus* from Chad.

The mistletoe family Viscaceae contains seven genera, two of which are featured on stamps: *Phoradendron* and *Viscum*. Although displaying these plants during the Christmas season originated in Europe, North Americans

Figure 3. Stamps of holoparasites in Rafflesiaceae. ***a***, *Rafflesia arnoldii*; ***b***, *Rafflesia azlanii*; ***c***, *Rafflesia kerrii*; ***d***, *Rafflesia lagascae*; ***e***, *Rafflesia micropylora*; ***f***, *Rafflesia pricei*; ***g***, *Rhizanthes lowii*; ***h***, *Sapria poilanei*.

continued the custom, substituting *Phoradendron* for *Viscum*. In 1964 the US Postal Service circulated a Christmas theme group of four stamps, one of which was *P. leucarpum*. In 1893, this mistletoe was chosen as the state floral emblem for the Oklahoma Territory in USA. Soon after Oklahoma became a state in 1907, controversy about the mistletoe ensued and the Indian blanket (*Gaillardia pulchella*, Asteraceae) became the state wildflower. That the mistletoe could not be a state flower or wildflower stems from the common misunderstanding that it is not a flowering plant. In 1982, Oklahoma issued a beautiful stamp featuring the scissor-tailed flycatcher (its state bird) and *P. leucarpum* whose seeds could be dispersed by this bird (Figure 2 *j*).

The European mistletoe, *Viscum album* is a popular parasitic plant for stamps, again owing to its Christmas symbolism. Two stamps issued by Hungary in 1963 were apparently the first to show this species, in both cases associating it with good luck. In 1974, Switzerland issued a mistletoe stamp beautifully illustrating *V. album* in fruit as part of its 'Poisonous Plants of the Forest' series, highlighting the fact that mistletoe fruits and seeds contain viscotoxins. European political entities that have issued *V. album* stamps include England, the Bailiwicks of Guernsey and Jersey (Figure 2 *k*), Sweden, Yugoslavia and the Netherlands. The Netherlands also issued a stamp in 2014 depicting the Yuletide custom of kissing under the mistletoe.

Malpighiales – Rafflesiaceae

The 'queen of parasites' is *Rafflesia*, some species of which have flowers over 1 m in diameter, the largest among all angiosperms[4]. The plant lacks stems, leaves and roots, and exists within the host vine (*Tetrastigma*) as a filamentous endophyte. Its presence is only revealed when the flower buds emerge and later open. It is no wonder that these unusual and record-breaking plants have been the subject of stamps in Thailand, Malaysia, Brunei, Indonesia and the Philippines. *Rafflesia arnoldii* is one of three national flowers of Indonesia.

Species misidentifications have occurred frequently with *Rafflesia* stamps. In some cases, a generalized image is shown with just the genus *Rafflesia* indicated. In other cases the *Rafflesia* illustration suggests a species, such as in Malaysia (2007) where *R. arnoldii* is shown with a hornbill bird. Similarly, the stamp issued by Indonesia in 1989 clearly shows *R. micropylora* from Sumatra (Figure 3 *e*). In 1979, Malaysia issued a series of *Rafflesia* stamps, each individualized for one of its 13 states. While, the name on the stamp was *R. hasseltii*, the image showed either *R. arnoldii* or *R. gadutensis* (two similar species). Indonesia erred in the opposite direction regarding its 2012 stamps. The grouping of four stamps each showed a quarter of a *Rafflesia* flower, identified as *R. arnoldii* when in fact it was *R. pricei* from Kalimantan (Figure 3 *f*). Fortunately, *R. arnoldii* was properly illustrated and identified on other stamps from Indonesia in 1992 (Figure 3 *a*), 1993 and 2008. Other correct identifications include *R. azlanii* (Malaysia, 2013; Figure 3 *b*), *R. kerii* (Thailand 2006; Figure 3 *c*), *R. micropylora* (Indonesia, 2002) and *R. pricei* (Brunei Darussalam, 2000). At the time when the Philippines *Rafflesia* stamp was issued (2007), this species was known as *R. manillana*, but later taxonomic work[24] named it as *R. lagascae* (Figure 3 *d*). Both of the other genera in Rafflesiaceae have also been featured on stamps. *Rhizanthes lowii*, whose bizarre flower is fringed with worm-like appendages, was showcased on the 2000

Figure 4. Parasites in various families. Lauraceae: ***a***, *Cassytha filiformis*. Hydnoraceae: ***b***, *Hydnora africana*. Cynomoriaceae: ***c***, *Cynomorium coccineum*. Krameriaceae: ***d***, *Krameria lappacea*. Convolvulaceae: ***e***, *Cuscuta epithymum*. Representative members of parasite families not yet present on stamps. ***f***, *Pilostyles thurberi* (Apodanthaceae); ***g***, *Cytinus ruber* (Cytinaceae); ***h***, *Mitrastema yamamotoi* (Mitrastemonaceae); ***i***, *Pholisma culiacana* (Lennoaceae).

stamp from Brunei Darussalam (Figure 3 *g*). Finally, an accurate and strikingly beautiful painting of *Sapria poilanei* was issued by Thailand in 2006 (Figure 3 *h*).

Laurales – Lauraceae

Cassytha, popularly known as love vine, is a genus of about 20 species, most of which occur in Australia. One species, *C. filiformis*, is pantropical, often reaching remote islands where it forms dense masses of stems that indiscriminately parasitize many different plant species. Under its Medicinal Plant Series, the Marshall Islands issued a stamp in 1985 that well illustrated *C. filiformis* (Figure 4 *a*). Tea made from this species is considered an aphrodisiac in the Bahamas.

Piperales – Hydnoraceae

Hydnoraceae includes *Hydnora* of the Old World and *Prosopanche* of the New World. *Hydnora* has been described as 'the strangest plant in the world'[25] and its vegetative and floral morphology bear this out. These holoparasites form angular pilot roots and haustorial roots that attach to host roots. No stems or leaves are formed; only a fleshy flower with a brown, rough exterior and a pink or orange smooth interior, the part of the flower visited by pollinating beetles. In its Parasitic Plant Series in 1991, the Republic of Transkei (now part of South Africa) issued a stamp (Figure 4 *b*) showing the flower of *Hydnora africana* with its *Euphorbia* host plants in the background.

Saxifragales – Cynomoriaceae

Cynomorium coccineum (Cynomoriaceae) has been used for thousands of years by ancient people for food, medicine and dyeing. Arabs call the plant 'tarthuth'; Bedouins ate the interior portions of fresh young stems, prepared infusions of older stems to treat colic or stomach ulcers, or dried and pulverized the plant for use as a condiment with meat dishes[26]. Following the Crusades, the Knights Hospitaller from Jerusalem relocated to Malta where they continued the medicinal use of *Cynomorium* that they learned from the Muslims. The site called Fungus Rock where the 'Maltese mushroom' grew was thereafter vigorously guarded. Despite its appearance, *Cynomorium* is certainly not a mushroom as its position within the

angiosperm phylogeny was confirmed using DNA sequencing[27]. Under a mushroom theme, however, *Cynomorium* was featured on a 1993 stamp by Bahrain (Figure 4 *c*).

Zygophyllales – Krameriaceae

At the end of the alphabet for angiosperm orders is Zygophyllales, containing two families: Zygophyllaceae and Krameriaceae. The former includes lignum vitae (*Guaiacum*) notable for having one of the densest woods in the world, and creosote bush (*Larrea tridentata*) which produces ring clones over 11,000 years old. Krameriaceae contains the genus *Krameria* with about 23 species commonly called rhatany. The flowers of *Krameria* have showy sepals and some petals are modified into glands. The fruit is globose and covered with spines. The Federated States of Micronesia issued a group of ten stamps of plants used in traditional medicine, none of which was native to Micronesia. One of these was *K. lappacea* (Figure 4 *d*) (synonym *K. triandra*) that constitutes the true rhatany of commerce[28]. This plant has been used by Andean people to stanch blood flow, clean their teeth and in the treatment of combat diarrhoea, mouth ulcers, etc.

Solanales – Convolvulaceae

Within the large family Convolvulaceae, which includes morning glory vines, a lineage of parasitic plants exists that is commonly called dodder. The genus *Cuscuta* contains over 200 species of vines which may be hemiparasitic or holoparasitic[8]. Although the vast majority of species do not harm the crop plants, some such as *C. campestris* can attack diverse crops, particularly legumes[29]. The Bailiwick of Guernsey is the only political entity that has shown a dodder species on a stamp (Figure 4 *e*). In 1994, it issued a stamp with a beautiful painting of *C. epithymum* parasitic on *Ulex europaeus* (Fabaceae) along with the Dartford Warbler (*Sylvia undata*). As the name implies, this dodder usually uses thyme (*Thymus*) as its host plant, but other hosts can also be parasitized.

Parasitic plants not on stamps

Four orders and families of holoparasites are not currently represented on stamps (Figure 4 *f–i*). Three of these families were once considered to be related to Rafflesiaceae, but molecular phylogenetic work showed that they were all in different orders[30]. The first is Apodanthaceae (Cucurbitales) which includes the genus *Pilostyles* (Figure 4 *f*). These holoparasites have tiny flowers that emerge from the branches of legume host trees and shrubs. The genus is widely distributed with species in North and South America, Africa, the Middle East and Australia. The next ex-Rafflesiaceae family is Cytinaceae (Malvales) which includes the genus *Cytinus* (Figure 4 *g*) in the Old World and *Bdallophytum* in the New World. The third ex-Rafflesiaceae family is Mitrastemonaceae (Ericales) which includes only the genus *Mitrastema* (Figure 4 *h*) with two disjunct species, *M. yamamotoi* in East Asia and *M. matudae* in Mexico. Who could have guessed that these three lineages were related respectively, to cucumber, okra and blueberries. The order Boraginales contains the family Lennoaceae with just two genera, *Lennoa* and *Pholisma* (Figure 4 *i*), distributed in the western US and Mexico. The inflorescences of these holoparasites emerge from the desert sand and display a tight cluster of tubular flowers. *Pholisma sonorae*, an endangered plant species in the southwestern US, is called 'sand food' because native Americans consumed it. Parasitic plants from all four of these lineages would make fascinating and informative stamps that highlight the unique biodiversity of their respective regions.

In conclusion, approximately 46 political units have issued parasitic plant stamps, with the highest numbers coming from Indonesia (seven) and Malaysia (six). Interestingly, the African country of Burkina Faso also has six. The small territory, Baliwick of Guernsey has five stamps. Large regions that have rich parasite floras, such as Central Asia, South America and Australia, have no parasitic plant stamps. We hope that this article will encourage more representation of these incredible organisms on stamps.

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