

# Population Genomics of Yams: Evolution and Domestication of *Dioscorea* Species



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**Abstract** Yam is a collective name of tuber crops belonging to the genus *Dioscorea*. Yam is important not only as a staple food crop but also as an integral component of society and culture of the millions of people who depend on it. However, due to its regional importance, yam has long been regarded as an “orphan crop” lacking a due global attention. Although this perception is changing with recent advances in genomics technologies, domestication processes of most yam species are still ambiguous. This is mainly due to the complicated evolutionary history of *Dioscorea* species caused by frequent hybridization and polyploidization, which is possibly caused by dioecy that imposed obligate outcrossing to the species of *Dioscorea*. In this chapter, we provide an overview of the evolution of *Dioscorea* and address the domestication of yam from population genomics perspectives by

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focusing on the processes of hybridization and polyploidization. A review is given to the recent population genomics studies on the hybrid origin of *D. rotundata* in West and Central Africa, the global dispersion of *D. alata* through human migrations, and the whole-genome duplication of the South America species of *D. trifida*. In the end, we give a summary of current understanding of sex-determination system in *Dioscorea*.

**Keywords** Dioecy · *Dioscorea* · Domestication · Evolution · Genetic diversity · Hybridization · Polyploidy · Population genomics · Sex determination · Yam

## 1 Introduction

Yam is a collective name of tuber crops belonging to the genus *Dioscorea*. In 2018, the global yam production was around 72.6 million tons (FAOSTAT 2018). The major yam species include *Dioscorea rotundata*, *D. alata*, *D. trifida*, *D. polystachya*, and *D. esculenta* (Arnau et al. 2010). White Guinea yam (*D. rotundata*) is the most important yam worldwide, mainly grown in West and Central Africa, especially Côte d’Ivoire, Ghana, Togo, Benin, Nigeria and Cameroon, the region known as the “yam belt”, which accounts for ~92.5% of the total world yam production (FAOSTAT 2018). Yam is a staple crop in many tropical countries, and it also plays important roles in society and culture of the people in the major yam-growing regions (Coursey 1972; Obidiegwu and Akpabio 2017; Obidiegwu et al. 2020). However, due to its localized importance, yam has been regarded as an “orphan crop” and received considerably less research attention compared to the major crop species.

The genetic improvement of yam is urgently needed for the food security of yam-growing regions, but it is constrained by various abiotic and biotic factors (Mignouna et al. 2003). For example, the entire genus *Dioscorea* is characterized by dioecy, with male and female flowers borne on separate individuals, which imposes obligate outcrossing to the species in the genus. Due to its dioecy, farmers clonally propagate yams to maintain its germplasms, and true seeds are rarely used as the starting materials for planting. However, this clonal propagation reduces the genetic diversity, which causes the vulnerability to plant diseases. Also, the clonal propagation causes the difficulty of purging deleterious mutations from the germplasms like in cassava (Ramu et al. 2017). To achieve effective yam improvement by overcoming these constraints, we need to answer key questions in yam genetics and genomics including: (1) what is the genetic relationships between cultivated yams and their wild relatives, and how the domestication of yam happened? (2) how to deploy *Dioscorea* genetic diversity to improve agronomic traits of cultivated yams? (3) how dioecy of *Dioscorea* is genetically controlled and how we can manipulate it to make an efficient cross breeding? Thanks to the recent development of genome sequencing technologies, we can now address these questions using

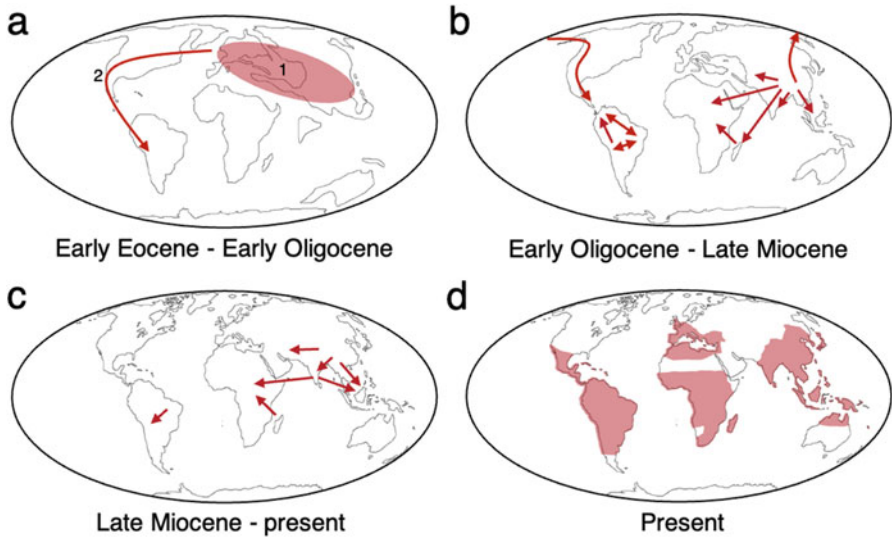
population genomics approaches. In this chapter, we review the latest findings of the domestication of yam from population genomics perspectives.

## 2 The Genus *Dioscorea*: Its Origin and Botanical Characteristics

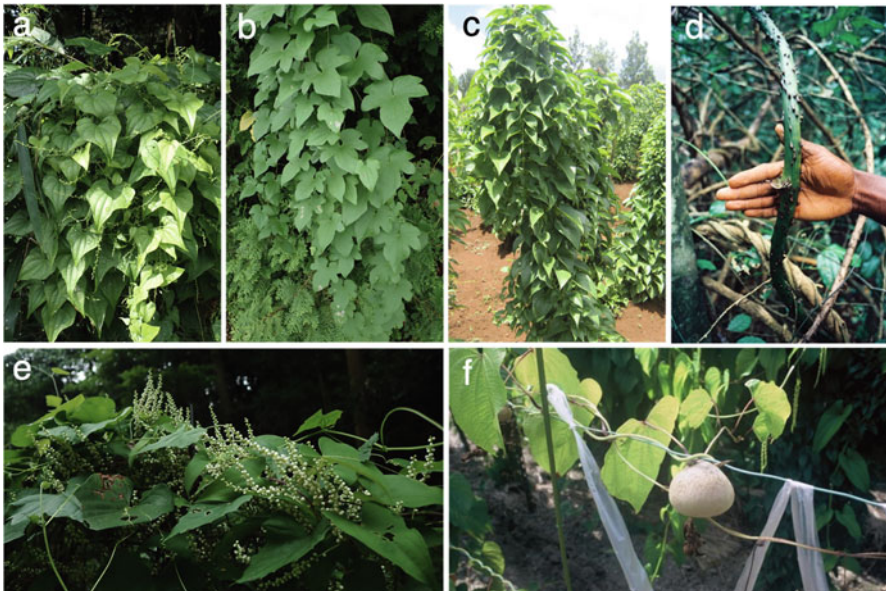
The genus *Dioscorea*, which consists of approximately 630 species, is the largest one in the family Dioscoreaceae of monocotyledons (WCSP 2020). It is widely distributed in the tropical and temperate regions and occurs in diverse environments from forests to grasslands (Wilkin et al. 2005; Maurin et al. 2016; Viruel et al. 2016). Several studies have been conducted on the phylogenetic relationships of species in *Dioscorea*. Previously, intrageneric taxa have been proposed based on morphological characters (Uline 1898; Knuth 1924; Prain and Burkill 1936, 1939; Burkill 1960; Huber 1998). However, diagnostic keys and delineation of taxa varied according to the authors. Recently, phylogenetic analyses have been conducted based on chloroplast DNA (cpDNA) sequences and nuclear gene sequences (for review, see Noda et al. 2020). Noda et al. (2020) provided a large-scale phylogenetic tree containing 183 species and proposed dividing *Dioscorea* into two subgenera (*Dioscorea* and *Helmia*), with 11 major clades and 27 sections/species groups.

*Dioscorea* likely originated in the Laurasian Palaeartic between the Late Cretaceous and the Early Eocene (Fig. 1). In the Eocene and Oligocene, *Dioscorea* expanded to the southern region by long-distance dispersal or migration by land bridges. In the Oligocene and Miocene, main *Dioscorea* lineages experienced divergence events on a worldwide scale. In the Miocene and Pliocene, some lineages dispersed into new areas. The number of biogeographical speciation events seems to have decreased after the Quaternary period began (Maurin et al. 2016; Viruel et al. 2016; Couto et al. 2018).

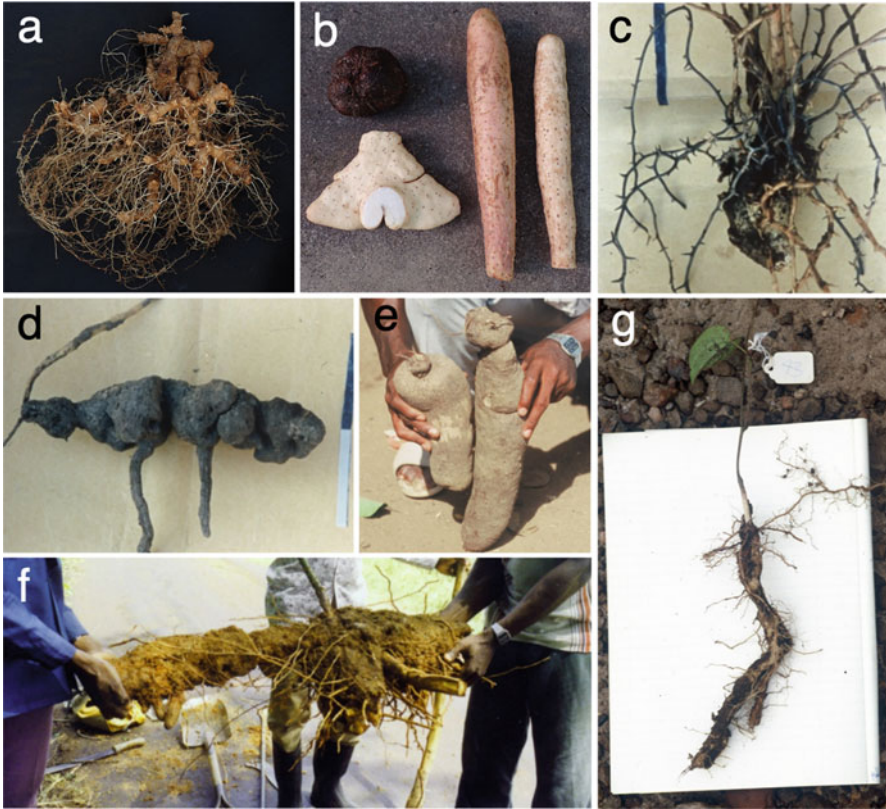
The majority of *Dioscorea* species are perennial herbaceous climbers with simple or compound leaves and reproduce sexually and/or clonally (Fig. 2). Flowers in *Dioscorea* are mostly dioecious with male and female flowers borne on separate individuals, and multiple sex-determination systems were reported in the genus (see Table 2 and Sect. 6). Most species produce winged seeds and capsular, six-seeded fruits, while some species have wingless seeds, samaroid or berry fruits (Caddick et al. 2002; Noda et al. 2020). In addition to sexual reproduction, *Dioscorea* species propagate clonally by bulbils, rhizomes, or tubers. Bulbils are aerial tubers that are formed in the axils of leaves or bracts of some *Dioscorea* species (Fig. 2f). They are mainly consumed as food, but also used as folk medicine in many cultures (Ikiriza et al. 2019). Bulbils are generally brown-colored and have small tubercles over their surface, but their shape and size vary in the different species (Murty and Purnima 1983). *D. bulbifera* (also known as aerial yam) is the major bulbil-producing species and is characterized by considerable bulbil shape diversity (Terauchi et al. 1991).



**Fig. 1** Biogeographical origin and distribution of *Dioscorea* species (Viruel et al. 2016). (a) *Dioscorea* likely originated in the Laurasian Palaeartic in the Late Cretaceous and the Early Eocene (1) and then dispersed from Asia to South America (2). (b) In the Oligocene and Miocene, *Dioscorea* mainly expanded to the southern region. (c) Some lineages dispersed into new areas in the Miocene and Pliocene, but speciation events decreased in the Quaternary. (d) Geographical distribution in the present era. (Maps are based on C. R. Scotese's PALEOMAP project; [www.scotese.com](http://www.scotese.com))



**Fig. 2** Morphological diversity of the above-ground parts of *Dioscorea* species. (a) *D. tokoro*, (b) *D. quinqueloba*, (c) *D. rotundata*, (d) a stem of *D. mangelotiana* with thorns, (e) flowers of *D. japonica*, (f) a bulbil of *D. bulbifera*



**Fig. 3** Rhizomes and tubers of *Dioscorea* species. (a) rhizomes of *D. tokoro*, (b) Tukuneimo group (left top), Ichoimo group (left bottom), Nagaïmo group (right) in *D. polystachya*, (c) *D. praehensilis*, (d) *D. minutiflora*, (e) *D. rotundata* (left), *D. cayenensis* (right), (f) *D. mangelotiana*, (g) *D. abyssinica*

Rhizomes and tubers represent morphologically diverse structures that serve as underground starch storage organs (Fig. 3). Because these storage organs serve as food sources for various wild animals, they have evolved defense traits. For example, *D. praehensilis* has crown roots with spines to protect tubers from burrowing or digging animals (Fig. 3c). Some species of the African clade have thick corky barks covering the pachycaul structure that may provide protection against fire and herbivores (Scott 1897; Maurin et al. 2016). In addition, *Dioscorea* species produce diverse secondary metabolites such as saponins, alkaloids, and tannins that serve a variety of functions including defense against herbivores (Coursey 1967). Chemical components of some species have medicinal values (Liu et al. 2008; Dutta 2015).

### 3 Ploidy in *Dioscorea*

Basic chromosome number of *Dioscorea* is  $\times = 10$  in the section *Stenophora*. However, in the section *Enantiophyllum* that includes the major cultivated species, the basic chromosome number is  $\times = 20$  (Scarcelli et al. 2005; Arnau et al. 2009). Our survey of the available literature shows that at least 33% of the species in the genus *Dioscorea* have variable ploidy levels including within the same species (Table 1). As we discuss in the later sections, *Dioscorea* species have undergone several hybridization events that sometimes led to changes in the ploidy levels. Information on ploidy is important to apply the correct population genomics approaches for the study of *Dioscorea*. For example, if the sequence reads obtained from a polyploid individual are aligned to a consensus haploid reference genome, variant calling based on the assumption of diploid genome may lead to wrong genotyping results.

**Table 1** The various ploidy levels of *Dioscorea* species

Species <sup>a</sup>	Chromosome number	References
<i>D. abyssinica</i> Hochst.	2n = 40	Miège (1954)
<i>D. aculeata</i> Webstar	2n = 40	Martin and Ortiz (1963)
<i>D. alata</i> L.	2n = 40, 60, 80	Arnau et al. (2009)
<i>D. alata</i> var. <i>purpurea</i> Roxb.	2n = 80	Ramachandran (1968)
<i>D. althaeoides</i> Knuth	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. asclepiadea</i> Prain & Burkill	2n = 40	Takeuchi et al. (1970)
<i>D. aspersa</i> Prain & Burkill	2n = 40	Chin et al. (1985)
<i>D. balcanica</i> Košanin	2n = 20	Miège (1954)
<i>D. banzhuana</i> Pei & Ting	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. batatas</i> Decne.	2n = 140, 144	Nakajima (1933), Smith (1937)
<i>D. belophylla</i> Voigt	2n = 50, 80, 100	Raghavan (1958, 1959)
<i>D. benthamii</i> Prain & Burkill	2n = c. 100	Chin et al. (1985)
<i>D. bernoulliana</i> Prain & Burkill	2n = 36	Martin and Ortiz (1966)
<i>D. biformifolia</i> Pei & Ting	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. bulbifera</i> L.	2n = 36, 40, 54, 60, 80, 98–100	Smith (1937), Miège (1954), Raghavan (1958)
<i>D. bulbifera</i> var. <i>bulbifera</i> L.	2n = 40	Paul and Debnath (2019)
<i>D. caucasica</i> Lipsky	2n = 20	Meurman (1925)
<i>D. cayenensis</i> Lam.	2n = 36, 54, 80, 140	Smith (1937), Miège (1954), Martin and Ortiz (1963)
<i>D. ceratandra</i> Uline	2n = 36	Martin and Ortiz (1963)
<i>D. chingii</i> Prain & Burkill	2n = 20	Kiangsu Institute of Botany (1976)

(continued)

**Table 1** (continued)

Species <sup>a</sup>	Chromosome number	References
<i>D. cirrhosa</i> Lour.	2n = 40	Chin et al. (1985)
<i>D. cirrhosa</i> var. <i>cylindrica</i> Ting & Chang	2n = 40	Chin et al. (1985)
<i>D. colletii</i> Hook.f.	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. colletii</i> var. <i>hypoglauca</i> (Palibin) Pei & Ting	2n = 40	Kiangsu Institute of Botany (1976)
<i>D. composita</i> Hemsl.	2n = 36, 54	Martin and Ortiz (1963, 1966)
<i>D. convolvulacea</i> Schlect. & Cham.	2n = 36	Martin and Ortiz (1963)
<i>D. deltoidea</i> Wall.	2n = 20, 40	Raghavan (1958), Mehra and Sachdeva (1976)
<i>D. discolor</i>	2n = 40	Smith (1937)
<i>D. dumetorum</i> Pax	2n = 36, 40, 45, 54	Miège (1954), Baquar (1980)
<i>D. esculintlensis</i> Matuda	2n = 36	Martin and Ortiz (1966)
<i>D. esculenta</i> Burkill	2n = 40, 60, 80, 90, 100	Miège (1954), Cox et al. (1958), Raghavan (1958), Chin et al. (1985)
<i>D. esculenta</i> (Cherukizhengu)	2n = 100	Ramachandran (1968)
<i>D. esculenta</i> (Nanakizhengu)	2n = 90	Ramachandran (1968)
<i>D. exalata</i> Ting & Chang	2n = 60, 80	Chin et al. (1985)
<i>D. fargesii</i> Franch.	2n = 64	Smith (1937)
<i>D. floribunda</i> Mart. & Gal.	2n = 36, 54, 72, 144	Martin and Ortiz (1963, 1966)
<i>D. fordii</i> Prain & Burkill	2n = 40	Chin et al. (1985)
<i>D. friedrichsthali</i> R.Knuth	2n = 36	Martin and Ortiz (1963)
<i>D. futschuensis</i> Uline	2n = 40	Kiangsu Institute of Botany (1976)
<i>D. glabra</i> Roxb.	2n = 40	Mehra and Sachdeva (1976)
<i>D. gracillima</i> Miq.	2n = 20, 40	Nakajima (1933), Takeuchi et al. (1970)
<i>D. hamiltonii</i>	2n = 40	Paul and Debnath (2019)
<i>D. hastata</i> J. Miège	2n > 120	Miège (1954)
<i>D. hemsleyi</i> Prain & Burkill	2n = 60	Pei et al. (1979)
<i>D. henryi</i> (Prain & Burkill) Ting	2n = 40	Chin et al. (1985)
<i>D. hirtiflora</i> Benth.	2n = 40	Miège (1954)
<i>D. hispida</i> Dennst.	2n = 40	Raghavan (1958)
<i>D. hondurensis</i> R. Knuth	2n = 36	Martin and Ortiz (1966)
<i>D. izuensis</i> Akahori	2n = 20	Takeuchi et al. (1970)
<i>D. japonica</i> Thunb.	2n = 40, 80, 100	Nakajima (1933), Araki et al. (1983), Chin et al. (1985)
<i>D. kamoensis</i> Kunth	2n = 40, 60	Chin et al. (1985)
<i>D. macroura</i> Harms.	2n = 40	Smith (1937)

(continued)

**Table 1** (continued)

Species <sup>a</sup>	Chromosome number	References
<i>D. mangenotiana</i> J. Miège	2n = 72, 80	Miège (1954)
<i>D. melanophyma</i> Prain & Burkill	2n = 40	Chin et al. (1985)
<i>D. mexicana</i> Guillemain	2n = 36	Martin and Ortiz (1966)
<i>D. minutiflora</i> Engl.	2n > 120	Miège (1954)
<i>D. nentaphylla</i> L.	2n = 120	Chin et al. (1985)
<i>D. nipponica</i> Makino	2n = 20, 40	Takeuchi et al. (1970), Kiangsu Institute of Botany (1976)
<i>D. nipponica</i> var. <i>rosthornii</i> Prain & Burkill	2n = 40	Kiangsu Institute of Botany (1976)
<i>D. nitens</i> Prain & Burkill	2n = 60	Chin et al. (1985)
<i>D. nummularia</i> Lam.	2n = 60, 100, 120	Lebot et al. (2017)
<i>D. opposita</i> Thunb.	2n = 140	Araki et al. (1983)
<i>D. oppositifolia</i> L.	2n = 40, 140, 138–142	Smith (1937), Raghavan (1958), Chin et al. (1985)
<i>D. oppositifolia</i> var. <i>linnaei</i> Prain & Burkill	2n = 40	Ramachandran (1968)
<i>D. paniculata</i> Michx	2n = 36	Martin and Ortiz (1966)
<i>D. panthaica</i> Prain & Burkill	2n = 40	Kiangsu Institute of Botany (1976)
<i>D. parviflora</i> C. T. Ting	2n = 20	Pei et al. (1979)
<i>D. pentaphylla</i> L.	2n = 40, 50, 60, 80, 120, 144	Smith (1937), Raghavan (1958, 1959), Chin et al. (1985), Paul and Debnath (2019)
<i>D. pentaphylla</i> var. <i>jacquemontii</i> Prain & Burkill	2n = 40, 80	Raghavan (1958)
<i>D. pentaphylla</i> var. <i>linnaei</i> Prain & Burkill	2n = 40, 80	Raghavan (1958)
<i>D. pentaphylla</i> var. <i>rheedei</i> Prain & Burkill	2n = 40	Ramachandran (1968)
<i>D. persimilis</i> Prain & Burkill	2n = 40	Chin et al. (1985)
<i>D. poilanei</i> Prain & Burkill	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. polygonoides</i> Humb. & Bonpl.	2n = 36, 54	Martin and Ortiz (1963, 1966)
<i>D. polystachya</i> Turcz. (Ichoimo group)	2n = 100	Babil et al. (2013)
<i>D. polystachya</i> Turcz. (Nagaimo group)	2n = 140	Babil et al. (2013)
<i>D. polystachya</i> Turcz. (Tsukuneimo group)	2n = 100	Babil et al. (2013)
<i>D. praehensilis</i> Benth.	2n = 40	Miège (1954)
<i>D. preussii</i> Pax	2n = 40	Miège (1954)
<i>D. pubera</i> Blume	2n = 40	Raghavan (1958)
<i>D. pyrenaica</i> Bord.	2n = 24	Miège (1954)

(continued)



**Table 1** (continued)

Species <sup>a</sup>	Chromosome number	References
<i>D. quaternata</i> Gmel.	2n = 36, 54	Jensen (1937), Martin and Ortiz (1966)
<i>D. quinqueloba</i> Thunb.	2n = 20	Smith (1937)
<i>D. reticulata</i> C. Gay	2n = 61	Smith (1937)
<i>D. rotundata</i> Poir.	2n = 40, 60	Martin and Ortiz (1963), Baquar (1980)
<i>D. sansibarensis</i> Pax.	2n = 40	Miège (1954)
<i>D. sativa</i> L.	2n = 40	Sharma and De (1956)
<i>D. sativa</i> Thunb.	2n = 80	Ramachandran (1962)
<i>D. septemloba</i> Thunb.	2n = 20, 40	Takeuchi et al. (1970), Kiangsu Institute of Botany (1976)
<i>D. septemloba</i> var. <i>sititoana</i>	2n = 40	Takeuchi et al. (1970)
<i>D. shimperana</i> Hochst ex Kunth	2n = 80	Baquar (1980)
<i>D. simulans</i> Prain & Burkill	2n = 20	Kiangsu Institute of Botany (1976)
<i>D. sinuata</i> Vell.	2n = 24, 34 (male), 36 (female)	Meurman (1925), Suessenguth (1921)
<i>D. smilacifolia</i> de Wild.	2n > 120	Miège (1954)
<i>D. spiculiflora</i>	2n = 36	Martin and Ortiz (1963)
<i>D. spinosa</i> Roxb.	2n = 90	Ramachandran (1962)
<i>D. subcalva</i> Prain & Burkill	2n = 60	Pei et al. (1979)
<i>D. subcalva</i> var. <i>submollis</i> (Knuth) Ling & Ting	2n = 60	Chin et al. (1985)
<i>D. tentaculigera</i> Prain & Burkill	2n = 40	Pei et al. (1979)
<i>D. tenuipes</i> Franch. & Savat.	2n = 20, 30, 40	Takeuchi et al. (1970)
<i>D. tokoro</i> Makino	2n = 20	Nakajima (1933)
<i>D. tomentosa</i> Koenig	2n = 40, 60	Raghavan (1959)
<i>D. trifida</i>	2n = 40, 60 <sup>b</sup> , 80	Bousalem et al. (2006, 2010)
<i>D. villosa</i> L.	2n = 60	Smith (1937)
<i>D. wallichii</i> Hook.f.	2n = 40	Raghavan (1959)
<i>D. yunnanensis</i> Prain & Burkill	2n = 40	Chin et al. (1985)
<i>D. zingiberensis</i> Wright	2n = 20, 30, 40	Kiangsu Institute of Botany (1976), Xiaoqin et al. (2003)
<i>Tamus communis</i> L. <sup>c</sup>	2n = 48	Meurman (1925)
<i>Tamus edulis</i> Lowe <sup>c</sup>	2n = 96	Borgen (1974)

<sup>a</sup>Species name used in the references<sup>b</sup>2C DNA content suggests the existence of the triploid *D. trifida* (Bousalem et al. 2010)<sup>c</sup>Synonym of *D. communis* (L.) Caddick & Wilkin

## 4 Reference Genome Sequences for *Dioscorea*

A reliable reference genome sequence is indispensable for genome diversity studies of a species. The first chromosome-level reference genome obtained for *Dioscorea* species was that of *D. rotundata* (Tamiru et al. 2017). The size of *D. rotundata* genome was estimated to be ~570-Mbp using flow cytometry and *k*-mer analyses of genome sequences. The genome contained 26,198 protein coding genes. White Guinea yam genome sequence is distant from those of other monocotyledon species including Poales (*Oryza* and *Brachypodium*), Arecales (*Elaeis* and *Phoenix*), and Zingiberales (*Musa*), indicating that *Dioscorea* lineage was split from other monocotyledons early in the evolution. Publication of the reference genome, which also reported a DNA marker for sex identification in *D. rotundata*, has served as a catalyst for further studies into genomes of not only *D. rotundata* (Scarcelli et al. 2019; Bhattacharjee et al. 2020; Zhang et al. 2020; Sugihara et al. 2020) but also of *D. alata* (Cormier et al. 2019a, b; Sharif et al. 2020) and the pathogens associated with yams such as yam mosaic virus (Silva et al. 2019). *D. rotundata* scaffolds were generated by combining two types of Illumina short reads: paired-end and mate-pair jump reads. The mate-pair jump reads bridged the contigs assembled using paired-end short reads, with the gaps between the contigs represented with “N” for missing bases. The scaffolds were then ordered to generate a chromosome-level reference genome guided by a linkage map generated by the DNA markers of restriction site associated DNA (RAD)-tags (Baird et al. 2008) using the pseudo-testcross mapping method (Grattapaglia and Sederoff 1994). This reference genome has been shared with the wider scientific community via Ensembl (Howe et al. 2019; [ftp://ftp.ensemblgenomes.org/pub/plants/release-48/fasta/dioscorea\\_rotundata](ftp://ftp.ensemblgenomes.org/pub/plants/release-48/fasta/dioscorea_rotundata)).

Recently, the reference genome of *D. rotundata* has been updated with long reads generated by Oxford Nanopore Technologies (Sugihara et al. 2020). Long read-based de novo genome assembly resulted in longer contigs with a minimum number of missing bases, unlike those constructed by mate-pair jump reads. The newly generated contigs were also ordered using a linkage map generated by massive number of single nucleotide polymorphism (SNP) markers, instead of RAD-markers, obtained from whole-genome re-sequencing of 156  $F_1$  progeny. This reference genome has been made available via Ensembl (Howe et al. 2019) as *D. rotundata* reference genome ver. 2 ([https://plants.ensembl.org/Dioscorea\\_rotundata/Info/Index](https://plants.ensembl.org/Dioscorea_rotundata/Info/Index)).

Reference genomes of two other *Dioscorea* species are also available in the public database. The recent chromosome-level reference genome of *D. alata* is yet to be published, but it is accessible on YamBase (<https://yambase.org/>). Additionally, the reference genome of *D. dumetorum*, which was generated by sequencing with Oxford Nanopore Technologies, has been reported (Siadjeu et al. 2020; <https://pub.uni-bielefeld.de/record/2941469>). Both *D. rotundata* and *D. alata* belong to the botanical section Enantiophyllum. The *D. dumetorum* reference genome represents the first genome sequenced from the section Lasiophyton. These multiple reference genomes will facilitate the comparative genomics and pangenome of *Dioscorea* species and be especially useful for the analysis of the transition of the sex-determination locus within *Dioscorea* (Cormier et al. 2019a; see Sect. 6).

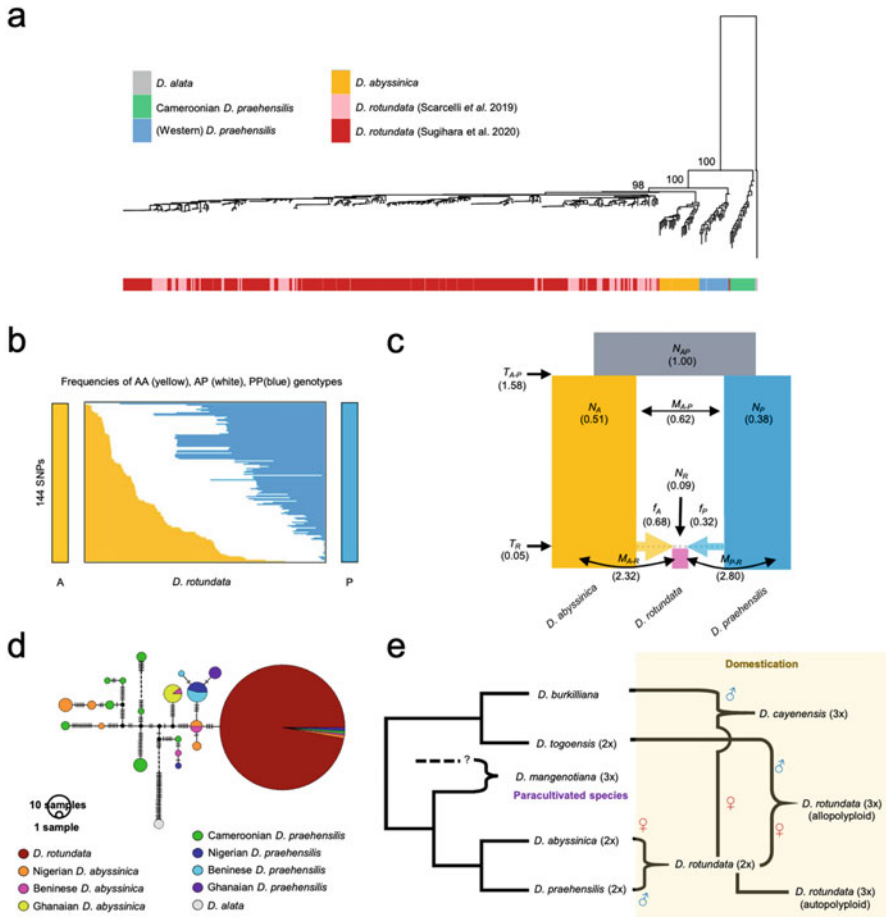
## 5 Origin and Domestication of *Dioscorea* Species

Yams of different *Dioscorea* species are believed to be independently domesticated in different continents: *D. rotundata* and *D. cayenensis* in West and Central Africa, *D. alata* in Southeast Asia, and *D. trifida* in South America. However, our knowledge of their origins has been limited until recently. This is mainly due to the frequent hybridization and polyploidization of many species including *D. rotundata* (Terauchi et al. 1992; Scarcelli et al. 2006; Chair et al. 2010; Girma et al. 2014; Scarcelli et al. 2017; Sugihara et al. 2020) and *D. alata* (Chair et al. 2016; Sharif et al. 2020). The recent population genomics studies have started unveiling the domestication processes of the major species (Scarcelli et al. 2019; Sugihara et al. 2020; Sharif et al. 2020).

### 5.1 Origin and Domestication of Guinea Yam

White Guinea yam, *D. rotundata*, is a true cultigen and the wild species *D. abyssinica* and *D. praehensilis* have been proposed as its two candidate progenitors (Coursey 1976a, b; Terauchi et al. 1992; Scarcelli et al. 2006; Chair et al. 2010; Girma et al. 2014; Scarcelli et al. 2017; Magwé-Tindo et al. 2018). *D. abyssinica* and *D. praehensilis* are distributed in savannah and rainforest areas, respectively, of West and Central Africa. By comparing whole-genome sequences of 80 *D. rotundata*, 29 *D. abyssinica*, 26 *D. praehensilis* from West Africa (Western *D. praehensilis*), and 18 *D. praehensilis* from Cameroon (Cameroonian *D. praehensilis*), Scarcelli and colleagues recently proposed that *D. rotundata* was domesticated from *D. praehensilis* in the northern part of Benin within the Niger River basin (Scarcelli et al. 2019). This report is a major contribution towards elucidating the origin of Guinea yam. However, after a careful reassessment of the Scarcelli et al. (2019) data and results, we reached at a different conclusion (Sugihara et al. 2020).

Our study included genome sequences of 336 *D. rotundata* accessions in addition to the *D. rotundata* and wild species accessions analyzed by Scarcelli et al. (2019). First, we conducted clustering analysis and flow cytometry analysis of our 336 *D. rotundata* accessions. Based on these results, we classified 308 accessions as diploid and 28 accessions as triploid. Focusing on the diploid *D. rotundata* accessions, we attempted to elucidate their phylogenetic relationships with the wild relative species; *D. abyssinica*, Western *D. praehensilis*, and Cameroonian *D. praehensilis* as reported by Scarcelli et al. (2019). We reconstructed a rooted neighbor-joining tree of four African yam taxa using *D. alata*, an Asian species, as an outgroup (Fig. 4a). In our result, *D. rotundata* was genetically closer to *D. abyssinica* than to *D. praehensilis*, which was not consistent to Scarcelli's hypothesis indicating that *D. rotundata* was directly domesticated from *D. praehensilis*. To test whether *D. rotundata* was derived from *D. abyssinica* or



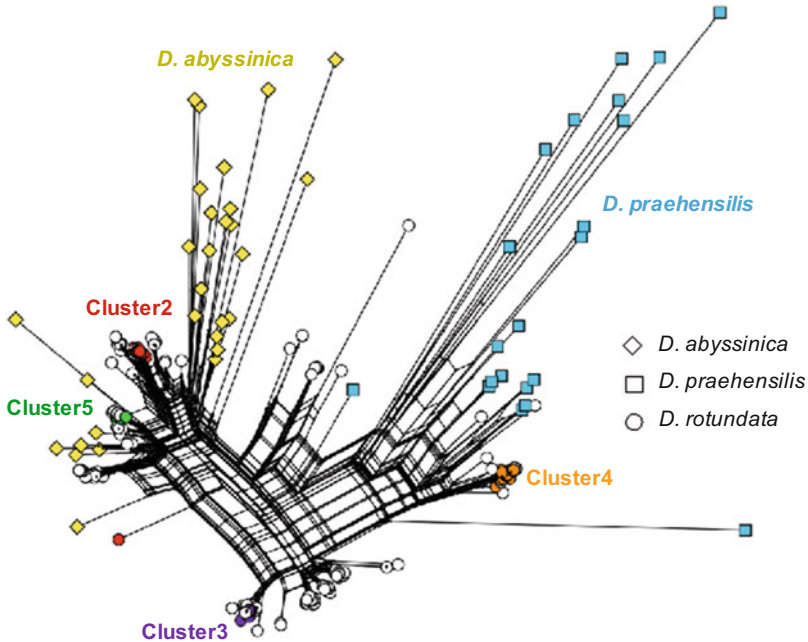
**Fig. 4** Domestication history of Guinea yam. **(a)** Neighbor-joining tree of four African yam taxa reconstructed using *D. alata* as an outgroup (adopted from Sugihara et al. 2020, Fig. 1c). **(b)** Frequencies of individuals homozygous for *D. abyssinica* allele (A: indicated by yellow color), homozygous for *D. praehensilis* allele (P: indicated by blue color), and heterozygous for A and P (indicated by white color) among the 388 *D. rotundata* sequences as studied for 144 SNPs (adopted from Sugihara et al. 2020, Fig. 2b). **(c)** Demographic history of *D. rotundata* as inferred by  $\partial a \partial i$  (Gutenkunst et al. 2009).  $N$ ,  $T$ ,  $M$ , and  $f$  represent a relative population size from the ancestral population ( $N_{AP}$ ), divergence time, migration rate, a fraction of genomic contribution, respectively. The  $\partial a \partial i$  analysis inferred the hybrid origin of *D. rotundata* with the high migration rates between *D. rotundata* and the two wild relatives (adopted from Sugihara et al. 2020, Fig. 2c). **(d)** Haplotype network of the whole plastid genomes of 416 *D. rotundata* (including the triploid accessions), 68 accessions of wild relative species, and two *D. alata* accessions used as the outgroup. The number of vertical dashes represents the number of mutations (adopted from Sugihara et al. 2020, Fig. 3a). **(e)** Reticulated evolutionary history of Guinea yam (Sugihara et al. 2020; Girma et al. 2014). *D. rotundata* (white Guinea yam) is derived from a homoploid hybridization between *D. abyssinica* and *D. praehensilis*. *D. cayenensis* (yellow Guinea yam) and the majority of triploid *D. rotundata* are derived from the polyploid hybridization between a female diploid *D. rotundata* and a male African wild yam. At least four species contributed to the gene pool of Guinea yam

*D. praehensilis*, we focused on the allele frequencies on 144 SNPs which were oppositely fixed in *D. abyssinica* and *D. praehensilis* (Fig. 4b). If *D. rotundata* was derived from either of *D. abyssinica* or *D. praehensilis*, allele frequencies of the analyzed SNPs should be highly skewed to either of the candidate progenitors. However, the allele frequencies of *D. rotundata* were intermediate. This observation suggested a hybrid origin of *D. rotundata* between *D. abyssinica* and *D. praehensilis*. To conform this hypothesis, we compared the three evolutionary models by  $\partial a \partial i$  which assesses evolutionary models with their likelihood based on the site frequency spectrum (Gutenkunst et al. 2009). The first model was that *D. rotundata* had been derived from *D. abyssinica*. The second model was that *D. rotundata* had been derived from *D. praehensilis* (Scarcelli's hypothesis). The third model was that *D. rotundata* had been hybrid-derived between *D. abyssinica* and *D. praehensilis*. As a result,  $\partial a \partial i$  showed the highest likelihood in the third model (the hybrid origin of *D. rotundata*) out of the three models.

Our finding suggested that *D. rotundata* is most likely a homoploid hybrid between *D. abyssinica* and *D. praehensilis* (Fig. 4b, c; Sugihara et al. 2020). Homoploid hybrid speciation is the formation of a new hybrid species without altering the ploidy levels of the parents (Mallet 2007). The origin of *D. rotundata* by hybridization seems to be recent when compared with timing of the speciation of *D. praehensilis* from *D. abyssinica* (Fig. 4c, d). Genomic contributions from *D. abyssinica* and *D. praehensilis* during the hybridization event were estimated to be ~68% and 32%, respectively (Fig. 4c). The relative population size of *D. rotundata* is much smaller than those of its wild relatives, which indicates that *D. rotundata* was affected by domestication bottleneck. Chloroplast DNA is predominantly inherited maternally in angiosperms. We extracted chloroplast DNA sequences from the whole-genome sequence reads and studied its polymorphisms in our samples. A chloroplast DNA haplotype network suggested that *D. abyssinica* and *D. praehensilis* were the maternal and paternal parents of *D. rotundata*, respectively (Fig. 4d, e; Sugihara et al. 2020). The hybrid origin of white Guinea yam was initially proposed by Coursey in 1976 based on morphological comparisons (Coursey 1976a). Our results from genome analyses support his hypothesis that spontaneous hybridization between wild yams could have occurred at the artificial "dump heaps" created by people living in the savannah between the forest and the Sahara (Coursey 1976b).

The most common cases of origin of crops by hybridization accompanies polyploidization (also known as allopolyploidization) as exemplified by bread wheat (*Triticum aestivum*) (Peng et al. 2011), banana (*Musa acuminata*) (Heslop-Harrison and Schwarzacher 2007), cotton (*Gossypium* spp.) (Zhang et al. 2015), and canola (*Brassica napus*) (Chalhoub et al. 2014). The homoploid hybrid speciation in *D. rotundata* is unique in that its domestication did not involve polyploidization.

We hypothesize that Guinea yam has been established by the process of "ennoblement" (Dumont and Vernier 2000; Mignouna and Dansi 2003; Scarcelli et al. 2006; Chaïr et al. 2010). "Ennoblement" is a traditional farmers' practice that involves collecting tubers of wild yams from the bush and forest and planting them in their fields, and it likely contributes to the genetic diversity of yam through hybridization and introgression (Jarvis and Hodgkin 1999; Scarcelli et al. 2006;



**Fig. 5** Genetic relationship among *D. rotundata* and its wild progenitors around the *SWEETIE* gene. A Neighbor-Net (adopted from Sugihara et al. 2020, Fig. 4c) was constructed by SplitsTree (Huson and Bryant 2006). Based on STRUCTURE analysis, five clusters (cluster 1–5) were defined in Sugihara et al. (2020). In this analysis, the accessions in cluster 1 were removed because they were triploid. Based on this result, the gene of cluster 2 and 5 were genetically close to *D. abyssinica*, while that of cluster 4 was genetically close to *D. praezensilis*. This different genetic relationship in the different clusters indicate the introgressions from both wild progenitors

Chair et al. 2010). Similar farmers' practices of sympatrically planting crop wild relatives and cultivars often occur in the centers of origin of domesticated plants (Jarvis and Hodgkin 1999).

The locus of the *SWEETIE* gene is an example that the crop wild relatives contributed to the genetic diversity of *D. rotundata*. The *SWEETIE* gene is known to be involved in sugar flux (Veyres et al. 2008a, b). In the diploid *D. rotundata*, this locus showed the signature of extensive introgressions from *D. abyssinica* and *D. praezensilis* (Fig. 5). We identified the introgressions by applying  $f_4$  statistic (Reich et al. 2009) of population genomics to our diploid *D. rotundata* accessions and its wild progenitors as analyzed in Scarcelli et al. (2019). The  $f_4$  statistic can detect genomic regions showing discordant topologies among different genetic groups of *D. rotundata* with respect to *D. abyssinica* and *D. praezensilis*. We hypothesize that this locus was under selection.

In addition to the majority of diploid accessions, triploid accessions of *D. rotundata* have been identified by flow cytometry analysis (Girma et al. 2014; Sugihara et al. 2020). These triploid *D. rotundata* accessions seem to have been

derived from a hybridization between the diploid *D. rotundata* and the wild yam species *D. togoensis* (Fig. 4e; Girma et al. 2014). Since the chloroplast sequences of the triploid *D. rotundata* were shared with the diploid *D. rotundata*, their maternal and paternal parents are likely the diploid *D. rotundata* and *D. togoensis*, respectively (Fig. 4d; Sugihara et al. 2020). Successful interspecific crosses between *D. rotundata* and *D. togoensis* were also reported (Girma et al. 2014). The triploid *D. rotundata* formed by autopolyploidization seems to be the minority as compared to those formed by allopolyploidization (Girma et al. 2014). It is not easy to distinguish the triploid *D. rotundata* accessions from the diploid accessions based on morphology. However, some morphological traits, such as the presence of bark patches, absence of waxiness, and dark green leaf color, have been shown to correlate with ploidy level (Girma et al. 2014). Agricultural importance of the triploid *D. rotundata* is yet to be studied.

*D. cayenensis* (yellow Guinea yam) is another species that is likely a triploid hybrid between the diploid *D. rotundata* and the rainforest-adapted wild species *D. burkilliana* (Fig. 4e; Terauchi et al. 1992; Girma et al. 2014). Based on chloroplast DNA polymorphisms, it was suggested that diploid *D. rotundata* is the maternal parent of *D. cayenensis* (Terauchi et al. 1992). Using nuclear ribosomal DNA polymorphisms (Terauchi et al. 1992) and Genotype-by-Sequencing (GBS) analysis (Girma et al. 2014), it was inferred that *D. burkilliana* is the paternal parent. *D. cayenensis* has a woody corm above the fleshy tuber, and this trait is shared with *D. burkilliana*. Interestingly, *D. burkilliana* is also subjected to “ennoblement” together with *D. abyssinica* and *D. praehensilis* (Mignouna and Dansi 2003), which probably contributed to its hybridization with *D. rotundata*.

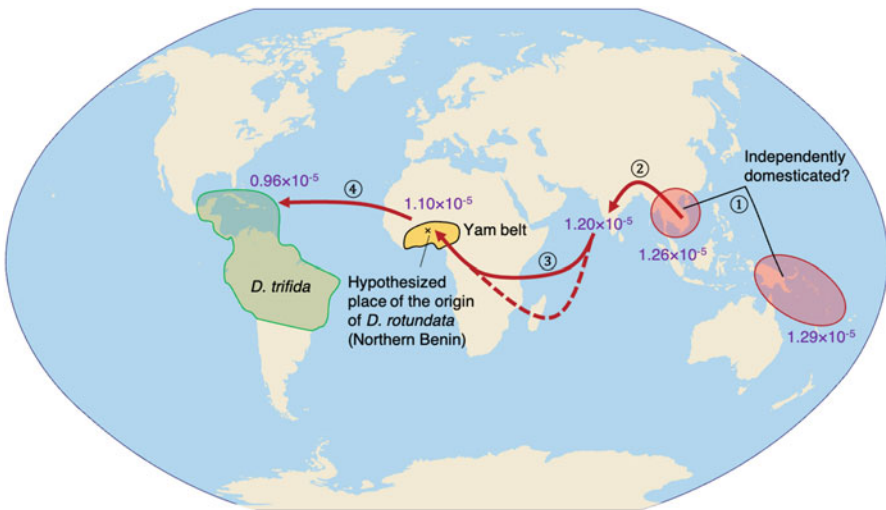
*D. mangelotiana* (syn. *D. baya*) is genetically close to Guinea yam (Girma et al. 2014; Magwé-Tindo et al. 2018). Previously, *D. mangelotiana* and *D. baya* were considered different species. However, a recent study proposed *D. mangelotiana* as the adult form of *D. baya* (Magwé-Tindo et al. 2018). *D. mangelotiana* is a rainforest-adapted wild species characterized by spiny stems and the production of very big tubers (Figs. 2d and 3f; Dounias 2001). The bases of its fleshy edible tubers are attached to very large woody corms, which probably provide protection from herbivores. In Southern Cameroon, *D. mangelotiana* has long been subjected to “paracultivation” by the Baka Pygmies (Dounias 2001). “Paracultivation” is the exploitation and maintenance of wild plants in their original/natural environments (Dounias 2001). Intriguingly, *D. mangelotiana* was reported as a triploid species (Girma et al. 2014) with a large number of heterozygous DNA markers, which probably suggests that it may be an allopolyploid. However, no research has been carried out to date to identify the ancestors of *D. mangelotiana*.

## 5.2 Origin and Domestication of *D. alata*

*D. alata* (greater yam) is widely cultivated in pantropical regions (Asia, the Pacific, Africa, and the Caribbean) in contrast to *D. rotundata* that is restricted to Africa and

the Caribbean. This worldwide dispersion of *D. alata* occurred mainly through human migrations (Sharif et al. 2020). As discussed above, the domestication process of *D. rotundata* seems mainly driven by hybridization and introgression. By contrast, the domestication of *D. alata* was mainly driven by vegetative propagation and autopolyploidization, which caused erratic or no flowering in this species (Arnau et al. 2010; Sharif et al. 2020). This predominant vegetative propagation in *D. alata* is in line with its very low nucleotide diversity ( $\pi = 0.96 \sim 1.29 \times 10^{-5}$  in Fig. 6; Sharif et al. 2020) as compared with the higher level of nucleotide diversity in *D. rotundata* ( $\pi = 1.48 \times 10^{-3}$ ) (Sugihara et al. 2020).

Sharif et al. (2020) used genome sequence analysis of 643 accessions spanning four continents to study the dispersion route of *D. alata*, which confirmed the region around tropical Eastern Asia as the geographical origin of *D. alata*. This finding supports the previous proposal by Burkill (1960) that *D. alata* was originated in the tropical Eastern Asia. Additionally, Sharif and colleagues hypothesized that *D. alata* was domesticated independently in the Mainland Southeast Asia and the Pacific (① in Fig. 6). Their hypothesis is based on the early divergence between the two regions estimated for *D. alata* (Sharif et al. 2020) as well as the estimated date of early human settlement of Sahul (at least 50,000 years ago) (Bird et al. 2019). After the divergence between the subgroups of Mainland Southeast Asia and the Pacific, *D. alata* reached the Indian subcontinent (② in Fig. 6). According to their demographic inference, there was a continuous migration between the Indian subcontinent



**Fig. 6** Global dispersion of *D. alata* (Sharif et al. 2020) and distributions of other cultivated yam species. Figures in purple color represent nucleotide diversities of the diploid *D. alata* accessions in different regions. *D. alata* was originated in Southeast Asia (①). After its domestication in Southeast Asia, it reached Africa via the Indian Peninsula (② and ③), and finally reached the Caribbean (④) from Africa. The introduction to Africa might be through either Madagascar (broken line in ③) or East Africa via the Swahili coast (solid line in ③). The gradual reduction in *D. alata* nucleotide diversities clearly suggests the founder effects



and the Pacific. From the Indian subcontinent, *D. alata* reached Africa (③ in Fig. 6). Since the African and Madagascar *D. alata* are genetically closer to that of the Indian subcontinent than to that from the Mainland Southeast Asia, this dispersion seems to have occurred via the Indian subcontinent (Sharif et al. 2020). The detailed route of how *D. alata* reached Africa is still unclear. However, it might be through either Madagascar or East Africa via the Swahili coast (③ in Fig. 6). The relatively low nucleotide diversity of African accessions suggests a founder effect from the Indian subcontinent (Sharif et al. 2020). From Africa, *D. alata* was introduced into the Caribbean (④ in Fig. 6) most probably during the Colombian exchange, which introduced African crops to the tropical America (Boivin et al. 2012). The lowest nucleotide diversity of the Caribbean accessions suggests a strong founder effect from Africa (Sharif et al. 2020; Fig. 6). Taken together, the decreasing nucleotide diversity of *D. alata* clearly reflects the route for its dispersion.

The distribution of the clonal and polyploid accessions of *D. alata* also reflects the route of dispersion of the species (Sharif et al. 2020). Approximately 68% of the inferred clonal clusters (multi-locus lineages in Sharif et al. 2020) had an intercontinental distribution. The Caribbean accessions had the highest number of the intercontinentally shared clonal clusters, while those of Asia had the lowest. Therefore, the distribution of the clonal clusters reflects dispersion of this species through vegetative propagation. The dispersion route of *D. alata* was also reflected in the distribution of its polyploid accessions. Most of the polyploid accessions are genetically close to either the Asian or the Pacific accessions. This suggests that the polyploidization of *D. alata* occurred several times before migration of the species from Asia and the Pacific to Africa and the Caribbean. Moreover, most triploid accessions were genetically closer to the Asian lineages rather than to the Pacific lineages. This suggests that most triploid accessions were derived from Asia.

The wild progenitor of *D. alata* is still unknown. However, some studies revealed that *D. alata* is phylogenetically close to the wild species *D. nummularia*, *D. transverse*, and *D. hastifolia* (Malapa et al. 2005; Chair et al. 2016). Especially, *D. nummularia*, a species native to Melanesia and Island Southeast Asia, is also subjected to a “paracultivation”-like practice (Dounias 2001; Chair et al. 2016). Interestingly, cultivars of natural hybrid between *D. alata* and *D. nummularia* have been reported and known as “strong yam” by farmers of Vanuatu (Chair et al. 2016). These interspecific hybrids were treated as unidentified taxa or erroneously assigned to *D. transverse* (Malapa et al. 2005; Chair et al. 2016). This mis-assignment is probably related to their potential hybrid status (Chair et al. 2016). Recently, researchers have started paying attention to the diversity of *D. nummularia* (Lebot et al. 2017) and attempts are made to introduce the resistance trait of *D. nummularia* against the anthracnose disease caused by *Colletotrichum* pathogens into *D. alata* by artificial hybridization (Lebot et al. 2019). Although the cross between *D. alata* and *D. nummularia* resulted in fertile seeds, *D. nummularia* is not regarded as a direct ancestor of *D. alata* (Chair et al. 2016). Further population genomics study is needed by including multiple accessions of *D. nummularia*, *D. transverse*, and *D. hastifolia* to clarify the origin of *D. alata*.

### 5.3 *Origin and Domestication of D. trifida*

*D. trifida* of the section *Macrogynodium* was domesticated in South America and is commonly referred to as the indigenous “Amerindian” yam. Genetic segregation study and cytogenetics suggested that the cultivated *D. trifida* is autotetraploid ( $2n = 4\times = 80$ ) (Bousalem et al. 2006), while a wild *D. trifida* with diploid genome ( $2n = 2\times = 40$ ) was found in French Guyana (Bousalem et al. 2010). A phylogenetic study based on amplified fragment length polymorphism (AFLP) clearly separated the cultivated ( $4\times$ ) and wild ( $2\times$ ) *D. trifida* (Bousalem et al. 2010). A region where the diploid *D. trifida* predominate was also found. *D. trifida* represents a clear case that whole-genome duplication may have played an important role in the domestication of *Dioscorea*. The autopolyploidization is not a preferred subject in population genomics, but this may help to calibrate the time when the polyploidization happened.

### 5.4 *Origin and Domestication of D. dumetorum*

*D. dumetorum*, known as the “trifoliate yam” because of its trifoliate leaves, belongs to the section *Lasiophyton*. *D. dumetorum* is widely consumed in West and Central Africa and occurs in both cultivated and wild forms. Despite its high yielding nature and nutritional richness, severe postharvest hardening of the tubers makes *D. dumetorum* a minor crop (Sefa-Dedeh and Afoakwa 2002). Genetic diversity study of *D. dumetorum* revealed that the accessions from Togo and Nigeria had the highest genetic diversity (Sonibare et al. 2010). This indicates that the center of genetic diversity and the possible origin of *D. dumetorum* might be around Togo and Nigeria. Another study focusing on the accessions from Cameroon identified gene flow and admixture among the accessions, which is probably caused by farmers’ breeding practices (Siadjeu et al. 2018). The same study revealed different ploidy levels in *D. dumetorum* and showed that diploids and triploids have different geographical distributions in Cameroon. Interestingly, population genomics study showed that the distribution of the triploid *D. dumetorum* was positively correlated with the region containing a higher level of gene flow (Siadjeu et al. 2018).

## 6 *Evolution of Sex in Dioscorea Species*

Most *Dioscorea* species are dioecious, bearing male and female flowers on separate individuals. This sexual system affects genetics and population genomics of the genera and consequently deserves a special attention. Dioecious plants account for ~5–6% of angiosperm species (Renner 2014). Based on its scattered taxonomic distribution, dioecy is suggested to have evolved recently and independently from

hermaphroditic co-sexual ancestors (Renner and Ricklefs 1995; Charlesworth 2002). Many studies have focused on understanding the process of this large-scale convergent evolution from co-sexual to dioecy in plants. To elucidate the process, sex-determination systems have been studied in several taxa (Akagi et al. 2016, 2019; Harkess et al. 2020).

In *Dioscorea*, multiple sex-determination systems have been reported by cytological observations and molecular analyses (Table 2). As part of our work on the genetics of *D. tokoro*, a wild species from East Asia, we studied the inheritance and segregation pattern of AFLP markers in an  $F_1$  family derived from a cross between male and female *D. tokoro* plants, which suggested an XY/XX (male/ female) sex-determination system in this species (Terauchi and Kahl 1999). Although most *Dioscorea* species have male heterogametic sex-determination system, female heterogametic sex-determination system (ZZ/ZW) and extra chromosomes in female (XO/XX) have also been reported (Table 2). Sex change of individuals was observed in *D. rotundata* having female heterogametic sex-determination system (ZZ/ZW) (Tamiru et al. 2017). Here, we review the sex-determination systems of ZZ/ZW and XY/XX that occur in *D. rotundata* and *D. alata*, respectively.

Sex in *D. rotundata* is regulated by a female-specific genomic region that we recently identified by QTL-seq analysis of an  $F_1$  progeny segregating for sex (Tamiru et al. 2017). QTL-seq is an NGS-based bulked segregant analysis (BSA) method to identify the genomic regions underlying traits of interest using progeny derived from crosses made between cultivars/lines showing contrasting phenotypes for the traits (Takagi et al. 2013; Itoh et al. 2019). To identify the genomic region associated with sex in *D. rotundata*, QTL-seq was applied to sequences generated for male and female DNA pools prepared from an  $F_1$  progeny derived from a cross between male and female plants. Accordingly, a candidate genomic region was detected on chromosome 11 using SNP markers that were heterozygous in the female parent whereas no candidate regions were detected when SNP markers heterozygous in the male parent were used. The candidate genomic region showed significant structural differences between the male and female sequences. PCR amplification and short read mapping analysis further identified a female-specific region within the candidate genomic region delineated by QTL-seq. These results suggest that the sex-determination system of *D. rotundata* is ZZ/ZW (male/female), not XO/XX (male/female).

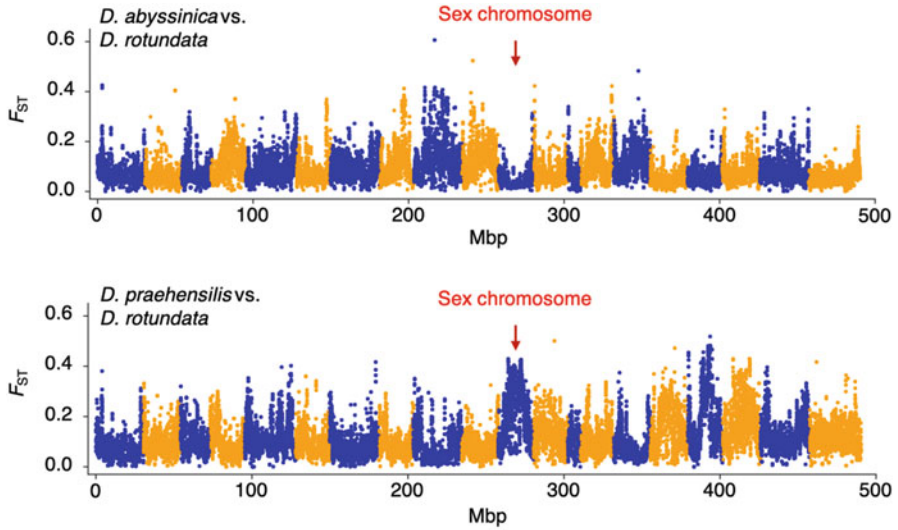
A DNA maker, “sp16,” was developed within the female-specific (*W*-) genomic region of *D. rotundata* for prediction of sex of the plant at the seedling stage (Tamiru et al. 2017). The usefulness of the DNA marker has been demonstrated in diverse *D. rotundata* accessions (Agre et al. 2020; Denadi et al. 2020). However, the marker type was not perfectly associated with sex, suggesting the manifestation of sex is unstable in *D. rotundata* over a time period (Tamiru et al. 2017). Sex change is widely known in plants and animals (Policansky 1982). Interestingly, this sex change was rarely observed in the male *D. rotundata* plants, suggesting a gene on the *W*-region with “sp16” marker seems to suppress maleness, and its effect is unstable.

**Table 2** Reported sex-determination systems in *Dioscorea*

Species	Sex-determination system	Methods	Reference
<i>D. alata</i> L.	XY	QTL detection	Cormier et al. (2019a)
<i>D. bulbifera</i> L.	XY	Cytological observations	Ramachandran (1962)
<i>D. deltoidea</i> Wall.	ZW	Cytological observations	Bhat and Bindroo (1980)
<i>D. discolor</i>	<sup>a</sup>	Cytological observations	Smith (1937)
<i>D. fargesii</i> Franch.	<sup>a</sup>	Cytological observations	Smith (1937)
<i>D. gracillima</i> Miq.	XY	Cytological observations	Nakajima (1937)
<i>D. japonica</i> Thunb.	XY	Cytological observations	Nakajima (1942)
<i>D. macroura</i> Harms.	<sup>a</sup>	Cytological observations	Smith (1937)
<i>D. pentaphylla</i> L.	XY	Cytological observations	Ramachandran (1962)
<i>D. reticulata</i> C. Gay	XO	Cytological observations	Smith (1937)
<i>D. rotundata</i>	ZW	QTL detection	Tamiru et al. (2017)
<i>D. sinuata</i> Vell.	XO	Cytological observations	Meurman (1925)
<i>D. spinosa</i> Roxb.	XY	Cytological observations	Ramachandran (1962)
<i>D. tokoro</i> Makino	XY	AFLP analysis	Terauchi and Kahl (1999)
<i>D. tomentosa</i> Koenig	XY	Cytological observations	Ramachandran (1962)

<sup>a</sup>Heteromorphic chromosomes were reported but no information about sex determination system

In our recent study, we also investigated the genomic contribution of *D. abyssinica* and *D. praehensilis* to *D. rotundata* chromosome-wise (Fig. 7; Sugihara et al. 2020). The chromosome 11 of *D. rotundata* harboring the sex-determination locus was highly skewed towards that of *D. abyssinica*. As described in the previous Sect. 5.1 above, *D. rotundata* is likely a hybrid species derived from *D. abyssinica* and *D. praehensilis*, and the genetic divergences from both wild progenitors are basically similar across the genome (Sugihara et al. 2020). However, of all the chromosomes, chromosome 11 of *D. rotundata* had the shortest genetic distance from that of *D. abyssinica* and the largest genetic distance from that of *D. praehensilis* (Sugihara et al. 2020). Similar interspecies divergence differences between autosomes and sex chromosome have also been reported in the dioecious plant species of the genus *Silene* (Hu and Filatov 2016).



**Fig. 7** Genomic scan of  $F_{ST}$  values between cultivated yam (*D. rotundata*) and two wild species *D. abyssinica* (top) and *D. praehensilis* (bottom) (adopted from Sugihara et al. 2020, Fig. 2d). Sliding window analysis was conducted with 100-kb window and 20-kb step. Chromosome 11 of *D. rotundata* containing the sex-determining locus shows the shortest distance to that of *D. abyssinica* and the largest distance to that of *D. praehensilis*

*D. alata* has a male heterogametic sex-determination system (XY/XX) (Cormier et al. 2019a), which is like the majority of *Dioscorea* species (Table 2). *D. alata* belongs to the section Enantiophyllum with *D. rotundata*, a species with a female heterogametic sex-determination system (ZZ/ZW). Interestingly, the genomic region associated with sex of *D. alata* was identified on linkage group 6, which also corresponded to chromosome 6 of *D. rotundata* (Cormier et al. 2019a). The sex-determination locus of *D. rotundata* was identified on chromosome 11 (Tamiru et al. 2017), suggesting the transition of sex-determination system from XY to ZW occurred in the section Enantiophyllum. A similar transition of sex-determination system was reported in the genus *Populus*. Most species *Populus* have the XY sex-determination system, while *P. alba* has the ZW sex-determination system (Müller et al. 2020).

As discussed above, the genus *Dioscorea* contains many dioecious species with divergent sex-determination systems. Transition of sex-determination systems are presumably involved in species divergence (Kumar et al. 2014). Further genomics research in *Dioscorea* species will help identify the causative genes involved in sex determination and to clarify how the sex-determination systems have diversified in the genus. Such information will also allow us to manipulate sex of plants for effective cross breeding of yam crops.

## 7 Conclusions and Future Perspectives

Population genomics and cytogenetics studies have revealed important domestication processes in *Dioscorea* species, but many questions still remain. For example, we still do not know the key traits and the genes involved in yam domestications, although some studies have identified genes showing signature of selection in *D. rotundata* including *SWEETIE* gene in our study (Akakpo et al. 2017; Scarcelli et al. 2019; Sugihara et al. 2020). *D. abyssinica* and *D. praehensilis*, the wild relatives of *D. rotundata*, are subjected to an ongoing practice of “ennoblement.” Additionally, it has been shown that the most cultivars introduced by “ennoblement” are indeed hybrids between the cultivated and wild yams (Scarcelli et al. 2006). These findings probably indicate that the wild species cannot directly be domesticated to become cultivars and that hybridization was necessary to generate white Guinea yam cultivars. Similar interspecific hybridization was also reported in *D. alata* (Chair et al. 2016). Consequently, analyzing hybridization is important to understand what attributes characterize *D. rotundata* and other cultivated yams. Probably, *D. rotundata* was established as a cultivar as a result of heterosis derived from the hybridization between *D. abyssinica* and *D. praehensilis*.

Understanding the genomes of crop wild relatives would facilitate efficient breeding programs. Crop wild relatives are expected to have potentially beneficial alleles that are not available in the cultivars. The farmers unconsciously introduce these beneficial alleles to the cultivars presumably by “ennoblement.” Since the genomic regions containing the beneficial alleles should be affected by selective sweeps, population genomics analyses may be able to identify these regions (Akakpo et al. 2017; Scarcelli et al. 2019; Sugihara et al. 2020). Currently, there is no evidence that these candidate selective sweeps affected any phenotypes. However future functional studies of the identified genes would reveal their impact on the change of traits in the crops.

Another standing question is how many times the domestication processes occurred in the various cultivated *Dioscorea* species. A recent study hypothesized multiple domestication processes of *D. alata* in separate regions (Sharif et al. 2020). The cultivated yam landraces from Southern Ethiopian are phylogenetically close to the cultivated gene pools of *D. rotundata*, but they were clearly separate from Nigerian *D. rotundata* (Tamiru et al. 2007). Although the model-based population genetics/genomics is needed to infer the detailed demographic history, this result may suggest independent domestication processes of *D. rotundata* in Ethiopia (or East Africa) and Nigeria.

In this chapter, the importance of hybridization and polyploidization for the domestication of *Dioscorea* species has been discussed. Some of these events appear to have played an important role in yam domestication. In recent years, our knowledge of yam domestication has dramatically improved thanks to the advances in sequencing technologies and statistical methods for population genomics analysis. These developments also allowed us to identify, among others, the transition of the sex-determination system in the section *Enantiophyllum*. Future studies should

further unravel the complex evolutionary history of *Dioscorea* species including hybridization, polyploidization, and sexual/asexual propagation.

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