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Characterization and delineation of two infraspecific taxa of *Dioscorea esculenta* (Lour.) Burkill: The leaf architecture approach

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Abstract. *Antonio MA, Buot Jr. IE. 2021. Characterization and delineation of two infraspecific taxa of Dioscorea esculenta (Lour.) Burkill: The leaf architecture approach. Biodiversitas 22: 1783-1789.* The current taxonomic treatment for the wild and cultivated species of *Dioscorea esculenta* Lour. (Burkill) presented them as two different varieties. However, there are confusions among botanists and farmers. So, leaf architecture analysis was done to investigate whether leaf architecture data would support their current taxonomic treatment. The varieties showed variability in several characteristics indicating their distinct identity from each other. Based on general leaf characters, they differ in all the parameters observed. But on venation characters, evident variation was seen only on the number of basal veins and secondary vein angle of divergence. Nevertheless, the two varieties resemble each other in a number of characters, *i.e.* campylodromous primary veins, brochidodromous secondary veins, presence of intermarginal and intersecondary veins, admedially ramified tertiary veins, and well-developed areolation. Dendrogram generated from cluster analysis agrees with and supports above leaf architectural examination, suggesting the two varieties to be recognized as separate taxa. But the current taxonomic treatment naming them as var. *spinosa* and var. *fasciculata* seemed to have dragged the cultivated plant into the classification system generally used for wild plants. Thus, the proposed name for the cultivated plant is *D. esculenta 'fasciculata'* while that of the wild plant remains as *D. esculenta* var. *spinosa*.

Keywords: *Dioscorea esculenta* var. *spinosa*, *Dioscorea esculenta* var. *fasciculata*, leaf anatomy, leaf morphology, venation patterns

INTRODUCTION

Dioscorea L. is a genus of more than 600 species of herbaceous or viny plants in the family Dioscoreaceae. The genus had been expanded with the recent circumscription subsuming the monotypic genera *Borderea, Epipetrum, Rajania, Nanarapenta, Tamus*, etc. following the phylogenetic analysis done by Caddick et al. *(*2002). Morphological diversity, which is partly attributed to the plants' wide geographic distribution, is reported in the genus. Such diversity, including the various local names used for them (Prain and Burkill 1913) triggered difficulties in identification. Thus, names and nomenclatural errors proliferated in the genus (Raz 2016).

There are 17 *Dioscorea* species which are reported in the Philippines (Pelser et al 2011). Except for the cultivated *Dioscorea alata* L. (greater yam, or ubi), *Dioscorea esculenta* (Lour.) Burkill (lesser yam or tugui) and *Dioscorea bulbifera* (aerial yam or ubi-bunga), the rest of the species grow in the wild.

Pelser et al. (2011) listed two varieties of *D. esculenta*: namely var. *fasciculata* (Roxb.) Prain and Burkill as the entirely cultivated plants devoid of thorny roots, and var. *spinosa* (Prain) R. Knuth as the cultigen and wild plants well-provided with thorny roots. Current taxonomic treatment, generally based on genetic status (cultivated vs. wild) and tuber morphology, seemed confusing to the botanists and farmers and the production sector. Antonio (2008) characterized the wild and cultivated varieties in terms of morphology. The varieties were observed similar in several leaf, stem and inflorescence characteristics but differ in terms of the spines on the anchor roots, tuber size and shape, and stolon length. Since plant morphology exhibits phenotypic plasticity, there is a need to supplement morphological data with more stable characters. In 2001, Roth-Nebelsick et al. (2001) hypothesized that leaf venation patterns such as anastomoses are genetically fixed. Since then, leaf architecture approach has gained importance and utilization in a range of applications such as in systematic botany. Among the studies on the application of leaf architecture techniques include characterization and species delineation in the genera *Psychotria* (Banaticla and Buot 2004) and *Hoya* (Salvaña and Buot 2014; Villareal and Buot 2015; Jumawan and Buot 2016; Torrefiel and Buot 2017; Tan and Buot 2018; Baltazar and Buot 2019), and families Malvaceae (Laraño and Buot 2010), Combretaceae (Baroga and Buot 2004) and Cucurbitaceae (Rao and Rao 2015).

This taxonomic investigation using leaf architecture approach was done in relation to the wild and cultivated *D. esculenta* and *D. alata* (outgroup) to determine whether leaf architecture data will support the current taxonomic treatment given to the two varieties of *D. esculenta* plants.

MATERIALS AND METHODS

Thirty leaf samples each of cultivated and wild *D. esculenta*, and *D. alata* (outgroup) were randomly collected from planted accessions at the field genebank of the Mariano Marcos State University, City of Batac, Ilocos Norte, Philippines (Figure 1). The collected leaf samples were pressed and oven-dried. Samples were examined using a dissecting microscope. Their leaf architecture was described following the leaf architecture characters and terminologies of Hickey (1973) and the Leaf Architecture Working Group (1999). Length and width were measured using ruler while angles of divergence were measured using a protractor. The studied leaf samples were deposited at the Plant Biology Division Herbarium (PBDH) at the Institute of Biological Sciences, University of the Philippines Los Baños, College, Laguna, Philippines.

A dichotomous key to the three taxa was constructed using leaf architecture characters. Cluster analysis was also conducted using PAST ver. 3.23 (Hammer et al. 2019) to determine and estimate the genetic relationship of the two varieties of *D. esculenta*, together with the outgroup *D. alata*. Twenty-eight leaf characters were used, and data were transformed into a scale of 1 to 3 depending on the values or data obtained. Dendrograms were constructed using unweighted pair-group average (UPGMA) as the algorithm, and Euclidean distance as the similarity index.

RESULTS AND DISCUSSION

General morphology of *Dioscorea esculenta* var. *spinosa* and *D. esculenta* var. *fasciculata*

In aid of presenting the distinct identity of the two varieties of *D. esculenta*, an understanding of their general morphology is deemed necessary. Both taxa shared characters such as left-twining habit, spiny stem and leaf petiole, cordate and pubescent leaves, spike inflorescence (Figure 2) with flowers bearing six petals and six stamens, multiple tubers covered with roots throughout the surface, and uniform off-white tuber flesh. The wild plant *D. esculenta* var. *spinosa*, on the other hand, can be easily distinguished from the cultivated *D. esculenta* var. *fasciculata* by having numerous spines on the anchor roots, big and multiple tubers of varied shapes, and long stolons on which the tubers are suspended. Meanwhile, the cultivated *D. esculenta* var. *fasciculata* has sparse spines to nil in the anchor roots, and very short stolons, making the small tubers close to each other or clustered immediately at stem base (Table 1). Other distinguishing morphological features are observed in Table 1. While plant morphology is phenotypically plastic, these distinguishing characters still provide additional evidence delineating the two varieties.

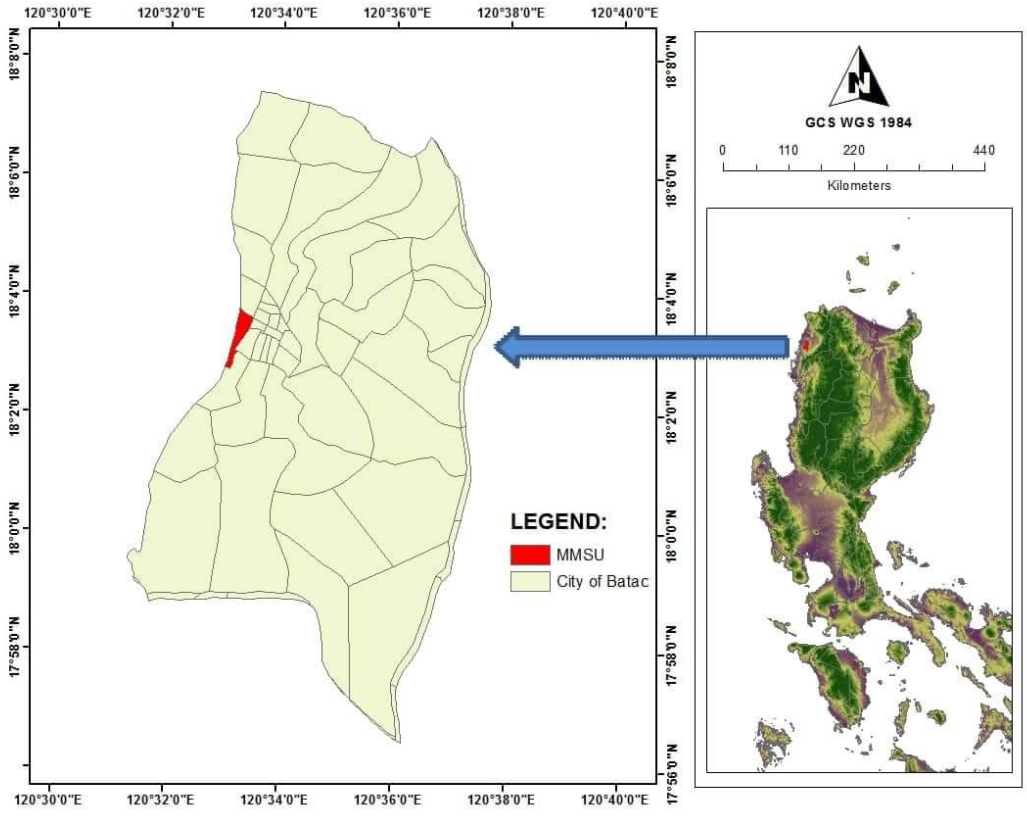


Figure 1. The City of Batac, which situates the MMSU field genebank, is located in the northwestern portion of the Philippines. The map was generated using ArcGIS v. 10.1 by Engr. RT Utrera, MMSU, City of Batac, Ilocos Norte.

A **B**

Figure 2. Leaf and inflorescence morphology of *Dioscorea esculenta* var. *spinosa* (A) and *D. esculenta* var. *fasciculata* (B). (Photo by M.A. Antonio)

Table 1. Distinguishing morphological characters of *Dioscorea esculenta* var. *spinosa* and *D. esculenta* var. *fasciculata*

Character	***D. esculenta* var. *spinosa*** **Exsicc. *Antonio 6893* (PBDH)**	***D. esculenta* var. *fasciculata*** **Exsicc. *Antonio 6894* (PBDH)**
Vine color	Purplish green as most dominant	Brownish green as most dominant
Vine spines	Fewer spines at stem base, becoming denser up the stem	Dominant at stem base, diminishes up the stem
Vine pubescence	Moderate	Slightly more than sparse
Leaf lobe	No measurable distance between leaf lobes	Distance between leaf lobes intermediate (between narrow and distant)
Petiole length	Shorter or of the same length as the blade	Longer or of the same length as the blade
Petiole color	Dominantly brownish green	Dominantly all green
Leaf density	High	sparse to intermediate
Tuber size	Big (19.3 cm long x 10.1 cm diameter) (Biggest tuber harvested 3.5 kg)	Small (about 8.52 cm long x 4.75 cm diameter) (Biggest tuber harvested 0.4 kg)
Stolon	Tubers subtended in long stolon (about 100 cm)	Stolon none, tubers clumped at stem base
Anchor roots	With numerous spines	Sparse to nil

Table 2. General blade characteristics of the two varieties of *Dioscorea esculenta* and *D. alata* (outgroup)

Character	***D. esculenta* var. *spinosa*** **Exsicc. *Antonio 6893* (PBDH)**	***D. esculenta* var. *fasciculata*** **Exsicc. *Antonio 6894* (PBDH)**	***D. alata* (outgroup)** **Exsicc. *Antonio 6895* (PBDH)**
Pubescence	Both sides	Ventral side	None
Blade length (mm)	74-105 (Mean: 86)	50-91 (Mean: 72.833)	117-173 (Mean: 150.42)
Blade width (mm)	86-140 (Mean: 112.23)	56-107 (Mean: 81.083)	87-164 (Mean: 141.83)
Blade area (mm2)	4586.67-9800 (Mean: 6465.31)	1866.67-6430.67 (Mean: 4109.94)	6786-18914.67 (Mean: 14398.28)
Blade class	Mesophyll	Notophyll	Majority mesophyll, few macrophyll
Length-width ratio	1:0.615-1:0.931 (Mean: 1 : 0.773)	1:0.832-1:0.956 (Mean: 1:0.902)	1:0.963-1:1.345 1:1.078

Leaf architectural characteristics of *Dioscorea esculenta* var. *spinosa* and *D. esculenta* var. *fasciculata*

In terms of general blade characters, the two varieties of *D. esculenta* showed variability in all six characters examined (Table 2). The *D. esculenta* var. *spinosa* has pubescence on both ventral and dorsal sides, mesophyll blade class and is intermediate to *D. esculenta* var. *fasciculata* and *D. alata* (outgroup) in terms of blade length, width and area, and leaf-width ratio. The *D. esculenta* var. *fasciculata*, on the other hand, has pubescence on the ventral side, notophyll blade class and gave the smallest measurements in all blade size parameters. Comparing the outgroup *D. alata*, it is non-pubescent, generally mesophyll (although few samples were rated macrophyll), and had the biggest leaf blade measurements among the three taxa. There was no general leaf character shared by the two *D. esculenta* species.

Table 3. General venation characteristics of the two varieties of *Dioscorea esculenta* and *D. alata* (outgroup)

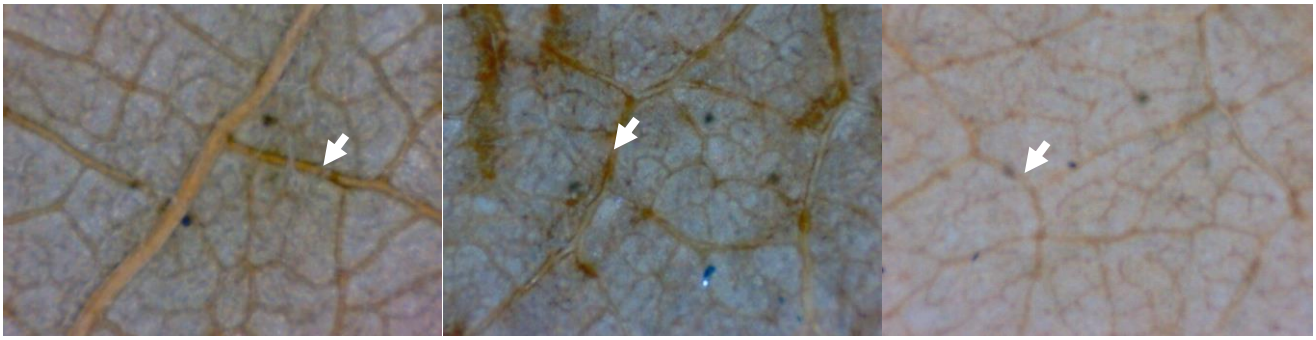
Character	***D. esculenta* var *spinosa*** **Exsicc. *Antonio 6893* (PBDH)**	***D. esculenta* var *fasciculata*** **Exsicc. *Antonio 6894* (PBDH)**	***D. alata*** **Exsicc. *Antonio 6895* (PBDH)**
Primary vein category	Campylodromous	Campylodromous	Campylodromous
No. of basal veins	9-10	7-9	7-9; majority
	One to two primary veins distichously branching-numerous	A primary vein distichously branching-rare	A primary vein distichously branching-rare
Primary vein size	Weak	Weak	Weak
Vein width (cm)	0.3-0.7 (Mean: 0.49)	0.4-0.5 (Mean: 0.508)	0.9-1.1 (Mean: 0.983)
Vein width/blade width	0.219-0.814 (Mean: 0.450)	0.476-1.11 (Mean: 0.662)	0.549-1.034 (Mean: 0.715)
Primary vein course	Curved	Curved	Curved
Secondary vein Category	Brochidodromous	Brochidodromous	Brochidodromous
Secondary vein angle of divergence	Wide acute	Moderately acute	Moderately acute
Secondary vein thickness	Moderate	Moderate	Fine
Secondary vein course	Sinuous, branched	Sinuous, branched	Sinuous, branched
Behavior of loop-forming branches	Joining superadjacent secondary at obtuse angle	Joining superadjacent secondary at obtuse angle	Joining superadjacent secondary at obtuse angle
Secondary vein spacing	Irregular	Irregular	Irregular
Intramarginal vein	Present	Present	Present
Intersecondary vein	Present	Present	Present
Tertiary vein course	Admedially ramified	Admedially ramified	Exmedially ramified
Tertiary vein pattern	Random reticulate	Random reticulate	Random reticulate
Tertiary vein angle to primary veins	Obtuse	Obtuse	Obtuse
Quarternary vein category	Regular polygonal reticulate	Regular polygonal reticulate	Regular polygonal reticulate
Pentanary vein category	Dichotomizing	Dichotomizing	Dichotomizing
Areolation	Well developed	Well developed	Moderately developed
Freely-ending veins	1-branched to 2 or more-branched	1-branched to 2-or more branched	1-branched to 2-or more branched
Highest order	5	5	6

The two varieties of *D. esculenta* are similar in majority (18 out of 22) of the venation characters observed (Table 3, Figure 3). They include campylodromous primary vein, weak primary vein size, curved primary vein course, brochidodromous secondary vein, sinuous and branched secondary vein course, loop-forming branches joining superadjacent secondary at obtuse angle, irregular secondary vein spacing, present intramarginal and intersecondary veins, random reticulate tertiary vein, obtuse tertiary-primary vein angle, regular polygonal reticulate quarternary vein, and 1-branched to 2-or more branched FEVS, among others. They differ in terms of the number of basal veins, vein width, vein width to blade width ratio and secondary vein angle of divergence.

The *D. esculenta* var. *spinosa* is so distinct from *D. esculenta* var. *fasciculata* and *D. alata* for having the highest number of basal veins (9-10) with very often occurrence of distichous branching in one or two of the primary veins nearest the blade margin (Table 3). It also has wide acute secondary vein angle of divergence in contrast to the moderately acute angle of divergence exhibited by the two other taxa.

Variation in the venation patterns of the two varieties is evident in the lower vein categories, particularly on the basal, primary and secondary veins. In contrast, variation in higher vein categories starting at the tertiary level is reported in *Hoya* by Tan and Buot (2018), and Torrefiel and Buot (2017).

In comparison with the outgroup *D. alata*, the two varieties exhibit greater variation from *D. alata*, differing in six out of 22 venation characters. Such variation is observed on the basal, secondary and tertiary veins and areolation. This observation corroborates the report of Hickey (1973) that there is high degree of interspecific variation on venation patterns, which is taxonomically important in distinguishing and identifying plant species from each other.



A B C

Figure 3. Leaf venation of *Dioscorea esculenta* var. *spinosa* (A), *D. esculenta* var. *fasciculata* (B), and *D. alata*, outgroup (C). Arrows pointing at secondary veins indicate moderate veins in A and B and fine veins in C. (Photo by M.A. Antonio)

Key to the three *Dioscorea* taxa

1a. Primary vein campylodromous, vein size weak, secondary vein brochidodromous, loop-forming branches at obuse angle with secondary vein ……. 2
1b. Primary vein not campolydromous, vein size moderate to massive, Secondary vein not brochidodromous, loop-forming branches join at non-obtuse angle …… 4

2a. Secondary vein thickness moderate, tertiary vein admedially ramified, areolation well-developed ....…… 3
2b. Secondary vein thickness fine to threadlike, tertiary vein exmedially ramified, areolation moderately developed …… ……. …… *D. alata*

3a. Basal veins 9-10, one to two basal veins very often dischitously branched, secondary vein angle of divergence wide acute, blade class mesophyll ……. …….. *D. esculenta* var. *spinosa*
3b. Basal veins 7-9, one to two basal veins rarely dischitously branched, secondary vein angle of divergence moderately acute, blade class notophyl ….. *D. esculenta* var. *fasciculata*

Venation patterns are taxonomically important for interspecific delineation because their orientation and quantitative characters are relatively stable at the species level (Roth-Nebelsick et al. 2001; Fang et al. 2002; Buot 2020). Observed variations in the two varieties of *D. esculenta* also suggest that venation patterns could also be used as diagnostic tool for infraspecific delineation, although such variation is to a lesser extent. In addition, Sun et al. (2017) used venation patterns in delineating the different sections of genus *Dioscorea.* Together with morphology and chemical composition, venation patterns were used in restructuring the composition of the different sections of *Dioscorea* sampled in China.

Descriptions of the leaf architecture characters of the *Dioscorea esculenta* varieties

***Dioscorea esculenta* (Lour.) Burkill var. *spinosa*: Exsicc. Antonio 6893 (PBDH):** Leaves pubescent on both sides; blade 74 to 105 cm long, 86 to 140 cm wide, mesophyll, 1:0.615 to 1:0.931 leaf length-width ratio; primary vein campylodromous, basal veins 9 to 10, one to two basal veins very often distichously branched, primary vein size weak, course curved; secondary vein brochidodromous, angle of divergence wide acute, thickness moderate, sinuous, branched, loop-forming branches at obtuse angle with secondary vein, spacing irregular; intramarginal and intersecondary veins present; tertiary vein admedially ramified, random reticulate, angle obuse with primary vein; quarternary vein regular polygonal reticulate; pentanary vein dichotomizing; areolation well developed; free ending veins 1-branched to 2-or more-branched.

***Dioscorea esculenta* (Lour.) Burkill var. *fasciculata*: Exsicc. Antonio 6894 (PBDH):** Leaves pubescent underside; blade 50 to 91 cm long, 56 to 107 cm wide, notophyll, 1:0.832 to 1:0.956 leaf length-width ratio; primary vein campylodromous, basal veins 7 to 9, basal vein rarely distichously branched, primary vein size weak, course curved; secondary vein brochidodromous, angle of divergence moderately acute, thickness moderate, sinuous, branched, loop-forming branches at obtuse angle with secondary vein, spacing irregular; intramarginal and intersecondary veins present; tertiary vein admedially ramified, random reticulate, angle obtuse with primary vein; quarternary vein regular polygonal reticulate; pentanary vein dichotomizing; areolation well developed; free ending veins 1-branched to 2-or more-branched.

Delineating the *Dioscorea* spp. using leaf architecture

Cluster analysis using UPGMA (Figure 4) illustrated a distinction between the three taxa of *Dioscorea. D. alata* diverged from the two varieties of *D. esculenta* at a distance coefficient of 35. Truncating the tree, the two *D. esculenta* varieties joined together earlier at a distance coefficient of 22, thus indicating greater similarity with each other than with *D. alata.*

The divergence of the two *D. esculenta* varieties at a relatively lower distance coefficient (22) indicates lesser differences of the two taxa. Number of basal veins, distichous branching of primary veins, secondary vein angle of divergence, blade class and pubescence are distinguishing characters that separate the two *D. esculenta* varieties (Table 3). Data from leaf architecture and plant morphology confer current taxonomic treatment as distinct varieties of *D. esculenta.*

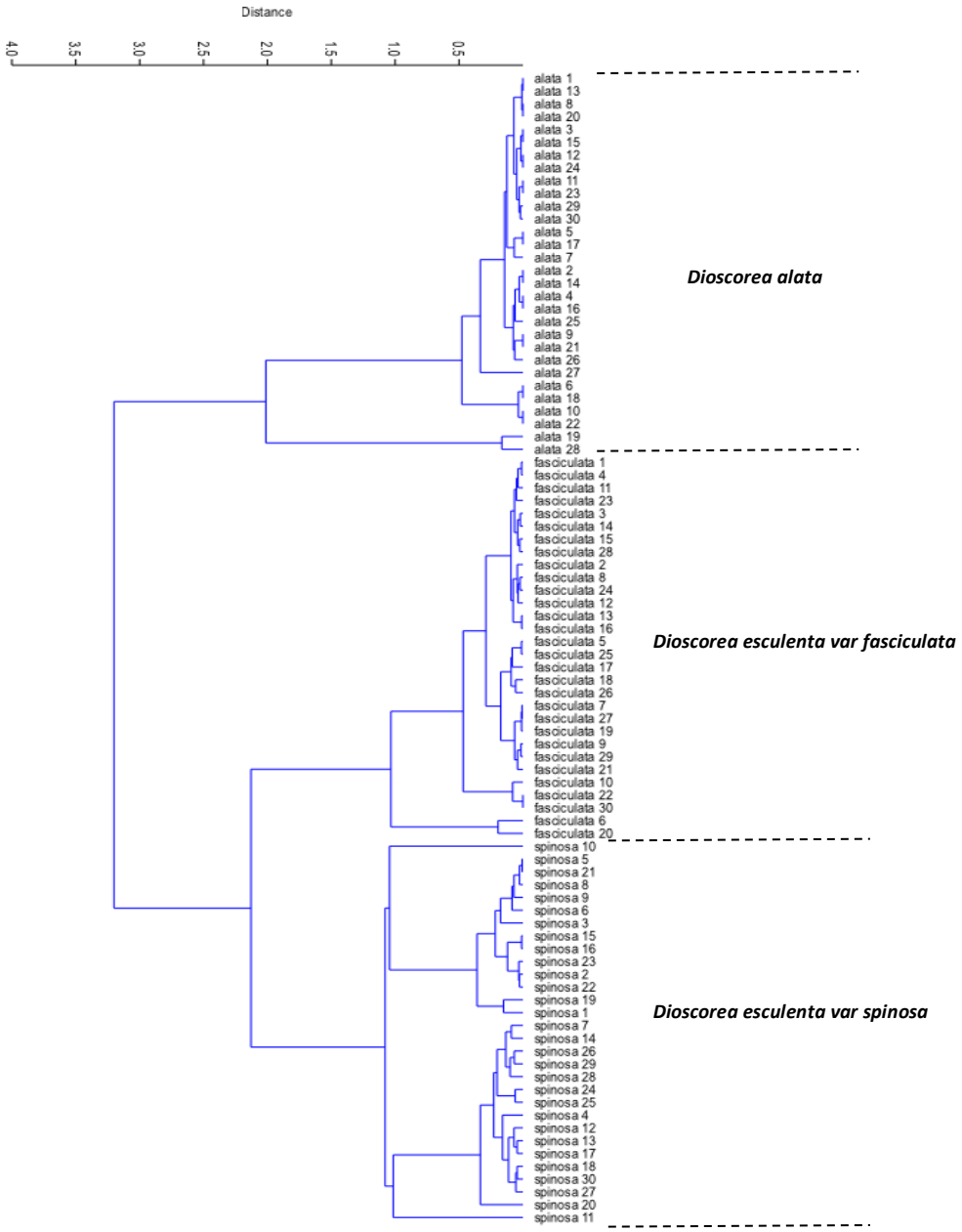


Figure 4. Unweighted pair-group average (UPGMA) clustering approach

However, the current name was given to *D. esculenta* var. *fasciculata* presents a contradiction to the rules of the International Code of Nomenclature for Cultivated Plants (ICNCP) (ISHS 2016). Since *D. esculenta* var. *fasciculata* is a cultivated variety, it should be treated under the ICNCP. So, following the ICNCP rules, a revision on the name of the cultivated variety is hereby proposed as: *D. esculenta* '*fasciculata*'. *D. esculenta* var. *fasciculata* is now considered a synonym of *D. esculenta* '*fasciculata*'. Meanwhile, the name of the wild variety remains as *D. esculenta* var. *spinosa.*

In the present study, leaf architecture is a useful tool for characterizing, delineating and classifying species. Results obtained from the analysis of *D. esculenta* and *D. alata* support their current species identity. Same approach was also helpful in delineating the infraspecific taxa of *D. esculenta* but to a lesser extent. A few venation characters, coupled with morphological characters, distinguish the two varieties of *D. esculenta*. Following the rules of ICNCP, *D. esculenta* var. *fasciculata* is proposed to be revised into *D. esculenta* '*fasciculata*'. The name *D. esculenta* var. *spinosa* for the wild variety remains.

Further, it is recommended that studies using other approaches such as floral and petiole anatomy be conducted to supplement the present results. Molecular studies are likewise recommended to confirm morphological and anatomical observations.

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