

Curvature analysis of seed silhouettes in the Euphorbiaceae

Emilio Cervantes^{1*}, José Javier Martín-Gómez¹, Diego Gutiérrez del Pozo², and Ángel Tocino^{3*}

¹ Instituto de Recursos Naturales y Agrobiología, Consejo Superior de Investigaciones Científicas, Cordel de Merinas 40, 37008 Salamanca, Spain; ecervant@usal.es, jjavier.martin@irnasa.csic.es

² Herbario Amazónico del Ecuador ECUAMZ, Universidad Estatal Amazónica, Carretera Tena a Puyo Km. 44, Carlos Julio Arosemena Tola 150950, Napo, Ecuador; diego.gutierrez.pozo@gmail.com

³ Departamento de Matemáticas, Facultad de Ciencias, Universidad de Salamanca, Plaza de la Merced 1-4, 37008 Salamanca, Spain; bacon@usal.es

* Correspondence: ecervant@usal.es; bacon@usal.es

Abstract: The Euphorbiaceae is a large, diverse and cosmopolitan family of monoecious or dioecious trees, shrubs, herbs, and lianas. Their name comes from *Euphorbia*, one of the largest genera in the Angiosperms with close to 2000 species and a complex taxonomy. Many of their members have an economic interest with multiple applications including pharmaceutical, nutritional and others. The seeds of the Euphorbiaceae develop in schizocarps and have a diversity of shape that has proven useful for species identification and classification. Nevertheless, analytical quantitative methods can be the subject of further development for the application of seed morphology in the taxonomy of this family. With this objective, measurements of size (area, perimeter, length and width), and shape (circularity, aspect ratio, roundness and solidity) in seed images of 230 species representative of the main taxonomic groups of Euphorbiaceae are presented, and curvature analysis applied to 19 species. Seed images corresponding to many species of this family present a tetragonal pattern with a curvature peak in the apical pole and three in the basal pole. The results of curvature analysis are discussed in relation with other morphological properties revealing new aspects of seed morphology of taxonomic application.

Keywords: curvature; geometry; morphometry; shape quantification

1. Introduction

The Euphorbiaceae Juss. is a diverse and cosmopolitan family consisting of monoecious or dioecious trees, shrubs, herbs, and lianas. The family is well represented in the tropics, and some of its members are succulents that resemble cacti and produce a milky sap. Included in the large order of Malpighiales [1], the Euphorbiaceae is the fifth largest family in the Angiosperms with about 7500 species in 300 genera [2], and, after restructuring leaving only the unlobed species [3,4], it was divided in three subfamilies: Acalyphoideae, with about 120 genera grouped in 17 tribes [5], Crotonoideae and Euphorbioideae, with close to 70 genera in 12 and 5 tribes **each respectively** [6]. The family receives its name after *Euphorbia* L., one of the largest genera of the Angiosperms with about 2000 species and a complex taxonomy. The genus was named after Euphorbus, the physician to king Juba of Mauretania, that was himself a given naturalist and the discoverer of *Euphorbia regis-jubae* J.Gay, now native of the Canary Islands. Other members of the family have their names associated with therapeutical properties such as *Jatropha* L., that etymologically means medicinal food. Members of the Euphorbiaceae have applications in the oil industry, as well as in the pharmaceutical and cosmetic industry such as *Ricinus communis* L. and *Jatropha curcas* L. [7,8]. The latex of *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg. is the basis of natural rubber [9]. Secondary metabolites of the genus *Euphorbia* are the basis for multitude of medical applications [10,11]. Many species also produce

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edible roots (*Manihot esculenta* Crantz.) or fruits (*Aleurites moluccanus* (L.) Willd., *Caryodendron orinocense* H.Karst. or *Plukenetia volubilis* L.).

Euphorbiaceae seeds vary greatly in size and shape, often being small to medium-in size, and their surface can be either smooth (shiny or faint) or wrinkled, with various degrees of ornamentation. The seed coat is usually hard and may have an outer layer called the caruncle, a fleshy outgrowth that is often involved in attracting ants for seed dispersal (myrmecochory) [12,13,14]. Other means of seed dispersal may involve explosive dehiscence [15] and diverse types of zoochory [16]. In some species the seeds contain alkaloids, diterpenes, and cyanogenic glycosides, that can deter herbivores and pathogens.

Seed surface structure and general seed morphology have often been used in the taxonomy of the Euphorbiaceae [17–37], in the description of subgenera [27,28], sections or subsections [17,22,25], and to discriminate between closely related species [30,31,32]. For example, Khan used seed characters as diagnostic in a key to the species distributed in Turkey [25], and the description of 14 Turkish species of *Euphorbia* by Genç and Kültür was based on the seed or/and caruncle shape and size, and seed surface sculpture [26]. In their classification of the subgen. *Athymalus*, Peirson et al mention a characteristic shape of the sections *Pseudacalypha* and *Crotonoides*, with seeds wider at the base and with one or more furrows encircling the entire seed [34]. Seed shape is also frequently used in the taxonomy of subgen. *Chamaesyce* [35], *Esula* [36] and *Euphorbia* [37].

The curvature of a plane curve measures the rate at which the tangent line varies per unit distance travelled along the curve. In plants, curvature was first measured in the root apex of *Arabidopsis* Heinh. (Brassicaceae), showing reduced values in ethylene-insensitive mutants (*etr1-1* and *ein2-1*) [38], or with hydrogen peroxide treatment [39]. In addition, morphotypes were differentiated by curvature analysis in wheat kernels [40] and in the seeds of cultivated grapevine varieties [41]. Measurement of curvature has been recently applied to seeds of the Cucurbitaceae and the Vitaceae [42,43]. The protocol to determine curvature in the curve formed by the image of a natural organ is based on Bézier curves representing the corresponding silhouettes [44]. The method of curvature analysis applied here to seed morphological analysis in the Euphorbiaceae can be useful in the study of phylogenetic relationships between the species, as well as for the description, identification, and classification of species in this family.

2. Materials and Methods

2.1. Plant Materials

The seeds analyzed for general morphological measurements are listed in Table A1 (Appendix A), together with their sources. Their images are shown in Figures S1 to S11 (see Supplementary Materials).

2.2. Photography

Seed photographs were taken with a Sony α 5100 camera (Sony, Tokyo, Japan), equipped with an objective AF-S NIKKOR 18-55 mm 1:3.5-5.6 G II ED (Nikon, Tokyo, Japan).

2.3. General morphological descriptors

Seed area (A), perimeter (P), length of the major axis (L), length of the minor axis (W), aspect ratio ($AR = L/W$), circularity (C), roundness (R), and solidity (S) were measured with the Image J program (version v1.8.0) [45,46,47,48,49].

2.4. Curvature analysis

To measure the variations in curvature along the seed image profile, the seed silhouettes were approximated by Bézier curves [44]. Bézier approximated polynomials were derived from the coordinates extracted using the Analyze Line Graph tool of the software Image J [45]. Seed images (JPEG, typically 100 ppp) were opened in Image J, converted to 8-bit, and thresholds adjusted. The contour corresponding to the silhouette was selected, and a new threshold was defined prior to the corresponding line graph analysis to obtain the x and y coordinates that will be used to calculate the Bézier curve and the corresponding curvature function in Mathematica according to published protocols [38,39,40,41].

Note that curvature depends on the size of the figure. Curvature was given in mm^{-1} ; so a curvature of 10 corresponds to a circumference of 100 microns, and a curvature of 2 corresponds to a circumference of 0.5 mm. The curvature of the curve is given as a parametric function defined in the interval $[0,1]$. The *Mean curvature* is the mean value of this curvature function, i.e. its Riemann integral divided by the interval length. The *Ratio of Maximum to mean curvature*, i.e. the result of dividing the maximum curvature by the mean curvature, close to 1 indicates a silhouette approaching a circumference with radius equal to the inverse of the *Mean curvature* value. Curvature ratios diverging from 1 indicate low circularity.

2.5. Statistical Analysis

Due to lack of normal distributions of the measurements in some populations, Kruskal Wallis test was applied for mean comparisons instead of ANOVA. Analysis was done with IBM SPSS statistics v29 (SPSS 2022), and p values below 0.05 were considered significant. The coefficient of variation (CV) was calculated as the ratio of the standard deviation to the mean $\times 100$ [50].

3. Results

3.1. General morphological descriptors

The following sections present the results of size and shape measurements for species in the subfamilies Acalyphoideae, Crotonoideae and Euphorbioideae (Tables B1 to B6 in Appendix B).

3.1.1. Subfamily Acalyphoideae

Supplementary Figure S1 (see Supplementary Materials) shows images of the 14 species analyzed in this subfamily. Table B1 (Appendix B) gives a summary of their morphological measurements. Area ranged between 0.72 and 321.89 mm^2 , perimeter between 3.33 and 69.24 mm. Length and width were between 1.11 and 22.25 and 0.82 and 18.42 mm respectively. In all these cases, the minimum values were for *Acalypha virginica* Benth., and the maximum for *Plukenetia volubilis* L.

Exceptionally low values of circularity and solidity (0.39 and 0.908, respectively) were observed for *Macaranga winkleri* Pax & K.Hoffm., while for the other species these values ranged from 0.67 (*Mercurialis annua* L.) to 0.89 (*Adelia triloba* (Müll.Arg.) Hemsl), for circularity; and between 0.973 (*Chrozophora tinctoria* (L.) A.Juss.) to 0.996 (*A. triloba*) for solidity.

3.1.2. Subfamily Crotonoideae

Supplementary Figure S2 (see Supplementary materials) shows images of the 16 species analyzed in this subfamily. Table B2 gives a summary of their morphological measurements. Area ranged from 6.50 to 638.27 mm^2 , perimeter from 9.99 to 102.01 mm. Length and width were between 3.39 and 38.62, and 2.19 and 23.44 mm respectively. Maximum values for area, perimeter and length corresponded to *Elateriospermum tapos* Blume, while minimum values for all these measurements corresponded to *Croton* species. Circularity values ranged from 0.72 to 0.88, and solidity from 0.974 to 0.994.

3.1.3. Subfamily Euphorbioideae.

Seeds of this subfamily were analyzed in *Hura crepitans* L. (tribe Hureae) and in several species of the genus *Euphorbia* (tribe Euphorbieae), subgen. *Athymalus* (Figure S3; Table B3), *Chamaesyce* (Figures S4 and S5; Table B4), *Esula* (Figures S6, S7 and S8; Table B5), and *Euphorbia* (Figures S9 and S10, Table B6).

Table 1 shows the mean values and coefficients of variation for all the measurements in the three subfamilies. Differences were observed in area, perimeter, length and width between the Euphorbioideae (smaller seeds) and the other two subfamilies. Circularity and solidity were smaller in the Euphorbioideae than in the Crotonoideae, aspect ratio

was lower in the Acalyphoideae than in the Euphorbioideae and solidity was higher in the Crotonoideae than in the Euphorbioideae. Size measurements (A, P, L, W) had higher coefficients of variation than the shape measurements, in particular solidity, for all subfamilies.

Table 1. Means and coefficients of variation (between brackets) of size and shape measurements in three subfamilies of Euphorbiaceae. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity. Different superscript letters in the same column indicate significant differences (p<0.05) in the Kruskal Wallis test.

Subfamily	N	A	P	L	W	C	AR	R	S
Acalyphoideae	15	45.77 ^b (184.2)	20.79 ^b (84.0)	6.59 ^b (89.9)	5.09 ^b (89.6)	0.74 ^{ab} (19.9)	1.29 ^a (14.8)	0.79 ^b (14.7)	0.978 ^{ab} (2.1)
Crotonoideae	18	141.47 ^b (152.3)	35.86 ^b (88.2)	12.16 ^b (90.0)	8.52 ^b (92.8)	0.78 ^b (7.7)	1.43 ^{ab} (21.3)	0.73 ^{ab} (20.4)	0.987 ^b (0.7)
Euphorbioideae	198	10.98 ^a (510.0)	9.63 ^a (93.1)	3.09 ^a (90.5)	2.26 ^a (112.8)	0.74 ^a (14.0)	1.44 ^b (20.5)	0.72 ^a (18.4)	0.977 ^a (1.6)

Table 2 shows the comparison of morphological measurements between the four subgenera of Euphorbia. Differences between subgenera were found for all measurements, with size measurements smaller in *Chamaesyce*, higher in *Athymalus*, and intermediate in *Esula* and *Euphorbia*. Circularity and solidity values were higher in subgen. *Euphorbia*.

Table 2. Means and coefficients of variation (between brackets) of size and shape measurements in the subgenera of Euphorbia. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity. Different superscript letters in the same column indicate significant differences (p<0.05) in the Kruskal Wallis test.

Subgen.	N	A	P	L	W	C	AR	R	S
<i>Athymalus</i>	23	9.86 ^c (151.1)	11.51 ^c (47.8)	3.55 ^c (48.4)	2.85 ^c (53.9)	0.75 ^a (10.3)	1.26 ^a (11.5)	0.80 ^c (11.3)	0.975 ^a (1.7)
<i>Chamaesyce</i>	48	4.04 ^a (109.8)	7.27 ^a (60.2)	2.33 ^a (61.0)	1.64 ^a (60.0)	0.73 ^a (12.2)	1.45 ^b (15.2)	0.71 ^b (14.9)	0.976 ^a (1.4)
<i>Esula</i>	80	4.85 ^b (56.9)	8.95 ^b (32.0)	2.97 ^{bc} (31.1)	1.89 ^b (34.0)	0.72 ^a (15.6)	1.57 ^c (19.2)	0.66 ^a (18.4)	0.974 ^a (1.9)
<i>Euphorbia</i>	44	5.67 ^b (110.4)	8.80 ^b (41.0)	2.75 ^b (39.2)	2.25 ^b (47.4)	0.79 ^b (12.5)	1.28 ^a (22.4)	0.81 ^c (16.4)	0.984 ^b (1.3)

3.2. Curvature analysis in seed silhouettes

The following sections present an analysis of curvature in species of the subfamilies Acalyphoideae (section 3.2.1), Crotonoideae (section 3.2.2) and Euphorbioideae (3.2.3).

3.2.1. Curvature analysis in species of the Acalyphoideae

Curvature was analyzed in the seed silhouettes of *Acalypha virginica* L., *Adelia triloba* (Müll.Arg.) Hemsl., *Ricinus communis* L., *Mercurialis annua* L., *Chrozophora tinctoria* L. and *Plukenetia volubilis* L. Table 3 shows the summary results of the maximum and mean curvature values, and the corresponding quotient in the seeds of these species. *Acalypha virginica* shows a maximum point of curvature corresponding to the apical side of the seed (Figure 1), in contrast with the almost constant value around 0.5 observed along the

silhouette in the seed of *A. triloba*, with some variation in the basal part (Figure 2). A curvature of 0.5 mm⁻¹ corresponds to a circumference of radius equal to 2 mm.

Table 3. Mean values of Maximum, Mean, and Maximum to Mean curvature ratios in representative species of the Acalyphoideae, Crotonoideae and Hureae. Between parentheses, number of seeds analyzed.

Species	Maximum curvature (mm ⁻¹)	Mean curvature (mm ⁻¹)	Max. to Mean curvature ratio
<i>Acalypha virginica</i> L. (1)	26.3	2.5	10.5
<i>Adelia triloba</i> (Müll.Arg.) Hemsl. (1)	0.9	0.5	1.8
<i>Ricinus communis</i> L. (1)	0.9	0.2	4.5
<i>Mercurialis annua</i> L. (4)	9.2	1.5	4.8
<i>Crozophora tintoria</i> (L.) A. Juss. (3)	6.9	0.6	11.5
<i>Plukenetia volubilis</i> L. (2)	0.9	0.09	10
<i>Jatropha curcas</i> L. (1)	0.6	0.2	3
<i>Hura crepitans</i> L (3)	0.4	0.07	5.7

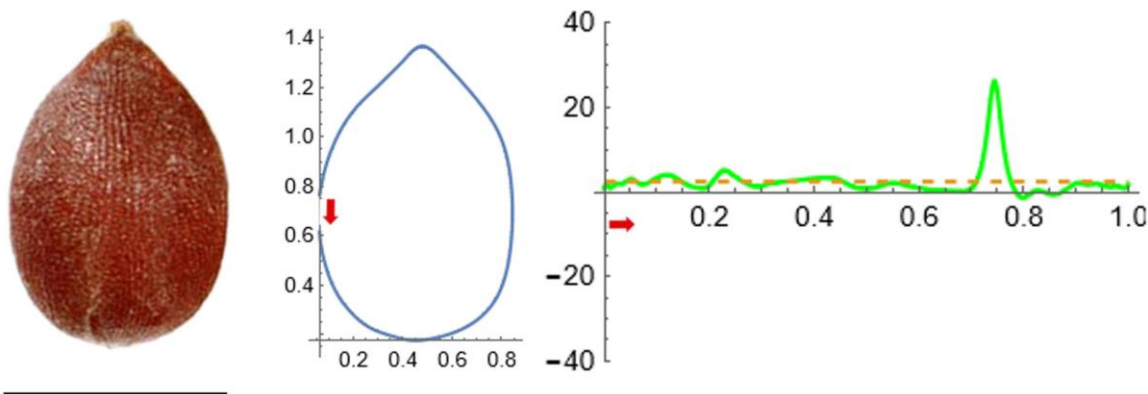


Figure 1. Curvature analysis in *Acalypha virginica* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

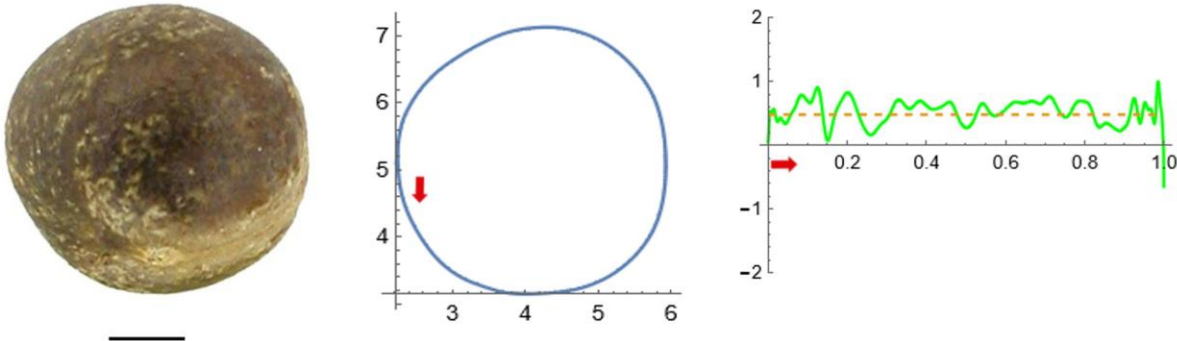


Figure 2. Curvature analysis in *Adelia triloba* (Müll.Arg.) Hemsl. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

R. communis shows two maximum curvature values in the apical region of the seed. In this case, the caruncle gives a prominent zone resulting in a double peak of maximum curvature (see Figure 3).

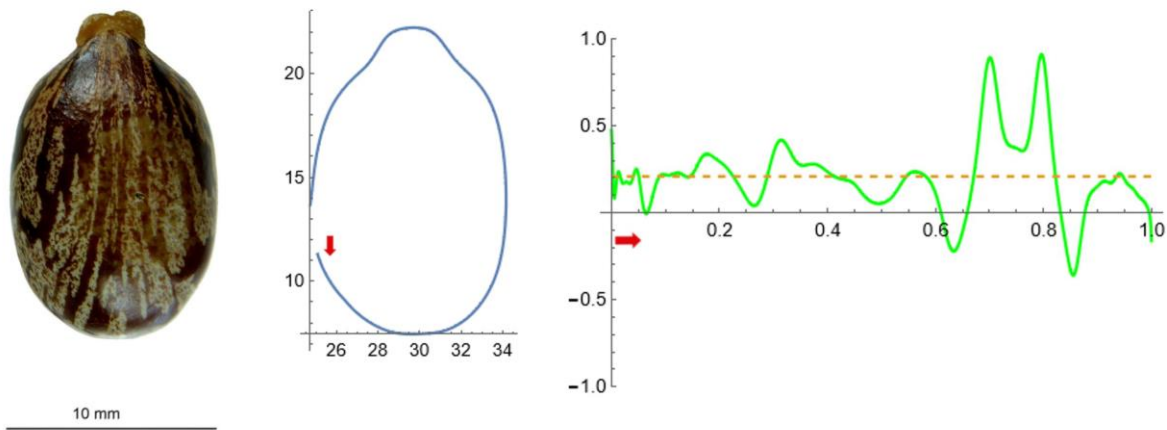


Figure 3. Curvature analysis in *Ricinus communis* L. Left: Seed image (bar represents 10 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

The seeds of *M. annua*, *C. tintoria* and *P. volubilis* showed one peak of high curvature corresponding to the apical region and three or more peaks in their basal regions. The curvature values in these regions are shown in Table 4, and the corresponding images in Figures 4, 5 and 6. Whereas in *M. annua* (Figure 4) curvature values were higher in the apical pole, in both *C. tintoria* (Figure 5) and *P. volubilis* (Figure 6), the maximum curvature values were observed in the basal pole, in a lateral peak in *Crozophora*, and corresponding to the central peak in *Plukenetia*. ANOVA revealed significant differences in the curvature values in the apical pole between *M. annua* and the other two species, and between *M. annua* and *C. tintoria* in the central peak of the basal pole.

Table 4. Curvature values in the apical pole and three basal peaks in seed images of *Mercurialis annua*, *Chrozophora tintoria*, and *Plukenetia volubilis*. Between parentheses, number of seeds analyzed.

Species	Apical pole	Basal pole (left, central and right peaks)
<i>Mercurialis annua</i> L. (4)	9.8	3.8; 5.2; 4.2
<i>Crozophora tintoria</i> (L.) A. Juss. (3)	1.6	5.0; 2.7; 3.2
<i>Plukenetia volubilis</i> L. (2)	3.8	3.9; 8.2; 3.8

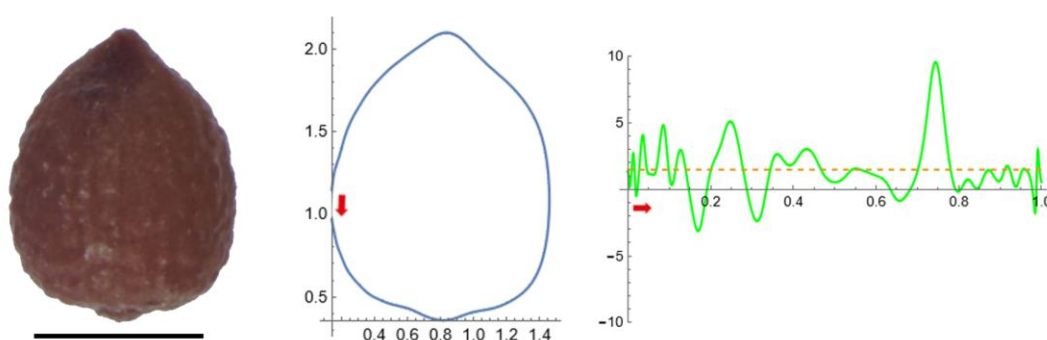


Figure 4. Curvature analysis in *Mercurialis annua* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

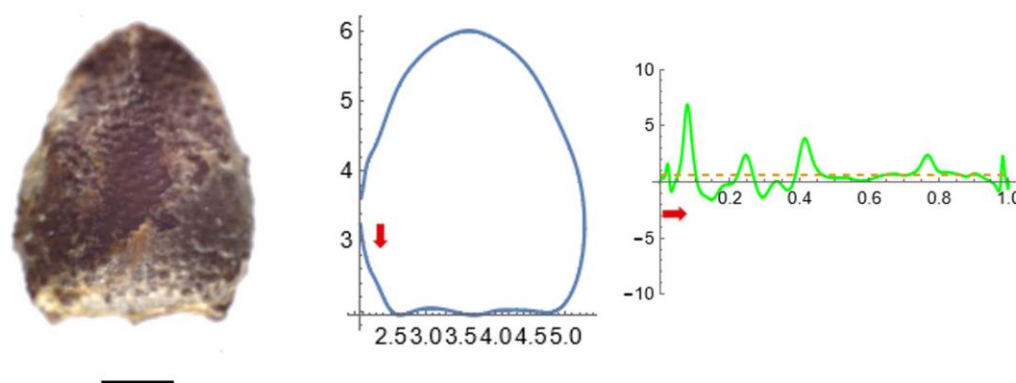


Figure 5. Curvature analysis in *Crozophora tintoria* (L.) A. Juss. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

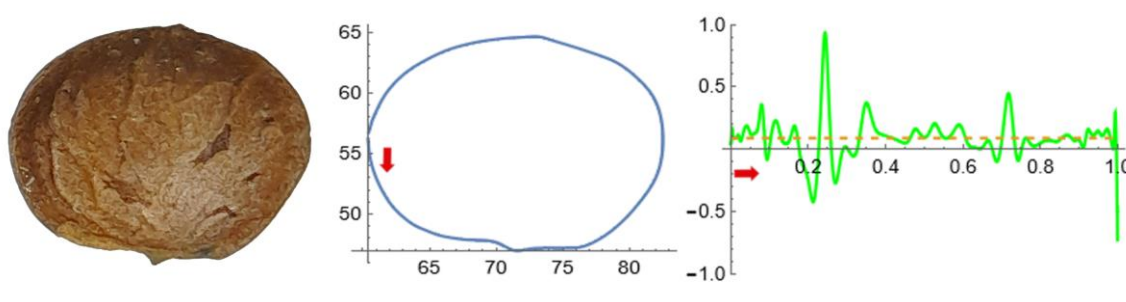


Figure 6. Curvature analysis in *Plukenetia volubilis* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

3.2.2. Curvature analysis in *Jatropha curcas* (Subfam. Crotonoideae, tribe Jatropheae)

Figure 7 presents the analysis of curvature in a representative seed of *Jatropha curcas* (Subfam. Crotonoideae, tribe Jatropheae), showing a point of maximum curvature corresponding to the apical region and regions of high curvature in their basal regions (Figure 7).

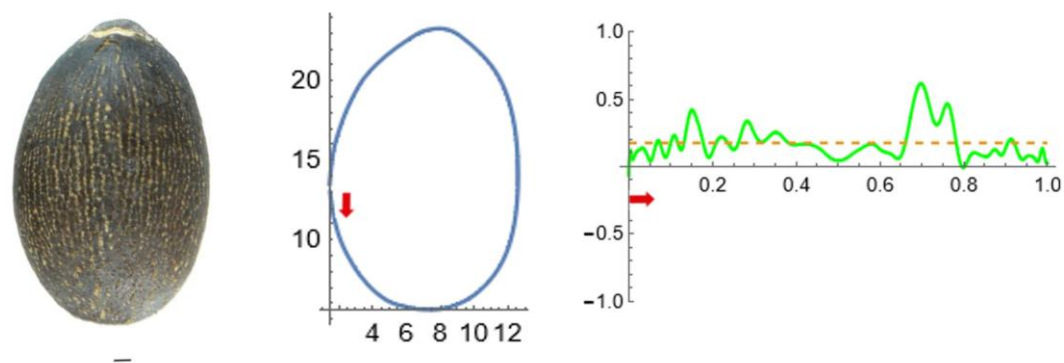


Figure 7. Curvature analysis in *Jatropha curcas* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

3.2.3. Curvature analysis in the Euphorbioideae

Curvature analysis was applied to seed images of *Hura crepitans* L. (tribe Hureae), and to species of *Euphorbia* belonging to subgen. *Chamaesyce*, *Esula*, and *Euphorbia* (tribe Euphorbieae). Table 5 shows the results of maximum and mean curvature values in the seeds of these species.

Table 5. Maximum, mean, and Maximum to Mean curvature ratio in representative species of the Euphorbioideae. Between parentheses, number of seeds analyzed.

Species	Maximum curvature	Mean curvature	Max. to Mean curvature ratio*
<i>Hura crepitans</i> (3)	0.35	0.07	5
<i>E. gentilis</i> (1)	3.6	0.6	6.0
<i>E. hirta</i> L. (1)	22.3	2.8	8.0
<i>E. rhombifolia</i> Boiss. (1)	10.0	1.5	6.7
<i>E. helioscopica</i> L. (3)	3.3	0.8	4.1
<i>E. pithyusa</i> L. (1)	6.8	0.9	7.6
<i>E. serrata</i> L. (3)	10	0.8	12.5
<i>E. gossypina</i> Pax (1)	5.7	0.9	6.3
<i>E. lamarckii</i> Sweet (3)	6.1	0.8	7.6
<i>E. peplus</i> L. (6)	5.5	1.9	2.9
<i>E. paralias</i> L. (3)	3.8	0.8	4.8
<i>E. segetalis</i> L. (1)	3.8	1.2	3.2
<i>E. amygdaloides</i> (2)	7.4	1.2	6.2

A unique peak of maximum curvature corresponds to the micropile region in *Hura crepitans* L. (Figure 8), and the mean curvature was 0.07, the lowest value of this subfamily, corresponding to a circumference of radius =14.3 mm.

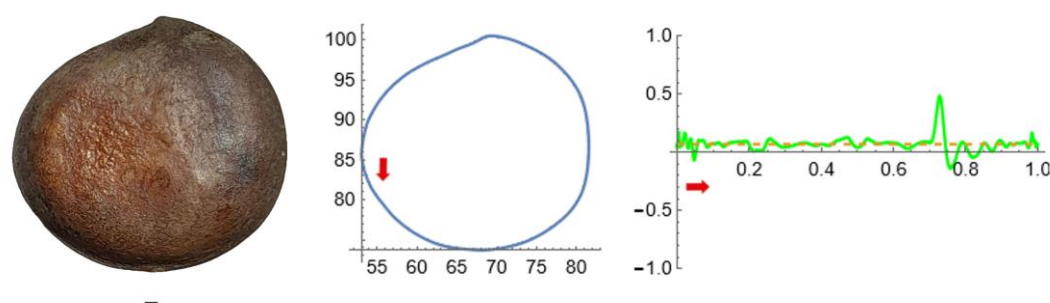


Figure 8. Curvature analysis in *Hura crepitans* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

In the *Euphorbia* species, values of maximum curvature ranged from 3.3 to 22.3, while mean curvatures ranged from 0.6 to 2.8. The lowest value of mean curvature corresponded to *E. gentilis* N.E.Br. (Figure 9), and the highest to *E. hirta* (Figure 10), both in subgen. *Chamaesyce*. The maximum and mean curvature values in *E. rhombifolia*, also in this subgenus, were intermediate between these two species. The seeds of these three species showed three points of high curvature corresponding to the vertices of their triangular shape.

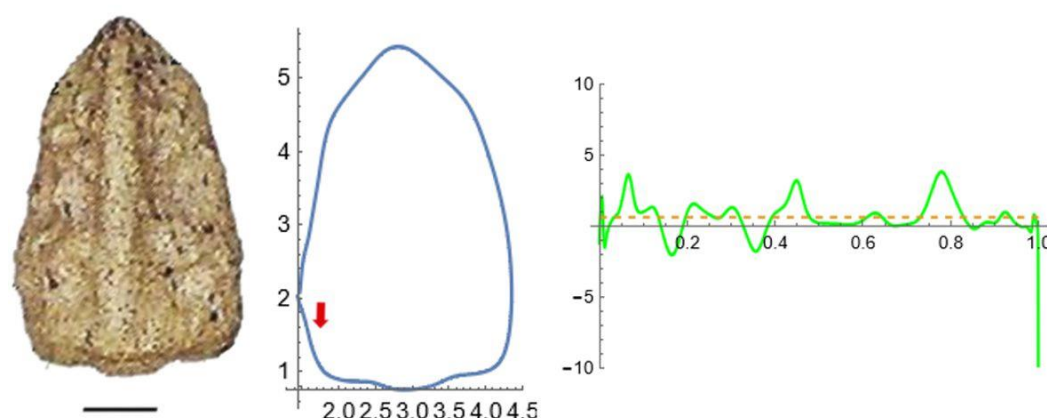


Figure 9. Curvature analysis in *Euphorbia gentilis* N. E. Br. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

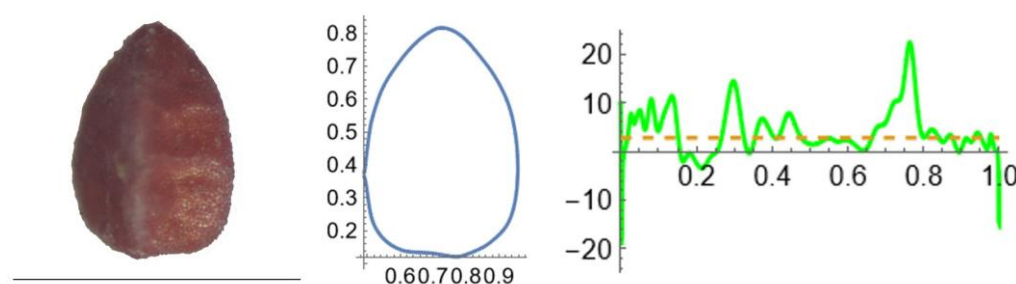


Figure 10. Curvature analysis in *Euphorbia hirta* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

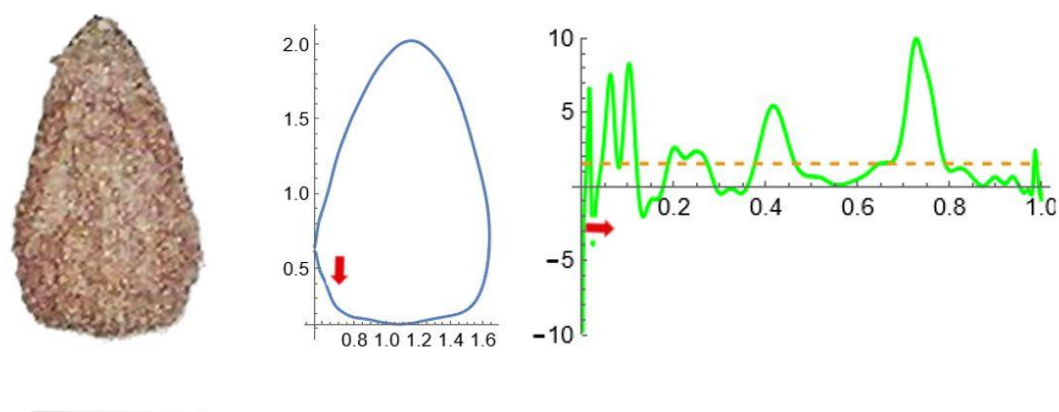


Figure 11. Curvature analysis in *Euphorbia rhombifolia* Boiss. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

Figures 12 to 21 show the results of curvature analysis in species of *Euphorbia* belonging to subgen. *Esula* (Figures 12 to 20), and *Euphorbia* (Figure 21). The silhouettes of *E. pithyusa* and *E. serrata* shared a squared shape (stadium), with three or more points of curvature at the basis and one in their upper side (Figures 12 and 13).

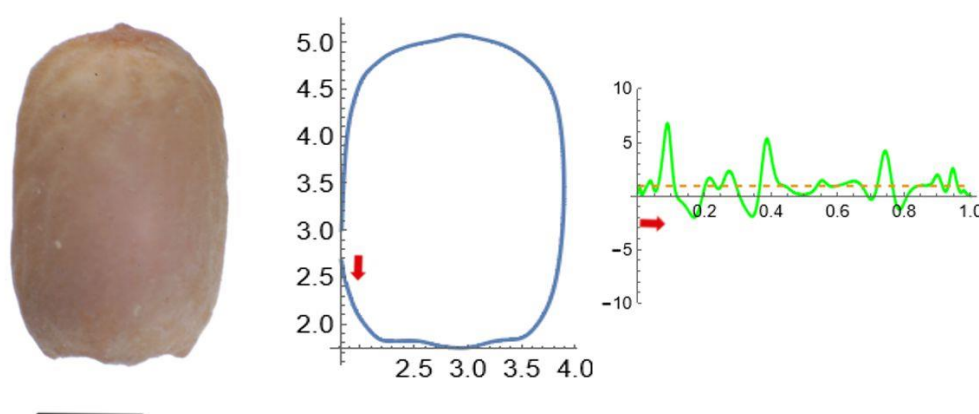


Figure 12. Curvature analysis in *Euphorbia pithyusa* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

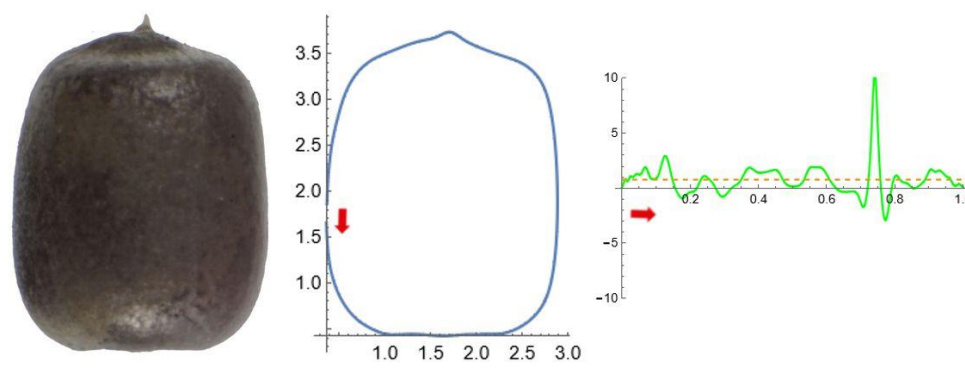


Figure 13. Curvature analysis in *Euphorbia serrata* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

Approximately triangular, or triangular-squared shapes with single points of high curvature in the apex and three or more points of high curvature at the basis were also observed in other species of *Euphorbia* as *E. gossypina* (Figure 14), *E. lamarckii* (Figure 15), *E. peplus* (Figure 16), *E. paralias* (Figure 17), *E. segetalis* (Figure 18), and *E. amygdaloides* (Figure 19).

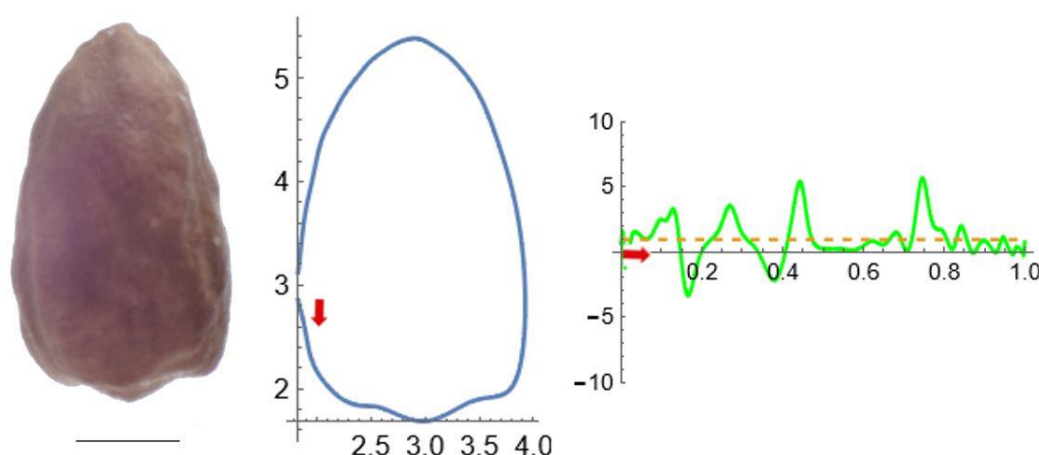


Figure 14. Curvature analysis in *Euphorbia gossypina* Pax. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

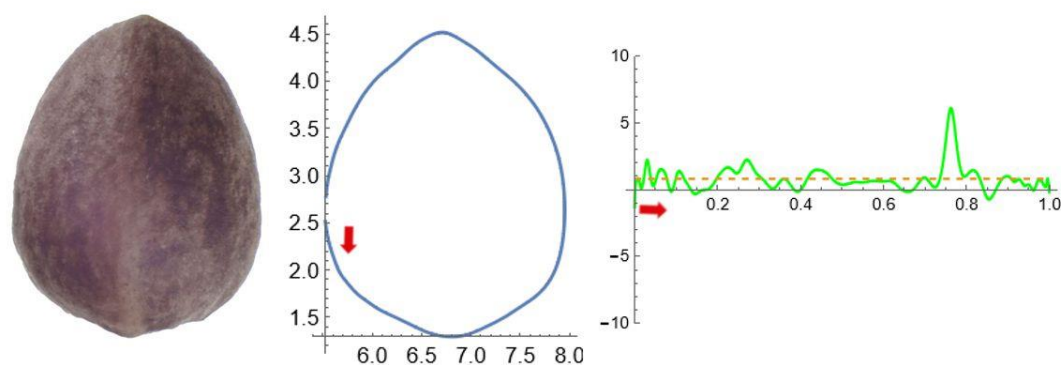


Figure 15. Curvature analysis in *Euphorbia lamarckii* Sweet. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

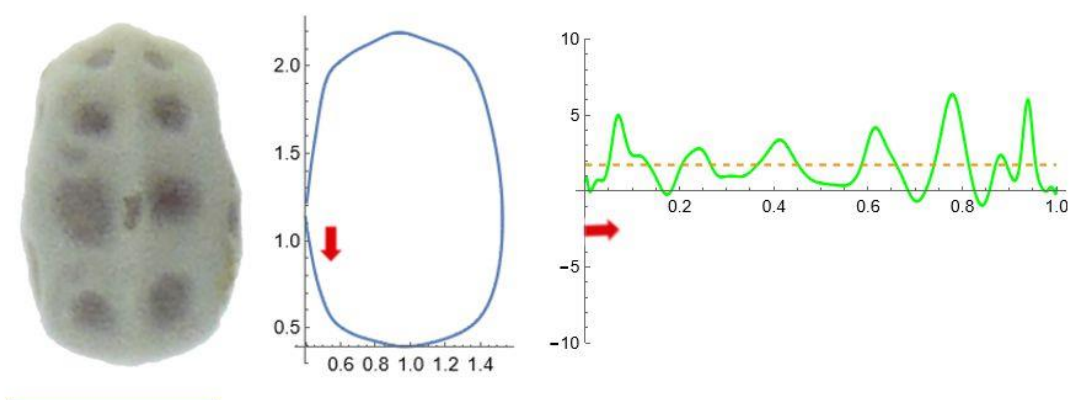


Figure 16. Curvature analysis in *Euphorbia peplus* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

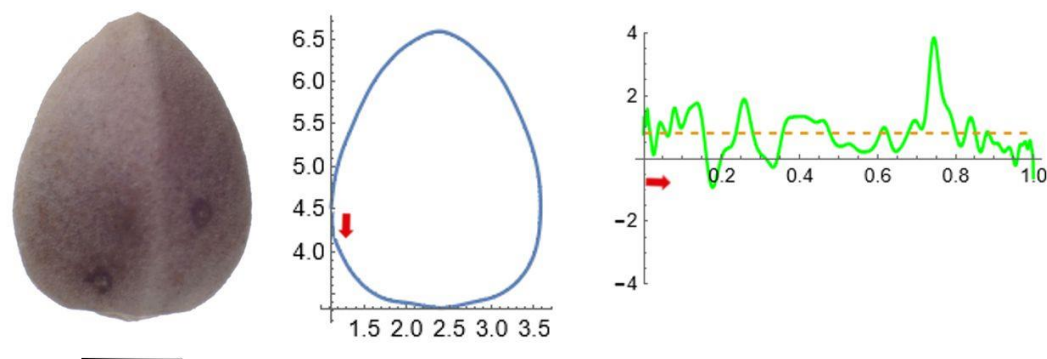


Figure 17. Curvature analysis in *Euphorbia paralias* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

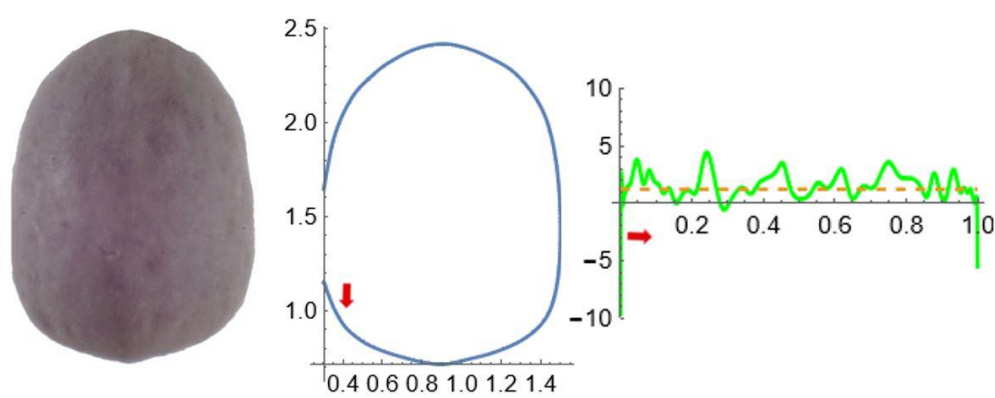


Figure 18. Curvature analysis in *Euphorbia segetalis* L. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

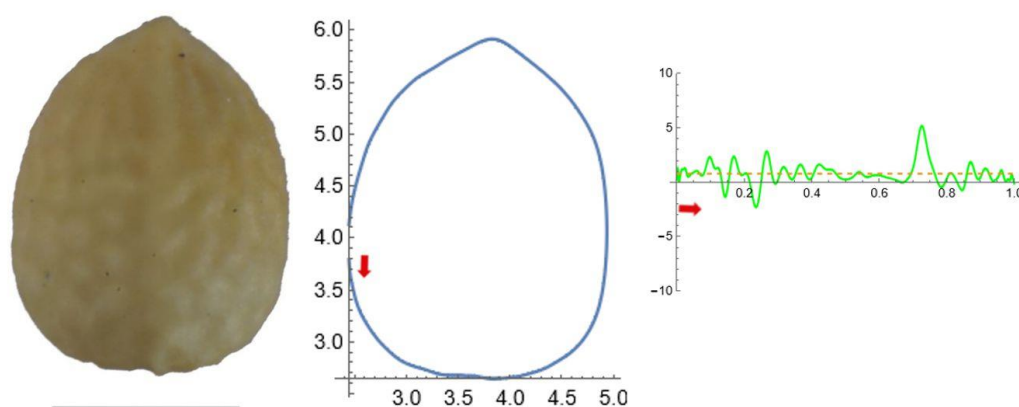


Figure 19. Curvature analysis in *Euphorbia amygdaloides* subsp. *amygdaloides*. Left: Seed image (bar represents 1 mm). Center: Bézier curve representing seed silhouette. Right: Variation of curvature along the Bézier curve. Dashed line (orange) indicates Mean curvature.

4. Discussion

The seeds of the Euphorbiaceae have an interesting variation in seed shape that is better understood with the basis of seed development in the schizocarp, a dry, dehiscent fruit that splits upon maturation into multiple single-seeded segments called mericarps [51,52,53,54]. In *Euphorbia*, before being released, these segments remain attached to a central column, known as the carpophore. In most species of the family, mature seeds have two distinct asymmetries. Firstly, an apical-basal asymmetry, with a wider basal part corresponding to the chalazal end and a narrower apical part close to the micropile. Secondly, the seed develops a larger dorsal part corresponding to the outside of the fruit, while the ventral part, smaller, remains close to the carpophore [54]. Following this general scheme, and oriented in their dorsal side, the seed images of most species resemble geometric figures with bilateral symmetry. Exceptions to this rule are the seeds of *Plukenetia* in the Acalyphoideae and those of *H. crepitans* in the Hureae, both of which lack bilateral symmetry. In some species there is little difference between the apical and basal parts of the seed, or between the dorsal and ventral parts, and the seed is almost spherical, corresponding to circular images such as those observed in *A. triloba*, *C. castaneifolium* (tribe Adelieae, fam. Acalyphoideae), and species of *Tragia* or *Dalechampia* (tribe Plukenetieae, fam. Acalyphoideae). Maximum to mean curvature ratios close to one were observed in these seeds,

corresponding to curvature values of a rounded silhouette. However, in the dorsal images of most species of the Euphorbiaceae, seed elongation results in figures with bilateral symmetry, that resemble polyhedra. In consequence, well oriented two-dimensional seed images show the shapes of figures resembling modified triangles, squares, pentagons or hexagons. In some cases, surface protrusions result in reduced circularity [49].

Solidity is the most stable (less variable) of the seed measurements in the Euphorbiaceae. This fact has been shown in other plant families [42,43,55,56]. In general, Euphorbiaceae seeds have high solidity values, higher than those reported for *Silene* and *Vitis* species, and close to those of Cucurbitaceae species. This means that seed images resemble convex geometric figures with little (or no) surface protuberances. Interestingly, in the genus *Euphorbia*, solidity is higher in subgen. *Euphorbia* than in the other three subgenera. Differences between subfamilies were found in other morphological measurements. Thus, area was smaller in the Euphorbioideae, and higher in the Crotonoideae; circularity was higher in the Crotonoideae than in the Euphorbioideae, and roundness higher in the seeds of the Acalyphoideae than in the Euphorbioideae.

Mature seeds of most species in the Euphorbiaceae have a polarity with a marked difference between an apical pole corresponding to the micropile and a basal pole, corresponding to the chalaza. In terms of curvature this basal-polar asymmetry corresponds to higher values in the apical pole. In most examined seeds, major changes in curvature are concentrated around both the apical and basal poles, with the lateral regions of the seed silhouette being smoother. Among the species studied in the families Acalyphoideae and Crotonoideae, high polarity with single or double peaks of maximum curvature in the apical pole, and lower and almost constant curvature values in the basal pole have been observed in *Acalypha virginica*, and *Ricinus communis* in the Acalypheae, *Jatropha curcas* in the Jatrophaeae. More detailed analyses may reveal whether curvature peaks in the basal pole of seeds in these species are associated with specific varieties or growth in different conditions.

In the Euphorbiaceae the seed silhouettes take sinuous forms similar to those described for some species of the Cucurbitaceae (*Momordica* sp., [42]), and the Vitaceae [57]. A tetragonal pattern with a curvature peak in the apical pole and three or more curvature peaks in the basal pole occurs in the seeds of *Mercurialis annua*, *Chrozophora tinctoria*, and *Plukenetia volubilis*, as well as in many species of *Euphorbia* analyzed, including species in the four subgen. *Athymalus*, *Chamaesyce*, *Esula* and *Euphorbia*. The curvature values in the poles as well as in the lateral protuberances may differ between species. For example, among the Acalyphoideae, curvature values in the apical pole are higher than in the basal pole for *Mercurialis annua*, but the inverse occurs in *Chrozophora tinctoria* and *Plukenetia volubilis*. Thus, variation in curvature along the seed surface reveals aspects of seed geometry that may be associated with genetic or developmental peculiarities.

In relation to taxonomy, there are taxonomic groups with defined seed morphological patterns as the pyramidal shape in the species of Sect. *Anisophyllum*, Subsect. *Hypericifoliae* in *Euphorbia* subgen. *Chamaesyce* [35] or a more rounded-oval pattern in subgen. *Esula* [37].

Genomic data are published for species in the Euphorbiaceae such as *Hevea brasiliensis*, *Manihot esculenta*, *Jatropha curcas*, and *Ricinus communis* [58,59,60,61], and recently *Euphorbia peplus* has been proposed as a model system for the study of the production of plant latex [61]. Given the peculiarities of seed morphology in this genus, the system may offer new possibilities to study the interaction between seed geometry and developmental conditions and implement the role of the former in taxonomy.

5. Conclusions

Seed images of the Euphorbiaceae show an apical basal polarity and bilateral symmetry. The seeds of *Plukenetia* in the Acalyphoideae and those of *Hura crepitans* in the *Hurea* are exceptions to this rule lacking bilateral symmetry. Many species of this family

show one or two curvature peaks in the apical pole and three or more curvature peaks in the basal pole allowing the application of curvature measurements in taxonomy based on statistical differences between peaks. Curvature measurements may contribute to the application of seed morphology in the taxonomy of this family.

Supplementary Materials: Supplementary figures (Figures S1 to S11) with seed images of used in the general morphological measurements (Tables 1,2 and B1 to B6) and Mathematica (.nb) files for the curvature analysis in Figures 1 to 19 can be downloaded at: <https://zenodo.org/urls/13306745>.

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Data Availability Statement: We encourage all authors of articles published in MDPI journals to share their research data. In this section, please provide details regarding where data supporting reported results can be found, including links to publicly archived datasets analyzed or generated during the study. Where no new data were created, or where data is unavailable due to privacy or ethical restrictions, a statement is still required. Suggested Data Availability Statements are available in section “MDPI Research Data Policies” at <https://www.mdpi.com/ethics>.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Seed images used in the present work with indication of their sources.

Taxa and Species	Source of the images [reference]
Subfam. Acalyphoideae	
Tribe Acalypheae, subtribe Acalyphinae	
<i>Acalypha virginica</i> Benth.	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
Tribe Acalypheae, subtribe Adrianinae	
<i>Adriana quadripartita</i> (Labill.) Müll.Arg.	South Australian seed conservation Centre https://spapps.environment.sa.gov.au/SeedsOfSA/speciesinformation.html?rid=277
<i>Adriana tomentosa</i> (Thunb.) Gaudich.	https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:338254-1
Tribe Acalypheae, subtribe Cleidiinae	
<i>Cleidion castaneifolium</i> Müll.Arg.	https://malpighiales.myspecies.info/taxonomy/term/113/media
Tribe Acalypheae, subtribe Macaranginae	
<i>Macaranga bancana</i> (Miq.) Müll.Arg.	Tiansawat et al. 2014 [63]
<i>Macaranga gigantea</i> (Rchb.f. & Zoll.) Müll.Arg.	Tiansawat et al. 2014 [63]
<i>Macaranga hypoleuca</i> (Rchb.f. & Zoll.) Müll.Arg.	Tiansawat et al. 2014 [63]

<i>Macaranga winkleri</i> Pax & K.Hoffm.	Tiansawat et al. 2014 [63]
Tribe Acalypheae, subtribe Mercurialinae	
<i>Mercurialis annua</i> L.	Herbarium IRNASA-CSIC
Tribe Acalypheae, subtribe Ricininae	
<i>Ricinus communis</i> L.	Herbarium IRNASA-CSIC
Tribe Adeliaeae	
<i>Adelia triloba</i> (Müll.Arg.) Hemsl.	Steven Paton, Smithsonian Institute: https://biogeodb.stri.si.edu/bioinformatics/dfm/metas/view/7230
Tribe Chrozophoreae, subtribe Crozophorinae	
<i>Chrozophora tinctoria</i> (L.) A.Juss.	Herbarium IRNASA-CSIC
Tribe Chrozophoreae, subtribe Ditaxinae	
<i>Caperonia palustris</i> (L.) A.St.-Hil.	USDA: https://plants.usda.gov/home/plantProfile?symbol=CAPA11 [64]
Tribe Plukenetieae	
<i>Plukenetia volubilis</i> L.	Acquired in local market in the city of Puyo (Ecuador).
Subfam. Crotonoideae	
Tribe Adenoclineae	
<i>Tetrorchidium andinum</i> Müll. Arg.	Steven Paton, Smithsonian Institute: https://biogeodb.stri.si.edu/bioinformatics/dfm/metas/view/11451
Tribe Aleuritidae	
<i>Aleurites moluccanus</i> (L.) Willd.	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
<i>Vernicia fordii</i> (Hemsl.) Airy-Shaw	https://plants.usda.gov/home/plantProfile?symbol=VEFO [64]
Tribe Codiaeae	
<i>Codiaeum variegatum</i> (L.) Rumph. ex A.Juss.	From disturbed environments in Ecuador and returned to nature after being photographed.
Tribe Crotoneae	
<i>Croton capitatus</i> Michx.	https://plants.usda.gov/home/plantProfile?symbol=CRCA6 [64]
<i>Croton glandulosus</i> L.	https://plants.usda.gov/home/plantProfile?symbol=CRGL2 [64]
<i>Croton gossypifolius</i> Vahl.	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
<i>Croton lechlerii</i> Müll.Arg.	From disturbed environments in Ecuador and returned to nature after being photographed.
<i>Croton monanthogynus</i> Michx	https://plants.usda.gov/home/plantProfile?symbol=CRMO6 [64]
<i>Croton setiger</i> Hook.	https://plants.usda.gov/home/plantProfile?symbol=CRSE11 [64]
<i>Croton texensis</i> (Klotzsch) Müll.Arg.	https://plants.usda.gov/home/plantProfile?symbol=CRTE4 [64]
Tribe Elateriospermeae	
<i>Elateriospermum tapos</i> Blume	https://www.nparks.gov.sg/florafaunaweb/flora/2/8/2875
Tribe Gelonieae	
<i>Suregada lanceolata</i> (Willd.) Kuntze	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
Tribe Jatropeae	
<i>Jatropha acanthophylla</i> Loefgr.	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
<i>Jatropha curcas</i> L.	

Tribe Manihoteae	
<i>Cnidoscolus texanus</i> (Müll.Arg.) Small	https://plants.usda.gov/home/plantProfile?symbol=CRSE11 [64]
<i>Manihot esculenta</i> Crantz	https://www.delta-intkey.com/famfs/www/euphor.htm [62]
Tribe Micrandreae	
<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	https://www.feedipedia.org/node/39 [65]
Subfam. Euphorbioideae	
Tribe Hureae	
<i>Hura crepitans</i> L.	Acquired in local market in the city of Puyo (Ecuador).
<i>Hura polyandra</i> Baill.	[62]
Tribe Hippomaneae	
<i>Sebastiania klotzschiana</i> (Müll.Arg.) Müll.Arg.	[62]
Tribe Euphorbieae	
Gen. <i>Euphorbia</i> L.	
Subgen. <i>Athymalus</i>	
Sect. <i>Antso</i>	
<i>E. antso</i> Denis	[34]
Sect. <i>Pseudacalypha</i>	
<i>E. hadramautica</i> Baker	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Sect. <i>Crotonoides</i> Bruyns & P.E. Berry	
<i>E. benthamii</i> Hiern	[34]
Sect. <i>Balsamis</i> Webb & Berthelot	
<i>E. adenensis</i> Deflers syn. <i>Euphorbia balsamifera</i> subsp. <i>adenensis</i> (Deflers) P.R.O.Bally	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. larica</i> Boiss.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. neospinescens</i> Bruyns	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Sect. <i>Anthacanthae</i>	
Subsect. <i>Florispiniae</i>	
<i>E. bubalina</i> Boiss.	[18]
<i>E. clandestina</i> Jacq.	[18]
<i>E. cumulata</i> R.A. Dyer	[18]
<i>E. meloformis</i> Aiton	https://www.euphorbia-international.org/euphorbias/cultivation/about_euph_cultivation_seed.htm
Subsect. <i>Pseudeuphorbium</i> Pax	
<i>E. dregeana</i> E.Mey. ex Boiss.	[34]
Subsect. <i>Medusea</i>	
<i>E. albipollinifera</i> L.C.Leach	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. arida</i> N.E. Br.	[18]
<i>E. braunsii</i> N.E.Br.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]

<i>E. caput-medusae</i> L.	[18]
<i>E. colliculina</i> A.C. White, R.A. Dyer & B. Sloane	[18]
<i>E. davyi</i> N.E. Br.	[18]
<i>E. decepta</i> N.E. Br.	[18]
<i>E. duseimata</i> R.A. Dyer	[18]
<i>E. esculenta</i> Marloth	[18]
<i>E. filiflora</i> Marloth	[18]
<i>E. multiceps</i> A. Berger	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. pentstemon</i> Marloth ex A.C. White, R.A. Dyer & B. Sloane	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Subgen. <i>Chamaesyce</i> Raf.	
Sect. <i>Espinosa</i> Pax & K. Hoffm.	
<i>E. espinosa</i> Pax	<i>Euphorbia</i> Seed Atlas-Part 1 [35,66]
<i>E. guerichiana</i> Pax	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Sect. <i>Articulofrutosae</i> Bruyns	
<i>Euphorbia burmanni</i> E. Mey. ex Boiss.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. ephedroides</i> E. Mey. ex Boiss.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. exilis</i> L.C. Leach	<i>Euphorbia</i> Seed Atlas-Parts 1,6 [66,69]
<i>E. gentilis</i> N.E. Br.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. racemosa</i> E. Mey. ex Boiss. (41)	<i>Euphorbia</i> Seed Atlas-Part 6 [69] (Syn <i>E. spartaria</i>)
<i>E. rhombifolia</i> Boiss.	<i>Euphorbia</i> Seed Atlas-Parts 1, 6 (syn. <i>E. mundii</i> en 12) [5,6,35]
<i>E. tenax</i> Burch.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Sect. <i>Cheirolepidium</i> Boiss.	
<i>E. cheirolepis</i> Fisch. & C.A. Mey. ex Karelin	[35]
<i>E. petiolata</i> Banks & Sol.	[35]
Sect. <i>Frondosae</i> Bruyns	
<i>E. transvaalensis</i> Schltr.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
Sect. <i>Tenellae</i> Pax & K. Hoffm.	
<i>E. phylloclada</i> Boiss.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
Sect. <i>Gueinzia</i> Riina	
<i>E. gueinzii</i> Boiss.	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
Sect. <i>Crossadenia</i>	
<i>E. goyazensis</i> Boiss.	[35]
<i>E. sarcodes</i> Boiss.	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
<i>E. sessilifolia</i> Klotzsch ex Boiss.	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
Sect. <i>Anisophyllum</i> Roep.	
Subsect. <i>Hypericifoliae</i> Boiss.	
<i>E. adenoptera</i> Bertol.	[70]
<i>E. bahiensis</i> (Klotzsch & Garcke) Boiss.	[70]

<i>E. chamaesyce</i> L.	[75]
<i>E. foliolosa</i> Boiss.	[70]
<i>E. geyeri</i> Engelm. & A.Gray	https://www.minnesotawildflowers.info/flower/geyers-spurge#lboxg-14
<i>E. glyptosperma</i> Engelm.	https://www.minnesotawildflowers.info/flower/geyers-spurge#lboxg-14
<i>E. hirta</i> L.	From disturbed environments in Ecuador and returned to nature after being photographed.
<i>E. humifusa</i> Willd.	[76]
<i>E. hyssopifolia</i> L.	From disturbed environments in Ecuador and returned to nature after being photographed.
<i>E. indica</i> Lam.	[76]
<i>E. maculata</i> L.	https://seedidguide.idseed.org/?s=Euphorbia&et_pb_searchform_submit=et_search_process&et_pb_include_posts=yes&et_pb_include_pages=yes https://www.minnesotawildflowers.info/flower/geyers-spurge#lboxg-14 https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-mac.html
<i>E. nutans</i> Lag.	https://plants.usda.gov/home/plantProfile?symbol=CHNU9 [64]
<i>E. ocellata</i> Durand & Hilg.	Photo by D. Walters & C. Southwick [71]
<i>E. ophthalmica</i> Pers.	[70]
<i>E. polycarpa</i> Benth.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-pol.html
<i>E. potentilloides</i> Boiss.	[70]
<i>E. prostrata</i> Aiton	[70]
<i>E. serpens</i> Kunth	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-ser.html [71]
<i>E. setosa</i> (Boiss.) Müll.Arg.	[70]
<i>E. thymifolia</i> L.	From disturbed environments in Ecuador and returned to nature after being photographed..
Sect. <i>Poinsettia</i> (Graham) Baill.	
Subsect. <i>Stormieae</i> Croizat	
<i>E. heterophylla</i> L.	[70]
<i>E. zonosperma</i> Müll.Arg.	[70]
Sect. <i>Alectorroctonum</i> (Schltdl.) Baill.	
<i>E. adiantoides</i> Lam.	From disturbed environments in Ecuador and returned to nature after being photographed.
<i>E. californica</i> Benth.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. cotinifolia</i> L.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. graminea</i> Jacq.	From disturbed environments in Ecuador and returned to nature after being photographed.
<i>E. hexagona</i> Nutt. ex Spreng.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. insulana</i> Vell.	[70]
<i>E. marginata</i> Pursh	https://plants.usda.gov/home/plantProfile?symbol=EUMA8 [64]

<i>E. mauritanica</i> L.	<i>Euphorbia</i> Seed Atlas Part 1 [66]
<i>E. sciadophila</i> Boiss.	[70]
Subgen. <i>Esula</i> Pers.	
Sect. <i>Lagascae</i> Lázaro	
<i>E. lagascae</i> Spreng.	<i>Euphorbia</i> Seed Atlas Part 2 [67]
<i>E. phymatosperma</i> Boiss. & Gaill.	[76]
Sect. <i>Lathyris</i> Durmort	
<i>E. lathyris</i> L.	<i>Euphorbia</i> Seed Atlas Part 2 [67]
Sect. <i>Holophyllum</i> (Prokh.) Prokh.	
<i>E. wallichii</i> Hook.f.	[36]
Sect. <i>Helioscopia</i> Dumort.	
<i>E. acanthothamnus</i> Heldr. & Sartori ex Boiss.	[66]
<i>E. altissima</i> var. <i>altissima</i>	[75]
<i>E. altissima</i> var. <i>glabrescens</i> Boiss. ex M.S.Khan	[75]
<i>E. epithymoides</i> L.	http://pe.ibcas.ac.cn/en/
<i>E. grisophylla</i> M.L.S.Khan	[75]
<i>E. helioscopia</i> L.	Herbarium IRNASA-CSIC [36]
<i>E. illirica</i> Lam.	[72]
<i>E. macrocarpa</i> Boiss. & Buhse	[76]
<i>E. microsphaera</i> Boiss.	[75]
<i>E. oblongata</i> Griseb	[72]
<i>E. orientalis</i> L.	[75]
<i>E. platyphyllos</i> L.	[72]
<i>E. purpurea</i> (Raf.) Fernald	[36]
<i>E. pterococca</i> Brot.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. rhabdotosperma</i> Radcl.-Sm.	[75]
<i>E. rhytidosperra</i> Boiss. & Balansa	[75]
<i>E. spathulata</i> Lam.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-spa.html
<i>E. squamigera</i> Loisel.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. stricta</i> L.	[72]
Sect. <i>Myrsiniteae</i> (Boiss.) Lojac.	
<i>E. myrsinites</i> L.	https://plants.usda.gov/home/plantProfile?symbol=EUMY2 [64]
<i>E. oxyphylla</i> Boiss.	[36]
<i>E. rigida</i> M.Bieb	[72]
Sect. <i>Pithyusa</i> (Raf.) Lázaro	
<i>E. cheiradenia</i> Boiss. & Hohen.	[26]
<i>E. erythron</i> Boiss. & Heldr.	[26]

<i>E. falcata</i> L.	https://www.i-flora.com/en/the-smartphone-apps/iflora-deutschland/species/art/show/euphorbia-falcata-1.html
<i>E. gaillardotii</i> Boiss. & C.I.Blanche	[74]
<i>E. glareosa</i> Pall. ex M.Bieb.	[70, 26]
<i>E. macroclada</i> Boiss.	[26]
<i>E. nicaeensis</i> All.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. niciciana</i> Borbás ex Novák	[26]
<i>E. pannonica</i> Host	[26]
<i>E. pestalozzae</i> Boiss.	[26]
<i>E. petrophila</i> C.A.Mey.	[26]
<i>E. pisidica</i> Hub.-Mor. & M.S.Khan	[26]
<i>E. pithyusa</i> L.	Herbarium IRNASA-CSIC
<i>E. seguieriana</i> Neck.	[26]
<i>E. smirnovii</i> Geltman	[26]
<i>E. thessala</i> (Formánek) Degen & Dörfel.	[26]
<i>E. yildirimlii</i> Dinç	[26]
sect. <i>Sclerocyathium</i> (Prokh.) Prokh	
<i>E. bungei</i> Boiss.	[76]
sect. <i>Calyptratae</i> Geltman	
<i>E. connata</i> Boiss.	[76]
Sect. <i>Chylogala</i> (Fourr.) Prokh.	
<i>E. aleppica</i> L.	[74]
<i>E. heteradena</i> Jaub. & Spach	[76]
<i>E. retusa</i> Forssk.	[36]
<i>E. serrata</i> Forssk	[36]
sect. <i>Szovitsiae</i> Geltman	
<i>E. szovitsii</i> Fisch. & C.A. Mey	[75]
Sect. <i>Patellares</i>	
<i>E. amygdaloides</i> subsp. <i>amygdaloides</i> (Syn. <i>E. sylvatica</i>)	Herbarium IRNASA-CSIC
<i>E. characias</i> L.	Herbarium IRNASA-CSIC (Collected at Botanical Garden, Porto, Portugal) [72]
<i>E. erubescens</i> Boiss.	[76]
Sect. <i>Herpetorhizae</i> (Prokh.) Prokh.	
subsect. <i>Aucheriae</i> Geltman & Pahlevani	
<i>E. aucheri</i> Boiss.	[76]
Subsect. <i>Oppositifoliae</i> Boiss.	
<i>E. densa</i> Schrenk	[36]
Sect. <i>Guyoniana</i> Molero & Riina	
<i>E. guyoniana</i> Boiss. & Reut.	[36]
Sect. <i>Pachycladae</i> (Boiss.) Tutin	
<i>E. dendroides</i> L.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]

<i>E. terracina</i> L.	[26]
Sect. <i>Biumbellatae</i> Molero & Riina	
<i>E. biumbellata</i> Poir.	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
Sect. <i>Exiguae</i> (Geltman) Riina & Molero	
<i>E. dracunculoides</i> subsp. <i>inconspicua</i> (Ball) Maire	[73]
<i>E. exigua</i> subsp. <i>merinoi</i> M.Láinz	[73]
<i>E. medicaginea</i> Boiss.	[36]
Sect. <i>Aphyllis</i> Webb & Berthel.	
Subsect. <i>Macaronesicae</i> Molero & Barres	
<i>E. lamarckii</i> Sweet	Herbarium IRNASA-CSIC (Collected at Botanical Garden, Porto, Portugal)
<i>E. pedroi</i> Molero & Rovira	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
Subsect. <i>Africanae</i> Molero & Barres	
<i>E. berotica</i> N.E.Br.	[36]
<i>E. gossypina</i> Pax.	Herbarium IRNASA-CSIC (Collected at Botanical Garden, Porto, Portugal)
Sect. <i>Paralias</i> Dumort.	
<i>E. paralias</i> L.	Herbarium IRNASA-CSIC (Collected at Valadares beach, near Porto, Portugal)
<i>E. portlandica</i> L.	<i>Euphorbia</i> Seed Atlas-Part 2 [67]
<i>E. taurinensis</i> All.	[72]
<i>E. segetalis</i> L.	Herbarium IRNASA-CSIC (Collected at Valadares beach, near Porto, Portugal)
Sect. <i>Tithymalus</i> (Gaertn.) Roep.	
<i>E. commutata</i> Engelm. ex A.Gray	[36]
<i>E. crenulata</i> Engelm.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-cre.html
<i>E. peplus</i> L.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-pep.html [71]
Sect. <i>Arvales</i>	
<i>E. arvalis</i> subsp. <i>longistyla</i>	[73]
<i>E. normannii</i> Schmalh. ex Lipsky	[74]
<i>E. sulcata</i> Lens ex Loisel	[73]
Sect. <i>Esula</i>	
<i>E. agraria</i> M.Bieb	[72]
<i>E. buhsei</i> Boiss.	[76]
<i>E. esula</i> L.	https://seedidguide.idseed.org/?s=Euphorbia&et_pb_searchform_submit=et_search_process&et_pb_include_posts=yes&et_pb_include_pages=yes
<i>E. lucida</i> Waldst. & Kit.	Julia Scher, Federal Noxious Weeds Disseminules, USDA APHIS PPQ, Bugwood.org
Subgen. <i>Euphorbia</i>	
Sect. <i>Numulariopsis</i>	
<i>E. chrysophylla</i> (Klotzsch & Garcke) Klotzsch ex Boiss.	[70]

<i>E. cordeiroae</i> P.Carrillo & V.W.Steinm.	[70]
<i>E. elodes</i> Boiss.	[70]
<i>E. papillosa</i> A.St.-Hil.	[70]
<i>E. peperomioides</i> Boiss.	[70]
<i>E. rhabdodes</i> Boiss.	[70]
Sect. <i>Crepidaria</i>	
<i>E. cymbifera</i> (Schltdl.) V.W.Steinm.	Delta-Inkey https://www.delta-intkey.com/famfs/images/euphor22.jpg [62]
Sect. <i>Stachydium</i>	
<i>E. comosa</i> Vell.	[70]
Sect. <i>Tirucalli</i>	
<i>E. alcicornis</i> Baker	Delta-Inkey https://www.delta-intkey.com/famfs/images/euphor14.jpg [62]
Sect. <i>Goniostema</i>	
<i>E. leuconeura</i> Boiss.	https://commons.wikimedia.org/wiki/File:Euphorbia_leuconeura_seeds.png Barbusoligolepis, CC BY-SA 3.0 < https://creativecommons.org/licenses/by-sa/3.0/ >, via Wikimedia Commons
<i>E. alfredii</i> Rauh	https://www.euphorbia-international.org/euphorbias/cultivation/about_euph_cultivation_seed.htm
Sect. <i>Euphorbia</i>	
<i>E. barnardii</i> A.C.White, R.A.Dyer & B.Sloane	<i>Euphorbia</i> Seed Atlas-Part 5 [68]
<i>E. baylissii</i> L.C. Leach	[18]
<i>E. bougeyi</i> L.C.Leach (200)	<i>Euphorbia</i> Seed Atlas-Part 5 [68]
<i>E. breviararticulata</i> Pax	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. buruana</i> Pax	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. bussei</i> var. <i>kibwezensis</i> (N.E.Br.) S.Carter	[18]
<i>E. cactus</i> Ehrenb. ex Boiss.	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. caerulescens</i> Haw.	<i>Euphorbia</i> Seed Atlas-Part 5 [68]
<i>E. clivicola</i> R.A.Dyer	<i>Euphorbia</i> Seed Atlas-Part 5 [68]
<i>E. cooperi</i> N.E.Br. ex A.Berger	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. cuneneana</i> L.C. Leach	[18]
<i>E. grandidens</i> Haw.	[18]
<i>E. griseola</i> Pax	[18]
<i>E. heterospina</i> S.Carter	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. ingens</i> E.Mey. ex Boiss.	[18]
<i>E. ingenticapsa</i> L.C. Leach	[18]
<i>E. jubata</i> L.C. Leach	[18]
<i>E. knuthii</i> Pax	[18]
<i>E. neococcinea</i> Bruyns ?	<i>Euphorbia</i> Seed Atlas-Part 1 [66] (https://www.euphorbia-international.org/euphorbias/cultivation/about_euph_cultivation_seed.htm)

<i>E. nubigena</i> L.C.Leach	https://www.euphorbia-international.org/euphorbias/cultivation/about_euph_cultivation_seed.htm
<i>E. nyikae</i> Pax ex Engl.	[18]
<i>E. otjipembana</i> L.C.Leach	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. proballyana</i> L.C.Leach	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. robecchii</i> Pax	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. seretii</i> De Wild.	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. subsalsa</i> Hiern	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. teixeirae</i> L.C.Leach	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. tholicola</i> L.C.Leach	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. tortirama</i> R.A.Dyer (syn. <i>E. groenewaldi</i> R.A.Dyer)	<i>Euphorbia</i> Seed Atlas-Part 1 [66]
<i>E. vandermerwei</i> R.A.Dyer	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. virosa</i> Willd	[18]
<i>E. waterbergensis</i> R.A.Dyer	<i>Euphorbia</i> Seed Atlas-Part 6 [69]
<i>E. zoutpansbergensis</i> R.A.Dyer	<i>Euphorbia</i> Seed Atlas-Part 6 [69]

Appendix B

Table B1. Summary of morphological measurements in species of the subfamily Acalyphoideae. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

Tribe, subtribe	N	A	P	L	W	C	AR	R	S
Acalypheae, Acalyphinae									
<i>Acalypha virginica</i> Benth.	2	0.72	3.33	1.11	0.82	0.81	1.35	0.74	0.978
Acalypheae, Adrianinae									
<i>Adriana quadripartita</i> (Labill.) Müll.Arg	1	16.97	17.56	5.92	3.65	0.69	1.63	0.62	0.979
<i>Adriana tomentosa</i> (Thunb.) Gaudich.	1	24.53	20.23	6.36	4.91	0.75	1.30	0.77	0.976
Acalypheae, Cleidiinae									
<i>Cleidion castaneifolium</i> Müll.Arg.	1	37.96	23.72	7.03	6.88	0.85	1.02	0.98	0.989
Acalypheae, Macaranginae									
<i>Macaranga bancana</i> (Miq.) Müll.Arg.	1	9.18	11.84	3.57	3.28	0.82	1.09	0.92	0.994
<i>Macaranga gigantea</i> (Rchb.f. & Zoll.) Müll.Arg.	1	12.87	14.65	4.97	3.30	0.75	1.51	0.66	0.990
<i>Macaranga hypoleuca</i> (Rchb.f. & Zoll.) Müll.Arg.	1	8.27	11.34	3.82	2.76	0.81	1.39	0.72	0.991
<i>Macaranga winkleri</i> Pax & K.Hoffm.		3.12	10.06	2.19	1.81	0.39	1.21	0.83	0.908
Acalypheae, Mercurialinae									
<i>Mercurialis annua</i> L.	20	1.80	5.79	1.70	1.34	0.67	1.26	0.79	0.983
Acalypheae, Ricininae									
<i>Ricinus communis</i> L.	50	107.05	40.83	14.33	9.51	0.81	1.51	0.66	0.975
Adelieae									
<i>Adelia triloba</i> (Müll.Arg.) Hemsl.	1	12.02	13.06	4.02	3.81	0.89	1.05	0.95	0.996
Chrozophoreae, Ditaxinae									
<i>Caperonia palustris</i> (L.) A.St.-Hil.	1	5.76	9.81	2.80	2.62	0.75	1.07	0.94	0.976

Chrozophoreae, Chrozophorinae									
<i>Chrozophora tinctoria</i> (L.) A.Juss.	20	10.83	18.15	4.11	3.35	0.42	1.23	0.82	0.973
Plukenetieae									
<i>Plukenetia volubilis</i> L.	5	321.89	69.24	22.25	18.42	0.84	1.21	0.83	0.989
Mean values subfam. Acalyphoideae	106	45.77	20.79	6.59	5.09	0.74	1.29	0.79	0.978

Table B2. Summary of morphological measurements in species of the subfamily Crotonoideae. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

Tribe	N	A	P	L	W	C	AR	R	S
Adenoclineae									
<i>Tetrorchidium andinum</i> Müll.Arg.	1	12.81	13.89	4.38	3.73	0.83	1.17	0.85	0.985
Aleuritidae									
<i>Aleurites moluccanus</i> (L.) Willd.	1	593.44	93.47	27.84	27.14	0.85	1.02	0.98	0.992
<i>Vernicia fordii</i> (Hemsl.) Airy Shaw	1	228.69	62.15	20.63	14.12	0.74	1.46	0.68	0.975
Codiaeae									
<i>Codiaeum variegatum</i> (L.) Rumph. ex A.Juss.	5	17.97	16.30	5.28	4.33	0.85	1.22	0.82	0.995
Crotoneae									
<i>Croton capitatus</i> Michx.	1	6.55	10.72	3.81	2.19	0.72	1.74	0.57	0.980
<i>Croton glandulosus</i> L.	1	7.46	10.97	3.60	2.64	0.78	1.36	0.73	0.987
<i>Croton gossypifolius</i> Vahl.	5	6.50	9.99	3.39	2.44	0.82	1.39	0.72	0.974
<i>Croton monanthogynus</i> Michx.	1	6.72	10.60	3.54	2.42	0.75	1.47	0.68	0.979
<i>Croton setiger</i> Hook.	1	14.50	16.29	5.10	3.62	0.69	1.41	0.71	0.987
<i>Croton texensis</i> (Klotzsch) Müll.Arg.	1	13.16	14.26	4.22	3.97	0.81	1.06	0.94	0.992
Elateriospermeae									
<i>Elateriospermum tapos</i> Blume	1	638.27	102.01	38.62	21.04	0.77	1.84	0.55	0.992
Gelonieae									
<i>Suregada lanceolata</i> (Willd.) Kuntze	1	13.72	14.84	4.25	4.11	0.78	1.03	0.97	0.978
Jatropheae									
<i>Jatropha acanthophylla</i> Loefgr.	1	107.49	43.95	17.13	7.99	0.70	2.14	0.47	0.989
<i>Jatropha curcas</i> L.	20	153.23	49.95	17.72	10.99	0.77	1.61	0.62	0.993
Manihoteae									
<i>Cnidoscolus texanus</i> (Müll.Arg.) Small	1	128.00	48.99	16.86	9.67	0.67	1.74	0.57	0.978
<i>Manihot esculenta</i> Crantz	1	63.01	31.04	11.15	7.20	0.82	1.55	0.65	0.993
Micrandreae									
<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	1	493.65	84.17	26.82	23.44	0.88	1.14	0.87	0.994
Mean values subfam. Crotonoideae	54	141.46	35.86	12.16	8.52	0.78	1.43	0.73	0.99

Table B3. Summary of morphological measurements in species of *Euphorbia*, subgen. *Athymalus*, sections *Anthacanthae* and *Balsamis*. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

Section, subsection	A	P	L	W	C	AR	R	S
Sect <i>Antso</i> P.E.Berry								

<i>E. antso</i> Denis	77.04	33.79	10.56	9.29	0.85	1.14	0.88	0.996
Sect. <i>Pseudacalypha</i> Boiss								
<i>E. hadramautica</i> Baker	2.38	6.30	1.98	1.53	0.76	1.30	0.77	0.965
Sect. <i>Crotonoides</i> Bruyns & P.E. Berry								
<i>E. benthamii</i> Hiern	1.45	5.34	1.48	1.25	0.64	1.19	0.84	0.951
Sect. <i>Balsamis</i> Webb & Berthelot								
<i>E. balsamifera</i> Aiton	1.78	5.15	1.53	1.49	0.843	1.027	0.974	0.986
<i>E. larica</i> Boiss.	6.92	10.32	3.33	2.65	0.817	1.256	0.796	0.985
<i>E. neospinescens</i> Bruyns	7.95	12.89	4.07	2.48	0.601	1.64	0.61	0.96
Sect. <i>Anthacanthae</i> Lem.								
Subsect. <i>Florispinae</i> Haw								
<i>E. bubalina</i> Boiss.	9.47	11.95	3.69	3.27	0.83	1.13	0.89	0.990
<i>E. clandestina</i> Jacq.	5.02	8.76	2.72	2.35	0.82	1.16	0.86	0.987
<i>E. cumulata</i> R.A. Dyer	4.77	8.79	2.94	2.07	0.78	1.42	0.70	0.987
<i>E. meloformis</i> Aiton	3.16	7.01	2.15	1.87	0.810	1.15	0.87	0.988
subsect. <i>Pseudeuphorbium</i> Pax								
<i>E. dregeana</i> E.Mey. ex Boiss.	11.28	12.83	3.80	3.78	0.86	1.01	0.99	0.992
Subsect. <i>Medusea</i> (Haw.) Pax & K. Hoffm.								
<i>E. albipollinifera</i> L.C.Leach	5.74	10.69	3.11	2.35	0.63	1.32	0.76	0.971
<i>E. arida</i> N.E. Br.	8.98	13.03	3.76	3.04	0.67	1.24	0.81	0.947
<i>E. braunsii</i> N.E.Br.	8.80	12.14	3.64	3.08	0.75	1.18	0.84	0.974
<i>E. caput-medusae</i> L.	7.33	11.01	3.47	2.69	0.76	1.29	0.77	0.979
<i>E. colliculina</i> A.C. White, R.A. Dyer & B. Sloane	8.95	13.06	4.08	2.80	0.66	1.46	0.69	0.962
<i>E. davayi</i> N.E. Br.	8.43	11.63	3.72	2.89	0.78	1.29	0.78	0.980
<i>E. decepta</i> N.E. Br.	7.75	11.35	3.62	2.73	0.76	1.33	0.75	0.984
<i>E. duseimata</i> R.A. Dyer	5.53	9.39	3.02	2.33	0.79	1.30	0.77	0.987
<i>E. esculenta</i> Marloth	6.83	10.59	3.40	2.56	0.77	1.33	0.75	0.982
<i>E. filiflora</i> Marloth	11.23	14.46	4.04	3.54	0.68	1.14	0.88	0.953
<i>E. multiceps</i> A.Berger	6.92	11.11	3.31	2.67	0.71	1.24	0.81	0.983
<i>E. pentops</i> Marloth ex A.C.White, R.A.Dyer & B.Sloane	9.11	13.06	4.12	2.81	0.67	1.46	0.68	0.932
Mean values subgen. <i>Athymalus</i>	9.86	11.51	3.55	2.85	0.75	1.26	0.80	0.97

Table B4. Summary of morphological measurements in species of *Euphorbia*, subgen. *Chamaesyce*.
A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

Section, subsection	N	A	P	L	W	C	AR	R	S
Sect. <i>Espinosae</i> Pax & K. Hoffm.									
<i>E. espinosa</i> Pax	1	16.71	16.65	5.52	3.86	0.76	1.43	0.70	0.978
<i>E. guerichiana</i> Pax	1	10.48	13.12	4.08	3.27	0.77	1.25	0.80	0.973
Sect. <i>Articulofruticosae</i> Bruyns									
<i>E. burmanni</i> E.Mey. ex Boiss.	1	1.73	5.44	1.93	1.14	0.74	1.69	0.59	0.983
<i>E. ephedroides</i> E.Mey. ex Boiss.	1	3.16	8.06	2.53	1.59	0.61	1.60	0.63	0.974
<i>E. exilis</i> L.C.Leach	1	2.70	7.50	2.28	1.51	0.60	1.52	0.66	0.972
<i>E. gentilis</i> N.E.Br.	1	10.57	14.06	4.63	2.91	0.67	1.59	0.63	0.971
<i>E. racemosa</i> E.Mey. ex Boiss.	1	3.21	8.26	2.61	1.56	0.59	1.67	0.598	0.958
<i>E. rhombifolia</i> Boiss.	1	1.55	5.99	1.88	1.05	0.54	1.79	0.56	0.967

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<i>E. tenax</i> Burch.	1	3.35	7.79	2.26	1.88	0.69	1.20	0.83	0.978
Sect. <i>Cheirolepidium</i> Boiss.									
<i>E. cheirolepis</i> Fisch. & C.A.Mey. ex Karelin	1	7.34	11.61	4.06	2.30	0.68	1.76	0.57	0.977
<i>E. petiolata</i> Banks & Sol.	1	6.65	11.53	4.12	2.06	0.63	2.00	0.50	0.954
Sect. <i>Frondosae</i> Bruyns									
<i>E. transvaalensis</i> Schltr.	1	17.63	17.85	5.97	3.76	0.70	1.59	0.63	0.974
Sect. <i>Tenellae</i> Pax & K. Hoffm.									
<i>E. phylloclada</i> Boiss.	1	11.35	14.34	4.78	3.02	0.69	1.58	0.63	0.969
Sect. <i>Gueinziae</i> Riina									
<i>E. gueinzii</i> Boiss.	1	9.49	14.36	3.85	3.14	0.58	1.23	0.82	0.939
Sect. <i>Crossadenia</i>									
<i>E. goyazensis</i> Boiss.	1	5.02	9.22	2.91	2.20	0.74	1.32	0.76	0.967
<i>E. sarcodes</i> Boiss.	1	3.81	7.81	2.48	1.95	0.79	1.27	0.79	0.983
<i>E. sessilifolia</i> Klotzsch ex Boiss.	1	8.73	12.12	3.95	2.81	0.75	1.41	0.71	0.980
Sect. <i>Anisophyllum</i> Roep.									
Subsect. <i>Hypericifoliae</i> Boiss.									
<i>E. adenoptera</i> Bertol.	1	0.54	2.93	1.01	0.68	0.79	1.49	0.67	0.985
<i>E. bahiensis</i> (Klotzsch & Garcke) Boiss.	1	1.48	4.68	1.47	1.28	0.85	1.15	0.87	0.990
<i>E. chamaesyce</i> L.	1	1.54	4.93	1.78	1.10	0.80	1.63	0.62	0.993
<i>E. foliolosa</i> Boiss.	1	0.81	3.50	1.16	0.89	0.83	1.29	0.77	0.991
<i>E. geyeri</i> Engelm. & A.Gray	1	0.88	3.71	1.26	0.89	0.80	1.42	0.71	0.990
<i>E. glyptosperma</i> Engelm.	1	0.46	2.88	1.01	0.58	0.70	1.75	0.57	0.979
<i>E. hirta</i> L.	12	0.41	2.52	0.84	0.62	0.81	1.37	0.73	0.989
<i>E. humifusa</i> Willd.	1	0.65	3.30	1.16	0.72	0.75	1.62	0.62	0.986
<i>E. hyssopifolia</i> L.	12	0.80	3.48	1.12	0.91	0.84	1.23	0.81	0.989
<i>E. indica</i> Lam.	1	0.89	3.67	1.24	0.91	0.83	1.36	0.73	0.990
<i>E. maculata</i> L.	1	0.17	1.70	0.55	0.41	0.76	1.34	0.75	0.978
<i>E. nutans</i> Lag.	1	0.74	3.59	1.19	0.80	0.73	1.49	0.67	0.984
<i>E. ocellata</i> Durand & Hilg.	1	1.07	3.99	1.33	1.03	0.84	1.30	0.77	0.993
<i>E. ophthalmica</i> Pers.	1	0.53	2.91	1.01	0.66	0.79	1.53	0.66	0.986
<i>E. polycarpa</i> Benth.	1	0.37	2.70	0.95	0.50	0.64	1.92	0.52	0.982
<i>E. potentilloides</i> Boiss.	1	1.06	3.96	1.31	1.03	0.85	1.26	0.79	0.990
<i>E. prostrata</i> Aiton	1	0.54	2.96	1.00	0.69	0.78	1.45	0.69	0.977
<i>E. serpens</i> Kunth	1	0.68	3.23	1.14	0.76	0.82	1.51	0.66	0.992
<i>E. setosa</i> (Boiss.) Müll.Arg.	1	1.20	4.38	1.45	1.05	0.78	1.38	0.72	0.977
<i>E. thymifolia</i> L.	12	0.41	2.59	0.90	0.58	0.76	1.56	0.64	0.981
Sect. <i>Poinsettia</i> (Graham) Baill.									
Subsect. <i>Stormieae</i> Croizat									
<i>E. heterophylla</i> L.	1	5.04	9.05	2.58	2.49	0.77	1.03	0.97	0.966
<i>E. zonosperma</i> Müll.Arg.	1	5.66	10.19	2.96	2.43	0.69	1.22	0.82	0.935
Sect. <i>Alectoroctonum</i> (Schltdl.) Baill.									
<i>E. adiantoides</i> Lam.	20	1.58	7.20	1.67	1.20	0.38	1.38	0.72	0.909
<i>E. californica</i> Benth.	1	4.84	8.96	2.66	2.32	0.76	1.15	0.87	0.981
<i>E. cotinifolia</i> L.	1	4.46	8.44	2.58	2.20	0.79	1.18	0.85	0.985
<i>E. graminea</i> Jacq.	2	1.44	5.42	1.53	1.20	0.62	1.27	0.79	0.960
<i>E. hexagona</i> Nutt. ex Spreng.	1	5.10	9.23	2.87	2.26	0.75	1.27	0.79	0.984

<i>E. insulana</i> Vell.	1	5.18	9.48	3.14	2.10	0.72	1.49	0.67	0.975
<i>E. marginata</i> Pursh	1	11.96	13.61	4.23	3.60	0.81	1.17	0.85	0.976
<i>E. mauritanica</i> L.	1	10.19	13.22	4.80	2.70	0.73	1.78	0.56	0.983
<i>E. sciadophla</i> Boiss.	1	0.70	3.50	1.06	0.84	0.72	1.28	0.78	0.963
Mean values subgen. <i>Chamaesyce</i>	101	4.04	7.27	2.33	1.64	0.73	1.45	0.71	0.98

Table B5. Summary of morphological measurements in species of *Euphorbia*, subgen. *Esula*. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

Section, subsection	N	A	P	L	W	C	AR	R	S
Sect. <i>Lagascae</i> Lázaro									
<i>E. lagascae</i> Spreng.	1	8.98	12.99	4.36	2.63	0.67	1.66	0.60	0.970
<i>E. phymatosperma</i> Boiss. & Gaill.	1	6.54	11.34	3.70	2.25	0.64	1.65	0.61	0.961
Sect. <i>Lathyris</i> Durmort									
<i>E. lathyris</i> L.	1	13.69	14.45	5.11	3.41	0.82	1.50	0.67	0.994
Sect. <i>Holophyllum</i> (Prokh.) Prokh.									
<i>E. wallichii</i> Hook.f.	1	12.42	13.52	4.34	3.65	0.85	1.19	0.84	0.993
Sect. <i>Helioscopia</i> Dumort.									
<i>E. acanthothamnos</i> Heldr. & Sartori ex Boiss.	1	1.66	4.98	1.68	1.26	0.84	1.33	0.75	0.993
<i>E. altissima</i> var. <i>altissima</i> .	1	4.67	8.40	2.88	2.07	0.83	1.39	0.72	0.991
<i>E. altissima</i> var. <i>glabrescens</i> Boiss. ex M.S.Khan	1	4.58	8.16	2.69	2.17	0.86	1.24	0.81	0.995
<i>E. epithymoides</i> L.	1	4.21	8.18	2.58	2.07	0.79	1.25	0.80	0.98
<i>E. grisophylla</i> M.L.S.Khan	1	10.55	12.45	3.97	3.39	0.86	1.17	0.85	0.992
<i>E. helioscopia</i> L.	10	2.76	6.97	2.19	1.60	0.71	1.37	0.73	0.973
<i>E. illirica</i> Lam.	1	9.48	11.91	3.64	0.16	0.84	1.10	0.91	0.992
<i>E. macrocarpa</i> Boiss. & Buhse	1	7.60	10.54	3.30	2.93	0.86	1.13	0.89	0.992
<i>E. microsphaera</i> Boiss.	1	3.44	7.14	2.38	1.84	0.85	1.29	0.77	0.993
<i>E. oblongata</i> Griseb	1	3.49	7.23	2.45	1.81	0.84	1.36	0.74	0.994
<i>E. orientalis</i> L.	1	8.84	11.63	3.87	2.91	0.82	1.33	0.75	0.986
<i>E. platyphyllos</i> L.	1	3.12	6.93	2.26	1.76	0.82	1.28	0.78	0.992
<i>E. purpurea</i> (Raf.) Fernald	1	8.93	11.90	3.75	3.03	0.79	1.24	0.81	0.985
<i>E. pterococca</i> Brot.	1	1.39	5.09	1.51	1.17	0.67	1.29	0.78	0.973
<i>E. rhabdotosperma</i> Radcl.-Sm.	1	3.45	7.55	2.53	1.74	0.76	1.46	0.69	0.978
<i>E. rhytidosperra</i> Boiss. & Balansa	1	7.10	10.19	3.36	2.69	0.86	1.25	0.80	0.994
<i>E. spathulata</i> Lam.	1	1.55	5.10	1.59	1.24	0.75	1.29	0.78	0.977
<i>E. squamigera</i> Loisel.	1	5.67	9.62	3.12	2.32	0.77	1.35	0.74	0.988
<i>E. stricta</i> L.	1	1.93	5.34	1.75	1.40	0.85	1.26	0.80	0.994
Sect. <i>Myrsiniteae</i> (Boiss.) Lojac.									
<i>E. myrsinites</i> L.	1	6.46	10.66	3.80	2.17	0.71	1.76	0.57	0.978
<i>E. oxyphylla</i> Boiss.	1	10.79	15.74	4.92	2.80	0.55	1.76	0.57	0.954
<i>E. rigida</i> M.Bieb	1	9.36	15.91	4.84	2.46	0.47	1.97	0.51	0.931
Sect. <i>Pithyusa</i> (Raf.) Lázaro									
<i>E. cheiradenia</i> Boiss. & Hohen.	1	7.05	13.66	4.18	2.15	0.48	1.94	0.52	0.943
<i>E. erythron</i> Boiss. & Heldr.	1	3.67	8.20	2.92	1.60	0.69	1.82	0.55	0.979
<i>E. falcata</i> L.	1	1.27	5.03	1.71	0.95	0.63	1.80	0.55	0.968

<i>E. glareosa</i> Pall. ex M.Bieb.	1	3.26	7.36	2.65	1.57	0.76	1.69	0.59	0.989
<i>E. macroclada</i> Boiss.	1	3.59	8.05	2.87	1.60	0.70	1.80	0.56	0.975
<i>E. nicaeensis</i> All.	1	6.94	12.36	4.07	2.17	0.57	1.88	0.53	0.957
<i>E. niciana</i> Borbás ex Novák	1	2.10	5.86	2.07	1.29	0.77	1.61	0.62	0.987
<i>E. pannonica</i> Host	1	2.79	6.67	2.27	1.56	0.79	1.45	0.69	0.986
<i>E. pestalozzae</i> Boiss.	1	5.05	10.75	3.49	1.84	0.55	1.90	0.53	0.935
<i>E. petrophila</i> C.A.Mey.	1	2.81	7.44	2.67	1.34	0.64	1.99	0.50	0.965
<i>E. pisidica</i> Hub.-Mor. & M.S.Khan	1	3.67	9.16	3.16	1.48	0.55	2.14	0.47	0.942
<i>E. pithyusa</i> L.	1	6.02	9.79	3.44	2.23	0.79	1.54	0.65	0.987
<i>E. seguieriana</i> Neck.	1	3.18	7.36	2.67	1.52	0.74	1.75	0.57	0.977
<i>E. smirnovii</i> Geltman	1	5.48	10.81	4.02	1.73	0.59	2.32	0.43	0.958
<i>E. thessala</i> (Formánek) Degen & Dörfel.	1	4.46	9.57	3.44	1.65	0.61	2.09	0.48	0.957
<i>E. yildirimlii</i> Dinç	1	4.64	9.09	3.32	1.78	0.71	1.87	0.54	0.982
Sect. <i>Sclerocyathium</i> (Prokh.) Prokh									
<i>E. bungei</i> Boiss.	1	5.29	10.29	3.06	2.20	0.63	1.39	0.72	0.948
Sect. <i>Calyptratae</i> Geltman									
<i>E. connata</i> Boiss.	1	6.02	13.81	3.57	2.15	0.40	1.66	0.60	0.946
Sect. <i>Chylogala</i> (Fourr.) Prokh.									
<i>E. aleppica</i> L.	1	5.42	9.09	2.95	2.34	0.82	1.26	0.79	0.985
<i>E. heteradena</i> Jaub. & Spach	1	5.76	11.14	3.86	1.90	0.58	2.03	0.49	0.955
<i>E. retusa</i> Forssk.	1	9.15	14.34	5.40	2.16	0.56	2.50	0.40	0.942
<i>E. serrata</i> Forssk	6	8.86	12.77	4.11	2.74	0.68	1.50	0.67	0.976
Sect. <i>Szovitsiae</i> Geltman									
<i>E. szovitsii</i> Fisch. & C.A. Mey	1	0.30	2.52	0.81	0.47	0.60	1.72	0.581	0.958
Sect. <i>Patellares</i> (Prokh.) Frajman									
<i>E. amygdaloides</i> subsp. <i>amygdaloides</i>	1	2.64	6.44	2.06	1.63	0.80	1.26	0.79	0.987
<i>E. characias</i> L.	2	6.30	9.85	3.29	2.44	0.82	1.35	0.74	0.992
<i>E. erubescens</i> Boiss.	1	6.78	12.98	3.78	2.28	0.51	1.66	0.60	0.934
Sect. <i>Herpetorhizae</i> (Prokh.) Prokh.									
Subsect. <i>Oppositifoliae</i> Boiss.									
<i>E. densa</i> Schrenk	1	2.00	6.47	2.22	1.15	0.60	1.94	0.52	0.946
Sect. <i>Guyoniana</i> Molero & Riina									
<i>E. guyoniana</i> Boiss. & Reut.	1	6.15	12.10	3.89	2.01	0.53	1.93	0.52	0.955
Sect. <i>Pachycladae</i> (Boiss.) Tutin									
<i>E. dendroides</i> L.	1	6.54	10.04	3.18	2.62	0.82	1.21	0.83	0.991
<i>E. terracina</i> L.	1	3.02	8.31	2.54	1.52	0.55	1.68	0.60	0.937
Sect. <i>Biumbellatae</i> Molero & Riina									
<i>E. biumbellata</i> Poir.	1	5.66	10.05	3.58	2.01	0.70	1.78	0.56	0.966
Sect. <i>Exiguae</i> (Geltman) Riina & Molero									
<i>E. dracunculoides</i> subsp. <i>inconspicua</i> (Ball) Maire	1	1.91	6.63	2.05	1.18	0.55	1.74	0.58	0.928
<i>E. exigua</i> subsp. <i>merinoi</i> M.Laínz	1	0.56	3.00	0.98	0.73	0.79	1.35	0.74	0.987
<i>E. medicaginea</i> Boiss.	1	4.14	8.76	3.09	1.71	0.68	1.81	0.55	0.96
Sect. <i>Aphyllis</i> Webb & Berthel.									
Subsect. <i>Macaronesicae</i> Molero & Barres									
<i>E. lamarckii</i> Sweet	4	5.96	9.39	3.10	2.45	0.85	1.27	0.79	0.994
<i>E. pedroi</i> Molero & Rovira	1	4.17	8.36	2.94	1.81	0.75	1.62	0.62	0.980

Table B6. Summary of morphological measurements in species of *Euphorbia*, subgen. *Euphorbia*. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio, R, Roundness; S, Solidity.

[illegible]

<i>E. barnardii</i> A.C.White, R.A.Dyer & B.Sloane	1	0.39	2.38	0.75	0.65	0.86	1.158	0.864	0.991
<i>E. baylissii</i> L.C. Leach	1	3.14	6.78	2.11	1.89	0.86	1.12	0.90	0.987
<i>E. bougheyi</i> L.C.Leach	1	7.60	11.34	3.50	2.76	0.74	1.27	0.789	0.987
<i>E. breviariculata</i> Pax	1	11.66	13.51	4.09	3.63	0.80	1.13	0.89	0.988
<i>E. buruana</i> Pax	1	4.10	8.42	2.54	2.06	0.73	1.23	0.81	0.985
<i>E. bussei</i> var. <i>kibwezensis</i> (N.E.Br.) S.Carter	1	9.92	12.05	3.84	3.29	0.86	1.17	0.86	0.993
<i>E. cactus</i> Ehrenb. ex Boiss.	1	4.71	8.36	2.73	2.20	0.85	1.24	0.807	0.990
<i>E. caerulescens</i> Haw.	1	3.96	7.75	2.37	2.13	0.83	1.11	0.898	0.990
<i>E. clivicola</i> R.A.Dyer	1	3.20	7.25	2.38	1.71	0.77	1.39	0.719	0.984
<i>E. cooperi</i> N.E.Br. ex A.Berger	1	6.26	9.67	2.95	2.70	0.84	1.09	0.914	0.988
<i>E. cuneneana</i> L.C. Leach	1	2.69	6.41	2.05	1.67	0.82	1.23	0.81	0.983
<i>E. grandidens</i> Haw.	1	5.05	8.62	2.80	2.30	0.86	1.22	0.82	0.993
<i>E. griseola</i> Pax	1	3.75	7.33	2.24	2.14	0.88	1.05	0.96	0.993
<i>E. heterospina</i> S.Carter	1	3.10	7.19	2.17	1.82	0.76	1.19	0.838	0.980
<i>E. ingens</i> E.Mey. ex Boiss.	1	7.74	10.81	3.64	2.70	0.83	1.35	0.74	0.991
<i>E. ingenticapsa</i> L.C. Leach	1	11.57	13.24	4.12	3.58	0.83	1.15	0.87	0.991
<i>E. jubata</i> L.C. Leach	1	3.09	6.67	2.05	1.92	0.87	1.07	0.94	0.991
<i>E. knuthii</i> Pax	1	5.28	8.91	2.62	2.57	0.84	1.02	0.98	0.989
<i>E. neococcinea</i> Bruyns	1	3.61	11.97	3.34	1.37	0.32	2.43	0.411	0.933
<i>E. nubigena</i> L.C.Leach	1	3.77	8.48	2.45	1.96	0.66	1.25	0.803	0.981
<i>E. nyikae</i> Pax ex Engl.	1	11.94	13.23	3.99	3.81	0.86	1.05	0.96	0.994
<i>E. otjipembana</i> L.C.Leach	1	2.14	6.21	2.08	1.31	0.70	1.59	0.628	0.971
<i>E. proballyana</i> L.C.Leach	1	2.36	6.17	1.94	1.55	0.78	1.25	0.800	0.985
<i>E. robecchii</i> Pax	1	13.21	14.12	4.44	3.79	0.83	1.17	0.85	0.992
<i>E. seretii</i> De Wild.	1	5.69	9.14	2.78	2.60	0.86	1.07	0.935	0.990
<i>E. subsalsa</i> Hiern	1	1.95	5.66	1.89	1.31	0.77	1.44	0.694	0.979
<i>E. teixeirae</i> L.C.Leach	1	4.80	8.82	2.66	2.30	0.78	1.15	0.866	0.987
<i>E. tholicola</i> L.C.Leach	1	2.39	6.31	1.98	1.54	0.75	1.28	0.780	0.981
<i>E. tortirama</i> R.A.Dyer (syn. <i>E. groenewaldi</i> R.A.Dyer)	1	7.82	11.14	3.23	3.08	0.79	1.05	0.951	0.990
<i>E. vandermerwei</i> R.A.Dyer	1	5.22	8.87	2.71	2.45	0.84	1.11	0.904	0.989
<i>E. virosa</i> Willd	1	40.93	24.48	7.41	7.04	0.86	1.05	0.95	0.994
<i>E. waterbergensis</i> R.A.Dyer	1	4.17	7.88	2.38	2.24	0.85	1.06	0.942	0.991
<i>E. zoutpansbergensis</i> R.A.Dyer	1	3.17	6.85	2.07	1.96	0.85	1.06	0.946	0.989
Mean values subgen. <i>Euphorbia</i>	44	5.67	8.80	2.75	2.25	0.79	1.28	0.81	0.984

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