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Curvature Analysis of Seed Silhouettes in the Euphorbiaceae

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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 in multiple applications, including pharmaceutical, nutritional, and others. The seeds of the Euphorbiaceae develop in schizocarps and have a diversity of shapes that have 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 is 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 the curvature analysis are discussed in relation to other morphological properties, revealing new aspects of seed morphology of taxonomic application.

Keywords: curvature; geometry; morphometry; shape quantification

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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 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 unilobed species [3,4], it was divided into three subfamilies: Acalyphoideae, with about 120 genera grouped in 17 tribes [5], and 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, who was himself a given naturalist and the discoverer of *Euphorbia regis-jubae* Webb & Berthel., an endemism of the Canary Islands. Other members of the family have their names associated with therapeutical properties, such as *Jatropha* L., which etymologically means medicinal food. Members of the Euphorbiaceae have applications in the oil industry, as well as in the pharmaceutical and cosmetic industries, 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 a multitude of medical applications [10,11]. Many species also produce 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 with one or two outer layers and an outgrowth called the caruncle, a fleshy outgrowth that is often involved in attracting ants for seed dispersal (myrmecochory) [12–14]. 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 [10,11].

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 [30–32]. For example, Khan used seed characteristics as a key diagnostic feature for 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. *Chamaesyze* [35], *Esula* [36], and *Euphorbia* [37]. The application of new, quantitative methods based on curvature analysis [38–44] to seed morphology may contribute to the taxonomy of Euphorbiaceae.

The curvature of a plane curve measures the rate at which the tangent line varies per unit distance traveled 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]. The 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 objectives of this work have been to apply the method of curvature analysis to seed morphology in the Euphorbiaceae to contribute to the understanding of complex seed shapes in this family and show that this method may 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–S11 (see Supplementary Materials). The low number of seeds considered in some cases (i.e., 1 seed for some species) is due to the absence of available images.

2.2. Photography

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

2.3. General Morphological Descriptors

The 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) [45–49].

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 their thresholds were 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 [38–41]. Note that the curvature depends on the size of the figure. The 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. A *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 a radius equal to the inverse of the *mean curvature* value. Curvature ratios diverging from 1 indicate low circularity.

2.5. Statistical Analysis

Statistical analyses were performed according to the available data, resulting in non-normal distributions of the measurements in some populations. Consequently, the 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 Description

Measurements of area, perimeter, length, width, circularity, aspect ratio, roundness, and solidity were obtained for the species in the subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae (Tables A2–A7 in Appendix B). A large range of variation was observed in all subfamilies. The comparison between subfamilies revealed differences in most measurements.

3.1.1. Subfamily Acalyphoideae

In the subfamily Acalyphoideae, the area ranged between 0.72 and 321.89 mm^2, the perimeter was between 3.33 and 69.24 mm, and the lengths and widths were between 1.11 and 22.25, 0.82, and 18.42 mm, respectively. In all these cases, the minimum values were for *Acalypha virginica* and the maximum values were for *Plukenetia volubilis.* (Supplementary Figure S1, Table A2).

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

3.1.2. Subfamily Crotonoideae

In the subfamily Crotonoideae, the area ranged from 6.50 to 638.27 mm^2, and the perimeter ranged from 9.99 to 102.01 mm. The lengths and widths were between 3.39 and 38.62, 2.19, and 23.44 mm, respectively. The maximum values for area, perimeter, and length corresponded to *Elateriospermum tapos*, while the minimum values for all these measurements corresponded to *Croton* species. The circularity values ranged from 0.72 to 0.88, and solidity ranged from 0.974 to 0.994. (Supplementary Figure S2, Table A3).

3.1.3. Subfamily Euphorbioideae

Seeds of this subfamily were analyzed in *H. crepitans* (tribe Hureae) and in several species of the genus *Euphorbia* (tribe Euphorbieae), including the subgen. *Athymalus*

(Figure S3; Table A4), *Chamaesyce* (Figures S4 and S5; Table A5), *Esula* (Figures S6–S8; Table A6), and *Euphorbia* (Figures S9 and S10, Table A7).

Differences were observed in area, perimeter, length, and width between the Euphorbioideae (smaller seeds) and the other two subfamilies (Table 1). The circularity and solidity were smaller in the Euphorbioideae than in the Crotonoideae, the aspect ratio was lower in the Acalyphoideae than in the Euphorbioideae, and the solidity was higher in the Crotonoideae than in the Euphorbioideae. Size measurements (A, P, L, and W) had higher coefficients of variation than the shape measurements, in particular solidity, for all subfamilies.

Table 1. The morphological measurements in three subfamilies of the Euphorbiaceae. The means and coefficients of variation (between brackets) in size and shape measurements in three subfamilies of Euphorbiaceae. N is the number of seeds analyzed. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio; R, Roundness; S, Solidity. The 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)

The comparison of morphological measurements between subgenera of Euphorbia revealed differences, with size measurements smaller in *Chamaesyce*, higher in *Athymalus*, and intermediate in *Esula* and *Euphorbia*. Circularity and solidity values were higher in the subgen. *Euphorbia* (Table 2).

Table 2. The morphological measurements in the subgenera of *Euphorbia*. The means and coefficients of variation (between brackets) in size and shape measurements in the subgenera of *Euphorbia*. N is the number of seeds analyzed. A, Area; P, Perimeter; L, Length; W, Width; C, Circularity; AR, Aspect Ratio; R, Roundness; S, Solidity. The 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
Athymalus	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)
Chamaesyce	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)
Esula	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)
Euphorbia	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

3.2.1. Curvature Analysis in Species of the Acalyphoideae

The curvature was analyzed in species representative of tribes Acalypheae, Adelieae, Crozophoreae, and Plukenetieae. The seeds of *Acalypha virginica*, *Mercurialis annua*, and *Ricinus communis* (Acalypheae) presented different patterns of curvature (Figure 1). *Acalypha virginica* showed a maximum point of curvature corresponding to the apical side of the seed (Figure 1A). The seeds of *M. annua* presented one peak of high curvature corresponding to the apical region and three or more peaks in their basal regions (Figure 1B). *R. communis* showed two maximum curvature values in the apical region of the seed (Figure 1C). In this case, the caruncle gave a prominent zone, resulting in a double peak of maximum curvature.

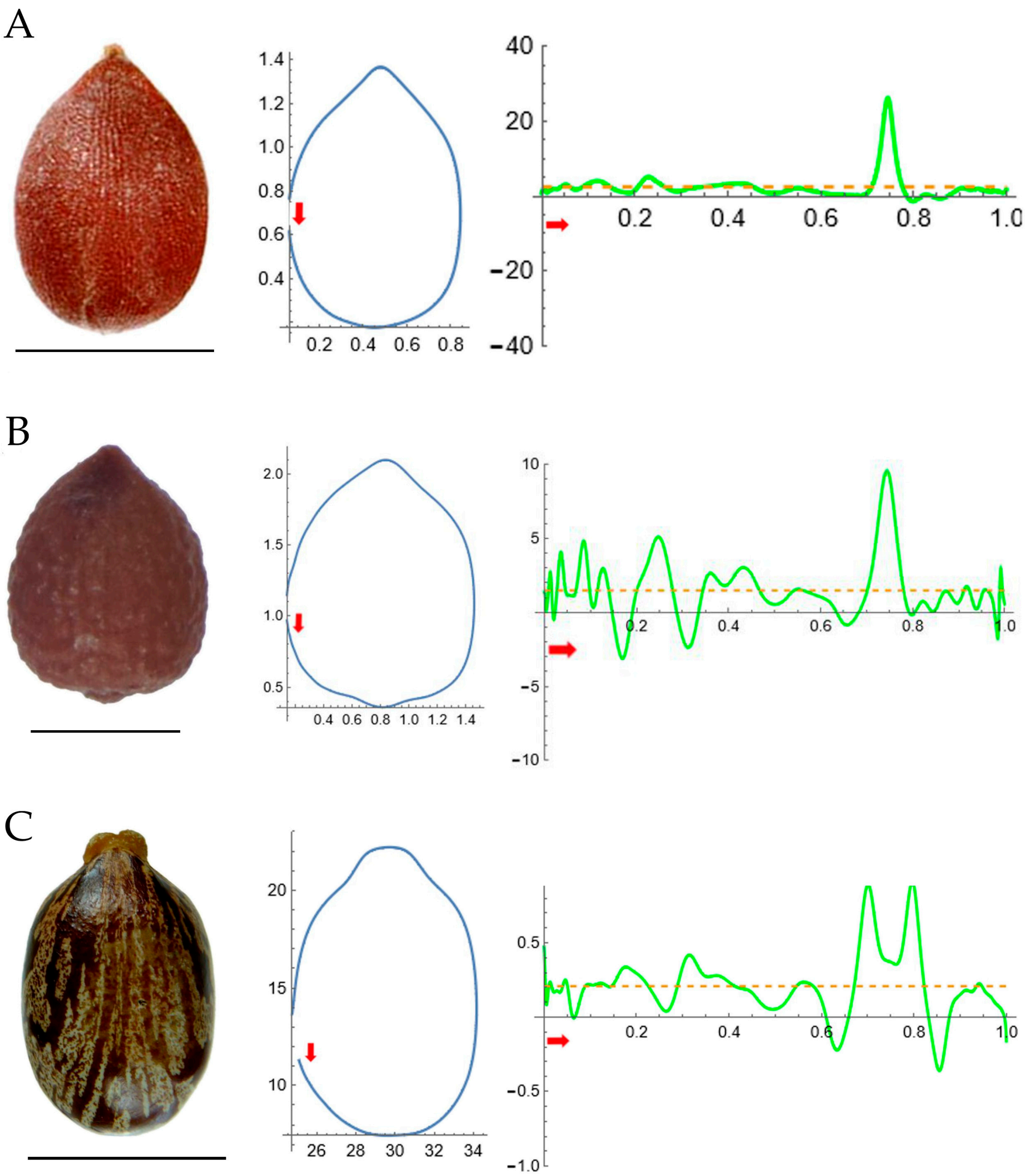

Figure 1. Curvature analysis in species of the Acalyphoideae, in the tribe Acalypheae. (**A**) *Acalypha virginica* L. (**B**) *Mercurialis annua* L. (**C**) *Ricinus communis* L. (**Left**): The seed images (the bar represents 10 mm). (**Center**): Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

The seeds of *Adelia triloba*, *Chrozophora tinctoria*, and *Plukenetia volubilis* were analyzed in the tribes Adelieae, Chrozophoreae, and Plukenetieae, respectively (Figure 2). An almost constant value of curvature around 0.5 was observed along the silhouette in the seed of *A. triloba*, with some variation in the basal part (Figure 2A). The curvature value of 0.5 mm^{-1} corresponds to a circumference of radius equal to 2 mm. The seeds of *M. annua* (Figure 2B), *C. tinctoria*, and *P. volubilis* showed one peak of high curvature corresponding to the apical region and three or more peaks in their basal regions. Curvature values for all these species are given in Table 3.

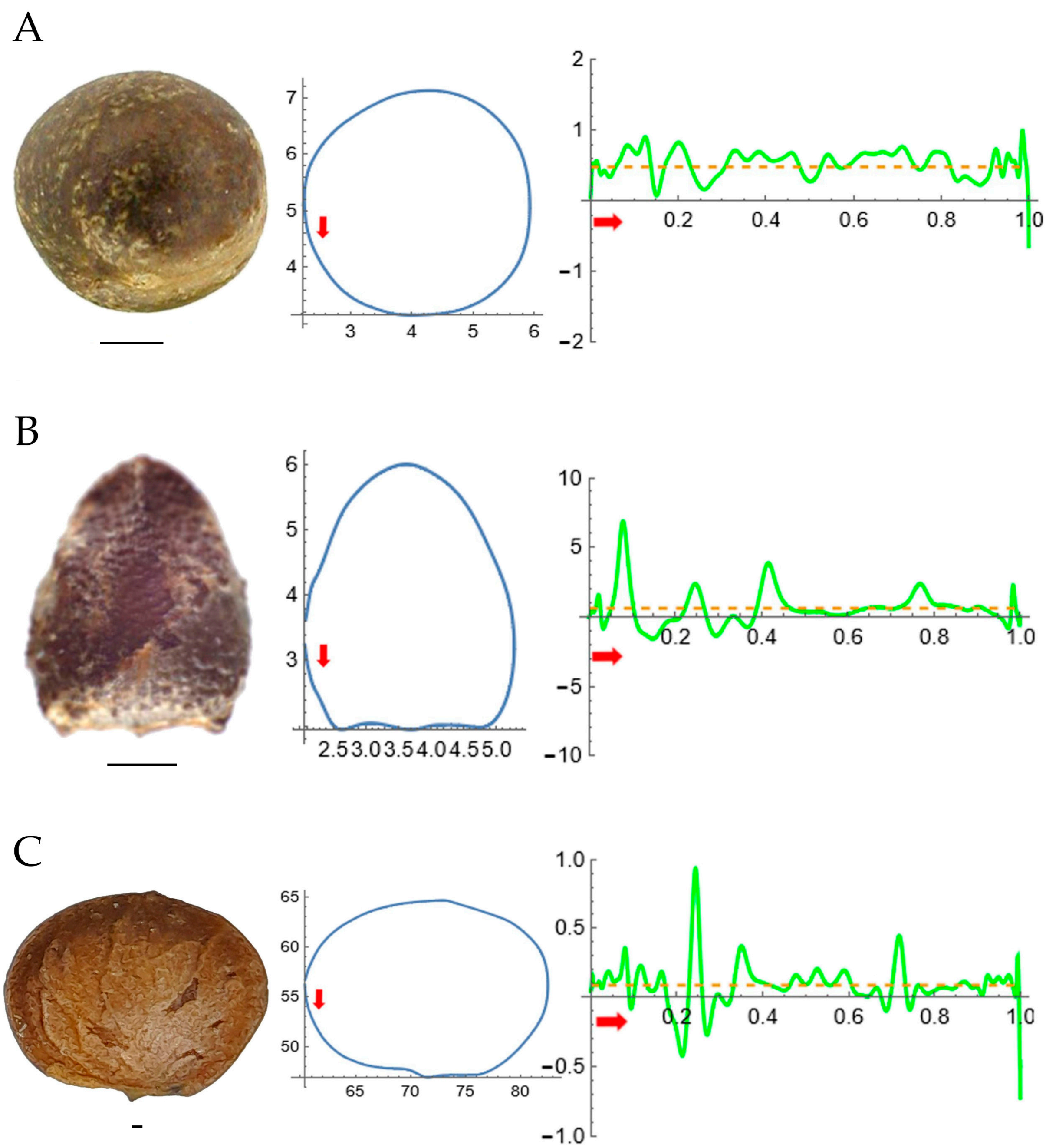

Figure 2. Curvature analysis in species of the Acalyphoideae, in the tribes Adelieae, Crozophoreae, and Plukenetieae. (**A**) *Adelia triloba* (Müll.Arg.) Hemsl. (**B**) *Crozophora tinctoria* (L.) A.Juss. (**C**) *Plukenetia volubilis* L. (**Left**): The seed image (the bar represents 1 mm). (**Center**): The Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

The seeds of *M. annua*, *C. tentoria*, and *P. volubilis* showed one peak of high curvature corresponding to the apical region and three or more peaks in their basal regions. The detailed curvature values in these regions are shown in Table 4. Whereas in *M. annua* (Figure 1B), the curvature values were higher in the apical pole, in both *C. tinctoria* (Figure 2B) and *P. volubilis* (Figure 2C), the maximum curvature values were observed in the basal pole, as well as 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. tinctoria* in the central peak of the basal pole.

Table 3. The curvature measurements in species of the subfamilies Acalyphoideae and Crotonoideae. The mean values of maximum, mean, and maximum to mean curvature ratios in representative species of the Acalyphoideae and Crotonoideae. Between parentheses are the number of seeds analyzed.

Species	Maximum Curvature (mm^{-1})	Mean Curvature (mm^{-1})	Max. to Mean Curvature Ratio
Acalypha virginica L. (1)	26.3	2.5	10.5
Mercurialis annua L. (4)	9.2	1.5	4.8
Ricinus communis L. (1)	0.9	0.2	4.5
Adelia triloba (Müll.Arg.) Hemsl. (1)	0.9	0.5	1.8
Crozophora tinctoria (L.) A.Juss. (3)	6.9	0.6	11.5
Plukenetia volubilis L. (2)	0.9	0.09	10
Jatropha curcas L. (1)	0.6	0.2	3

Table 4. Curvature analysis in species of the subfam. Acalyphoideae. The values in the apical pole and three basal peaks in the seed images of *Mercurialis annua*, *Chrozophora tinctoria*, and *Plukenetia volubilis.* Between parentheses are the number of seeds analyzed.

Species	Apical Pole	Basal Pole (Left, Central and Right Peaks)
Mercurialis annua L. (4)	9.8	3.8; 5.2; 4.2
Crozophora tinctoria (L.) A.Juss. (3)	1.6	5.0; 2.7; 3.2
Plukenetia volubilis L. (2)	3.8	3.9; 8.2; 3.8

3.2.2. Curvature Analysis in *Jatropha curcas* (Subfam. Crotonoideae, Tribe Jatropheae)

The seeds of *J. curcas* (Subfam. Crotonoideae, tribe Jatropheae) present a point of maximum curvature corresponding to the apical region and regions of high curvature in their basal regions (Figure 3).

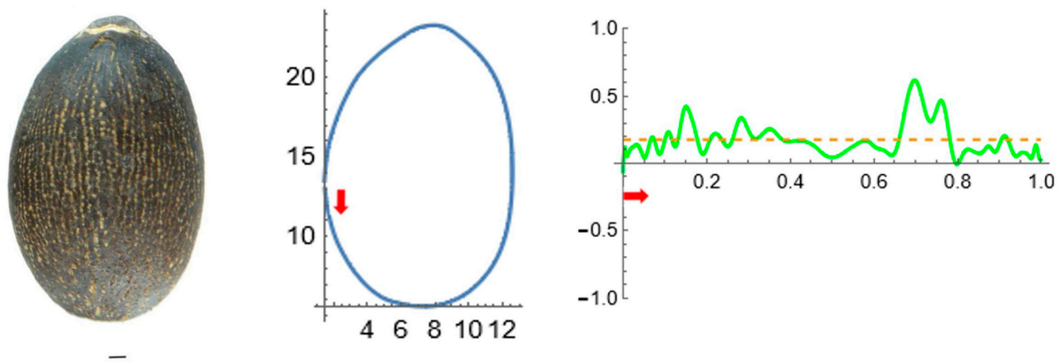

Figure 3. Curvature analysis in *Jatropha curcas* L. (**Left**): The seed image (the bar represents 1 mm). (**Center**): The Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

3.2.3. Curvature Analysis in the Euphorbioideae

Curvature analysis was applied to the seed images of *Hura crepitans* L. (tribe Hureae) and to species of *Euphorbia* belonging to the subgen. *Chamaesyce*, *Esula*, and *Euphorbia* (tribe Euphorbieae) (Table 5).

A unique peak of maximum curvature corresponds to the micropilar region in *Hura crepitans* L. (Figure 4), and the mean curvature was 0.07, the lowest value of this subfamily, corresponding to a circumference of radius = 14.3 mm.

Table 5. Curvature analysis in species of the Euphorbioideae. The maximum, mean, and maximum to mean curvature ratios in representative species of the Euphorbioideae. Between parentheses are the number of seeds analyzed.

Species	Maximum Curvature	Mean Curvature	Max. to Mean Curvature Ratio
Hura crepitans L. (3)	0.4	0.07	5
E. gentilis N.E.Br. (1)	3.6	0.6	6.0
E. hirta L. (1)	22.3	2.8	8.0
E. rhombifolia Boiss. (1)	10.0	1.5	6.7
E. helioscopia L. (3)	3.3	0.8	4.1
E. pithyusa L. (1)	6.8	0.9	7.6
E. serrata L. (3)	10	0.8	12.5
E. gossypina Pax (1)	5.7	0.9	6.3
E. lamarckii Sweet (3)	6.1	0.8	7.6
E. peplus L. (6)	5.5	1.9	2.9
E. paralias L. (3)	3.8	0.8	4.8
E. segetalis L. (1)	3.8	1.2	3.2
E. amygdaloides L. (2)	7.4	1.2	6.2

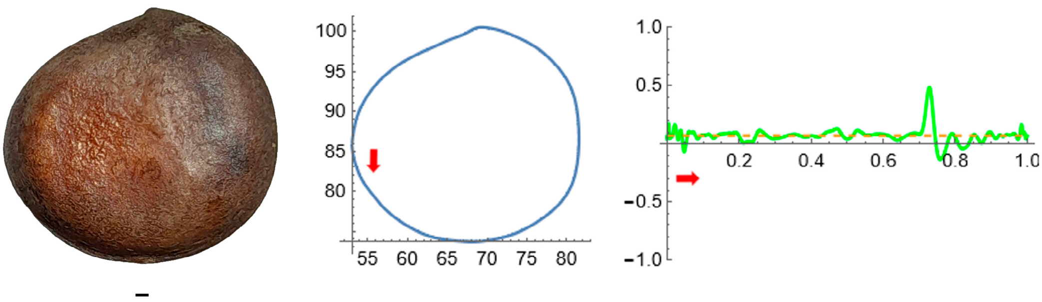

Figure 4. Curvature analysis in *Hura crepitans* L. (**Left**): The seed image (the bar represents 1 mm). (**Center**): The Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

In the species of *Euphorbia*, values of the maximum curvature ranged from 3.3 to 22.3, while mean curvatures ranged from 0.6 to 2.8. The seeds of *E. hirta* (Figure 5), *E. helioscopia*, and *E. rhombifolia* showed three points of high curvature corresponding to the vertices of their triangular shape.

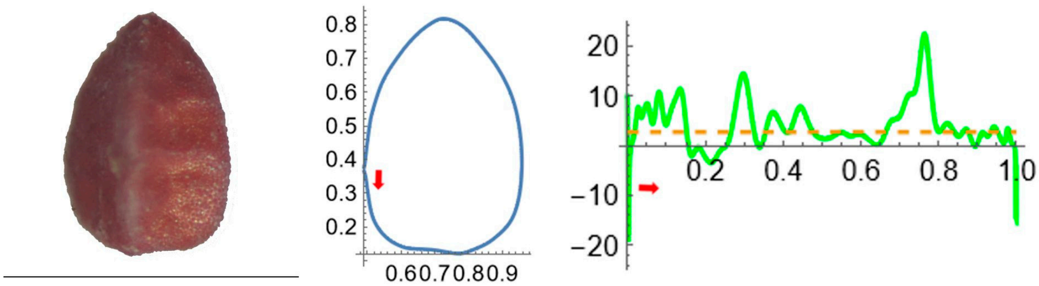

Figure 5. Curvature analysis in *Euphorbia hirta* L. (**Left**): The seed image (bar represents 1 mm). (**Center**): The Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

Curvature analysis was done in species of *Euphorbia* belonging to the subgen. *Esula* (Figures 6 and 7). 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 on their upper side

(Figure 6A,B). Approximately triangular or triangular-square 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, such as *E. amygdaloides* subsp. *amygdaloides* (Figure 6C). Squared or polygonal 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, such* as *E. gossypina*, *E. lamarckii,* (*E. paralias* (Figure 7A), *E. segetalis* (Figure 7B), and *E. peplus* (Figure 7C).

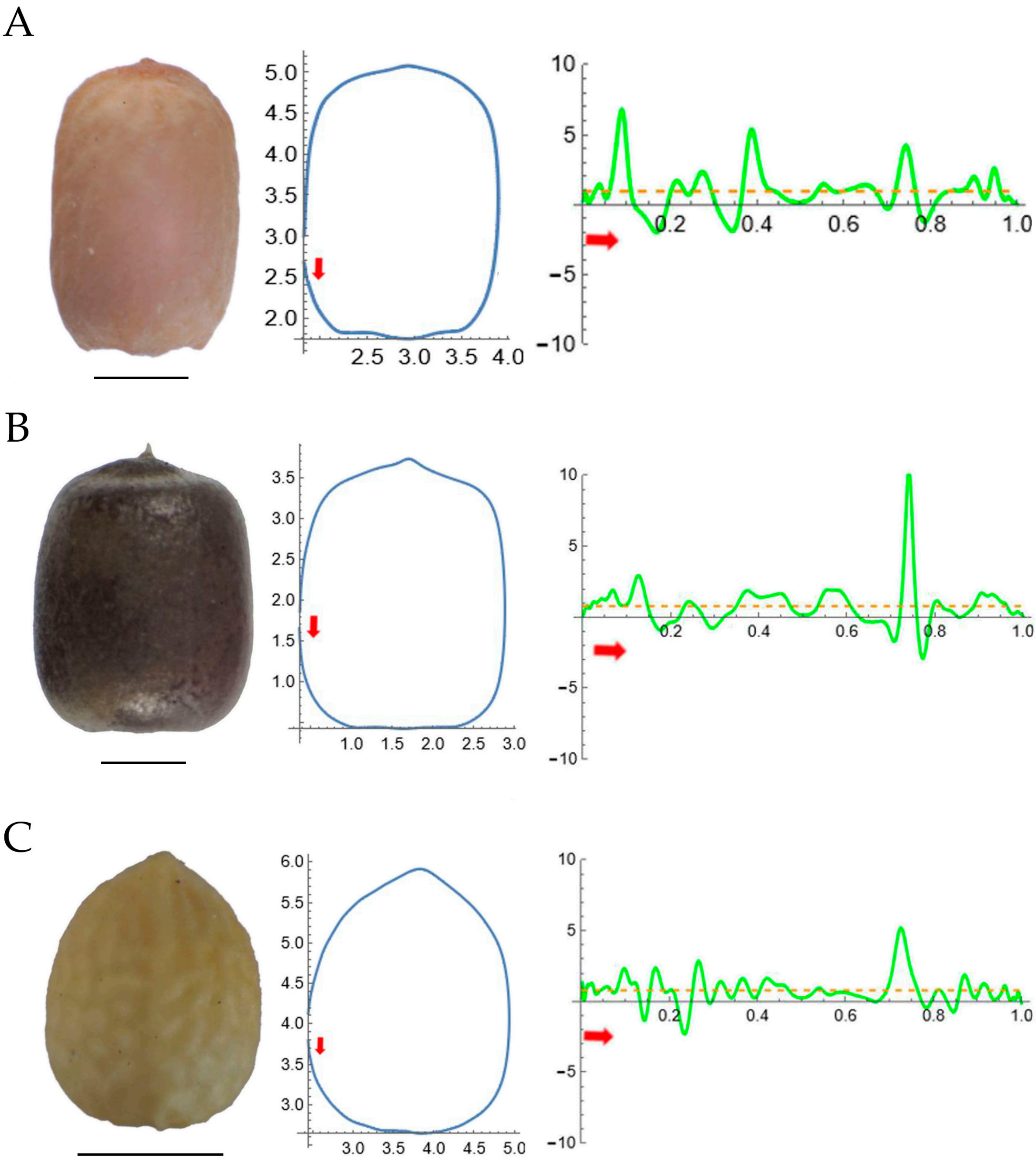

Figure 6. Curvature analysis in species of the *Euphorbia* subgen. *Esula*. (**A**) *Euphorbia pithyusa* L. (**B**) *Euphorbia serrata* L. (**C**) *Euphorbia amygdaloides* subsp. *amygdaloides.* (**Left**): The seed image (the bar represents 1 mm). (**Center**): the Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

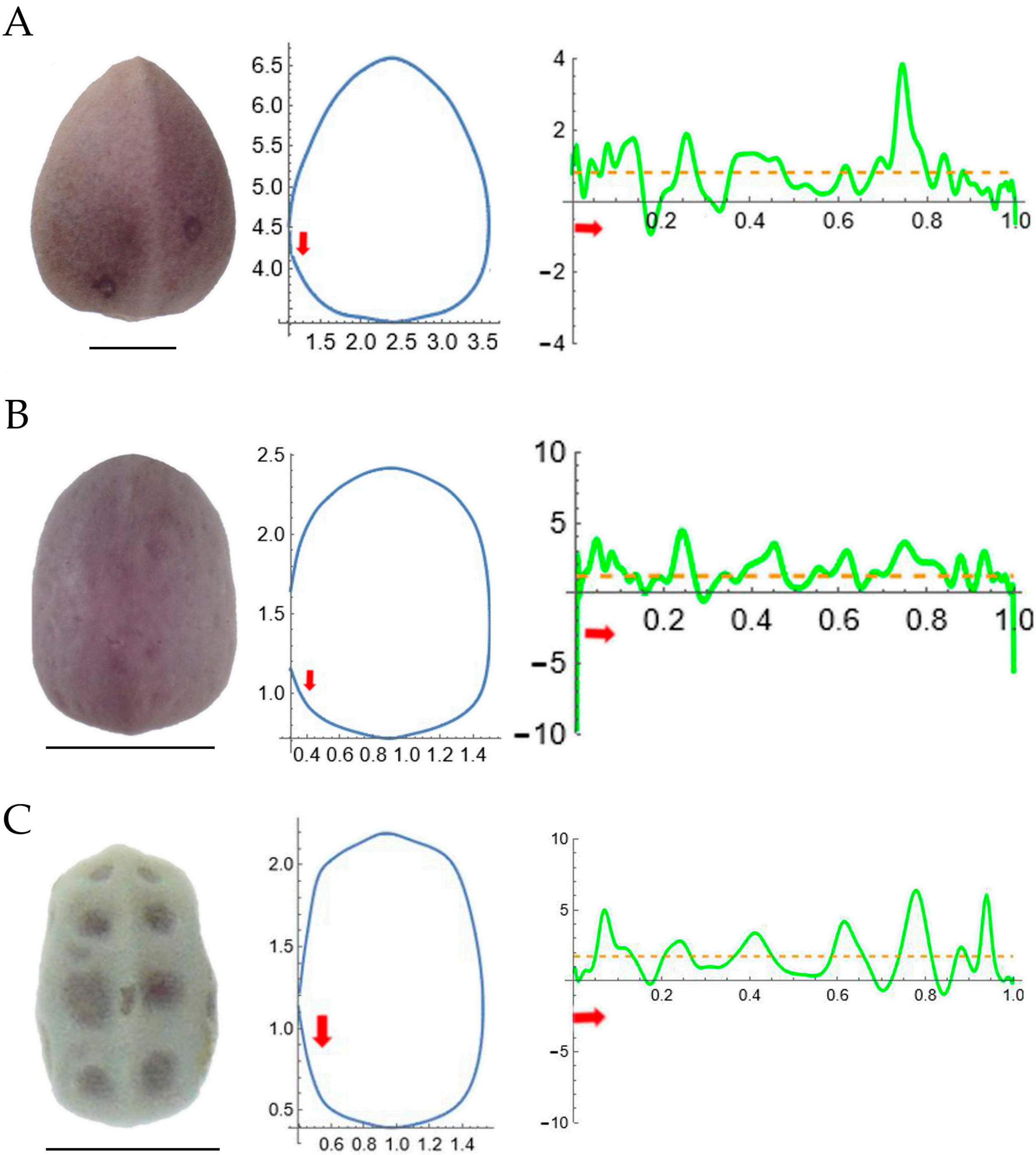

Figure 7. Curvature analysis in the *Euphorbia* subgen. *Esula*. (**A**) *Euphorbia paralias* L. (**B**) *Euphorbia segetalis* L. (**C**) *Euphorbia peplus* L. (**Left**): The seed image (the bar represents 1 mm). (**Center**): The Bézier curve, representing the seed silhouettes. (**Right**): The variation in curvature along the Bézier curve. The dashed line (orange) indicates the mean curvature. The green line shows curvature values along the curve. The red arrows indicate the direction of curvature measurement.

4. Discussion

4.1. Variations in Seed Shape According to Fruit Type

The range of variation in seed shape in seeds of the Euphorbiaceae is better understood by the basis of seed development in the schizocarp, a dry, dehiscent fruit that splits upon maturation into a variable number of segments called mericarps [51–54]. In *Euphorbia*, before being released, these segments remain attached to a central column known as the carpophore. The number of mericarps was not related to seed size in the species of this study. The present analysis included species with large seeds (larger than 2 cm, such as *J. curcas* or *Aleurites moluccanus* (L.) Willd.) which have up to three mericarps, and other species with bulky seeds, such as *Plukenetia* and *Hura*, which come from fruits with a higher number of mericarps.

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 is smaller and remains close to the carpophore [51–54]. Following this general scheme and oriented on their dorsal side, the seed images of most species resemble geometric figures with bilateral symmetry. Exceptions to this rule are the seeds of *P. volubilis* in the subfam. Acalyphoideae and those of *H. crepitans* in the subfam. Hureae, both of which lack bilateral symmetry. While capsules with up to 3 mericarps allow the seeds to have more space around the central carpophore during development and thus acquire greater sphericity, in contrast, when the schizocarp divisions are greater than 4, the smaller space around the carpophore makes these seeds more flattened, with the lateral view being wider than the dorsal or ventral view, as happens with the seeds of *P. volubilis*, which has fruits with 4 to 6 mericarps [55], and *H. crepitans*, whose fruits often have 11–14 mericarps [56], thus losing bilateral symmetry.

4.2. Curvature Analysis in Different Taxonomic Groups

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, subfam. Acalyphoideae), and species of *Tragia* or *Dalechampia* (tribe Plukenetieae, subfam. 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 polygons. 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 Euphorbiaceae. This result has been shown in other plant families, such as the Caryophyllaceae, Cucurbitaceae, Vitaceae, and others [42,43,57,58]. In general, Euphorbiacaeae seeds have high solidity values, higher than those reported for *Silene* L. (Caryophyllaceae) and *Vitis* L. (Vitaceae) species and close to those of Cucurbitaceae species. This means that the seed images resemble convex geometric figures with little (or not very abundant) surface protuberances. Differences between subfamilies were found in the area, as well as in the circularity and solidity. The area, circularity, and solidity were smaller in the Euphorbioideae than in the Crotonoideae, and roundness was higher in the seeds of the Acalyphoideae than in the Euphorbioideae. In the genus *Euphorbia*, the area was higher in the subgen. *Athymalus* and lower in the subgen. *Chamaesyze*. Solidity was higher in the subgen. *Euphorbia* than in the other three subgenera. This result is in contrast with Chen et al. [59], most probably due to the different species under study.

The 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 and in some species, for example, *Acalypha virginica*, and some species of *Euphorbia* (*E. pithyusa*, *E. serrata*), the highest curvature values in the apical pole correspond to the nucellar beak, a structure that is associated with the obturator during the embryonic development [51]. It may be of interest to investigate this aspect in more detail in these and other autochorous species, searching, for example, the relationship between maximum curvature values and the distance of the projection of the seeds. In most examined seeds, major changes in curvature are concentrated around both the apical and basal poles, with the lateral regions of the seed silhouettes being smoother. Among the species studied in the subfamilies Acalyphoideae and Crotonoideae, high polarity with single or double peaks of maximum curvature in the apical pole and lower almost constant curvature values in the basal pole have been observed in *A. virginica*, *R. communis* in the Acalypheae, and *J. curcas* in the Jatropheae. 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 like those described for some species of the Cucurbitaceae (*Momordica* sp., [42]) and the Vitaceae [43,58]. 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 *M. annua*, *C. tinctoria*, and *P. 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 *M. annua*, but the inverse occurs in *C. tinctoria* and *P. volubilis*. Thus, variation in curvature along the seed surface reveals aspects of seed geometry that may be associated with genetic or developmental peculiarities.

4.3. Relation Between Seed Shape and Dispersal Syndrome

Although seed shape and size are not directly related to dispersal mechanisms, in cases of zoochory, a relationship exists where larger seeds are transported by mammals or birds and smaller seeds by ants [4,12,59–61]. Nevertheless, most species have autochory [4], alone or in combination with other dispersion types, like myrmecochory [14,59–64]. This explosive seed dispersal includes large seeds without bilateral symmetry, like *H. crepitans* [65], as well as seeds with two or a maximum of three mericarps, like *Euphorbia paralias* or *E. maculata*, having, therefore, bilateral symmetry.

Many species of the Euphorbiaceae, such as *E. comosa* and *E. neococcinea* in subgen. *Euphorbia*, *E. neospinescens* in subgen. *Athymalus, E. petiolata* in subgen. *Chamaesyce*, as well as species of *Croton* and *Ricinus*, have a caruncle and are myrmecochorous [12–14,59–61]. The presence of a caruncle can regulate differences in explosive dispersal distance, favoring primary or secondary dispersal mechanisms [64]. Variations in surface curvature associated with the size and shape of the caruncle may provide clues about preferential transport by different insect populations or the relative relevance of these characters in different taxonomic groups. Curvature analysis may also provide information related to the taxonomy of larger seeds formed within flesh indehiscent capsules, as in some species of *Plukenetia*, that are dispersed by mammals [62].

4.4. Implications of Seed Shape in Taxonomy

In the genus *Euphorbia*, there are taxonomic groups with defined seed morphological patterns that are applied to discriminate between species [17,18,26,32,34–37], for example, the pyramidal shape in the species of Euphorbia sect. Anisophyllum subsect. Hypericifoliae and subgen. Chamaesyce [35], or a more rounded-oval pattern in subgen. *Esula* [36].

Genomic data are published for species in the Euphorbiaceae, such as *Hevea brasiliensis*, *Manihot esculenta*, *J. curcas*, and *R. communis* [66–69]. Recently, *E. peplus* has been proposed as a model system for the study of the production of plant latex [69]. 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

The seeds of the Euphorbiaceae show an apical basal polarity and bilateral symmetry. The seeds of *P. volubilis* in the Acalyphoideae and those of *H. crepitans* in the Hureae are exceptions to this rule, lacking bilateral symmetry due to their high number of mericarps per fruit. The number of fruit mericarps does not affect seed size in the Euphorbiaceae family but does affect seed shape, especially with respect to their axes of symmetry.

Differences in morphological measurements were found between subfamilies, as well as between subgenera of *Euphorbia*. Curvature analysis provides a new tool to interpret the seed morphology in this family. 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. The maximum curvature values correspond to the nucellar beak, a structure that is associated with the obturator during embryonic development, and thus are related to autochory.

Curvature measurements may contribute to the application of seed morphology in the taxonomy of this family. Further curvature analysis, focusing on specific taxonomic groups, may be an interesting technique for explaining possible correlations between shape and dispersal syndromes.

Supplementary Materials: Supplementary figures (Figures S1–S11) with the seed images used in the general morphological measurements (Tables 1, 2 and A2–A7) and the Mathematica (.nb) files for the curvature analysis in the figures can be downloaded at: https://zenodo.org/uploads/13306745, accessed on 2 September 2024.

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Appendix A

Table A1. The seed images used in the present work, with an indication of their sources.

Taxa and Species	Source of the Images [Reference]
Subfam. Acalyphoideae	
Tribe Acalypheae, subtribe Acalyphinae	
Acalypha virginica L.	[70]
Tribe Acalypheae, subtribe Adrianinae	
Adriana quadripartita (Labill.) Müll.Arg.	South Australian seed conservation Centre https://spapps.environment.sa.gov.au/SeedsOfSA/speciesinformation.html?rid=277, accessed on 2 September 2024.
Adriana tomentosa (Thunb.) Gaudich.	https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:338254-1, accessed on 2 September 2024.
Tribe Acalypheae, subtribe Cleidiinae	

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
Cleidion castaneifolium Müll.Arg.	https://malpighiales.myspecies.info/taxonomy/term/113/media, accessed on 2 September 2024.
Tribe Acalypheae, subtribe Macaranginae	
Macaranga bancana (Miq.) Müll.Arg.	[71]
Macaranga gigantea (Rchb.f. and Zoll.) Müll.Arg.	[71]
Macaranga hypoleuca (Rchb.f. & Zoll.) Müll.Arg.	[71]
Macaranga winkleri Pax & K.Hoffm.	[71]
Tribe Acalypheae, subtribe Mercurialinae	
Mercurialis annua L.	Herbarium IRNASA-CSIC
Tribe Acalypheae, subtribe Ricininae	
Ricinus communis L.	Herbarium IRNASA-CSIC
Tribe Adelieae	
Adelia triloba (Müll.Arg.) Hemsl.	Steven Paton, Smithsonian Institute: https://biogeodb.stri.si.edu/bioinformatics/dfm/metas/view/7230, accessed on 2 September 2024.
Tribe Chrozophoreae, subtribe Crozophorinae	
Chrozophora tinctoria (L.) A.Juss.	Herbarium IRNASA-CSIC
Tribe Chrozophoreae, subtribe Ditaxinae	
Caperonia palustris (L.) A.St.-Hil.	[72].
Tribe Plukenetieae	
Plukenetia volubilis L.	Acquired in local market in the city of Puyo (Ecuador).
Subfam. Crotonoideae	
Tribe Adenoclineae	
Tetrorchidium andinum Müll.Arg.	Steven Paton, Smithsonian Institute: https://biogeodb.stri.si.edu/bioinformatics/dfm/metas/view/11451, accessed on 2 September 2024.
Tribe Aleuritidae	
Aleurites moluccanus (L.) Willd.	[70]
Vernicia fordii (Hemsl.) Airy-Shaw	[72].
Tribe Codiaeae	
Codiaeum variegatum (L.) Rumph. ex A.Juss.	From urban gardens in city of Puyo (Ecuador).
Tribe Crotoneae	
Croton capitatus Michx.	[72]
Croton glandulosus L.	[72]
Croton gossypifolius Vahl	[70]
Croton lechlerii Müll.Arg.	From disturbed environments in Ecuador and returned to nature after being photographed.
Croton monanthogynus Michx	[72]
Croton setiger Hook.	[72]
Croton texensis (Klotzsch) Müll.Arg.	[72]
Tribe Elateriospermeae	
Elateriospermum tapos Blume	https://www.nparks.gov.sg/florafaunaweb/flora/2/8/2875, accessed on 2 September 2024.

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
Tribe Gelonieae	
Suregada lanceolata (Willd.) Kuntze	[70]
Tribe Jatropheae	
Jatropha sp.	[70,72].
Jatropha curcas L.	
Tribe Manihoteae	
Cnidoscolus texanus (Müll.Arg.) Small	[72]
Manihot esculenta Crantz	[70]
Tribe Micrandreae	
Hevea brasiliensis (Willd. ex A.Juss.) Müll.Arg.	[73]
Subfam. Euphorbioideae	
Tribe Hureae	
Hura crepitans L.	Acquired in local market in the city of Puyo (Ecuador).
Hura polyandra Baill.	[70]
Tribe Hippomaneae	
Sebastiania klotzschiana (Müll.Arg.) Müll.Arg.	[70]
Tribe Euphorbieae	
Gen. *Euphorbia* L.	
Subgen. *Athymalus*	
Sect. *Antso*	
E. antso Denis	[34]
Sect. *Pseudacalypha*	
E. hadramautica Baker	[34]
Sect. *Crotonoides* Bruyns & P.E. Berry	
E. benthamii Hiern	[34]
Sect. *Balsamis* Webb & Berthelot	
E. adenensis Deflers syn. *Euphorbia balsamifera* subsp. *adenensis* (Deflers) P.R.O.Bally	[20]
E. larica Boiss.	[20]
Sect. *Anthacanthae*	
Subsect. *Florispinae*	
E. bubalina Boiss.	[24]
E. clandestina Jacq.	[24]
E. cumulata R.A. Dyer	[24]
E. meloformis Aiton	https://www.euphorbia.de/seedgallery.html, accessed on 15 November 2024
Subsect. *Pseudeuphorbium* Pax	
E. dregeana E.Mey. ex Boiss.	[34]
Subsect. *Medusea*	
E. albipollinifera L.C.Leach	[20]
E. arida N.E. Br.	[24]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
E.braunsii N.E.Br.	[20]
E. caput-medusae L.	[34]
E. colliculina A.C. White, R.A. Dyer & B. Sloane	[24]
E. davyi N.E. Br.	[24]
E. decepta N.E. Br.	[24]
E. duseimata R.A. Dyer	[24]
E. esculenta Marloth	[24]
E. filiflora Marloth	[24]
E.multiceps A.Berger	[20]
E.pentops Marloth ex A.C.White, R.A.Dyer & B.Sloane	[20]
Subgen. *Chamaesyce* Raf.	
Sect. Espinosae Pax & K. Hoffm.	
E. espinosa Pax	[20]
E. guerichiana Pax	[20]
Sect. *Articulofruticosae* Bruyns	
Euphorbia burmanni E.Mey. ex Boiss.	[20]
E. ephedroides E.Mey. ex Boiss.	[20]
E. exilis L.C.Leach	[20,74]
E. gentilis N.E.Br.	[74]
E. racemosa E.Mey. ex Boiss. (41)	[74] (syn. *E. spartaria*)
E. rhombifolia Boiss.	[20,74] (syn. *E. caterviflora* en 74)
E. tenax Burch.	[20]
Sect. *Cheirolepidium* Boiss.	
E. cheirolepis Fisch. & C.A.Mey. ex Karelin	[35]
E. petiolata Banks & Sol.	[35]
Sect. *Frondosae* Bruyns	
E. transvaalensis Schltr.	[74]
Sect. *Tenellae* Pax & K. Hoffm.	
E. phylloclada Boiss.	[20]
Sect. *Gueinziae* Riina	
E. gueinzii Boiss.	[21]
Sect. *Crossadenia*	
E. goyazensis Boiss.	[35]
E.sarcodes Boiss.	[21]
E. sessilifolia Klotzsch ex Boiss.	[21]
Sect. *Anisophyllum* Roep.	
Subsect. *Hypericifoliae* Boiss.	
E. adenoptera Bertol.	[75]
E. bahiensis (Klotzsch & Garcke) Boiss.	[75]
E. chamaesyce L.	[76]
E. foliolosa Boiss.	[75]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
E. geyeri Engelm. & A.Gray	https://www.minnesotawildflowers.info/flower/geyers-spurge#lboxg-14, accessed on 2 September 2024.
E. glyptosperma Engelm.	https://www.minnesotawildflowers.info/flower/geyers-spurge#lboxg-14, accessed on 2 September 2024.
E. hirta L.	[75]
E. humifusa Willd.	[77]
E. hyssopifolia L.	[75]
E. indica Lam.	[77]
E. maculata L.	https://seedidguide.idseed.org/?s=Euphorbia&et_pb_searchform_submit=et_search_proccess&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, accessed on 2 September 2024.
E.nutans Lag.	[72]
E. ocellata Durand & Hilg.	[78] Photo by D. Walters and C. Southwick
E. ophthalmica Pers.	[75]
E. polycarpa Benth.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-pol.html, accessed on 2 September 2024.
E. potentilloides Boiss.	[75]
E. prostrata Aiton	[75]
E. serpens Kunth	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-ser.html [76], accessed on 2 September 2024.
E. setosa (Boiss.) Müll.Arg.	[75]
E. thymifolia L.	[75]
Sect. Poinsettia (Graham) Baill.	
Subsect. *Stormieae* Croizat	
E. heterophylla L.	[75]
E. zonosperma Müll.Arg.	[75]
Sect. *Alectoroctonum* (Schltdl.) Baill.	
E. adiantoides Lam.	From disturbed environments in Ecuador and returned to nature after being photographed.
E. californica Benth.	[74]
E. cotinifolia L.	[74]
E. graminea Jacq.	From disturbed environments in Ecuador and returned to nature after being photographed.
E. hexagona Nutt. ex Spreng.	[74]
E. insulana Vell.	[75]
E. marginata Pursh	[74]
E. mauritanica L.	*Euphorbia* Seed Atlas Part 1 [20]
E. sciadophila Boiss.	[75]
Subgen. *Esula* Pers.	

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
Sect. *Lagascae* Lázaro	
E. lagascae Spreng.	[21]
E. phymatosperma Boiss. & Gaill.	[77]
Sect. *Lathyris* Durmort	
E. lathyris L.	[21]
Sect. *Holophyllum* (Prokh.) Prokh.	
E. wallichii Hook.f.	[36]
Sect. *Helioscopia* Dumort.	
E. acanthothamnos Heldr. & Sartori ex Boiss.	[20]
E. altissima var. *altissima*	[75]
E. altissima var. *glabrescens* Boiss. ex M.S.Khan	[75]
E. epithymoides L.	http://pe.ibcas.ac.cn/en/, accessed on 16 June 2018.
E. grisophylla M.L.S.Khan	[75]
E. helioscopia L.	Herbarium IRNASA-CSIC
E. illirica Lam.	[78]
E. macrocarpa Boiss. & Buhse	[75,76]
E. microsphaera Boiss.	[75]
E. oblongata Griseb	[78]
E. orientalis L.	[75]
E. platyphyllos L.	[78]
E. purpurea (Raf.) Fernald	[36]
E. pterococca Brot.	[20]
E. rhabdotosperma Radcl.-Sm.	[76]
E. rhytidosperma Boiss. & Balansa	[76]
E. spathulata Lam.	https://idtools.org/id/weed-tool/key/GrapeSeedKey/Media/Html/fact_sheets/Eup-spa.html, accessed on 2 September 2024.
E. squamigera Loisel.	*Euphorbia* Seed Atlas-Part 1 [20]
E.stricta L.	[76]
Sect. *Myrsiniteae* (Boiss.) Lojac.	
E. myrsinites L.	https://plants.usda.gov/home/plantProfile?symbol=EUMY2 [69,76,78], accessed on 2 September 2024.
E. oxyphylla Boiss.	[36]
E.rigida M.Bieb	[78]
Sect. *Pithyusa* (Raf.) Lázaro	
E. cheiradenia Boiss. & Hohen.	[26,76]
E. erythrodon Boiss. & Heldr.	[26]
E. falcata L.	https://www.i-flora.com/en/the-smartphone-apps/iflora-deutschland/species/art/show/euphorbia-falcata-1.html [78], accessed on 2 September 2024.
E. gaillardotii Boiss. & C.I.Blanche	[75]
E. glareosa Pall. ex M.Bieb.	[24,26]
E. macroclada Boiss.	[26]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
E. nicaeensis All.	*Euphorbia* Seed Atlas-Part 1 [76]
E. niciciana Borbás ex Novák	[26,78]
E. pannonica Host	[26,78]
E. pestalozzae Boiss.	[26]
E. petrophila C.A.Mey.	[26]
E. pisidica Hub.-Mor. & M.S.Khan	[26]
E. pithyusa L.	Herbarium IRNASA-CSIC
E. seguieriana Neck.	[26]
E. smirnovii Geltman	[26]
E. thessala (Formánek) Degen & Dörfl.	[26]
E. yildirimlii Dinç	[26]
sect. *Sclerocyathium* (Prokh.) Prokh	
E. bungei Boiss.	[76]
sect. Calyptratae Geltman	
E. connata Boiss.	[76]
Sect. *Chylogala* (Fourr.) Prokh.	
E. aleppica L.	[75]
E. heteradena Jaub. & Spach	[76]
E. retusa Forssk.	[36]
E. serrata L.	[36]
sect. *Szovitsiae* Geltman	
E. szovitsii Fisch. & C.A. Mey	[76]
Sect. *Patellares*	
E. amygdaloides L. subsp. *amygdaloides* (Syn. *E. sylvatica*)	Herbarium IRNASA-CSIC, [78]
E. characias L.	Herbarium IRNASA-CSIC (Colected at Botanical Garden, Porto, Portugal)
E. erubescens Boiss.	[76]
Sect. *Herpetorhizae* (Prokh.) Prokh.	
subsect. Aucheriae Geltman & Pahlevani	
E. aucheri Boiss.	[77]
Subsect. *Oppositifoliae* Boiss.	
E. densa Schrenk	[20]
Sect. *Guyonianae* Molero & Riina	
E. guyoniana Boiss. & Reut.	[36]
Sect. *Pachycladae* (Boiss.) Tutin	
E. dendroides L.	[20]
E. terracina L.	[26]
Sect. *Biumbellatae* Molero & Riina	
E. biumbellata Poir.	[36]
Sect. *Exiguae* (Geltman) Riina & Molero	
E. dracunculoides subsp. *inconspicua* (Ball) Maire	[79]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
E. exigua subsp. *merinoi* M.Laínz	[79]
E. medicaginea Boiss.	[36]
Sect. *Aphyllis* Webb & Berthel.	
Subsect. *Macaronesicae* Molero & Barres	
E. lamarckii Sweet	Herbarium IRNASA-CSIC (Colected at Botanical Garden, Porto, Portugal)
E. pedroi Molero & Rovira	[21]
Subsect. *Africanae* Molero & Barres	
E. berotica N.E.Br.	[36]
E. gossypina Pax.	Herbarium IRNASA-CSIC (Colected at Botanical Garden, Porto, Portugal)
Sect. *Paralias* Dumort.	
E. paralias L.	Herbarium IRNASA-CSIC (Colected at Valadares beach, near Porto, Portugal)
E. portlandica L.	[21]
E. taurinensis All.	[80]
E. segetalis L.	Herbarium IRNASA-CSIC (Colected at Valadares beach, near Porto, Portugal)
Sect. *Tithymalus* (Gaertn.) Roep.	
E. commutata Engelm. ex A.Gray	[36]
E. crenulata Engelm.	[78]
E. peplus L.	Herbarium IRNASA-CSIC
Sect. *Arvales*	
E. arvalis subsp. *longistyla* (Litard. & Maire) Molero, Rovira & Vicens	[79]
E. normannii Schmalh. ex Lipsky	[81]
E. sulcata Lens ex Loisel	[79]
Sect. *Esula*	
E. agraria M.Bieb	[78]
E. buhsei Boiss.	[76]
E. esula L.	https://seedidguide.idseed.org/?s=Euphorbia&et_pb_searchform_submit=et_search_proccess&et_pb_include_posts=yes&et_pb_include_pages=yes, accessed on 2 September 2024.
E. lucida Waldst. & Kit.	Julia Scher, Federal Noxious Weeds Disseminules, USDA APHIS PPQ, Bugwood.org, accessed on 2 September 2024.
Subgen. *Euphorbia*	
Sect. *Numulariopsis*	
E. chrysophylla Klotzsch ex Boiss.	[75]
E. cordeiroae P.Carrillo & V.W.Steinm.	[75]
E. elodes Boiss.	[75]
E. papillosa A.St.-Hil.	[75]
E. peperomioides Boiss.	[75]
E. rhabdodes Boiss.	[75]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
Sect. *Crepidaria*	
E. cymbifera (Schltdl.) V.W.Steinm.	[70]
Sect. *Stachydium*	
E. comosa Vell.	[75]
Sect. *Tirucalli*	
E. alcicornis Baker	[70]
Sect. *Goniostema*	
E. leuconeura 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, accessed on 2 September 2024.
E. alfredii Rauh	https://www.euphorbia.de/seedgallery.html, accessed on 15 November 2024.
Sect. *Euphorbia*	
E. barnardii A.C.White, R.A.Dyer & B.Sloane	[82]
E. baylissii L.C. Leach	[24]
E. bougheyi L.C.Leach (200)	[24]
E. breviarticulata Pax	[20]
E. buruana Pax	[20]
E. bussei var. *kibwezensis* (N.E.Br.) S.Carter	[24]
E. cactus Ehrenb. ex Boiss.	[20]
E. caerulescens Haw.	[82]
E. clivicola R.A.Dyer	[82]
E. cooperi N.E.Br. ex A.Berger	[20]
E. cuneneana L.C. Leach	[24]
E. grandidens Haw.	[24]
E. griseola Pax	[24]
E. heterospina S.Carter	[82]
E. ingens E.Mey. ex Boiss.	[74]
E. ingenticapsa L.C. Leach	[44]
E. jubata L.C. Leach	[24]
E. knuthii Pax	[24]
E. neococcinea Bruyns	*Euphorbia* Seed Atlas-Part 1 [20] https://www.euphorbia.de/seedgallery.html, accessed on 15 November 2024
E. nubigena L.C.Leach	https://www.euphorbia.de/seedgallery.html, accessed on 15 November 2024
E. nyikae Pax ex Engl.	[24]
E. otjipembana L.C.Leach	[82]
E. proballyana L.C.Leach	[82]
E. virosa Pax	[24]
E. seretii De Wild.	[82]

Table A1. *Cont.*

Taxa and Species	Source of the Images [Reference]
E. subsalsa Hiern	[82]
E. teixeirae L.C.Leach	[82]
E. tholicola L.C.Leach	[82]
E. tortirama R.A.Dyer (syn. *E. groenewaldi* R.A.Dyer)	[24]
E. vandermerwei R.A.Dyer	[82]
E. virosa Willd	[24]
E. waterbergensis R.A.Dyer	[82]
E. zoutpansbergensis R.A.Dyer	[82]

Appendix B

Table A2. A summary of morphological measurements in the species of the subfamily Acalyphoideae. N is the number of seeds analyzed. 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									
Acalypha virginica	2	0.72	3.33	1.11	0.82	0.81	1.35	0.74	0.978
Acalypheae, Adrianinae									
Adriana quadripartita	1	16.97	17.56	5.92	3.65	0.69	1.63	0.62	0.979
Adriana tomentosa	1	24.53	20.23	6.36	4.91	0.75	1.30	0.77	0.976
Acalypheae, Cleidiinae									
Cleidion castaneifolium	1	37.96	23.72	7.03	6.88	0.85	1.02	0.98	0.989
Acalypheae, Macaranginae									
Macaranga bancana	1	9.18	11.84	3.57	3.28	0.82	1.09	0.92	0.994
Macaranga gigantea	1	12.87	14.65	4.97	3.30	0.75	1.51	0.66	0.990
Macaranga hypoleuca	1	8.27	11.34	3.82	2.76	0.81	1.39	0.72	0.991
Macaranga winkleri		3.12	10.06	2.19	1.81	0.39	1.21	0.83	0.908
Acalypheae, Mercurialinae									
Mercurialis annua	20	1.80	5.79	1.70	1.34	0.67	1.26	0.79	0.983
Acalypheae, Ricininae									
Ricinus communis	50	107.05	40.83	14.33	9.51	0.81	1.51	0.66	0.975
Adelieae									
Adelia triloba	1	12.02	13.06	4.02	3.81	0.89	1.05	0.95	0.996
Chrozophoreae, Ditaxinae									
Caperonia palustris	1	5.76	9.81	2.80	2.62	0.75	1.07	0.94	0.976
Chrozophoreae, Chrozophorinae									
Chrozophora tinctoria	20	10.83	18.15	4.11	3.35	0.42	1.23	0.82	0.973
Plukenetieae									
Plukenetia volubilis	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 A3. A summary of morphological measurements in the species of the subfamily Crotonoideae. N is the number of seeds analyzed. 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									
Tetrorchidium andinum	1	12.81	13.89	4.38	3.73	0.83	1.17	0.85	0.985
Aleuritidae									
Aleurites moluccanus	1	593.44	93.47	27.84	27.14	0.85	1.02	0.98	0.992
Vernicia fordii	1	228.69	62.15	20.63	14.12	0.74	1.46	0.68	0.975

Table A3. *Cont.*

Tribe	N	A	P	L	W	C	AR	R	S
Codiaeae									
Codiaeum variegatum	5	17.97	16.30	5.28	4.33	0.85	1.22	0.82	0.995
Crotoneae									
Croton capitatus	1	6.55	10.72	3.81	2.19	0.72	1.74	0.57	0.980
Croton glandulosus	1	7.46	10.97	3.60	2.64	0.78	1.36	0.73	0.987
Croton gossypiifolius	5	6.50	9.99	3.39	2.44	0.82	1.39	0.72	0.974
Croton monanthogynus	1	6.72	10.60	3.54	2.42	0.75	1.47	0.68	0.979
Croton setiger	1	14.50	16.29	5.10	3.62	0.69	1.41	0.71	0.987
Croton texensis	1	13.16	14.26	4.22	3.97	0.81	1.06	0.94	0.992
Elateriospermeae									
Elateriospermum tapos	1	638.27	102.01	38.62	21.04	0.77	1.84	0.55	0.992
Gelonieae									
Suregada lanceolata	1	13.72	14.84	4.25	4.11	0.78	1.03	0.97	0.978
Jatropheae									
Jatropha sp. (cited as *J. acanthophylla* Loefgr. in ref. [62])	1	107.49	43.95	17.13	7.99	0.70	2.14	0.47	0.989
Jatropha curcas	20	153.23	49.95	17.72	10.99	0.77	1.61	0.62	0.993
Manihoteae									
Cnidoscolus texanus	1	128.00	48.99	16.86	9.67	0.67	1.74	0.57	0.978
Manihot esculenta	1	63.01	31.04	11.15	7.20	0.82	1.55	0.65	0.993
Micrandreae									
Hevea brasiliensis	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 A4. 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 *Antso*								
E. antso	77.04	33.79	10.56	9.29	0.85	1.14	0.88	0.996
Sect. *Pseudacalypha*								
E. hadramautica	2.38	6.30	1.98	1.53	0.76	1.30	0.77	0.965
Sect. *Crotonoides*								
E. benthamii Hiern	1.45	5.34	1.48	1.25	0.64	1.19	0.84	0.951
Sect. *Balsamis*								
E. balsamifera	1.78	5.15	1.53	1.49	0.843	1.027	0.974	0.986
E. larica.	6.92	10.32	3.33	2.65	0.817	1.256	0.796	0.985
Euphorbia sp. (*E. neospinescens* Bruyns in [76])	7.95	12.89	4.07	2.48	0.601	1.64	0.61	0.96
Sect *Anthacanthae*								
Subsect. *Florispinae*								
E. bubalina	9.47	11.95	3.69	3.27	0.83	1.13	0.89	0.990
E. clandestina	5.02	8.76	2.72	2.35	0.82	1.16	0.86	0.987
E. cumulata	4.77	8.79	2.94	2.07	0.78	1.42	0.70	0.987
E. meloformis	3.16	7.01	2.15	1.87	0.810	1.15	0.87	0.988
subsect. *Pseudeuphorbium*								
E. dregeana.	11.28	12.83	3.80	3.78	0.86	1.01	0.99	0.992
Subsect. *Medusea*								
E. albipollinifera	5.74	10.69	3.11	2.35	0.63	1.32	0.76	0.971
E. arida.	8.98	13.03	3.76	3.04	0.67	1.24	0.81	0.947
E. braunsii.	8.80	12.14	3.64	3.08	0.75	1.18	0.84	0.974
E. caput-medusae	7.33	11.01	3.47	2.69	0.76	1.29	0.77	0.979
E. colliculina	8.95	13.06	4.08	2.80	0.66	1.46	0.69	0.962
E. davyi	8.43	11.63	3.72	2.89	0.78	1.29	0.78	0.980
E. decepta.	7.75	11.35	3.62	2.73	0.76	1.33	0.75	0.984

Table A4. *Cont.*

Section, Subsection	A	P	L	W	C	AR	R	S
E. duseimata	5.53	9.39	3.02	2.33	0.79	1.30	0.77	0.987
E. esculenta	6.83	10.59	3.40	2.56	0.77	1.33	0.75	0.982
E. filiflora	11.23	14.46	4.04	3.54	0.68	1.14	0.88	0.953
E.multiceps	6.92	11.11	3.31	2.67	0.71	1.24	0.81	0.983
E. pentops	9.11	13.06	4.12	2.81	0.67	1.46	0.68	0.932
Mean values subgen. *Athymalus*	9.86	11.51	3.55	2.85	0.75	1.26	0.80	0.97

Table A5. Summary of morphological measurements in species of *Euphorbia*, subgen. *Chamaesyce*. N is the number of seeds analyzed. 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. *Espinosae*									
E. espinosa	1	16.71	16.65	5.52	3.86	0.76	1.43	0.70	0.978
E. guerichiana	1	10.48	13.12	4.08	3.27	0.77	1.25	0.80	0.973
Sect. *Articulofruticosae*									
E. burmanni	1	1.73	5.44	1.93	1.14	0.74	1.69	0.59	0.983
E. ephedroides	1	3.16	8.06	2.53	1.59	0.61	1.60	0.63	0.974
E. exilis	1	2.70	7.50	2.28	1.51	0.60	1.52	0.66	0.972
E. gentilis	1	10.57	14.06	4.63	2.91	0.67	1.59	0.63	0.971
E. racemosa	1	3.21	8.26	2.61	1.56	0.59	1.67	0.598	0.958
E. rhombifolia	1	1.55	5.99	1.88	1.05	0.54	1.79	0.56	0.967
E. tenax	1	3.35	7.79	2.26	1.88	0.69	1.20	0.83	0.978
Sect. *Cheirolepidium*									
E. cheirolepis	1	7.34	11.61	4.06	2.30	0.68	1.76	0.57	0.977
E. petiolata	1	6.65	11.53	4.12	2.06	0.63	2.00	0.50	0.954
Sect. *Frondosae*									
E. transvaalensis	1	17.63	17.85	5.97	3.76	0.70	1.59	0.63	0.974
Sect. *Tenellae*									
E. phylloclada	1	11.35	14.34	4.78	3.02	0.69	1.58	0.63	0.969
Sect. *Gueinziae*									
E. gueinzii	1	9.49	14.36	3.85	3.14	0.58	1.23	0.82	0.939
Sect. *Crossadenia*									
E. goyazensis	1	5.02	9.22	2.91	2.20	0.74	1.32	0.76	0.967
E. sarcodes	1	3.81	7.81	2.48	1.95	0.79	1.27	0.79	0.983
E. sessilifolia	1	8.73	12.12	3.95	2.81	0.75	1.41	0.71	0.980
Sect. *Anisophyllum*									
Subsect. *Hypericifoliae*									
E. adenoptera	1	0.54	2.93	1.01	0.68	0.79	1.49	0.67	0.985
E. bahiensis	1	1.48	4.68	1.47	1.28	0.85	1.15	0.87	0.990
E. chamaesyce	1	1.54	4.93	1.78	1.10	0.80	1.63	0.62	0.993
E. foliolosa	1	0.81	3.50	1.16	0.89	0.83	1.29	0.77	0.991
E. geyeri	1	0.88	3.71	1.26	0.89	0.80	1.42	0.71	0.990
E. glyptosperma	1	0.46	2.88	1.01	0.58	0.70	1.75	0.57	0.979
E. hirta	12	0.41	2.52	0.84	0.62	0.81	1.37	0.73	0.989
E. humifusa	1	0.65	3.30	1.16	0.72	0.75	1.62	0.62	0.986
E. hyssopifolia	12	0.80	3.48	1.12	0.91	0.84	1.23	0.81	0.989
E. indica	1	0.89	3.67	1.24	0.91	0.83	1.36	0.73	0.990
E. maculata	1	0.17	1.70	0.55	0.41	0.76	1.34	0.75	0.978
E.nutans	1	0.74	3.59	1.19	0.80	0.73	1.49	0.67	0.984
E. ocellata	1	1.07	3.99	1.33	1.03	0.84	1.30	0.77	0.993
E. ophthalmica	1	0.53	2.91	1.01	0.66	0.79	1.53	0.66	0.986
E. polycarpa	1	0.37	2.70	0.95	0.50	0.64	1.92	0.52	0.982
E. potentilloides	1	1.06	3.96	1.31	1.03	0.85	1.26	0.79	0.990
E. prostrata	1	0.54	2.96	1.00	0.69	0.78	1.45	0.69	0.977

Table A5. *Cont.*

Section, Subsection	N	A	P	L	W	C	AR	R	S
E. serpens	1	0.68	3.23	1.14	0.76	0.82	1.51	0.66	0.992
E. setosa	1	1.20	4.38	1.45	1.05	0.78	1.38	0.72	0.977
E. thymifolia	12	0.41	2.59	0.90	0.58	0.76	1.56	0.64	0.981
Sect. *Poinsettia*									
Subsect. *Stormieae*									
E. heterophylla	1	5.04	9.05	2.58	2.49	0.77	1.03	0.97	0.966
E. zonosperma.	1	5.66	10.19	2.96	2.43	0.69	1.22	0.82	0.935
Sect. *Alectoroctonum*									
E. adiantoides	20	1.58	7.20	1.67	1.20	0.38	1.38	0.72	0.909
E. californica	1	4.84	8.96	2.66	2.32	0.76	1.15	0.87	0.981
E. cotinifolia	1	4.46	8.44	2.58	2.20	0.79	1.18	0.85	0.985
E. graminea	2	1.44	5.42	1.53	1.20	0.62	1.27	0.79	0.960
E. hexagona	1	5.10	9.23	2.87	2.26	0.75	1.27	0.79	0.984
E. insulana	1	5.18	9.48	3.14	2.10	0.72	1.49	0.67	0.975
E. marginata	1	11.96	13.61	4.23	3.60	0.81	1.17	0.85	0.976
E. mauritanica	1	10.19	13.22	4.80	2.70	0.73	1.78	0.56	0.983
E. sciadophla	1	0.70	3.50	1.06	0.84	0.72	1.28	0.78	0.963
Mean values subgen. *Chamaesyce*	101	4.04	7.27	2.33	1.64	0.73	1.45	0.71	0.98

Table A6. Summary of morphological measurements in species of *Euphorbia*, subgen. *Esula*. N is the number of seeds analyzed. 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. *Lagascae*									
E. lagascae	1	8.98	12.99	4.36	2.63	0.67	1.66	0.60	0.970
E. phymatosperma	1	6.54	11.34	3.70	2.25	0.64	1.65	0.61	0.961
Sect. *Lathyris*									
E. lathyris	1	13.69	14.45	5.11	3.41	0.82	1.50	0.67	0.994
Sect. *Holophyllum*									
E. wallichii	1	12.42	13.52	4.34	3.65	0.85	1.19	0.84	0.993
Sect. *Helioscopia*									
E. acanthothamnos	1	1.66	4.98	1.68	1.26	0.84	1.33	0.75	0.993
E. altissima Boiss. var. *altissima*.	1	4.67	8.40	2.88	2.07	0.83	1.39	0.72	0.991
E. altissima var. *glabrescens*	1	4.58	8.16	2.69	2.17	0.86	1.24	0.81	0.995
E. epithymoides	1	4.21	8.18	2.58	2.07	0.79	1.25	0.80	0.98
E. grisophylla	1	10.55	12.45	3.97	3.39	0.86	1.17	0.85	0.992
E. helioscopia	10	2.76	6.97	2.19	1.60	0.71	1.37	0.73	0.973
E. illirica	1	9.48	11.91	3.64	0.16	0.84	1.10	0.91	0.992
E. macrocarpa	1	7.60	10.54	3.30	2.93	0.86	1.13	0.89	0.992
E. microsphaera	1	3.44	7.14	2.38	1.84	0.85	1.29	0.77	0.993
E. oblongata	1	3.49	7.23	2.45	1.81	0.84	1.36	0.74	0.994
E. orientalis	1	8.84	11.63	3.87	2.91	0.82	1.33	0.75	0.986
E. platyphyllos	1	3.12	6.93	2.26	1.76	0.82	1.28	0.78	0.992
E. purpurea	1	8.93	11.90	3.75	3.03	0.79	1.24	0.81	0.985
E. pterococca	1	1.39	5.09	1.51	1.17	0.67	1.29	0.78	0.973
E. rhabdotosperma	1	3.45	7.55	2.53	1.74	0.76	1.46	0.69	0.978
E. rhytidosperma	1	7.10	10.19	3.36	2.69	0.86	1.25	0.80	0.994
E. spathulata	1	1.55	5.10	1.59	1.24	0.75	1.29	0.78	0.977
E. squamigera	1	5.67	9.62	3.12	2.32	0.77	1.35	0.74	0.988
E. stricta	1	1.93	5.34	1.75	1.40	0.85	1.26	0.80	0.994
Sect. *Myrsiniteae*									
E. myrsinites	1	6.46	10.66	3.80	2.17	0.71	1.76	0.57	0.978
E. oxyphylla	1	10.79	15.74	4.92	2.80	0.55	1.76	0.57	0.954
E.rigida	1	9.36	15.91	4.84	2.46	0.47	1.97	0.51	0.931

Table A6. *Cont.*

Section, Subsection	N	A	P	L	W	C	AR	R	S
Sect. *Pithyusa*									
E. cheiradenia	1	7.05	13.66	4.18	2.15	0.48	1.94	0.52	0.943
E. erythrodon	1	3.67	8.20	2.92	1.60	0.69	1.82	0.55	0.979
E. falcata	1	1.27	5.03	1.71	0.95	0.63	1.80	0.55	0.968
E. glareosa	1	3.26	7.36	2.65	1.57	0.76	1.69	0.59	0.989
E. macroclada	1	3.59	8.05	2.87	1.60	0.70	1.80	0.56	0.975
E. nicaeensis	1	6.94	12.36	4.07	2.17	0.57	1.88	0.53	0.957
E. niciciana	1	2.10	5.86	2.07	1.29	0.77	1.61	0.62	0.987
E. pannonica	1	2.79	6.67	2.27	1.56	0.79	1.45	0.69	0.986
E. pestalozzae	1	5.05	10.75	3.49	1.84	0.55	1.90	0.53	0.935
E. petrophila	1	2.81	7.44	2.67	1.34	0.64	1.99	0.50	0.965
E. pisidica	1	3.67	9.16	3.16	1.48	0.55	2.14	0.47	0.942
E. pithyusa	1	6.02	9.79	3.44	2.23	0.79	1.54	0.65	0.987
E. seguieriana	1	3.18	7.36	2.67	1.52	0.74	1.75	0.57	0.977
E. smirnovii	1	5.48	10.81	4.02	1.73	0.59	2.32	0.43	0.958
E. thessala	1	4.46	9.57	3.44	1.65	0.61	2.09	0.48	0.957
E. yildirimlii	1	4.64	9.09	3.32	1.78	0.71	1.87	0.54	0.982
Sect. *Sclerocyathium*									
E. bungei	1	5.29	10.29	3.06	2.20	0.63	1.39	0.72	0.948
Sect. *Calyptratae*									
E. connata	1	6.02	13.81	3.57	2.15	0.40	1.66	0.60	0.946
Sect. *Chylogala*									
E. aleppica	1	5.42	9.09	2.95	2.34	0.82	1.26	0.79	0.985
E. heteradena	1	5.76	11.14	3.86	1.90	0.58	2.03	0.49	0.955
E. retusa	1	9.15	14.34	5.40	2.16	0.56	2.50	0.40	0.942
E. serrata	6	8.86	12.77	4.11	2.74	0.68	1.50	0.67	0.976
Sect. *Szovitsiae*									
E. szovitsii	1	0.30	2.52	0.81	0.47	0.60	1.72	0.581	0.958
Sect. *Patellares*									
E. amygdaloides subsp. *amygdaloides*	1	2.64	6.44	2.06	1.63	0.80	1.26	0.79	0.987
E. characias	2	6.30	9.85	3.29	2.44	0.82	1.35	0.74	0.992
E. erubescens	1	6.78	12.98	3.78	2.28	0.51	1.66	0.60	0.934
Sect. *Herpetorhizae*									
Subsect. *Oppositifoliae*									
E. densa	1	2.00	6.47	2.22	1.15	0.60	1.94	0.52	0.946
Sect. *Guyonianae*									
E. guyoniana	1	6.15	12.10	3.89	2.01	0.53	1.93	0.52	0.955
Sect. *Pachycladae*									
E. dendroides	1	6.54	10.04	3.18	2.62	0.82	1.21	0.83	0.991
E. terracina	1	3.02	8.31	2.54	1.52	0.55	1.68	0.60	0.937
Sect. *Biumbellatae*									
E. biumbellata	1	5.66	10.05	3.58	2.01	0.70	1.78	0.56	0.966
Sect. *Exiguae*									
E. dracunculoides subsp. *inconspicua*	1	1.91	6.63	2.05	1.18	0.55	1.74	0.58	0.928
E. exigua subsp. *merinoi*	1	0.56	3.00	0.98	0.73	0.79	1.35	0.74	0.987
E. medicaginea.	1	4.14	8.76	3.09	1.71	0.68	1.81	0.55	0.96
Sect. *Aphyllis*									
Subsect. *Macaronesicae*									
E. lamarckii	4	5.96	9.39	3.10	2.45	0.85	1.27	0.79	0.994
E. pedroi	1	4.17	8.36	2.94	1.81	0.75	1.62	0.62	0.980
Subsect. *Africanae*									
E. berotica	1	5.42	9.77	2.90	2.38	0.71	1.22	0.82	0.959
E. gossypina	1	5.99	10.01	3.62	2.11	0.75	1.72	0.58	0.985
Sect. *Paralias*									
E. paralias	6	6.89	10.47	3.35	2.62	0.79	1.28	0.78	0.988
E. portlandica	1	2.57	7.19	2.50	1.31	0.62	1.91	0.53	0.961
E. segetalis	4	1.68	5.00	1.69	1.26	0.84	1.35	0.74	0.990
E. taurinensis	1	2.97	7.17	2.33	1.62	0.73	1.44	0.70	0.978

Table A6. *Cont.*

Section, Subsection	N	A	P	L	W	C	AR	R	S
Sect. *Tithymalus*									
E. commutata	1	1.63	4.98	1.62	1.28	0.82	1.26	0.79	0.986
E. crenulata	1	3.24	7.64	2.54	1.63	0.70	1.56	0.64	0.974
E. peplus	6	1.19	4.45	1.55	0.98	0.76	1.59	0.63	0.983
Sect. *Arvales*									
E. arvalis subsp. *longistyla*	1	1.70	5.85	1.93	1.12	0.62	1.72	0.58	0.963
E. normannii	1	3.847	7.913	2.76	1.775	0.77	1.555	0.64	0.99
E. sulcata	1	2.24	6.31	2.28	1.25	0.71	1.82	0.55	0.981
Sect. *Esula*									
E. agraria	1	3.54	7.42	2.39	1.89	0.81	1.26	0.79	0.987
E. buhsei	1	5.25	9.85	3.62	1.85	0.68	1.96	0.51	0.975
E. esula	1	2.98	7.08	2.37	1.60	0.75	1.49	0.67	0.988
E. lucida	1	3.57	7.66	2.68	1.70	0.76	1.58	0.63	0.988
Mean values subgen. *Esula*	116	4.84	8.95	2.97	1.89	0.71	1.57	0.66	0.974

Table A7. Summary of morphological measurements in species of *Euphorbia*, subgen. *Euphorbia*. N is the number of seeds analyzed. 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. *Nummulariopsis*									
E. chrysophylla	1	2.32	6.02	2.04	1.45	0.80	1.41	0.71	0.985
E. cordeiroae	1	2.19	5.86	1.96	1.43	0.80	1.37	0.73	0.981
E. elodes	1	0.71	3.36	1.13	0.80	0.79	1.41	0.71	0.974
E. papillosa	1	4.75	8.62	3.01	2.01	0.81	1.49	0.67	0.992
E. peperomioides	1	1.96	5.60	2.08	1.20	0.79	1.74	0.58	0.993
E. rhabdodes	1	2.45	6.29	2.09	1.50	0.78	1.39	0.72	0.977
Sect. *Crepidaria*									
E. cymbifera	1	9.51	12.80	4.17	2.90	0.729	1.436	0.696	0.968
Sect. *Stachydium*									
E. comosa	1	3.48	9.15	3.17	1.40	0.522	2.265	0.441	0.937
Sect. *Tirucalli*									
E. alcicornis	1	5.17	8.96	2.58	2.56	0.81	1.01	0.99	0.990
Sect. *Goniostema*									
E. leuconeura	1	4.73	8.59	2.80	2.15	0.804	1.302	0.768	0.983
E. alfredii	1	2.02	5.96	1.86	1.38	0.71	1.349	0.741	0.978
Sect. *Euphorbia*									
E. barnardii	1	0.39	2.38	0.75	0.65	0.86	1.158	0.864	0.991
E. baylissii	1	3.14	6.78	2.11	1.89	0.86	1.12	0.90	0.987
E. bougheyi	1	7.60	11.34	3.50	2.76	0.74	1.27	0.789	0.987
E. breviarticulata	1	11.66	13.51	4.09	3.63	0.80	1.13	0.89	0.988
E. buruana	1	4.10	8.42	2.54	2.06	0.73	1.23	0.81	0.985
E. bussei var. *kibwezensis*	1	9.92	12.05	3.84	3.29	0.86	1.17	0.86	0.993
E. cactus	1	4.71	8.36	2.73	2.20	0.85	1.24	0.807	0.990
E. caerulescens	1	3.96	7.75	2.37	2.13	0.83	1.11	0.898	0.990
E. clivicola	1	3.20	7.25	2.38	1.71	0.77	1.39	0.719	0.984
E. cooperi	1	6.26	9.67	2.95	2.70	0.84	1.09	0.914	0.988
E. cuneneana	1	2.69	6.41	2.05	1.67	0.82	1.23	0.81	0.983
E. grandidens	1	5.05	8.62	2.80	2.30	0.86	1.22	0.82	0.993
E. griseola	1	3.75	7.33	2.24	2.14	0.88	1.05	0.96	0.993
E. heterospina	1	3.10	7.19	2.17	1.82	0.76	1.19	0.838	0.980
E. ingens	1	7.74	10.81	3.64	2.70	0.83	1.35	0.74	0.991
E. ingenticapsa	1	11.57	13.24	4.12	3.58	0.83	1.15	0.87	0.991
E. jubata	1	3.09	6.67	2.05	1.92	0.87	1.07	0.94	0.991
E. knuthii	1	5.28	8.91	2.62	2.57	0.84	1.02	0.98	0.989
E. neococcinea	1	3.61	11.97	3.34	1.37	0.32	2.43	0.411	0.933

Table A7. *Cont.*

Section, Subsection	N	A	P	L	W	C	AR	R	S
E. nubigena	1	3.77	8.48	2.45	1.96	0.66	1.25	0.803	0.981
E. nyikae.	1	11.94	13.23	3.99	3.81	0.86	1.05	0.96	0.994
E. otjipembana	1	2.14	6.21	2.08	1.31	0.70	1.59	0.628	0.971
E. proballyana	1	2.36	6.17	1.94	1.55	0.78	1.25	0.800	0.985
E. robecchii	1	13.21	14.12	4.44	3.79	0.83	1.17	0.85	0.992
E. seretii	1	5.69	9.14	2.78	2.60	0.86	1.07	0.935	0.990
E. subsalsa	1	1.95	5.66	1.89	1.31	0.77	1.44	0.694	0.979
E. teixeirae	1	4.80	8.82	2.66	2.30	0.78	1.15	0.866	0.987
E. tholicola	1	2.39	6.31	1.98	1.54	0.75	1.28	0.780	0.981
E. tortirama	1	7.82	11.14	3.23	3.08	0.79	1.05	0.951	0.990
E. vandermerwei	1	5.22	8.87	2.71	2.45	0.84	1.11	0.904	0.989
E. virosa	1	40.93	24.48	7.41	7.04	0.86	1.05	0.95	0.994
E. waterbergensis	1	4.17	7.88	2.38	2.24	0.85	1.06	0.942	0.991
E. zoutpansbergensis	1	3.17	6.85	2.07	1.96	0.85	1.06	0.946	0.989
Mean values subgen. *Euphorbia*	44	5.67	8.80	2.75	2.25	0.79	1.28	0.81	0.984

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