RHEEDEA
Journal of the Indian Association for Angiosperm Taxonomy

RESEARCH ARTICLE

Vol. 34(5): 457–475 (2024)
ISSN: 0971-2313 (Print edition)
ISSN: 2582-2438 (Online edition)
https://dx.doi.org/10.22244/rheedea.2024.34.05.07

Systematic relevance of seed macro and micromorphology of *Evolvulus* (Convolvulaceae)

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Abstract: *Evolvulus* is one of the largest genera of Convolvulaceae, and most of the morphological traits evolved independently, making many of its species quite similar. Macro and micromorphological characters of the seed surface of 40 species were analyzed under a stereomicroscope and Scanning Electron Microscope (SEM). The sampling considered both morphological and distribution ranges of species. Nine characters varied among species and were compared by clustering (UPGMA) to investigate their sharing among the species studied. The variable seed traits show clear phenotypic differences among the species whose vegetative and reproductive traits are similar. In relation to infrageneric classification, seed morphology such as concave periclinal walls and smooth anticlinal walls shows a close affinity only between the species of *E.* sect. *Linoidei* and *E.* sect. *Lagopodini*. The results highlight the taxonomic importance of seed morphological traits to clarify the interspecific delimitation in *Evolvulus*.

Keywords: Morphology, Phenetic, Scanning electron microscopy, Taxonomy

Introduction

Seed morphology can be a source of valuable characters for taxonomy in different plant families such as Fabaceae (Karan, 1997; Abdel Khalik & Van der Maesen, 2002), Brassicaceae (Koul *et al.*, 2000; Abdel Khalik & Al-Juhani 2024); Plantaginaceae (Hassan & Khalik, 2014), Cucurbitaceae (Heneidak & Khalik, 2015), and Acanthaceae (Azevedo & Braz, 2018; Azevedo & Moraes, 2019). Traits that usually vary among species within these families are color, shape, the contour of epidermal cells, sinuosity of anticlinal walls, and sculpture of periclinal walls.

In Convolvulaceae (*c.* 2000 spp.), the seed morphology contributes to species delimitation in several genera such as *Convolvulus* L., *Cressa* L. (Khalik & Osman, 2007), *Distimake* Raf. (Khalik & Osman, 2007), *Evolvulus* L. (Ketjarun *et al.*, 2016), *Ipomoea* L. (Khalik & Osman, 2007; Khalik, 2013) and *Seddera* Hochst. (Khalik & Osman, 2007); and to the recognition of subgenera in *Cuscuta* (Abdel Khalik, 2006). A study of *Cuscuta* seeds was recently carried out with an evolutionary and anatomical focus (Olszewski, 2020). *Evolvulus*, the focus of the present study, had its seeds studied by Ketjarun *et al.* (2016) who addressed the micromorphology of three species (*E. alsinoides* (L.) L., *E. glomeratus* Nees & Mart., and *E. nummularius* (L.) L.), and concluding that these species could also be distinguished by their features of seeds.

Evolvulus L. comprises about 100 species, mainly distributed in environments with high light incidence of the Neotropical Seasonally Dry Forests (Ooststroom, 1934), of which 74 occur in Brazil, predominantly in the Cerrado and Caatinga domains (Simão-Bianchini & Silva, 2024). It is morphologically characterized by having two free styles, each with two filiform or clavate stigmas and glabrous seeds (Ooststroom,

Received: 31.10.2024; *Revised & Accepted*: 14.12.2024
Published Online: 31.12.2024

1934; Junqueira & Bianchini, 2006; Santos & Buril, 2020). Phylogenetic studies associated with reproductive characters indicate that the genus is possibly monophyletic (Stefanovic *et al.*, 2002).

Ooststroom (1934), in the most comprehensive monograph of the genus to date, circumscribed seven sections (*Evolvulus* sect. *Alsinoides* Meisn., *E.* sect. *Linoidei* Meisn., *E.* sect. *Lagopodini* Meisn., *E.* sect. *Paniculati* Peter., *E.* sect. *Passerinoidei* Meisn., *E.* sect. *Phyllostachyi* Meisn., *E.* sect. *Involucrati* Oosts.), based on different habits, leaf shape, indumentum and comparison between bract and sepal dimensions. However, these characters were proved to be inconsistent, due to overlapping between species from different sections. This reveals the need to explore other characteristics to provide morphological evidence that may be useful in future phylogenetic studies of *Evolvulus*.

Considering the taxonomic potential of *Evolvulus* seeds, this study aimed to investigate the taxonomic relevance of their morphology (macro and microcharacters) using a larger sample to aid in the delimitation of species and to understand their relationships within this genus. The study also aimed to answer the following questions:

a) Do the characters of *Evolvulus* seeds vary among populations inhabiting different types of vegetation?

b) Can the morphological characters of the seeds provide evidence that potentially indicates the monophyly of the sections within *Evolvulus*?

c) Do the seeds represent a promising source of characters for future evolutionary studies to investigate possible synapomorphies in *Evolvulus*?

Can seed morphology be used to elucidate taxonomic complexes within *Evolvulus*?

Materials & methods

Sampling and materials examined

Seeds were obtained from herbarium specimens HST, HUEFS, ME, PEUFR [acronyms following Thiers (2019) continuously updated] and during field expeditions in Caatinga, Cerrado, and Atlantic Rainforest dominium. We sampled 40 species of *Evolvulus*, representing 40% of the genus. This sampling includes representatives from all accepted *Evolvulus* sections except for *E.* sect. *Paniculati*, which is monospecific and endemic to Colombia. A list of voucher specimens and localities is provided in Table 1. To cover the range of morphological variation, we used three to five specimens for each specific taxon. For species widely distributed, we sampled individuals collected in different phytogeographic domains. We selected five to eight seeds from each specimen, and only mature and dried seeds were used for investigation.

Morphological analysis

Seeds were measured under a stereomicroscope (LEICA EZ4) using a digital caliper. For scanning electron microscopy (SEM), dry seeds were mounted on stubs with double adhesive tape, and coated with gold, followed by visualization and image capture using a Scanning Electron Microscope (Tescan VEGA3). All photomicrographs were taken at the Centro de Apoio a Pesquisa – CENAPESQ of the Universidade Federal Rural de Pernambuco. The classification and identification of the species followed the taxonomic study of Ooststroom (1934). The characters of the seed surface, such as cell outline, anticlinal walls, the relief of the cell boundaries, and curvature of the outer periclinal wall, were analyzed and described using the terminology of Barthlott (1981), Abdel Khalik and Maesen (2002), Khalik and Osman (2007).

Phenetic analysis

Evolvulus species were compared based on a set of 17 macro and micromorphological characters of the seeds, organized in a binary matrix (Table 2). The matrix was built in Microsoft Excel 2016 program and exported to PAST 2.17 program (Hammer *et al.*, 2001). Multivariate statistical methods (cluster analysis) were performed for

Table 1. List of vouchers used in the present study.

Sections/species	Voucher	Origin (Municipalities/state/bioma)
E.* sect. *Alsinoidei		
E. alsinoides (L.) L.	*Nelly Diego* 178 (MEXU)	Pedregal de San Angel, México (DF)
	G.S. Hinton 23366 (MEXU)	Parras, México (DF)
	J. Gregg 189 (MEXU)	Nuevo Leon, México (DF)
E. anagalloides Meisn.	*T.S. Nunes* 1146 (HUEFS)	Brasileira, Piauí (CAA)
	F.S. Araújo 395 (EAC)	Crateús, Ceará (CAA)
	A. Fernandes s.n. (EAC9798)	Guaraciaba do Norte, Ceará (CAA)
E. argyreus Choisy	*R.M. Harley* 57037 (HUEFS)	Santo Sé, Bahia (CAA)
	M.E.R.Junqueira 219 (HUEFS)	Morro do Chapéu, Bahia (CAA)
	T.S. Nunes 954 (HUEFS)	Xique-Xique, Bahia (CAA)
E. aurigenius Mart.	*D.G. Ernestino* 10 (CEN)	Brasília, Distrito Federal (CE)
	Márcio Verde 7356 (CEN)	Alto Paraíso, Goiás (CE)
	R. Romero et al. 2296 (HUFU)	São Roque, Minas Gerais (CE)
E. cardiophyllus Schltdl.	*L.P.Queiroz* 1759 (HUEFS)	Feira de Santana, Bahia (CAA)
	A. Fernandes s.n. (EAC11837)	Oeiras, Piauí (CAA)
	F.S. Araújo 1509 (EAC)	Crateús, Ceará (AF)
E. cordatus Moric.	*L.P. Queiroz* 10050 (HUEFS)	Remanso, Bahia (CAA)
	L. Moreira s.n. (ALCB)	Pilão Arcado, Bahia (CAA)
	F.S.E.Santo 07 (HVASF)	Afrânio, Pernambuco (CAA)
	F.D.S.Santos 567 (PEUFR)	Triunfo, Pernambuco (AF)
E. filipes Mart.	*M.A. Sousa* 1098 (HUEFS)	Sousa, Paraíba (CAA)
	F.S. Araújo 1515 (EAC)	Crateús, Ceará (AF)
	L.W.Lima-Verde s.n. (EAC)	Aiuaba, Ceará (AF)
E. flexuosus Mart.	*F.França* 5946 (HUEFS)	Xique-Xique, Bahia (CAA)
	M.L.S. Guedes 13568 (HUEFS)	M. São Francisco, Bahia (CAA)
	P.C.S.J.Torrend s.n. (ALCB3383)	Feira de Santana, Bahia (CAA)
E. frankenioides Moric.	*Andrade-Lima* 68 (IPA)	Inajá, Pernambuco (CAA)
	J.E.Gomes 144 (HST)	Alagoinha, Pernambuco (CAA)
	K.A.Silva 128 (IPA)	Petrolândia, Pernambuco (CAA)
E. gnaphalioides Moric.	*L.P. Queiroz* 15953	Morro do Chapéu, Bahia (CAA)
	A.C. Pereira 34 (HUEFS)	Morro do Chapéu, Bahia (CAA)
	M.J.G.Andrade 606 (HUEFS)	Morro do Chapéu, Bahia (CAA)
E. nummularius (L.) L.	*Chagas-Mota* 2787 (MAC)	Maceió, Alagoas (AF)
	L.P. Queiroz 4850 (PEUFR)	Barra, Bahia (CAA)
	A.M. Miranda et al. 2987 (PEUFR)	Paudalho, Pernambuco (CAA)

Sections/species	Voucher	Origin (Municipalities/state/bioma)
E. ovatus Fernald.	*A.M.S. Bitencourt et al.* 11 (EAC)	Irauçuba, Ceará (CAA)
	M.L.Guedes et al. 19646 (ALCB)	Piripiri, Piauí (CAA)
	G.C.Lima s.n. (IPA49695)	Cruzeta, Rio Grande do Norte (AF)
E. pohlli Meisn.	*E. Melo* 11763 (HUEFS)	Itatim, Bahia (CAA)
	C.C. Soares s.n. (BHCB53453)	Januária, Minas Gerais (CE)
	M. Aparecida 4389 (HST)	Monte Alegre, Goiás (CE)
	F.D.S. Santos 583 (PEUFR)	Castro Alves, Bahia (CAA)
E. pusillus Choisy	*J. Durigon* 316 (ICN)	Torres, Rio Grande do Sul (AF)
	P.P.A. Ferreira 74 (ICN)	Torres, Rio Grande do Sul (AF)
	D.B. Falkenberg 6656 (FLOR)	Florianópolis, Santa Catarina (AF)
E. rotundifolius (S.Watson) Hallier f.	*G.S. Hinton* 20834 (MEXU)	Galeana, México (DF)
	Hinton et al. 23404 (MEXU)	Cerro Viejo, México (DF)
	Hinton et al. 28418 (MEXU)	Acuña, México (DF)
E. saxifragus Mart.	*L.P. Félix et al. s.n.* (HST5872)	Triunfo, Pernambuco (AF)
	J.R. Maciel 890 (HVASF)	Monteiro, Paraíba (AF)
	A.M. Miranda 3077 (ALCB)	Triunfo, Pernambuco (AF)
E. sericeus Sw.	*A.V. Popovkin* 386 (HUEFS)	Entre Rios, Bahia (CAA)
	I.M. Bortolotto 89 (COR)	Corumbá, Mata Grosso do Sul (CE)
	B. Pickel 3547 (IPA)	São L. da Mata, Pernambuco (AF)
E. stellariifolius Ooststr.	*R.M. Castros* 1236 (HUEFS)	Senhor do Bonfim, Bahia (AF)
	R.M. Harley 54971 (HUEFS, ALCB)	Rio de Contas, Bahia (AF)
		Rio de Contas, Bahia (AF)
E.* sect. *Involucrati		
E. glomeratus Ness & Mart.	*S.M. Costa* 86 (ASE)	Poço Redondo, Sergipe (CAA)
	M.S. Castro s.n. (ALCB66346)	Canudos, Bahia (CAA)
	L.V. Vasconcelos 742 (HUEFS)	Jeremoabo, Bahia (CE)
E. saxatilis D. Santos & Buril	*F.D.S. Santos* 543 (PEUFR)	Tacoaritinga, Pernambuco (CAA)
E.* sect. *Lagopodini		
E. lagopodioides Meisn.	*A.G. Amaral* 2777 (CEN)	Alto Paraíso, Goiás (CE)
	J.N. Nakajima et al. 2323 (HUFU)	São Roque, Minas Gerais (CE)
	J.A. Rizzo 8798 (HUFU)	Cristalina, Goiás (CE)
E. pterocaulon Moric.	*D. Lopes s.n.* (HUFU18014)	Uberlândia, Minas Gerais (CE)
	T.S. Nunes 231 (HUEFS)	Rio de Contas, Bahia (CAA)
	E.O. Lenza 390 (HUFU)	Uberlândia, Minas Gerais (CE)
E. pterygophyllus Mart.	*R.M. Harley* 55938 (PEUFR)	Rio de Contas, Bahia (CAA),
	M. Barros et al. 2285 (PEUFR)	Brasília (CE)
E.* sect. *Linoidei	*R.S. Juliete* 595 (CEN)	Brasília (CE)

Sections/species	Voucher	Origin (Municipalities/state/bioma)
E. elaeagnifolius Dammer	*L.V. Vasconcelos* 732 (HUEFS)	Jeremoabo, Bahia (CAA)
	A. Fernandes s.n. (EAC13178)	Farias Brito, Ceará (CAA)
	J.R. Andrades 246 (PEUFR)	Coremas, Paraíba (CAA)
E. elegans Moric.	*M. Ataíde s.n.* (HST6769)	Ibimirim, Pernambuco (CAA)
	M.J.S. Lemos 05 (MAC)	Feira de Santana, Bahia (CAA)
	M.L. Guedes 12584 (ALCB)	Piatã, Bahia (CAA)
E. ericifolius var. *siguliflorus* Meisn.		
	E.B. Souza 4480 (HUEFS)	Granja, Ceará (CE)
	M.R.A. Mendes et al. 457 (PEUFR)	Piracuruca, Piauí (CAA)
	Roque N. et al. 3522 (ALCB)	Licínio de Almeida, Bahia (CAA)
E. ericifolius Mart.	*N.T.L. Pena* 1834 (VIES)	Nova Venécia, Espírito Santo (AF)
	Alves-Araújo et al. 1834 (VIES)	Nova Vnenécia, Espírito Santo (AF)
	C.S. Anderson 7203 (CEN)	Berizal, Minas Gerais (AF)
E. gypsophylloides Moric.	*A.M. Miranda* 6288 (EAC)	Jaguaribe, Ceará (CAA)
	D.A. Lima et al. 1272 (ASE)	Umbuzeiro, Paraiba (CAA)
	B. Freitas 151 (EAC)	Caridade, Ceará (CAA)
	F.D.S. Santos 595 (PEUFR)	Granja, Ceará (CE)
E. linoides Moric.		
	A.M. Miranda 6288 (EAC)	Jaguaribe, Ceará (CAA)
	Lima, D.A. et al. 1272 (ASE)	Umbuzeiro, Paraiba (CAA)
	B. Freitas 151 (EAC)	Caridade, Ceará (CAA)
E.* sect. *Passerinoidei		
E. daphnoides Moric.	*R.A. Silva* 1837 (HUEFS)	Glória, Bahia (CAA)
	J.G. Carvalho 2011 (HVASF)	Petrolândia, Pernambuco (CAA)
	L.P. Queiroz 7148 (HUEFS)	Canudos, Bahia (CAA)
E. genistoides Ooststr.	*O.J. Pereira et al.* 7463 (VIES)	Guarapari, Espírito Santos (AF)
	J.M.L. Gomes 2917 (VIES)	Caravelas, Bahia (AF)
	O.J. Pereira et al. 2205 (VIES)	Guarapari, Espirito Santo (AF)
	F.D.S. Santos 567 (PEUFR)	Brejinho de Ametista, Bahia (CAA)
E. imbricatus Mart.	*M.L. Guedes et al.* 25095 (ALCB)	Lagoa de Freitas, Bahia (AF)
	J.M.L. Gomes 2918 (VIES)	Caravelas, Bahia (AF)
	A.M. Miranda 4652 (EAC)	Caravelas, Bahia (AF)
E. jacobinus Moric.	*E.B. Miranda* 548 (HUEFS)	Abaíra, Bahia (CAA)
	M.N. Stapf 480 (HUEFS)	Ituberá, Bahia (CAA)
	J.C. Brito 81 (HUEFS)	Lençóis, Bahia (AF)
	F.D.S. Santos 588 (PEUFR)	Pico do Jabre, Paraiba (AF)

Sections/species	Voucher	Origin (Municipalities/state/bioma)
E. latifolius Ker Gawl.	*S.P. Gomes s.n.* (MAC37181)	Palmeira dos Índios, Alagoas (CAA)
	A.V. Popovkin 368 (HUEFS)	Entre Rios, Bahia (CAA)
	M.E. Junqueira 456 (CEN)	Cravolândia, Bahia (CAA)
E. phyllanthoides Moric.	*F.S. Araújo* 1562 (HUEFS)	Crateús, Ceará (AF)
	M.A. Figueiredo 244 (EAC)	João Pessoa, Rio Grande do Norte (CAA)
	J.G. Jardim 6231 (HUEFS)	Portalegre, Rio Grand do Norte (CAA)
E.* sect. *Phyllostachyi	*A.M. Giuliette* 2463 (HST)	Juazeiro, Bahia (CAA)
E. chamaepitys Mart.	*A.M. Giuliette* 1787 (HST)	Juazeiro, Bahia (CAA)
	H.F. Leitão-Filho et al. 1904 (HST)	Poços de Caldas, Minas Gerais (CE)
E. fuscus Meisn.		
	L.F. Souza 4754 (HJ)	Jataí, Goiás (CE)
	L.F. Souza 4638 (HJ)	Jataí, Goiás (CE)
	A.S. Aécio 1868 (CEN)	Cabeceira Grande, Minas Gerais (CE)
E. harleyi		
	G. Costa 57 (HUEFS)	Palmeira, Bahia (CE)
	J.E.Q. Farias 4428 (HUEFS)	Palmeira, Bahia (CE)
	F.D.S. Santos (PEUFR)	Rio de Contas, Bahia (CE)
E. helichrysoides Mart.		
	F. França 4172 (HUEFS)	Ibicara, Bahia (CE)
	L.V. Vasconcelos 422 (HST)	Palmeira, Bahia (CE)
	L.V. Vasconcelos 424 (HUEFS)	Palmeiras, Bahia (CE)
	F.D.S. Santos 586 (PEUFR)	Lenções, Bahia (AF)
E. kramerioides Mart.	*T. Mansur* 65 (BHCB)	Rio Acima, Minas Gerais (CE)
	M. Magalhães (BHCB)	Ouro Preto, Minas Gerais (CE)
	G.L. Pedrosa 2317 (OUPR)	Ouro Preto, Minas Gerais (CE)

the dataset. The phenogram was constructed using the UPGMA clustering algorithm, using the Euclidean distance (Sneath & Sokal, 1973).

Results

According to the analyses under stereomicroscope and scanning electron microscope (SEM), *Evolvulus* seeds present variation in both macroscopic (color, shape, and size) and microscopic characters (shape of epidermal cells, relief, and ornamentation of anticlinal cell walls, concavity, and ornamentation of the outer periclinal wall), important for the delimitation of species and the recognition of morphological clusters. These characters are summarized for each species studied in Table 3, while the stereomicroscope and SEM images are presented in Figures 1–3.

(i) General description of *Evolvulus* seeds

Seeds elliptical, ovoid, with two ventral faces and a convex dorsal one, or globoid without faces, black, brown, yellow or whitish, glabrous; 3–7-polygonal epidermis cells, irregular, sinuous or straight, smooth, wavy, folded or with fine folded anticlinal walls, elevated in relation to the periclinal walls, fluted or not; periclinal walls flat,

convex or concave, smooth, reticulated, folded, with fine folds, or striated.

(ii) Morphological Aspects

Seed color (Fig. 1a–i)

Seed color varies among species. They can be black (*E. anagalloides, E. aurigenius, E. filipes, E. nummularius, E. pohlli, E. pusillus, E. glomeratus, E. lagopodioides, E. ericifolius, E. ericifolius* var. *singuliflorus, E. gypsophylloides, E. linoides, E.daphnoides,E.jacobinus,E.latifolius,E.pterygophyllus*), yellowish (*E. convolvuloides* and *E. fuscus*) or brown (*E. alopecuroides, E. chamaepitys, E. argyreus, E. harley, E. imbricatus, E. flexuosus, E. helichrysoides, E. ovatus, E. rotundifolius, E. saxifragus, E. stellariifolius, E.saxatilis*) (Fig. 1a–c). Color variation was sometimes observed within the same individual of some species, ranging from black to brown (*E. alsinoides, E. elaeagnifolius*), black to yellowish (*E. diosmoides, E. cordatus, E. elegans, E. genistoides, E. phyllanthoides*) and brown to yellowish (*E. cardiophyllus, E. frankenioides, E. sericeus, E. pterocaulon*). From the analysed species, only *E. gnaphaloides* presented whitish seeds (Fig. 1d).

Seed shape (Fig. 1a–i)

Three shape patterns were recognized: elliptical, ovoid or globoid. Elliptical seeds comprise the largest group: *E. alopecuroides, E. alsinoides, E. anagalloides, E. cardiophyllus, E. convolvuloides, E. cordatus, E. diosmoides, E. elaeagnifolius, E. elegans, E. frankenioides, E. genistoides, E. glomeratus, E. gypsophylloides, E. harley, E. helichrysoides, E. jacobinus, E. latifolius, E. nummularius, E. pohlli, E. rotundifolius, E. saxatilis, E. saxifragus* (Fig. 1e). Ovoid seeds are found in *E. argyreus, E. aurigenius, E. daphnoides, E. ericifolius, E. ericifolius* var. *singuliflorus, E. filipes, E. flexuosus, E. gnaphaloides, E. lagopodioides, E. linoides, E. ovatus, E. pterygophyllus, E. pusillus, E. sericeus, E. stellarifolius, E. phyllanthoides, E. chamaepitys, E. fuscus* (Fig. 1f–h). Both elliptical and ovoid seeds have two flat ventral faces, and a convex dorsal face. The third group is composed only by *E. imbricatus* and *E. pterocaulon* that present globoid seeds (Fig. 1i; Table 2).

Seed size (Table 2)

To categorize seeds size, we considered small seeds < 2 mm long., and large > 2 mm long. The largest seeds were found in *E. cardiophyllus* (2.50–2.58 × 1.95–2.21 mm), *E. daphnoides* (2.87–2.96 × 2.17–2.47 mm), *E. diosmoides* (2.55–3.09 × 1.33–1.60 mm) and *E. pterocaulon* (2.56–2.62 × 1.73–1.85 mm); while the smaller ones were found in *E. saxifragus* (1.23–1.50 × 0.81–1.23 mm), *E. saxatilis* (1.25–1.42 × 1.4–1.26 mm) and *E. alsinoides* (1.26–1.31 × 1.4–1.18 mm).

Epidermal cell shape (Fig. 2a–i)

The epidermic cells were 3-4-gonal (*E. saxatilis*), 4–5-gonal (*E. chamaepitys, E. ericifolius, E. ericifolius* var. *singuliflorus, E. flexuosus, E. genistoides, E. gypsophylloides, E. jacobinus*), 5–7-gonal (*E. elegans*), polygonal elongated in one direction (*E. latifolius*) (Fig. 2a), or irregular and polygonal (found in the other species) (Fig. 2b).

Anticlinal cell wall boundaries (Figs. 2–3)

We found three variable characters of the anticlinal walls: sinuosity, ornamentation, and their position in relation to the periclinal wall. Based on sinuosity, the species can be divided into three groups, the first with wavy walls present in *E. latifolius* and *E. stellariifolius* (Fig. 2a); the second with sinuous walls, reported to *E. alsinoides, E. argyreus, E. aurigenius, E. cordatus, E. filipes, E. flexuosus, E. frankenioides, E. fuscus, E. glomeratus, E. harley, E. imbricatus, E. linoides, E. nummularius, E. ovatus, E. phyllanthoides, E. pohlli, E. pusillus, E. rotundifolius* and *E. sericeus* (Fig. 2b–c); and the last with straight walls, present in all other species studied (Fig. 2d).

The ornamentation of the anticlinal walls can vary from fine folds in *E. cordatus* and *E. ovatus* (Fig. 2e); folded in *E. daphnoides* and *E. stellariifolius* (Fig. 2f); or smooth in the other species (Fig. 2g). The anticlinal walls can be elevated in relation to the periclinal wall and fluted in *E. alsinoides, E. argyreus, E. cardiophyllus,*

E. flexuosus, E. frankenioides, E. glomeratus, E. jacobinus, E. lagopodioides, E. linoides, E. pterocaulon, E. pterygophyllus, E. saxatilis, E. stellariifolius (Fig. 2h); fluted in *E. anagalloides, E. elaeagnifolius* (Fig. 2i); or only elevated in the other species (Fig. 2g).

Outer periclinal cell wall (Fig. 3a–i)

The periclinal walls present two variable characters in the analyzed species of *Evolvulus*: concavity of the outer periclinal wall and type of ornamentation. The concavity varies from flat

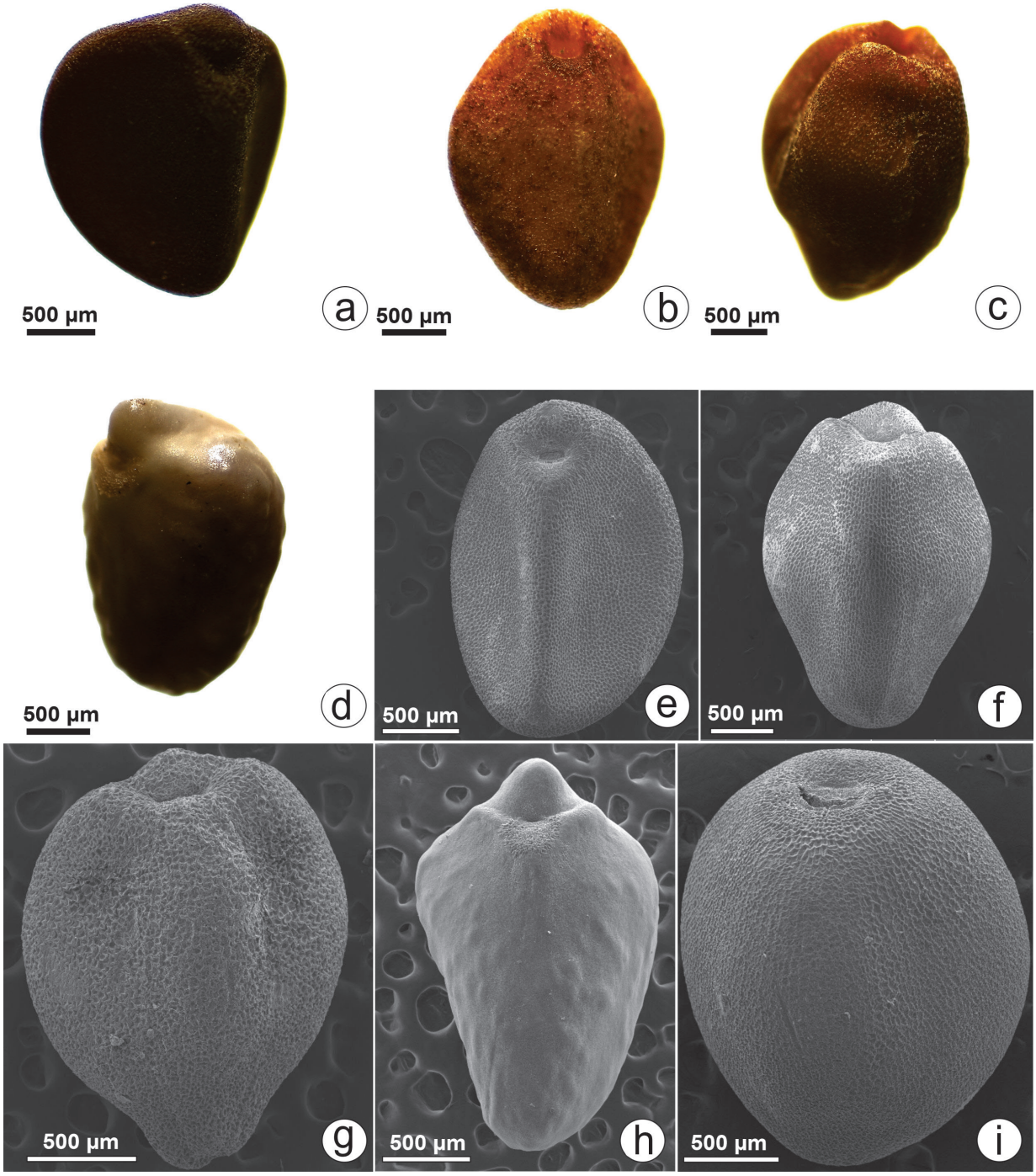

Fig. 1. Morphological aspects of *Evolvulus* seeds. Variation in seed color: **a**. Black seed of *E. nummularius* (L.) L.; **b**. Yellow seed of *E. convolvuloides* (Willd. ex Schult.) Stearn; **c**. Yellow seed of *E. phyllanthoides* Moric.; **d**. Whitish seed of *E. gnaphaloides* Moric.; **e**. Elliptically shaped seed in *E. nummularius*; **f**. Ovoid seed of *E. phyllanthoides*; **b**. Ovoid seed of *E. argyreus* Choisy; **h**. Ovoid seed of *E. gnaphaloides* Moric.; **i**. Globoid seed of *E. imbricatus* Mart. ex Colla.

in *E. anagalloides, E. chamaepitys, E. cordatus, E. elegans, E. ericifolius, E. ericifolius* var. *singuliflorus, E. filipes, E. gnaphaloides, E. gypsophylloides, E. harley, E. imbricatus, E. linoides, E. ovatus, E. pusillus, E. rotundifolius, E. saxatilis* (Fig. 3a); convex in *E. elaeagnifolius* (Fig. 3b), and concave in the other species (Fig. 3c). Regarding the type of ornamentation of the periclinal walls, the species can be divided into four groups. Smooth walls are found in *E. alsinoides, E. anagalloides,*

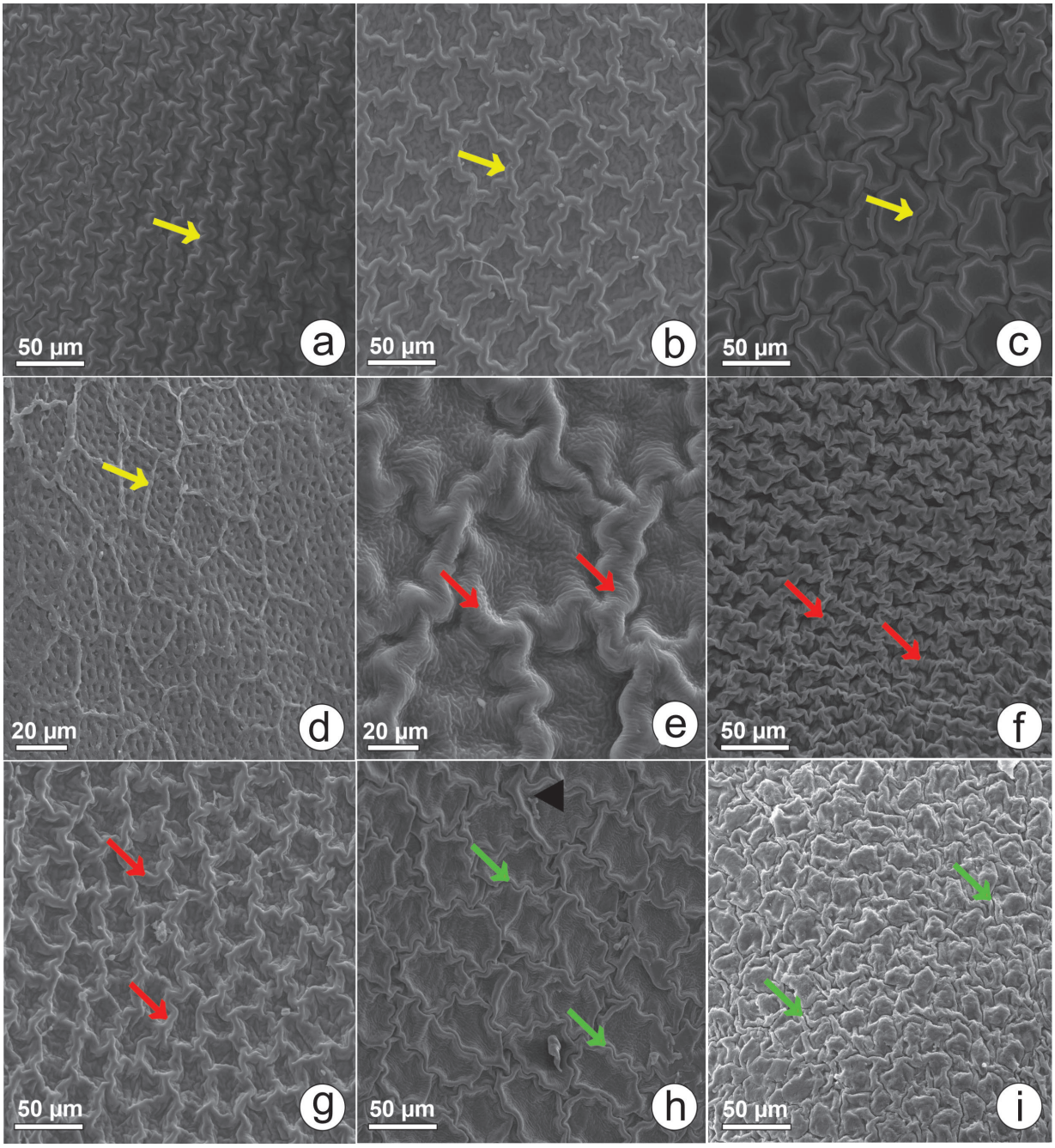

Fig. 2. Detail of the epidermal surface of *Evolvulus* seeds showing the shape of the epidermal cells, ornamentation, and sinuosity of the anticlinal walls. Yellow arrows show the sinuosity of the anticlinal walls; red arrows show the ornamentation of the anticlinal walls; and green arrows indicate the arrangement of the anticlinal walls in relation to the outermost periclinal wall: **a**. Elongated cells and wavy anticline walls in *E. latifolius* Ker Gawl.; **b**. Detail of the sinuous anticline walls of *E. rotundifolius* (S.Watson) Hallier f.; **c**. Slightly sinuous anticline walls in *E. flexuosus* Helwig; **d**. Straight anticline walls in *E. gnaphaloides*; **e**. Anticlinal walls ornamented with fine folds in *E. cordatus* Moric.; **f**. Bent anticline walls in *E. stellariifolius* Ooststr.; **g**. Smooth anticline walls in *E. nummularius* (L.) L.; **h**. Elevated and fluted anticlinal walls in *E. glomeratus* Nees & Mart.; **i**. Fluted and non-elevated anticlinal walls in *E. elaeagnifolius* Dammer.

E. diosmoides, E. elaeagnifolius, E. ericifolius, E. ericifolius var. *singuliflorus, E. flexuosus, E. filipes, E. genistoides, E. jacobinus, E. lagopodioides, E. linoides, E. phyllanthoides, E. pterygophyllus, E. sericeus* (Fig. 3a). Walls with thin folds occurs in *E. aurigenius, E. cardiophyllus, E. chamaepitys, E. cordatus, E. glomeratus, E. pohlli, E. pterocaulon* (Fig. 3d–e). Reticulated walls occur only in *E. gnaphaloides* (Fig. 3f), and folded walls occur in all other species (Fig. 3g–i).

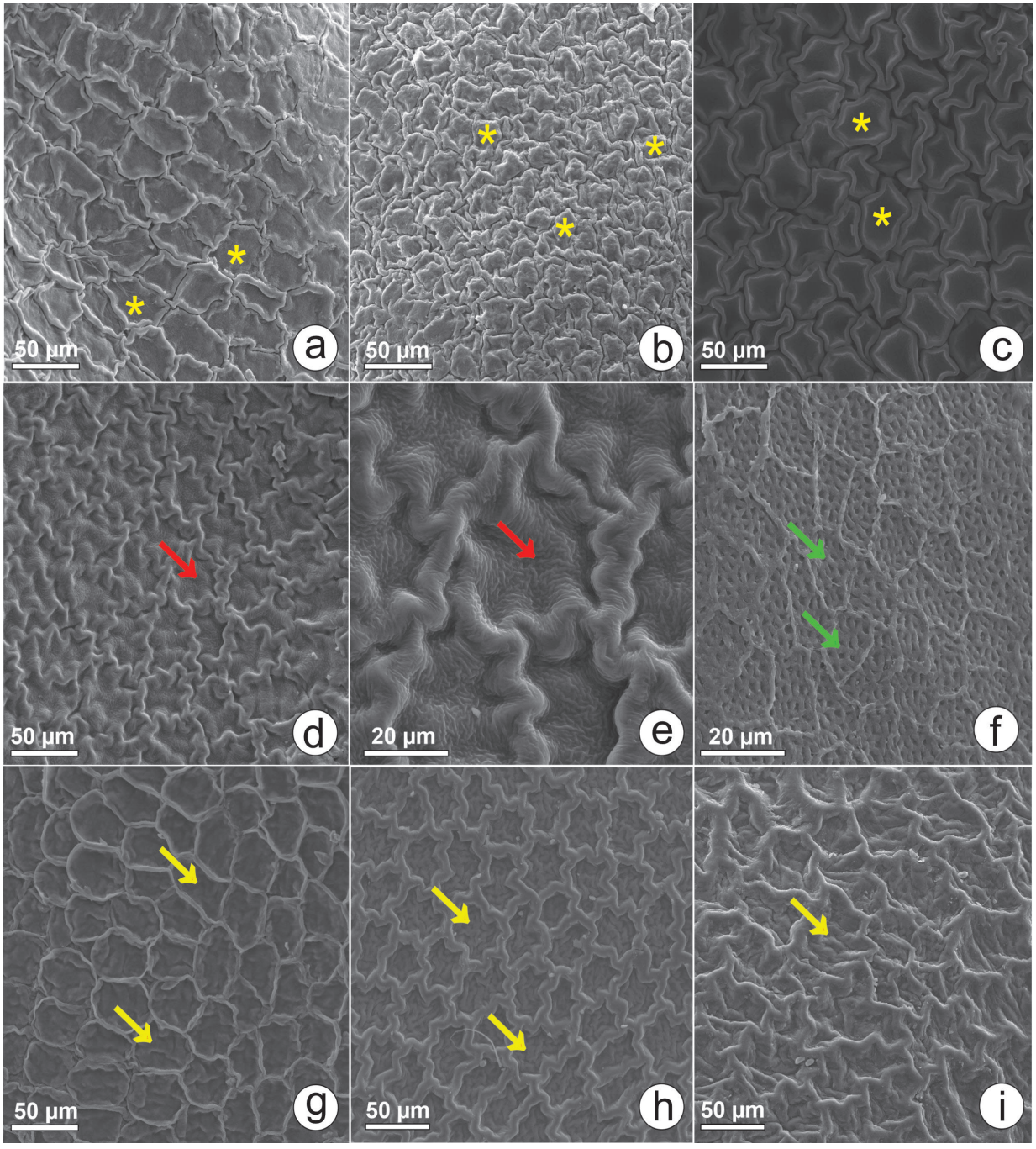

Fig. 3. Detail of the outer periclinal wall of the epidermis cells of *Evolvulus* seeds. Variation in concavity and periclinal wall ornamentation. Asterisks indicate the concavity of the outer periclinal wall, while arrows show ornamentation: **a**. Flat periclinal wall of *E. linoides* Moric.; **b**. Convex periclinal wall of *E. elaeagnifolius* Dammer; **c**. Concave periclinal wall of *E. genistoides* Oostrst.; **d**. Periclinal wall with fine folds of *E. cordatus* Moric. (red arrows); **e**. Detail of the ornamentation of the periclinal wall of *E. cordatus*; **f**. Reticulated periclinal walls of *E. gnaphaloides* Moric. (green arrows); **g-i**. Folded periclinal walls of *E. elegans* Moric., *E. rotundifolius* (S.Watson) Hallier **f**. and *E. imbricatus* Mart. ex Colla, respectively.

(iii) Phenetic analysis

The phenetic analysis resulted in a phenogram (Fig. 4a–g) that revealed the presence of seven groups in *Evolvulus*, according to the morphological characterization of the seeds. Group A is composed only of *E. gnaphaloides*, whose exclusively present reticulated anticlinal wall and whitish seeds. Group B comprises *E. cordatus, E. harleyi, E. helichrysoides, E. imbricatus, E. ovatus, E. pusillus, E. rotundifolius*, and *E. saxatilis*, which share a flat, folded periclinal wall (most) or with fine folds. Group C is composed of some species that belong to the sections *Alsinoidei, Involucrati, Passerinoidei*, and *Phyllostachyi*, which together have smooth anticlinal walls. Group D is formed by *E. alopecuroides* and E. *chamaeptys* (both belong to the *Phyllostachyi* section), which have straight and smooth anticline walls, flat periclinal walls with thin folds. Seeds shape is ovoid in E. *chamaepitys*, while in *E. alopecuroides* are elliptical. Group E is composed of species circumscribed in the *Linoidei* section (*E. elaeagnifolius, E. elegans, E. linoides, E. ericifolius, E. ericifolius* var. *singuliflorus* and *E. gypsophylloides*), and share smooth, straight anticlinal walls (sinuous in *E. linoides*), and flat periclinal walls (convex in *E. elaeagnifolius*). Group F is formed by only three species that belong to the *Lagopodini* section (*E. lagopodioides, E. pterocaulon* and *E. pterygophyllus*), which share straight and smooth anticline walls. Group G is composed of two species, *E. daphnoides* which belong to the section *Passerinoidei*, and *E. stellarifolius* which belong to the section *Alsinoidei*. Both species were grouped together by sharing folded anticlinal walls and concave and folded periclinal walls.

The macromorphological characters of the seeds do not corroborate the infrageneric classification, being variable, sometimes, within the same population. On the other hand, the characters associated with the anticline walls (sinuosity and ornamentation) should be investigated as a possible synapomorphy of the *Linoidei* section the light of molecular phylogeny, since all its species (*E. elaeagnifolius, E. elegans, E. linoides, E. ericifolius, E. ericifolius* var *singuliflorus* and *E. gypsophylloides*) have smooth and straight anticlinal walls. The

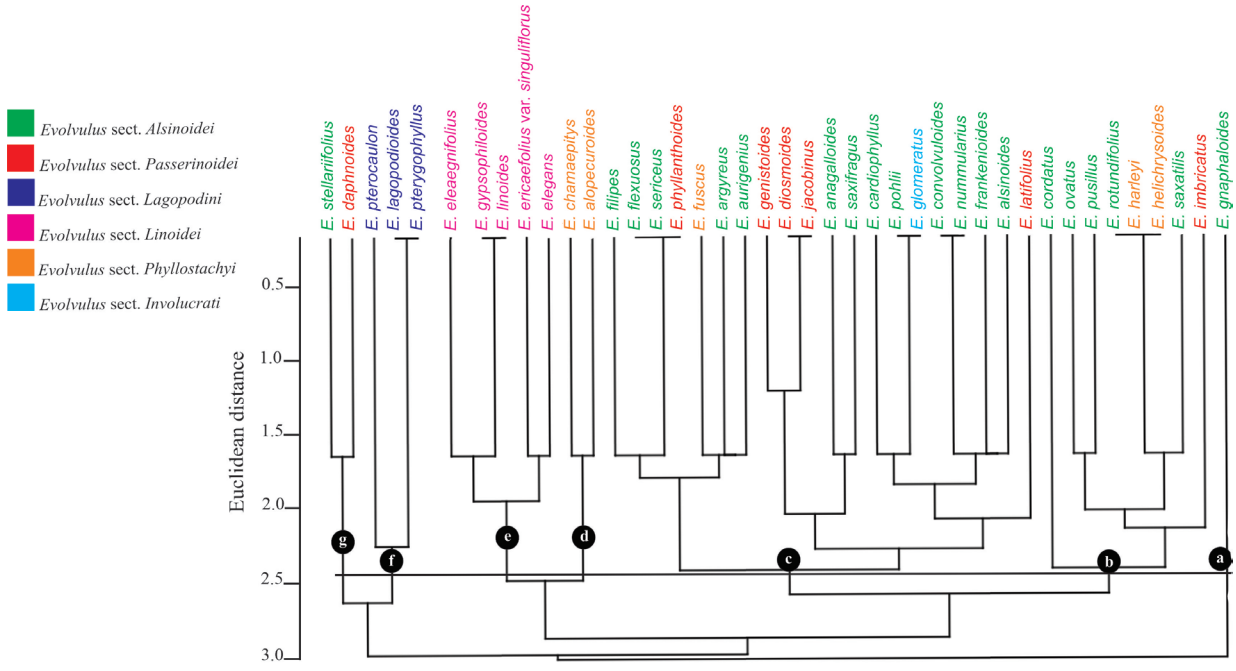

Fig. 4. Phenogram generated from the similarity of seed characters of the studied species of *Evolvulus*. Group: **a**. whitish seeds and reticulated anticline walls; **b**. flat periclinal wall, folded (most) or with fine folds; **c**. smooth anticline wall; d. straight and smooth anticlinal walls, flat periclinal walls with thin folds; **e**. smooth, straight anticline walls (sinuous in *E. linoides* Moric.), and flat periclinal walls (convex in *E. elaeagnifolius* Dammer); **f**. straight and smooth anticlinal walls; **g**. folded anticline walls and concave and folded periclinal walls.

Lagopodini section, represented here by three species (*E. lagopodioides*, *E. pterocaulon* and *E. pterygophyllus*) has straight and smooth anticline walls, but these character states also appear in several other species.

Discussion

(i) Taxonomic implications

Our results demonstrate that seed characters can be used to distinguish species in *Evolvulus* and provide insights for an infrageneric classification. Even though some of the traits can vary within an individual, features of the anticlinal and periclinal walls are stable at a specific level.

Although we recognize three groups of species from the seed's color (black, yellow, and brown seeds), it can sometimes vary in the same individual, such as in *E. alsinoides* and *E. cordatus*. This variation was also observed in species of other genera as in *Convolvulus*, whose seeds vary from black in *C. prostratus* Forssk and *C. schimperi* Boiss, to brown in *C. dorycnium* L. and *C. fatmensis* Kunze. Color variation within the same individual was reported for *C. hystrix*, where both yellow and brown seed coats are observed. *Evolvulus gnaphaloides* was the only studied species with whitish seeds. This species occurs exclusively in sandy dunes under high light incidence and low water potential (Junqueira & Bianchini, 2006), which may justify the color of its seeds as an adaptive advantage for this environment, as it confers greater retractability of light radiation, preventing the loss of water from the embryo until germination (Barthlott, 1981).

Neither the size categories nor shape patterns found here (elliptical, ovoid, and globoid) support the current infrageneric classification in *Evolvulus*. The same variation on shape was also observed in *Ipomoea* (Khalik & Osman, 2007) and in *Cuscuta* (Khalik, 2006). As for the seed microcharacters, the shape of the epidermal cells was variable among the species of the same section in *Evolvulus*.

The epidermal cells in *Evolvulus* have well-developed anticlinal walls, whose sinuosity forms three morphological patterns (wavy, sinuous, and straight) that do not correspond to the sections, as all of them were observed within the *Alsinoidei* section. On the other hand, the variation of these patterns helps to delimit morphologically similar pair of species, such as *E. glomeratus* and *E. saxatilis*, *E. nummularius* and *E. pohlii*, *E. cardiophyllus* and *E. latifolius* (Table 2). This variation was also observed in the delimitation of species of *Ipomoea* (Khalik & Osman, 2007).

The ornamentation patterns of the anticlinal walls (folded, fine folds, and smooth folds) were also incongruent with the infrageneric classification in *Evolvulus*, since they were all observed among species of *E.* sect. *Alsinoidei*. Despite this, it was possible to observe two well-defined groups of species, one with folded anticline walls and walls with thin folds, represented only by *E. gnaphaloides*, *E. ovatus*, *E. stellariifolius*, and another with smooth walls, represented by the other species in this section. On the other hand, smooth anticlinal walls were observed in species of *Involucrati*, *Lagopodini*, *Linoidei* and *Phyllostachyi* sections. These patterns were useful in delimiting species in *Ipomoea* (Khalik &Osman, 2007). Furthermore, they are useful in understanding phylogenetic relationships in other plant groups, such as in Cucurbitaceae (Heneidak & Khalik, 2014).

The patterns related to the elevation of the anticlinal walls in relation to the periclinal do not support the sections in *Evolvulus*, as all patterns were observed in the *Alsinoidei* section. The high anticline wall pattern is present in all representatives of the *Lagopodini* and *Phyllostachyi* sections, while the fluted pattern was observed only in *E. anagaloides* and *E. elaeagnifolius*, both belonging to different sections.

Flat or concave periclinal walls were observed in species from sections *Alsinoidei*, *Involucrati*, *Passerinoidei*, and *Phyllostachyi*, while in species from *E.* sect. *Lagopodini* only the concave pattern was observed. Species of *E.* sect. *Linoidei* present

concave or rarely convex walls in *E. elaeagnifolius*, possibly suggesting the autapomorphic nature of this species.

(ii) Ecological and biogeographic insights

Environmental changes usually affect the seed surface, as different carvings have different specialized functions, such as the regulation of embryo temperature (Johnson, 1975; Eller, 1979; Barthlott & Wollenweber, 1981). However, micromorphological patterns of seeds are genetically determined, conferring adaptive value to the species to survive in certain environmental conditions (Barthlott, 1981).

Evolvulus species often occur in Seasonally Dry Tropical Forest environments of the Neotropical region with high light incidence (Oostrstroom, 1934; Junqueira & Simão-Bianchini, 2006; BFG, 2018). This distribution may be related, together with other features, to the presence of seeds with an ornamented surface, giving them adaptive value to survive in these environments. Barthlott (1981) stated that species that inhabit environments with high light incidence usually have seeds with sculpted surfaces. Also, according to this author, these surfaces, such as sinuous anticlinal walls, function as a mechanism to control the temperature of the tegma by enlarging its surface, enhancing the effect of the reflectivity of solar radiation. Thus, this effect may be one of the factors that help to understand the adaptability of *Evolvulus* species for areas with high light incidence.

The surface characteristics of *Evolvulus* seeds appear to be unrelated to the geographic distribution of its species. Taxa widely distributed in the Americas, such as *E. alsinoides*, *E. ovatus* and *E. sericeus* (Oostrstroom, 1934) exhibit different patterns of character states on the surface of their seeds. The consistency of these characters can also be observed in the seeds of *I. cairica* (Khalik & Osman, 2007), whose distribution extends across the Americas (Wood *et al.,* 2020). The same can be observed in endemic species of the Caatinga domain, such as *E. anagaloides*, *E. daphnoides* and *E. elaeagnifolius*, which have different character states associated with anticlinal and periclinal walls.

On the other hand, most species of *E.* sect. *Linoidei* (*E. elegans*, *E. ericifolius* var. *singuliflorus* Meisn., *E. gypsophylloides*, *E. linoides*), despite having the same anticlinal and periclinal walls characteristics, they are distributed in different environments, such as Caatinga, Cerrado or Atlantic Forest. This was also observed by Khalik and Osman (2007) when analyzing the testa surface of *Ipomoea* and *Cuscuta* seeds, showing that populations inhabiting different environments have the same morphological patterns. If microcharacters of the seeds are genetically determined, not being affected by environmental conditions, as stated by Barthlott (1981), it can contribute to the delimitation of polymorphic species in *Evolvulus*.

Conclusion

The results presented here demonstrate that seed morphology supports the circumscription of two sections currently accepted for *Evolvulus*: *E.* sect. *Lagopodini* and *E.* sect. *Linoidei*. In addition to that, most of the seed characters do not vary among populations from different distribution areas, therefore, they are not influenced by environmental variables. Thus, we conclude that seed characters can be used to understand the morphological extremes of polymorphic species, and can be used to elucidate taxonomic complexes in *Evolvulus*. Furthermore, such characteristics may be useful for understanding possible relationships between species in light of future phylogenetic studies.

Acknowledgments

We express our gratitude to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a scholarship to the first author (Process No. 88882.436296/2019-01) and to Susan Casement for reviewing the English language of the manuscript.

Table 3. Seed morphological characters of the studied species in *Evolvulus*.

Section/species	Seeds color	Seed shape	Seed size (long x wide) mm	Epidermal cell shape	Anticlinal cell wall boundaries	Periclinal cell wall
E. sect. Alsinoides						
E. alsinoides (L.) L.	black to brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.26-1.31 × 1.4-1.18	irregular, polygonal cell	sinuous, smooth, raised-fluted	concave, smooth
E. anagalloides Meisn	Black	elliptic, 2 flat ventral faces, one convex dorsal face	1.74-1.90 × 1.24-1.87	irregular, polygonal cells	straight, smooth, fluted	flat, smooth
E. argyreus Choisy	Brown	ovoid, 2 flat ventral faces, one convex dorsal face	1.65-2.73 × 1.85-2.75	irregular, polygonal cells	sinuous, smooth, raised-fluted	concave, striate
E. aurigenius Mart.	Black	ovoid, 2 flat ventral faces, one convex dorsal face	2.46-2.93 × 1.53-1.87	irregular, polygonal cells	sinuous, raised, smooth	concave, fine folds
E. cardiophyllus Schltdl	brown to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	2.50-2.58 × 1.95-2.21	irregular, polygonal cells	straight, raised-fluted, smooth	concave, fine folds
E. convolvuloides Stearn	Yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	2.10-2.30 × 1.65-1.67	irregular, polygonal cells	sinuous, raised, smooth	concave, folded
E. cordatus Moric.	black to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	1.48-1.58 × 1.26-1.55	irregular, polygonal cells	sinuous, raised, fine folds	flat, fine folds
E. filipes Mart.	Black	ovoid, 2 flat ventral faces, one convex dorsal face	1.32-1.47 × 1.04-1.26	irregular, polygonal cell	sinuous, raised, smooth	flat, smooth
E. flexuosus Mart.	Brown	ovoid, 2 flat ventral faces, one convex dorsal face	2.16-2.43 × 1.53-1.76	4-5 gonal cell	sinuous, raised-fluted, smooth	concave, smooth
E. frankenioides Moric.	brown to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	1.75-1.81 × 1.11-1.26	irregular, polygonal cell	sinuous, raised-fluted, smooth	concave, striate
E. gnaphaloides Moric.	Whitish	ovoid, 2 flat or convex ventral faces, one convex dorsal face	1.77-2.31 × 1.23-1.83	irregular, polygonal cell	straight, raised, fine folds	flat, reticulate
E. nummularius (L.) L.	black	elliptic, 2 flat ventral faces, one convex dorsal face	1.87-2.08 × 1.52-1.58	irregular, polygonal cells	sinuous, raised, smooth	concave, folded
E. ovatus Fernald.	brown	ovoid, 2 flat ventral faces, one convex dorsal face	1.32-1.67 × 1.31-1.43	irregular, polygonal cell	sinuous, raised, fine folds	flat, folded
E. pohlli Meisn.	black	elliptic, 2 flat ventral faces, one convex dorsal face	1.55-1.65 × 1.22-1.27	irregular, polygonal cell	sinuous, raised, smooth	concave, fine folds

Section/species	Seeds color	Seed shape	Seed size (long x wide) mm	Epidermal cell shape	Anticlinal cell wall boundaries	Periclinal cell wall
E. pusillus Choisy	black	ovoid, 2 flat ventral faces, one convex dorsal face	1.68-2.0 × 1.25-1.55	irregular, polygonal cell	sinuous, raised, smooth	flat, folded
E. rotundifolius (S.Watson) Hallier f.	brown	elliptic, 2 flat ventral faces, one convex dorsal face	2.03-2.12 × 1.87-1.90	irregular, polygonal cells	sinuous, raised, smooth	flat, folded
E. saxifragus Mart.	brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.23-1.50 × 0.81-1.23	irregular, polygonal cell	sinuous, raised, smooth	flat, smooth
E. sericeus Sw.	brown to yellowish	ovoid, 2 flat ventral faces, one convex dorsal face	1.71-1.97 × 1.42-1.95	irregular, polygonal cell	sinuous, raised, smooth	concave, smooth
E. stellariifolius Ooststr.	brown	ovoid, 2 flat ventral faces, one convex dorsal face	1.28-1.64 × 0.93-1.14	irregular, polygonal cell	undulate, raised, fluted, folded	concave, folded
E.* sect. *Involucrati						
E. glomeratus Ness & Mart.	black	elliptic, 2 flat ventral faces, one convex dorsal face	2.12-2.22 × 1.75-1.84	polygonal cells	sinuous, raised, fluted, smooth	concave, fine folds
E. saxatilis D.Santos & Buril	brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.25-1.42 × 1.4-1.26	3-4polygonal	straight, raised, fluted, smooth	flat, folded
E.* sect. *Lagopodini						
E. lagopodioides Meisn.	black	ovoid, 2 flat ventral faces, one convex dorsal face	2.2-2.8 × 1.45-1.64	irregular cells	straight, raised, fluted, smooth	concave, smooth
E. pterygophyllus Mart.	black	ovoid, 2 flat ventral faces, one convex dorsal face	2.2-2.8 × 1.45-1.64	irregular cells	straight, raised, fluted, smooth	concave, smooth
E. pterocaulon Moric.	brown to yellowish	globoid, absence of faces	2.56-2.62 × 1.73-1.85	irregular cells	straight, raised, fluted, smooth	concave, fine folds
E.* sect. *Linoidei						
E. elaeagnifolius Dammer	black to brown	elliptic, 2 flat ventral faces, one convex dorsal face	2.26-2.28 × 1.66-1.82	irregular cells	straight, fluted, smooth, no raised	convex, smooth
E. elegans Moric.	black to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	1.47-1.67 × 1.18-1.55	5-7 gonal cells	straight, raised, smooth	flat, folded
E. ericifolius Mart.	black	ovoid, 2 flat ventral faces, one convex dorsal face	1.35-1.55 × 1.20-1.25	4-5 gonal cells	straight, raised, smooth	flat, smooth
E. ericifolius var. *singuliflorus* Meisn.	black	ovoid, 2 flat ventral faces, one convex dorsal face	1.40-1.64 × 1.23-1.28	4-5 gonal cells	straight, raised, smooth	flat, folded

Section/species	Seeds color	Seed shape	Seed size (long x wide) mm	Epidermal cell shape	Anticlinal cell wall boundaries	Periclinal cell wall
E. gypsophylloides Moric.	black	elliptic, 2 flat ventral faces, one convex dorsal face	1.91-2.21 × 1.55-1.69	4-5 gonal cells, elongate in one direction	straight, raised, smooth	flat, folded
E. linoides Moric.	black	ovoid, 2 flat ventral faces, one convex dorsal face	1.45-1.74 × 1.23-1.50	irregular cells	sinuous, raised, cancelled, smooth	flat, smooth
E.* sect. *Passerinoidei						
E. daphnoides Moric.	black	ovoid, 2 flat ventral faces, one convex dorsal face	2.87-2.96 × 2.17-2.47	irregular cells	straight, raised, folded	concave, folded
E. diosmoides Mart.	black to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	2.55-3.09 × 1.33-1.60	4-5 gonal cells	straight, raised, smooth	concave, smooth
E. genistoides Moric.	black to yellowish	elliptic, 2 flat ventral faces, one convex dorsal face	2.50-3.09 × 1.30-1.60	4-5 gonal cells	straight, raised, smooth	concave, smooth
E. imbricatus Mart.	brown	globoid, absence of faces	1.70-1.91 × 1.51-1.91	irregular cells	sinuous, raised, smooth	flat, folded
E. jacobinus Moric.	black	elliptic, 2 convex ventral faces, one convex dorsal face	1.29-1.67 × 1.18-1.55	4-5 gonal cells	straight, raised, cancelled, smooth	concave, smooth
E. latifolius Ker Gawl.	black	elliptic, 2 flat ventral faces, one convex dorsal face	2.41-2.85 × 1.63-2.11	elongate in one direction	undulate, raised, smooth	concave, folded
E. phyllanthoides Moric.	black to yellowish	ovoid, 2 flat ventral faces, one convex dorsal face	2.45-2.80 × 1.56-1.81	irregular, polygonal cells	sinuous, raised, smooth	concave, smooth
E.* sect. *Phyllostachyi						
E. alopecuroides Mart.	brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.44-1.50 × 1.48-1.55	4-5 gonal cells	straight, raised, smooth	flat, fine folds
E. chamaepitys Mart.	brown	ovoid, 2 flat ventral faces, one convex dorsal face	2.1-2.5 × 1.47-1.63	4-5 gonal cells	straight, raised, smooth	flat, fine folds
E. fuscus Meisn.	yellowish	ovoid, 2 flat ventral faces, one convex dorsal face	1.90-1.91 × 1.64-1.70	irregular cells	sinuous, raised, smooth	concave, folded
E. harley	brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.42-1.45 × 1.48-1.53	polygonal cells, elongate in one direction	sinuous, raised, smooth	flat, folded
E. helichrysoides Mart.	brown	elliptic, 2 flat ventral faces, one convex dorsal face	1.69-1.74 × 1.0-2.4	4-5 gonal cells	straight, raised, smooth	flat, fine folds

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Table 2. Binary matrix of macro and micromorphological characters of *Evolvulus* species. Values: 0=absence; 1=presence. abbreviations: os: ovoid seed; es: elliptical seed; gs: globoid seed; waw: wavy anticlinal walls; saw: sinuous anticlinal walls; staw: straight anticlinal walls; awtf: anticlinal wall with thin folds; awf: anticlinal walls folded; aws: anticlinal walls smooth; pwf: anticlinal walls flat; pwcx: periclinal walls convex; pwc: periclinal walls concave; pws: periclinal walls smooth; pwtf: periclinal walls with thin folds; pwr: periclinal walls reticulated; pwf: periclinal walls folded; pws: periclinal walls striate.

Species	os	es	gs	waw	siaw	staw	awtf	awf	as	pwf	pwcx	pwc	pws	pwtf	pwr	pwf	pws
E. alsinoides (L.) L.	0	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
E. anagalloides Meisn.	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0
E. argyreus Choisy	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1
E. aurigenius Mart.	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
E. cardiophyllus Schltdl	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0
E. convolvuloides Stearn	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0
E. cordatus Moric.	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0
E. filipes Mart.	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0
E. flexuosus Mart.	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
E. frankenioides Moric.	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1
E. gnaphaloides Moric.	1	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0
E. nbummularius (L.) L.	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0
E. ovatus Fernald.	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0
E. pohlli Meisn.	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
E. pusillus Choisy	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0
E. rotundifolius (S.Watson) Hallier f.	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0
E. saxifragus Mart.	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0
E. sericeus Sw.	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
E. stellariifolius Ooststr.	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0

Species	os	es	gs	waw	siaw	staw	awtf	awf	as	pwf	pwcx	pwc	pws	pwtf	pwr	pwf	pws
E. glomeratus Ness & Mart.	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0
E. saxatilis D.Santos & Buril	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0
E. lagopodioides Meisn.	1	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0
E. pterygophyllus Mart.	1	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0
E. pterocaulon Moric.	0	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	0
E. elaeagnifolius Dammer	0	1	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0
E. elegans Moric.	0	1	0	1	0	1	0	0	1	1	1	0	0	0	0	1	0
E. ericifolius Mart.	1	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0
E. ericifolius var. *siguliflorus* Meisn.	1	0	0	1	0	1	0	0	1	1	1	0	0	0	0	1	0
E. gypsophylloides Moric.	0	1	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0
E. linoides Moric.	1	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0
E. daphnoides Moric.	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0
E. diosmoides Mart.	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1
E. genistoides Moric.	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1
E. imbricatus Mart.	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0
E. jacobinus Moric.	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0
E. latifolius Ker Gawl.	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0
E. phyllanthoides Moric.	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
E. alopecuroides Mart.	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0
E. chamaepitys Mart.	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0
E. fuscus Meisn.	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0
E. harleyi C.V. da Silva & Sim.-Bianch.	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0
E. helichrysoides Mart.	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0