DIVERSIFICATION OF SEED CHARACTERS IN THE CLEOMACEAE

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Abstract

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A comprehensive analysis of seed coat micromorphology was performed with scanning electron microscopy on seeds of 24 of the 26 genera currently recognized in the family Cleomaceae. Micromorphological characters such as cell shape, shape and ornamentation of periclinal and anticlinal walls, epicuticular residues, hairs, and arils are presented. Analysis of seed coat characters show that they are a useful in differentiating lineages of the family. Some genera have highly specific characters with little variation and others have greater variability. Cleomaceae has undergone a systematic revision in the past decade producing a robust phylogenetic framework to interpret patterns of evolution. Results demonstrate that seed coat characters provide reliable support to the classification of genera in Cleomaceae and could inform evolutionary patterns in future studies.

TABLE OF CONTENTS

Page

ACKNOWLEDGMENT....................iii

ABSTRACT iv

LIST OF TABLES vi

LIST OF FIGURES vii

INTRODUCTION 1

METHODOLOGY 7

RESULTS 9

DISCUSSION 14

CONCLUSION…....................21

SEED DESCRIPTIONS…....................22

REFERENCES....................117

APPENDIX

CODING SCHEME FOR PHYLOGENETIC TREES 127

PHYLOGENETIC TREES WITH SEED CHARACTER STATES 131

LIST OF TABLES

Page

Table 1: Taxon Sampling..96

Table 2: Character Definitions..104

Table 3: Major Seed Coat Characters of Species..105

LIST OF FIGURES

Page

Figures 1–40: Seed SEM Images 56–95

INTRODUCTION

The role of seeds and seed coat characters in plant development and taxonomy—Seeds are fertilized and matured ovules that develop in the fruits of flowering plants. They provide a protective external barrier for the embryo until germination and nutrition for the developing seedling (Bhatnagar & Johri, 1972). Because most seedlings will not survive, a plant usually produces more ovules and seeds than will eventually become mature plants (Charlesworth, 1989; Kärkkäinen et al., 1999). This production can be limited by a number of factors including insufficient pollen to fertilize ovules (Charlesworth, 1989), not enough resources for all fruit to set or fertilized seeds to develop (Charlesworth, 1989; Evenari, 1984; Stanton et al., 1987), and various stresses during maturation or during germination (Kranner et al., 2010). The seed coat serves as a major barrier to the environment and potential stressors. In seeds with bitegmic ovules, the outer and inner integuments form the testal and tegmic mechanical layers respectively (Corner, 1974). Corner (1976) referred to endo-, meso-, and exotestal and endo-, meso-, and exotegmic seeds as those derived from the outer epidermis, middle, or inner layers of the outer and inner integuments (Baskin et al., 2000), and determined that the majority of plant families can be distinguished by the predominance of one layer over another.

Seed evolution is important to understand because it represents a major life history transition of the plant (Eriksson et al., 2000; Tiffney, 1984). Earliest evidence of angiosperm diversification come from fossils from the Early Cretaceous (Dilcher, 2000; Friis et al., 2015). Recent advances in microscopy have shown fossilized embryos and surrounding nutritive tissues from the Early Cretaceous (Friis et al., 2015) informing further hypotheses of seed evolution. Seed coats typically have been understood to have three main functions: protect the embryo, assist in dormancy, and aid in dispersal (Haughn & Chaudhury, 2005; Morris, 2000). Seed coat structures such as mucilage and hairs have evolved in some taxa to assist in these functions (Palací et al., 2004; Yang et al., 2012) and can be more prevalent in certain families and genera.

Seed morphology is diverse across angiosperms and investigations of seed characters can be used to understand character changes across a phylogeny and provide potential synapomorphies for clades. In a seminal work on seed coat characters of 5,000 species of angiosperms and 100 species of gymnosperms, Barthlott (1981) described primary, secondary, and tertiary sculpture of seed coats. In particular, secondary wall thickenings and the anticlinal walls outlining cells of the seed coat were high in taxonomic significance, potentially characterizing taxa between the species and genus-level (Barthlott, 1981). Macro- and micromorphological characters of plants are useful for the delimitation of species, genera, or higher ranks in many groups of flowering plants. Seeds are an underused resource that are readily available on herbarium sheets or collected from mature plants in the field. Of the different character traits of the plant, seed morphology has especially been demonstrated to be valuable in other families for defining taxa (Barthlott & Hunt, 2000; Bouman, 1995; Caddick et al., 2002; Ocampo et al., 2014; Simões et al., 2010).

Scanning electron microscopy (SEM) has long been used as a way to describe novel characters of plants, identify potential homologies, and place morphological characters within a systematic or phylogenetic framework. SEM analysis of seeds has helped in defining subfamilies and tribes of ginger (Benedict et al., 2015), subtribes of plantain and brassica (Ahedor & Elisens, 2015; Koul, 2000), and genera of Acanthaceae, Polemoniaceae, and Annonaceae (Al-Hakimi et al., 2015; Johnson et al., 2004; Tang et al., 2015).

The family Cleomaceae—Species of Cleomaceae are found on all continents except Antarctica with high diversity in South America, South and NE Africa, Australia, and SW Asia and more limited diversity in most temperate regions (Iltis, 1957). Several species, including *Gynandropsis gynandra*, *Corynandra viscosa*, and *Sieruela rutidosperma*, are known pantropical weeds (Iltis, 1960). Cleomaceae is thought to have a center of origin in SW Asia and Africa with radiations to pantropical areas (Cardinal-McTeague et al., 2016; Feodorova et al., 2010) and is hypothesized to have diverged from the core Brassicales in the Eocene (~50 Mya) (Cardinal-McTeague et al., 2016) suggesting a much older divergence than previously thought (Feodorova et al., 2010). Seed characters of Cleomaceae were first recognized as having systematic value in delimiting genera (Iltis et al., 2011) and species complexes (Kers 1966, 1969, 1973; Sánchez-Acebo, 2005, Iltis unpub. data). Recently, a species wide examination of seeds among the Indian and Australasian clades have been helpful in determining genera (Barrett et al., 2017).

Accurate classifications are the foundation for most biological research (Chase et al., 2016; Christenhusz et al., 2015; Wearn et al., 2013). Cleomaceae has undergone a major classification revision over the last decade. The family is well-supported as sister to Brassicaceae (Iltis et al., 2011), and the general consensus is that the Cleomaceae is best treated as a separate family from Brassicaceae (Iltis et al., 2011). Relationships among lineages within Cleomaceae have only become reasonably understood over the past decade (Barrett et al., 2017; Feodorova et al., 2010; Patchell et al., 2014). Historically, Cleomaceae was separated into ~15-18 genera (Patchell et al., 2014), most containing 1–36 species with the remaining 200+ placed in the type genus *Cleome*. Numerous studies have made it clear that *Cleome* s.l. is not monophyletic (Feodorova et al., 2010; J. C. Hall, Sytsma, & Iltis, 2002; Patchell et al., 2014). This has led to major generic reorganization of the family (Iltis & Cochrane, 2007; Cochrane & Iltis, 2014; Iltis & Cochrane, 2014; Roalson et al., 2015; Barrett et al., 2017; Roalson & Hall, 2017; Soares Neto et al., 2017; Thulin & Roalson, 2017). The current state of classification in Cleomaceae supports ~26 genera (Barrett et al., 2017; Roalson & Hall, 2017; Roalson, unpubl. data) based on combined molecular phylogenetic and morphological studies. Continued study of additional character variation can greatly assist our current understanding of morphological variation in Cleomaceae and help reconcile our understanding of lineage's characteristics.

Morphology—Cleomaceae has been distinguished from Brassicaceae based on the presence of palmately compound leaves, monosymmetric flowers with four sepals, four petals, and usually six stamens, dehiscent capsular fruits without a septum, and incumbent cotyledons (Hall et al., 2002; Iltis et al., 2011; Patchell et al., 2014). Furthermore, the seeds of Cleomaceae are distinctly dry, cochlidospermous or horseshoe-shaped with a testal invagination or cleft between the radicular and cotyledonar claws (Iltis et al., 2011; Kers, 1966, 1969, 1973). The seed cleft may be open or closed, and with or without a connecting membrane. Seeds also may be arillate or have wax-like residues.

Economic and pharmacological properties—Several species of Cleomaceae are used and valued for their nutritional and chemical properties. The young shoots and leaves of *Arivela viscosa* are eaten as a vegetable in NW India (Upadhyay, 2015). *Gynandropsis gynandra* and *Sieruela monophylla* are grown and eaten as annual herbs in South Africa (Dovie et al., 2007). *Arivela viscosa* is used for its biological activities including anti-malarial (Upadhyay, 2015) and anti-pyretic (Devi et al., 2003). Anti-bacterial properties have been discovered in the leaves of *A. viscosa* (Upadhyay, 2015) and in *Cleome arabica* and *Rorida droserifolia* in the form of essential oils (Muhaidat et al., 2015). The seeds of *A. viscosa* are used as a nutritive staple and as an insecticide (Upadhyay, 2015). Iltis (ined.) characterizes the pulverized seeds of some species of *Andinocleome* (*A. pilosa, A. anomala*) as an insecticide for fleas, maggots and chiggers. The seed oil profile of *A. viscosa* is similar to rapeseed and safflower oils (Upadhyay, 2015).

The purpose of this thesis—This project seeks to understand the diversification of the seed coat morphology among genera/lineages of Cleomaceae. In particular, what are the major seed coat modifications and how does their distribution among lineages relate to our understanding of lineage relationships. The starting hypotheses for this study based on initial comparisons of Cleomaceae seed coat variation included: 1) Seed coat characters, or a combination thereof, can substantiate circumscribed genera/lineages in Cleomaceae; and 2) The high diversity of seed coat characters within some genera may be explained by adaptation to different environmental niches associated with some of the specialized character states found in those lineages. I here note where seed variation may support hypotheses on adaptation, but testing these hypotheses is beyond the scope of this thesis.

METHODOLOGY

Seed surface ornamentation for ~120 species of Cleomaceae were imaged with scanning electron microscopy (SEM), characterized, and then this morphological variation was compared to recent phylogenetic studies to look at patterns of seed character changes across the phylogenetic hypothesis. Imaging took place from the Fall of 2015 to June of 2017.

Sampling—Mature seeds of ~120 species of 24 of 26 currently recognized genera were sampled from herbarium sheets from L, MO, NY, P, U, WAG, WS. Six seeds from each species were sampled. Nomenclature follows the currently revised generic concepts sensu Iltis, Cochrane, Roalson, and colleagues (Iltis & Cochrane, 2007; Cochrane & Iltis, 2014; Iltis & Cochrane, 2014; Roalson et al., 2015; Barrett et al., 2017; Roalson & Hall, 2017; Soares Neto et al., 2017; Thulin & Roalson, 2017; Roalson, unpubl. data). Samples were chosen based on the quality of plant material (mature seeds) for the samples available. All species, their authors, country of collection, collector number and herbarium code are listed in Table 1, with reference to the figure number if that specimen image was used.

Morphological and SEM studies—Seed dimensions (l x w) were measured with a digital caliper and recorded for each species. Seeds were fixed to specimen stubs with double-sided carbon tape and either gold sputter coated on a Technics Hummer V or left uncoated depending on which SEM machine was used. SEM images were taken with either a FEI Quanta 200F, Hitachi S-570, or Tescan Vega3 microscope at the Franceschi Microscopy and Imaging Center (FMIC) at Washington State University. Images were made at 20-30 kV for optimal resolution. Seed were imaged with four different magnifications (typically 30-50x, 100-200x, 350-500x, and 500x+, depending on the size of the seed) to get the overall picture of cell shape and morphological variability at multiple scales. Morphological characters and character states were chosen to describe the variability seen using descriptions from Cleomaceae literature (Iltis & Cochrane, 2014; Iltis et al., 2011; Iltis, 1952; Inda et al., 2008; Kers, 1966, 1969, 1973; Sánchez-Acebo, 2005) and from other families, particularly Brassicaceae (Kasem et al., 2011; Koul, 2000), and meta-analyses of seed coat function across diverse taxa (Barthlott, 1981, 1984; Koch et al., 2009). Major seed coat characters are defined in Table 2 with their associated character states. Sampled species and a listing of the character/character states present or absent are shown in Table 3. The characters chosen have been shown in previous studies to have the most value in delimiting taxa (Barthlott, 1981, 1984).

Phylogenetic analysis of seed coat characters—Species were coded for ten characters with 2-4 character states (Appendix, Table 1) in Mesquite v. 3.4 (Maddison & Maddison, 2018) and plotted on a phylogenetic tree modified from Roalson and Hall (2017), Barrett et al. (2017), and Patchell et al. (2014) using an unordered parsimony model. Separate trees were generated for each character and then compiled (Appendix, Fig. 1-10) to visualize patterns of character distribution between and within genera.

RESULTS

SEM analysis shows major seed coat characters that can group genera as reflected in recent phylogenetic hypotheses (Barrett et al., 2017; Roalson & Hall, 2017). A complete list of examined specimens and associated morphological characters are listed in Table 3. The character matrix used for the Mesquite analysis is provided in the Appendix (Table 1). The following section contains a synopsized account of the characters found in each genus. For expanded descriptions of each species sampled, see the 'Seed Descriptions' section of this thesis which also references seed images included here. SEM micrographs of each species sampled are found in Figures 1 – 40.

General patterns in seed coat characters among genera—*Cleome* s.s. (Fig. 1a – 5b) and *Rorida* species (Fig. 5c – 6b) have papillate periclinal walls that are blunt or tabular and with a scurfy or rugose texture. Cells are generally of uniform height with close cell boundaries obscuring the anticlinal walls. *Cleome* s.s. contains some species where the papillate walls extend to form hairs (Fig. 1e,1f, 3a, 3b, 4c, 4d, 5a, 5b) while *Rorida* does not. Species in these two genera have an open seed cleft. *Cleomella* species (Fig. 6c – 9d) have flat to concave periclinal walls that are rugose and a closed seed cleft. *Polanisia* species (Fig. 9e – 10b) have papillate, rugose cells with anticlinal walls that are wide. *Coalisina* (Fig. 10c – 12d) and *Kersia* (Fig. 13e – 15b) species have reticulations bounding groups of cells. Periclinal walls of *Kersia* species are concave and rugose. Periclinal walls of *Coalisina* are papillate with tabular projections (Fig. 12d) or concave with collapsed outer edges (Fig. 10f, 11f). Anticlinal walls of both genera are wide. Most *Coalisina* species have hairs on top of the reticulations (Fig. 11a, 11b, 11f, 12a – d) excluding *C. polyanthera* and *C. semitetrandra. Coalisina paradoxa* has indistinct hairs (Fig. 10c and 10d) and was not included to have this trait. *Arivela* species (Fig. 12e – 13b) have low radial crests and deeply rugose, papillate cells with wide anticlinal walls. *Arivela cleomoides* and *A. viscosa* both have open seed clefts but *A. cleomoides* is arillate (Fig. 13a, 13b) and *A. viscosa* is not (Fig.12e and 12f). *Areocleome* (*A. oxalidea*) has lobes that group cells with individual cells papillate with a rugose, pitted surface (Fig. 13c, 13d). Species in this genus have an open seed cleft. Monotypic *Gilgella* (*G. scaposa* – Fig. 15c, 15d*)* has papillate cells that are blunt or tabular with wide anticlinal walls, a thick epicuticlar residue, and open seed cleft. Monotypic *Thulinella* (*T. chrysantha* – Fig. 15e, 15f) has reticulations bounding groups of cells, with concave periclinal walls, wide anticlinal walls and an open seed cleft. Monotypic *Stylidocleome* (*S. brachycarpa* – Fig. 16a, 16b) has raised circumferential areas and flat to papillate cells that are wrinkled with wide anticlinal walls*.* The *Dipterygium* (*D. glaucum* – Fig. 16c, 16d) specimen shown and described is the indehiscent, single-seeded, winged fruit characteristic of this genus. The seed was not able to be released from the fruit wall for imaging. Because the fruit wall has taken the form of the structure underneath, there is reason to believe that some of the descriptions of the fruit also pertain to the seed (concave with wrinkled periclinal walls and a thick epicuticular residue). More work will need to be done to isolate and characterize the seed alone. *Corynandra* (Fig. 16e – 17b) has punctuated crests and concave, rugose periclinal walls. *Corynandra felina* has a closed seed cleft (Fig. 16e, 16f) and *C. chelidonii* has an open cleft (Fig. 17a, 17b). *Gynandropsis* (*G. gynandra* – Fig. 17c, 17d) has radial crests and raised circumferential areas forming reticulations grouping cells. Periclinal walls are concave with thick edges and seed has an open cleft. *Sieruela* (Fig. 17e – 25f) includes a lot of variability, including species with reticulations grouping cells (Fig. 19c, 19d, 20a, 20b, 23a, 23b, 24c, 24d, 25c, 25d), radial outgrowths (Fig. 18a, 18b, 19e, 19f), radial crests that are very low to medium high (Fig. 20c, 20d, 20e, 20f, 21c, 21d, 21e, 21f, 22e, 22f, 23c-f) or crests and reticulations (Fig. 21a, 21b, 22c, 22d, 24a, 24b, 25a, 25b). Periclinal walls can be flat to papillate with (Fig. 17e, 17f, 18c, 18d) or without a central, round to pointed papillae and with or without or epicuticular residues. Most have an open seed cleft. *Andinocleome* (Fig. 26a – 27f) generally has flat or concave to papillate cells periclinal walls that can be rugose to pitted with wide anticlinal walls. One species sampled (*Andinocleome magnifica* – Fig. 27e, 27f*)* shows punctuated crests. Two species have epicuticular residues (Fig. 26c, 26d, 27c, 27d) and all species have an open cleft. *Podandrogyne* (Fig. 28a – 29d) have pitted areas containing cells (28c – f, 29a, 29a -d). Periclinal walls can be papillate or concave and rugose. Most seeds sampled are arillate and can have an open or closed cleft. Monotypic "*Pterocleome*" (*Pterocleome stylosa* – Fig. 29e, 29f) has a circumferential 'wing' of elongated cells, papillate cells on the main body and wide anticlinal walls. *Melidiscus* (*M. gigantea* – Fig. 30a, 30b) seeds look very smooth and have a slight periclinal wall concavity and raised anticlinal walls with a closed cleft. *Cleoserrata* (Fig. 30c – 31d) seeds are variable, including punctuated radial crests (Fig. 30c – f, 31c, 31d) or a smooth seed surface (Fig. 31a, 31b, 31e, 31f). Periclinal walls can be have a rugose to very wrinkled surface and anticlinal walls can be wide, raised, or obscure. Seeds have an open or closed cleft. *Taranaya* (Figures 32a – 36b) seeds also show significant variability. They can have low circumferential ridges and radial outgrowths (Fig. 32a, 32b, 33e, 33f, 35a, 35b) or radial crests (32c – f, 33a, 33b, 34c – f, 35c, 35d, 36a, 36b). Periclinal walls can be papillate or concave, anticlinal walls can be raised (32a, 32b, 33e, 33f) or wide, and some species are arillate (Fig. 33a, 33d, 34d, 35d) and have long thin hairs on crest cells (Fig. 32d, 33b, 33d, 34d). *Dactylaena* (Figures 36c – 37f) seeds have reticulations grouping cells, papillate and rugose periclinal walls. Anticlinal walls are wide and grooved, and the seed cleft is closed. *Physostemon* (Figures 38a – 40d) seeds are quite variable. Seeds have low (Fig. 38e, 38f, 39a. 39b) to high (Fig. 38a, 38b) radial crests. Some species have circumferential raised areas (Fig. 38c, 38d, 38e, 38f). Three species show distinctive crests or projections: punctuated (Fig. 38c, 38d, 39e, 39f), thin spiked (Fig. 40a, 40b), and thick spiked (Fig. 40c, 40d). Periclinal walls can be papillate or concave and rugose or wrinkled (38b, 38f, 40b) with a tabular protrusion (Fig. 39b) or a stout micropapillae (39f, 40b, 40d). Anticlinal walls are wide and grooved and can be wrinkled (38b). Physostemon seeds have a closed cleft. *Mitostylus* (*M. procumbens* – Fig. 40e and f) has high radial crests. Periclinal walls are papillate and deeply rugose and anticlinal walls are wide and grooved, and seeds have an open cleft.

Distribution of characters on the phylogenetic tree—An open cleft was found in all sampled species of *Cleome* s.s., *Rorida*, *Polanisia*, *Areocleome, Kersia, Gilgella, Thulinella, Stylidocleome,* and *Andinocleome.* Most of the sampled species of *Coalisina*, and *Sieruela* had an open cleft. A closed seed cleft was found in *Cleomella, Dipterygium, Corynandra, Gynandropsis, “Pterocleome’,* and *Melidiscus, Tarenaya* and *Physostemon. Cleoserrata* species show open or closed clefts. Concave cells were found in all species of *Kersia, Thulinella, Dipterygium, Corynandra, Gynandropsis and Melidiscus* and most species of *Coalisina* and *Cleoserrata.* Papillate cells were found in *Cleome* s.s., *Rorida, Areocleome, Gilgella, Stylidocleome, "Pterocleome", Mitostylus* and most species of *Podandrogyne.* There was variability is periclinal wall shape in *Cleomella, Physostemon, Tarenaya, Andinocleome*, and *Sieruela.* Periclinal wall ornamentation was predominately rugose (of varying degrees) or a combination of surface textures (see Table 3). Exceptions were a scurfy texture in *Cleome ornithopodioides, C. stevensiana, C. iberica, Rorida droserifolia* and *R. polytricha*. A wrinkled surface is found in *Stylidocleome* and species of *Physostemon, Tarenaya, Andinocleome, Sieruela* and *Cleoserrata.* Anticlinal wall width was mostly wide and grooved to varying widths. There are raised anticlinal walls in *Melidiscus gigantea* and *Corynandra* and species of *Tarenaya* and *Cleoserrata*. Anticlinal wall ornamentation was only visible in a limited set of sampled species: as rugose in species of *Cleome* s.s., rugose or wrinkled in species of *Sieruela and Physostemon* and rugose in one species of *Dactylaena.* Punctuated crests are present in *Corynandra, Andinocleome* and *Cleoserrata.* Radial crests are found in *Gynandropsis, Sieruela, Tarenaya, Physostemon, Arivela* and *Mitostylus. Physostemon* has species that are punctuated, radial or spiked (*P. rotundifolium* and *P. tenuifolium*). Arillate species are present in *Tarenaya*, *Sieruela*, *Podandrogyne, Corynandra* (*C. felina*) and *Arivela* (*A. cleomoides*). Presence of epicuticular residues are found in species of *Andinocleome and Sieruela.* Seed hairs are found in species of *Cleome* s.s., *Coalisina* and *Tarenaya*. Reticulations are found in *Thulinella, Gynandropsis* and species of *Sieruela* and *Dactylaena* and all sampled species of *Coalisina* and *Kersia.*

DISCUSSION

Seed characters were chosen as to adequately describe the seeds and investigate if the characters could diagnose genera, without missing potential synapomorphies when coding and viewing them on the trees. Most characters in this study are homoplasious; however, due to the nature of the descriptions, characters that are described as the same between genera (e.g., hairs or papillae) may actually be of different origin and be convergent for different ecological or adaptive roles. We are not testing those hypotheses here, but the data presented should help future studies explore those issues. Future studies would benefit from more detailed refinement of characters and character states. Seeds are assumed to be of the same age, just before or at the time of silique dehiscence. Outgroup seeds from Brassicaceae seeds were not sampled for this project (Appendix Fig. 1 – 10) as the goal was not to test monophyly. We note this omission and recognize the analysis could have benefited with this sampling. Iltis et al. (2011) used seed morphology to support monophyly for the families Brassicaceae, Capparaceae and Cleomaceae, most notably a reniform shape for Brassicaceae and horse-shoe shaped for Cleomaceae (Iltis et al., 2011).

Character changes on the phylogenetic tree—Inda et al. (2008) describe an open or closed cleft as the least homoplasious of seed characters, which is supported by the findings here. The sister group to the rest of the family (*Cleome* s.s.*)* shows an open seed cleft along with other predominantly African and Southwest Asian lineages *Rorida, Coalisina, Kersia, Gilgella, Thulinella, Stylidocleome*, and *Sieruela*, and the Australasian lineages *Arivela* and *Areocleome.* A change to a closed cleft is seen in the later diverging New World lineage of *Physostemon, Tarenaya, Cleoserrata* (with a reversal in *C. melanosperma* and *C. speciosa*) and *Melidiscus.* The *Andinocleome* lineage shows variability of this character with derivation of a closed cleft in *Podandrogyne* (*P. jamesonii* and *P. macrophylla*), and *"Pterocleome"* (*C. stylosa*). A closed cleft is derived in *Cleomella* and in the clade that contains species of the Indian lineage *Corynandra* (*C. felina, C. cleomoides*) (Appendix, Fig. 1).

Different shaped reticulations are found in the seeds of many plant families (Barthlott, 1981; Barthlott, 1984) and have been useful in showing how genera ally with lineages based on this morphology (Koul, 2000). Reticulations are derived in predominately African distributed lineages *Coalisina, Kersia, Thulinella* (*T. chrysantha*), and species of *Sieruela* but also in *Dactylaena*, a New World, northern South American lineage (Appendix, Fig. 10). This trait is found primarily in desert species, suggesting an environmental adaptation, however further work is needed to verify this.

Epicuticular residues are derived in two places on the tree: in the clade that contains monotypic genus *Gilgella* (*G. scaposa*) and in the *Andinocleome* clade (*A. lechleri* and *A.* pilosa) (Appendix, Fig. 8). Epicuticular residues are seed surface residues that appear waxy and/or flaky. They have been cited as a possible strategy for seed dispersal by animals as the residue may contain highly nutritive waxes that are attractive to dispersers (Celedon-Neghme et al., 2008; Meisenburg & Fox, 2002). We distinguish here between an overall glaucous appearance of the seed (see Fig. 6c – f, 7e, 7f, 8a – f, 9a – d, 14c, 14d, 15e, 15f, 28a, 28b, 28e, 28f, 29a, 29b, 31e, 31f) and a build-up of residues. This trait needs to be further explored to determine potential homology.

Arils are derived in four different lineages: the Australasian lineage (*Arivela cleomoides*), Indian lineage (*Corynandra felina*), some members of *Sieruela* (*S. iberidella*, *S. schimperi* and *S. rutidosperma*), and *Tarenaya* (*T. aculeata*, *T. cordobensis*, *T. tucumanensis*, and *T. microcarpa*); however, evidence for arils in *Corynandra* is not supported by Barrett et al. (2017). Arils have been described by Iltis (ined), Iltis et al. (2011) and, as elaiosomes, are proposed as a method for seed dispersal by ants (Lengyel et al., 2010). Arils may be correlated with other seed coat traits such as hairs for ant dispersal (Schenk et al., 2016). Lipid rich arils may initially attract ants with subsequent dispersal by a hold onto seed hairs (Schenk et al., 2016).

Hairs are defined here as extended protrusions from a cell that are distinctly protruded beyond the seed surface. Hairs can be localized around the rims of the reticulations (see Fig. 11a, 11b, 11e, 11f, 12a – d) or crests (see Fig. 23d), can be restricted to the outer dorsal body (see Fig. 1e, 1f, 3a, 3b, 5a, 5b) or they can completely cover the seed (Fig. 4c, 4d). Hairs have multiple derivations in the clades of *Cleome* s.s., *Coalisina*, and subclades of *Sieruela* and *Tarenaya* (Appendix, Fig. 9). The morphology of the hairs in *Cleome* s.s. and *Coalisina* are more similar in their wide-based, tapered, and ribbon-like quality. The hairs of *Tarenaya* species have a uniform thread-like quality and are restricted as projections from crest cells. The seed hairs don't appear homologous; however, the current distributions of species with hairs are concentrated in desert areas of the Middle East, southern Africa and drier parts of South America (Bolivia, Paraguay, and Argentina) suggesting an ecological adaptation or dispersal strategy which needs to be explored in more detail in future work.

Radial crested species arise on the tree in *Arivela*, *Gynandropsis, Sieruela* and *Tarenaya* (Appendix, Fig. 6). Species in the clade containing *Physostemon* + *Dactylaena* all contain crests. There are radial crests in *D. pauciflora, D. microphylla, P. stenophyllum, P. hemsleyanum*, and *P. lanceolatum* with a possible apomorphy of spiked crests in *P. rotundifolium* and *P. tenuifolium*, which are sister to the remaining species and are found in no other sampled species on the tree. Both have elongated cells with a central, stout, papillae, but *P. tenuifolium* has thinner spikes with pointed cells at the end forming a barb (Fig. 40b) and those of *P. rotundifolium* are thicker and smoothly tapered at the end (Fig. 40d). Both of these species are distributed in Brazil which may have some ecological role for dispersal or local deposition. Punctuated-crested species are derived in *Corynandra, Andinocleome*, and *Cleoserrata.*

Papillate seed cells arise at the nodes leading to *Cleome* s.s., *Rorida,* the Australasian lineages of *Areocleome* and *Arivela, Dactylaena* + *Physostemon, Tarenaya,* and *Andinocleome* + *Podandrogyne* (Appendix, Fig. 2). Concave cells arise at the node leading to the clade of *Kersia, Corynandra* and allies. Concave cells predominate in *Kersia, Corynandra* and *Thulinella scaposa*, with papillate cells in *Stylidocleome brachycarpa* and *Gilgella scaposa*. Concave cells predominate in *Sieruela*, excluding *S. rutidosperma, S. schimperi* and *S. maculata*. Papillate cells predominate in the *Andinocleome/Podandrogyne* clade, excluding *A. chilensis, A. anomala,* and *A. lechleri* which are a sister group to the remaining species of the clade. *Cleoserrata* have concave cells with a possible reversion in *Cleoserrata speciose.* In the *Dactylaena* + *Physostemon* lineage, *Dactylaena* show papillate cells and *Physostemon* show concave with a possible reversal in *P. lanceolatum* and *P. stenophyllum.*

Curvature of the periclinal wall or outgrowths is shown to be systematically valuable (Barthlott, 1981); in particular it is useful for delimiting genera, even if there is some overlap of characters of some species (Al-Hakimi et al., 2015). Because of this, denser sampling, especially of the more speciose genera can provide further evidence of the usefulness of this character.

Similarly, periclinal wall ornamentation has been show useful in describing genera in Acanthaceae (Al-Hakimi et al., 2015). Rugose periclinal walls predominate on the tree (Appendix, Fig. 3). We define rugose here as having lines going in a similar direction and may be fine, medium, or deep in terms of depth and closeness of lines (see Table 3); however, the magnifications shown in the figures presented here do not show that level of detail. On the tree a scurfy texture is derived in *C. ornithopodioides* (*Cleome* s.s.) and *Rorida droserifolia* only. A wrinkled texture is defined here as having lines running in many directions and may appear cross-hatched and the lines may appear as at different depths (see Table 3 and 'Seed Descriptions'). Wrinkles are derived in Old World species of *Stylidocleome brachycarpa* and one species of *Sieruela* (*S. maculata*), and in New World species *Andinocleome lechleri*, *Tarenaya torticarpa*, and the *Physostemon* clade (excluding *P. hemsleyanum*, which has a rugose texture). What ecological adaptative value these might have is unclear.

Anticlinal wall shape (Appendix, Fig. 4) is mostly evident when wide and grooved, and this is the most homoplasious character state. Wide and grooved anticlinal walls are defined as a visible detection of a groove around the perimeter of cells (See Fig. 7d, 12f) and can be shallow or have varying widths. When the papillae have a significant length, or the cells are deflated, anticlinal wall detection was not possible. Raised anticlinal walls can be variable along the surface of the seed, depending if there are crests or undulations, and are most clearly evident in *C. felina* and *C. chelidonii* (*Corynandra* – Fig. 16f and 17b), *Melidiscus gigantea* (Fig. 30b), *Cleoserrata bahiana* (Fig. 31f) and *Tarenaya torticarpa* (Fig. 32b [not clear at this magnification]). Anticlinal wall ornamentation (Appendix Fig. 5) needs more sampling and quantification for detection. A rugose texture is derived in *C. coluteoides* (*Cleome* s.s. – Fig. 1d), *S. maculata* (*Sieruela* – Fig. 23f) and *D. microphylla* (*Dactylaena* – Fig. 37f). A wrinkled texture is derived in *P. stenophyllum* (*Physostemon* – Fig. 38b). Although Barthlott (1981, 1984) emphasizes the utility of anticlinal wall shape and ornamentation in systematics, these characters are the least useful here. Sometimes the outer edges of the periclinal walls were deflated and overlapping other cells making the distinction between periclinal and anticlinal walls challenging. Higher magnifications and a variety of angles when imaging seed cell boundaries will be helpful for future studies of this character's relevance in describing diversity.

Another character not reviewed here, but is worth noting, is oil-filled bulliform cells specific to some members of *Tarenaya* (see *T. pernambucensis* – Fig. 34e) that Iltis (ined.) thought might aid in dispersal. As stated, more robust sampling of this sprecies-rich genus will greatly help with characterizing this seed trait.

Limited seed fossil evidence in Cleomaceae—The crown age of the core Brassicales has been hypothesized as ~ 76 mya, and the crown age of Cleomaceae ~ 50 mya (Cardinal-McTeague et al., 2016). These authors used the *Palaeocleome lakensis* specimens from the lake locality of the Pipe-clay Series of south-east Dorset, U.K. as one of the calibration points for their dated phylogenetic hypothesis. These are putative seed fossils of the Cleomaceae – Brassicaceae node dated at ~ 47.8 mya (Cardinal-McTeague et al., 2016). Many of the surface features of these specimens resemble extant species, in particular a campylotropous shape with a deeply invaginated, membranous, seed cleft. However, there is dispute about the age of the fossils from this location and the association to *Cleome* (Chandler, 1962; Feodorova et al., 2010). Moreover, these seed surface attributes may be common for the earliest diverging lineages of Cleomaceae, therefore associating them with one extant lineage may be difficult.

Two other sources of fossil evidence need to be substantiated for Cleomaceae. One is a seed fossil from the Ballast Brook Formation, northwestern Banks Island, in the Canadian Arctic Archipelago whose paleobotanical record indicates a likely mid-Miocene age ~ 16 – 11 mya (Fyles et al., 1994). The seed specimen, called *Polanisia siberica* Nikitin, has an open seed cleft and hairless, acute reticulations similar to extant Old World species of *Kersia* (see Fig. 10c and d), specific to South Africa and Namibia. The other putative Cleomaceae fossils include the Russian seed fossil genus *Meloke,* from the Paleogene and Neogene (Arbuzova and Nikitin, 2003). Among them, *Meloke sibirica* has a smooth surface, rarely tuberculate (here as punctuated crests); *Meloke rugosissima* with a conical tuberculate surface; *Meloke ucrainica* with tall tubercules; and *Meloke macrosperma* with low circumferential wrinkles resembling extant species of *Cleomella*, in particular *Cleomella mexicana* (see Fig. 7 e and f; Arbuzova and Nikitin, 2003). It will require future work to assess where these fossils might be located in the

Cleomaceae phylogeny, but the dense sampling of Cleomaceae seeds here should facilitate the placement of the fossils.

Conclusions—The seed characters presented provide an initial comprehensive investigation of seed coat characters of Cleomaceae. Overall, these characters support the existing phylogeny and the descriptions provide information of diversity within and among genera. Open or closed cleft, reticulations, hairs, crests, arils, and periclinal wall shape are the most informative. More dense sampling of seeds, especially of the more speciose genera *Tarenaya* and *Sieruela* will assist in finer scale analysis.

SEED DESCRIPTIONS

Seed descriptions are arranged by genera according to Barrett et al. (2017) with current nomenclature. Genus name, author and book or journal are given as well as species name and author. Overviews of generic-level seed variation are provided, and major seed coat characters are expanded upon for species according to Table 3.

I. *Cleome* L., Sp. Pl. 2: 671. 1753.

Cleome s.s., which houses the type species of the family, *C. ornithopodioides* L., has three main groups of characters: domed papillate periclinal walls with a scurfy texture; papillae that are longitudinally incurved and tabular shaped with a deeply rugose texture; or a rough papillate texture with medium to long length wide, ribbon like hairs. The seed cleft is open in this genus.

1. *Cleome ornithopodioides* L. (Figure 1a and b)—Seeds are 1.25 x 1.6 mm.

Arrangement of epidermal cells – Cells are tetra- to penta-gonal. Periclinal walls are domed papillate and scurfy. Anticlinal walls are wide, grooved and shallow. Cells are a uniform height over the entirety of the seed. Open cleft. Cotyledonar claw has a shelf or incurvature.

2. *Cleome coluteoides* Boiss. (Figure 1c and d)—Seeds are 2.1 x 2.5 mm.

Arrangement of epidermal cells – Cells appear isodiametric. Periclinal walls are tabular-shaped papillate with a thick outer boundary and deeply rugose. Anticlinal walls appear wide in some areas and deeply rugose. Open cleft.

3. *Cleome socotrana* Balf.f. (Figure 1e and f)—Seeds are 1.0 x 1.25 mm.

Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are tabular-shaped papillate with a thick outer boundary and deeply rugose. Anticlinal walls are wide and grooved and rugose. There are wide hairs of medium length and a fine rugosity on the outer dorsal body. Open cleft.

4. ***Cleome stevensiana*** **Schult.f. (Figure 2a and b)—**Seeds are 1.1 x 1.6 mm. Arrangement of epidermal cells – Cells are tetra- to penta-gonal. Periclinal walls are domed and blunt papillate with a central depression and have a scurfy texture. Anticlinal walls are wide, grooved and shallow. Cells are of uniform height over the entirety of the seed. Open and very short cleft. Cotyledonar claw has a shelf or incurvature.

5. ***Cleome glaucescens*** **DC. (Figure 2c and d)—**Seeds are 2.25 x 2.75 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are tabular-shaped papillate that are sometimes infolded with a medium rugosity. Anticlinal walls are obscured by adjacent cells. Longer and wider tabular cells with a finer rugosity are present on the outer dorsal body. Open cleft.

6. ***Cleome turkmena*** **Bobrov (Figure 2e and f)—**Seeds are 1.25 x 1.7 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are a wide tabular-shaped papillate and deeply rugose. Tabs appear to be of uniform height. Anticlinal walls are obscured by the adjacent cells. Open cleft.

7. ***Cleome rupicola*** **Vicary (Figure 3a and b)—**Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are papillate with a rough undulating surface that is rugose and sometimes pitted. There are tabular, rugose papillae on the outer dorsal body. Anticlinal walls are obscured by the adjacent cells. Long, wide (~0.25 mm) hairs on the outer dorsal body with a fine rugosity. Open cleft.

8. *Cleome khorassanica* Bunge & Bien. ex Boiss. (Figure 3c and d)—Seeds are 1.5 x 1.3 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are domed to arched papillate with a bumpy texture and rugose at the lower cell margin. Anticlinal walls are wide, grooved and rugose. Cells are of uniform height over the entirety of the seed. Open cleft.

9. *Cleome heratensis* Bunge & Bien. ex Boiss. (Figure 3e and f)—Seeds are 0.8 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are papillate with a rough undulating surface that is rugose. Rugose tabular papillae are on the outer dorsal body. Anticlinal walls are obscured by the adjacent cells. Open cleft.

10. *Cleome iberica* DC. (Figure 4a and b)—Seeds are 1.25 x 1.6 mm. Arrangement of epidermal cells – Cells are tetra- to penta-gonal. Periclinal walls are domed papillate and scurfy. Anticlinal walls appear wide, grooved and shallow. Cells are a uniform height over the entirety of the seed. Open cleft. Slight thickening at the edges of the cotyledonar and radicular claws.

11. *Cleome arabica* L. (Figure 4c and d)—Seeds are 1.3 x 1.5 mm. Arrangement of epidermal cells – Cells appear isodiametric. Periclinal walls are papillate. There are wide, flat hairs of a medium length covering the entirety of the seed body. Hairs are finely rugose. Anticlinal walls are obscured by hairs. Open cleft.

12. *Cleome ariana* Hedge & Lamond (Figure 4e and f)—Seeds are 1.25 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are tabular-shaped papillate that are incurved lengthwise and medium rugose. Anticlinal walls are obscured by the adjacent cells. Papillae appear to be of uniform height over entirety of seed body. Open cleft.

13. *Cleome oxypetala* Boiss. (Figure 5a and b)—Seeds are 1.5 x 1.6 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are concave. There are long, ribbon-like flat hairs restricted to the outer dorsal body. Hairs are finely rugose changing to a medium rugosity at the base. Anticlinal walls appear narrow or are obscured by hairs. Open cleft.

II. *Rorida* J.F.Gmel., Syst. Nat., ed. 13 [bis]. 2(1): 260. 1791.

Seeds generally have papillate cells of uniform height with close cell boundaries. Papillae may be columnar, curved-conical or papillate and pinched with a rugose or scurfy texture. Anticlinal walls are generally wide and can be grooved. The seed cleft is open. This genus was less densely sampled (3 out of 12 species) than the other genera.

14. *Rorida fimbriata* (Vicary) M. Thulin & Roalson (Figure 5c and d)—Seeds are 0.8 x 0.8 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are papillate, pinched on the sides and medium rugose. Anticlinal walls are not evident by closeness of cell boundaries. Cells are sunken at the base giving appearance of wide spaces between papillae. Open invagination.

15. *Rorida droserifolia* (Forssk.) M. Thulin & Roalson (Figure 5e and f)—Seeds are 0.8 x 0.8 mm. Arrangement of epidermal cells – Cells are tetra- to penta-gonal. Periclinal walls are blunt papillate with a central depression and are scurfy. Anticlinal walls are wide, grooved and shallow. Cells are of uniform height over the entirety of the seed. Open and short cleft.

16. *Rorida polytricha* (Franch.) M. Thulin & Roalson (Figure 6a and b)—Seeds are 0.8 x 0.8 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are curved conical papillate and are scurfy. Anticlinal walls are obscured but there are wide spaces around papillae. Cells are of uniform height over the entirety of the seed. Open cleft.

III. *Cleomella* DC., Prod. Syst. 237. 1824.

Seeds show variability in overall seed shape and texture. Most species are distinctive in their obovoid shape (longer width than length) and sometimes have a flat, smooth appearance. Other character variability includes low punctuated or radial outgrowths that can be peaked, a roughened cell texture with the appearance of overlapping cells. Anticlinal walls are generally wide or obscured. Some species appear glaucous without build-up so were not included as having epicuticular residues in the analysis. The seed cleft is closed.

17. *Cleomella angustifolia* Torrey (Figure 6c and d)—Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells - Cells are rectangular tetra-gonal. There are undulating radial outgrowths that peak in some areas. Periclinal walls concave to slightly papillate depending on where they are located. Periclinal walls texture is fine to medium rugose with varied elevations of these lines. Some cells have thickened outer periclinal walls. Anticlinal walls are narrow. Slight glaucous surface. Closed cleft.

18. ***Cleomella hillmanii*** **Nelson var.** ***goodrichii*** **(Welsh) Holmgren (Figure 6e and f)—**Seeds are 2.3 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are concave and the edges appear to overlap. Outer periclinal walls are finely rugose and can be puckered. Anticlinal walls obscured due to overlapping cell edges. Slight glaucous surface. Closed cleft.

19. ***Cleomella hillmanii*** **Nelson var.** ***hillmanii*** **(Figure 7a and b)—**Seeds are 2.25 x 2.0 mm. Arrangement of epidermal cells – Cells are 5-7-gonal. Finely rugose, flat papillate cells fit together like puzzle pieces and are of uniform height. Anticlinal walls are grooved and appear shallow and flat. Arched outgrowths are on the extreme dorsal end of the seed that lay flat, pointed outwards. Closed cleft.

20. ***Cleomella longipes*** **Torrey (Figure 7c and d)—**Seeds are 2.25 x 2.0. Arrangement of epidermal cells – Cells are tetra to penta-gonal and abutted. Seed surface has an overall flat appearance. Periclinal walls are flat to concave with a medium to deep rugose texture. Anticlinal walls are wide and grooved. Closed cleft.

21. ***Cleomella mexicana*** **DC. (Figure 7e and f)—**Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal and abutted. There are low circumferential outgrowths. Periclinal walls are concave with a medium to deeply rugose texture. Anticlinal walls obscured by the close fit of adjacent cells. Slight glaucous surface. Cotyledonar claw has a lip around the perimeter. Closed cleft.

22. ***Cleomella obtusifolia*** **Torrey & Frémont (Figure 8a and b)—**Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are tetra to hepta-gonal and very closely abutted. Seed surface has an overall flat appearance. Periclinal walls are generally flat to slightly concave and rugose. Some cells show a depression in the center. Anticlinal walls not evident due to closeness of the cells. Slight glaucous surface. Closed cleft.

23. *Cleomella palmeriana* Torrey & Frémont (Figure 8c and d)—Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are tetra to hepta-gonal and are very closely abutted. Seed surface has an overall flat appearance. Periclinal walls are generally flat and rugose. Anticlinal walls not evident due to closeness of the cells. Slight glaucous surface. Closed cleft.

24. *Cleomella parviflora* Gray (Figure 8e and f)—Seeds are 1.75 x 1.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal on dorsal body and are closely abutted. Finely rugose, flat papillate cells fit together like puzzle pieces and are of uniform height. Anticlinal walls are grooved and appear shallow and flat. Slight glaucous surface. Closed cleft.

25. *Cleomella perennis* Iltis (Figure 9a and b)—Seeds are 2.0 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are concave and deeply rugose with thick outer boundaries. Anticlinal walls wide, grooved and shallow. Slight glaucous surface. Closed invagination.

26. *Cleomella plocasperma* Watson (Figure 9c and d)—Seeds are 2.0 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are papillate and deeply rugose. Anticlinal walls are wide and grooved. Slight glaucous surface. Closed invagination.

IV. *Polanisia* Raf., Amer. J. Sci. 1: 37. 1819.

Species have domed to flat papillate cells with a uniform height in *P. uniglandulosa* and varying heights in *P. dodecandra*. Periclinal walls are rugose and anticlinal walls are wide and grooved anticlinal walls.

27. *Polanisia uniglandulosa* (Cav.) DC. (Figure 9e and f)—Seeds are 2.5 x 2.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are slightly domed to flat papillate and rugose. Cells are generally of the same height. Anticlinal walls are wide, grooved and shallow. Open cleft.

28. *Polanisia dodecandra* (L.) DC. subsp. *dodecandra* (Figure 10a and b)—Seeds are 2.25 x 2.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are papillate and rugose with slight varying of height apices. Anticlinal walls are wide and grooved. Open cleft.

V. *Coalisina* Raf., Sylva Tellur. 114. 1838.

Cells are grouped in angular or rounded reticulations that may have hairs protruding out of the top of them in or have indistinct hairs. The hairs may be thin and tapered or shorter with a wide base. Periclinal wall shape can be concave with upturned or collapsed edges or papillate with tabular projections. Anticlinal walls are wide to obscured. The seed cleft is open except for *C. tenella*.

29. *Coalisina paradoxa* (R.Br. ex DC.) Roalson & JC Hall (Figure 10c and d) — Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are angular reticulations grouping cells with indistinct hairs. Periclinal walls are concave with collapsed outer edges that sometimes fall into the center of the cell or adjacent cell. Periclinal texture is deeply rugose. Anticlinal walls are wide and grooved but are sometimes obscured by outer periclinal walls. Open cleft.

30. ***Coalisina tenella*** **(L.f.) Roalson & JC Hall (Figure 10e and f)—**Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. Papillate cells make up the angular reticulations grouping cells. Cells inside reticulations have periclinal walls that are concave with collapsed outer edges that sometimes fall into the center of the cell or adjacent cell. Periclinal texture is medium rugose. Anticlinal walls are obscured by outer periclinal walls. Closed cleft.

31. ***Coalisina semitetrandra*** **(Sond.) Roalson & JC Hall (Figure 11a and b)—**Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are rounded reticulations grouping cells. Reticulations have hairs around the perimeter that are short and pointed with a wider base. Periclinal walls are tabular papillate with a sunken area around the base and are finely rugose. Anticlinal walls are grooved or obscured. Open cleft.

32. ***Coalisina polyanthera*** **(Schweinf. & Gilg ex Gilg) Roalson & JC Hall (Figure 11c and d)—**Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are elongated tetra-gonal. There are angular, rectangular reticulations grouping cells. Reticulations have higher radial walls than circumferential. Periclinal walls are slightly concave and are deeply rugose with striations that can extend over adjacent cells. Anticlinal walls are obscured. Open cleft.

33. ***Coalisina angustifolia*** **(Forssk.) Raf. subsp. *petersiana* (Klotzsch) Roalson & JC Hall (Figure 11e and f)—**Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are elongated tetra-gonal. There are angular reticulations grouping cells

with hairs around the perimeter. Hairs are pointed with a wider base and can be short to medium length around the same reticulation. Periclinal walls are concave with thick outer edges and are fine to medium rugose Anticlinal walls are wide and grooved. Open cleft.

34. *Coalisina angustifolia* (Forssk.) Raf. subsp. *angustifolia* (Figure 12a and b)— Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are rounded reticulations grouping cells. Reticulations have hairs around the perimeter that are medium length and less of a taper than other species. Periclinal walls are tabular papillate with a sunken area around the base and are finely rugose. Anticlinal are obscured. Open cleft.

35. *Coalisina angustifolia* (Forssk.) Raf. subsp. *diandra* (Burch.) Roalson & JC Hall var. *diandra* (Figure 12c and d)—Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are rounded reticulations grouping cells. Reticulations have hairs around the perimeter that are medium length and less of a taper than other species. Periclinal walls are tabular papillate with a sunken area around the base and are finely rugose. Anticlinal are wide and grooved. Open cleft.

VI. *Arivela* Raf., Sylva Tellur. 110. 1838.

Seeds have radial crests with deeply rugose raised striations forming surface bumps and wide and grooved anticlinal walls. *A. cleomoides* is arillate and *A. viscosa* is not. Species in this groups have an open seed cleft.

36*. Arivela viscosa* (L.) Raf. (Figure 12e and f)—Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Arrangement of epidermal cells – Cells are tetra-gonal. Seeds have low radial crests that are continuous. Periclinal walls are papillate and deeply rugose breaking and forming surface bumps. Anticlinal walls are wide and grooved. Open seed cleft.

37. *Arivela cleomoides* (F. Muell.) RL Barrett (Figure 13a and b)—Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are tetrta-gonal. Seeds have low radial crests that are continuous. Periclinal walls are papillate and deeply rugose to breaking and forming surface bumps. Anticlinal walls are wide and grooved. Seeds are arillate and have an open seed cleft.

VII. *Areocleome* RL Barrett & Roalson, Syst. Bot. 42: 694. 2017.

Seeds have a lobed surface. Cells have a rugose to pitted periclinal wall and wide anticlinal walls with an open seed cleft.

38. *Areocleome oxalidea* (F.Muell.) RL Barrett & Roalson (Figure 13c and d)— Seeds are 0.7 x 0.8 mm. Arrangement of epidermal cells – Cells are isodiametric. Cells are grouped on raised lobed projections. Periclinal walls are papillate and are rugose and pitted. Anticlinal walls are grooved and very wide and between lobed projections. Open cleft.

VIII. *Kersia* Roalson & JC Hall, Syst. Bot. 42: 925. 2017.

Seeds have reticulations that group cells. Reticulations may have sharp or rounded edges and may have higher radial walls that make up the reticulations. Periclinal walls are concave and may have upturned or deflated edges. Anticlinal walls are wide and grooved and may be shallow or obscured by adjacent cell. *K. foliosa* var. *lutea* shows epicuticular residues and *K. suffruticosa* is glaucous. The seed cleft is open.

39*. Kersia paxii* (Schinz) Roalson & JC Hall (**Figure 13e and f)—**Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Cells are grouped in reticulations that have sharp edges. Periclinal walls are concave and are finely rugose to bumpy. Anticlinal walls are wide, grooved and shallow. Open cleft.

40*. Kersia foliosa* (Hook.f.) Roalson & JC Hall var. *lutea* (Sond.) Roalson & JC Hall (Figure 14a and b)—Seeds are 0.8 x 0.8 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Cells are grouped in rounded reticulations. Periclinal walls are concave and are finely to medium rugose. Anticlinal walls are wide, grooved and shallow. Open cleft.

41*. Kersia suffruticosa* (Schinz) Roalson & JC Hall (Figure 14c and d)—Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Cells are grouped in elongated reticulations. Periclinal walls are concave and are finely rugose. Anticlinal walls are wide and grooved. Slight glaucous surface. Open cleft.

42*. Kersia kalachariensis* (Schinz) Roalson & JC Hall subsp. *kalachariensis* (Figure 14e and f)—Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Cells are grouped in elongated reticulations with higher radial walls than circumferential. Periclinal walls are concave with upturned edges and are finely rugose. Anticlinal walls are wide and grooved or obscured. Open cleft.

43*. Kersia kalachariensis* (Schinz) Roalson & JC Hall subsp. *namibensis* (Kers) Roalson & JC Hall (Figure 15a and b)—Seeds are 0.8 x 0.8 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Cells are grouped in rounded reticulations. Periclinal walls are concave with deflated edged and are finely rugose. Anticlinal walls are wide and grooved, shallow or obscured by outer periclinal walls of adjacent cells. Open cleft.

IX*. Gilgella* Roalson & JC Hall, Syst. Bot. 42: 925. 2017.

Monotypic genus. Seeds have papillate cells that can be blunt or pointed with very wide and grooved anticlinal walls. An epicuticular residue coats the whole seed.

44. *Gilgella scaposa* (DC.) Roalson & JC Hall (Figure 15c and d)—Seeds are 0.7 x 0.7 mm. Arrangement of epidermal cells – Cells are isodiametric. Periclinal walls are papillate and can be pointed or blunt. Periclinal wall texture is obscured by epicuticular residue covering the whole seed. Anticlinal walls are very wide and grooved around cells. Open cleft.

X. *Thulinella* Roalson & JC Hall, Syst. Bot. 42: 925. 2017.

Monotypic genus. Seeds have reticulations that bound groups of cells. Periclinal walls can be concave with upturned edges. Anticlinal walls are raised. Presence of a glaucous surface. The seed cleft is open.

45. *Thulinella chrysantha* (Decne.) Roalson & JC Hall (Figure 15e and f)—Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are shallow, hexagonal reticulations grouping cells. Periclinal walls are concave and rugose to pebbled. Anticlinal walls are wide and grooved. Slight glaucous surface. Open cleft.

XI. *Stylidocleome* Roalson & JC Hall, Syst. Bot. 42: 925. 2017.

Monotypic genus**.** Seeds have shallow depressions that group cells with raised circumferential walls. Periclinal walls are papillate and wrinkled. Anticlinal walls are wide and grooved, very shallow to flat. The seed cleft is open.

46. *Stylidocleome brachycarpa* (Vahl ex DC.) Roalson & JC Hall (Figure 16a and b)—Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are shallow depressions grouping cells. Raised circumferential bands of cells make up one of the walls of the depression. Periclinal walls are papillate to flat and wrinkled with lines directed towards the center of the cell. Anticlinal walls are wide and grooved, very shallow to flat. Slight incurvature of the cotyledonar cleft. Open cleft.

XII. *Dipterygium* Decne., Ann. Sci. Nat., Bot. ser. 2, 4: 66. 1835.

Fruits elongated longitudinally with concave periclinal walls that are deeply rugose with obscured anticlinal walls. Epicuticular residue and a closed cleft.

47. *Dipterygium glaucum* Decne. (Figure 16c and d)—Fruits are 4.0 x 3.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are radial outgrowths at wide intervals (~6 per seed). Periclinal walls are concave and deeply wrinkled with thick outer edges. Anticlinal walls are obscured. In the center of the fruit are funnel-shaped pits grouping cells. Thick, flaky epicuticular residue. Through the fruit wall, cleft seems closed.

XIII. *Corynandra* Schrad. ex Spreng., Syst. Veg., ed. 16, 4(2, Cur. Post.): 204. 1827.

Seeds have punctuated crests at varying intervals. Periclinal walls are concave and rugose. Anticlinal walls are raised. The seed cleft can be open or closed with an extended radicular claw.

48. *Corynandra felina* (L.f.) Cochrane & Iltis (Figure 16e and f)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are punctuated crests on the dorsal body. Periclinal walls are concave and deeply rugose. Anticlinal walls are thick and raised surrounding the cells. Extended radicular claw. Aril present. Closed cleft.

49. *Corynandra chelidoni* (L.f.) Cochrane & Iltis (Figure 17a and b)—Seeds are 1.5 x 1.3 mm. Arrangement of epidermal cells – Cells are isodiametric. There are punctuated crests on the dorsal body. Periclinal walls are concave and deeply rugose. Anticlinal walls are thick and raised surrounding the cells. Extended radicular claw. Closed cleft.

XIV. *Gynandropsis* DC., Prodr. [A. P. de Candolle] 1: 237. 1824.

Monotypic genus. Seeds have radial crests of medium height and raised circumferential areas forming reticulations that group cells. Periclinal walls are concave and rugose. Anticlinal walls are wide and grooved. The seed cleft is closed.

50. *Gynandropsis gynandra* (L.) Briq. (Figure 17c and d)—Seeds are 1.5 x 1.3 mm. Arrangement of epidermal cells – Cells are isodiametric. There are radial crests and raised circumferential areas forming reticulations grouping cells. Periclinal walls are concave with very thick outer edges and are deeply rugose. Anticlinal walls wide and grooved. Closed cleft.

XV. *Sieruela* Raf., Sylva Tellur. 112. 1838.

Seed characters can be highly variable. Many species have low to medium height radial crests and reticulations grouping cells. Periclinal walls can be flat with a central papillae to concave and can have varying textures. Anticlinal walls usually wide and grooved. Most species have an open seed cleft.

51. *Sieruela hanburyana* (Penz.) Roalson & JC Hall (Figure 17e and f)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are continuous radial crests of medium height. Periclinal walls have pointed papillae with a deeply rugose and pebbled surface. Anticlinal walls flat, wide and grooved. Open cleft.

52. *Sieruela stricta* (Klotzsch) Roalson & JC Hall (Figure 18a and b)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are raised radial outgrowth with rounded cells are on top of outgrowths and elongated cells in the rest of the dorsal body. Periclinal walls are concave and deeply rugose. Anticlinal walls are wide and grooved. Open cleft.

53. *Sieruela parvipetala* (R.A. Graham) Roalson & JC Hall (Figure 18c and d)— Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are continuous radial crests of medium height. Cells on top of the crests are globose with pointed papillae. Periclinal walls have flat and pointed papillae that span the width of the cell. Periclinal surface is deeply rugose. Anticlinal walls are wide, flat and grooved. Open cleft.

54. ***Sieruela boroensis*** **(Klotzsch) Roalson & JC Hall (Figure 18e and f)—**Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are shallow depressions grouping cells. Periclinal walls are papillate and flat and finely rugose. Anticlinal walls are thin and slightly raised. Closed cleft.

55. ***Sieruela macrophylla*** **(Klotzsch) Roalson & JC Hall (Figure 19a and b)—**Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are reticulations grouping cells. Shorter cells are on top of reticulations and elongated cells are in between. Periclinal walls are concave and finely rugose. Anticlinal walls are wide and grooved. Open cleft.

56. ***Sieruela briquetti*** **(Polhill) Roalson & JC Hall (Figure 19c and d)—**Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal with reticulations grouping cells. Periclinal walls are concave with thick outer edges and a medium rugose texture. Anticlinal walls are wide and grooved. Open cleft.

57. ***Sieruela hirta*** **(Klotzsch) Roalson & JC Hall (Figure 19e and f)—**Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are circumferential outgrowths. Periclinal walls are concave with thick outer edges that are deflated and rugose. Anticlinal walls are wide and grooved. Closed cleft.

58. ***Sieruela usambarica*** **(Pax ex Engl.) Roalson & JC Hall (Figure 20a and b)—**Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric with reticulations grouping cells. Periclinal walls are concave with thick outer edges and a central rounded to pinched protrusion. Periclinal wall texture is medium rugose. Anticlinal walls are wide and grooved. Open cleft.

59. *Sieruela iberidella* (Welw. ex Oliv.) Roalson & JC Hall (Figure 20c and d)— Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric with medium height radial crests. Periclinal walls are concave with thick outer edges and are deeply rugose. Anticlinal walls are wide and grooved or obscured by periclinal walls. Seeds are arillate and have an open cleft.

60. *Sieruela rutidosperma* (DC.) Roalson & JC Hall var. *rutidosperma* (Figure 20e and f)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells –Cells are isodiametric to elongated and there are medium to high radial crests. Periclinal walls are papillate and finely rugose. Anticlinal walls are wide and grooved. There is a round, vernicose spot at the vertex of the seed cleft. Aril present. Open cleft.

61. *Sieruela rutidosperma* (DC.) Roalson & JC Hall var*. burmannii* (Wight & Arn.) Roalson & JC Hall (Figure 21a and b)—Seeds are 1.25 x 1.0 mm. Arrangement of epidermal cells – Cells are isodiametric with medium radial crests and reticulations in between crests grouping cells. Periclinal walls are concave and finely rugose with a protrusion that spans the width of the cell. Protrusion is pebbled. Anticlinal walls are wide and grooved or obscured. Open cleft.

62. *Sieruela oxyphylla* (Burch.) Roalson & JC Hall var. *oxyphylla* (Figure 21c and d)—Seeds are 1.125 x 1.125 mm. Arrangement of epidermal cells – Cells are isodiametric with very low radial crests. Periclinal walls are concave and finely rugose with thickened to deflated and puckered outer edges. Anticlinal walls are wide and grooved or obscured by adjacent cells. Open short cleft.

63. ***Sieruela oxyphylla*** **(Burch.) Roalson & JC Hall var.** ***robusta*** **(Kers) Roalson & JC Hall (Figure 21e and f)—**Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric with very low radial crests. Periclinal walls are concave and finely rugose with thickened to deflated and puckered outer edges. Anticlinal walls are masked by adjacent periclinal walls. Open cleft. Longer radicular claw than var. *oxyphylla* with a u-shaped curvature to the cleft.

64. ***Sieruela strigosa*** **(Bojer) Roalson & JC Hall (Figure 22a and b)—**Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric with raised radial areas. Periclinal walls are concave with upturned edges and a medium rugosity. Cells on raised areas can be papillate with the same texture. Anticlinal walls are wide and grooved. Open cleft. Cleft is incurved towards the cotyledonar claw.

65. ***Sieruela kermesina*** **(Gilg & Gilg-Ben.) Roalson & JC Hall var.** ***plebeia*** **(Kers) Roalson & JC Hall (Figure 22c and d)—**Seeds are 2.0 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric with low radial crests and very defined reticulations in between crests grouping cells. Periclinal walls are concave with a medium rugosity. Cells on crests can be papillate with the same texture. Anticlinal walls are wide and grooved but mostly obscured by adjacent cells. Open and incurved cleft.

66. ***Sieruela micrantha*** **(Bojer) Roalson & JC Hall subsp.** ***leandrii*** **(Hadj-Moust.) Roalson & JC Hall (Figure 22e and f)—**Seeds are 1.0 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric with low to medium radial crests. Periclinal

walls are papillate with deeply rugose to pebbled. Anticlinal walls are wide, grooved and deeply rugose. Short, open cleft.

67. *Sieruela perrieri* (Hadj-Moust.) Roalson & JC Hall (Figure 23a and b)—Seeds are 700 x 700 μm. Arrangement of epidermal cells – Cells are isodiametric with isodiametric reticulations grouping cells. Periclinal walls are domed papillate with a wrinkled texture. Anticlinal walls are wide, grooved and wrinkled. Epicuticular residues. Open cleft.

68. *Sieruela conrathii* (Burtt Davy) Roalson & JC Hall (Figure 23c and d)—Seeds are 1.25 x 1.75 mm. Arrangement of epidermal cells – Cells are tetra-gonal with low to medium radial crests with sparse, fine and long hairs coming out of crest cells. Periclinal walls are flat papillate and have a deeply wrinkled texture. Anticlinal walls are wide and grooved. There is one central, blunt and conical papillae per cell. Open cleft.

69. *Sieruela maculata* (Sond.) Roalson & JC Hall (Figure 23e and f)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal with high radial crests. Periclinal walls are flat papillate and deeply wrinkled texture. Anticlinal walls are wide and grooved with a rugose texture. There is one central, blunt and conical papillae per cell. Open cleft.

70. *Sieruela rubella* (Burch.) Roalson & JC Hall (Figure 24a and b)—Seeds are 1.3 x 1.8 mm. Arrangement of epidermal cells – Cells are tetra- to penta-gonal with very low radial crests and reticulations in between crests grouping cells. Periclinal walls are very shallow concave with a rugose and pitted texture. Cells on the sides of the crests are pitted and rugose. Anticlinal walls are obscured by adjacent cells. There is one central, blunt and conical hair per cell. Radicular claw significantly longer than cotyledonar claw. Open cleft.

71. *Sieruela silvatica* (Gilg & Gilg-Ben.) Roalson & JC Hall (Figure 24c and d)— Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells. Periclinal walls are concave and deeply rugose. Anticlinal walls are wide and grooved. Radicular claw longer than cotyledonar claw. Open cleft.

72. *Sieruela coeruleo-rosea* (Gilg & Gilg-Ben.) Roalson & JC Hall (Figure 24e and f)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal with medium height radial crests. Periclinal walls are concave with a rugose texture. A rounded projection spans the width of the cells. Anticlinal walls are obscured by adjacent cells. There is one central, blunt and conical hair per cell. Radicular claw significantly longer than cotyledonar claw. Open cleft.

73. *Sieruela monophylla* (L.) Roalson & JC Hall (Figure 25a and b)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra- to penta-gonal with very low radial crests and reticulations in between crests grouping cells. Periclinal walls are very shallow concave with a rugose and pitted texture. Cells on the sides of the crests are pitted and rugose. Anticlinal walls are obscured by adjacent cells. There is one central, blunt and conical papillae per cell. Radicular claw significantly longer than cotyledonar claw. Open cleft.

74. *Sieruela elegantissima* (Briq.) Roalson & JC Hall (Figure 25c and d)—Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal with reticulations grouping cells. Periclinal walls are concave with a rugose and pitted texture. Anticlinal walls are wide and grooved. Radicular claw longer than cotyledonar claw. Open cleft.

75. *Sieruela schimperi* (Pax) Roalson & JC Hall (Figure 25e and f)—Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric with low radial crests. Periclinal walls are papillate and rugose. Anticlinal walls are wide and grooved. Seeds are arillate and have an open cleft.

XVI. *Andinocleome* Iltis & Cochrane, Novon 23: 51. 2014.

Periclinal walls can be concave or papillate. Many species have medium-high circumferential outgrowths on the outer dorsal body or punctuated crests. Concave periclinal walls have thick outer edges. Papillate periclinal walls are rugose and pitted, Anticlinal walls are wide and grooved or obscured. Species have an open seed cleft.

76. *Andinocleome chilensis* (DC.) Iltis, ined. (Figure 26a and b)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric and seed has an overall smooth appearance. Periclinal walls are concave, have thick outer walls often overlapping adjacent ones, and are rugose. Anticlinal walls are wide and grooved. Open cleft.

77. *Andinocleome pilosa* (Benth.) Iltis & Cochrane (Figure 26c and d)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are papillate rugose and pitted. Anticlinal walls are wide, grooved and shallow. Flaking epicuticular residues. Open cleft.

78. *Andinocleome anomala* (Kunth) Iltis, ined. (Figure 26e and f)—Seeds are 3.0 x 3.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are concave, deeply rugose and pitted. Some periclinal walls have thick edges that can obscure anticlinal walls. Open cleft.

79. ***Andinocleome moritziana*** **(Klotzsch ex Eichler) Iltis, ined. (Figure 27a and b)—** Seeds are 2.5 x 2.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal with circumferential outgrowths on outer dorsal body. Periclinal walls are papillate and deeply rugose. Anticlinal walls are wide and grooved. Open cleft.

80. ***Andinocleome lechleri*** **(Eichler) Iltis & Cochrane (Figure 27c and d)—**Seeds are 2.75 x 2.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal circumferential outgrowths. Periclinal walls are concave with thick outer edges. Periclinal wall texture is wrinkled. Anticlinal walls are obscured. Flaking epicuticular residues. Open cleft.

81. ***Andinocleome magnifica*** **(Briq.) Iltis & Cochrane (Figure 27e and f)—**Seeds are 3.0 x 3.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are punctuated crests on the dorsal body. Periclinal walls are concave with thick outer edges and are deeply rugose. Anticlinal walls are obscured. Open cleft.

XVII. ***Podandrogyne*** **Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 115. 1930.**

Periclinal walls are papillate or concave and rugose. Anticlinal walls wide and grooved. Most species are arillate and can have glaucous areas with an open or closed cleft.

82. ***Podandrogyne pulcherrima*** **(Standl.) Cochrane (Figure 28a and b)—**Seeds are 2.0 x 2.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Seed has an undulating surface. Periclinal walls are papillate and rugose. Anticlinal walls are wide and grooved. Aril present. Slight glaucous surface in some areas. Open cleft.

83. *Podandrogyne jamesonii* (Briq.) Cochrane (Figure 28c and d)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are raised surface and shallow pits areas over the seed surface. Periclinal walls are papillate and deeply rugose. Anticlinal walls are shallow, wide and grooved. Aril present. Closed cleft.

84. *Podandrogyne caucana* Cochrane (Figure 28e and f)—Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are very shallow depressions covering the seed surface. Periclinal walls are concave and rugose. Anticlinal walls are wide and grooved. Aril present. Slight glaucous surface in some areas. Closed cleft.

85. *Podandrogyne macrophylla* (Turcz.) Woodson (Figure 29a and b)—Seeds are 2.25 x 2.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are very shallow depressions covering the seed surface. Periclinal walls are papillate and rugose. Anticlinal walls are wide and grooved. Slight glaucous surface in some areas. Closed cleft.

86. *Podandrogyne densiflora* (Benth.) Iltis & Cochrane (Figure 29c and d)—Seeds are 3.0 x 2.75 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are very shallow depressions covering the seed surface. Periclinal walls are papillate and rugose. Anticlinal walls are wide and grooved. Aril present. Open cleft.

XVIII. *Pterocleome* Iltis, ined.

Seeds have long circumferential wings with elongated cells. Main dorsal body has stacked crests that lay flat. Cells are papillate with wide and grooved anticlinal walls.

87. *Pterocleome stylosa* (Eichler) Iltis, ined. (Figure 29e and f)—Seeds are 2.75 x 2.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal and columnar. There are layers of circumferential peaks that make up the dorsal body. Periclinal walls are papillate and smooth. Anticlinal walls are wide and grooved. Wing has columnar cells that are narrower than those on dorsal body. Periclinal walls on wing are papillate and smooth with wide and grooved anticlinal walls. Closed cleft.

XIX. *Melidiscus* Raf., Sylva Tellur. 110. 1838.

Seeds looks smooth overall and have very slight depressions over the seed body with a membrane joining the cotyledonar and radicular claws. Periclinal walls are slightly concave, flat and have a rugose and pitted texture. Anticlinal walls are raised. Cleft is closed.

88. *Melidiscus gigantea* (L.) Raf. (Figure 30a and b)—Seeds are 2.25 x 2.0 mm. Arrangement of epidermal cells – Cells are hexagonal. Overall appearance of seed is smooth. Periclinal walls are concave and flat, rugose and pitted. Anticlinal walls are of medium thickness and raised. Closed cleft with a membrane between the claws.

XX. *Cleoserrata* Iltis, Novon 17: 447. 2007.

Most species have short punctuated crests that can be pointed or blunt or connected by radial ridges. Periclinal walls are concave with thick outer edges or are papillate and finely rugose to rugose. Anticlinal walls are wide and grooved. Some species are glaucous. Under high magnification (1300x and 5000x – not presented here), *Cleoserrata bahiana* has a wrinkled surface that is continuous over the seed. Open or closed cleft.

89. *Cleoserrata paludosa* (Willd. ex Eichler) Iltis ex Soares Neto & Roalson (Figure 30c and d)—Seeds are 2.0 x 2.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are short punctuated radial crests that can be pointed or blunt with raised circumferential ridges. Periclinal walls are concave and finely rugose with thick outer edges that can be upturned. Anticlinal walls are wide, grooved and shallow. Closed cleft.

90. *Cleoserrata melanosperma* (S.Wats.) Roalson & Soares Neto (Figure 30e and f)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low, punctuated crests with radial ridges. Periclinal walls are concave and rugose and have thick outer edges that can be thicker and upturned at one end. Anticlinal walls are wide and grooved. Open cleft.

91. *Cleoserrata serrata* (Jacq.) Iltis (Figure 31a and b)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal and overall appearance of seed surface is smooth and grid-like. There are slightly raised circumferential areas that look like parallel lines. Periclinal walls are concave and finely rugose with thick outer edges. Anticlinal walls are wide and grooved. Closed cleft.

92. *Cleoserrata speciosa* (Raf.) Iltis (Figure 31c and d)—Seeds are 1.75 x 1.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are rounded, punctuated crests that have smooth columnar cells. Periclinal walls are papillate and rugose. Anticlinal walls are wide and grooved. Open cleft.

93. ***Cleoserrata bahiana*** **Iltis & MB Costa-e-Silva ex Soares Neto & Roalson (Figure 31e and f)—**Seeds are 2.5 x 2.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal and overall appearance of seed surface is smooth and grid-like. Periclinal walls are concave. Anticlinal walls are raised. Both periclinal and anticlinal walls have a continuous deeply wrinkled surface. Seed is glaucous over its entirety. Closed invagination.

XXI. ***Tarenaya*** **Raf., Sylva Tellur. 111. 1838.**

Seeds can have punctuated to radial crests of low, medium or high height. Periclinal walls can be concave to domed papillate with raised to wide and grooved anticlinal walls. Some crested species show hairs on the crests and some are arillate.

94. ***Tarenaya torticarpa*** **(Iltis & T.Ruiz Zapata) Soares Neto & Roalson (Figure 32a and b)—**Seeds are 2.25 x 2.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are low circumferential ridges and low radial outgrowths on the dorsal body. Periclinal walls are concave and wrinkled with thick outer walls. Anticlinal walls are narrow and raised. Closed cleft.

95. ***Tarenaya tucumanensis*** **(Iltis) Arana & Oggero (Figure 32c and d)—**Seeds are 3.0 x 2.75 mm. Arrangement of epidermal cells – Cells are isodiametric. There are high radial crests and circumferential ridges. The periclinal walls are papillate with a central rounded projection and are rugose. Anticlinal walls are wide, grooved and shallow. Some crest cells and cells around crests have a long, thin flattened hair projecting from them. Aril present. Closed cleft.

96. *Tarenaya rosea* (Vahl ex DC.) Soares Neto & Roalson (Figure 32e and f)— Seeds are 1.25 x 1.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are radial crests of medium height and circumferential ridges. Periclinal walls are papillate and deeply rugose to pebbled. Anticlinal walls are wide, grooved and shallow. Crest cells are larger and elongated with the same periclinal wall surface as described. Aril present. Closed cleft.

97. *Tarenaya aculeata* (L.) Soares Neto & Roalson (Figure 33a and b)—Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low radial crests. and circumferential ridges. Periclinal walls are papillate with a central rounded projection and are rugose. Anticlinal walls are wide, grooved and shallow. Some crest cells and cells around crests have a long, thin flattened hair projecting from them. Aril present. Closed cleft.

98. *Tarenaya cordobensis* (Eichler ex Griseb.) Arana & Oggero (Figure 33c and d)—Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low radial crests and circumferential ridges. The periclinal walls are papillate with a central rounded projection and rugose. Anticlinal walls are wide, grooved and shallow. Some crest cells and cells around crests have a long, thin flattened hair projecting from them. Aril present. Closed cleft.

99. *Cleome spinosa* Jacq. subsp. *longicarpa* Iltis, ined. (Figure 33e and f)—Seeds are 1.75 x 1.75 mm. Arrangement of epidermal cells – Cells are isodiametric. There are circumferential and radial ridges. Periclinal walls are concave and rugose. Anticlinal walls are raised. Closed cleft.

100. ***Tarenaya boliviensis*** **(Iltis) Soares Neto & Roalson (Figure 34a and b)—**Seeds are 1.75 x 1.25 mm. Arrangement of epidermal cells – Cells are tetra-gonal. Periclinal walls are concave and finely rugose. Outer edges of perclinal walls are thick and obscure anticlinal walls. Closed cleft.

101. ***Tarenaya eosina*** **(J.F. Macbr.) Soares Neto & Roalson (Figure 34c and d)—** Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are high radial crests and circumferential ridges. Periclinal walls are papillate with a central rounded projection and rugose. Anticlinal walls are wide, grooved and shallow. Some crest cells and cells around crests have a long, thin flattened hair projecting from them. Aril present. Closed cleft.

102. ***Tarenaya pernambucensis*** **Iltis & MB Costa-e-Silva ex Soares Neto & Roalson (Figure 34e and f)—**Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are high radial crests and circumferential ridges. Periclinal walls are papillate and deeply rugose to pebbled. Anticlinal walls are wide, grooved, and shallow. Crest cells are elongated with the same periclinal wall surface as described. Presence of bulliform cells in cleft. Closed cleft.

103. ***Tarenaya parviflora*** **(Kunth) Iltis (Figure 35a and b)—**Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low circumferential ridges and low radial outgrowths on the dorsal body. Periclinal walls are concave and rugose with the outer edges often folded toward center of cell or over adjacent cell. Anticlinal wall wide, grooved and shallow. Closed cleft

104. ***Tarenaya microcarpa*** **(Ule) Soares Neto & Roalson (Figure 35c and d)—**Seeds are 2.25 x 2.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low, radial crests of medium height and circumferential ridges. The periclinal walls are papillate, domed and rugose. Anticlinal walls are wide, grooved and shallow. Crest cells are elongated with concave periclinal walls with thick outer edges. Aril present. Closed cleft.

105. *Tarenaya hassleriana* (Chodat) Iltis (Figure 35e and f)—Seeds are 2.0 x 2.0 mm. Arrangement of epidermal cells – Cells are tetra-gonal and overall appearance of seed surface is smooth and grid-like. There are circumferential ridges that look like parallel lines. Periclinal walls are concave and rugose with thick outer edges. Anticlinal walls are obscured. Closed cleft.

106. *Tarenaya curvispina* MB Costa-e-Silva & Iltis ex Soares Neto & Roalson (Figure 36a and b)—Seeds are 1.0 x 1.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are high radial crests and circumferential ridges. Periclinal walls are papillate and deeply rugose to pebbled. Anticlinal walls are wide, grooved and very shallow. Crest cells are large elongated with the same periclinal wall surface as described. Presence of bulliform cells in cleft. Closed cleft.

XXII. *Dactylaena* Scrad. ex Schult.f., Syst. Veg. 7: ix, in obs. 1829.

Seeds show rectangular reticulations with papillate cells within them. Periclinal walls are papillate or domed papillate and deeply rugose. Anticlinal walls are generally wide and grooved and can be shallow. Seeds have a closed cleft.

107. *Dactylaena boliviensis* Iltis (Figure 36c and d)—Seeds are 1.75 x 1.75 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells with the radial walls of the reiculations higher than the circumferential walls. Periclinal walls are papillate and rugose. Anticlinal walls are shallow, wide and grooved. Closed invagination.

108. ***Dactylaena pauciflora*** **Griseb. (Figure 36e and f)—**Seeds are 1.5 x 1.55 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells with the radial walls of the reiculations higher than the circumferential walls. Periclinal walls are papillate and deeply rugose. Anticlinal walls are wide and grooved. Closed cleft.

109. ***Dactylaena micrantha*** **Schrad. ex Schult.f. (Figure 37a and b)—**Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells with the radial walls of the reiculations higher than the circumferential walls. Periclinal walls are domed or slightly pinched papillate with a rough and deeply rugose texture with sunken areas. Anticlinal walls are very wide, grooved and shallow. Closed cleft.

110. ***Dactylaena pohliana*** **Eichler (Figure 37c and d)—**Seeds are 2.0 x 2.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells with the radial walls of the reiculations higher than the circumferential walls. Periclinal walls are domed papillate and rugose. Anticlinal walls are wide, grooved and shallow. Closed cleft.

111. ***Dactylaena microphylla*** **Eichler (Figure 37e and f)—**Seeds are 2.0 x 2.0 mm. Arrangement of epidermal cells – Cells are isodiametric. There are reticulations grouping cells with the radial walls of the reiculations higher than the circumferential walls. Periclinal walls are domed papillate and rugose. Anticlinal walls are wide grooved, shallow and rugose. Closed cleft.

XXIII. *Physostemon* Mart. & Zucc., Flora 7: 139. 1824.

Seeds have medium, high radial, thin or thick spiked crests with or without circumferential ridges. Periclinal walls can be papillate or concave with a tabular protrusion or pointed papillae, rugose or wrinkled. Anticlinal walls are wide and grooved. Seeds have a closed cleft.

112. *Physostemon stenophyllum* (Klotzsch ex Urb.) Iltis (Figure 38a and b)— Seeds are 2.0 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric and have high radial crests. Periclinal walls are papillate and wrinkled. Anticlinal walls are wide, grooved, shallow and wrinkled. Closed cleft.

113. *Physostemon guianensis* (Aubl.) Malme (Figure 38c and d)—Seeds are 1.5 x 1.25 mm. Arrangement of epidermal cells – Cells are mostly tetra-gonal and isodiametric near the crests. There are punctuated crests and circumferential ridges. Periclinal walls are papillate and rugose. Anticlinal walls are mostly wide and shallow becoming wider and more deeply grooved near the crests. Closed crest. Radicular claw elongated.

114. *Physostemon humilis* (Rose) Iltis (Figure 38e and f)—Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low radial crests and circumferential ridges. Periclinal walls are papillate and wrinkled with tabular protrusions. Anticlinal walls are wide, grooved and rugose. Closed cleft.

115*. Cleome tenuis* S. Watson (Figure 39a and b)—Seeds are 1.25 x 1.25 mm. Arrangement of epidermal cells – Cells are isodiametric. There are low radial crests and circumferential ridges. Periclinal walls are papillate and wrinkled with tabular protrusions. Anticlinal walls are wide, grooved, shallow and rugose. Closed cleft.

Note*—Cleome tenuis* was considered part of *Cleome* section *Physostemon* by Iltis (1959), but has never had a nomenclatural combination made within *Physostemon*. As it has yet to be included in a phylogenetic analysis, we are grouping it here with the *Physostemon* species but not making any nomenclatural changes.

116. *Physostemon lanceolatum* Mart. & Zucc. (Figure 39c and d)—Seeds are 2.0 x 1.75 mm. Arrangement of epidermal cells – Cells are isodiametric. There are high radial crests. Periclinal walls are papillate and wrinkled with cells papillate flat and wrinkled closer to the crests. Anticlinal walls are wide, grooved and very shallow. Closed cleft.

117. *Physostemon hemsleyanum* (Bullock) R.C. Foster (Figure 39e and f)—Seeds are 2.5 x 2.5 mm. Arrangement of epidermal cells – Cells are tetra-gonal. There are high punctuated radial crests. Periclinal walls are concave to flat, rugose and pitted with one stout central papillae that is pointed. Anticlinal walls are wide, grooved and very shallow. Closed cleft.

118. *Physostemon tenuifolium* Mart. & Zucc. (Figure 40a and b)—Seeds are 3.75 x 3.75 mm. Arrangement of epidermal cells – Cells are isodiametric. There are irregularly spaced, long and thin spikes. Cells on the spikes are columnar and smooth with a central, pointed papillae. Periclinal walls are concave and wrinkled with a tabular projection that spans the length of the cell. Anticlinal walls obscured. Closed cleft.

119. *Physostemon rotundifolium* Mart. & Zucc. (Figure 40c and d)—Seeds are 3.0 x 2.5 mm. Arrangement of epidermal cells – Cells are isodiametric. There are irregularly spaced, thick spikes and other rounded protrusions on the seed body. Cells on the spikes are columnar, concave with a non-central, blunt papillae. Periclinal walls are concave and wrinkled with a with a tabular projection that spans the length of the cell. Anticlinal walls obscured. Closed cleft.

XXIV. *Mitostylis* Raf., Sylva Tellur. 114. 1838.

Seeds have high radial crests with papillate and rugose periclinal walls. Anticlinal walls are wide and seed cleft is closed.

120. *Mitostylus procumbens* (Jacq.) Raf. (Figure 40e and f)—Seeds are 1.5 x 1.5 mm. Arrangement of epidermal cells – Cells are elongated tetra-gonal. There are high radial crests. Periclinal walls are papillate and deeply rugose. Anticlinal walls are wide, grooved and shallow. Open cleft.

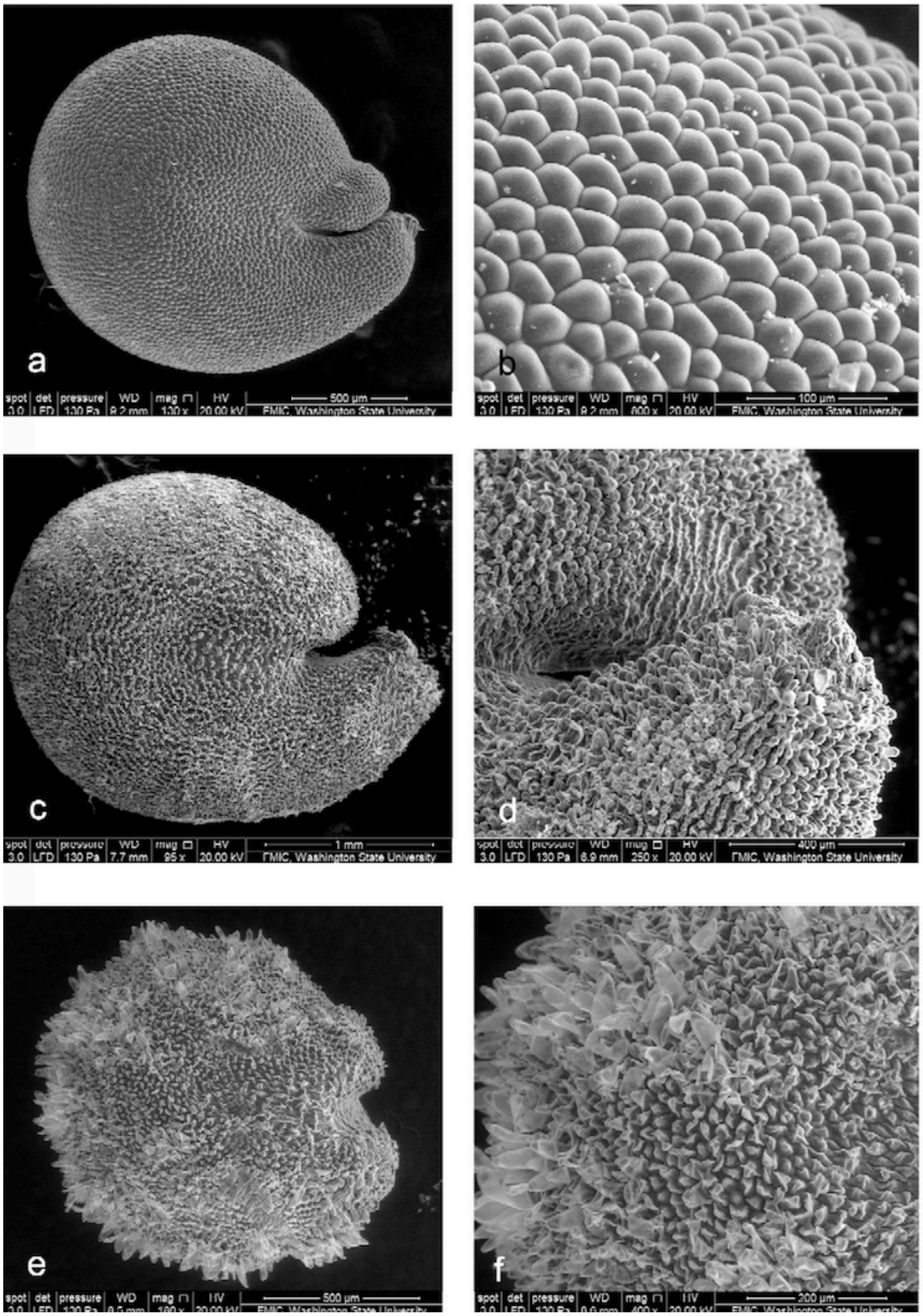

Figure 1: (a and b) *Cleome ornithopodioides* at 500 µm and 100 µm. (c and d) *Cleome coluteoides* at 1.0 mm and 400 µm. (e and f) *Cleome socotrana* at 500 µm and 200 µm.

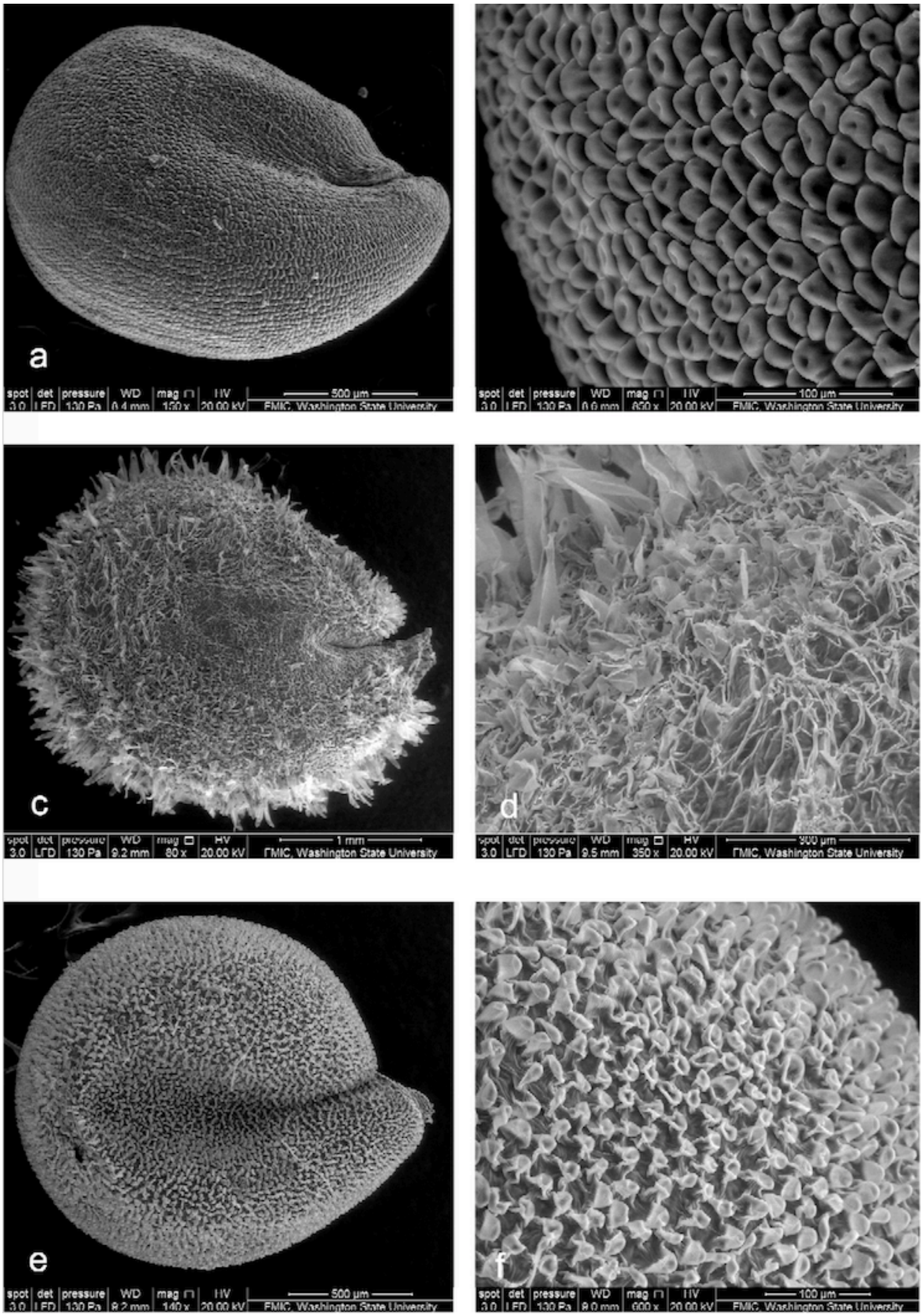

Figure 2: (a and b) *Cleome stevensiana* at 500 μm and 100 μm.
(c and d) *Cleome glaucescens* at 1.0 mm and 300 μm. (e and f) *Cleome turkmena* at 500 μm and 100 μm.

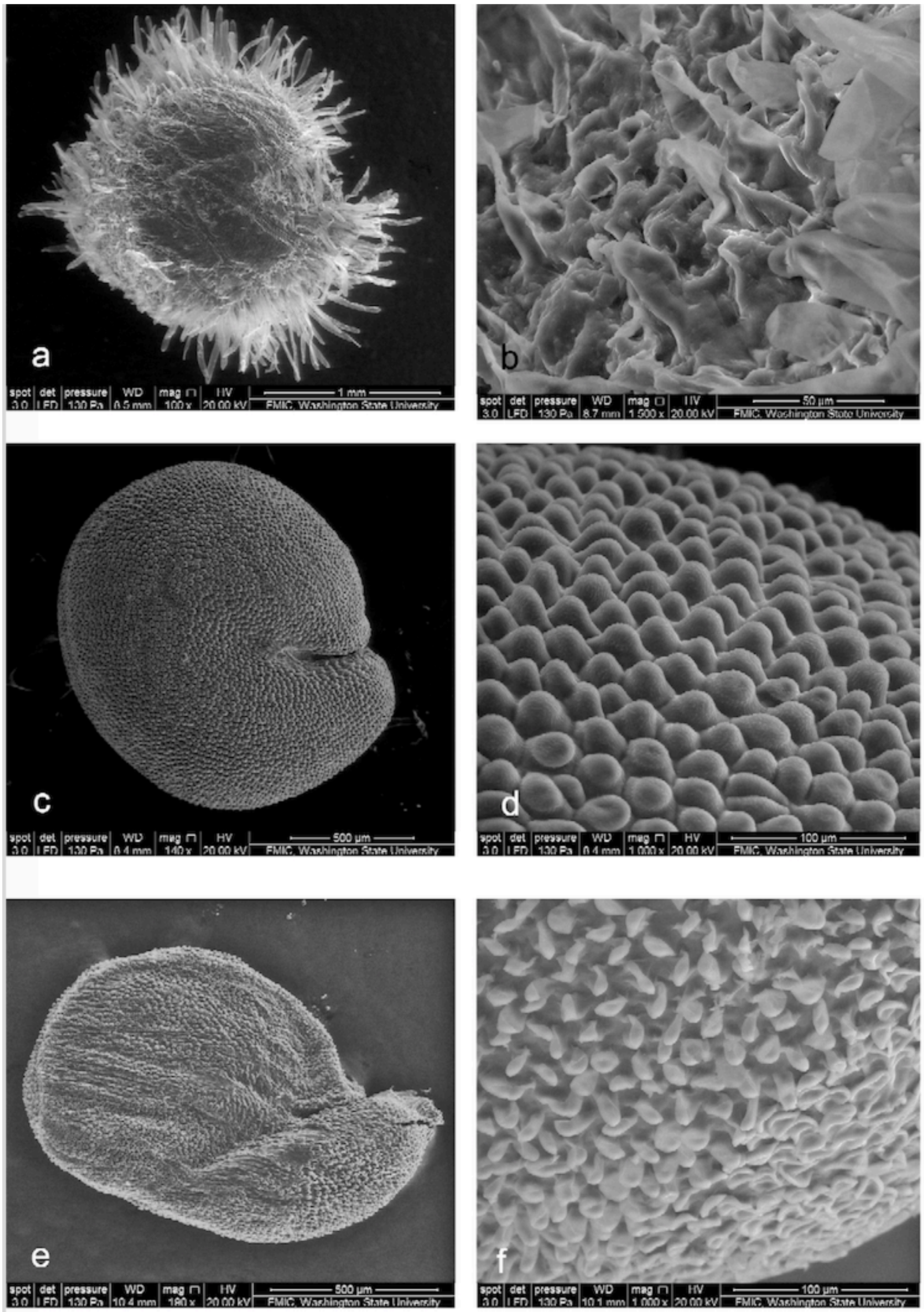

Figure 3: (a and b) *Cleome rupicola* at 1.0 mm and 50 μm. (c and d) *Cleome khorassanica* at 500 μm and 100 μm. (e and f) *Cleome heratensis* at 500 μm and 100 μm.

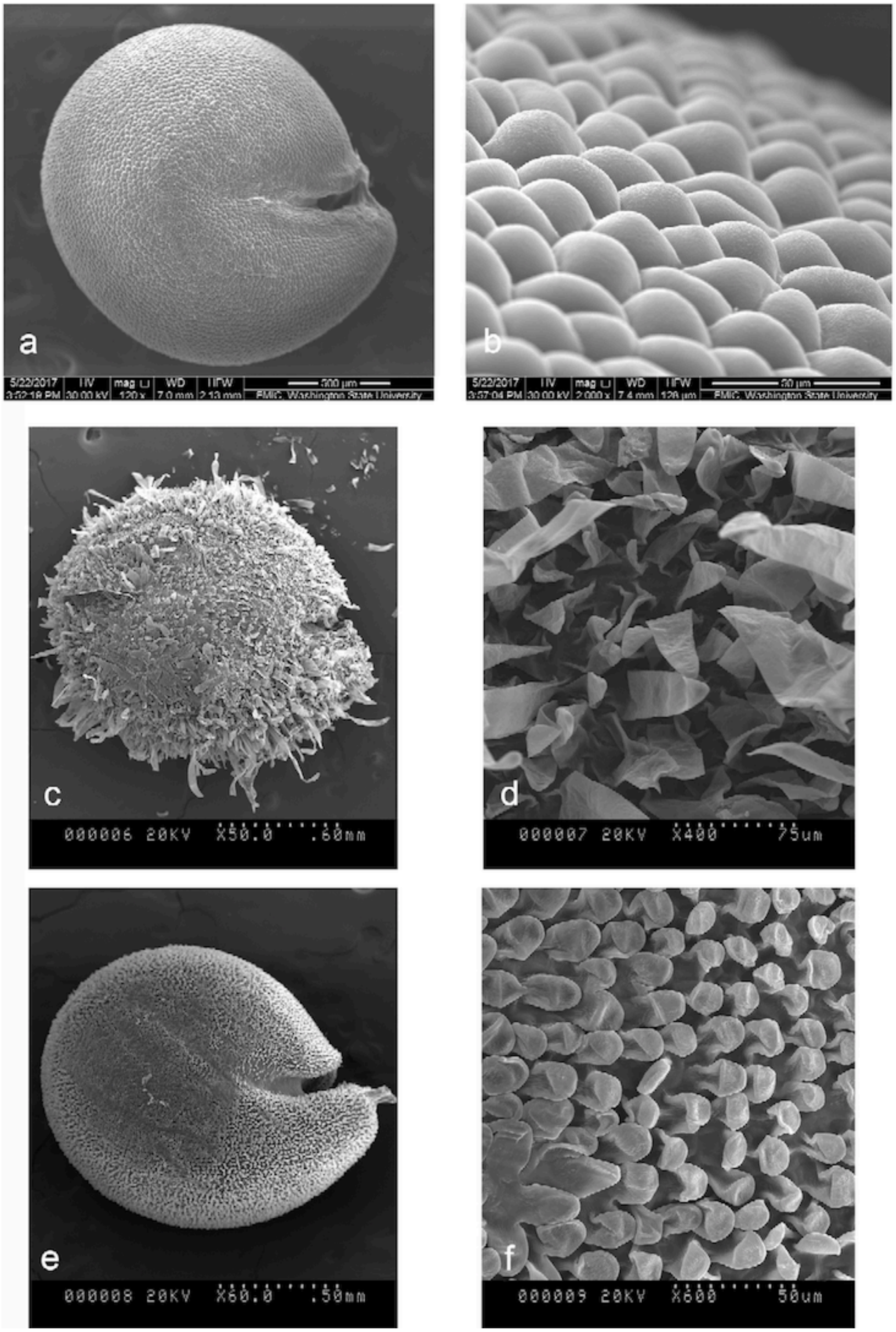

Figure 4: (a and b) *Cleome iberica* at 500 μm and 50 μm. (c and d) *Cleome arabica* at 0.6 mm and 75 μm. (e and f) *Cleome ariana* at 0.5 mm and 50 μm.

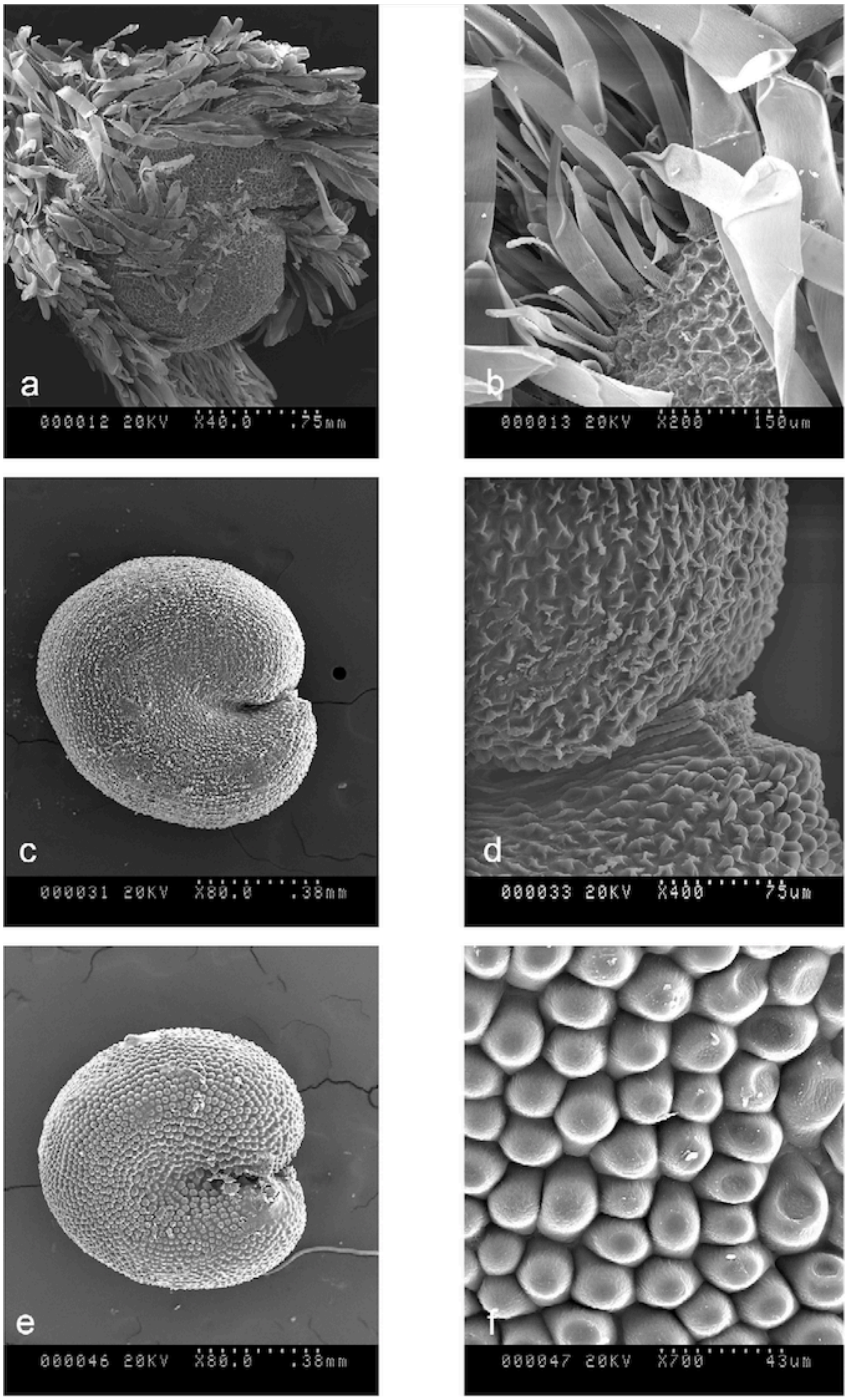

Figure 5: (a and b) *Cleome oxypetala* at 0.75 mm and 150 μm. (c and d) *Rorida fimbriata* at 0.38 mm and 75 μm. (e and f) *Rorida droserifolia* at 0.38 mm and 43 μm.

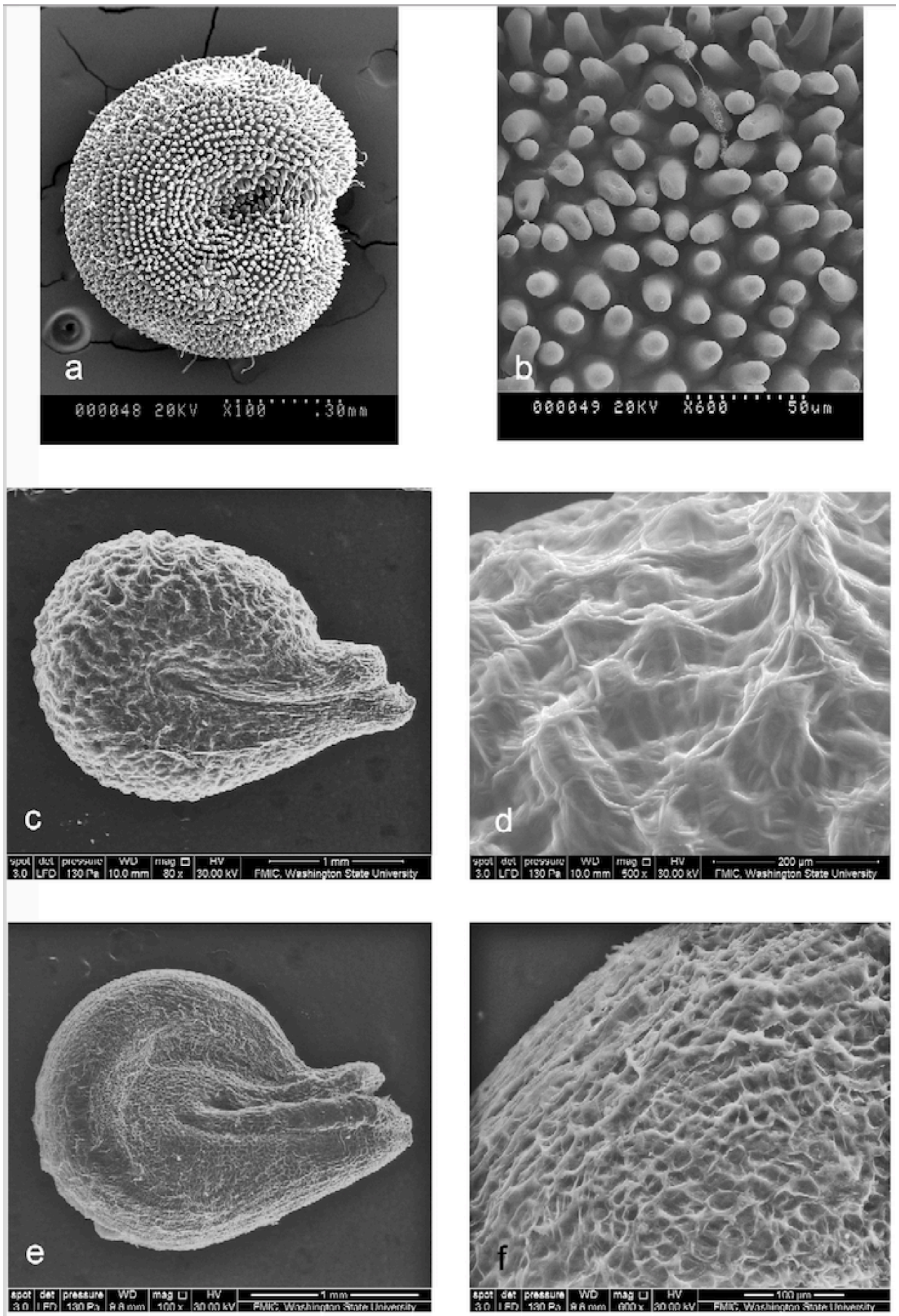

Figure 6: (a and b) *Rorida polytricha* at 0.3 μm and 50 μm. (c and d) *Cleomella angustifolia* at 1.0 mm and 50 μm. (e and f) *Cleomella hillmanii* var. *goodrichii* at 1.0 mm and 100 μm.

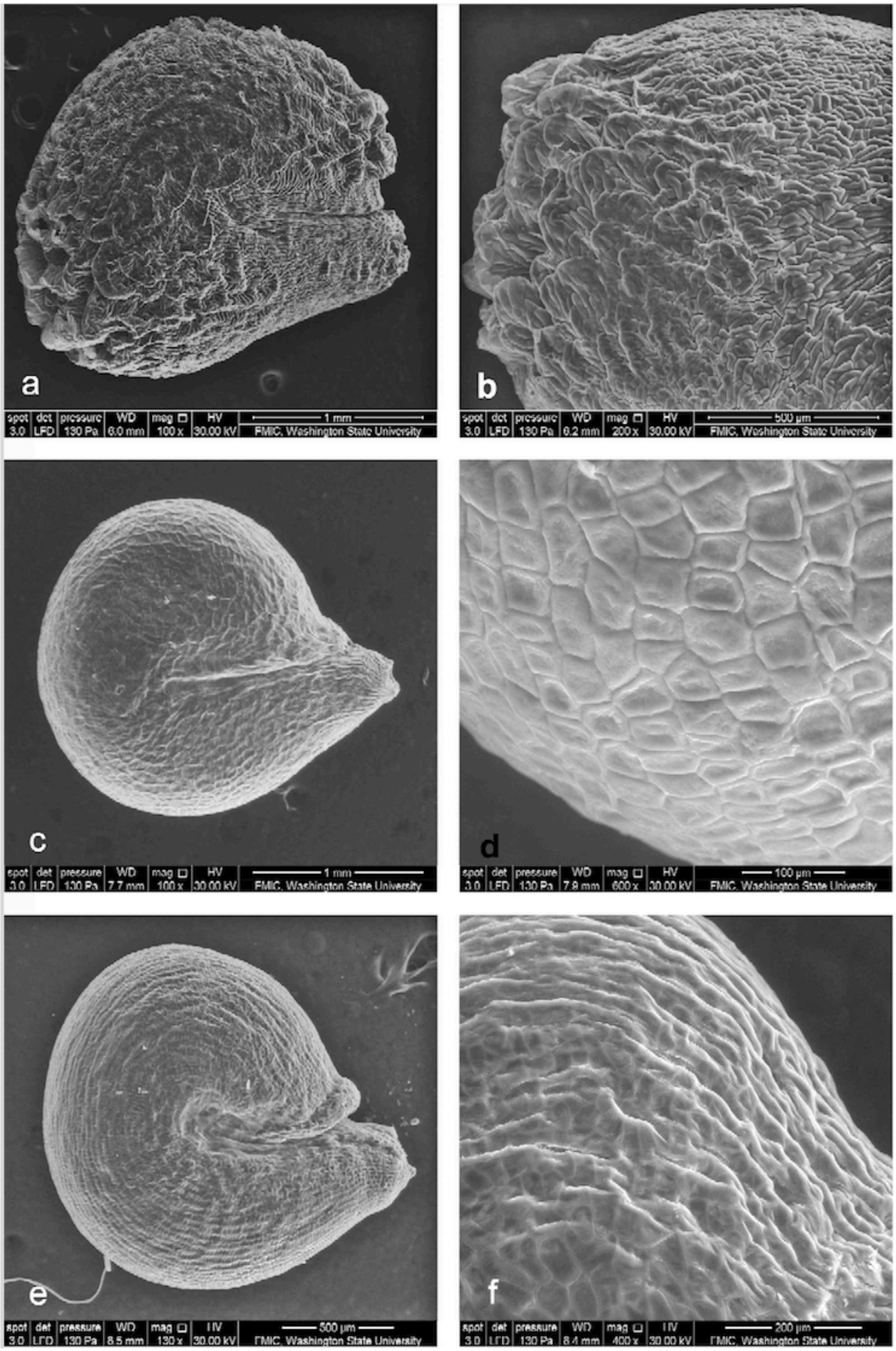

Figure 7: (a and b) *Cleomella hillmanii* var. *hillmanii* at 1.0m and 500 μm. (c and d) *Cleomella longipes* at 1.0 mm and 100 μm. (e and f) *Cleomella mexicana* at 500 μm. and 200 μm.

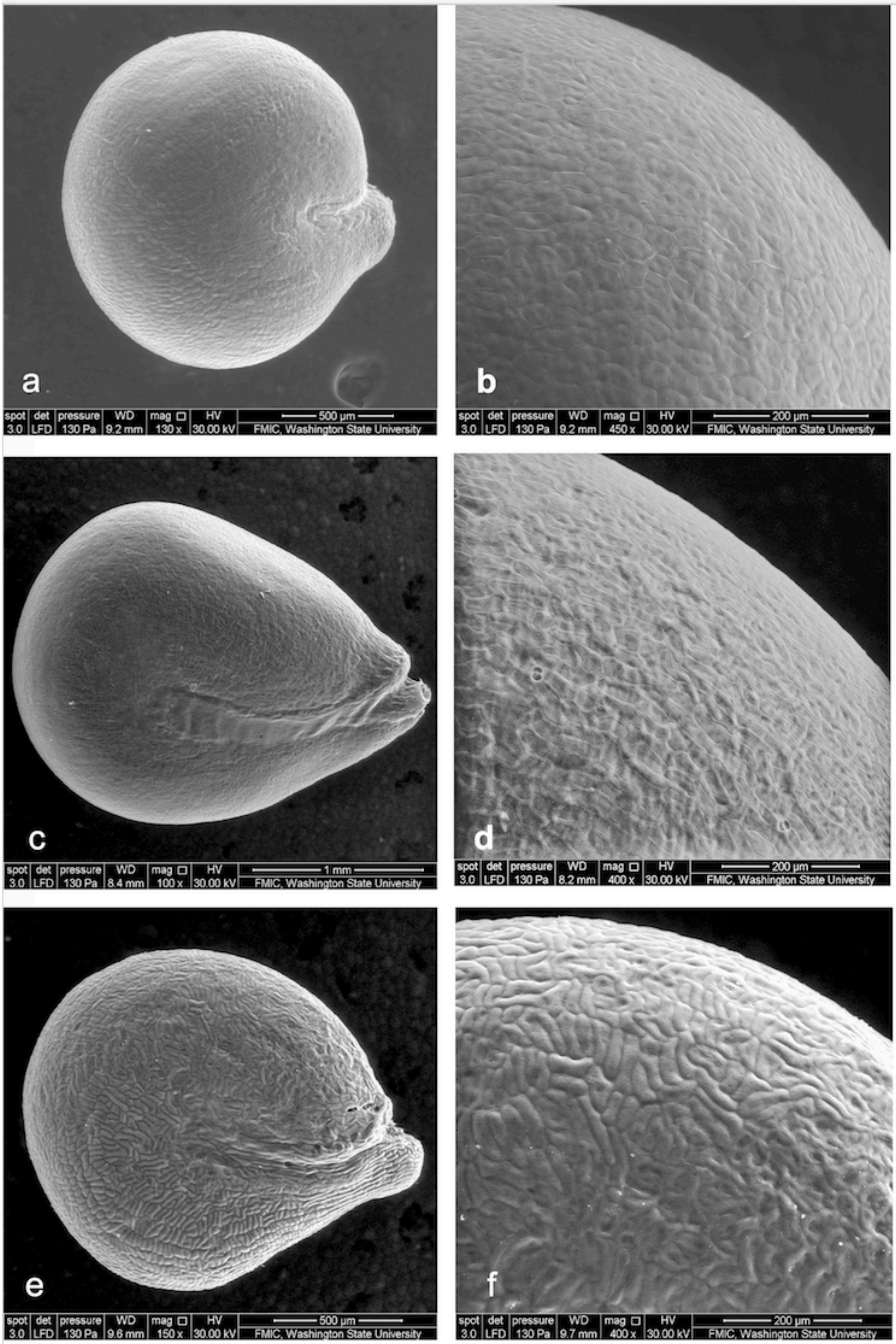

Figure 8: (a and b) *Cleomella obtusifolia* at 500 μm and 200 μm. (c and d) *Cleomella palmeriana* at 1.0 mm and 200 μm. (e and f) *Cleomella parviflora* at 500 μm. and 200 μm.

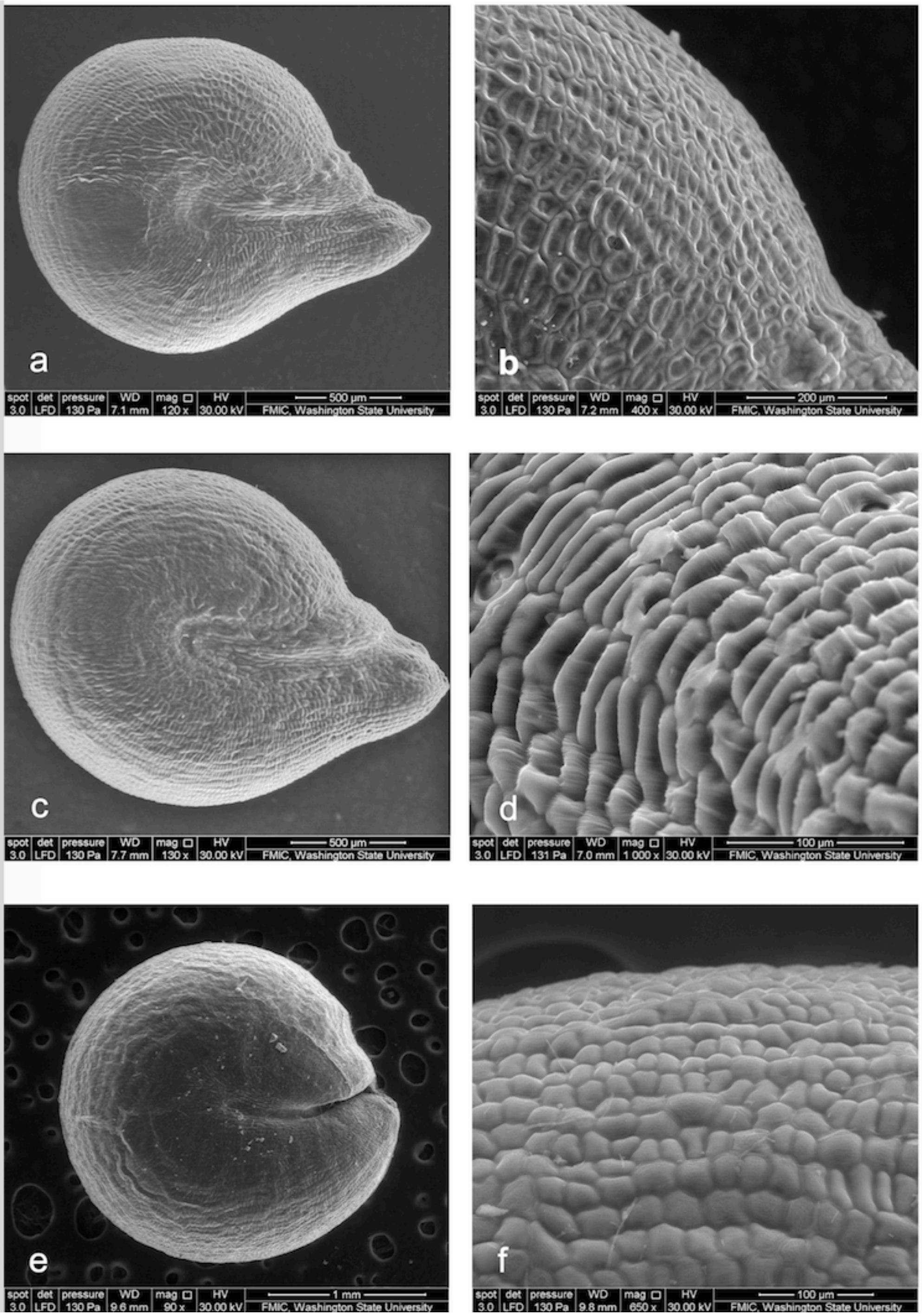

Figure 9: (a and b) *Cleomella perennis* at 500 μm and 200 μm. (c and d) *Cleomella plocasperma* at 500 μm and 100 μm. (e and f) *Polanisia uniglandulosa* at 1.0 mm. and 100 μm.

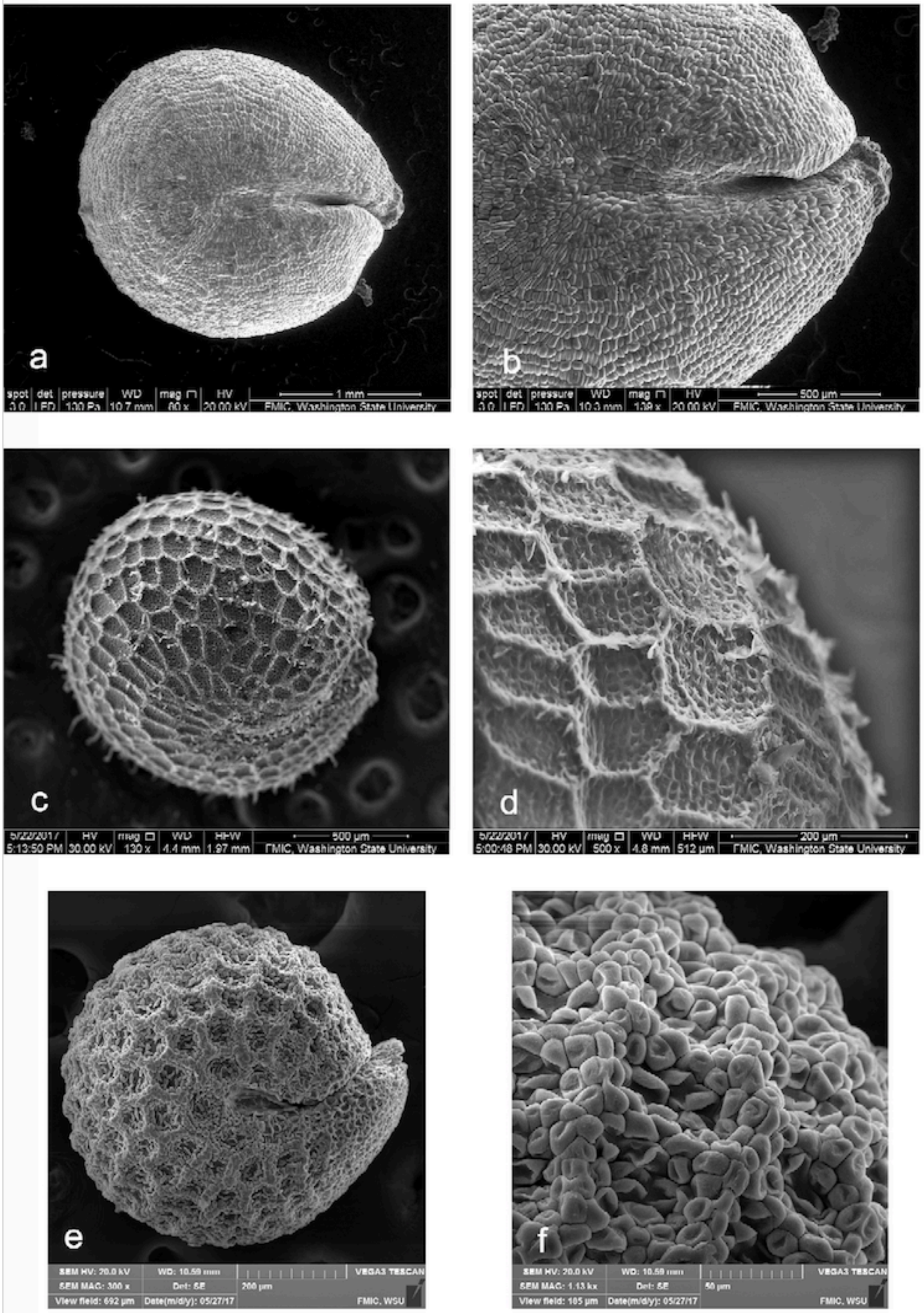

Figure 10: (a and b) *Polanisia dodecandra* at 1.0 mm and 500 µm. (c and d) *Coalisina paradoxa* at 500 µm and 200 µm. (e and f) *Coalisina tenella* at 200 µm and 500 µm.

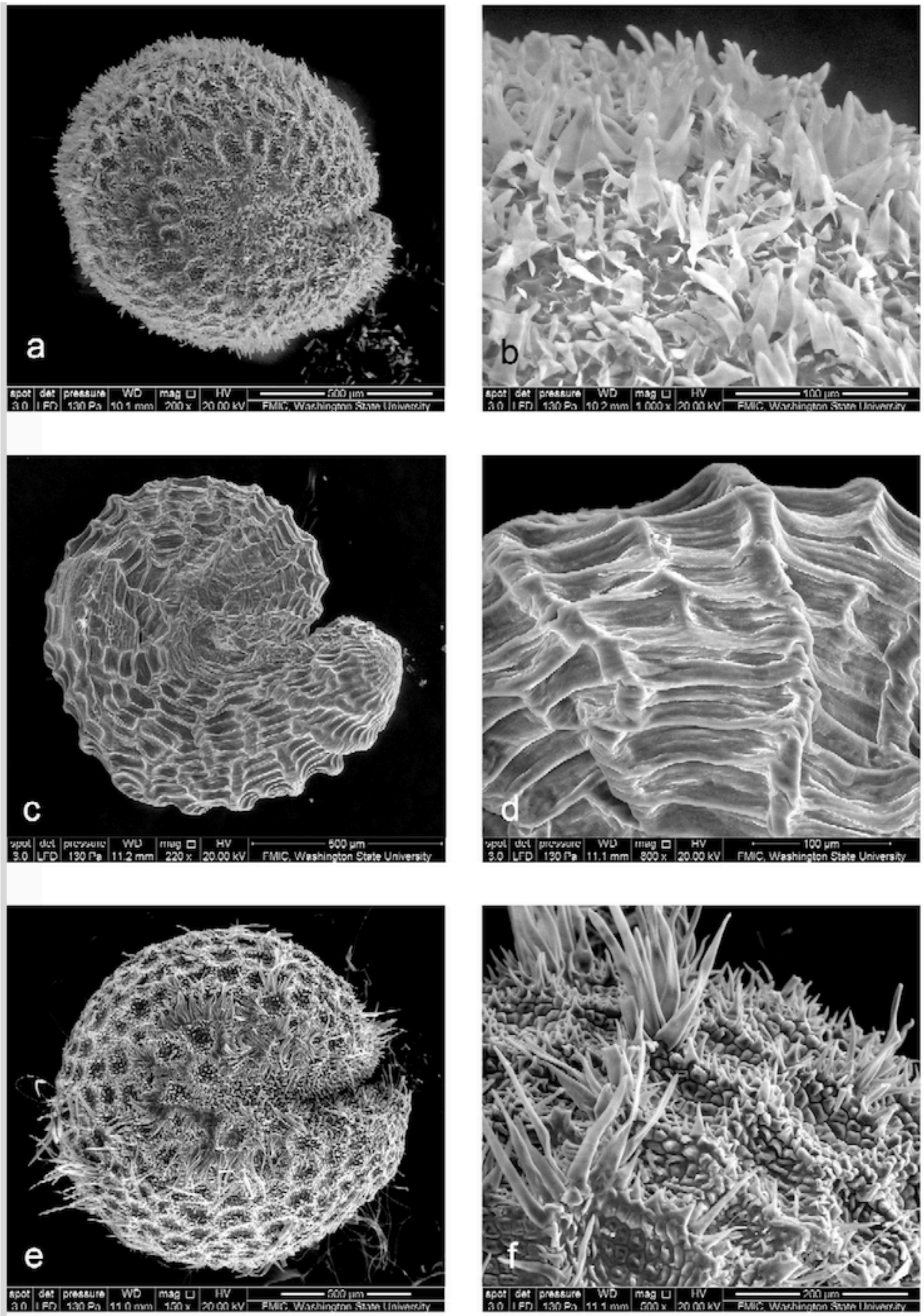

Figure 11: (a and b) *Coalisina semitetrandra* at 500 μm and 100 μm. (c and d) *Coalisina polyanthera* at 500 μm and 100 μm. (e and f) *Coalisina angustifolia* subsp. *petersiana* at 500 μm and 200 μm.

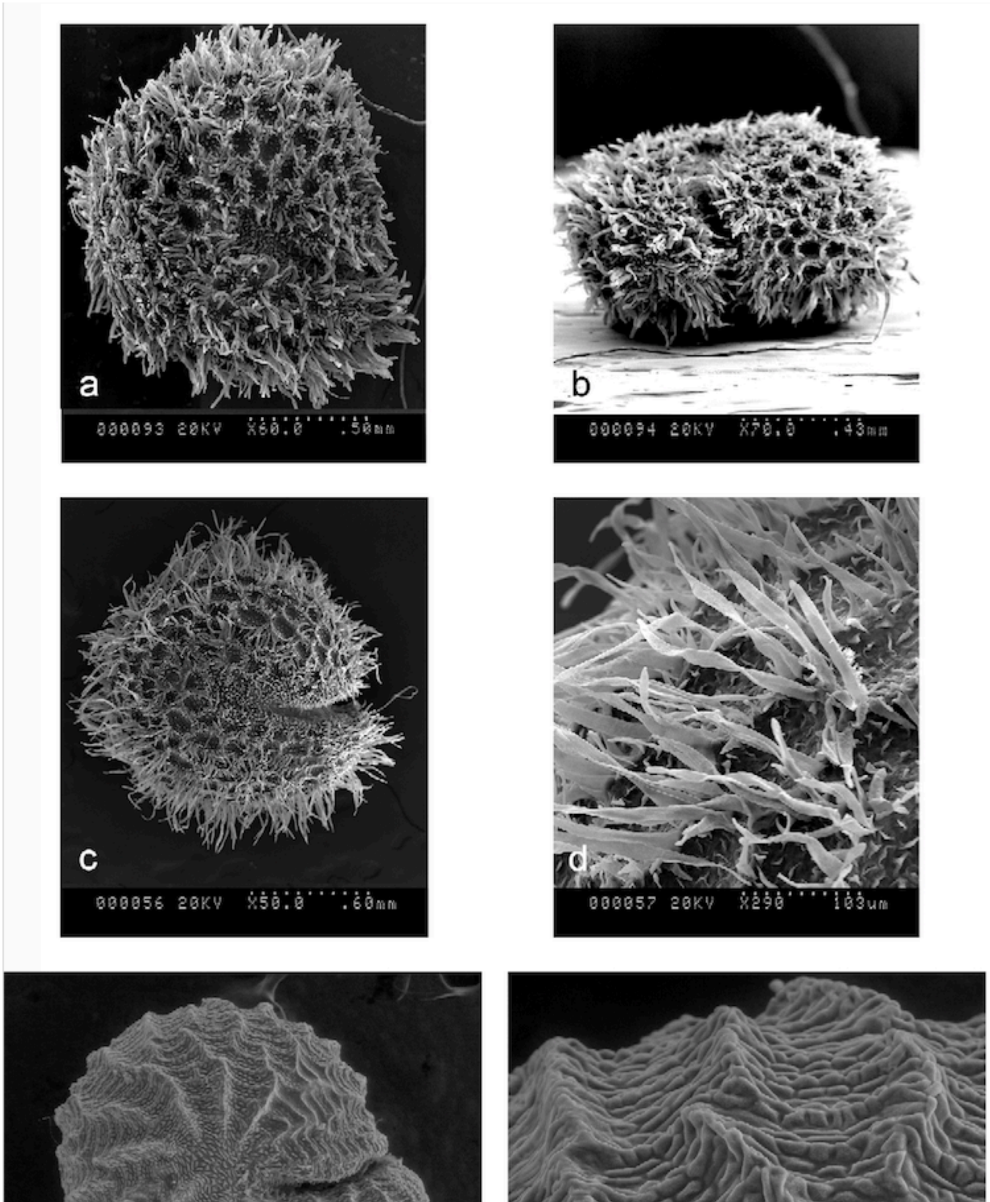

Figure 12: (a and b) *Coalisina angustifolia* subsp. *angustifolia* at 0.5 mm and 0.43 mm. (c and d) *Coalisina angustifolia* subsp. *diandra* at 0.6 mm and 103 mm. (e and f) *Arivela viscosa* at 500 μm and 100 μm.

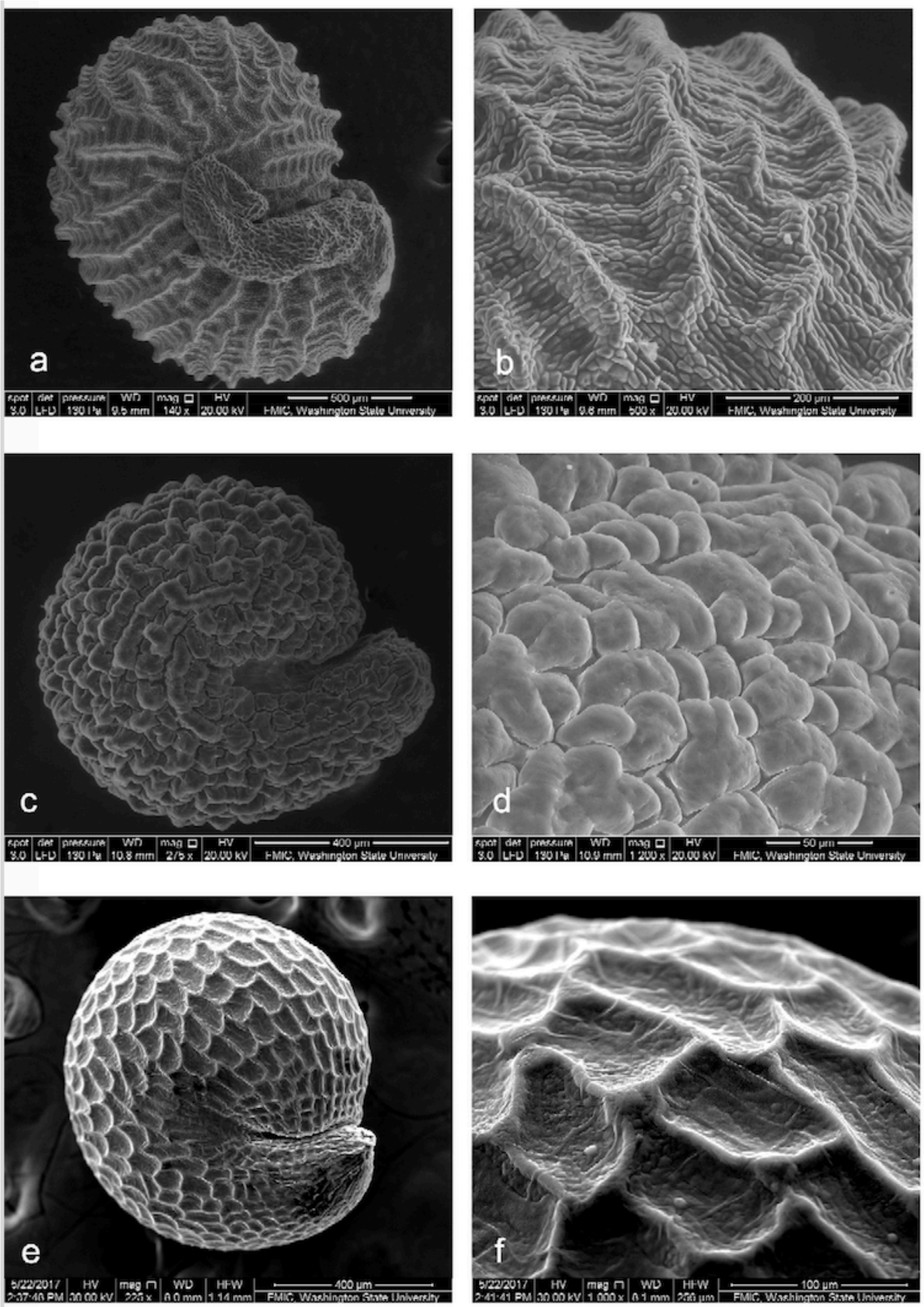

Figure 13: (a and b) *Arivela cleomoides* at 500 μm and 200 μm. (c and d) *Areocleome oxalidea* at 400 μm and 50 μm. (e and f) *Kersia paxii* at 400 μm and 100 μm.

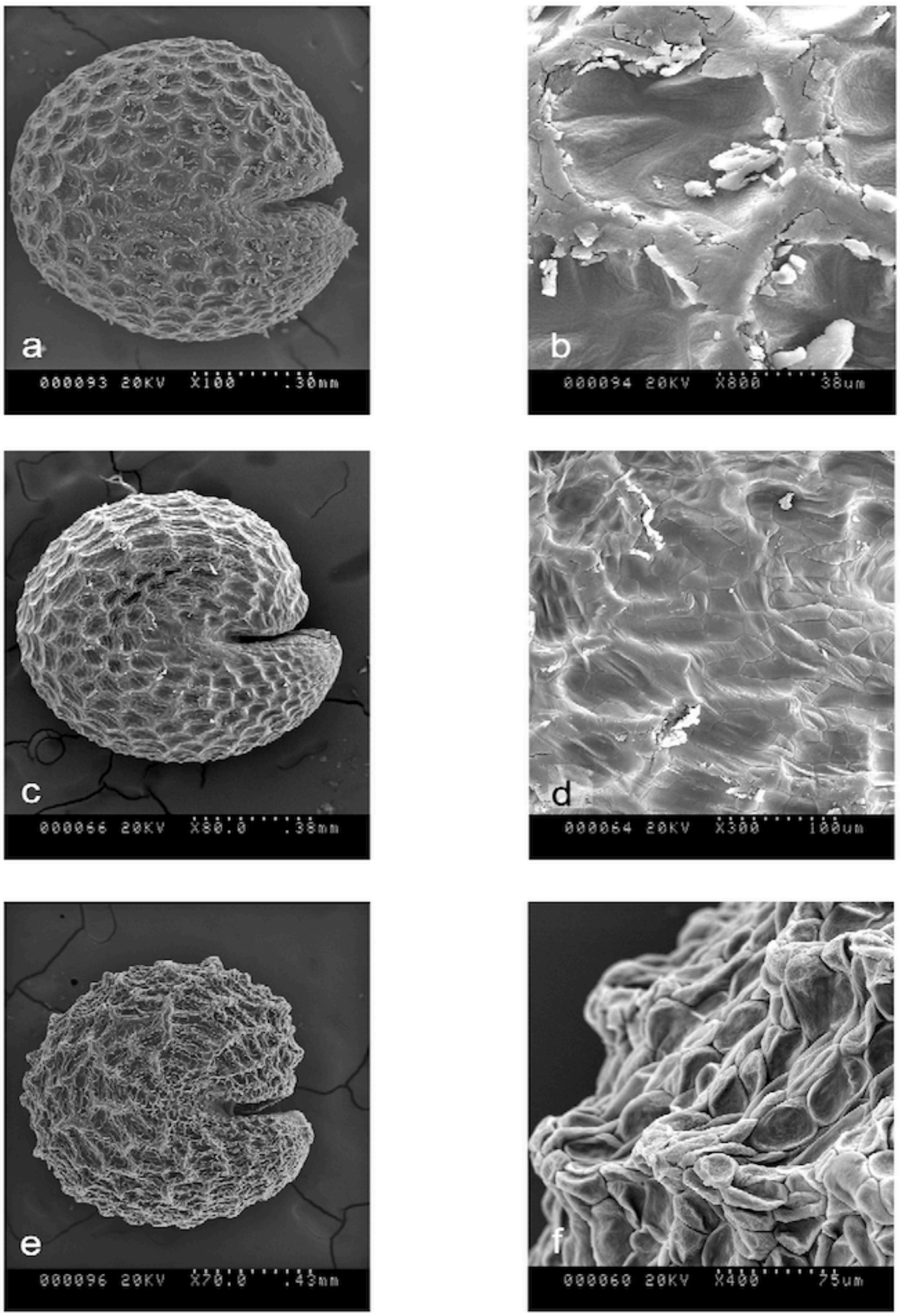

Figure 14: (a and b) *Kersia foliosa* var. *lutea* at 0.3 mm and 0.38 mm. (c and d) *Kersia suffruticosa* at 0.38 mm and 100 µm. (e and f) *Kersia kalachariensis* subsp. *kalachariensis* at 0.43 mm and 75 mm.

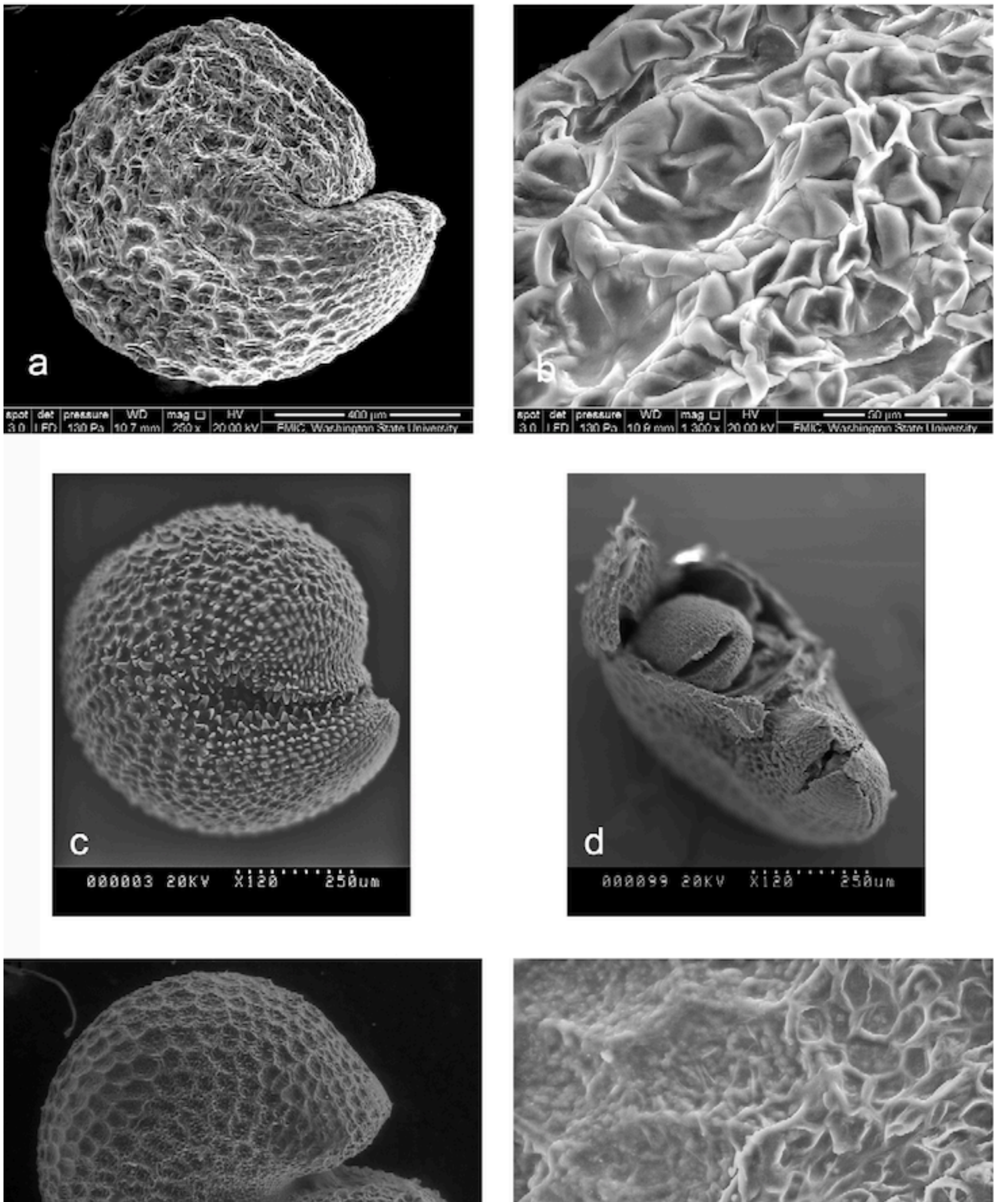

Figure 15: (a and b) *Kersia kalachariensis* subsp. *namibensis* at 400 μm and 50 μm. (c and d) *Gilgella scaposa* at 250 μm and 250 μm. (e and f) *Thulinella chrysantha* at 500 μm and 100 μm.

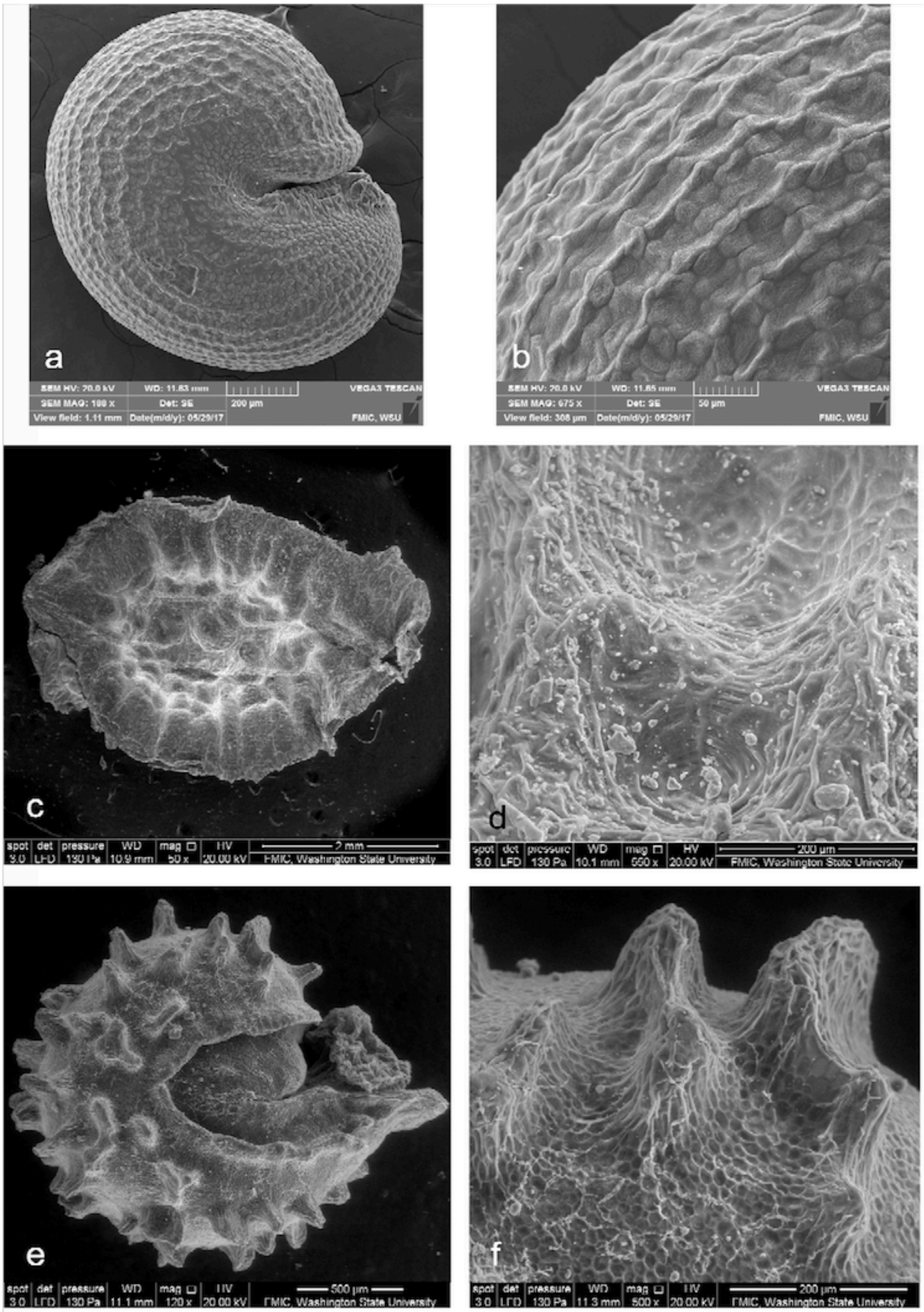

Figure 16: (a and b) *Stylidocleome brachycarpa* at 200 μm and 50 μm. (c and d) *Dipterygium glaucum* (fruit) at 2.0 mm and 200 μm. (e and f) *Corynandra felina* at 500 μm and 200 μm.

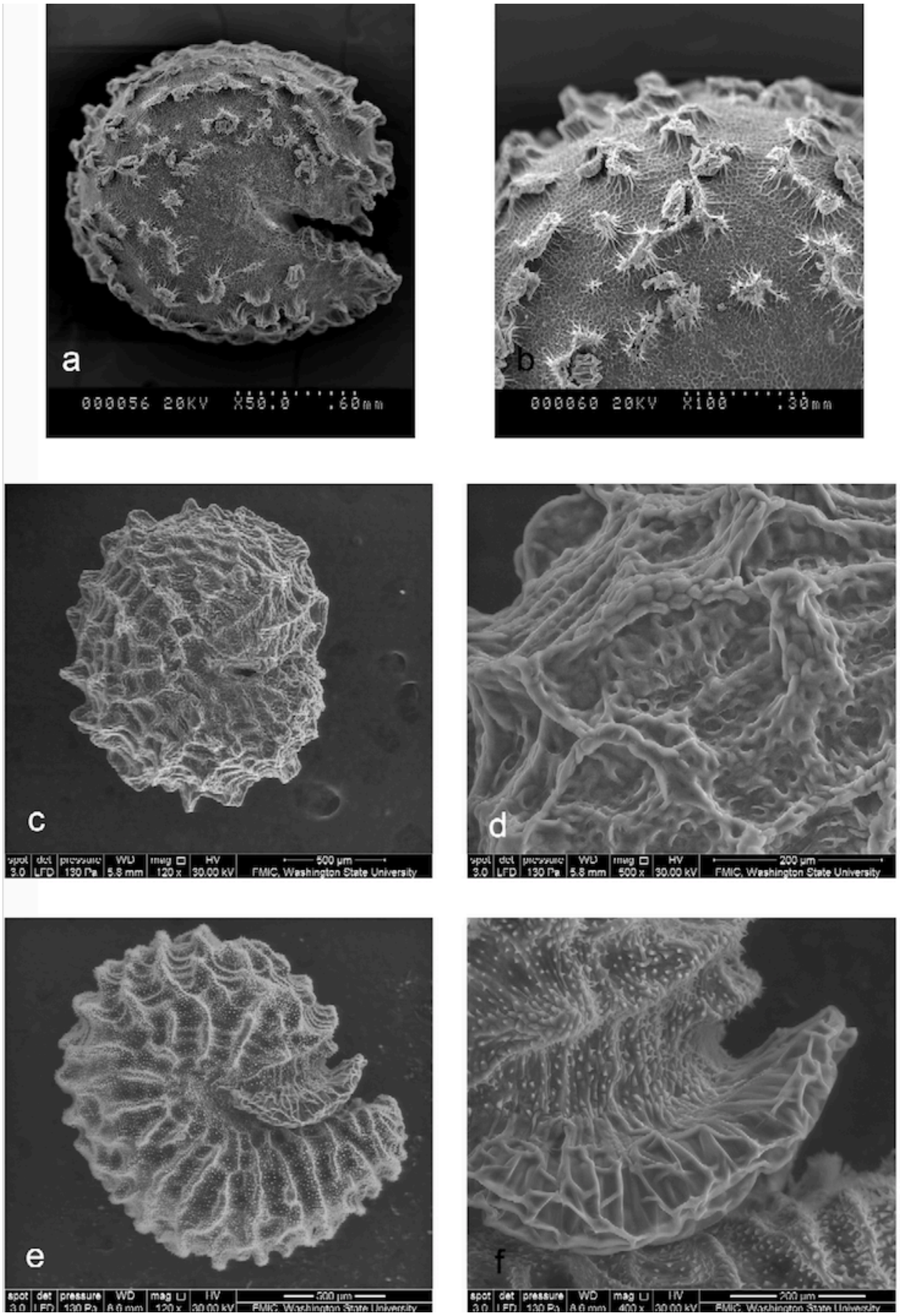

Figure 17: (a and b) *Corynandra chelidonii* at 0.6 mm and 0.3 mm. (c and d) *Gynandropsis gynandra* at 500 μm and 200 μm. (e and f) *Sieruela hanburyana* at 500 μm and 200 μm.

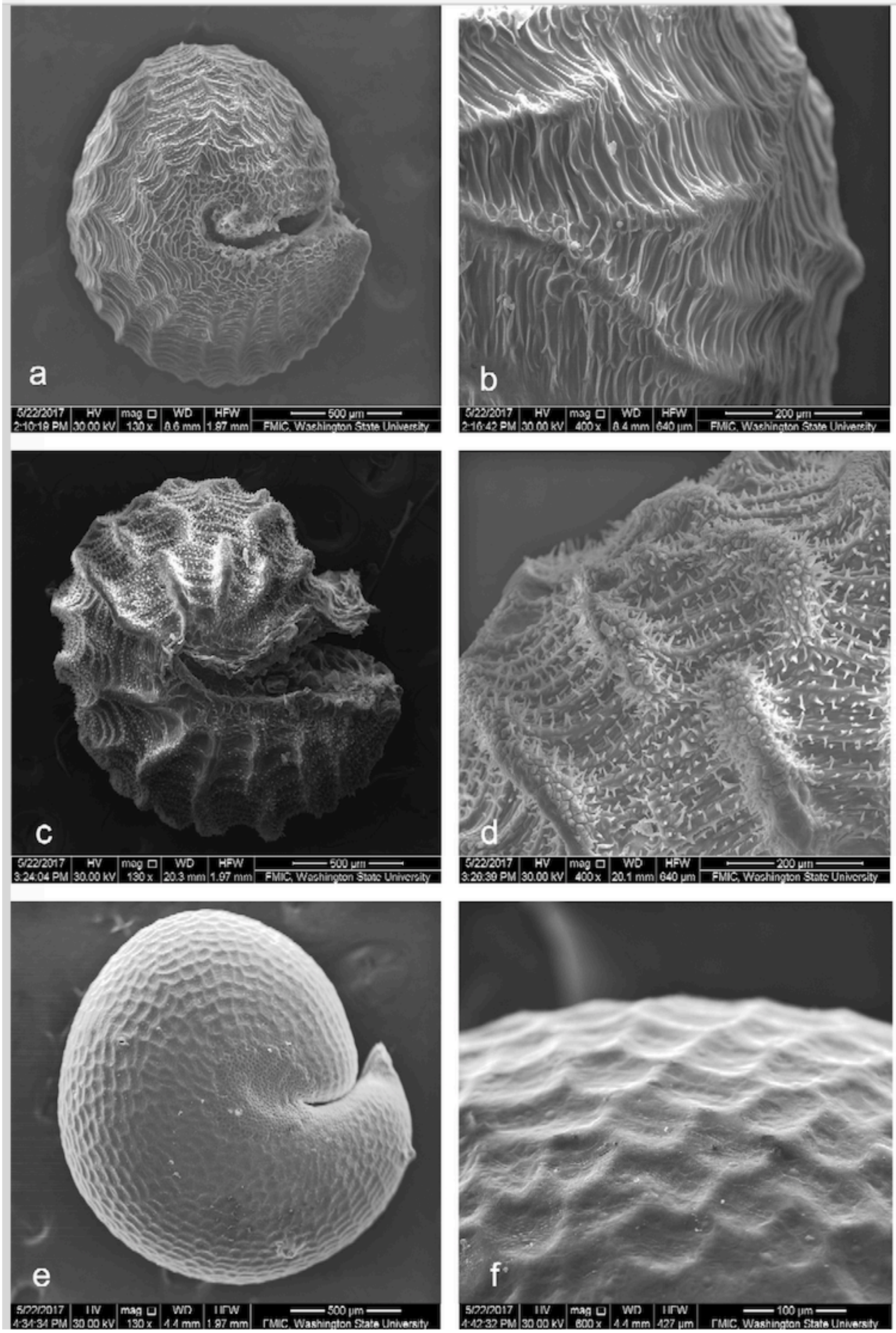

Figure 18: (a and b) *Sieruela stricta* at 500 μm and 200 μm. (c and d) *Sieruela parvipetala* at 500 μm and 200 μm. (e and f) *Sieruela boroensis* at 500 μm and 100 μm.

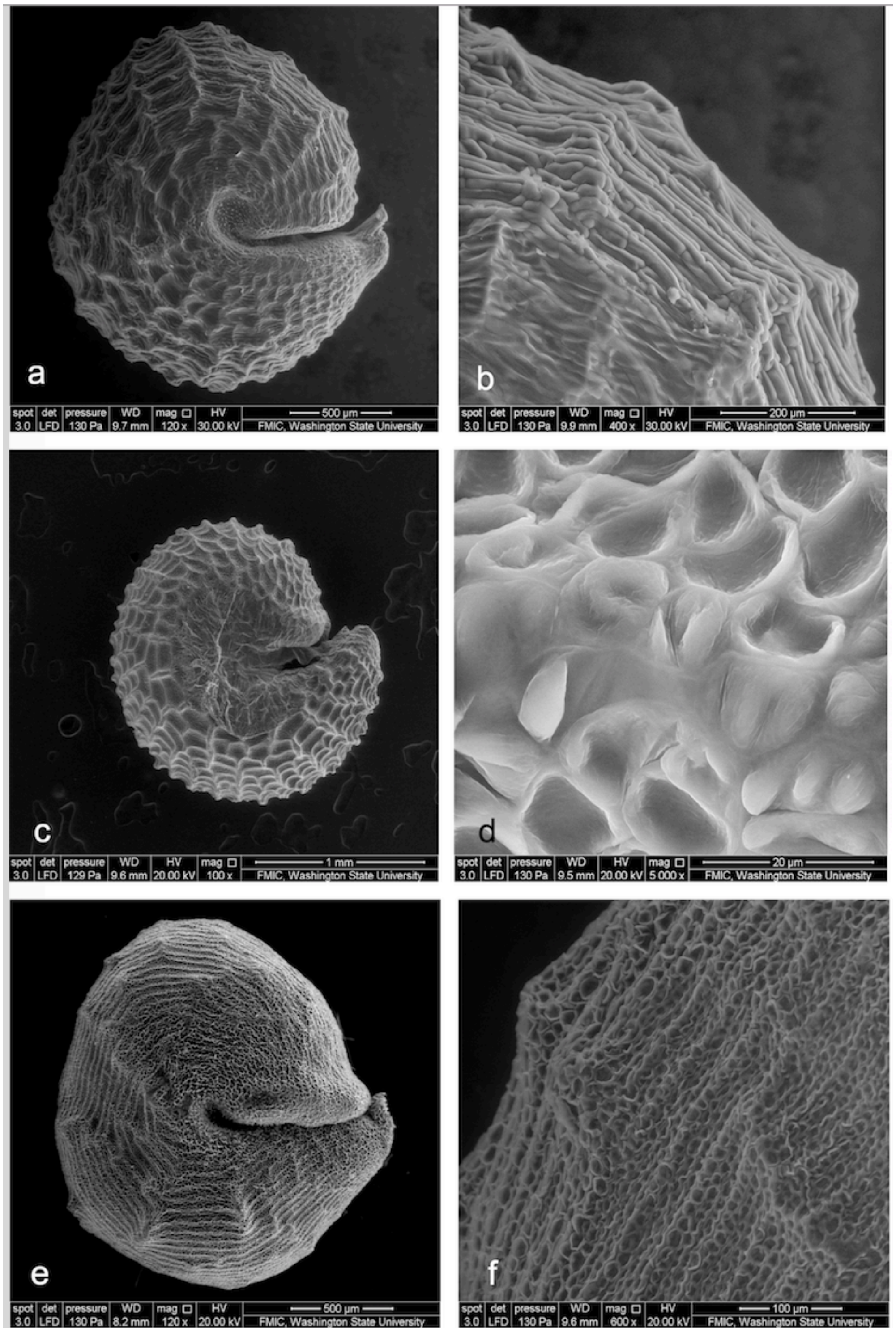

Figure 19: (a and b) *Sieruela macrophylla* at 500 μm and 200 μm. (c and d) *Sieruela briquetti* at 1.0 mm and 200 μm. (e and f) *Sieruela hirta* at 500 μm and 100 μm.

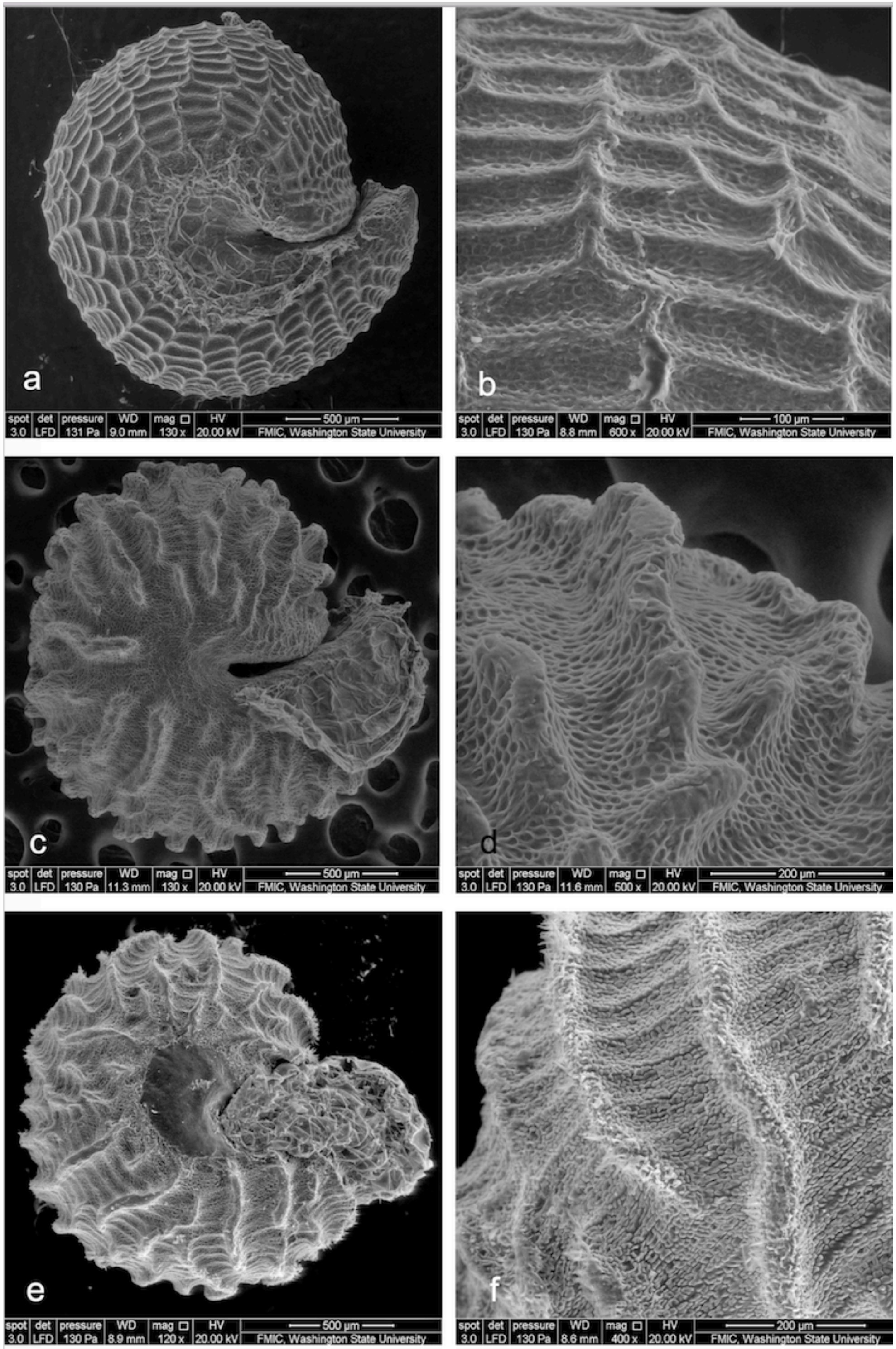

Figure 20: (a and b) *Sieruela usambarica* at 500 μm and 100 μm. (c and d) *Sieruela iberidella* at 500 μm and 200 μm. (e and f) *Sieruela rutidosperma* var. *rutidosperma* at 500 μm and 200 μm.

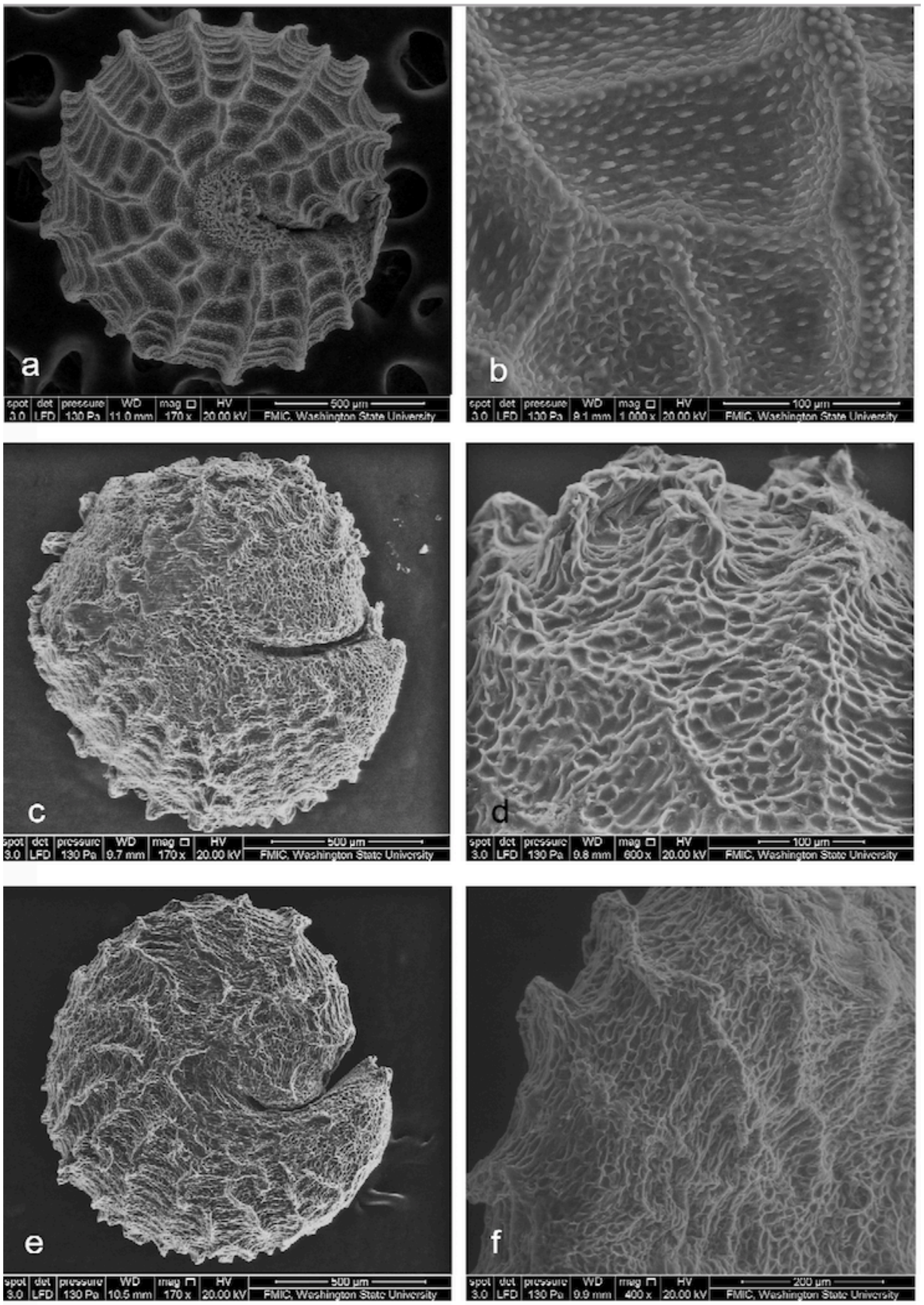

Figure 21: (a and b) *Sieruela rutidosperma* var. *burmanii* at 500 μm and 100 μm. (c and d) *Sieruela oxyphylla* var. *oxyphylla* at 500 μm and 100 μm. (e and f) *Sieruela oxyphylla* var. *robusta* at 500 μm and 200 μm.

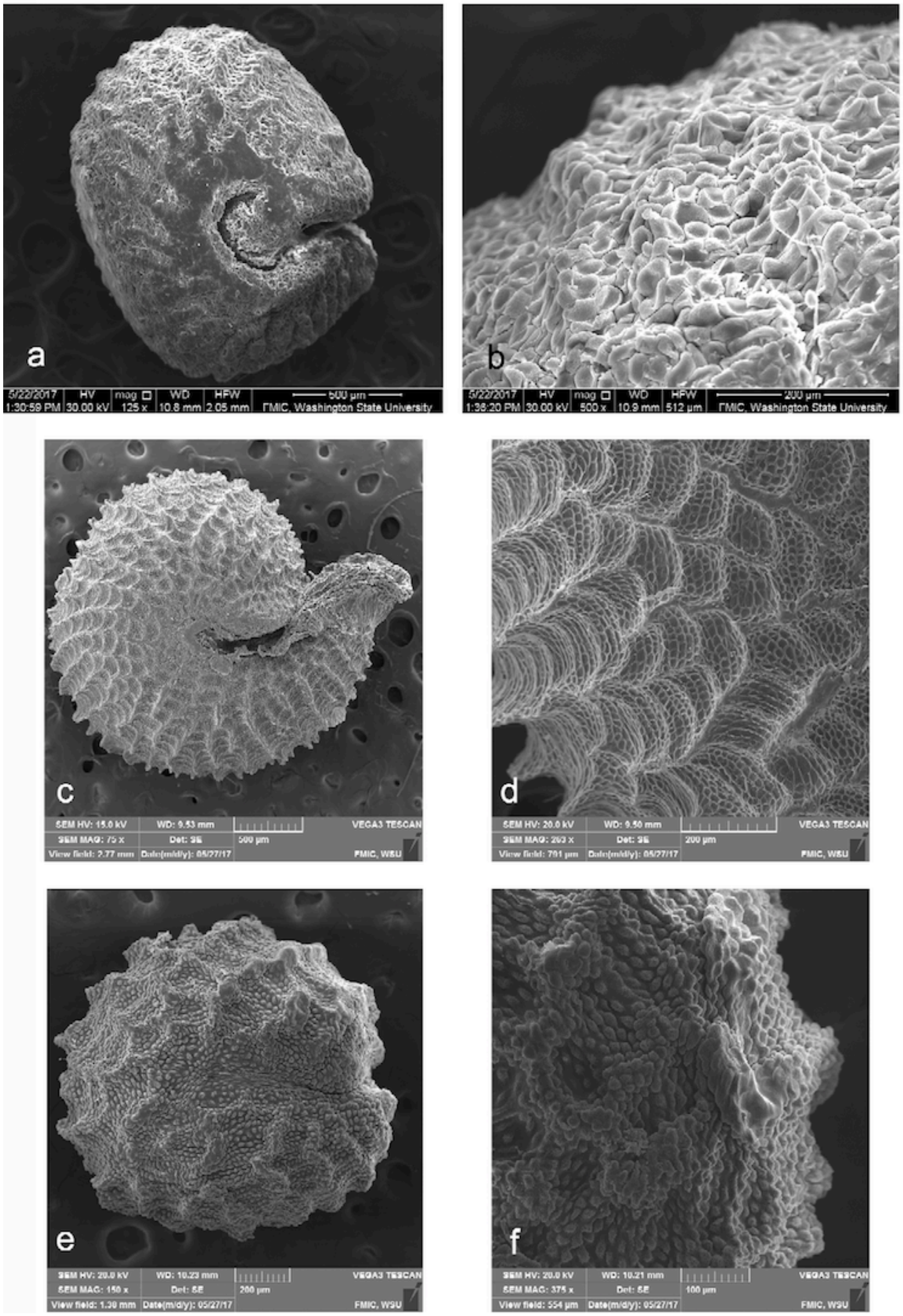

Figure 22: (a and b) *Sieruela strigosa* at 500 μm and 200 μm. (c and d) *Sieruela kermesina* var. *plebeia* at 500 μm and 200 μm. (e and f) *Sieruela micrantha* at 500 μm and 200 μm.

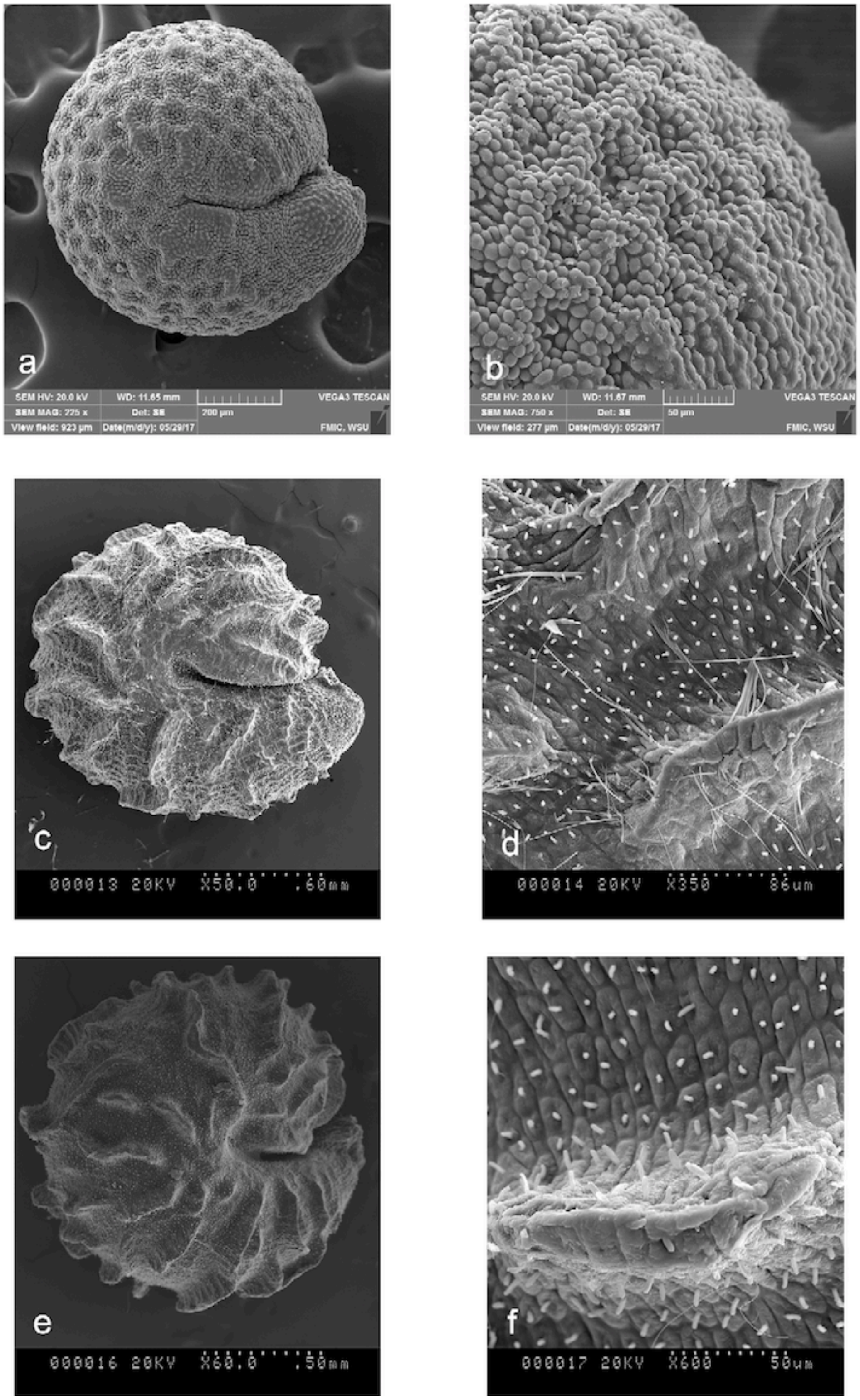

Figure 23: (a and b) *Sieruela perrieri* at 200 μm and 50 μm. (c and d) *Sieruela conrathii* at 0.6 mm and 86 μm.200 μm and 50 μm. (e and f) *Sieruela maculata* at 0.5 mm and 50 μm.

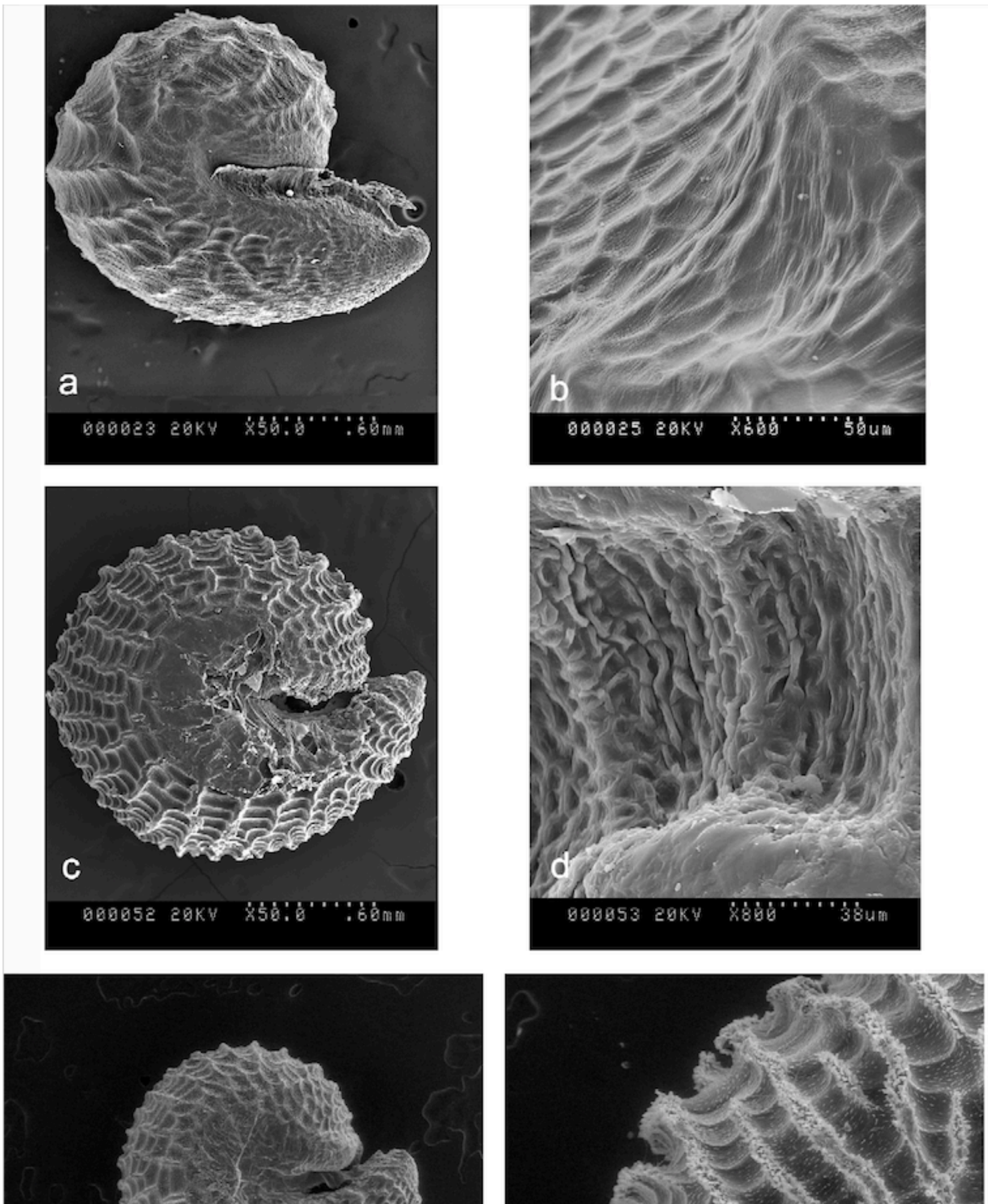

Figure 24: (a and b) *Sieruela rubella* at 0.6 mm and 50 μm. (c and d) *Sieruela silvatica* at 0.6 mm and 38 μm. (e and f) *Sieruela coerulea-rosea* at 1.0 mm and 400 μm.

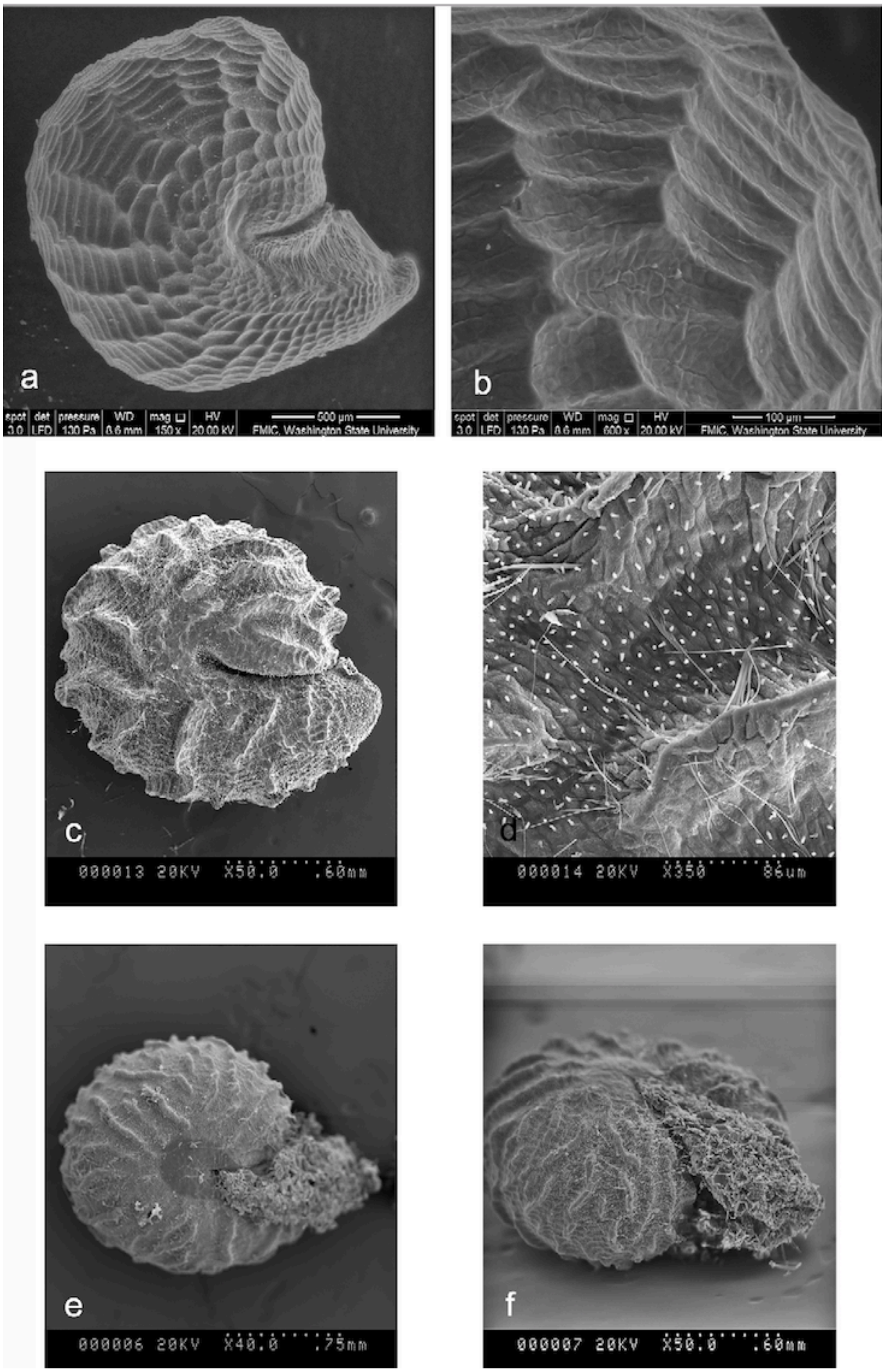

Figure 25: (a and b) *Sieruela monophylla* at 500 μm and 400 μm. (c and d) *Sieruela elegantissima* at 0.6 mm and 86 μm. (e and f) *Sieruela schimperi* at 0.75 mm and 0.6 mm.

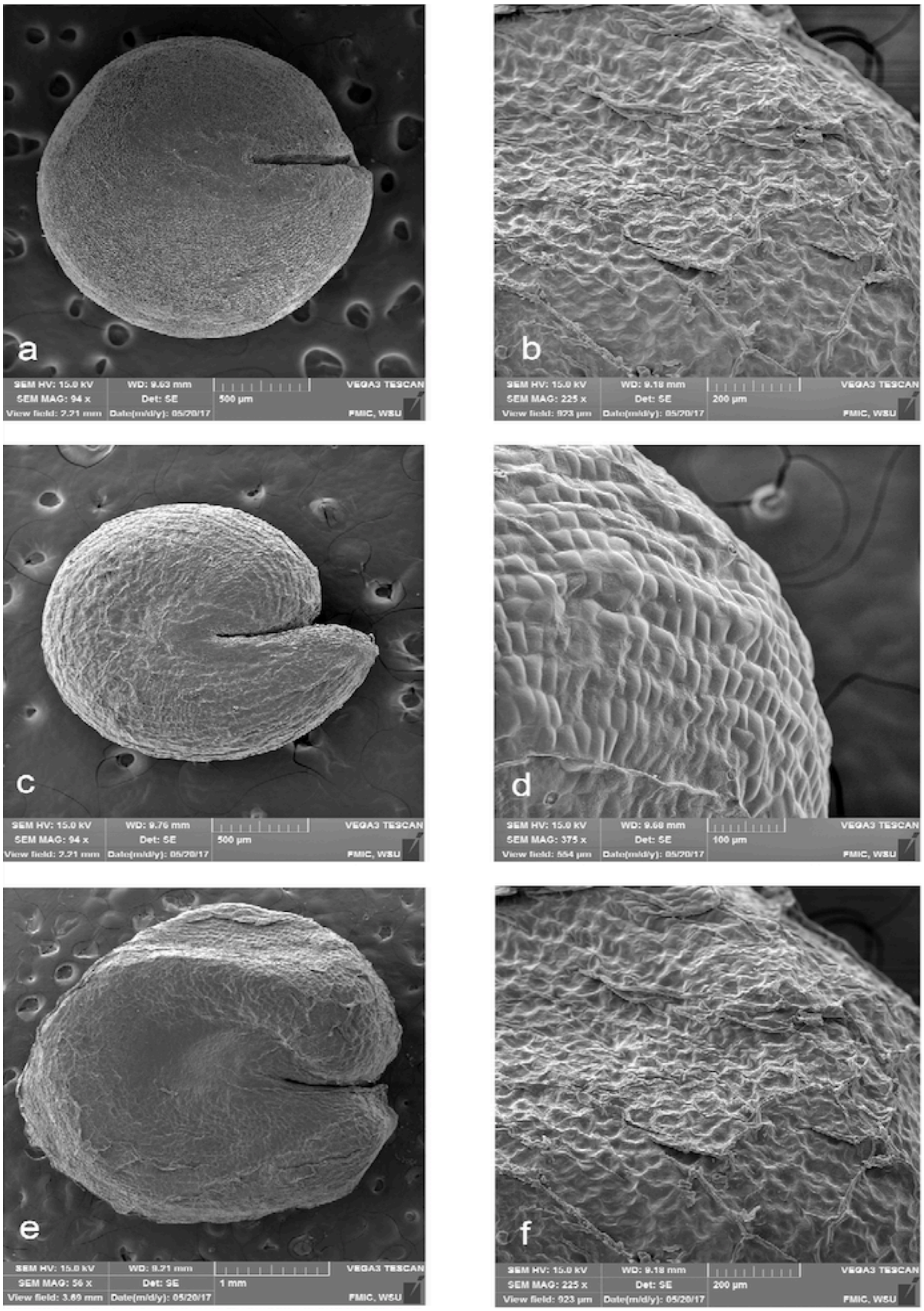

Figure 26: (a and b) *Andinocleome chilensis* at 500 μm and 200 μm. (c and d) *Andinocleome pilosa* at 500 μm and 100 μm. (e and f) *Andinocleome anomala* at 1.0 mm and 200 μm.

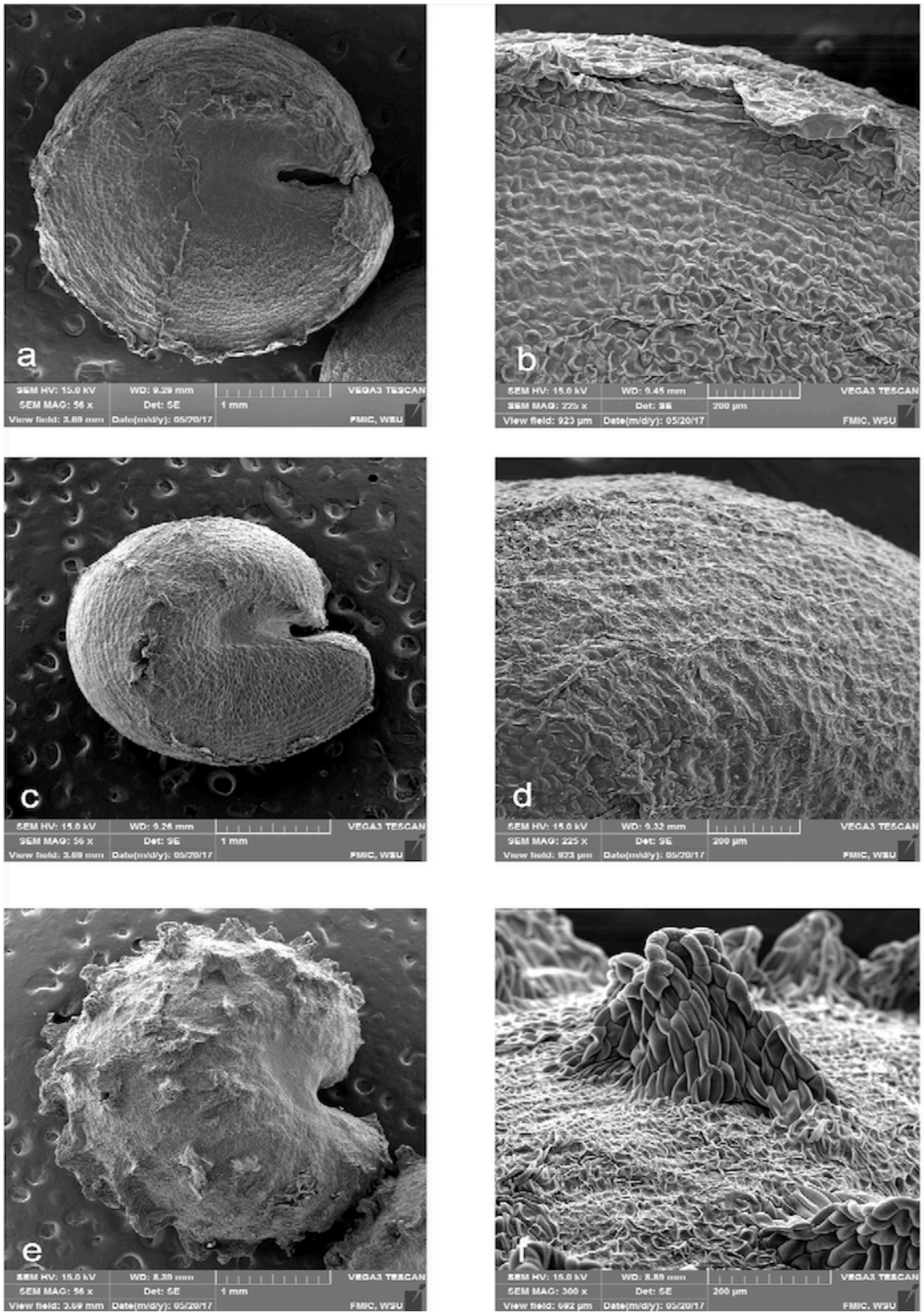

Figure 27: (a and b) *Andinocleome moritziana* at 1.0 mm and 200 μm. (c and d) *Andinocleome lechleri* at 1.0 mm and 200 μm. (e and f) *Andinocleome magnifica* at 1.0 mm and 200 μm.

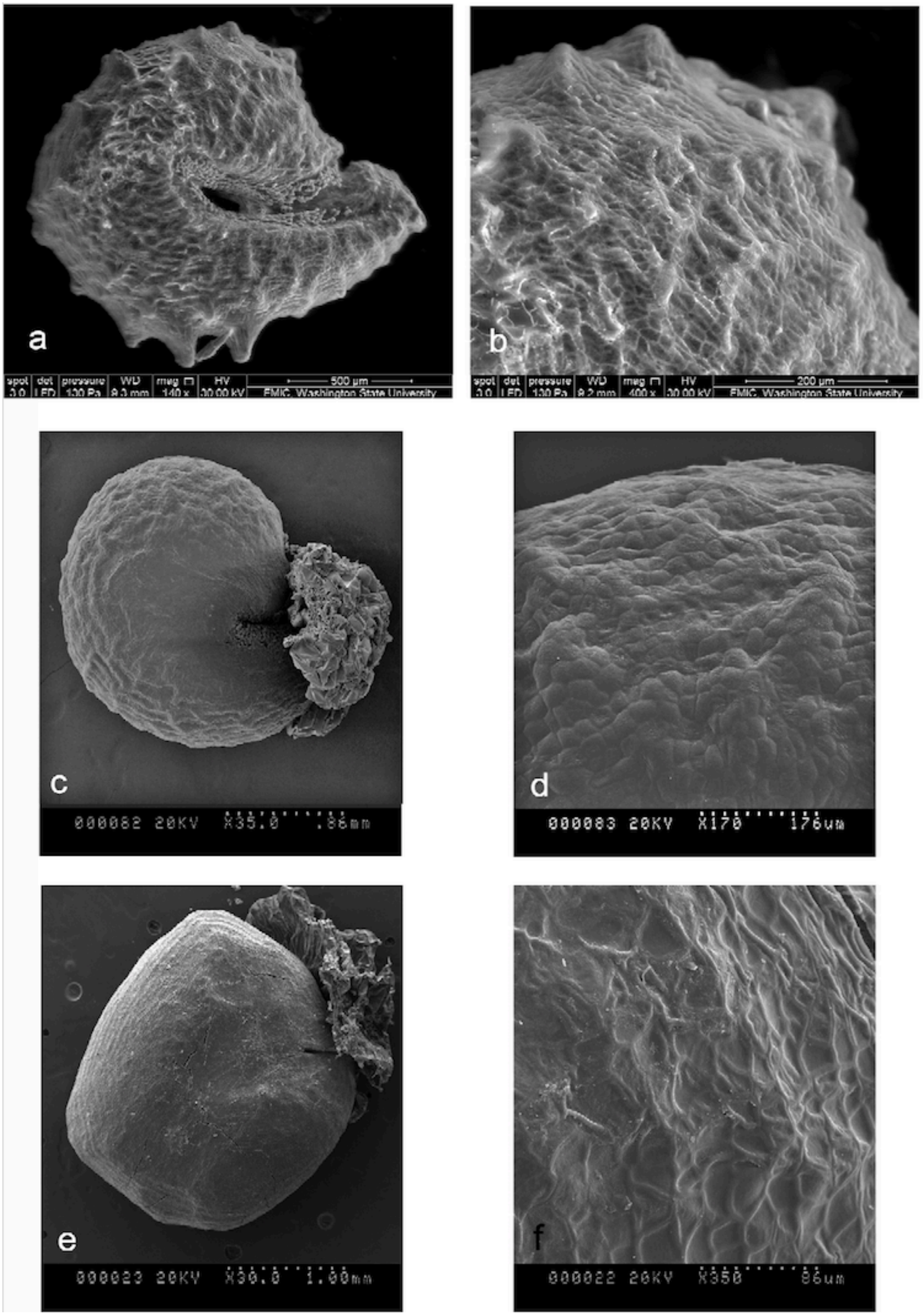

Figure 28: (a and b) *Podandrogyne pulcherrima* at 500 μm and 200 μm. (c and d) *Podandrogyne jamesonii* at 0.86 mm and 176 μm. (e and f) *Podandrogyne caucana* at 1.0 mm and 86 μm.

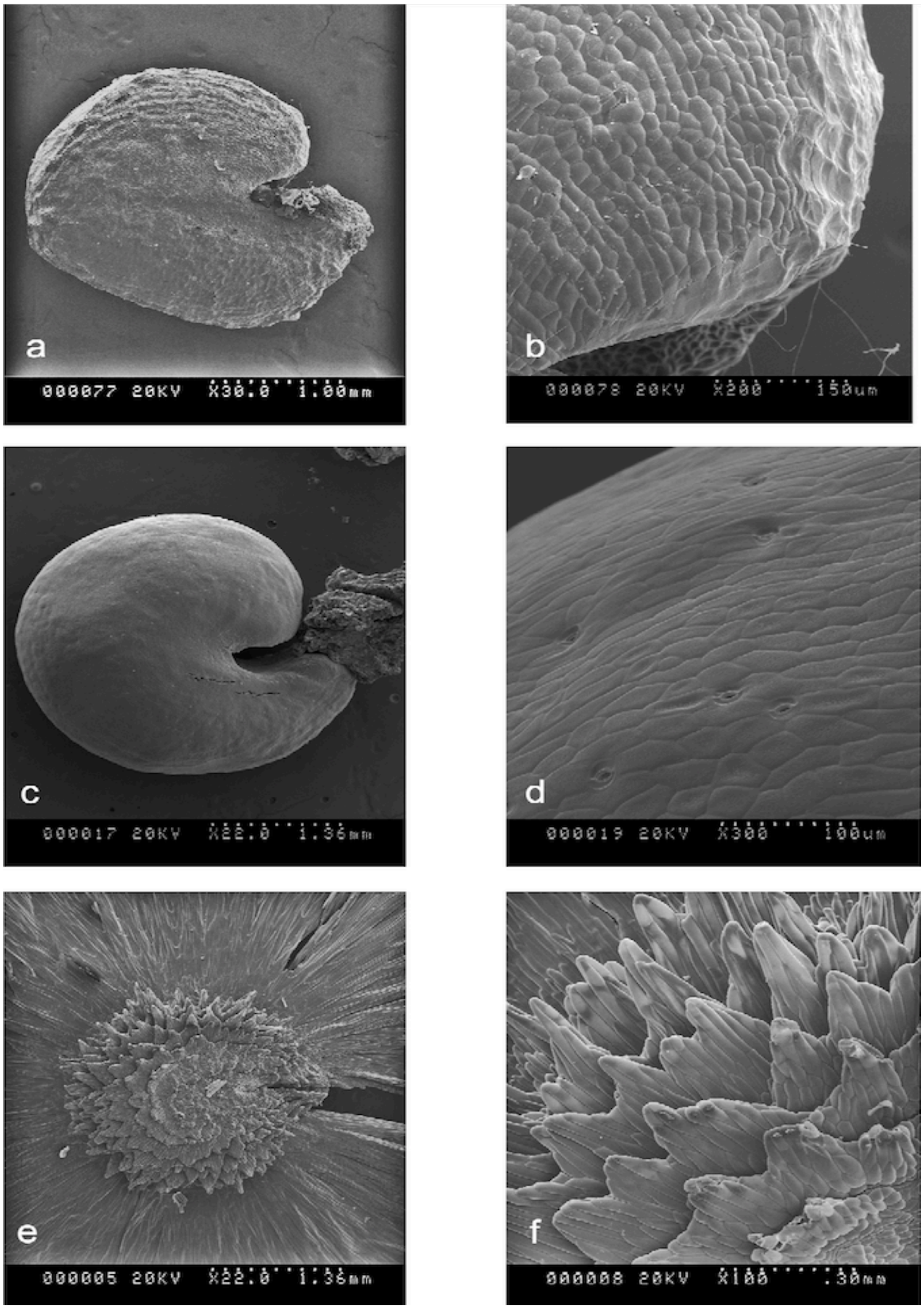

Figure 29: (a and b) *Podandrogyne macrophylla* at 1.0 mm and 150 μm. (c and d) *Podandrogyne densiflora* at 1.0 mm and 100 μm. (e and f) *Cleome stylosa* at 1.36 mm and 0.3 mm.

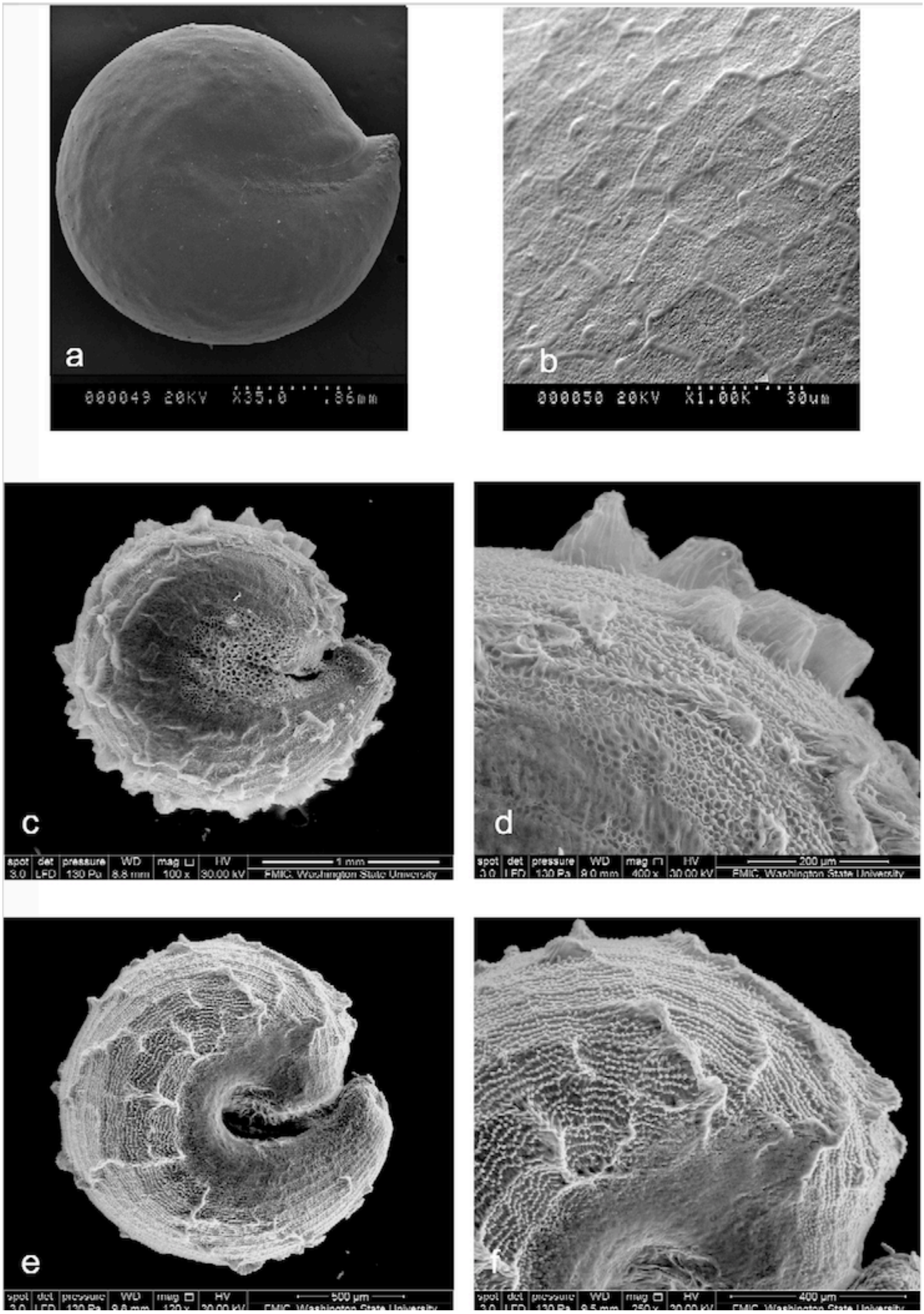

Figure 30: (a and b) *Melidiscus gigantea* at 0.86 mm and 30 μm. (c and d) *Cleoserrata paludosa* at 1.0 mm and 200 μm. (e and f) *Cleoserrata melanosperma* at 500 μm and 400 μm.

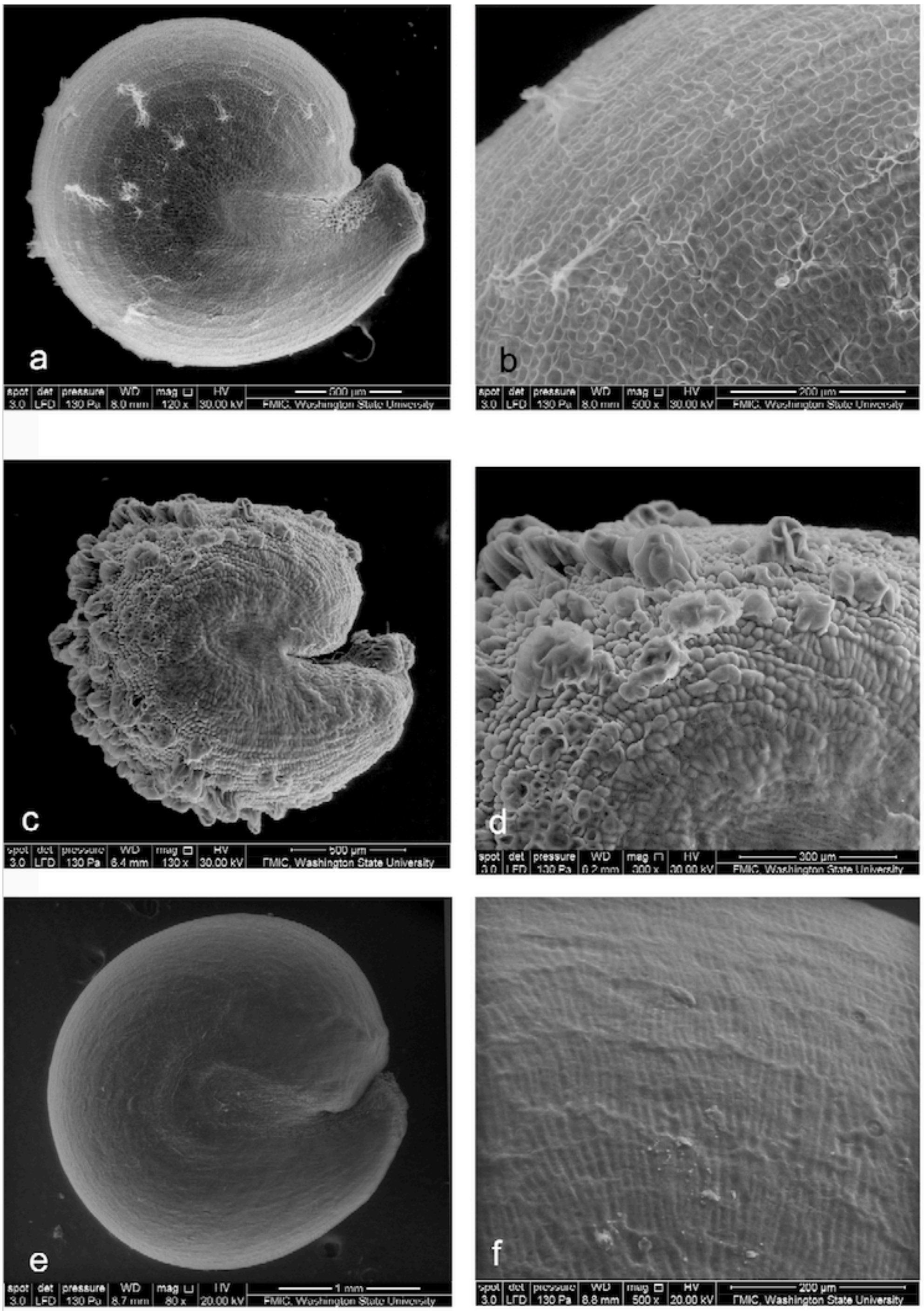

Figure 31: (a and b) *Cleoserrata serrata* at 500 μm and 200 μm. (c and d) *Cleoserrata speciosa* at 500 μm and 300 μm. (e and f) *Cleoserrata bahiana* at 1.0 mm and 200 μm.

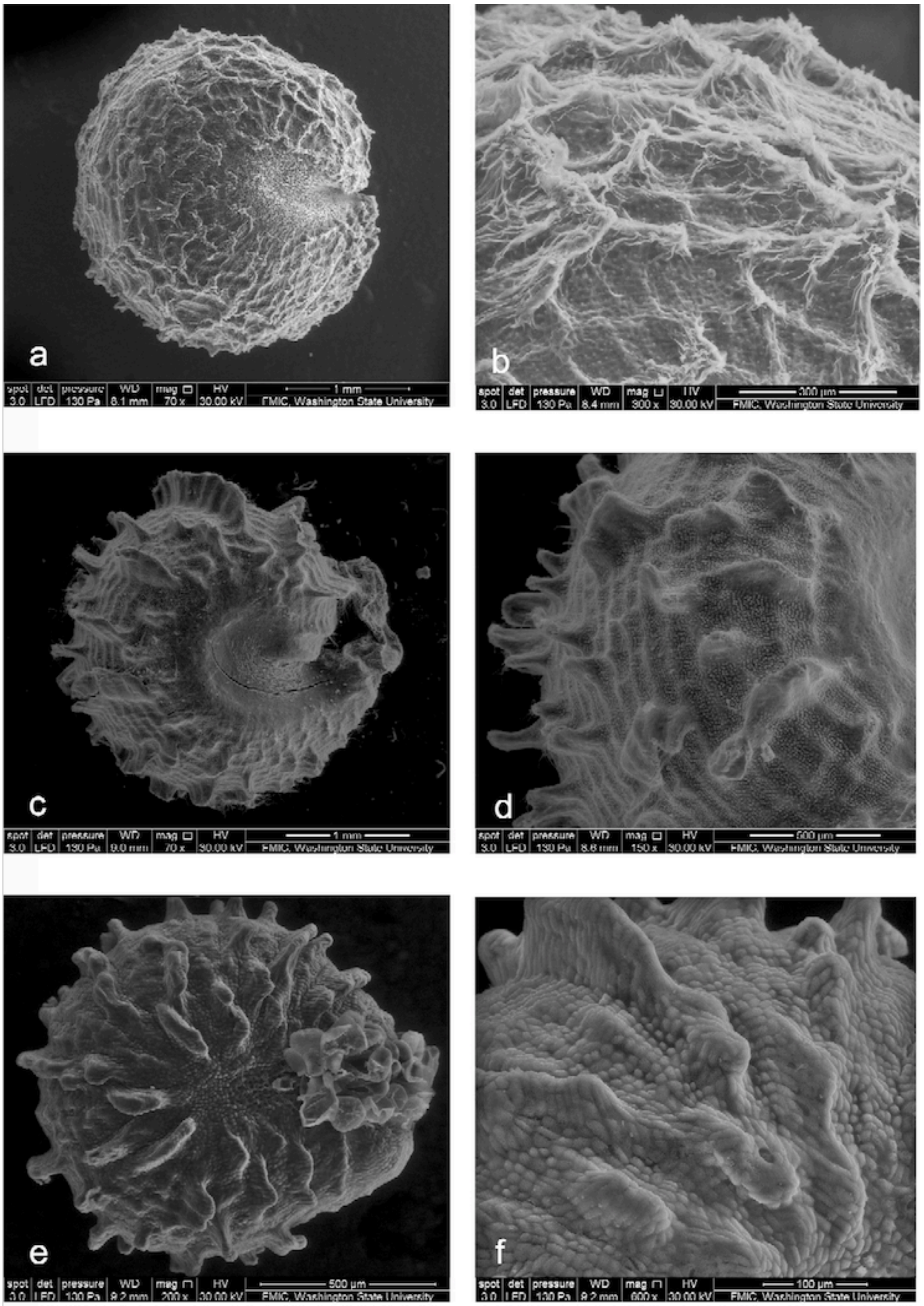

Figure 32: (a and b) *Tarenaya torticarpa* at 1.0 mm and 300 µm. (c and d) *Tarenaya tucumanensis* at 1.0 mm and 500 µm. (e and f) *Tarenaya rosea* at 500 µm and 100 µm.

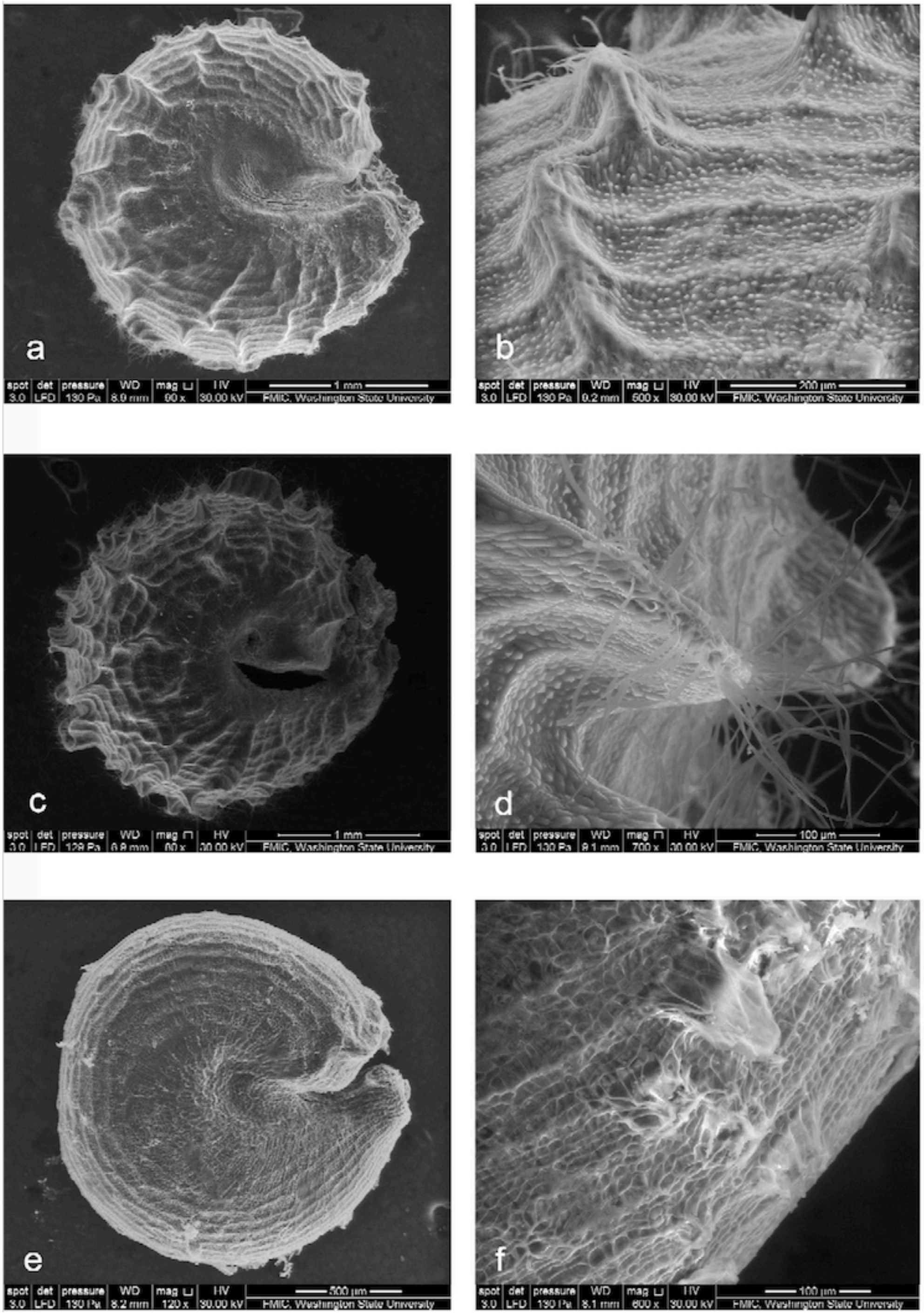

Figure 33: (a and b) *Tarenaya aculeata* at 1.0 mm and 200 μm. (c and d) *Tarenaya cordobensis* at 1.0 mm and 100 μm. (e and f) *Cleome spinosa* subsp. *longicarpa* at 500 μm and 100 μm.

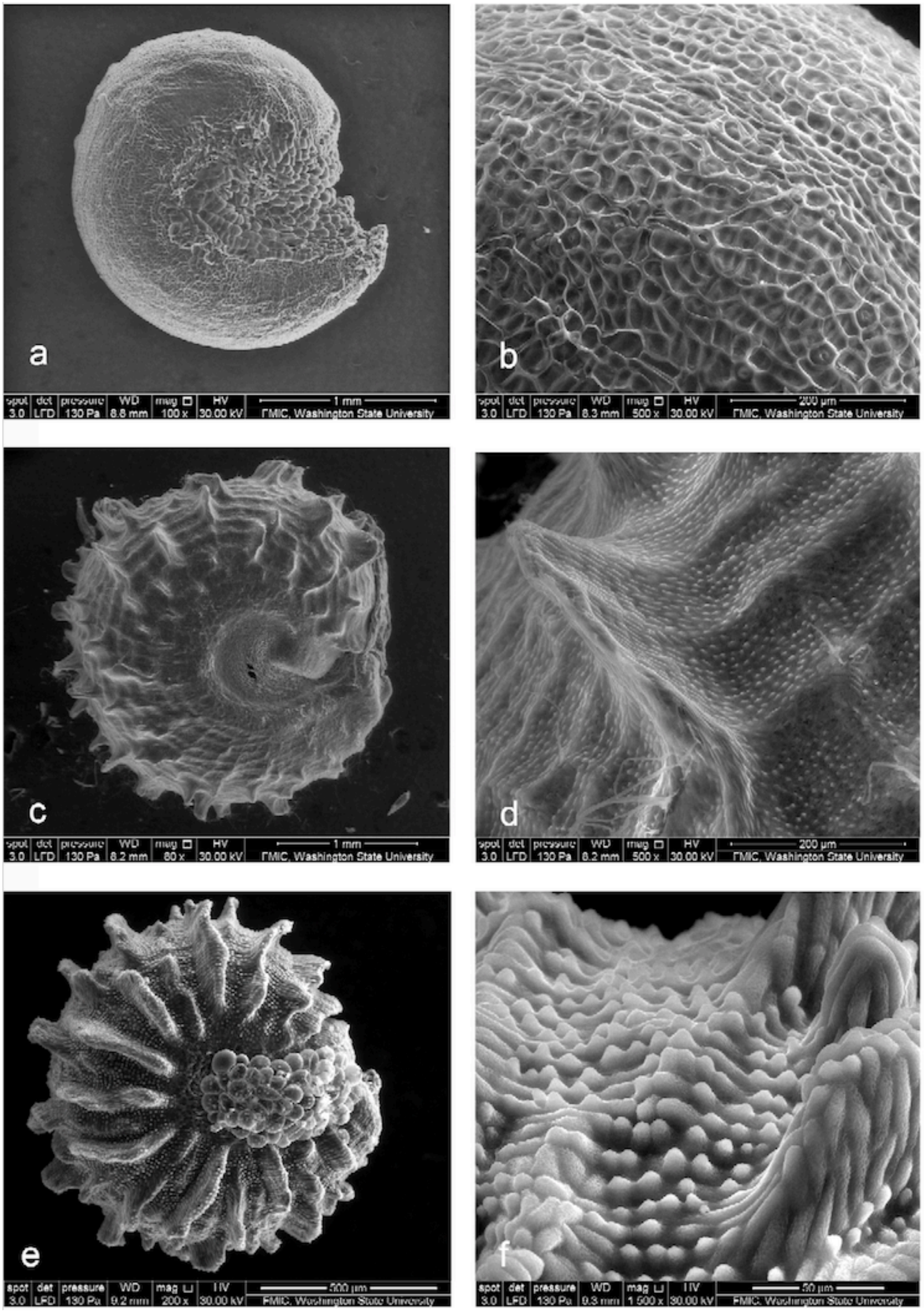

Figure 34: (a and b) *Tarenaya boliviensis* at 1.0 mm and 200 μm. (c and d) *Tarenaya eosina* at 1.0 mm and 200 μm. (e and f) *Tarenaya pernambucensis* at 500 μm and 50 μm.

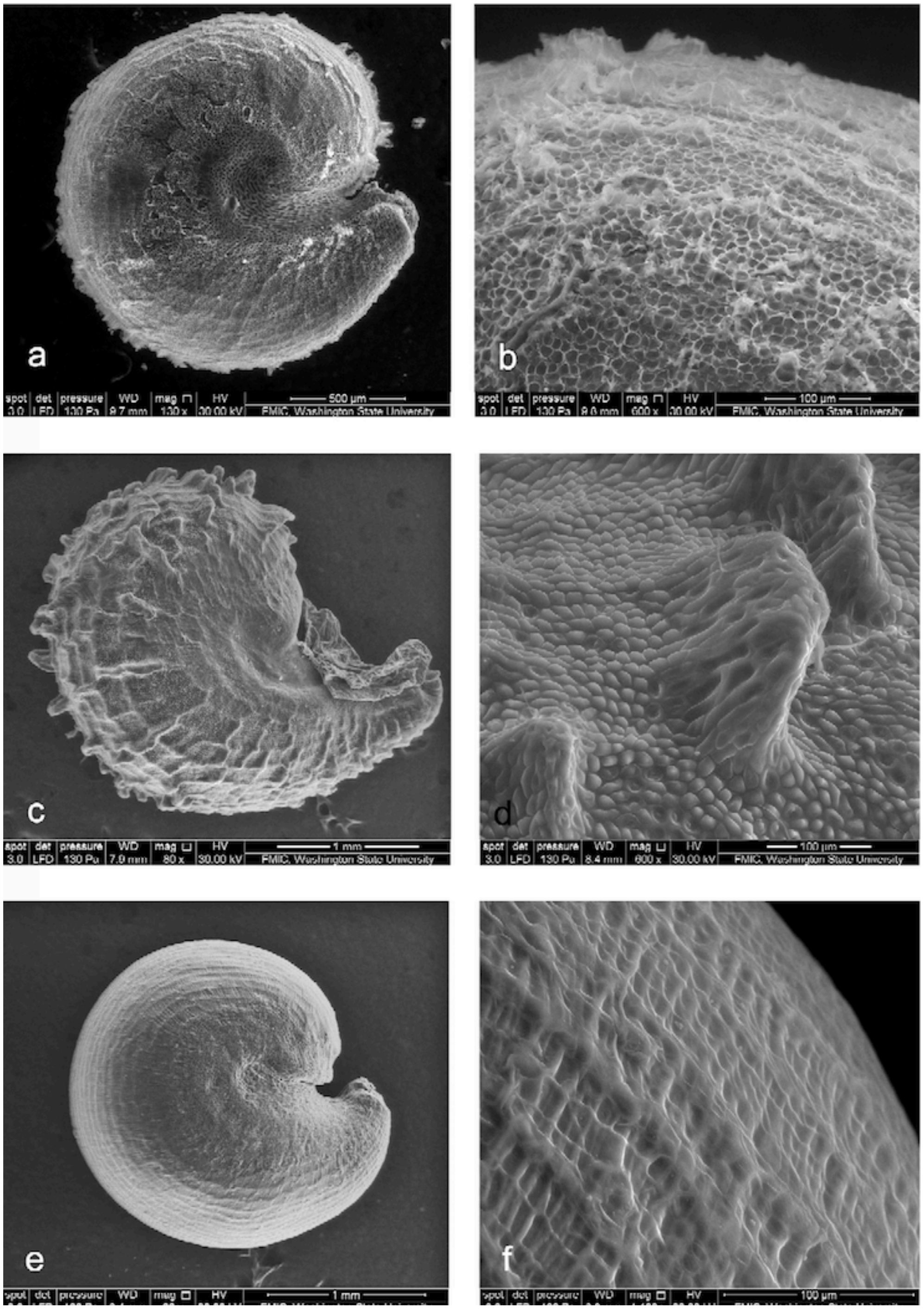

Figure 35: (a and b) *Tarenaya parviflora* at 500 μm and 100 μm. (c and d) *Tarenaya microcarpa* at 1.0 mm and 100 μm. (e and f) *Tarenaya hassleriana* at 1.0 mm and 100 μm.

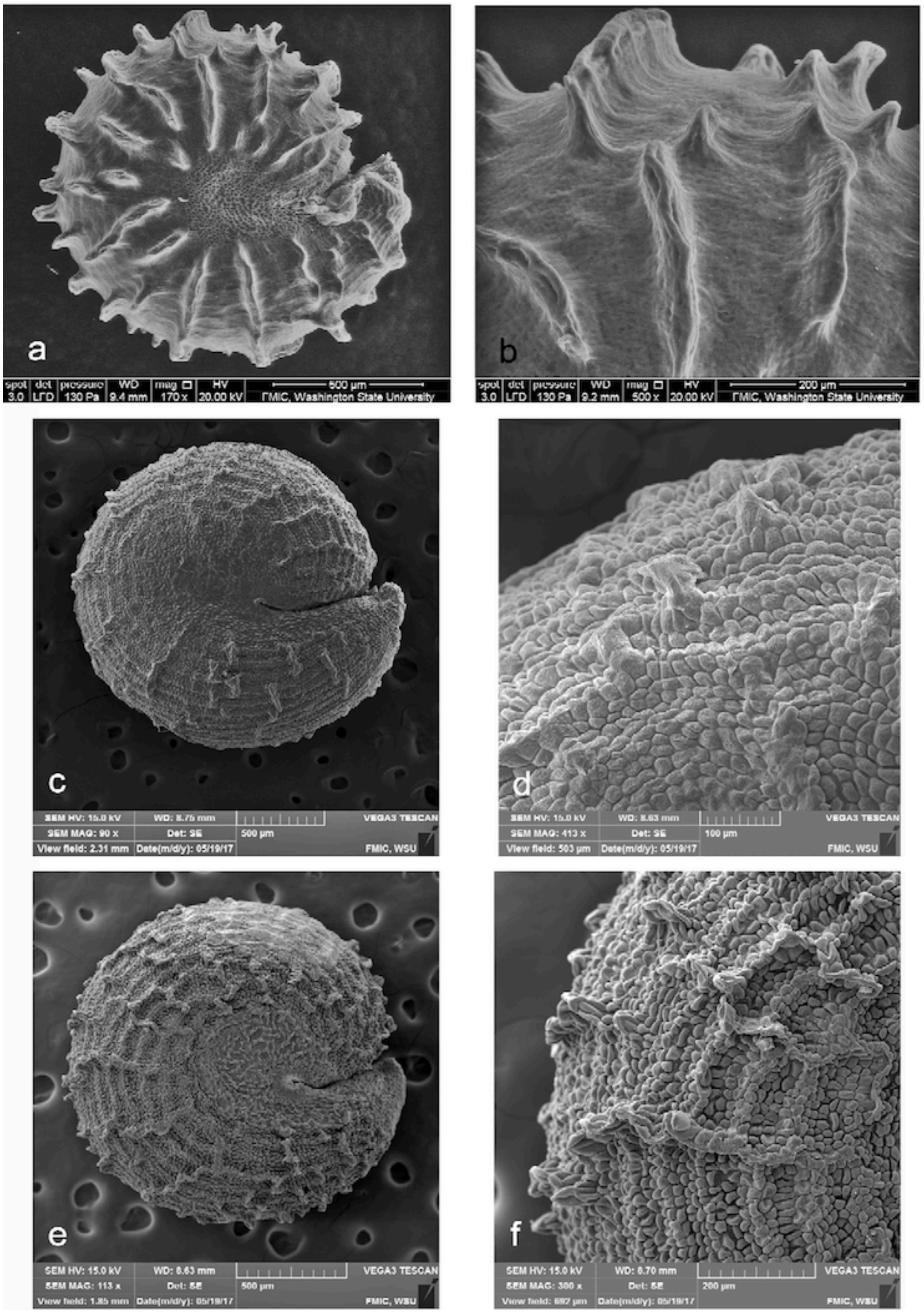

Figure 36: (a and b) *Tarenaya curvispina* at 500 μm and 200 μm. (c and d) *Dactylaena boliviensis* at 500 μm and 100 μm. (e and f) *Dactylaena pauciflora* at 500 μm and 200 μm.

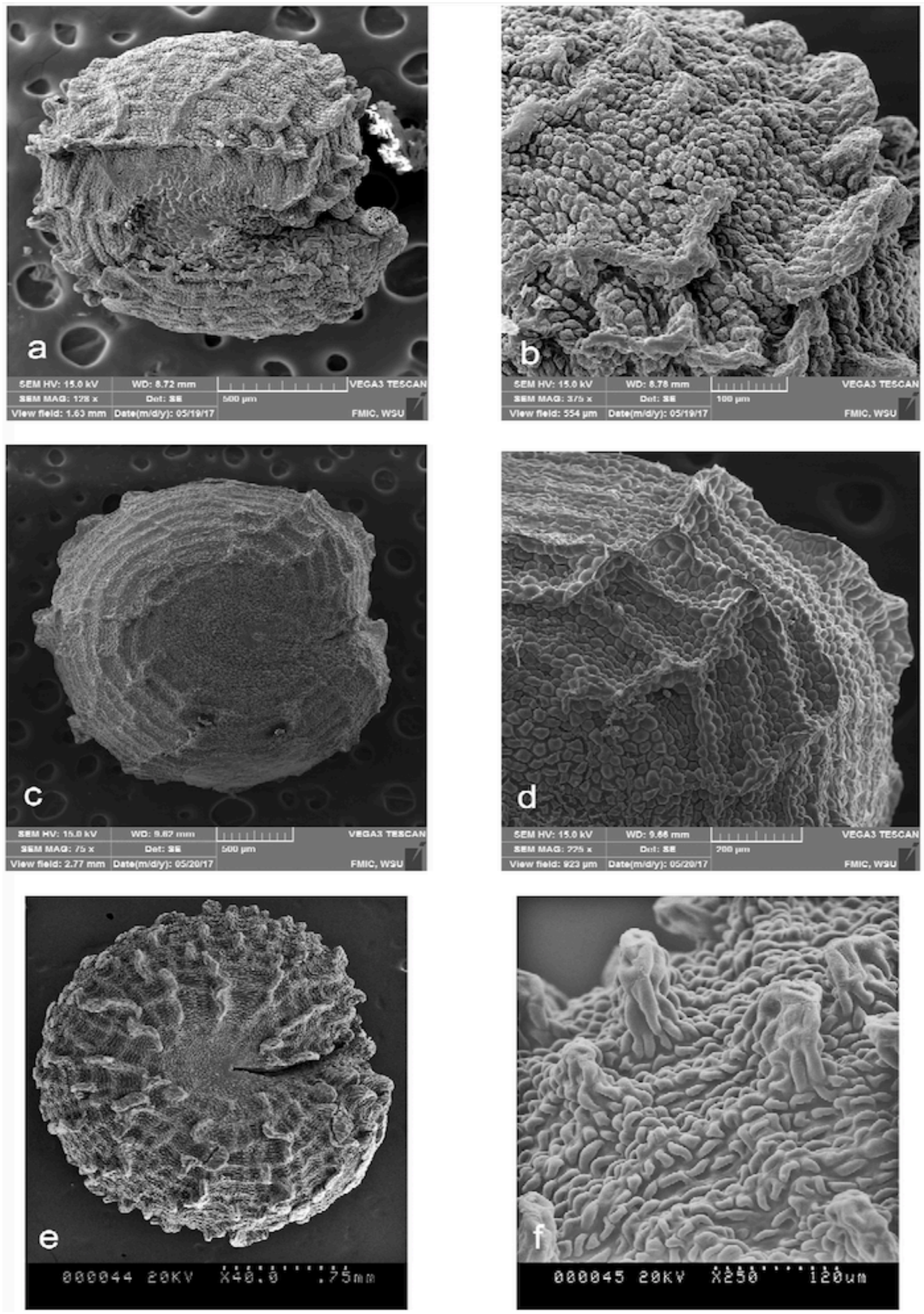

Figure 37: (a and b) *Dactylaena micrantha* at 500 μm and 100 μm. (c and d) *Dactylaena pohliana* at 500 μm and 200 μm. (e and f) *Dactylaena microphylla* at 0.75 mm and 120 μm.

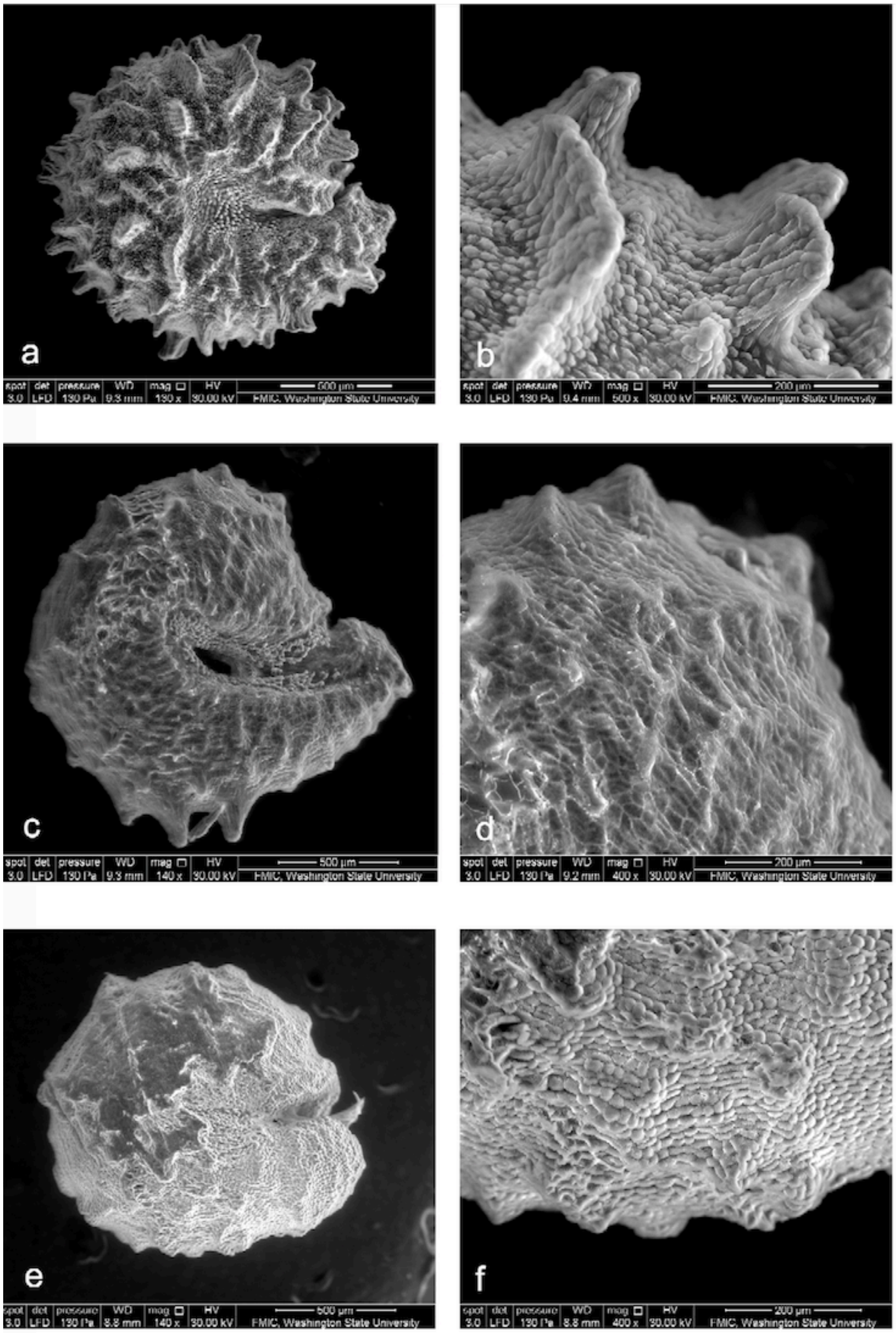

Figure 38: (a and b) *Physostemon stenophyllum* at 500 μm and 200 μm. (c and d) *Physostemon guianensis* at 500 μm and 200 μm. (e and f) *Physostemon humilis* at 500 μm and 200 μm.

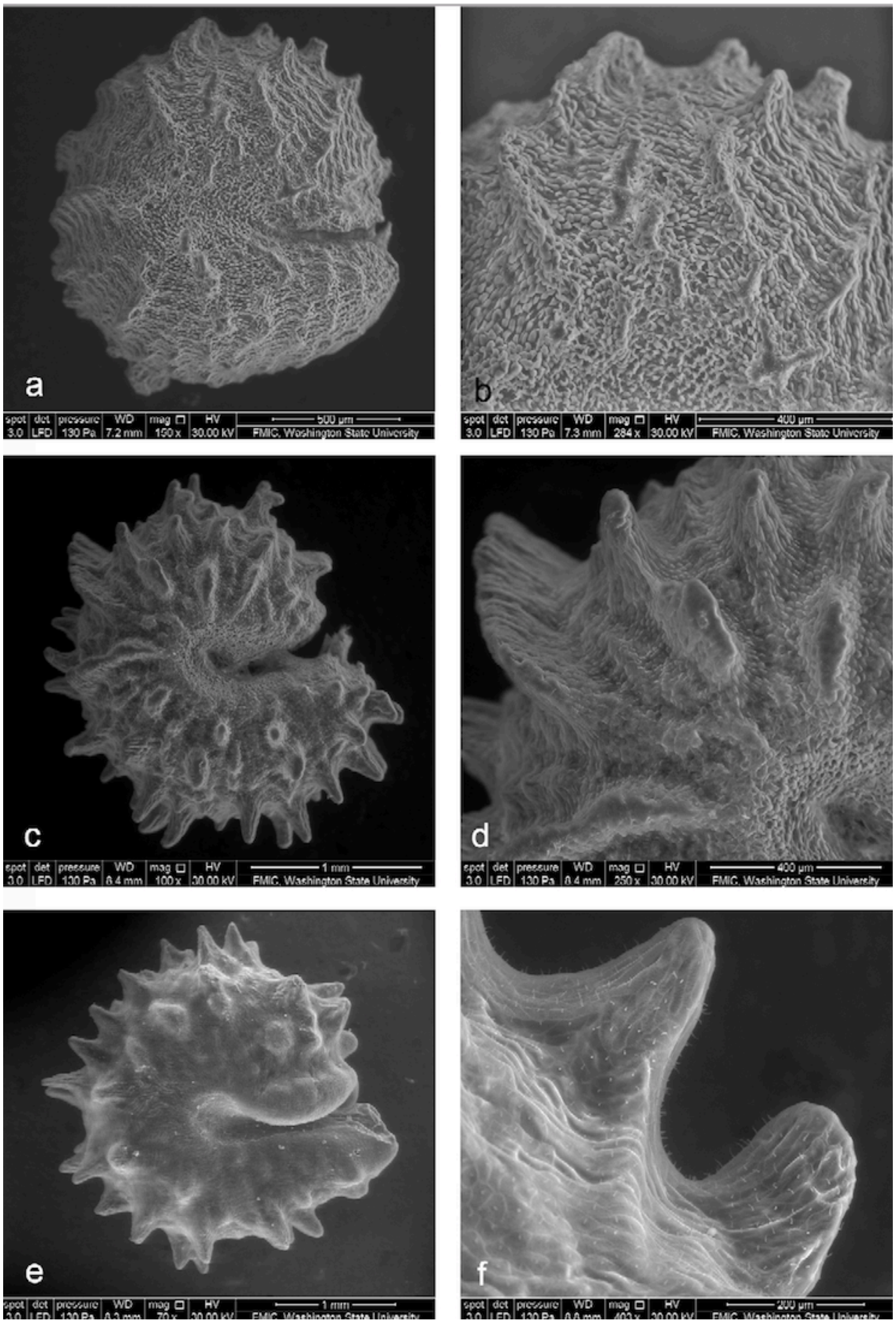

Figure 39: (a and b) *Cleome tenuis* at 500 μm and 400 μm. (c and d) *Physostemon lanceolatum* at 1.0 mm and 400 μm. (e and f) *Physostemon hemsleyanum* at 1.0 mm and 200 μm.

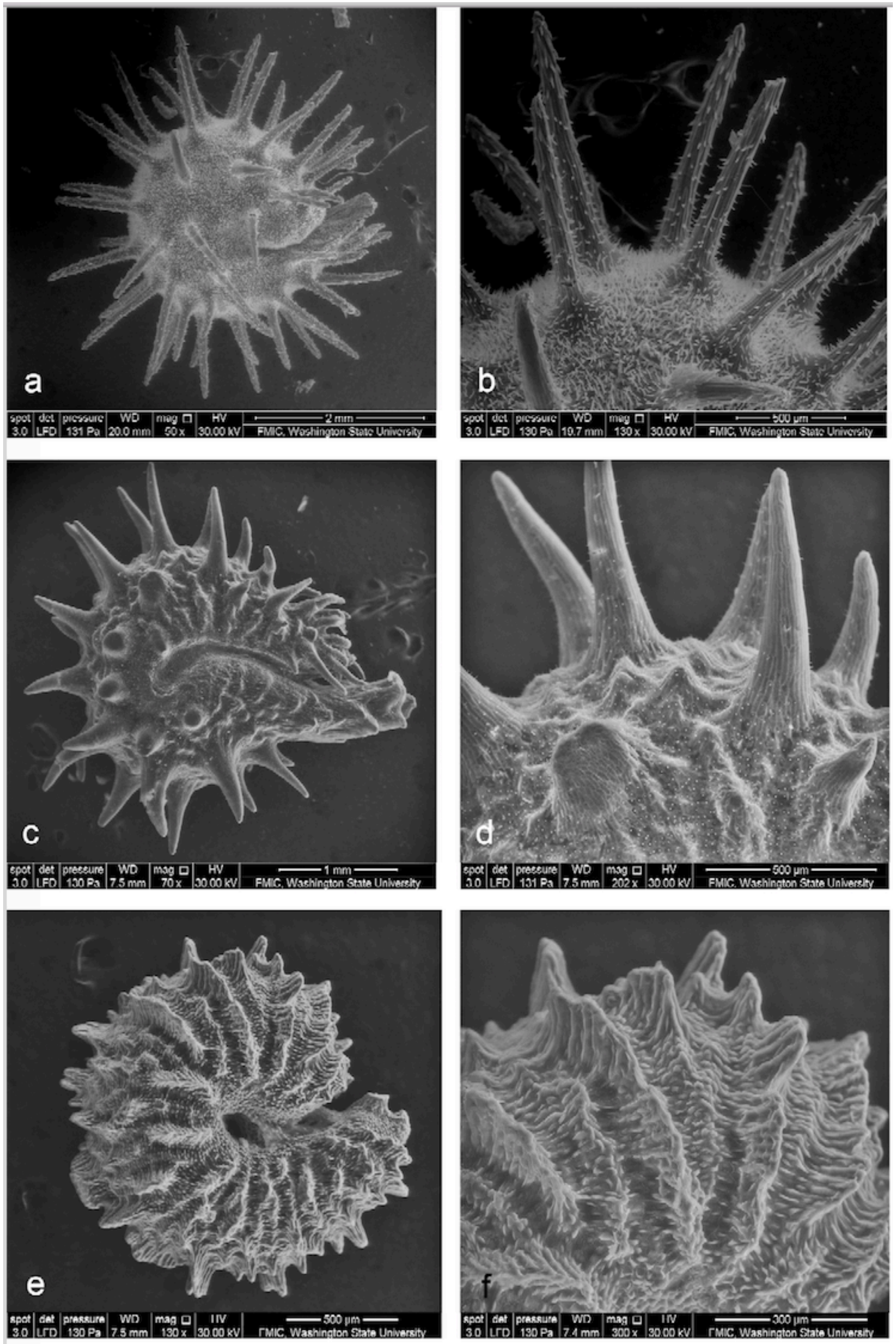

Figure 40: (a and b) *Physostemon tenuifolium* 2.0 mm and 500 μm. (c and d) *Physostemon rotundifolium* at 1.0 mm and 500 μm. (e and f) *Mitostylus procumbens* 500 μm and 300 μm.

Table 1: List of all species of Cleomaceae that were sampled for this study and information from herbarium sheets. Images used in plates are indicated in reference plate no. column.

Genus or species and author	**Country, collector no., herbarium**	**Plate reference no.**
***Cleome* L.**		
Cleome ornithopodioides L.	Georgia, 2056, MO	1
Cleome ornithopodioides L.	Armenia, 04-0777, MO	
Cleome ornithopodioides L.	Georgia, 1843, MO	
Cleome coluteoides Boiss.	Iran, 223, MO	1
Cleome socotrana Balf. f	Yemen, 12504, E	1
Cleome socotrana Balf. f	Yemen, M8621, E	
Cleome stevensiana Schult.	Azerbaijan, 4029, E	2
Cleome glaucescens DC.	Iraq, R. Wheeler Haines s.n., E	2
Cleome turkmena Bobrov	Turkmenistan, 1053, MO	2
Cleome rupicola Vicary	Oman, 3429, E	3
Cleome khorassanica Bunge & Bien. ex Boiss.	Iran, 18824, MO	3
Cleome heratensis Bunge & Bien. ex Boiss	Afghanistan, 4935, E	3
Cleome iberica DC.	Armenia, V. Vasak s.n., WAG	4
Cleome arabica L.	Israel, 10032, E	4
Cleome ariana Hedge & Lamond	Afghanistan, W9510, E	4
Cleome oxypetala Boiss.	Iran, D56165, E	5
***Rorida* J.F. Gmelin**		
Rorida fimbriata (Vicary) M. Thulin & Roalson	Tajikistan, A. Czukavina, G. Kinzikaeva, V. Czevtaeva s.n., E	5

Rorida fimbriata (Vicary) M. Thulin & Roalson	Tajikistan, A. Czukavina, G. Kinzikaeva, V. Czevtaeva s.n., MO	
Rorida droserifolia (Forssk.) M. Thulin & Roalson	Libya, 4876, MO	5
Rorida polytricha (Franch.) M. Thulin & Roalson	Oman, 3033, E	6
***Cleomella* DC.**		
Cleomella angustifolia Torrey	US, 13360, NY	6
Cleomella hillmanii Nelson *var. goodrichii* (Welsh) Holmgren	US, 27517, NY	6
Cleomella hillmanii Nelson	US, 14700, NY	7
Cleomella longipes Torrey	US, 13845, NY	7
Cleomella mexicana DC.	Mexico, 3293, NY	7
Cleomella obtusifolia Torrey & Frémont	US, 5000, NY	8
Cleomella palmeriana Jones	US, 4258, NY	8
Cleomella parviflora Gray	US, 15694, NY	8
Cleomella perennis Iltis	Mexico, 74105, NY	9
Cleomella plocasperma Watson	US, 3306, NY	9
***Polanisia* Raf.**		
Polanisia uniglandulosa (Cav.) DC.	Mexico, 3007, MO	9
Polanisia dodecandra (L.) DC. subsp. *dodecandra*	US, 1092, MO	10
***Coalisina* Raf.**		
Coalisina paradoxa (RBr. ex DC.) Roalson & JC Hall	Ethiopa, 12800, WAG	10
Coalisina tenella (L.f.) Roalson & JC Hall	Madagascar, 936, P	10
Coalisina semitetrandra (Sond.) Roalson & JC Hall	SW Africa, 8492, WAG	11
Coalisina polyanthera (Schweinf. & Gilg ex Gilg) Roalson & JC Hall	Cameroon, 2061, P	11
Coalisina angustifolia (Forssk.) Raf. subsp. *petersiana* (Klotzsch) Roalson & JC Hall	South Africa, 125, WAG	11

Coalisina angustifolia (Forssk.) subsp. *angustifolia*	South Africa, 10335, MO	12
Coalisina angustifolia (Forssk.) subsp. *angustifolia*	Ethiopia, 3318, MO	
Coalisina angustifolia (Forssk.) Raf. subsp. *diandra* (Burch.) Roalson & JC Hall var. *diandra*	Ethiopia, 9804, MO	12
***Arivela* Raf.**		
Arivela viscosa (L.) Raf.	Ghana, 1351, MO	12
Arivela cleomoides (F. Muell.) RL Barrett	Australia, 622, MO	13
***Areocleome* RL Barrett & Roalson**		
Areocleome oxalidea (F. Muell.) RL Barrett & Roalson	Australia, 3958, NY	13
***Kersia* Roalson & JC Hall**		
Kersia paxii (Schinz) Roalson & JC Hall	Namibia, 6525, WAG	13
Kersia foliosa (Hook.f.) Roalson & JC Hall var. *lutea* (Sond.) Roalson & JC Hall	South Africa, 5342, MO	14
Kersia suffruticosa (Schinz) Roalson & JC Hall	Namibia, 9236, PRE	14
Kersia kalachariesis (Schinz) Roalson & JC Hall subsp. *kalachariensis*	South Africa, 118/35 PRE	
Kersia kalachariesis (Schinz) Roalson & JC Hall subsp. *kalachariensis*	South Africa, 1759, PRE	14
Kersia kalachariensis (Schinz) Roalson & JC Hall subsp. namibensis (Kers) Roalson & JC Hall	South Africa, 5554, WAG	15
***Gilgella* Roalson & JC Hall**		
Gilgella scaposa (DC.) Roalson & JC Hall	Ethiopia, 2346, PRE	15
***Thulinella* Roalson & JC Hall**		
Thulinella chrysantha (Decne.) Roalson & JC Hall	Saudi Arabia, 7074, E	15
Thulinella chrysantha (Decne.) Roalson & JC Hall	Libya, 4952, MO	
***Stylidocleome* Roalson & JC Hall**		

Stylidocleome brachycarpa (Vahl ex DC.) Roalson & JC Hall	Ethiopia, 10, 186, WAG	16
***Dipterygium* Decne.**		
Dipterygium glaucum Decne.	Yemen, 7471, NY	16
Dipterygium glaucum Decne.	Egypt, 2669, WAG	
***Corynandra* Schrad. ex Spreng.**		
Corynandra felina (L.f.) Cochrane & Iltis	India, 3520, E	16
Corynandra chelidonii (L.f.) Cochrane & Iltis	Ceylon, 1341, MO	17
Corynandra chelidonii (L.f.) Cochrane & Iltis	Ceylon, 7389, MO	
***Gynandropsis* DC.**		
Gynandropsis gynandra (L.) Briq.	South Africa, 8395, PRE	17
Gynandropsis gynandra (L.) Briq.	Ceylon, 10675, MO	
***Sieruela* Raf.**		
Sieruela hanburyana (Penz.) Roalson & JC Hall	Kenya, 10867, MO	17
Sieruela stricta (Klotzsch) Roalson & JC Hall	Mozambique, 555, WAG	18
Sieruela parvipetala (R.A. Graham) Roalson & JC Hall	Kenya, 48, WAG	18
Sieruela boroensis (Klotzsch) Roalson & JC Hall	Mozambique, 7153, WAG	18
Sieruela macrophylla (Klotzsch) Roalson & JC Hall	Botswana, 5037, PRE	19
Sieruela briquetii (Polhill) Roalson & JC Hall	Tanzania, 285, MO	19
Sieruela hirta (Klotzsch) Roalson & JC Hall	Malawi, 1659, MO	19
Sieruela hirta (Klotzsch) Roalson & JC Hall	South Africa, 3033, PRE	
Sieruela usambarica (Pax ex Engl.) Roalson & JC Hall	Tanzania, 7683, MO	20
Sieruela iberidella (Welw. ex Oliv.) Roalson & JC Hall	Cameroon, 8612, MO	20
Sieruela rutidosperma (DC.) Roalson & JC Hall var. *rutidosperma*	Ghana, 2323, MO	20

Sieruela rutidosperma (DC.) Roalson & JC Hall var. *rutidosperma*	Gabon, 6709, MO	
Sieruela rutidosperma (DC.) Roalson & JC Hall var. *burmannii* (Wight & Arn.) Roalson & JC Hall	Ceylon, 8851, MO	21
Sieruela oxyphylla (Burch.) Roalson & JC Hall var. *oxyphylla*	Namibia, 82, PRE	
Sieruela oxyphylla (Burch.) Roalson & JC Hall var. *oxyphylla*	South Africa, 3235, PRE	21
Sieruela oxyphylla (Burch.) Roalson & JC Hall var. *robusta* (Kers) Roalson & JC Hall	South Africa, 6239, PRE	21
Sieruela strigosa (Bojer) Roalson & JC Hall	Somalia, 1823, 6677, WAG	22
Sieruela kermesina (Gilg & Gilg-Ben.) Roalson & JC Hall var. *plebeia* (Kers) Roalson & JC Hall	Angola, 3628, P	22
Sieruela micrantha (Bojer) Roalson & JC Hall subsp. *leandrii* (Hadj-Moust.) Roalson & JC Hall	Madagascar, 312, P	22
Sieruela perrieri (Hadj-Moust.) Roalson & JC Hall	Madagascar, 29531, P	23
Sieruela conrathii (Burtt Davy) Roalson & JC Hall	South Africa, 594612, PRE	23
Sieruela maculata (Sond.) Roalson & JC Hall	South Africa, 1167, PRE	23
Sieruela rubella (Burch.) Roalson & JC Hall	South Africa, 908, PRE	24
Sieruela silvatica (Gilg & Gilg-Ben.) Roalson & JC Hall	Tanzania, 2953, MO	24
Sieruela silvatica (Gilg & Gilg-Ben.) Roalson & JC Hall	Tanzania, 6573, MO	
Sieruela coeruleo-rosea (Gilg & Gilg-Ben.) Roalson & JC Hall	Cameroon, 2420, MO	24
Sieruela monophylla (L.) Roalson & JC Hall	Sudan, 6276, MO	25
Sieruela elegantissima (Briq.) Roalson & JC Hall	Namibia, 7710, PRE	25
Sieruela elegantissima (Briq.) Roalson & JC Hall	Namibia, 9157, MO	
Sieruela schimperi (Pax) Roalson & JC Hall	Burundi, 10689, MO	25

***Andinocleome* Iltis & Cochrane**		
Andinocleome chilensis (DC.) Iltis, ined.	Chile, 10727, MO	26
Andinocleome pilosa (Benth.) Iltis & Cochrane	Nicaragua, 3174, MO	26
Andinocleome anomala (Kunth) Iltis, ined.	Ecuador, 5589, MO	26
Andinocleome anomala (Kunth) Iltis, ined.	Ecuador, 1633, MO	
Andinocleome moritziana (Klotzsch ex Eichler) Itlis, ined.	Venezuela, 121991, MO	27
Andinocleome lechleri (Eichler) Iltis & Cochrane	Bolivia, 30194, MO	27
Andinocleome magnifica (Briq.) Iltis & Cochrane	Mexico, 25874, MO	27
***Podandrogyne* Ducke**		
Podandrogyne pulcherrima (Standl.) Cochrane	Costa Rica, 10090, MO	28
Podandrogyne jamesonii (Briq.) Cochrane	Ecuador, 7723, MO	28
Podandrogyne caucana Cochrane	Colombia, 3770, MO	28
Podandrogyne macrophylla (Turcz.) Woodson	Venezuela, 3315, MO	29
Podandrogyne densiflora (Benth.) Iltis & Cochrane	Colombia, 2749, MO	29
***"Pterocleome"* Iltis, ined.**		
Pterocleome stylosa (Eichler) Iltis, ined.	Colombia, 23699, MO	29
***Melidiscus* Raf.**		
Melidiscus gigantea (L.) Raf.	Venezuela, 4987, MO	30
***Cleoserrata* Iltis**		
Cleoserrata paludosa (Willd. ex Eichler) Iltis ex Soares Neto & Roalson	Bolivia, 37760, MO	30
Cleoserrata melanosperma (S. Wats.) Roalson & Soares Neto	Mexico, 98-853, NY	30
Cleoserrata serrata (Jacq.) Iltis	Costa Rica, 1224, MO	31

Cleoserrata serrata (Jacq.) Iltis	Nicaragua, 27397, MO	
Cleoserrata speciosa (Raf.) Iltis	El Salvador, 340, MO	31
Cleoserrata bahiana Iltis & MB Costa-e-Silva ex Soares Neto & Roalson	Brazil, 21972, WIS	31
***Tarenaya* Raf.**		
Tarenaya torticarpa (Iltis & T. Ruiz Zapata) Soares Neto & Roalson	Venezuela, 7791, MO	32
Tarenaya tucumanensis (Iltis) Arana & Oggero	Paraguay, 4224, MO	32
Tarenaya rosea (Vahl ex DC.) Soares Neto & Roalson	Brazil, 9216, MO	32
Tarenaya aculeata (L.) Soares Neto & Roalson	Bolivia, 33688, MO	33
Tarenaya cordobensis (Eichler ex Griseb.) Arana & Oggero	Argentina, 3105, MO	33
Cleome spinosa Jacq. subsp. *longicarpa* Iltis, ined.	Cameroon, 7326, MO	33
Tarenaya boliviensis (Iltis) Soares Neto & Roalson	Bolivia, 1062, MO	34
Tarenaya boliviensis (Iltis) Soares Neto & Roalson	Bolivia, 2230A, MO	
Tarenaya eosina (J.F. Macbr.) Soares Neto & Roalson	Paraguay, 49647, MO	34
Tarenaya pernambucensis Iltis & MB Costa-e-Silva ex Soares Neto & Roalson	Brazil, 1513, MO	34
Tarenaya parviflora (Kunth) Iltis	Bolivia, 53022, MO	35
Tarenaya microcarpa (Ule) Soares Neto & Roalson	Brazil, 16861, MO	35
Tarenaya hassleriana (Chodat) Iltis	South Africa, 6742, PRE	35
Tarenaya curvispina MB Costa-e-Silva & Iltis ex Soares Neto & Roalson	Brazil, 58318, WIS	36
***Dactylaena* Schrad. ex Schult.f.**		
Dactylaena boliviensis Iltis	Bolivia, 50049, MO	36
Dactylaena pauciflora Griseb.	Bolivia, 3385, MO	36

Dactylaena micrantha Schrad. ex Schult.f.	US, 8357, MO	37
Dactylaena pohliana Eichler	Brazil, 21992, NY	37
Dactylaena microphylla Eichler	Brazil, 51126, MO	37
***Physostemon* Martius**		
Physostemon stenophyllum (Klotzsch ex Urb.) Iltis	Venezuela, 2866, MO	38
Physostemon guianensis (Aubl.) Malme	Costa Rica, 662, MO	38
Physostemon humilis (Rose) Iltis	Guatemala, MG757, MO	38
Cleome tenuis S. Watson	Mexico, 94-640, MO	39
Physostemon lanceolatum Mart. & Zucc.	Belize, 1682, MO	39
Physostemon hemsleyanum (Bullock) RC Foster	Mexico, 51157, MO	39
Physostemon tenuifolium Mart. & Zucc.	Brazil, 16325, E	40
Physostemon rotundifolium Mart. & Zucc.	Brazil, 27032, NY	40
***Mitostylis* Raf.**		
Mitostylis procumbens (Jacq.) Raf.	Jamaica, 37944, MO	40
Mitostylis procumbens (Jacq.) Raf.	Grand Cayman, 51036, MO	

Table 2: Definitions of major characters used in the seed descriptions and analyses. Character states used in this study are listed in the definition part of the table.

Character	Definition
Cleft	Space between the cotyledonar and radicular claw. Space can be open or closed with or without a membrane connecting the two claws. Character states: open or closed.
Periclinal Wall Shape	Curvature of the outer epidermal cell wall. Cells can be convex (papillate) or concave. Papillae can have different shapes. Character states: papillate, concave.
Periclinal Wall Ornamentation	Texture on the periclinal wall. Character states: rugose, wrinkled, scurfy.
Anticlinal Wall Shape	Cell walls that are perpendicular to the outer epidermal layer. Character states: grooved or raised.
Anticlinal Wall Ornamentation	Texture on the anticlinal wall. Character states: rugose and wrinkled.
Crests	An elevated group of cells that takes on a certain shape and height. Character states: radial, punctuated, spiked.
Aril	A fleshy or pulpy outgrowth of the seed that takes the form of an appendage. Character states: presence or absence.
Epicuticular Residue	A wax-like surface or build-up on the epidermis of the seed. Character states: presence or absence.
Hairs	A multicellular strand that can take on different forms such as thread or ribbon-like and can be located at different areas of the seed. Character states: presence or absence.
Reticulations	Surface depressions that group cells. Outline of reticulation can take different forms. Character states: presence or absence.

Table 3: Major seed coat characters for species shown in Figures 1–40 and in the 'Seed Description' section.

Species	Characters									
	Cleft	Periclinal wall	Periclinal wall - ornamentation	Anticlinalwall - thickness	Anticlinal wall - ornamentation	Crests	Aril	Epicuticular Residue	Hairs/shape/ texture	Reticulations
***Cleome* L.**										
Cleome ornithopodioides L.	open	papillate –domed	scurfy	wide/grooved		no	no	no	no	no
Cleome coluteoides Boiss.	open	papillate –tabular	deeply rugose	wide/grooved	deeply rugose	no	no	no	no	no
Cleome socotrana Balf.f.	open	papillate –tabular	deeply rugose	wide/grooved	rugose	no	no	no	wide/flat/ finely rugose	no
Cleome stevensiana Schult.	open	papillate –domed	scurfy	wide/grooved		no	no	no	no	no
Cleome glaucescens DC.	open	papillate –tabular	medium rugose			no	no	no	no	no
Cleome turkmena Bobrov	open	papillate –tabular	deeply rugose			no	no	no	wide/flat/ finely rugose	no
Cleome rupicola Vicary	open	papillate	rugose/pitted			no	no	no	wide/flat/ finely rugose	no
Cleome khorassanica Bunge & Bien. ex Boiss.	open	papillate –domed	rugose/bumpy	wide/grooved shallow	rugose	no	no	no	no	no
Cleome heratensis Bunge & Bien. ex Boiss	open	papillate	medium rugose			no	no	no	no	no
Cleome iberica DC.	open	papillate –domed	scurfy	wide/grooved shallow		no	no	no	no	no

Cleome arabica L.	open	papillate				no	no	no	wide, flat/finely rugose	no
Cleome ariana Hedge & Lamond	open	papillate –tabular	medium rugose			no	no	no	no	no
Cleome oxypetala Boiss.	open	concave				no	no	no	ribbon-like/finely rugose	no
***Rorida* J.F.Gmelin**										
Rorida fimbriata (Vicary) M. Thulin & EH Roalson	open	papillate –pinched	medium rugose			no	no	no	no	no
Rorida droserifolia (Forssk.) M. Thulin & EH Roalson	open	papillate –blunt	scurfy	wide/grooved shallow		no	no	no	no	no
Rorida polytricha (Franch.) M. Thulin & EH Roalson	open	papillate -conical	scurfy			no	no	no	no	no
***Cleomella* Candolle**										
Cleomella angustifolia Torrey	closed	concave	fine - medium rugose	narrow/ shallow		no	no	no	no	no
Cleomella hillmanii Nelson var. *goodrichii* (Welsh) Holmgren	closed	concave	finely rugose			no	no	no	no	no
Cleomella hillmanii Nelson	closed	papillate -flat	finely rugose	wide/grooved shallow		no	no	no	no	no
Cleomella longipes Torrey	closed	concave	medium/deeply rugose	wide/grooved		no	no	no	no	no
Cleomella mexicana DC.	closed	concave	medium/deeply rugose			no	no	no	no	no
Cleomella obtusifolia Torrey & Frémont	closed	papillate -flat	rugose			no	no	no	no	no

Cleomella palmeriana Jones	closed	papillate -flat	rugose			no	no	no	no	no
Cleomella parviflora Gray	closed	papillate -flat	finely rugose	wide/grooved shallow		no	no	no	no	no
Cleomella perennis Iltis	closed	concave	deeply rugose	wide/grooved shallow		no	no	no	no	no
Cleomella plocasperma Watson	closed	papillate -flat	deeply rugose	wide/grooved		no	no	no	no	no
***Polanisia* Raf.**										
Polanisia uniglandulosa (Cav.) DC.	open	papillate -domed to flat	rugose	wide/grooved shallow		no	no	no	no	no
Polanisia dodecandra (L.) DC. subsp. *dodecandra*	open	papillate	rugose	wide/grooved		no	no	no	no	no
***Coalisina* Raf.**										
Coalisina paradoxa (R Br. Ex DC.) Roalson & JC Hall	open	concave	deeply rugose	wide grooved		no	no	no	no/ indistinct	yes
Coalisina tenella (L.f) Roalson & JC Hall	closed	concave	medium rugose			no	no	no	no	yes
Coalisina semitetrandra (Sond.) Roalson & JC Hall	open	papillate -tabular	finely rugose	grooved		no	no	no	short/ pointed	yes
Coalisina polyanthera (Schweinf. & Gilg ex Gilg) Roalson & JC Hall	open	concave	deeply rugose			no	no	no	no	yes
Coalisina angustifolia (Forssk.) Raf. subsp. *petersiana* (Klotzsch) Roalson & JC Hall	open	concave	fine/medium rugose	wide/grooved		no	no	no	short/ medium pointed	yes
Coalisina angustifolia (Forssk.) Raf. subsp. *angustifolia*	open	papillate/ tabular	finely rugose	wide/grooved		no	no	no	medium/less tapered	yes

Coalisina angustifolia (Forssk.) Raf. subsp. *diandra* (Burch.) Roalson & JC Hall var. *diandra*	open	papillate/ tabular	finely rugose	wide/grooved		no	no	no	medium/less tapered	yes
***Arivela* Raf.**										
Arivela viscosa (L.) Raf.	open	papilllate	deeply rugose/bumpy	wide/grooved		radial-low	no	no	no	no
Arivela cleomoides (F. Muell.) RL Barrett	open	papilllate	deeply rugose	wide/grooved		radial-low	yes	no	no	no
***Areocleome* RL Barrett & Roalson**										
Areocleome oxalidea (F. Muell.) RL Barrett & Roalson	open	papillate	rugose/ pitted	wide/grooved		no	no	no	no	no
***Kersia* EH Roalson**										
Kersia paxii (Schinz) Roalson & JC Hall	open	concave	finely rugose-bumpy	wide/grooved shallow		no	no	no	no	yes
Kersia foliosa (Hook.f.) Roalson & JC Hall var. *lutea* (Sond.) Roalson & JC Hall	open	concave	fine - medium rugose	wide/grooved shallow		no	no	no	no	yes
Kersia suffruticosa (Schinz) Roalson & JC Hall	open	concave	finely rugose	wide/grooved		no	no	no	no	yes
Kersia kalachariesis (Schinz) Roalson & JC Hall subsp. *kalachariensis*	open	concave	finely rugose	wide/grooved		no	no	no	no	yes

Kersia *kalachariensis* (Schinz) Roalson & JC Hall subsp. *namibensis* (Kers) Roalson & JC Hall	open	concave	finely rugose	wide/grooved		no	no	no	no	yes
***Gilgella* Roalson & JC Hall**										
Gilgella scaposa (DC.) Roalson & JC Hall	open	papillate -pointed		very wide/grooved		no	no	yes	no	no
***Thulinella* Roalson & JC Hall**										
Thulinella chrysantha (Decne.) Roalson & JC Hall	open	concave	rugose/ pebbled	wide/grooved shallow		no	no	no	no	yes
***Stylidocleome* Roalson & JC Hall**										
Stylidocleome brachycarpa (Vahl ex DC.) Roalson & JC Hall	open	papillate -flat	wrinkled	wide/grooved shallow		no	no	no	no	no
***Dipterygium* Decne.**										
Dipterygium glaucum Decne. (fruit)	closed	concave	deeply rugose			no	no	yes	no	no
***Corynandra* Schrad. ex Spreng**										
Corynandra felina (L.f.) Cochrane & Iltis	closed	concave	deeply rugose	raised		punct-uated	yes	no	no	no
Corynandra chelidonii (L.f.) Cochrane & Iltis	closed	concave	deeply rugose	raised		punct-uated	no	no	no	no
***Gynandropsis* DC.**										
Gynandropsis gynandra (L.) Briq.,	closed	concave	deeply rugose	wide/grooved		radial-med.	no	no	no	yes
***Sieruela* Raf.**										

Sieruela hanburyana (Penz.) Roalson & JC Hall	open	papillate -pointed	rugose/pebbled	wide/grooved		radial -med.	no	no	no	yes
Sieruela stricta (Klotzsch) Roalson & JC Hall	open	concave	deeply rugose	wide/grooved		no	no	no	no	no
Sieruela parvipetala (R.A. Graham) Roalson & JC Hall	open	papillate -pointed	deeply rugose	wide/grooved		radial -med.	no	no	no	no
Sieruela bororensis (Klotzsch) Roalson & JC Hall	closed	papillate -flat	finely rugose	raised		no	no	no	no	no
Sieruela macrophylla (Klotzsch) Roalson & JC Hall	open	papillate	finely rugose	wide/grooved		no	no	no	no	yes
Sieruela briquetii (Polhill) Roalson & JC Hall	open	concave	medium rugose	wide/grooved		no	no	no	no	yes
Sieruela hirta (Klotzsch) Roalson & JC Hall	closed	concave	rugose	wide/grooved		no	no	no	no	no
Sieruela usambarica (Pax ex Engl.) Roalson & JC Hall	open	concave	medium rugose	wide/grooved		no	no	no	no	yes
Sieruela iberidella (Welw. ex Oliv.) Roalson & JC Hall	open	concave	deeply rugose	wide/grooved		radial -med.	yes	no	no	no
Sieruela rutidosperma (DC.) Roalson & JC Hall var. *rutidosperma*	open	papillate	finely rugose	wide/grooved		radial -med./ high	yes	no	no	no
Sieruela rutidosperma (DC.) Roalson & JC Hall var. *burmannii* (Wight & Arn.) Roalson & JC Hall	open	concave	finely rugose	wide/grooved		radial -med.	no	no	no	yes
Sieruela oxyphylla (Burch.) Roalson & JC Hall var. *oxyphylla*	open	concave	finely rugose	wide/grooved		radial -very low	no	no	no	no

Sieruela oxyphylla (Burch.) Roalson & JC Hall var. *robusta* (Kers) Roalson & JC Hall	open	concave	finely rugose	wide/grooved		radial -very low	no	no	no	no
Sieruela strigosa (Bojer) Roalson & JC Hall	open	concave	medium rugose	wide/grooved		no	no	no	no	no
Sieruela kermesina (Gilg & Gilg-Ben.) Roalson & JC Hall var. *plebeia* (Kers) Roalson & JC Hall	open	concave	medium rugose			radial -low	no	no	no	yes
Sieruela micrantha (Bojer) Roalson & JC Hall subsp. *leandrii* (Hadj-Moust.) Roalson & JC Hall	open	papillate	rugose/pebbled	wide/grooved	deeply rugose	radial -low/ med.	no	no	no	no
Sieruela perrieri (Hadj-Moust.) Roalson & JC Hall	open	papillate -domed	wrinkled	wide/grooved	wrinkled	no	no	yes	no	yes
Sieruela conrathii (Burtt Davy) Roalson & JC Hall	open	papillate -flat	wrinkled	wide/grooved		radial -med.	no	no	no	no
Sieruela maculata (Sond.) Roalson & JC Hall	open	papillate -flat	wrinkled	wide/grooved	rugose	radial -high	no	no	no	no
Sieruela rubella (Burch.) Roalson & JC Hall	open	concave	rugose/pitted			radial -low	no	no	no	no
Sieruela silvatica (Gilg & Gilg-Ben.) Roalson & JC Hall	open	concave	deeply rugose	wide/grooved			no	no	no	yes
Sieruela coeruleo-rosea (Gilg & Gilg-Ben.) Roalson & JC Hall	open	concave	rugose			radial -med.	no	no	no	no
Sieruela monophylla (L.) Roalson & JC Hall	open	concave	rugose/pitted			radial -low	no	no	no	yes
Sieruela elegantissima (Briq.) Roalson & JC Hall	open	concave	rugose/pitted	wide/grooved		no	no	no	no	yes
Sieruela schimperi (Pax) Roalson & JC Hall	open	papillate	rugose	wide/grooved		radial -low	no	no	no	no
***Andinocleome* Iltis & Cochrane**										

Andinocleome chilensis (DC.) Iltis, ined.	open	concave	rugose	wide/grooved		no	no	no	no	no
Andinocleome pilosa (Benth.) Iltis & Cochrane	open	papillate -flat	rugose/pitted	wide/grooved shallow		no	no	yes	no	no
Andinocleome anomala (Kunth) Iltis, ined.	open	concave	rugose/pitted			no	no	no	no	no
Andinocleome moritziana (Klotzsch ex Eichler) Iltis, ined.	open	papillate -flat	deeply rugose	wide/grooved		no	no	no	no	no
Andinocleome lechleri (Eichler) Iltis & Cochrane	open	concave	wrinkled			no	no	yes	no	no
Andinocleome magnifica (Briq.) Iltis & Cochrane	open	concave	deeply rugose			punct-uated	no	no	no	no
***Podandrogyne* Ducke**										
Podandrogyne pulcherrima (Standl.) Cochrane	open	papillate -flat	rugose	wide/grooved		no	yes	no	no	no
Podandrogyne jamesonii (Briq.) Cochrane	closed	papillate -flat	deeply rugose	wide/grooved		no	yes	no	no	no
Podandrogyne caucana Cochrane	closed	concave	rugose	wide/grooved		no	yes	no	no	no
Podandrogyne macrophylla (Turcz.) Woodson	closed	papillate	rugose	wide/grooved		no	no	no	no	no
Podandrogyne densiflora (Benth.) Iltis & Cochrane	open	papillate	rugose	wide/grooved		no	yes	no	no	no
***"Pterocleome"* Iltis ex EH Roalson**										
Pterocleome stylosa (Eichler) Iltis, ined.	closed	papillate	smooth	wide/grooved		no	no	no	no	no
***Melidiscus* Rafinesque**										
Melidiscus gigantea (L.) Raf.	closed	concave -flat	rugose/pitted	raised		no	no	no	no	no
***Cleoserrata* Iltis**										

Cleoserrata paludosa (Willd. ex Eichler) Iltis ex Soares Neto & Roalson	closed	concave	rugose	wide/grooved		punct-uated				
Cleoserrata melanosperma (S. Watson)	open	concave	rugose	wide/grooved		punct-uated	no	no	no	no
Cleoserrata serrata (Jacq.) Iltis	closed	concave	finely rugose	wide/grooved		no	no	no	no	no
Cleoserrata speciosa (Raf.) Iltis	open	papillate	rugose	wide/grooved		punct-uated	no	no	no	no
Cleoserrata bahiana Iltis & Costa e Silva, ined.	closed	concave	wrinkled	raised		no	no	no	no	no
***Tarenaya* Rafinesque**										
Tarenaya torticarpa (Iltis & T. Ruiz Zapata) Soares Neto & Roalson	closed	concave	wrinkled	raised		no	no	no	no	no
Tarenaya tucumanensis (Iltis) Arana & Oggero	closed	papillate	rugose	wide/grooved shallow		radial -high	yes	no	yes, long, thin	no
Tarenaya rosea (Vahl ex DC.) Soares Neto & Roalson	closed	papillate	rugose/pebbled	wide/grooved shallow		radial -med.	yes	no	no	no
Tarenaya aculeata (L.) Soares Neto & Roalson	closed	papillate	rugose	wide/grooved shallow		radial -low	yes	no	yes, long, thin	no
Tarenaya cordobensis (Eichler ex Griseb.) Arana & Oggero	closed	papillate	rugose	wide/grooved shallow		radial -low	yes	no	no	no
Cleome spinosa Jacq. subsp. *longicarpa* Iltis, ined.	closed	concave	rugose	raised		no	no	no	yes, long, thin	no
Tarenaya boliviensis (Iltis) Soares Neto & Roalson	closed	concave	finely rugose			no	no	no	no	no
Tarenaya eosina (J.F. Macbr.) Soares Neto & Roalson	closed	papillate	rugose	wide/grooved shallow		radial -high	yes	no	yes, long, thin	no
Tarenaya pernambucensis Iltis & MB Costa-e-Silva ex Soares Neto & Roalson	closed	papillate	rugose/ pebbled	wide/grooved		radial -high	no	no	no	no
Tarenaya parviflora (Kunth) Iltis	closed	concave	rugose	wide/grooved		no	no	no	no	no

Tarenaya microcarpa (Ule) Soares Neto & Roalson	closed	papillate/ domed	rugose	wide/grooved		radial-low	yes	no	no	no
Tarenaya hassleriana (Chodat) Iltis	closed	concave	rugose			no	no	no	no	no
Tarenaya curvispina MB Costa-e-Silva & Iltis ex Soares Neto & Roalson	closed	papillate	rugose/pebbled	wide/grooved		radial-high	no	no	no	no
***Dactylaena* Scrad. ex Schult.f.**										
Dactylaena boliviensis Iltis	closed	papillate -domed	deeply rugose	wide/groove		no	no	no	no	yes
Dactylaena pauciflora Griseb.	closed	papillate	rugose	wide/grooved		no	no	no	no	yes
Dactylaena micrantha Schrad. ex Schult.f.	closed	papillate -tabular pinched	deeply rugose	wide/grooved		no	no	no	no	yes
Dactylaena pohliana Eichler	closed	papillate -domed	rugose	wide/grooved shallow		no	no	no	no	yes
Dactylaena microphylla Eichler	closed	papillate	rugose	wide/grooved shallow	rugose	no	no	no	no	yes
***Physostemon* Mart. & Zucc.**										
Physostemon stenophyllum (Klotzsch ex Urb.) Iltis	closed	papillate	rugose	wide/grooved shallow	wrinkled	radial-high	no	no	no	no
Physostemon guianensis (Aubl.) Malme	closed	papillate	rugose	wide/grooved shallow		punct-uated	no	no	no	no
Physostemon humilis (Rose) Iltis	closed	papillate	wrinkled	wide/grooved shallow	rugose	radial-low	no	no	no	no
Cleome tenuis S. Watson	closed	papillate	wrinkled	wide/grooved shallow	rugose	radial-low	no	no	no	no
Physostemon lanceolatum Mart. & Zucc.	closed	papillate	wrinkled	wide/grooved		radial-high	no	no	no	no

Physostemon hemsleyanum (Bullock) RC Foster	closed	concave -flat	rugose/pitted	wide/grooved shallow		radial -high	no	no	no	no
Physostemon tenuifolium Mart. & Zucc.	closed	concave	wrinkled			spiked -thin	no	no	no	no
Physostemon rotundifolium Mart. & Zucc.	closed	concave	wrinkled			spiked -thick	no	no	no	no
***Mitostylus* Raf.**										
Mitostylus procumbens (Jacq). Raf.	open	papillate	deeply rugose	wide/grooved shallow		radial -high	no	no	no	no

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APPENDIX

Table 1: Coding scheme for phylogenetic trees

Taxon \ Character	Cleft	Periclinal Wall Shape	Periclinal Wall Ornamentation	Anticlinal Wall Thickness	Anticlinal Wall Ornamentation	Crests	Aril	Epicuticular Residue	Hairs	Reticulations
A arabica	?	?	?	?	?	?	?	?	?	?
A thaliana	?	?	?	?	?	?	?	?	?	?
B nigra	?	?	?	?	?	?	?	?	?	?
B rapa	?	?	?	?	?	?	?	?	?	?
A saxatile	?	?	?	?	?	?	?	?	?	?
I oppositifolia	?	?	?	?	?	?	?	?	?	?
N officinale	?	?	?	?	?	?	?	?	?	?
S altissimum	?	?	?	?	?	?	?	?	?	?
S pinnata	?	?	?	?	?	?	?	?	?	?
B vulgaris	?	?	?	?	?	?	?	?	?	?
C bursa pastoris	?	?	?	?	?	?	?	?	?	?
Ph rotundifolium	closed	concave	wrinkled	?	?	spikes	absent	absent	absent	absent
Ph tenuifolium	closed	concave	wrinkled	?	?	spikes	absent	absent	absent	absent
T chalapensis	?	?	?	?	?	?	?	?	?	?
Ph lanceolatum	closed	papillate	wrinkled	wide	?	radial	absent	absent	absent	absent
Ph stenophyllum	closed	papillate	wrinkled	wide	wrinkled	radial	absent	absent	absent	absent
Cor felina	closed	concave	rugose	raised	?	punctuated	present	absent	absent	absent
S aspera	?	?	?	?	?	?	?	?	?	?
Cor simplicifolia	?	?	?	?	?	?	?	?	?	?
Cor chelidonii (1)	closed	concave	rugose	raised	?	punctuated	absent	absent	absent	absent
Cor chelidonii (2)	?	?	?	?	?	?	?	?	?	?
D microphylla	closed	papillate	rugose	wide	rugose	radial	absent	absent	absent	present
Cleo speciosa (1)	open	papillate	rugose	wide	?	punctuated	absent	absent	absent	absent
Cleo speciosa (2)	?	?	?	?	?	?	?	?	?	?
Cleo melanosperma	open	concave	rugose	wide	?	punctuated	absent	absent	absent	absent
Ph hemsleyanum	closed	concave	rugose	wide	?	radial	absent	absent	absent	absent
Cleo paludosa (1)	closed	concave	rugose	wide	?	punctuated	absent	absent	absent	absent
Cleo paludosa (2)	?	?	?	?	?	?	?	?	?	?
M arborea	?	?	?	?	?	?	?	?	?	?
M gigantea (1)	closed	concave	rugose	raised	?	?	absent	absent	absent	absent
M gigantea (2)	?	?	?	?	?	?	?	?	?	?
T torticarpa	closed	concave	wrinkled	raised	?	?	absent	absent	absent	absent
T siliculifera	?	?	?	?	?	?	?	?	?	?
T rosea	closed	papillate	rugose	wide	?	radial	absent	absent	absent	absent
T spinosa (2)	?	?	?	?	?	?	?	?	?	?
T parviflora	closed	concave	rugose	wide	?	?	absent	absent	absent	absent
T aculeata	closed	papillate	rugose	wide	?	radial	present	absent	present	absent
T afrospina	?	?	?	?	?	?	?	?	?	?
T microcarpa	closed	papillate	rugose	wide	?	radial	present	absent	absent	absent
T crenopetala	?	?	?	?	?	?	?	?	?	?
T diffusa	?	?	?	?	?	?	?	?	?	?

T cordobensis	closed	papillate	rugose	wide	?	radial	present	absent	present	absent
T tucamanensis	closed	papillate	rugose	wide	?	radial	present	absent	present	absent
C werdermannii	?	?	?	?	?	?	?	?	?	?
T titubans	?	?	?	?	?	?	?	?	?	?
T domingensis	?	?	?	?	?	?	?	?	?	?
T pernambucensis	closed	papillate	rugose	wide	?	radial	absent	absent	absent	absent
T spinosa (1)	?	?	?	?	?	?	?	?	?	?
T houtteana	?	?	?	?	?	?	?	?	?	?
T boliviensis	closed	concave	rugose	?	?	?	absent	absent	absent	absent
T trachycarpa	?	?	?	?	?	?	?	?	?	?
An pilosa	open	papillate	rugose	wide	?	?	absent	present	absent	absent
D pauciflora	closed	papillate	rugose	wide	?	radial	absent	absent	absent	present
Di glaucum	closed	concave	wrinkled	?	?	?	absent	present	absent	absent
G gynandra	closed	concave	rugose	wide	?	radial	absent	absent	absent	absent
Po chiriquensis	?	?	?	?	?	?	?	?	?	?
Po jamesonii	closed	papillate	rugose	wide	?	?	present	absent	absent	absent
Po macrophylla	closed	papillate	rugose	wide	?	?	absent	absent	absent	absent
Po mathewsii	?	?	?	?	?	?	?	?	?	?
Po pulcherrima	open	papillate	rugose	wide	?	?	present	absent	absent	absent
Po decipiens	?	?	?	?	?	?	?	?	?	?
C stylosa	closed	papillate	?	wide	?	?	absent	absent	absent	absent
An chilensis	open	concave	rugose	wide	?	?	absent	absent	absent	absent
An moritziana	open	papillate	rugose	wide	?	?	absent	absent	absent	absent
An anomala	open	concave	rugose	?	?	?	absent	absent	absent	absent
An lechleri	open	concave	wrinkled	?	?	?	absent	present	absent	absent
S strigosa	open	concave	rugose	wide	?	?	absent	absent	absent	absent
Co paradoxa	open	concave	rugose	wide	?	?	absent	absent	absent	present
Co angustifolia	open	papillate	rugose	?	?	?	absent	absent	present	present
C angustifolia sub diandr	open	papillate	rugose	wide	?	?	absent	absent	present	present
Cl arborea	?	?	?	?	?	?	?	?	?	?
Cl longipes	closed	concave	rugose	wide	?	?	absent	absent	absent	absent
Cl obtusifolia	closed	concave	rugose	wide	?	?	absent	absent	absent	absent
Cl lutea	?	?	?	?	?	?	?	?	?	?
Cl serrulata	?	?	?	?	?	?	?	?	?	?
Cl platycarpa	?	?	?	?	?	?	?	?	?	?
Cl oxystylioides	?	?	?	?	?	?	?	?	?	?
Cl refracta	?	?	?	?	?	?	?	?	?	?
Gi scaposa	open	papillate	?	wide	?	?	absent	present	absent	absent
Pol dodecandra	open	papillate	rugose	wide	?	?	absent	absent	absent	absent
Pol uniglandulosa	open	papillate	rugose	wide	?	?	absent	absent	absent	absent
C ornithopodioides	open	papillate	scurfy	wide	?	?	absent	absent	absent	absent
R droserifolia	open	papillate	scurfy	wide	?	?	absent	absent	absent	absent

R fimbriata	open	papillate	rugose	?	?	?	absent	absent	absent	absent
R quinquenervia	?	?	?	?	?	?	?	?	?	?
C violacea	?	?	?	?	?	?	?	?	?	?
C rupicola	open	papillate	rugose	?	?	?	absent	absent	present	absent
C coluteoides	open	papillate	rugose	wide	rugose	?	absent	absent	absent	absent
C schweinforthii	?	?	?	?	?	?	?	?	?	?
C amblyocarpa (1)	?	?	?	?	?	?	?	?	?	?
C ambylocarpa (2)	?	?	?	?	?	?	?	?	?	?
C arabica	open	papillate	?	?	?	?	absent	absent	present	absent
S elegantissima	open	concave	rugose	wide	?	?	absent	absent	absent	present
C khorassanica	open	papillate	rugose	wide	?	?	absent	absent	absent	absent
C turkmena	open	papillate	rugose	?	?	?	absent	absent	absent	absent
C linearifolia	?	?	?	?	?	?	?	?	?	?
K foliosa	open	concave	rugose	wide	?	?	absent	absent	absent	present
K kalachariensis (2)	open	concave	rugose	wide	?	?	absent	absent	absent	present
K kalachariensis (1)	?	?	?	?	?	?	?	?	?	?
St brachycarpa	open	papillate	wrinkled	wide	?	?	absent	absent	absent	absent
Th chrysantha	open	concave	rugose	wide	?	?	absent	absent	absent	present
Ar oxalidea (1)	open	papillate	rugose	wide	?	?	absent	absent	absent	absent
Ar oxalidea (2)	?	?	?	?	?	?	?	?	?	?
Ar oxalidea (3)	?	?	?	?	?	?	?	?	?	?
Ar. oxalidea (4)	?	?	?	?	?	?	?	?	?	?
C arenitensis	?	?	?	?	?	?	?	?	?	?
C bundeica	?	?	?	?	?	?	?	?	?	?
C linophylla	?	?	?	?	?	?	?	?	?	?
C microaustralica (1)	?	?	?	?	?	?	?	?	?	?
A cleomoides (1)	open	papillate	rugose	wide	?	radial	present	absent	absent	absent
C kenealleyi	?	?	?	?	?	?	?	?	?	?
A cleomoides (2)	?	?	?	?	?	?	?	?	?	?
C microaustralica (2)	?	?	?	?	?	?	?	?	?	?
C tetrandra (1)	?	?	?	?	?	?	?	?	?	?
C tetranda (2)	?	?	?	?	?	?	?	?	?	?
A viscosa (1)	open	papillate	rugose	wide	?	radial	absent	absent	absent	absent
A viscosa (2)	?	?	?	?	?	?	?	?	?	?
A viscosa (3)	?	?	?	?	?	?	?	?	?	?
A viscosa (4)	?	?	?	?	?	?	?	?	?	?
A viscosa (5)	?	?	?	?	?	?	?	?	?	?
A viscosa (6)	?	?	?	?	?	?	?	?	?	?
A viscosa (7)	?	?	?	?	?	?	?	?	?	?
Ar arenitensis	?	?	?	?	?	?	?	?	?	?
C uncifera (1)	?	?	?	?	?	?	?	?	?	?

C uncifera (2)	?	?	?	?	?	?	?	?	?	?
C uncifera sub microphyl	?	?	?	?	?	?	?	?	?	?
C breyeri	?	?	?	?	?	?	?	?	?	?
S oxyphylla	open	concave	rugose	wide	?	?	absent	absent	absent	absent
S macrophylla	open	concave	rugose	wide	?	?	absent	absent	absent	present
S maculata	open	papillate	wrinkled	wide	rugose	radial	absent	absent	absent	absent
S iberidella	open	concave	rugose	wide	?	radial	present	absent	absent	absent
S schimperi	open	papillate	rugose	wide	?	radial	present	absent	absent	absent
S rutidosperma	open	papillate	rugose	wide	?	radial	present	absent	present	absent
S hirta	closed	concave	rugose	wide	?	?	absent	absent	absent	absent
C burtii	?	?	?	?	?	?	?	?	?	?
C monochroma	?	?	?	?	?	?	?	?	?	?
S densifolia	?	?	?	?	?	?	?	?	?	?
S monophylla (1)	open	concave	rugose	?	?	radial	absent	absent	absent	present
S monophylla (2)	?	?	?	?	?	?	?	?	?	?
S monophylla (3)	?	?	?	?	?	?	?	?	?	?
S allamanii	?	?	?	?	?	?	?	?	?	?
S briquetii	open	concave	rugose	wide	?	?	absent	absent	absent	present
S usambarica	open	concave	rugose	wide	?	?	absent	absent	absent	present

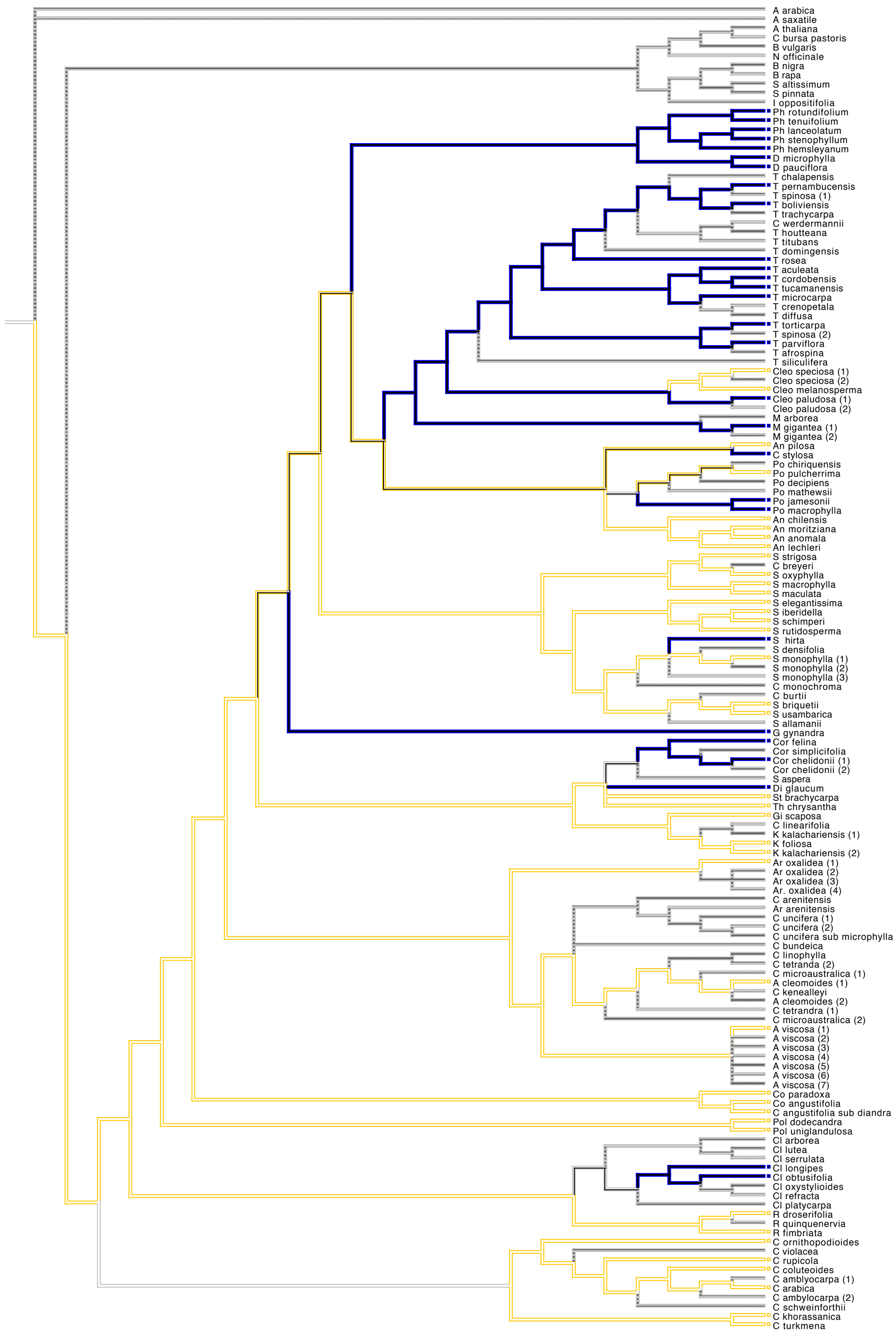

Figure 1: Ancestral character mapping of an open and closed cleft indicates that a closed cleft was derived at the node leading to the New World clades and in *Cleomella*. Blue line indicates a closed cleft; orange indicate an open cleft; grey lines indicate non-coded taxa or missing data.

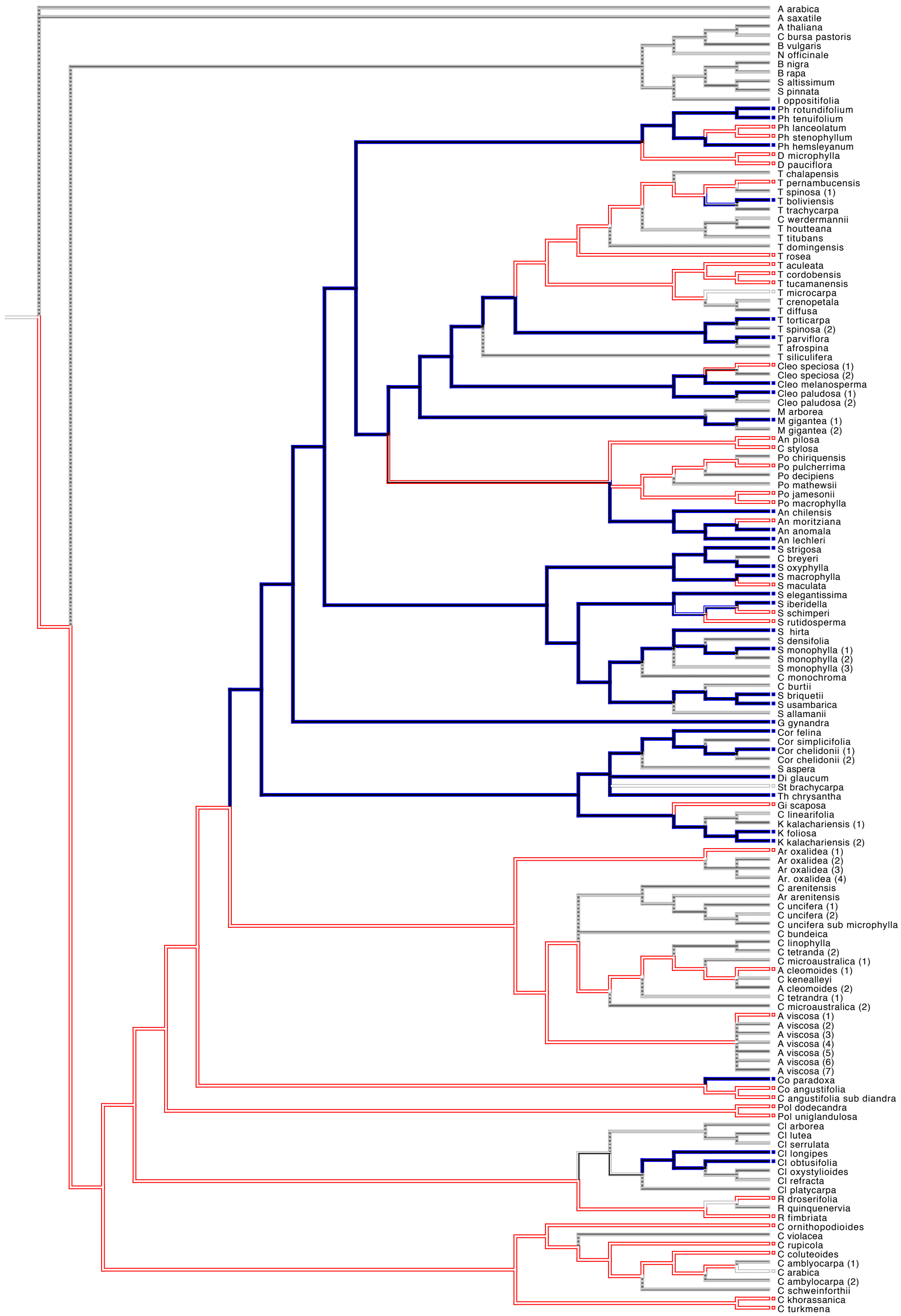

Figure 2: Ancestral character mapping of periclinal wall shape indicates major derivations of a concave wall at the node leading to the African and New World clades clades. Blue lines indicate concave walls; red lines indicate papillate walls; grey lines indicate non-coded taxa or missing data.

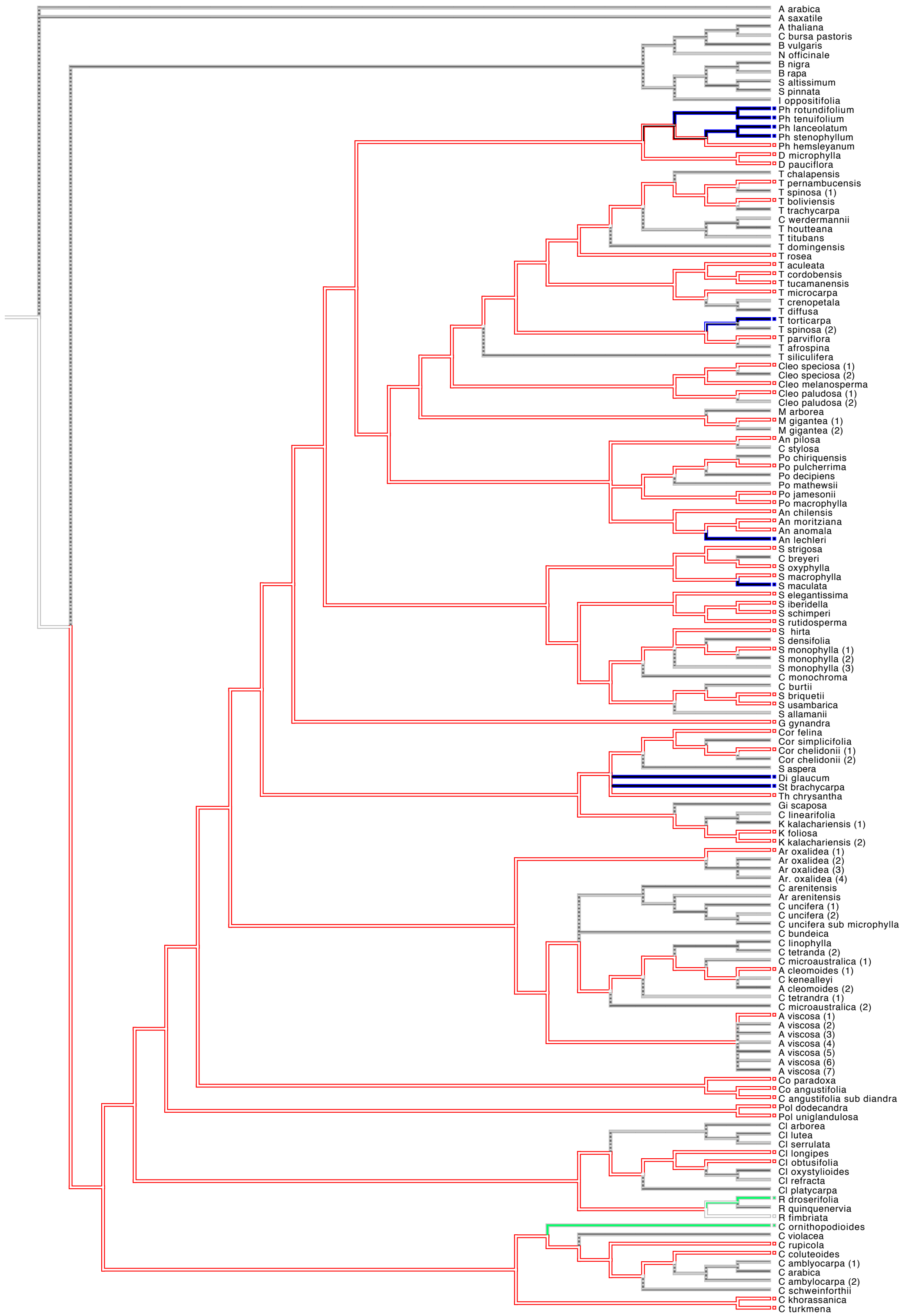

Figure 3: Ancestral character mapping of an periclinal wall ornamentation indicates a derived state of scurfy in *Cleome* s.s. and *Rorida* and wrinkled in *Stylidocleome*, species of *Sieruela, Andinocleome, Tarenaya* and *Physostemon*. Green lines indicate scurfy; blue lines indicate wrinkled; red lines indicate rugose; grey lines indicate non-coded taxa or missing data.

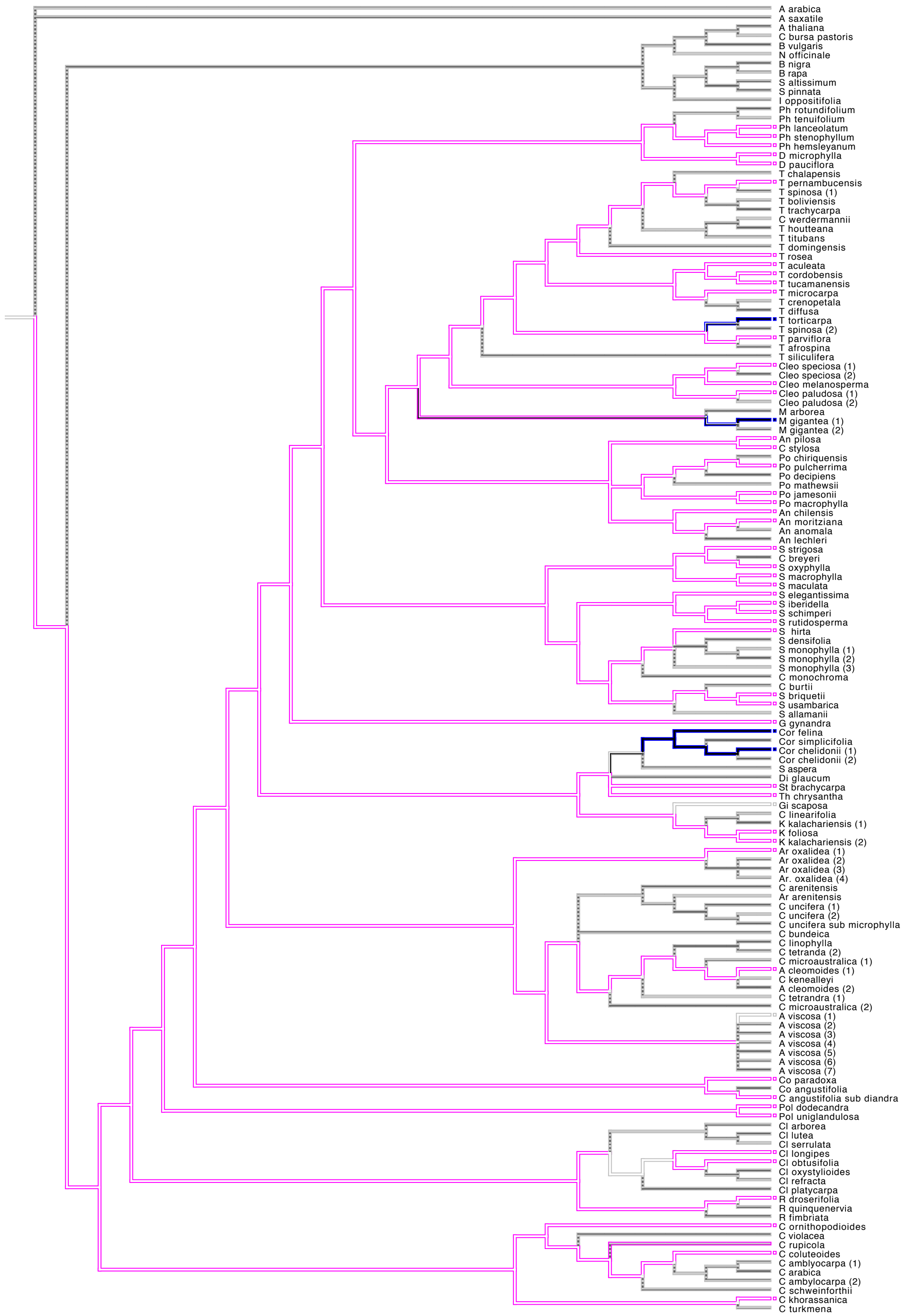

Figure 4: Ancestral character mapping of an anticlinal wall thickness indicates a derived raised state in *Corynandra* and *Melidiscus* and one species of *Tarenaya.* Blue lines indicate a raised wall; pink lines indicate wide and grooved; grey lines indicate non-coded taxa, missing data or species that have obscured anticlinal walls.

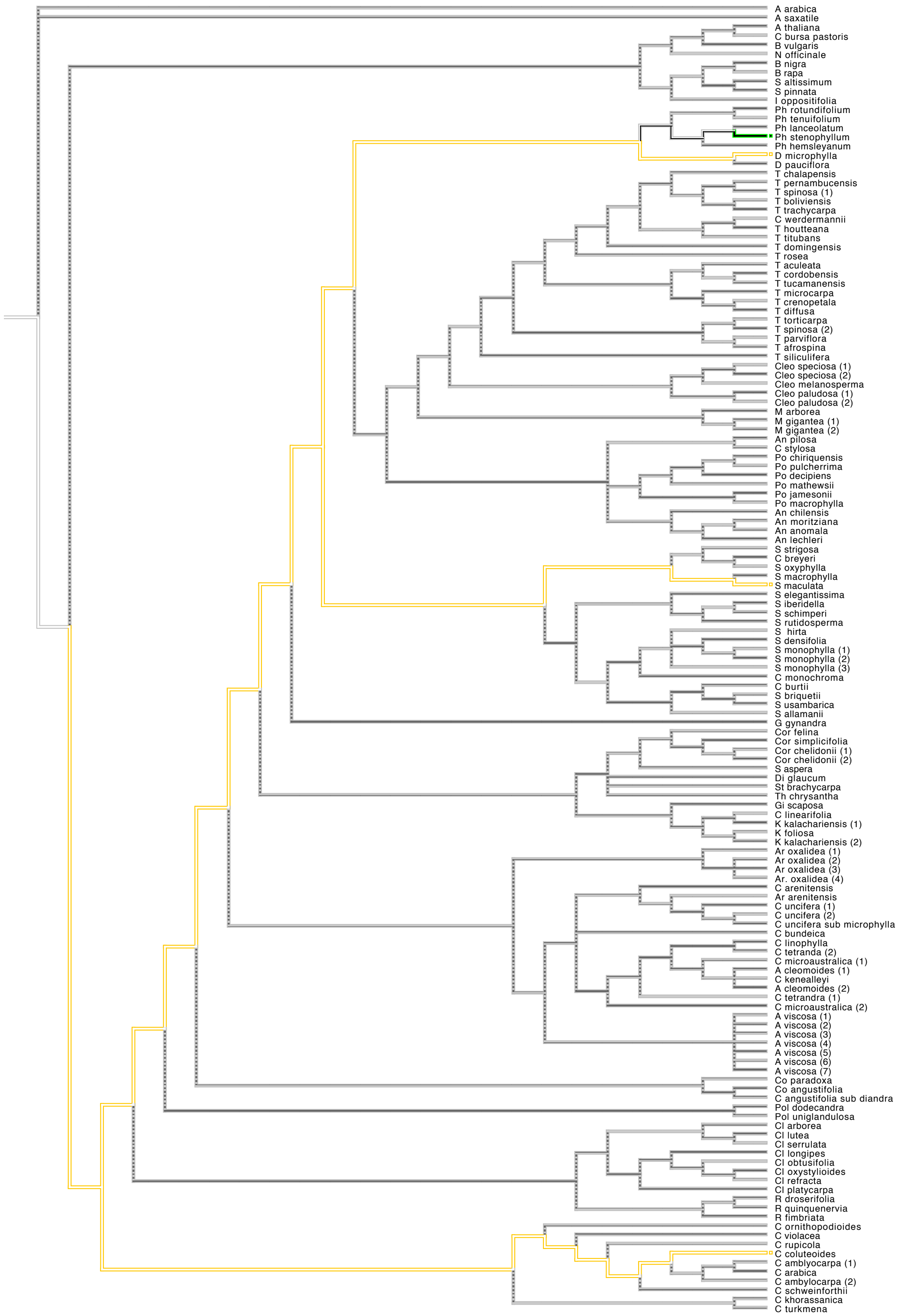

Figure 5: Ancestral character mapping of an anticlinal wall ornamentation indicates one derivation of a wrinkled state in *Physostemon stenophyllum.* Yellow lines indicate rugose walls; green line indicates wrinkled; grey lines indicate non-coded taxa, missing data or species that had obscured anticlinal walls or ornamentation was undiagnosable in images.

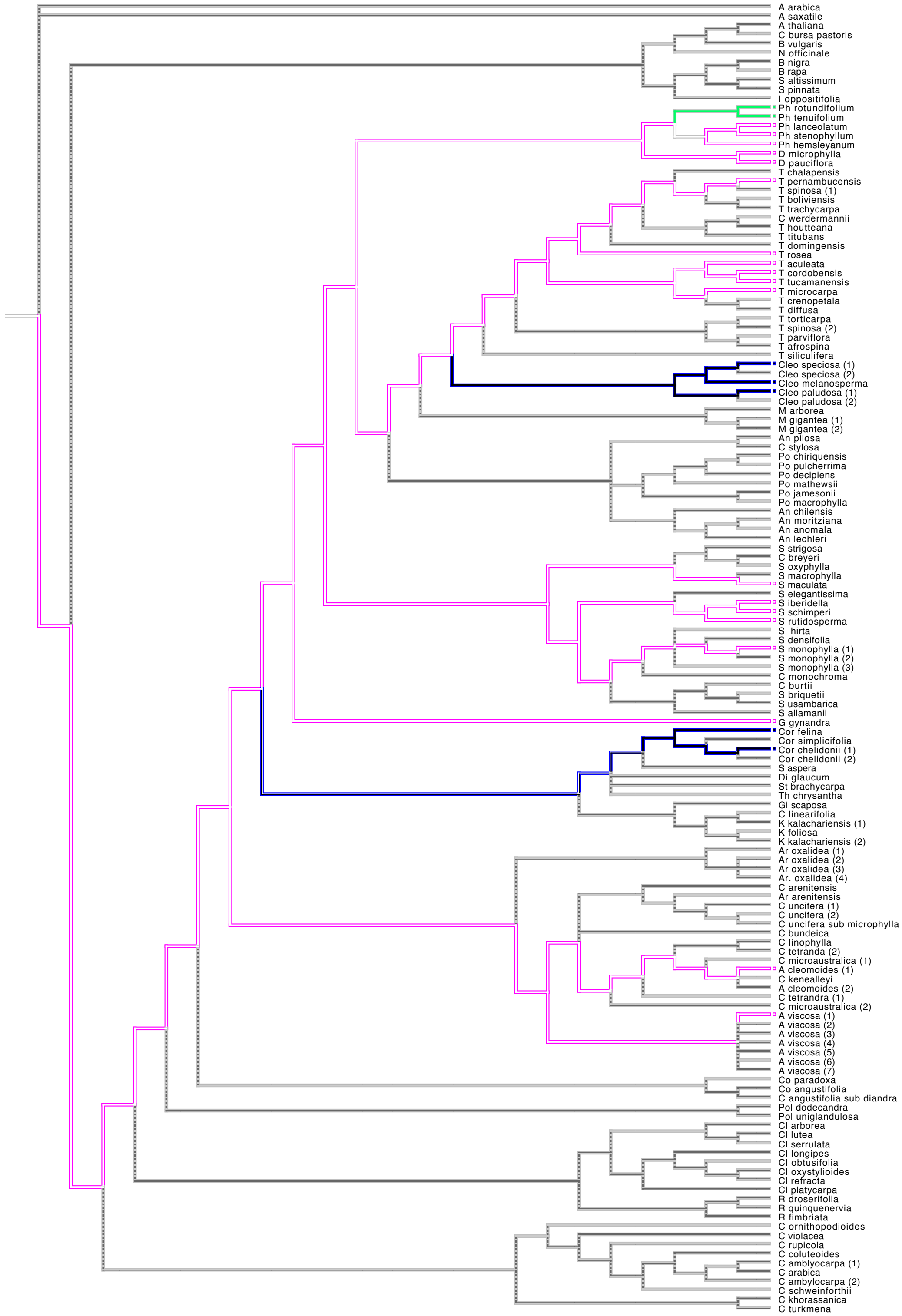

Figure 6: Ancestral character mapping of crests indicate a derivation of punctuated crests in *Corynandra* and *Cleoserrata* and spiked crests in *Physostemon*. Pink lines indicate radial crests; blue lines indicate punctuated; green lines indicate spiked; grey lines indicate non-coded taxa or missing data.

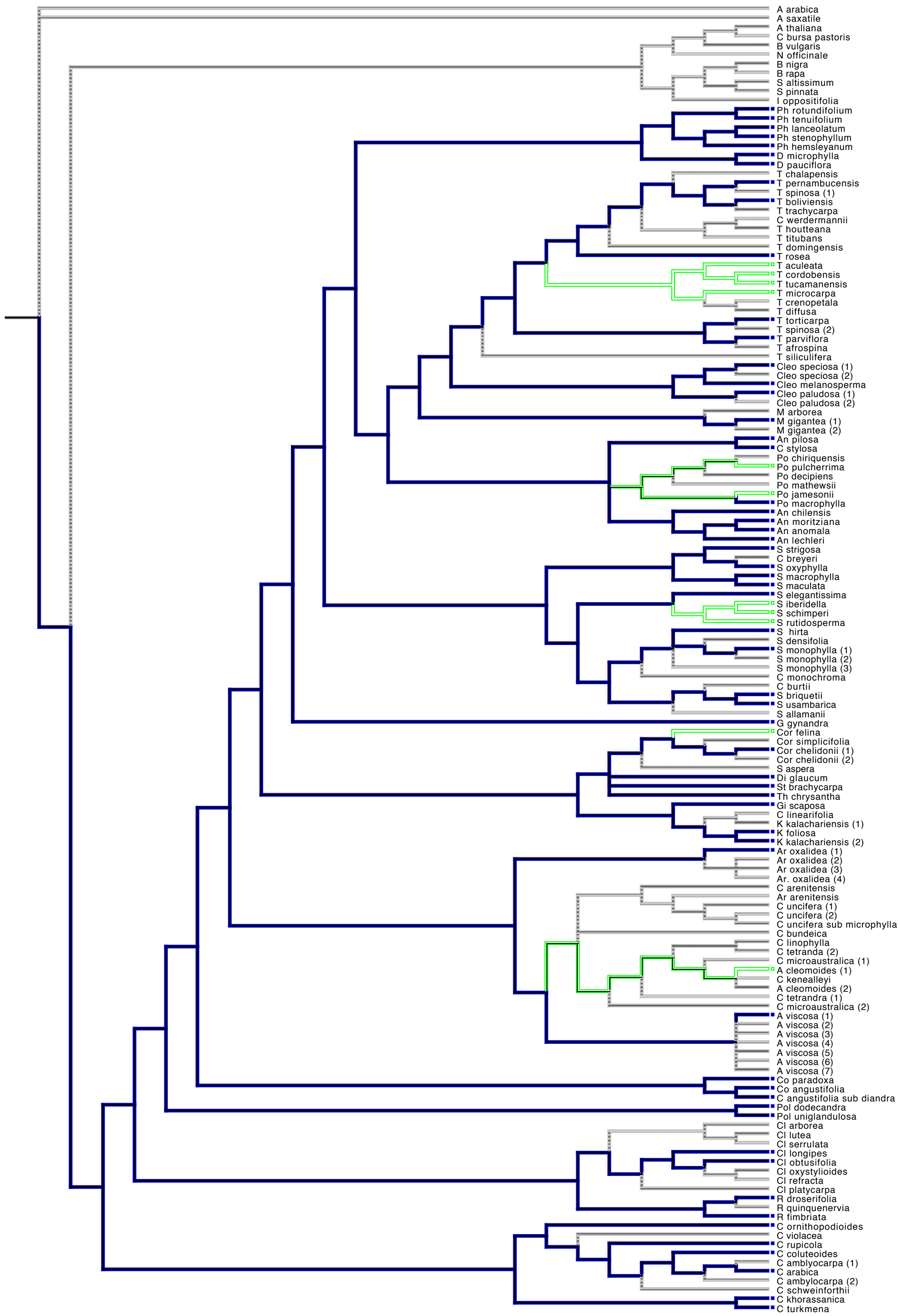

Figure 7: Ancestral character mapping of aril indicates a derived state of arils in *Arivela* and *Corynandra, Sieruela, Podandrogyne* and *Tarenaya.* Green lines indicate presence of arils; blue lines indicate absence; grey lines indicate non-coded taxa or missing data.

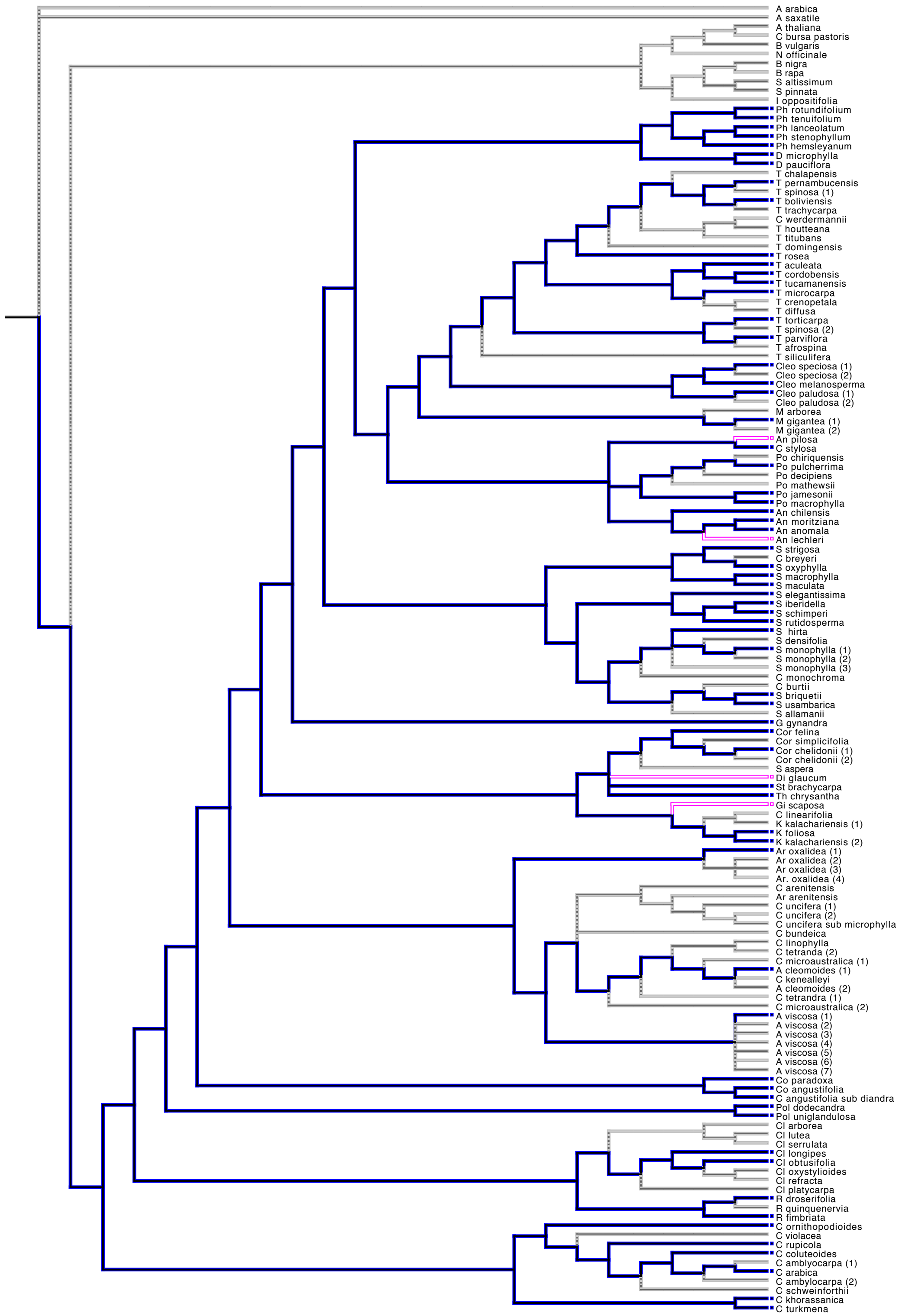

Figure 8: Ancestral character mapping of epicuticular residues indicate a derived state in *Gilgella* and *Andinocleome.* Pink lines indicate presence of epicuticular residues; blue lines indicate absence; grey lines indicate non-coded taxa or missing data.

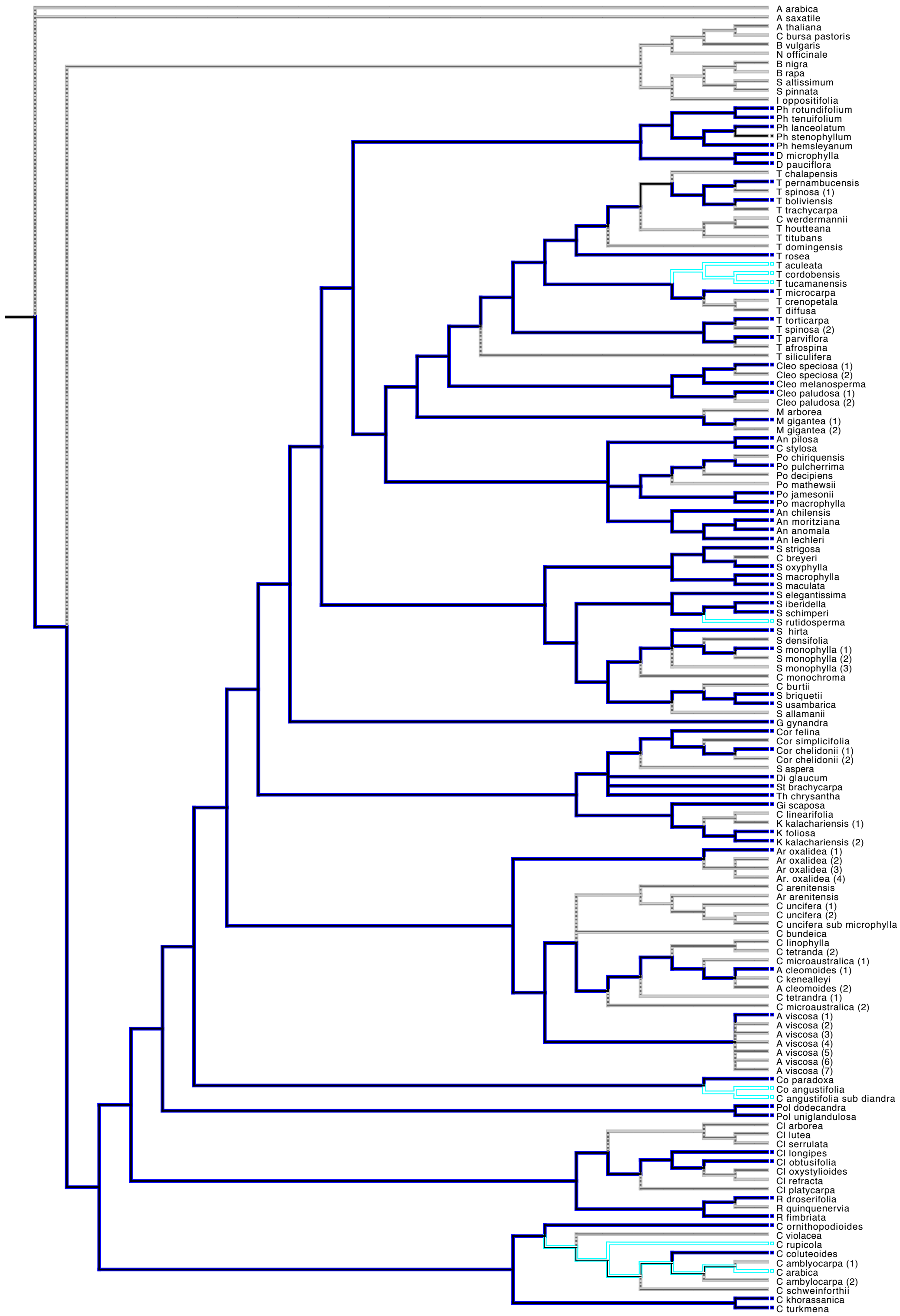

Figure 9: Ancestral character mapping of hairs indicate a derived state of hairs in *Cleome s.s., Coalisina,* one species *of Sieruela* and in *Tarenaya.* Light blue lines indicate presence of hairs; blue lines indicate absence; grey lines indicate non-coded taxa or missing data.

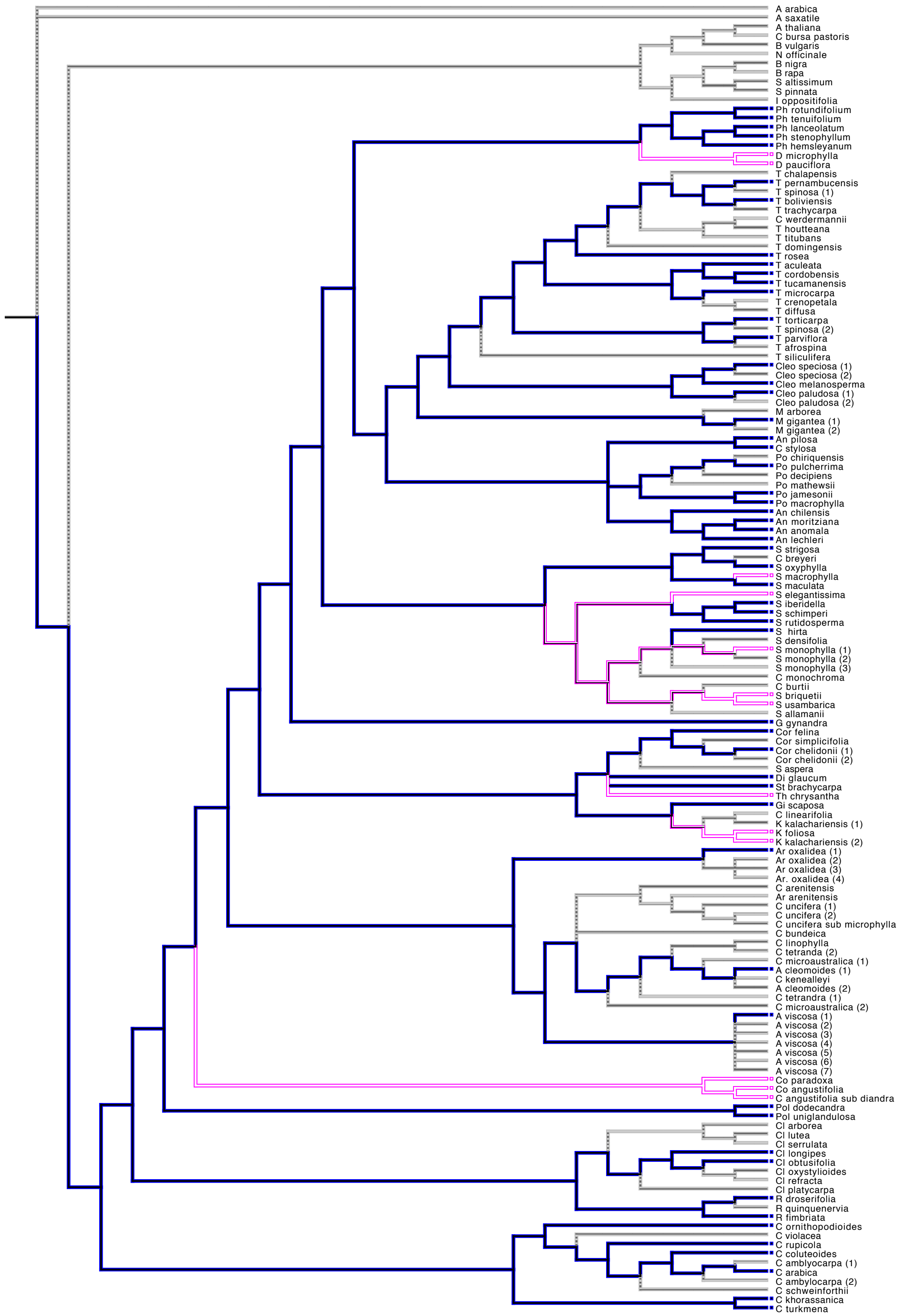

Figure 10: Ancestral character mapping of reticulations indicate a derived state of reticulations in *Coalisina, Kersia, Thulinella, Sieruela* and *Dactyleana.* Pink lines indicate presence of reticulations; blue lines indicate absence; grey lines indicate non-coded taxa or missing data.