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The form, structure and size of *Lithops* N.E.Br. seeds and the taxonomic implications

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Summary: The seeds of all the taxa of the genus *Lithops* N.E.Br. are hereby described following their study by both digital dissection microscope and scanning electron microscopy. This information is used together with all other taxonomically important data to suggest the best possible classification for the genus. As a consequence of this new information, *L. bella*, *L. dendritica* and *L. eberlanzii* are reinstated as full species whilst four varieties are elevated to subspecies status. The varieties of *L. karasmontana* are no longer recognised except for var. *aiaisensis* which is transferred to *L. eberlanzii* due to its identical seeds. *L. dendritica* now comprises of four subspecies, all of which have seeds vastly different from *L. pseudotruncatella*, under which they were formerly classified.

Zusammenfassung: Die Samen aller Taxa der Gattung *Lithops* N.E.Br. werden hiermit nach der Untersuchung sowohl mit dem digitalen Präparationsmikroskop als auch mit dem Rasterelektronenmikroskop beschrieben. Diese Informationen werden zusammen mit allen anderen taxonomisch wichtigen Daten verwendet, um die bestmögliche Klassifikation für die Gattung vorzuschlagen. Aufgrund dieser neuen Informationen werden *L. bella*, *L. dendritica* und *L. eberlanzii* wieder als eigene Arten anerkannt, während vier Varietäten in den Status einer Unterart erhoben werden. Die Varietäten von *L. karasmontana* werden nicht mehr anerkannt, mit Ausnahme von *L. karasmontana* var. *aiaisensis*, die aufgrund ihrer identischen Samen zu *L. eberlanzii* gestellt wird. *L. dendritica* besteht nun aus vier Unterarten, die alle ganz andere Samen haben als *L. pseudotruncatella*, zu der sie früher gestellt wurden.

Introduction

To date, the classification of taxa within the genus *Lithops* N.E.Br. has primarily been based on the morphological characteristics of the plants and more specifically the leaf surface patterns and colour of the leaves. Due to the intra- and inter-population variations seen in these plants, a plethora of taxa names have been assigned to *Lithops* especially during the past century until the taxonomic classification was somewhat stabilised by Cole (1988) and Cole & Cole (2005). This classification was largely accepted. The earlier work by Dugdale (1971) on the anatomy and, in particular, the distribution of tanniniferous idioblast cells provided some useful information on the relationships of the subspecies and varieties of *Lithops* but did not have a major influence on the accepted classification. Likewise, the reflecting microscope study of *Lithops* seeds (Jump, 1981) highlighted possible relationships between species but ultimately did not influence their classification as this important work was largely overlooked. More recent attempts at gaining an insight into the relationships of *Lithops* species on a molecular level were also not successful (Kellner *et al.,* 2011) mainly because of the lack of measurable genetic diversity as a result of the very recent evolution of members of the Aizoaceae (Wallace, 1990; Klak *et al.,* 2003, 2004).

As part of a larger publication on succulents in general, Cole & Cole (2017) did not list any varieties in the *Lithops* classification that they presented. This was the result of publication restrictions and not because the authors no longer recognised the varieties as described by Cole & Cole (2005). The 2017 publication must thus be seen as a compacted version of the 2005 publication.

Furthermore, a major overhaul of the classification of the *Lithops* genus as suggested by Jainta, (2019) was based solely on the morphology of the vegetative parts of the plants (as seen in habitat), and therefore failed to take into account other key morphological features that aid the classification of taxa. However, a recent molecular study by Loots (2019) and Loots *et al.* (2019) on the relationships between *Lithops* species of Namibia has provided some useful information and suggested some changes in the classification within the genus.

The morphological parameters, mostly based on differences in the features of the leaf surface, used to determine the taxonomic position of *Lithops* taxa are very plastic due to their adaptions to local conditions and are therefore not always reliable. Differences in reproductive features are generally more meaningful and stable in determining relationships between plant taxa. However, the minimal differences seen between the flowers and seed capsules of different *Lithops* taxa, are also useful in some instances but do not consistently aid in their classification (Jump, 1981). By con-

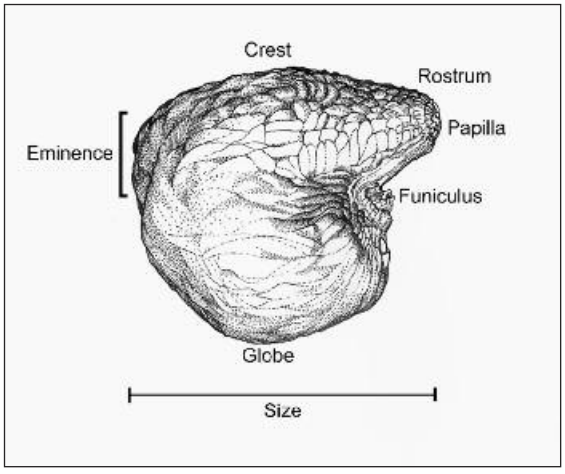

Figure 1. External features of *Lithops* seeds.

trast, the morphology of *Lithops* seeds can be helpful in determining relationships within the genus. Although morphologically similar seeds do not necessarily denote a close relationship between diverse taxa within species, they might indicate an affinity between them. On the other hand, a marked difference in seed morphology, structure or size is a good basis for considering taxa not to be closely related (Jump, 1981), especially if this is consistent with other evidence such as leaf morphology, tanniniferous idioblast patterns, flower size and colour or genetic similarities.

The aim of this study was to determine the fine structure of the seeds of all the presently recognised taxa of *Lithops* and to use this information together with all other relevant features to suggest the best possible classification for the genus.

Material and methods

Seeds of all the species, to varietal level, of the genus *Lithops* as listed by Cole & Cole (2005) and Hammer (2010) as well as new taxa described after these publications (Cole, 2006; Cole, 2012; Earlé & Uijs, 2019) were examined.

Lithops seeds were described and measured as they appear in colour and seen with a digital dissection microscope (DDM) at a magnification of about 40X - 100X. The seeds were measured using the DDM with the aid of a 0.01 mm stage micrometre. At least 30 individual seeds of each taxon were measured to calculate their mean length. The mean lengths obtained were compared to the mean lengths given by Hammer (2010) as taken from Wallace (1988) (Table 1).

For scanning electron microscopy (SEM), seeds were first coated with gold using an Emitech K550X sputter coater (Quorum Tech Ltd., East Grinstead, U.K.). Samples were then observed using a FEI Quanta 200 microscope (ThermoFischer Scientific) typically operating at 10keV and a beam size of 3µm. The resulting images further highlighted the surface structure of the seeds. Images obtained from at least three individual seeds of each taxon were then studied and described.

Results and Discussion

The basic *Lithops* seed consists of a globe and a rostrum with the crest often prominent and in some seeds protruding backwards past the globe to form a visible eminence (Figure 1). In some seeds a small papilla is attached to the tip of the rostrum. The globe of the seed is described as rounded, round and partly flattened, flattened or indented (see Table 2). Seeds with an indented globe were the result of two definite bulges of the globe. In *Lithops lesliei* the globe bulges below the rostrum and often protrudes forwards to form a pout (see below).

The surface of the seeds was either smooth, wave-like rugose or covered in tubercles that could either be interlocking or individual. The pattern of the rugosity of the seed surface was described as uniform, when the entire seed displayed the same rugosity, or the surface showed a bi-rugosity pattern when the globe and the crest/rostrum had different rugosity patterns (Table 2 & Figure 2).

The structure of the seeds and the taxonomic implications

***Lithops amicorum* Cole (2006):** The seeds of *L. amicorum* have a creamy yellow to yellow brown rounded globe and a distinct bi-rugosity tuberculate pattern. The smooth to wave-like rugosity on the globe merges into an area of small flat tubercles towards the crest which is yellow brown and forms ill-defined rows of tubercles on the medium sized brown coloured rostrum (Figure 3A). The mean size of individual seeds is 0.69 mm. The recent genetic investigations by Loots *et al.* (2019) found this species to be closely related to *Lithops karasmontana* and suggested that it should be considered a subspecies. Although the seeds are somewhat similar in structure, *L. amicorum* has much larger seeds than *L. karasmontana*. Furthermore, the unique blue grey colour of the plants, the widely different leaf surface patterns and geographical separation from *L. karasmontana* are considered enough to retain *L. amicorum* as a stand-alone species at present.

***Lithops aucampiae* L. Bolus (1932):** The seeds of all the taxa in *L. aucampiae* are somewhat similar in that they are all a light brown to yellow brown colour but there are small differences between the seeds of the lower taxa. These large seeds (Table 1) all have a ventrally flattened globe with a slight wave-like rugosity. Only the short straight rostrum (often bending slightly upwards) has a surface that is slightly more rugose with ill-defined flat tubercles arranged in rows (Figures 3B–E). The seeds of var. *koelemanii* (de Boer) Cole (1960) have a ventrally flattened globe but are different in that they are uniformly covered in indistinct tubercles that form ridges on the ventral part of the globe (Figure 3C). Both varieties of subsp. *euniceae* (de Boer) Cole (1966) have slightly deeper wave lines on the anterior part of the flattened globe as well as on the crest area and the deep waves present as ridges on the ventral part of the globe and towards the tip of the rostrum (Figures 3D–E). Since the seeds of all the

taxa share a similar overall shape with only slight differences in their rugosity the suggestion by Jainta (2019) that subsp. *euniceae* should be regarded as a separate species on the basis of its isolated distribution and the 'relatively uniform and prominent markings at their outer margins' is not regarded as substantial enough to warrant its status as a separate species. The seeds of the two varieties of subsp. *euniceae* are identical but the yellowish or pinkish grey colour and the consistently fine marginal markings of var. *fluminalis* Cole (1970) separate this variety from var. *euniceae.* The tanniniferous idioblast patterns of all four of the taxa within *L. aucampiae* are different and are probably an indication of the intra-species variability.

***Lithops bromfieldii* L. Bolus (1934):** Cole & Cole (2005) considered this species to have four varieties, namely var. *bromfieldii, glaudinae* (de Boer) Cole (1960)*, insularis* (L. Bolus) Fearn (1937) and *mennellii* (L. Bolus) Fearn (1937). The seeds of var. *insularis* are slightly larger than the other varieties (0.82 *vs.* 0.73 mm) but otherwise the seeds are all identical, having a flattened to minimally indented globe with a uniformly smooth surface and are yellow brown with a darker brown rostrum (Figures 3G–H & 4A–B). Although there is some overlap in the leaf surface characters of the varieties, they are easily recognizable as different varieties especially if grown in cultivation to their full potential. Jump (1981) also showed that the seeds of these varieties were identical and concluded that they should not be regarded as different species as had been suggested by earlier researchers. The current SEM study confirms the results of Jump (1981), that var. *glaudinae* is clearly a variety of *L. bromfieldii.* The suggestion by Jainta (2017, 2019) that var. *glaudinae* should instead be regarded as a separate species due to the metallic looking dots on the face surface of the leaves cannot be supported.

***Lithops coleorum* S.A. Hammer & R. Uijs (1994):** The seeds of this species have a bi-rugosity pattern with the rounded, yellow brown globe showing a rough wave-like rugosity merging into individual tubercles on the crest of the seed and well-defined rows of flat tubercles towards the tip of the long brown coloured rostrum (Figure 4C). The mean length of individual seeds is 0.72mm.

***Lithops comptonii* L. Bolus (1930):** The seeds of the two varieties recognised in this species are somewhat similar with both having a rounded globe and long rostrum (Figures 4D–E). The seeds are yellow brown with the tips of the tubercles being a dark brown colour giving the seed a spotted appearance. The constant difference between the seeds of the two varieties is that the small tubercles on the globe of var. *comptonii* are ill-defined and the ventral part of the globe thus has a rough wave-like rugosity pattern and the seeds overall have a bi-rugosity pattern (Figure 4D). In var. *weberi* (Nel) Cole (1940) the individual tubercles are well separated from each other and the seed is uniformly covered in well-defined tubercles (Figure 4E). Since the varieties are easily identified due to their consistently different leaf patterns in addition to the differences in the seeds described here, there is no justification to lump these two varieties into a single taxon as suggested by Janita (2017, 2019). The seeds of the varieties measured during this study (Table 1) are slightly larger (0.68/0.62 *vs.* 0.57/0.56mm) than those reported by Hammer (2010).

***Lithops dinteri* Schwantes (1927):** The division of this species into three subspecies seems to be justified if both the growth forms of the adult plants and the structure of the seeds are considered. Subsp. *dinteri* is currently divided into two varieties, var. *dinteri* and *brevis* (L. Bolus) Fearn (1932). The seeds of both varieties are identical in that the rounded globe and the rest of the seed is uniformly covered in medium-sized individual tubercles (Figures 5B–D). The slight difference in the presentation of adult plants, with var. *brevis* tending to have either no or fewer red dots on the leaf face than var. *dinteri,* makes the validity of these two varieties questionable (Earlé & Mouton, 2013; Earlé, 2016). Therefore the two varieties are henceforth synonymised under subsp. *dinteri.* The growth forms of the two other subspecies, *frederici* (Cole) Cole (1973) and *multipunctata* (de Boer) Cole (1966) are so different from each other and from subsp. *dinteri* that there is no doubt that these are valid taxa. Subsp. *frederici* are small plants, which rarely, even in cultivation, grow larger than 20mm x 12mm with a very pronounced convex upper leaf surface not seen in the other varieties while adult plants of subsp. *multipunctata* are large with individual heads that can measure up to 33 x 20mm and an upper leaf surface that is flat or only slightly convex even in fully turgid plants. This variance is further confirmed by the slight differences in the seed structures. Although both show a tendency of bi-rugosity with the surface of the rounded globe being wave-like merging into small individual tubercles towards the crest and rostrum (c.f. Figures 5B & C), the tubercles are larger but more widely spread in subsp. *multipunctata* (Figure 5D) and the seeds are slightly smaller than the other subspecies (0.50 *vs.* 0.54/0.55mm; Table 1). Our observations do not support the proposal by Jainta (2017, 2019) who argued that all the *L. dinteri* taxa should be regarded as the same and combined with *Lithops dorotheae* and *Lithops schwantesii* subsp. *schwantesii* var. *marthae.* [also see *Lithops dorotheae* and *Lithops schwantesii*].

***Lithops divergens* L. Bolus (1934):** This species is currently considered to consist of two varieties, var. *divergens* and *amethystina.* The growth forms of these two taxa are different as are the sizes and structures of their seeds. The seeds of var. *divergens* are light brown to dark brown and show a marked bi-rugosity pattern with the rounded globe being smooth merging into large flat tubercles towards the crest with neatly aligned rows of tubercles towards the rostrum tip (Figures 5F). The mean length of the seeds is 0.58mm (rel-

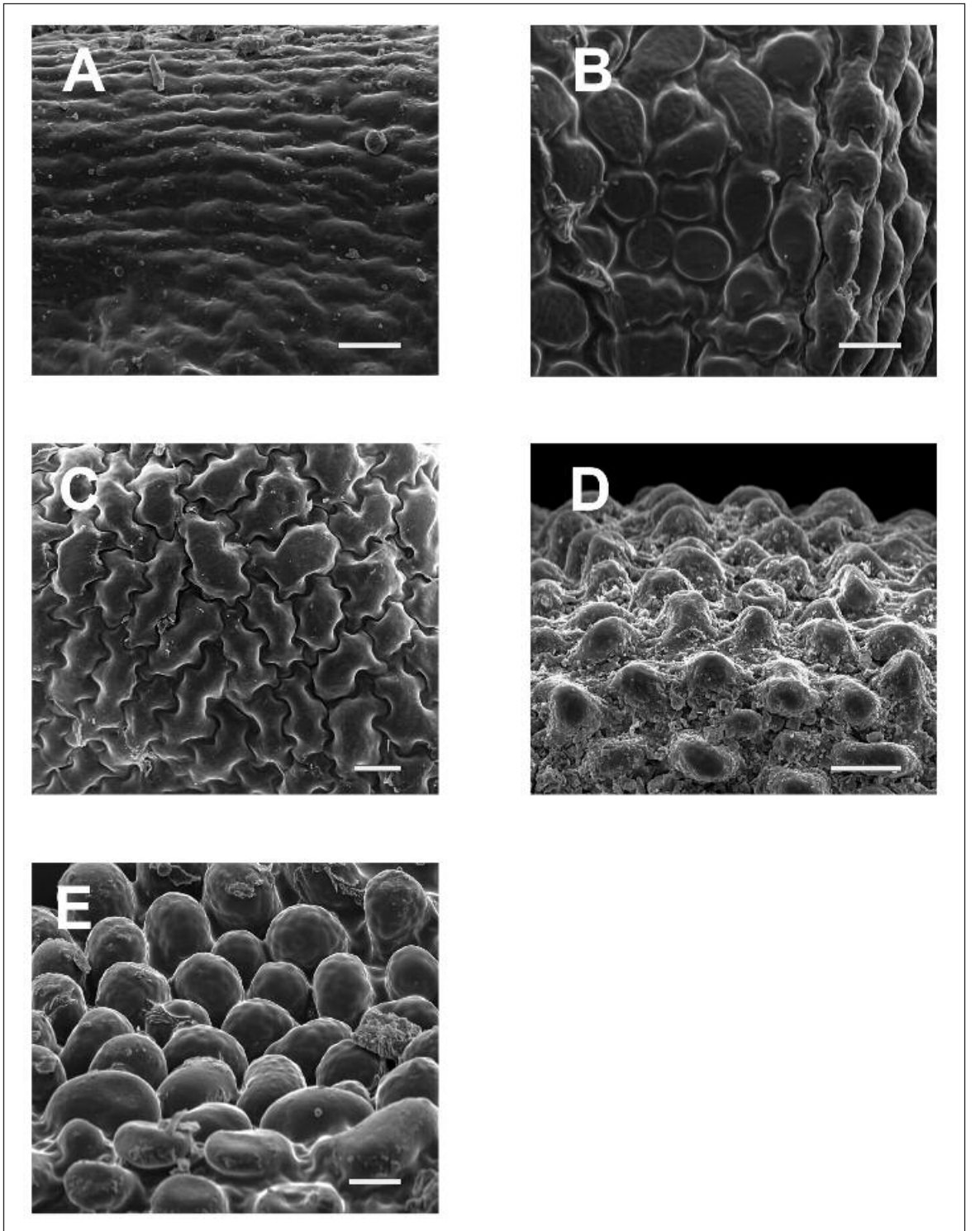

Figure 2. Surface features of *Lithops* seeds. **(A)** Wave-like rugosity, *L. hallii* var. *hallii* (scale bar = 100µm). **(B)** Flat tubercles, *L. dorotheae* (50µm). **(C)** Interlocking tubercles, *L. bella* (50µm). **(D)** Small individual tubercles, *L. naureeniae* (50µm). **(E)** Large individual tubercles, *L. lesliei* subsp. *lesliei* var. *lesliei* (100µm).

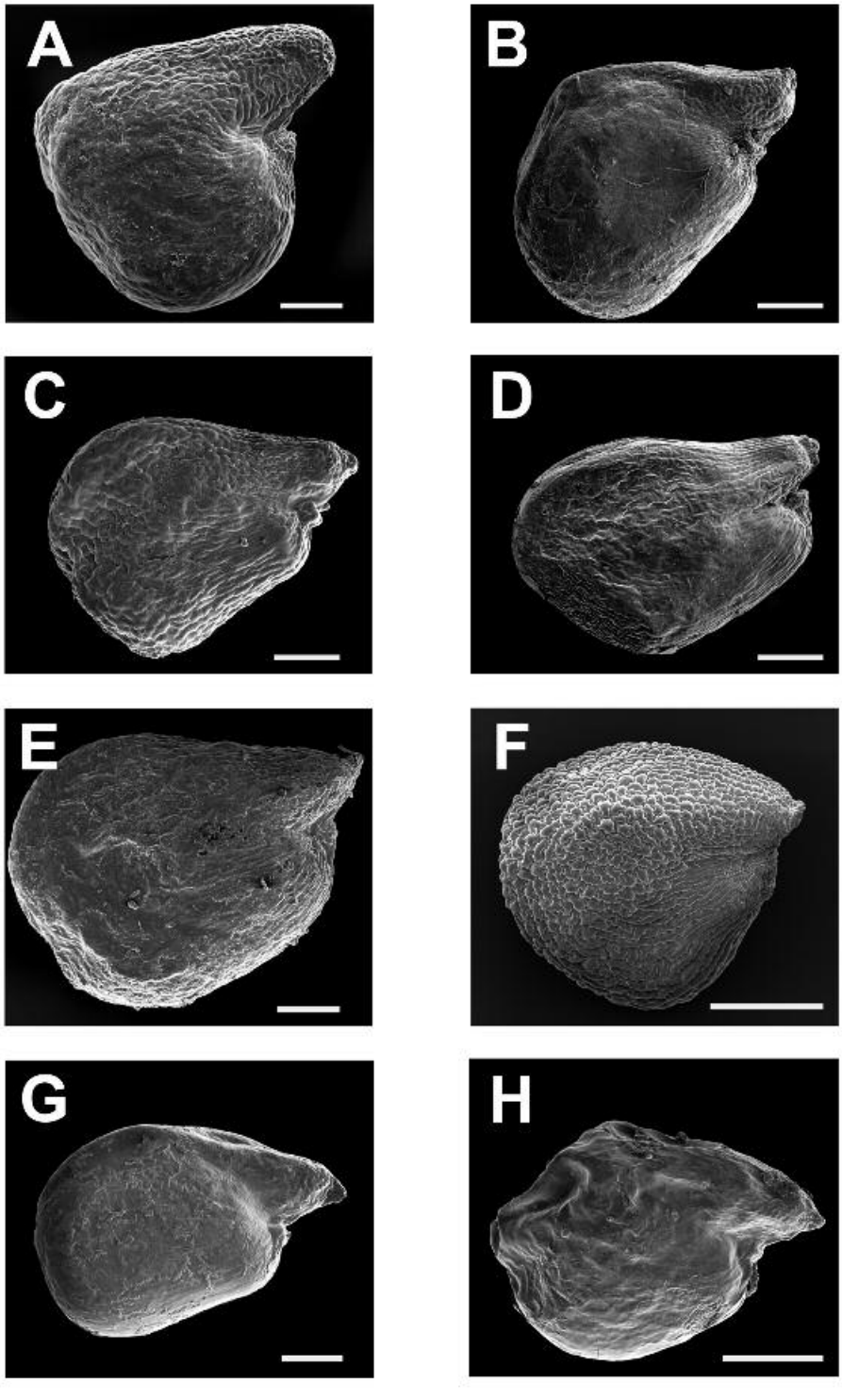

Figure 3. (A) *Lithops amicorum*. **(B)** *Lithops aucampiae* subsp. *aucampiae* var. *aucampiae*. **(C)** *Lithops aucampiae* subsp. *aucampiae* var. *koelemanii*. **(D)** *Lithops aucampiae* subsp. *euniceae* var. *euniceae*. **(E)** *Lithops aucampiae* subsp. *euniceae* var. *fluminalis*. **(F)** *Lithops bella*. **(G)** *Lithops bromfieldii* var. *bromfieldii*. **(H)** *Lithops bromfieldii* var. *glaudinae*. (scale bar = 200μm).

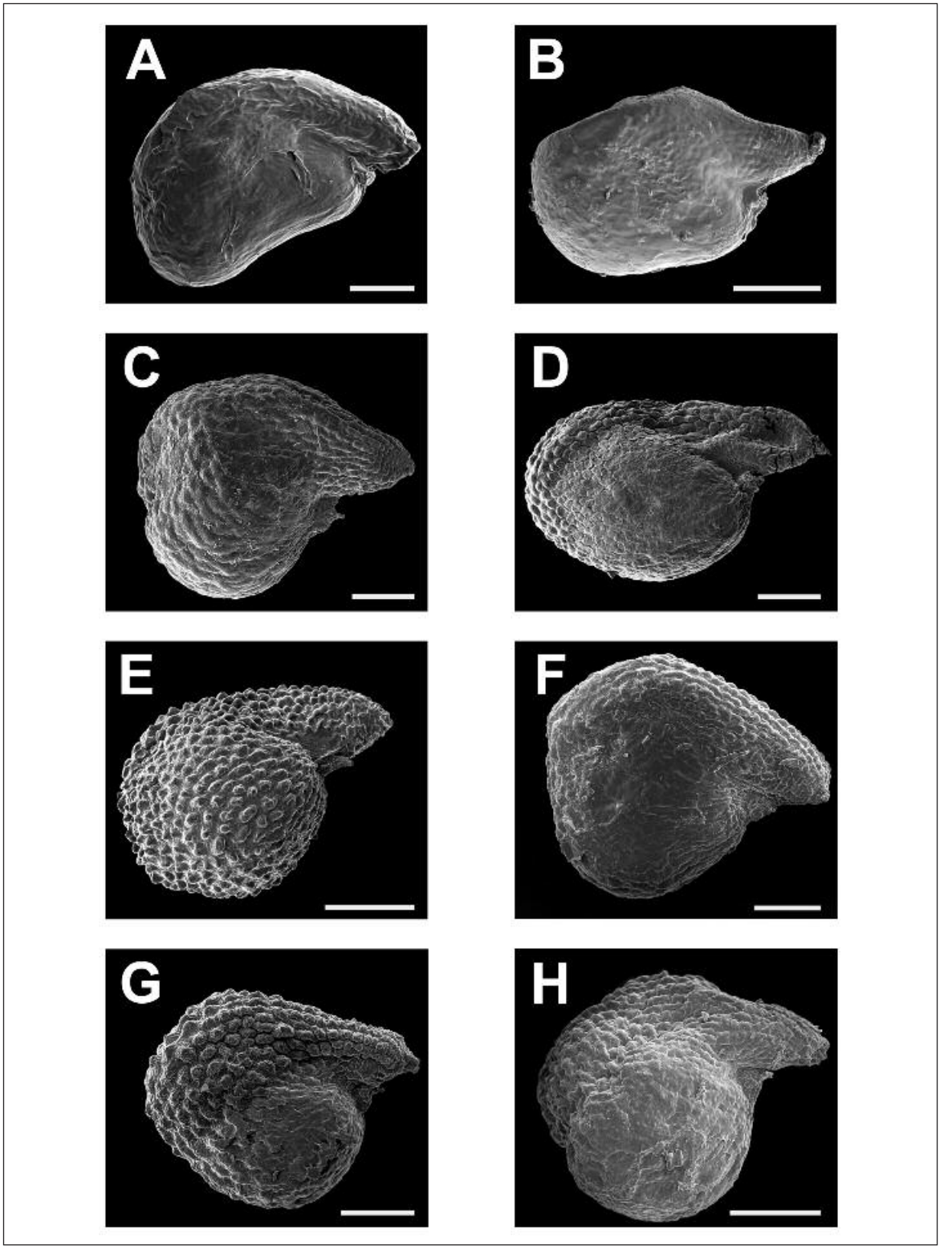

Figure 4. (A) *Lithops bromfieldii* var. *insularis.* **(B)** *Lithops bromfieldii* var. *mennellii.* **(C)** *Lithops coleorum.* **(D)** *Lithops comptonii* var. *comptonii.* **(E)** *Lithops comptonii* var. *weberi.* **(F)** *Lithops dendritica* subsp. *archerae.* **(G)** *Lithops dendritica* subsp. *dendritica.* **(H)** *Lithops dendritica* subsp. *groendrayensis.* (scale bar = 200μm).

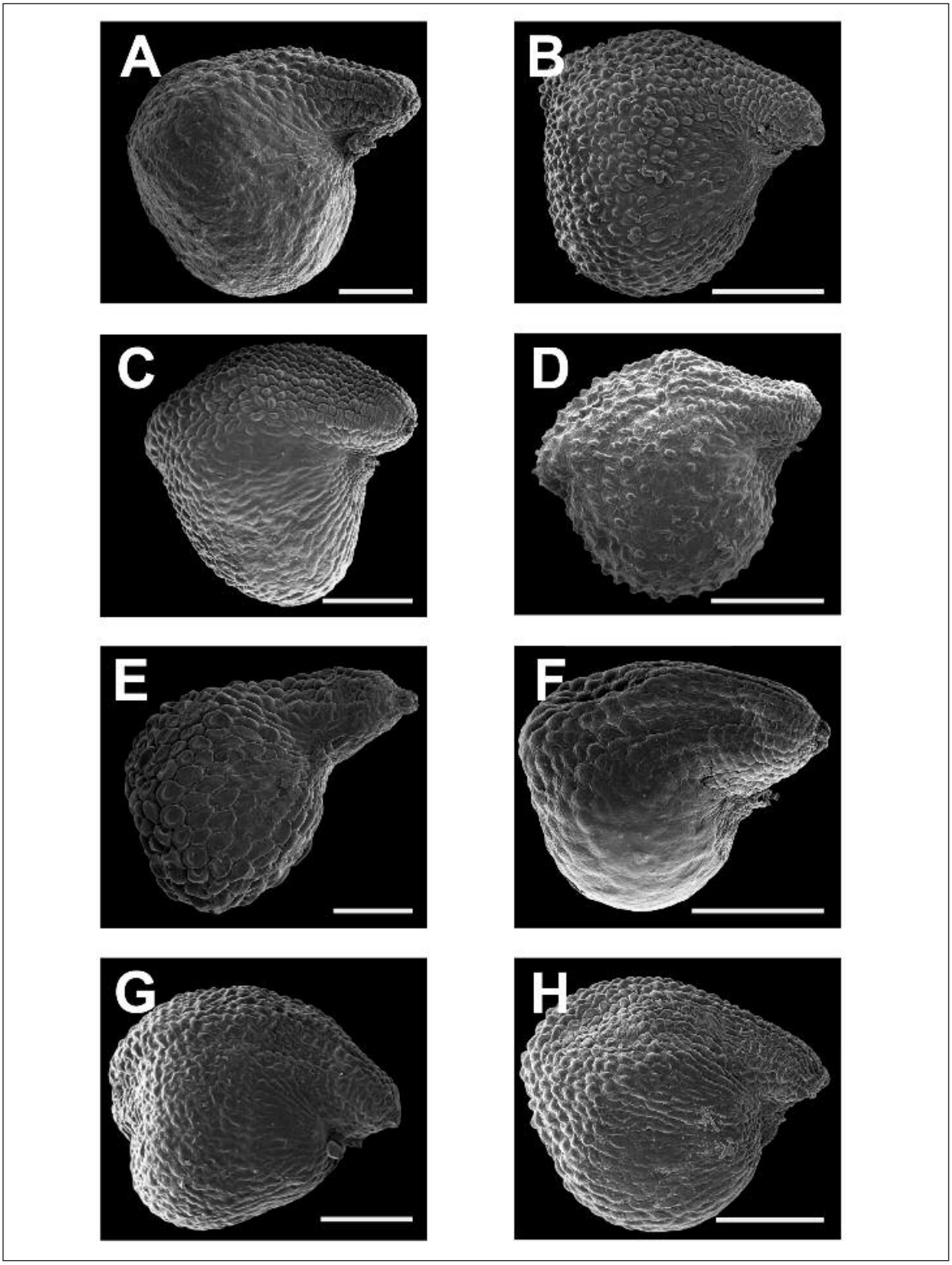

Figure 5. (A) *Lithops dendritica* subsp. *schoemanii.* **(B)** *Lithops dinteri* subsp. *dinteri.* **(C)** *Lithops dinteri* subsp. *frederici.* **(D)** *Lithops dinteri* subsp. *multipunctata.* **(E)** *Lithops divergens* subsp. *amethystina.* **(F)** *Lithops divergens* subsp. *divergens.* **(G)** *Lithops dorotheae.* **(H)** *Lithops eberlanzii* var. *aiaisensis.* (scale bar = 200µm).

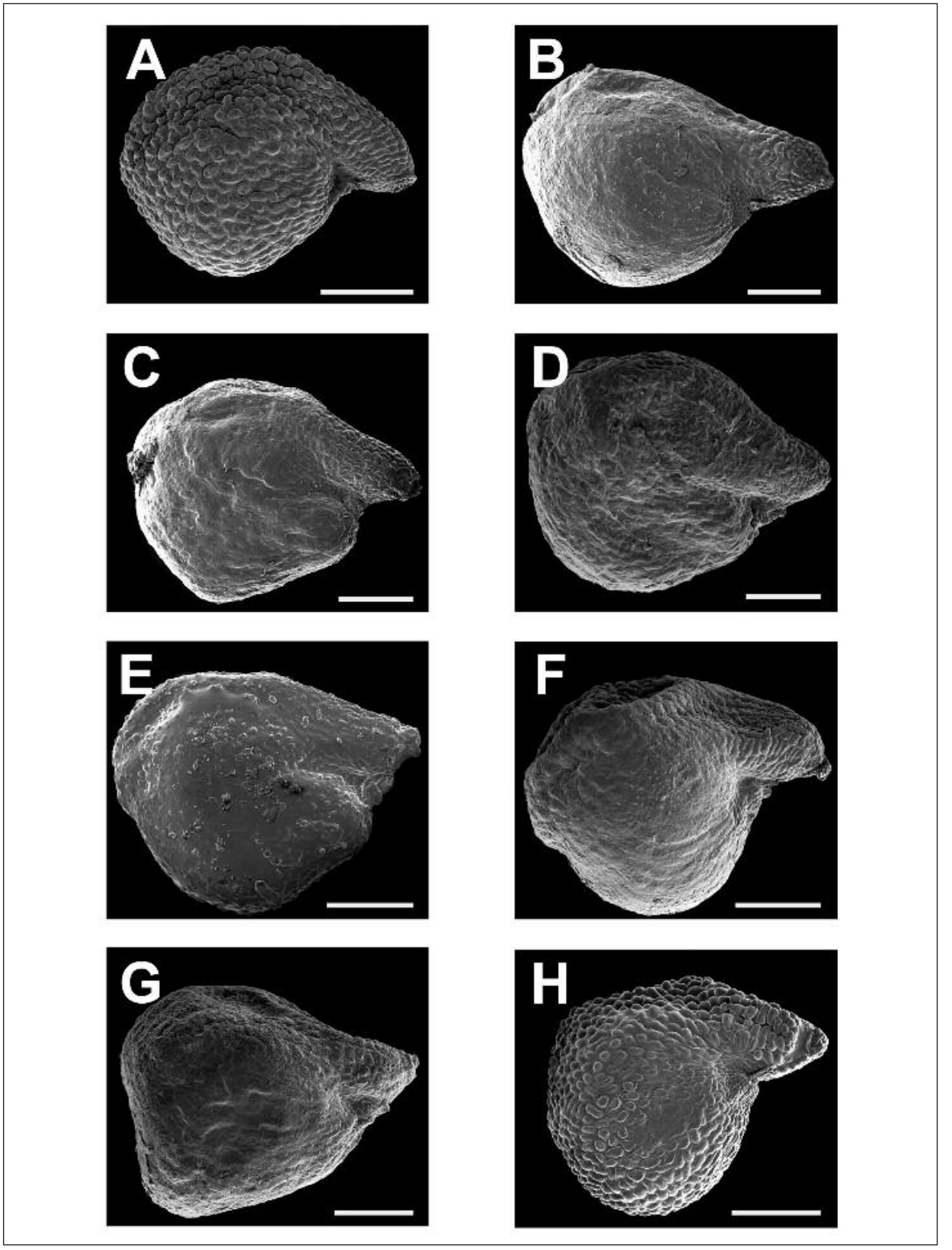

Figure 6. (A) *Lithops eberlanzii* var. *eberlanzii.* **(B)** *Lithops francisci.* **(C)** *Lithops fulviceps* var *fulviceps.* **(D)** *Lithops fulviceps* var. *lactinea.* **(E)** *Lithops fulviceps* var. *laevigata.* **(F)** *Lithops gesinae* subsp. *annae.* **(G)** *Lithops gesinae* subsp. *gesinae.* **(H)** *Lithops geyeri.* (scale bar = 200μm).

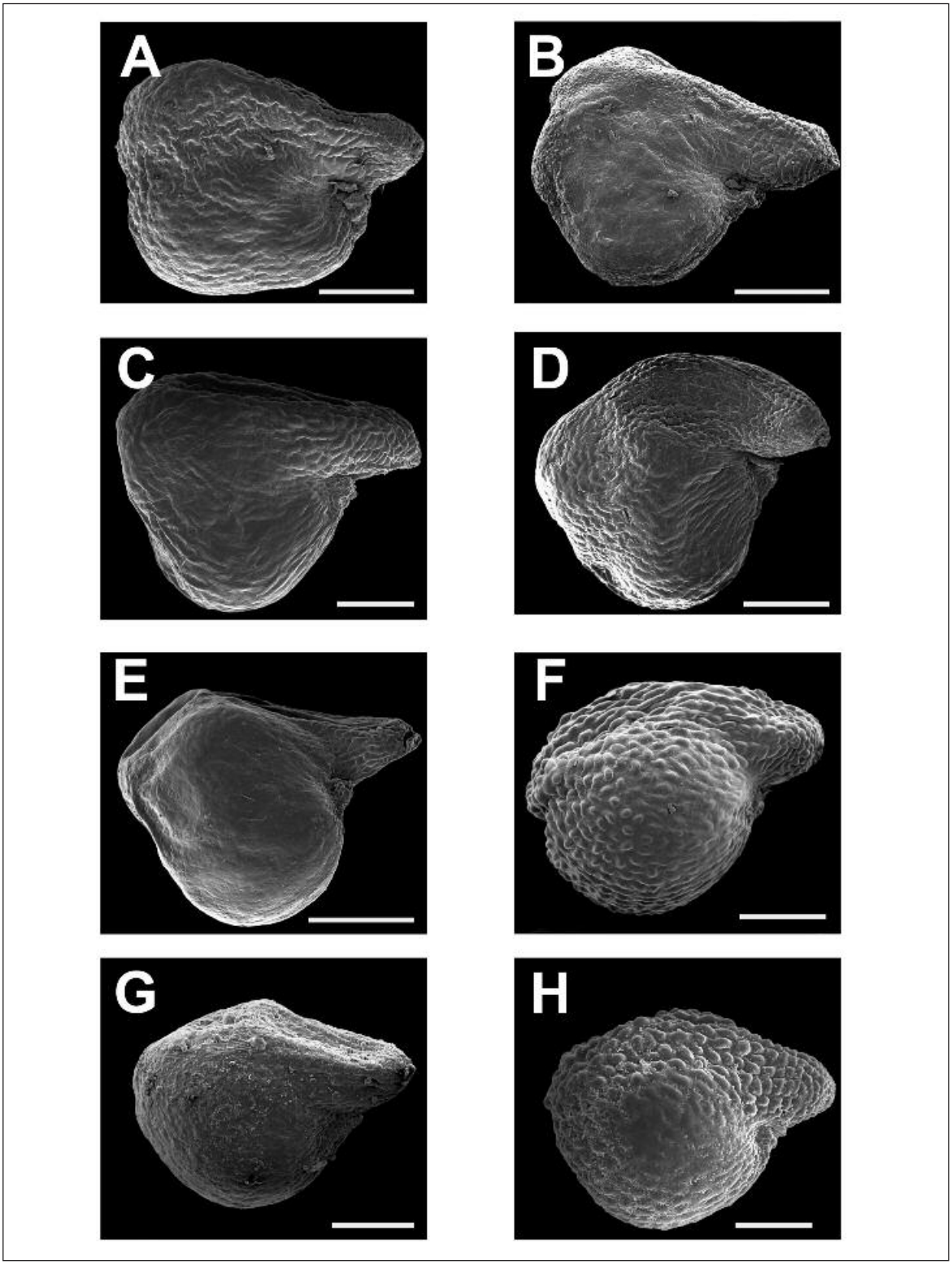

Figure 7. (A) *Lithops gracilidelineata* subsp. *brandbergensis.* **(B)** *Lithops gracilidelineata* subsp. *gracilidelineata.* **(C)** *Lithops gracilidelineata* subsp. *waldroniae.* **(D)** *Lithops hallii* var. *hallii.* **(E)** *Lithops hallii* var. *ochracea.* **(F)** *Lithops helmutii.* **(G)** *Lithops hermetica.* **(H)** *Lithops herrei.* (scale bar = 200µm).

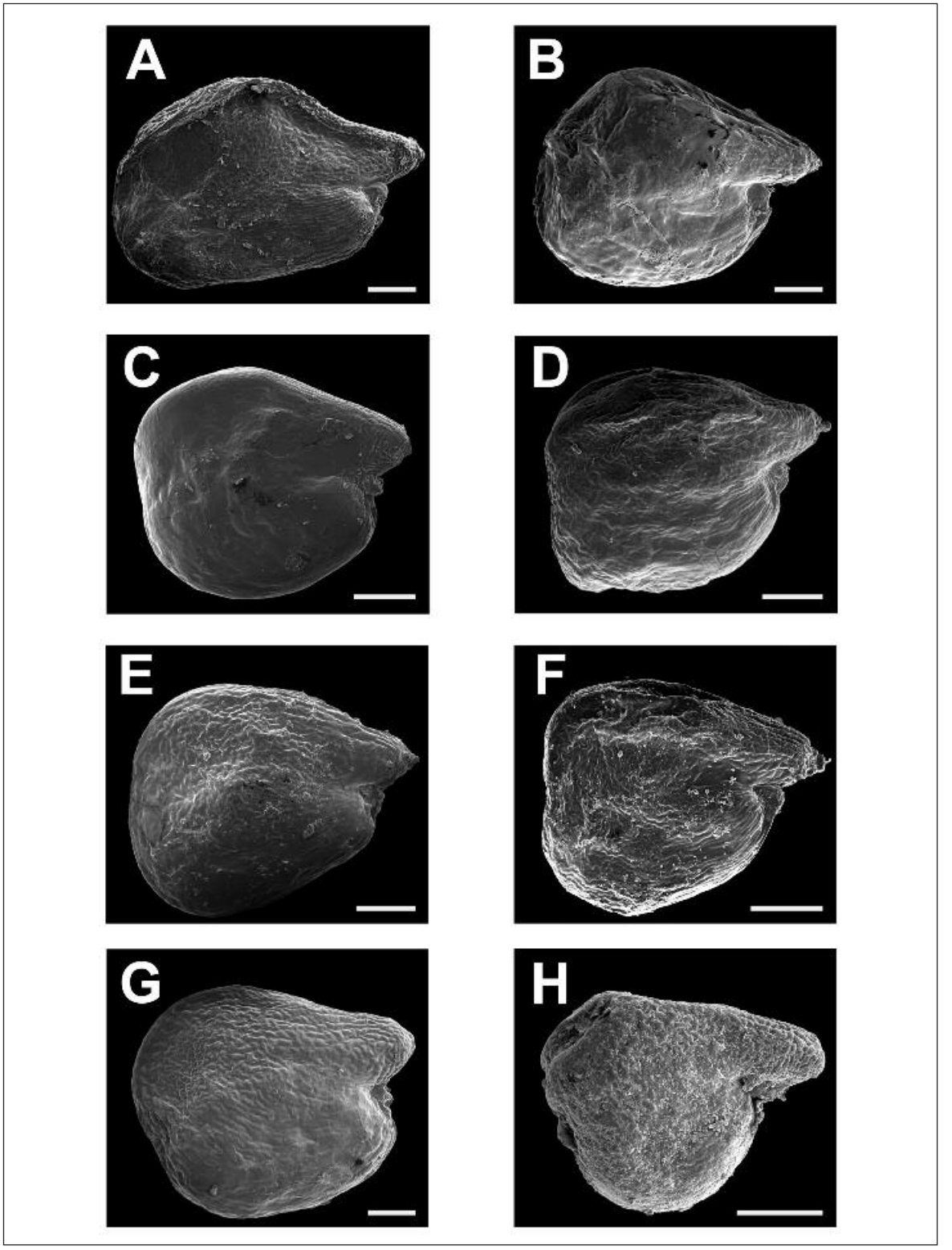

Figure 8. (A) *Lithops hookeri* var. *dabneri*. **(B)** *Lithops hookeri* var. *elephina*. **(C)** *Lithops hookeri* var. *hookeri*. **(D)** *Lithops hookeri* var. *lutea*. **(E)** *Lithops hookeri* var. *marginata*. **(F)** *Lithops hookeri* var. *subfenestrata*. **(G)** *Lithops hookeri* var. *susannae*. **(H)** *Lithops julii* subsp. *fulleri* var. *brunnea*. (scale bar = 200μm).

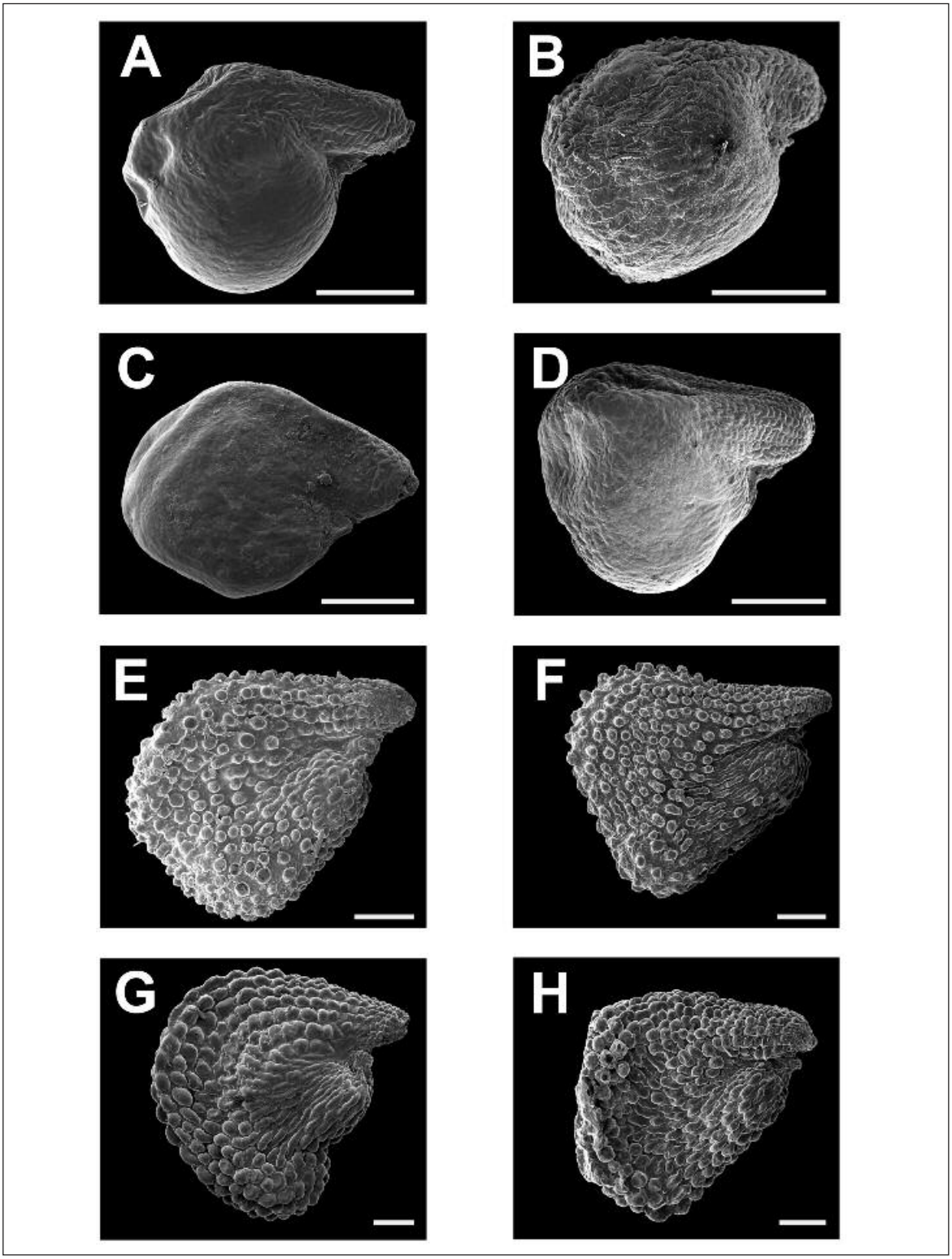

Figure 9. (A) *Lithops julii* subsp. *fulleri* var. *fulleri.* **(B)** *Lithops julii* subsp. *fulleri* var. *rouxii.* **(C)** *Lithops julii* subsp. *julii.* **(D)** *Lithops karasmontana.* **(E)** *Lithops lesliei* subsp. *burchellii.* **(F)** *Lithops lesliei* subsp. *lesliei* var. *hornii.* **(G)** *Lithops lesliei* subsp. *lesliei* var. *lesliei.* **(H)** *Lithops lesliei* subsp. *lesliei* var. *mariae.* (scale bar = 200μm)**.**

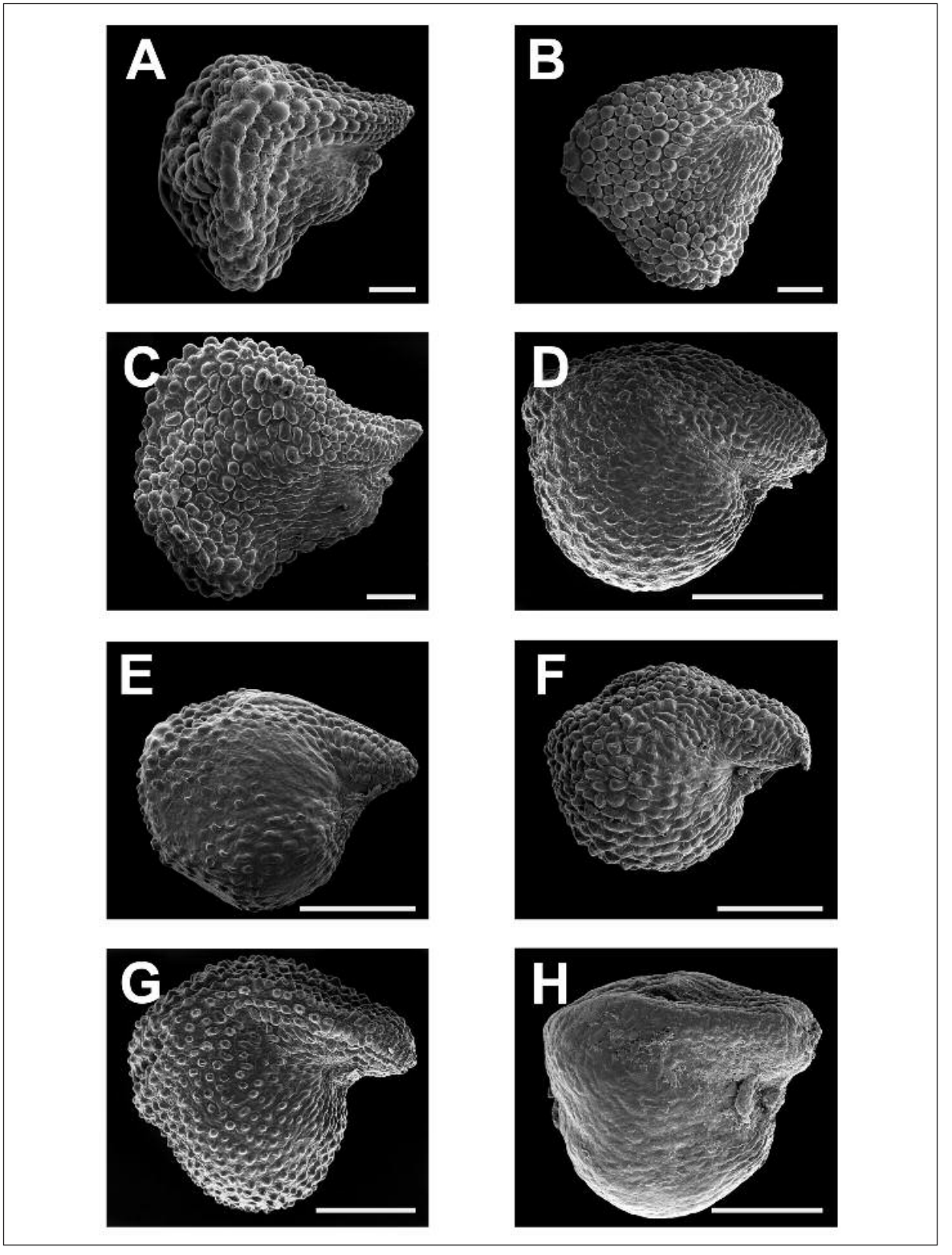

Figure 10. (A) *Lithops lesliei* subsp. *lesliei* var. *minor*. **(B)** *Lithops lesliei* subsp. *lesliei* var. *rubrobrunnea*. **(C)** *Lithops lesliei* subsp. *lesliei* var. *venteri*. **(D)** *Lithops marmorata* var. *elisae*. **(E)** *Lithops marmorata* var. *marmorata*. **(F)** *Lithops meyeri*. **(G)** *Lithops naureeniae*. **(H)** *Lithops olivacea* var. *nebrownii*. (scale bar = 200μm)**.**

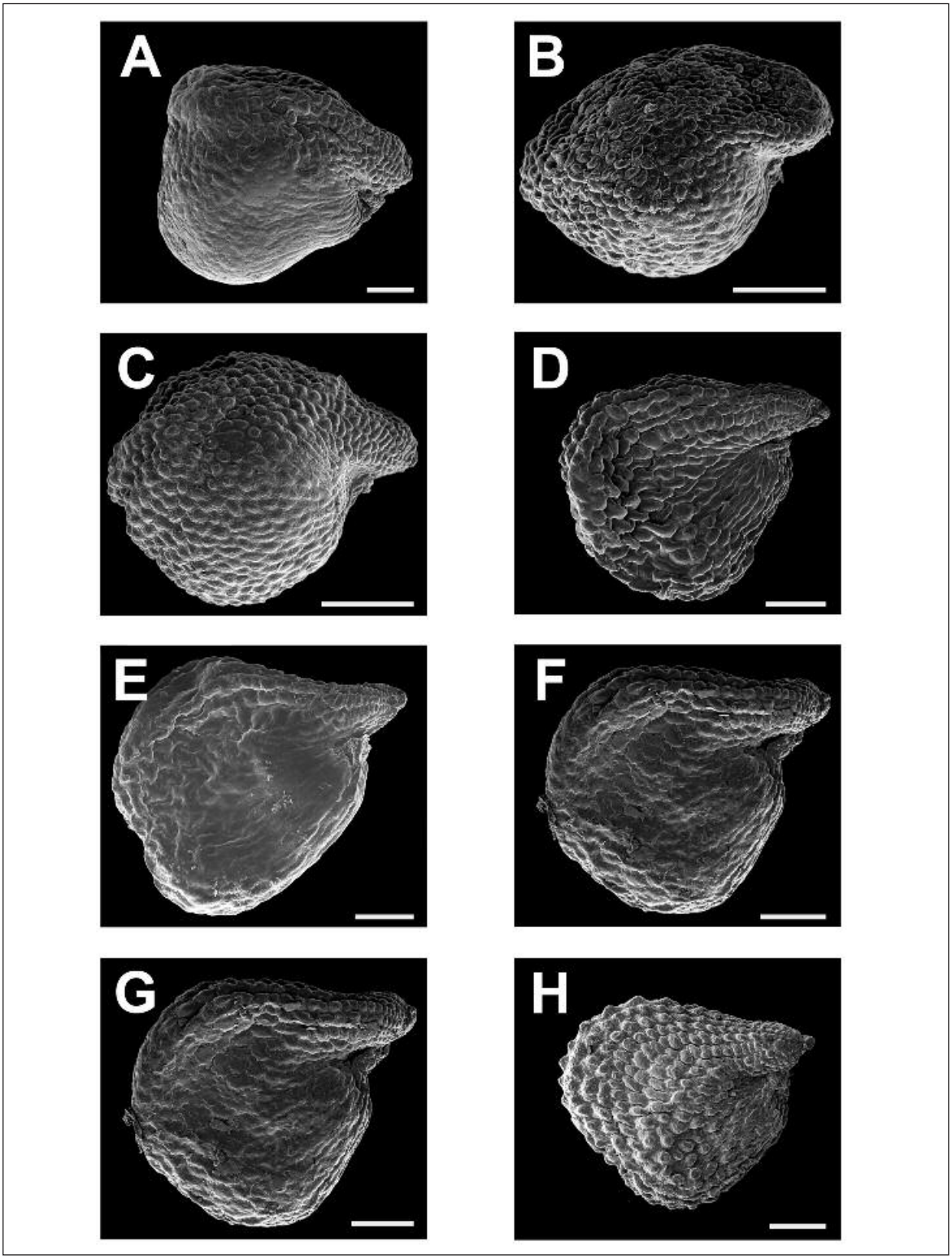

Figure 11. (A) *Lithops olivacea* var. *olivacea.* **(B)** *Lithops optica.* **(C)** *Lithops otzeniana.* **(D)** *Lithops pseudotruncatella* var. *elisabethiae.* **(E)** *Lithops pseudotruncatella* var. *pseudotruncatella* *mundtii-type plants. **(F)** *Lithops pseudotruncatella* var. *pseudotruncatella.* **(G)** *Lithops pseudotruncatella* var. *riehmerae.* **(H)** *Lithops pseudotruncatella* var. *volkii.* (scale bar = 200µm).

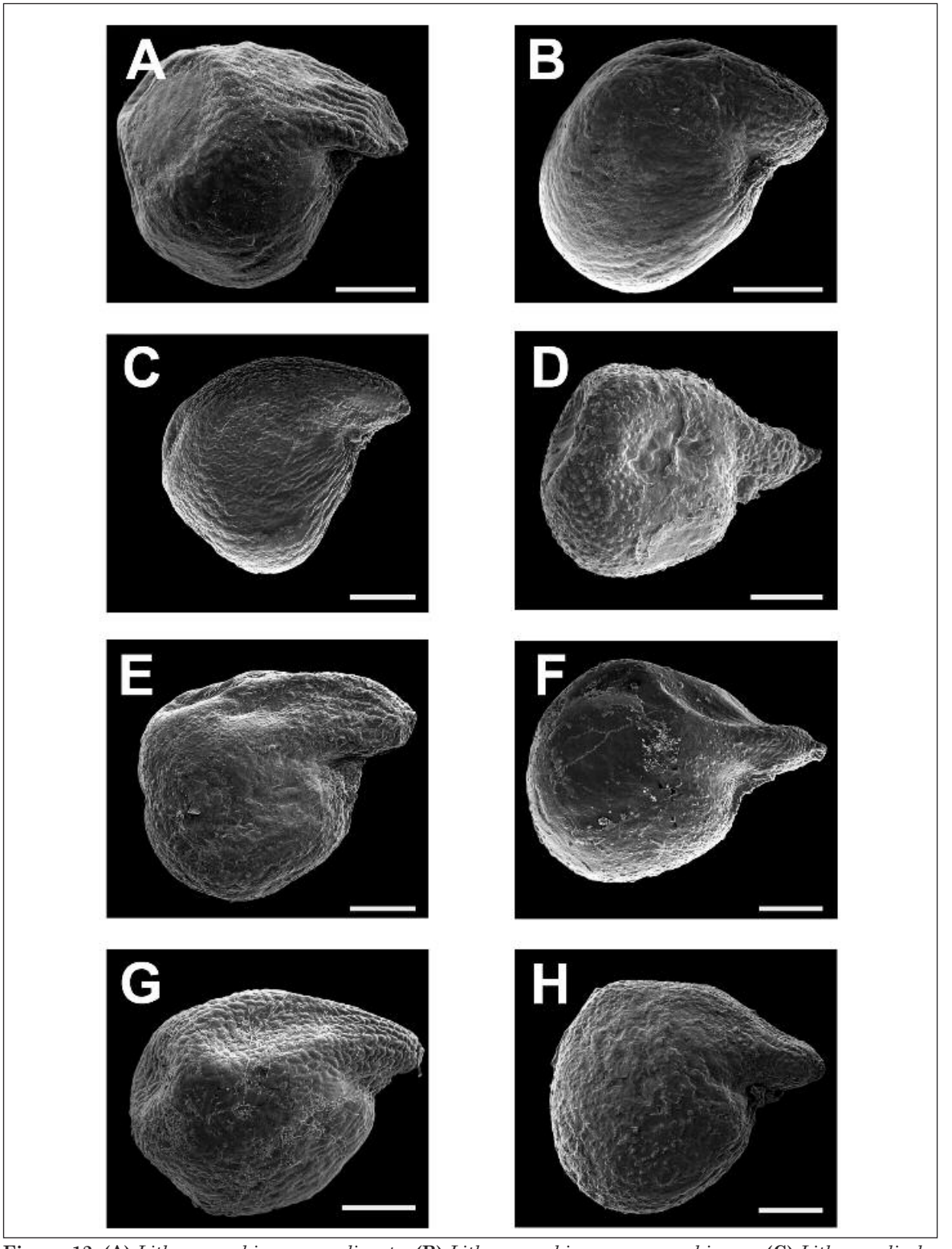

Figure 12. (A) *Lithops ruschiorum* var. *lineata.* **(B)** *Lithops ruschiorum* var. *ruschiorum.* **(C)** *Lithops salicola.* **(D)** *Lithops schwantesii* subsp. *gebseri.* **(E)** *Lithops schwantesii* subsp. *schwantesii* var. *marthae.* **(F)** *Lithops schwantesii* subsp. *schwantesii* var. *rugosa.* **(G)** *Lithops schwantesii* subsp. *schwantesii* var. *schwantesii.* **(H)** *Lithops schwantesii* subsp. *schwantesii* var. *urikosensis.* (scale bar = 200μm).

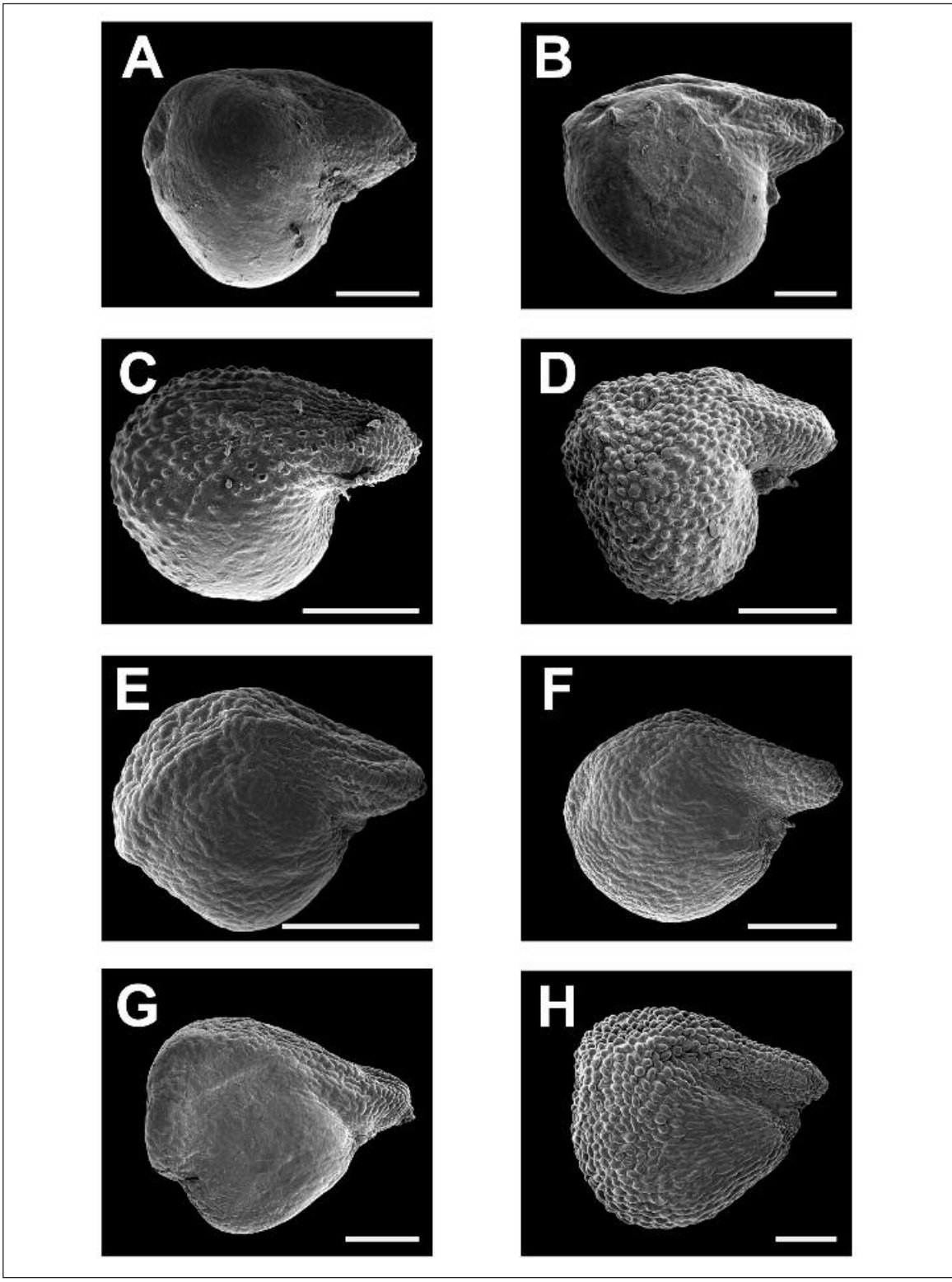

Figure 13. (A) *Lithops terricolor.* **(B)** *Lithops vallis-mariae.* **(C)** *Lithops verruculosa* var. *glabra.* **(D)** *Lithops verruculosa* var. *verruculosa.* **(E)** *Lithops villetii* subsp. *deboeri.* **(F)** *Lithops villetii* subsp. *kennedyi*. **(G)** *Lithops villetii* subsp. *villetii.* **(H)** *Lithops viridis.* (scale bar = 200µm).

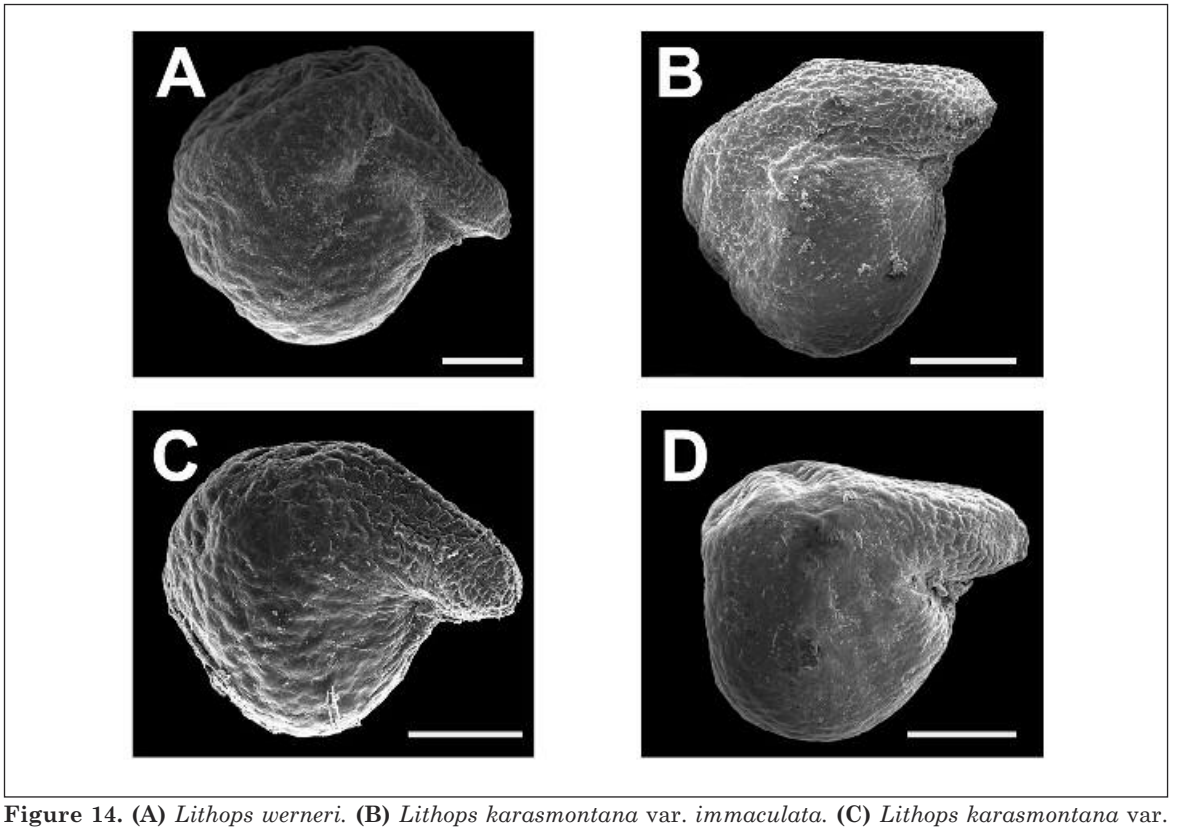

Figure 14. (A) *Lithops werneri.* **(B)** *Lithops karasmontana* var. *immaculata.* **(C)** *Lithops karasmontana* var. *lericheana.* **(D)** *Lithops karasmontana* var. *tischeri.* (scale bar = 200µm.

atively small for the genus). The seeds of var. *amethystina* de Boer (1961) are brown to dark brown in colour with a rounded globe, a thick rostrum and are uniformly covered in large individual tubercles with some showing an interlocking pattern on the ventral part of the globe (Figure 5E). The mean length of seeds of var. *amethystina* is larger at 0.65mm. There is no overlap in the ranges of the size of the seeds (Table 1). Furthermore, the plants have very different growth forms in that var. *divergens* has the characteristic rugose 'frosted glass' leaf surface which is flat or only slightly convex in turgid plants with sharp edges at both the outer and inner margins of the leaf (Figure 15A & B). This is in sharp contrast to the prominent convex leaf surface of var. *amethystina* which is rounded towards the leaf edge and the largely smooth leaf surface even in plants that are not fully turgid (Figure 15C & D). Because of the marked differences in the seeds and the growth forms of these two taxa, they are hereby elevated to subspecies status.

***Lithops dorotheae* Nel (1939):** The closeness of the relationship between *Lithops dorotheae* and the different taxa of *L. dinteri* has often been commented on (see Cole & Cole, 2005; Hammer, 2010). The seeds of *L. dorotheae* have a rounded to partly flattened globe. The wave-like rugosity of the globe merges into flat interlocking tubercles on the crest and rostrum (Figure 5G). This is in stark contrast to the rounded globe of *Lithops dinteri* which is uniformly covered in small individual tubercles (Figures 5B–D). The seeds are yellow brown with a darker brown area around the hilum and measure 0.60mm (Table 1). The difference in seed morphology together with the sharply defined margins and clear rubrications separate *L. dorotheae* from *L. dinteri* and *L. dorotheae* is hereby retained as a standalone species.

***Lithops francisci* (Dinter & Schwantes) N.E.Br. (1925):** These seeds are yellow brown often possessing a brown coloured rostrum and a rounded globe with a smooth surface. There are only a few small flat tubercles at the tip of the medium-length rostrum (Figure 6B). The seeds of *L. francisci* differ slightly from both *L. gesinae* and *L. hermetica* (see Figures 6F–G and 7G) in the extent to which rugosity occurs on the globe and the seeds are much smaller (0.61mm *vs.* 0.73/0.74mm for *L. gesinae* and 0.81mm for *L. hermetica*; Table 1). Although the seed structure probably indicates a close relationship between these three species, the colours of the leaves and their growth forms are very different. *L. francisci* are an overall grey colour and the plants tend to grow tall thus exposing the sides of the plant which is usually below the level of the soil surface. This contrasts with the growth habit of *L. hermetica* where the plants do not grow tall even in cultivation or under low light intensity conditions. *Lithops gesinae* are brown to beige or greenish coloured plants with

subsp. *annae* characteristically being monocephalic. The molecular study of the *Lithops* species of Namibia (Loots, 2019) found there to be some relationship between *L. francisci* and *L. hermetica* but this was not considered a close enough relationship to warrant taxonomic changes. The submission by Jainta (2019) that *L. francisci, L. gesinae* and *L. hermetica* should be regarded as a single species cannot be supported due to the slight differences in seed morphology, structure and size, the differences in tanniniferous idioblast patterns (Cole & Cole, 2005) as well as the vastly different growth forms observed between the species especially in cultivation when the plants can grow to their full potential. [see also *L. gesinae* and *L. hermetica*]

Lithops fulviceps **(N.E.Br.) N.E.Br. (1925):** Three varieties are recognised in this species; var. *fulviceps,* var. *lactinea* Cole (1973) and var. *laevigata* Cole (2006). The seeds of all three are yellow brown with a darker brown rostrum. They are also similar in shape with a flattened globe, but the rugosity pattern of the globe is very smooth in var. *laevigata* (Figure 6E) and smooth to having a wave-like rugosity in var. *fulviceps* (6C) while in var. *lactinea* the entire seed has a wave-like rugosity (6D). The very short rostrum of var. *laevigata* lacks tubercles while the medium length rostrum and crest areas of the other two varieties possess ill-defined interlocking tubercles. The seeds are of a similar size in the range 0.73–0.80mm (Table 1). The observed differences in the seed structure together with the readily recognisable differences in the plants (as described by Cole & Cole (2005) and Cole (2006)), indicates that the observed differences are distinctive enough to retain the varietal status of the three taxa but the differences are not distinctive enough to justify reclassification

Lithops gesinae **de Boer (1955):** The two varieties of this species currently recognised, var. *gesinae* and var. *annae* have different seeds. The seeds of var. *gesinae* have a flattened globe with a wave-like rugosity pattern and some ill-defined tubercles towards the tip of the rostrum (Figure 6G). In contrast, var. *annae* (de Boer) Cole (1956) shows a rounded globe with wave-like rugosity and much more prominent tubercles in rows on the crest and rostrum (Figure 6F). The seeds of var. *gesinae* are also much larger than those of var. *annae* (Table 1) although Hammer (2010) mentioned that one colony of var. *gesinae* (SH2003) have seeds that measure only 0.68mm which is much smaller than the mean of 0.82mm as measured during this study. Furthermore, these two varieties are very different in habit and growth form both in habitat and cultivation. In var. *gesinae* multi-headed plants are the norm (Figure 16A). By contrast, var. *annae* are largely monocephalic (Figure 16B) and in a colony of more than 500 plants only single headed plants could be seen. Furthermore, the varieties have different tanniniferous idioblast patterns (Cole & Cole, 2005) and var. *annae* is much less convex with larger individual heads than var. *gesinae* when fully turgid. Because of these significant differences the varieties are hereby elevated to subspecies status. [also see *Lithops francisci* and *Lithops hermetica*].

Lithops geyeri **Nel (1943):** The seeds of *L. geyeri* are brown, have a rounded globe with a long rostrum and are uniformly covered in medium sized densely packed individual tubercles (Figure 6H). The seeds measure 0.61mm in length (Table 1). They are morphologically (except for their size) nearly identical to those of the other members of the group of *Lithops* with diverging leaves i.e., *L. meyeri, L. helmutii,* and *L. herrei.* Although Jainta (2019) argued that *L. geyeri* and *L. herrei* cannot be separated in the wild, they are easily separated when in flower since *L. geyeri* has large flowers (25.3–30.5mm ø) whilst the flowers of *L. herrei* are consistently much smaller (14.0–18.6mm ø). The growth form of these two species are also very different, especially when in cultivation. *L. geyeri* are usually double headed plants while *L. herrei* form large, multi-headed clusters both in habitat and in cultivation.

Lithops gracilidelineata **Dinter (1928):** This species is separated into subsp. *brandbergensis* (de Boer) Cole (1963) and subsp. *gracilidelineata* with the latter comprising of var. *gracilidelineata* and var. *waldroniae* de Boer (1963). The seeds of all three of these taxa are different (Figures 7A–C). Subsp. *brandbergensis* have seeds with a flattened globe and a heavy wave-like rugosity merging into the interlocking tubercles towards the crest and along the short rostrum where the tubercles merge into flat individuals at the tip of the rostrum (Figure 7A). The seeds are the largest of this species measuring 0.80mm in length. The small (0.65mm) seeds of var. *gracilidelineata* have a rounded globe usually with a very prominent eminence and have a smooth to minimally wave-like rugose surface with only a few large flat tubercles towards the tip of the long rostrum (Figure 7B). The seeds of var. *waldroniae* are 0.76mm in length and have a rounded globe with fine wave-like rugosity on the surface and occasionally a few small, flat tubercles on the long rostrum (Figure 7C). The distinction between var. *gracilidelineata* and var. *waldroniae* on morphological grounds is described as rather tenuous (Cole & Cole, 2005) being based essentially on the depth of the valleys on the surface of the leaves and thus a matter of degree. However, since the flowers of var. *waldroniae* are much smaller, the seeds are consistently larger and there is a clear difference in the structure of the seeds between these two taxa, the varietal status of *waldroniae* is justified. The seeds of subsp. *brandbergensis* are distinctive enough and if the bright coloured leaves of the plants are considered, these plants should be retained as a valid subspecies.

Lithops hallii **de Boer (1957):** The two varieties of this species, var. *hallii* and var. *ochracea* (de Boer) Cole (1962), possess marked differences in seed morphology. The rounded globe of var. *hallii* has a wave-like rugosity merging into flat faintly interlocking

tubercles towards the crest and on the thick, rostrum (Figure 7D). The round globe of var. *ochracea* is very smooth with much fewer rugose tubercles towards the tip of the rostrum (Figure 7E). The seeds of both varieties are yellow brown with the rostrum being a darker brown colour. The plants from Cole colony C087 called **salicola reticulata* are believed to be a natural hybrid between *L. hallii* and the reticulata form of *L. salicola*. They have seeds which resemble those of *L. hallii* with a thick and long rostrum. The faintly interlocking tubercles also occur in *L. salicola*, but the seeds are more uniformly wave-like rugose and the rostrum is very short.

***Lithops helmutii* L. Bolus (1933):** The seeds of this species are 0.54mm in length, yellow brown, have a rounded globe and are uniformly covered in medium sized individual tubercles with a medium length rostrum (Figure 7F). The eminence is prominent in most seeds.

***Lithops hermetica* D.T. Cole (2000):** The seeds of *L. hermetica* have a rounded globe with a uniformly smooth to slightly wave-like rugosity and only a few ill-defined flat tubercles at the tip of the rostrum and around the hilum (Figure 7G). The seeds are yellow brown with only the rostrum tip and a small area around the hilum a darker brown colour. The mean length of individual seeds is 0.70mm. [also see *L. francisci* and *L. gesinae*].

***Lithops herrei* L. Bolus (1932):** The seeds of *L. herrei* are light brown to brown, have a rounded globe and are uniformly covered in medium sized tubercles which are slightly flattened to form a rugose wave-like pattern on the ventral part of the globe (Figure 7H). The rostrum is of medium length and the seeds measure 0.60mm. [also see *L. optica* and *L. geyeri*].

***Lithops hookeri* (Berger) Schwantes (1908):** At present seven varieties are recognised in *L. hookeri*. The sizes of the seeds of all these varieties varies between 0.89–1.13mm (Table 1). The seeds of var. *hookeri,* var. *elephina* (Cole) Cole (1970) and var. *lutea* (de Boer) Cole (1964) are similarly shaped with the globe being rounded to marginally flattened and with a short rostrum (Figures 8B–D). Varieties *hookeri* and *elephina* are uniformly very smooth with only ill-defined flat tubercles at the tip of the rostrum. By comparison, var. *lutea* shows a marginally more wave-like rugosity on the globe but is also smoother than the other four varieties. These three varieties were also considered by Cole & Cole (2005) to form a group which are closer related to each other than to any of the other varieties. The seeds of the other four recognised varieties all have more pronounced flattened globes with a more obvious wave-like rugosity merging into more prominent waves towards the crest and rostrum (Figures 8A, E–G). Varieties *marginata* (Nel) Cole (1964)*, susannae* (Cole) Cole (1970) and *dabneri* (L. Bolus) Cole (1965) have identical seeds and were also considered to form a closely related group by Cole & Cole (2005). However, they are not morphologically similar enough to be regarded as a single taxon. The seeds of var. *subfenestrata* are the most rugose showing ill-defined interlocking tubercles on the sides of the seeds and neat rows of small tubercles towards the rostrum tip (Figure 8F). The plants are also readily distinguished from the other varieties, having a 'polished' leaf surface, and are thus morphologically easily recognised as a separate variety. The tanniniferous idioblast pattern of all the varieties is very similar, only differing slightly in the subjectively determined density of the cells and is thus not of any taxonomic value in this case. Although the distinction between the seven varieties of *L. hookeri* is tenuous, especially if only the leaf surface morphology and colour is considered, there is not enough convincing evidence to change the *status quo* and all the varieties are retained for the present.

***Lithops julii* (Dinter & Schwantes) N.E.Br. (1925):** Two subspecies, subsp. *julii* and *fulleri* (N.E.Br.) Fearn (1927) are currently recognised in *L. julii* with subsp. *fulleri* further divided into three varieties, *brunnea* de Boer (1962) , *fulleri* and *rouxii* (de Boer) Cole (1964). The small seeds of all the taxa are reasonably similar in length between 0.53–0.60mm, but they differ in structure. The surface of the globe of subsp. *julii* is smooth and only at the tip of the rostrum are ill-defined flat tubercles present (Figure 9C). The seeds of var. *brunnea* and var. *fulleri* are similar to each other with the globe having a smooth wave-like rugosity, increasing in rugosity towards the crest and forming rows of tubercles on the long rostrum (Figures 8H, 9A). The seeds of var. *rouxii* are very different in that the rounded globe and medium sized rostrum is uniformly covered in medium sized individual tubercles (Figure 9B). This difference was also noted by Jump (1981) but not acknowledged by Cole (1988), Cole & Cole (2005) or Jainta (2019) in assessing the status of this taxon. The marked differences in the seeds of subsp. *julii* and subsp. *fulleri* as well as the morphologically constant feature of a 'lip smear' on both sides of the flower fissure in subsp. *julii,* justifies the continued recognition of these two subspecies and does not support the proposal by Jainta (2017, 2019) that *Lithops julii* should be a single species with no lower taxa recognised. In subsp. *fulleri* the recognition of var. *brunnea* is also justified as these plants are morphologically easily identified by their leaf colour both in the field and in cultivation. Var. *rouxii* is hereby elevated to subspecies status based on the marked differences in seed structure from other taxa in the species, combined with the morphologically consistent feature of the 'stitching pattern' on the edges of the leaves, despite the face surface patterns being variable. Furthermore, the tanniniferous idioblast patterns of subsp. *julii* are very different from those of subsp. *fulleri* and subsp. *rouxii* (the latter two are identical) (Cole & Cole, 2005) which supports the argument for the divisions as set out above.

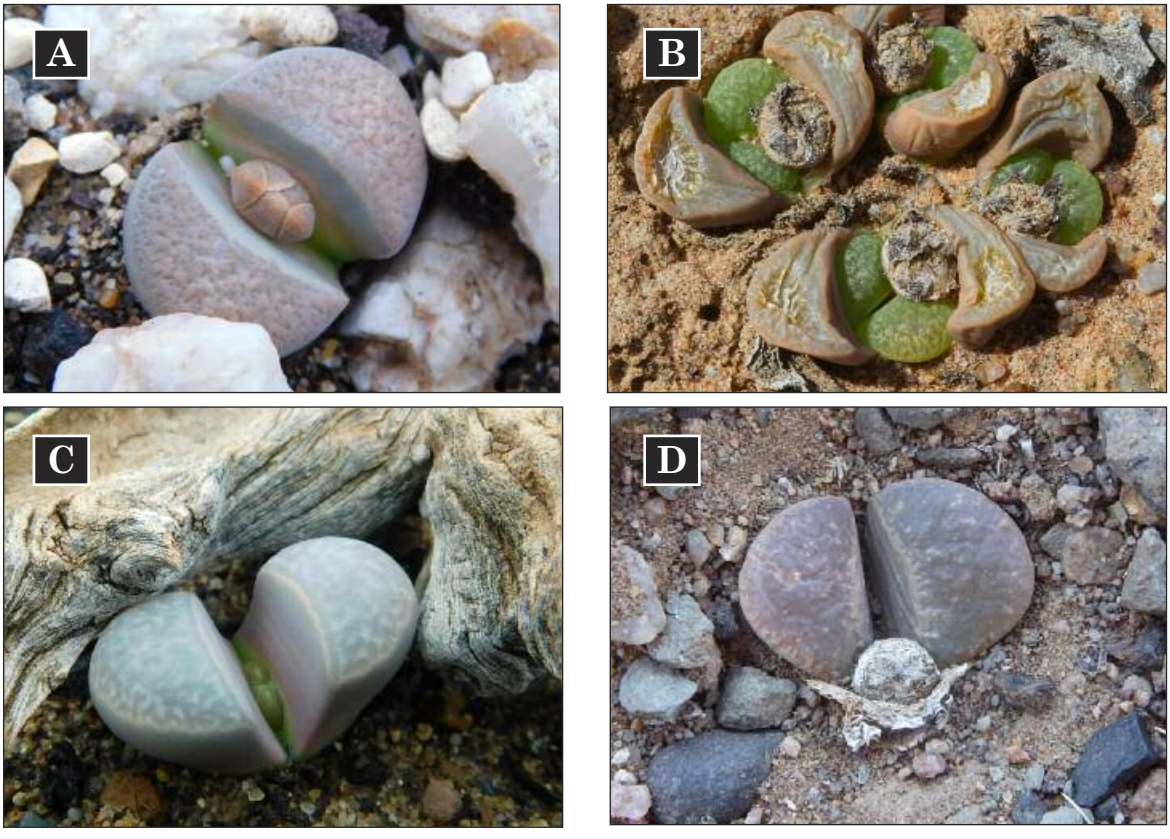

Figure 15. (A) *Lithops divergens* subsp. *divergens* in cultivation. **(B)** *Lithops divergens* subsp. *divergens* with new leaves emerging in habitat **(C)** *Lithops divergens* subsp. *amethystina* in cultivation. **(D)** *Lithops divergens* subsp. *amethystina* in habitat.

***Lithops karasmontana* (Dinter & Schwantes) N.E.Br. (1920):** The seeds of *L. karasmontana* have a rounded globe with a medium to long rostrum showing a bi-rugosity pattern. The globe has a minimal wave-like rugosity with small flat tubercles arranged in rows on the rostrum. The seeds are 0.57mm in length. At present subsp. *karasmontana* is represented by five varieties, var. *aiaisensis* (de Boer) Cole (1964), *karasmontana, immaculata* Cole (2012), *lericheana* Dinter & Schwantes) Cole (1925) and *tischeri* Cole (1973). The seeds of the latter four varieties are all identical (cf. Figure 9D & Figure 14B–D). This together with the observation that colonies of var. *karasmontana* contain plants indistinguishable from vars. *immaculata, lericheana* and *tischeri*., suggests an over classification and these varieties should no longer be recognised (also see Earlé, 2014). In the recent molecular study on Namibian *Lithops* Loots (2019) found the genetic variation between the varieties of *L. karasmontana* to be very low (1%) and concluded that these varieties should not be recognised. In contrast, var. *aiaisensis* has seeds that are markedly different from those of *L. karasmontana* (c.f. Figures 5H & 9D). They are, however, nearly identical to those of subsp. *eberlanzii* (Figure 6A) and the plants also morphologically closely resemble the *erniana witputzensis type plants of this subspecies. Furthermore, the tanniniferous idioblast pattern of var. *aiaisensis* is identical to that of subsp. *eberlanzii* (Dinter & Schwantes) Cole (1925) and this variety is thus probably more closely related to subsp. *eberlanzii*.

Subsp. *eberlanzii* was recently combined with subsp. *bella* by Loots *et al.* (2019) into a single subspecies under *L. karasmontana* on the evidence of some genetic similarities. However, the seeds of subsp. *eberlanzii* (Figure 6A) are readily distinguished from *L. karasmontana* (Figure 9D) as well as from subsp. *bella* (Figure 3F). Subsp. *eberlanzii* occurs in a strip from just north of Aus in the Namib desert southwards to about 50km north of Rosh Pinah. Over this distribution there are three distinct forms of this taxon. The leaves of the northern form have a face surface showing mostly thin rubrication markings (Figure 17A) while the form south of Aus (*erniana type) has very prominent and usually broad leaf surface markings (Figure 17B). At the southern edge of its distribution the larger plants are usually without any facial markings (*erniana witputzensis type) (Figure 17C) The seeds of all three of these forms are identical, having a rounded globe with the seeds uniformly covered in medium sized individual tubercles. Because of highly distinctive seeds, *Lithops eberlanzii* (Dinter & Schwantes) N.E.Br. is hereby elevated to full species status. The former *L. karasmontana* var. *aiaisensis* is

Figure 16. (A) *Lithops gesinae* subsp. *gesinae* in habitat in the Namtib Mountains, Namibia. **(B)** *Lithops gesinae* subsp. *annae* in habitat near Helmeringhausen, Namibia.

also hereby transferred to *L. eberlanzii* as a variety as discussed above (Figure 17D).

The seeds of subsp. *bella* (as currently recognised) have a unique structure with a rounded to anterior flattened globe covered uniformly in interlocking tubercles and a very short rostrum (Figure 3F). At 0.66mm in length they are larger than any of the other taxa formerly classified under *L. karasmontana.* The seeds are very different in structure from both *L. karasmontana* and the current subsp. *eberlanzii* (cf. Figures 3F, 9D & 6A). As previously mentioned, Loots *et al.* (2019) combined subsp. *bella* and subsp. *eberlanzii* as a result of genetic similarities while Jainta (2019) also combined these two taxa reasoning that 'small differences in the markings are obviously the result of adaptations to the different substrates in which they live'. The present study of seed structure does not support these views and subsp. *bella* is hereby reinstated to full species status as originally described: *Lithops bella* N.E.Br. (1922) without combining it with other taxa.

***Lithops lesliei* (N.E.Br.) N.E.Br. (1912):** In this species two subspecies, subsp. *lesliei* and *burchellii* Cole (1988) are currently recognised. The large seeds of all the *L. lesliei* taxa are nearly identical being dark brown and having a deep rounded or indented globe often with an anterior 'pout' and a short rostrum. In some individual seeds the crest is very rounded giving the seed a fan-like appearance. The seeds are immediately recognisable, being uniformly covered in large individual tubercles (Figure 2E) in rows that mostly merge to form prominent ridges towards the 'pout' (Figures 9E–H & 10A–C). Some seeds of var. *lesliei* display a pronounced interlocking of the tubercles on the side of the seeds, a feature rarely seen across the genus (see *L. pseudotruncatella* below). The seeds of subsp. *burchellii* and var. *hornii* de Boer (1966) have slightly smaller tubercles that are less densely packed (Figures 9E–F). These two taxa also have the smallest seeds of the species at 0.96 and 1.02mm, respectively while all the other taxa have seeds larger than 1.05mm (Table 1). Although seed structure *per se* does not distinguish between taxa of this species, all the varieties of subsp. *lesliei* are easily recognisable based on the morphology and colour of the leaves as described by Cole & Cole (2005) and these varieties are therefore retained.

The unique leaf facial pattern of dark slate grey to black thin lines and dots extending over the leaf edges and the overall grey colour of subsp. *burchellii* make these plants easy to distinguish from the rest of the subsp. *lesliei* varieties except for var. *venteri* which is also largely grey and of which this subspecies was once considered to be a local form (Cole & Cole, 2005). Although the recognition of subsp. *burchellii* at this level is somewhat tentative, based largely on leaf pattern and geographical isolation (Cole & Cole, 2005), there is not enough convincing evidence at present to change the *status quo* and this subspecies is thus retained.

***Lithops marmorata* (N.E.Br.) N.E.Br. (1920):** The seeds of the two varieties of *L. marmorata,* var. *marmorata* and var. *elisae* (de Boer) Cole (1961) are different in their presentation of tubercles on the surface of the seed (Figures 10D–E). The seeds have a rounded globe usually with a prominent eminence. The flat tubercles on the globe of var. *elisae* are arranged uniformly in a wave-like pattern over the seed becoming organised in rows towards the tip of the short rostrum (Figure 10D). On the seeds of var. *marmorata* the tubercles are mostly distributed individually and generally lack the wave-like arrangement (Figure 10E). In both varieties the seeds are yellow brown with the rostrum a darker brown. As each of the tubercles have a dark brown tip, the seeds appear spotted. Although there is some overlap in the facial patterns of individual plants between the var. *marmorata* and var. *elisae* in habitat colonies (Cole & Cole, 2005; Hammer, 2010; Earlé *et al.,* 2017), there are colonies that are pure

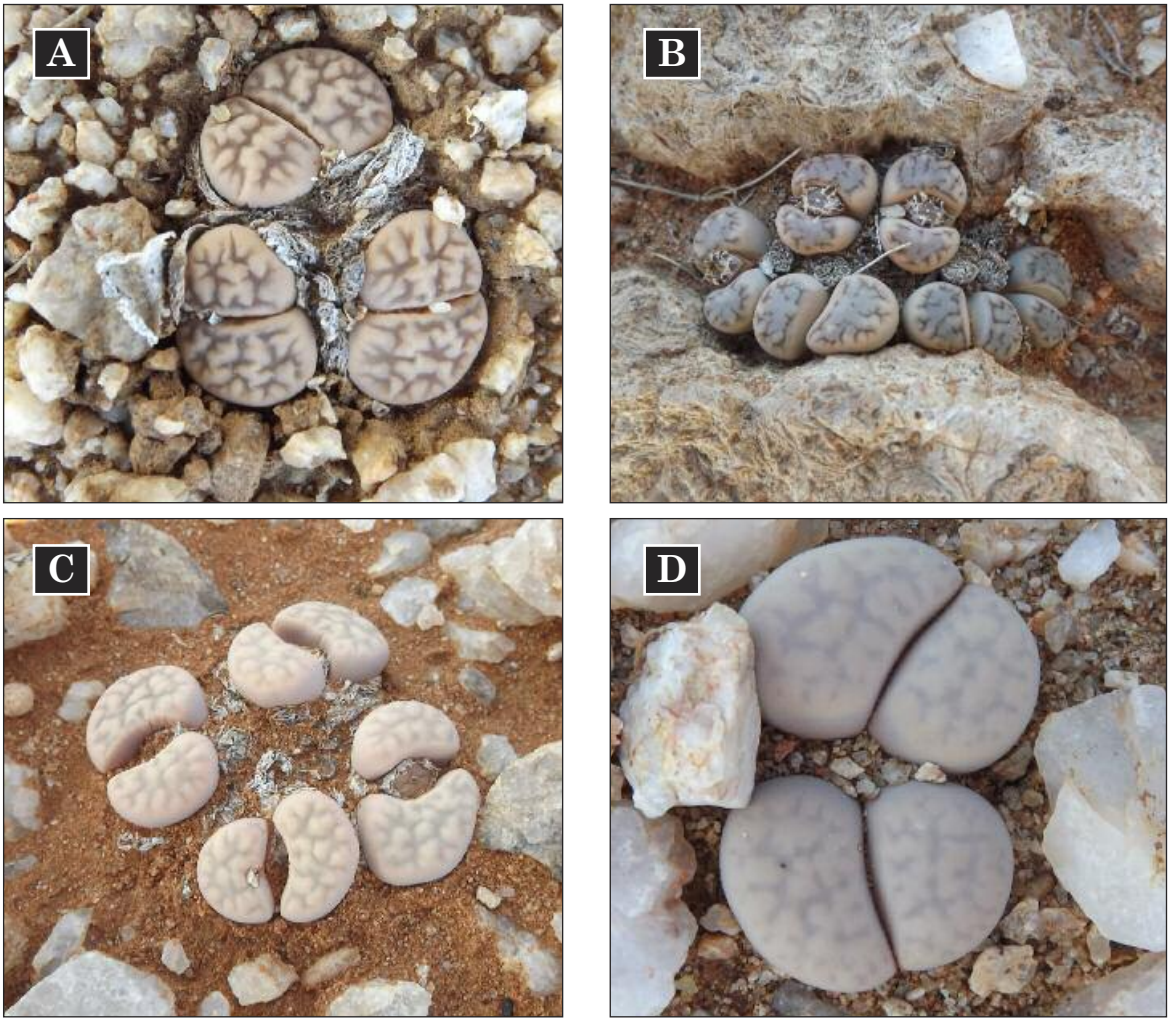

Figure 17 (A) *Lithops eberlanzii* var. *eberlanzii,* the northern form from the Halenberg, Namibia in habitat. (B) *Lithops eberlanzii* var. *eberlanzii,* the well-marked *erniana form in habitat south of Aus, Namibia. (C) *Lithops eberlanzii* var. *eberlanzii,* the pale *erniana witputzensis form in habitat at Witpeuts, north of Rosh Pinah. (D) *Lithops eberlanzii* var. *aiaisensis,* in habitat east of Ai-Ais, Namibia.

stands of var. *elisae.* When var. *elisae* plants are grown in cultivation to their full potential they are readily distinguished from var. *marmorata* as they invariably grow asymmetric pairs of leaves with one leaf smaller and usually lower than the larger leaf. The seeds of both varieties are amongst the smallest of the genus (Table 1). Because of the differences in the morphology of the plants and seed structure, the two varieties are maintained.

***Lithops meyeri* L. Bolus (1932):** The seeds of *L. meyeri* have a rounded globe and are uniformly covered in medium sized individual tubercles which are arranged in rows on the rostrum (Figure 10F). Most of the seeds are a light brown to brown in colour with a dark brown rostrum. The tips of each tubercle are a darker colour than the rest of the back-ground and this gives the seeds a spotted appearance. The papilla is often retained on the tip of the rostrum of the small seeds.

***Lithops naureeniae* D.T. Cole (1980):** The seeds of this species possess a rounded globe with a prominent eminence and are uniformly covered in small individual tubercles neatly arranged in rows on the crest and towards the tip of the short rostrum (Figure 10G). The globe is yellow-brown to light brown with the rostrum a darker brown colour. The tips on the tubercles are dark brown and against the lighter brown background, this gives the seeds a spotted appearance.

***Lithops olivacea* L. Bolus (1929):** Although the seeds of both varieties of *L. olivacea* are small (Table 1) and yellow brown, there are differences in their fine structure. Var. *olivacea* displays bi-rugosity with a rounded globe and prominent eminence. The globe rugosity is smooth to wave-like merging into prominent tubercles on the crest and the very short rostrum (Figure 11A). This contrasts with seeds of var. *nebrownii* Cole (1988) where the entire seed surface is uniformly

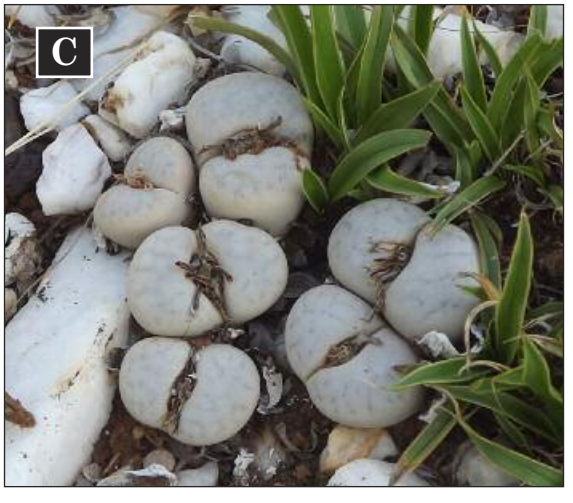

Figure 18 (A) *Lithops pseudotruncatella* subsp. *pseudotruncatella* var. *pseudotruncatella* in habitat south of Windhoek, Namibia. (B) *Lithops pseudotruncatella* subsp. *pseudotruncatella* var. *riehmerae* in habitat near Windhoek, Namibia. (C) *Lithops pseudotruncatella* subsp. *volkii* in habitat south of Windhoek, Namibia

smooth to faintly wave-like rugose (Figure 10H). The reddish-brown colouration of the plants with the characteristic deep fissures of var. *nebrownii* morphologically distinguish these plants from var. *olivacea*. That these two varieties should be maintained is supported by their markedly different seed structure.

***Lithops optica* (Marloth) N.E.Br. (1910):** The light brown to brown coloured seeds of this species have a rounded globe and a medium length rostrum. The globe has flat tubercles arranged in a wave-like fashion that merge into medium sized individual tubercles towards the crest and rostrum (Figure 11B). Loots *et al.* (2019) reported a close genetic relationship between *L. optica* and *L. herrei* concluding that *L. herrei* should be absorbed under *L. optica*. The seeds of these two species are similar which would help confirm this relationship (c.f. Figures 7H & 11B). Furthermore, the seed capsules of these two species are very similar in that they both have a characteristic dark red line around the capsule just below the rim which is unique in the genus. However, the two species have different coloured flowers, with the flowers of *L. herrei* a yellow (often dark) with a white centre, while *L. optica* has white flowers often with a pink flush. It is obvious that there is a gradient of morphological forms in *L. optica* from the typical smallish open-windowed plants in the northern populations through to the 'maculate form' in the southern populations. The latter are larger, with islands on the windows and more closely resemble *L. herrei*. The seeds of the northern populations are larger (0.64mm; Table 1) than those of the southern 'maculata form' (0.55mm; Hammer, 2010). Despite the seemingly close relationship of these two species, they are retained here as separate species mainly because of differences in flower colouration, patterns of tanniniferous idioblasts (Cole & Cole, 2005) and their growth habits.

***Lithops otzeniana* Nel (1937):** The seeds have a rounded globe with a prominent eminence and a medium long rostrum. They are uniformly covered in medium sized tubercles which form waves on the seed globe and neat rows towards the tip of the rostrum (Figure 11C). The seeds are yellow brown to brown with the rostrum a slightly darker brown colour. The tips of the tubercles are dark brown giving the seeds a spotted appearance. The seeds measured during this

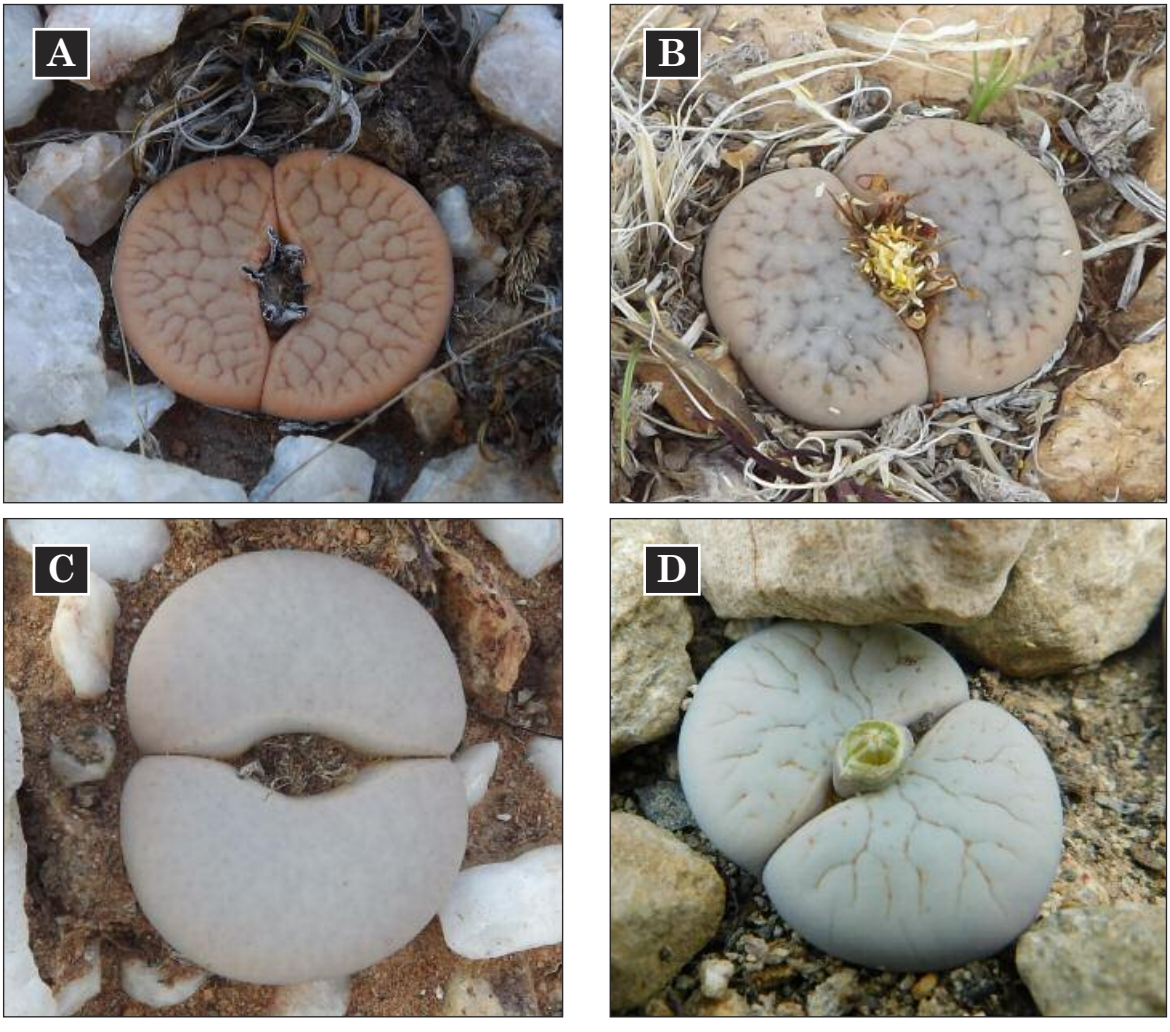

Figure 19 (A) *Lithops dendritica* subsp. *dendritica* in habitat near Nauchas, Namibia. (B) *Lithops dendritica* subsp. *archerae* in habitat in the Namib-Naukluft Park, Namibia. (C) *Lithops dendritica* subsp. *groendrayensis* in habitat near Karanas, Namibia. (D) *Lithops dendritica* subsp. *schoemanii* in habitat at the Namib-Naukluft Mountains, Namibia.

study were larger (0.65mm) than the value (0.55mm) given by Hammer (2010).

***Lithops pseudotruncatella* (Berger) N.E.Br. (1908):** At present this species is divided into six subspecies with subsp. *pseudotruncatella* containing three varieties. The diversity in both the structure and size of the seeds of the different taxa does not, however, support their current classification. Plants of *L. pseudotruncatella* typically form multi-headed clusters both in habitat and cultivation (Figure 18A) except for var. *riehmerae* which are usually double-headed plants. The seeds of all the varieties of subsp. *pseudotruncatella* have flat but mostly prominent tubercles often arranged in waves on a slightly flattened seed globe and merging into larger tubercles on the crest and rostrum of the seed (Figures 11D & F–G). On the side of the globe, close to the crest, there is an area where the tubercles are of the interlocking type. The northern var. *elisabethiae* (Dinter) de Boer & Boom (1933) has the most prominent tubercles (Figure 11D) while in the eastern populations, the *mundtii-type plants, the tubercles on the globe are the least prominent (Figure 11E). Although the seeds of var. *riehmerae* Cole (1987) (Figure 11G) are identical to those of var. *pseudotruncatella*, the plants are consistently both smaller and greyer in colour, forming double-headed plants (Figure 18B) which are confined to one small population. This is therefore considered enough to warrant retention of this variety in the absence of evidence to the contrary. The patch of interlocking tubercles on the sides of the seeds are visible in all subsp. *pseudotruncatella* seeds examined but the seeds of subsp. *volkii* (Schwantes ex de Boer & Boom) Cole (1961) lack these and have prominent tubercles uniformly covering the seeds instead (Figure 11H). These differences in the seed structure and the easily

recognisable bluish-white plants (Figure 18C) alongside their isolated, one population status is enough to retain these plants as a subspecies of *L. pseudotruncatella.*

The seeds of the other four currently recognised subspecies of *L. pseudotruncatella,* namely subsp. *archerae* (de Boer) Cole (1967)*, dendritica* (Nel) Cole (1946)*, groendrayensis* (Jacobsen) Cole (1961) and *schoemanii* Earlé & Uijs (2019) do not support their placement in *L. pseudotruncatella*. The seeds of these four taxa are all smaller than *L. pseudotruncatella* seeds and in the case of subsp. *dendritica* and subsp. *groendrayensis*, the seeds are 25–30% smaller (0.63 and 0.64mm *vs.* 0.87mm; Table 1). Their seeds have a rounded globe (*vs.* the flattened globe of all other *L. pseudotruncatella* taxa) and show a marked bi-rugosity structure of the seed surface. A wave-like rugosity of the globe is common to all four subspecies as is the merging of this into an area of more prominent tubercles on the crest and rostrum (Figures 4G–H). In subsp. *schoemanii* the tubercles are less prominent (Figure 5A) and only present on the rostrum. The similarity of the seeds of these subspecies appears to indicate that they are closely related as was found in the genetic study of Loots *et al.* (2019). The geographical ranges of subsp. *dendritica* and subsp. *groendrayensis* meet at a few colonies just south of Rehoboth, Namibia. In these colonies the plants of subsp. *dendritica* are all smaller that subsp. *groendrayensis* while the hybrids are again much larger than any of these two subspecies (Earlé & Schoeman, 2012) probably indicating hybrid vigour. Although the plants in some colonies of subsp. *dendritica* are mostly red brown in colour, other colonies (e.g. Cole colonies C384 and C245) contain mostly plants that are grey or greyish brown and thus morphologically resembling subsp. *groendrayensis* more closely but for the smaller size of the individual plants. The other two subspecies, subsp. *archerae* (Figure 19B) and *schoemanii* (Figure 19D) occur much further south and are readily separated from subsp. *dendritica* (Figure 19A) and *groendrayensis* (Figure 19C) based on differences in leaf morphology and in the case of subsp. *schoemanii,* the unique calcrete habitat and very large size of the plants (Earlé & Uijs, 2019). Considering the above, subsp. *dendritica* is hereby restored to full species status: *Lithops dendritica* Nel (1946) with four subspecies, namely subsp. *archerae, dendritica, groendrayensis* and *schoemanii*.

***Lithops ruschiorum* (Dinter & Schwantes) N.E.Br.(1925):** The seeds of the two varieties of this species are identical except that the size of var. *ruschiorum* is much smaller at 0.64mm while var. *lineata* (Nel) Cole (1946) seeds are 0.78mm long. The rounded globe is smooth to faintly wave-like rugose with flat individual tubercles on the short, thick rostrum (Figures 12A–B). In both varieties the globe of the seed is light brown (sometimes mainly brown in var. *lineata*) with the crest and rostrum being a dark brown. The characteristic leaf colour of var. *lineata* together with the difference in seed size and the slight difference in the tanniniferous idioblast patterns of these two varieties warrant that they are retained as separate varieties.

***Lithops salicola* L. Bolus (1936):** The rounded globe of the seeds of *L. salicola* has a wave-like rugosity merging to faint interlocking waves on the crest and short rostrum (Figure 12C). The seeds are yellow brown with the rostrum being a darker brown colour. The seeds are different from *L. hallii* (Figures 7D–E) whose *salicola reticulata form is regarded as a natural hybrid with *L. salicola* and which has a seed size intermediate between those of *L. hallii* and *L. salicola* (*L. hallii* 0.61mm, – *L. hallii* *salicola reticulata 0.66mm, – *L. salicola* 0.76mm). [also see *L. hallii*]

***Lithops schwantesii* Dinter (1928):** Two subspecies of *L. schwantesii* are currently recognised. Subsp. *gebseri* (de Boer) Cole (1964) is extinct at the type locality where a long-term reintroduction programme is ongoing (Earlé *et al*., 2017). Subsp. *schwantesii* is further divided into four readily identifiable varieties, var. *marthae* (Loesch & Ticher) Cole (1936)*, rugosa* (Dinter) de Boer & Boom (1928)*, schwantesii* and *urikosensis* (Dinter) de Boer & Boom (1928) (Earlé *et al.,* 2019). This study has discovered that the seed globe is rounded to marginally flattened in all the *L. schwantesii* taxa (Figures 12D–H). The surface of the seeds in the globe area has a smooth to slightly wave-like rugosity merging into irregular rows of flat tubercles on the crest of some individual seeds of var. *schwantesii* and on the rostrum in all the taxa. Subsp. *gebseri* has the smallest seeds (0.77mm) with the varieties of subsp. *schwantesii* being slightly larger (0.79–0.84mm). This evidence showing that the seeds of the lower taxa are nearly identical suggests a close relationship which was also indicated by the genetic studies of Loots (2019). Despite an occasional overlap of the features on the upper leaf surface of the plants from different colonies, the lower taxa are easily separated morphologically, and the *status quo* is thus maintained. The putative relationship between var. *marthae* and *L. dinteri* was first suggested by Fearn (1970). This was rejected by Jump (1981) as the markedly tuberculate seeds of *L. dinteri* (see Figures 5B–D) are very much smaller (0.55mm) than those of the largely smooth to wave-like rugose seeds of var. *marthae* (0.79mm; Figure 12E). The recent suggestion by Jainta (2017, 2019) that var. *marthae* should be reclassified as *L. dinteri* is not supported by the current study.

***Lithops terricolor* N.E.Br. (1922):** The rounded globe has a smooth surface with very indistinct rugosity towards the tip of the very thick rostrum (Figure 13A). The seeds are a yellow-brown colour with a brown rostrum and measure 0.56mm. However, the 'Prince Albert form' has somewhat smaller seeds at 0.51mm according to Hammer (2010).

Table 1. Seeds sizes of *Lithops* taxa measured in this study and compared to Hammer (2010).

Lithops taxon	Mean seed size (mm)	Range (mm)	n	Mean seed size (Hammer 2010)
L. amicorum	0.69	0.60–0.71	50	No data
L. aucampiae subsp. *aucampiae* var. *aucampiae*	0.98	0.92–1.10	50	0.95
L. aucampiae subsp. *aucampiae* var. *koelemanii*	0.94	0.92–0.97	40	0.94
L. aucampiae subsp. *euniceae* var. *euniceae*	0.97	0.96–0.99	30	0.95
L. aucampiae subsp. *euniceae* var. *fluminalis*	0.99	0.97–1.01	30	1
L. bella	0.66	0.64–0.69	100	0.64
L. bromfieldii subsp. *bromfieldii* var. *bromfieldii*	0.73	0.70–0.79	40	0.75
L. bromfieldii subsp. *bromfieldii* var. *glaudinae*	0.73	0.73–0.74	30	0.74
L. bromfieldii subsp. *bromfieldii* var. *insularis*	0.82	0.80–0.87	30	0.8
L. bromfieldii subsp. *bromfieldii* var. *mennellii*	0.73	0.70–0.75	30	0.75
L. coleorum	0.72	0.69–0.76	30	0.68
L. comptonii subsp. *comptonii*	0.68	0.61–0.70	40	0.57
L. comptonii subsp. *weberi*	0.62	0.56–0.65	30	0.56
L. dendritica subsp. *dendritica*	0.63	0.62–0.67	40	0.65
L. dendritica subsp. *archerae*	0.87	0.83–0.89	50	0.8
L. dendritica subsp. *groendrayensis*	0.64	0.61–0.67	40	0.61
L. dendritica subsp. *schoemanii*	0.75	0.72–0.76	50	No data
L. dinteri subsp. *dinteri*	0.55	0.53–0.58	30	0.53
L. dinteri subsp. *frederici*	0.54	0.53–0.57	30	0.53
L. dinteri subsp. *multipunctata*	0.5	0.48–0.5.0	30	0.5
L. divergens subsp. *divergens*	0.58	0.52–0.59	50	0.57
L. divergens subsp. *amethystina*	0.65	0.61–0.67	50	0.63
L. dorotheae	0.6	0.54–0.61	50	0.53
L. eberlanzii var. *eberlanzii*	0.61	0.60–0.61	50	0.61
L. eberlanzii var. *aiaisensis*	0.58	0.56–0.62	50	0.57
L. francisci	0.6	0.58–0.61	30	0.61
L. fulviceps var. *fulviceps*	0.74	0.72–0.75	50	0.74
L. fulviceps var. *lactinea*	0.8	0.77–0.81	50	0.77
L. fulviceps var. *laevigata*	0.73	0.71–0.75	50	No data
L. gesinae subsp. *gesinae*	0.82	0.77–0.85	40	0.74[1]
L. gesinae subsp. *annae*	0.71	0.69–0.74	40	0.73
L. geyeri	0.61	0.60–0.64	30	0.62
L. gracilidelineata subsp. *gracilidelineata* var. *gracilidelineata*	0.65	0.60–0.67	50	0.6
L. gracilidelineata subsp. *gracilidelineata* var. *waldroniae*	0.76	0.72–0.79	50	0.72
L. gracilidelineata subsp. *brandbergensis*	0.8	0.76–0.82	40	0.74
L. hallii var. *hallii*	0.61	0.54–0.66	30	0.54[2]
L. hallii var. *ochracea*	0.55	0.50–0.59	30	0.52

Lithops taxon	Mean seed size (mm)	Range (mm)	n	Mean seed size (Hammer 2010)
L. helmutii	0.54	0.50–0.55	30	0.53
L. hermetica	0.7	0.68–074	30	No data
L. herrei	0.6	0.57–0.6.1	50	0.58
L. hookeri var. *hookeri*	0.89	0.85–0.92	50	0.89
L. hookeri var. *dabneri*	0.99	0.97–1.09	40	1
L. hookeri var. *elephina*	1.13	0.96–1.17	40	0.95
L. hookeri var. *lutea*	0.93	0.83–0.97	30	0.85
L. hookeri var. *marginata*	0.95	0.91–0–0.99	30	0.92
L. hookeri var. *subfenestrata*	0.91	0.88–0.94	30	0.9
L. hookeri var. *susannae*	0.96	0.91–0.98	30	0.85
L. julii subsp. *julii*	0.6	0.57–0.67	50	0.54
L. julii subsp. *fulleri* var. *fulleri*	0.53	0.50–0.55	30	0.53
L. julii subsp. *fulleri* var. *brunnea*	0.53	0.49–0.55	30	0.52
L. julii subsp. *rouxii*	0.53	0.49–0.56	30	0.5
L. karasmontana	0.57[3]	0.53–0.60	120	0.54
L. lesliei subsp. *lesliei* var. *lesliei*	1.12	1.00–1.17	30	1.14
L. lesliei subsp. *lesliei* var. *hornii*	1.02	0.99–1.12	30	0.96
L. lesliei subsp. *lesliei* var. *mariae*	1.05	1.00–1.12	30	1.06
L. lesliei subsp. *lesliei* var. *minor*	1.23	1.09–1.28	30	1.13
L. lesliei subsp. *lesliei* var. *rubrobrunnea*	1.12	1.00–1.17	30	1.14
L. lesliei subsp. *lesliei* var. *venteri*	1.05	1.00–1.10	30	1.06
L. lesliei subsp. *burchellii*	0.96	0.92–0.99	30	0.95
L. marmorata var. *marmorata*	0.48	0.40–0.51	30	0.46
L. marmorata var. *elisae*	0.5	0.45–0.52	30	0.49
L. meyeri	0.5	0.48–0.53	30	0.46
L. naureeniae	0.57	0.54–0.60	30	0.5
L. olivacea var. *olivacea*	0.52	0.49–0.53	30	0.5
L. olivacea var. *nebrownii*	0.5	0.45–0.53	30	0.54
L. optica	0.64	0.62–0.68	40	0.62[4]
L. otzeniana	0.65	0.59–0.69	50	0.55
L. pseudotruncatella subsp. *pseudotruncatella* var. *pseudotruncatella*	0.875	0.80–0.90	40	0.87[5]
L. pseudotruncatella subsp. *pseudotruncatella* var. *elisabethiae*	0.91	0.85–0.97	30	0.91
L. pseudotruncatella subsp. *pseudotruncatella* var. *riehmerae*	0.9	0.84–0.92	30	0.88
L. pseudotruncatella subsp. *volkii*	0.89	0.86–0.91	30	0.89
L. ruschiorum var. *ruschiorum*	0.64	0.62–0.69	50	0.61
L. ruschiorum var. *lineata*	0.78	0.75–0.79	40	0.78
L. salicola	0.76	0.73–0.81	30	0.71

Lithops taxon	Mean seed size (mm)	Range (mm)	n	Mean seed size (Hammer 2010)
L. schwantesii subsp. *schwantesii* var. *schwantesii*	0.82	0.77–0.84	50	0.78
L. schwantesii subsp. *schwantesii* var. *marthae*	0.79	0.76–0.80	40	0.78
L. schwantesii subsp. *schwantesii* var. *rugosa*	0.84	0.77–0.87	30	0.83
L. schwantesii subsp. *schwantesii* var. *urikosensis*	0.83	0.81–0.85	30	0.81
L. schwantesii subsp. *gebseri*	0.77	0.73–0.79	30	0.74
L. terricolor	0.56	0.54–0.63	40	0.63[6]
L. vallis-mariae	0.72	0.70–0.75	40	0.74
L. verruculosa var. *verruculosa*	0.47	0.45–0.49	40	0.46
L. verruculosa var. *glabra*	0.54	0.50–0.55	40	0.5
L. villetii subsp. *villetii*	0.65	0.58–0.72	40	0.66 (0.57–0.77)
L. villetii subsp. *deboeri*	0.5	0.44–0.53	40	0.49 (0.46–0.52)
L. villetii subsp. *kennedyi*	0.55	0.54–0.56	40	0.56
L. viridis	0.82	0.79–0.83	40	0.79
L. werneri	0.89	0.84–0.97	50	0.64

[1]The seeds from the Hammer collection SH2003 are much smaller, at 0.68mm, than the mean for the subspecies.
[2]The *salicola reticulata type plants of *Lithops hallii* var. *hallii* have larger seeds at 0.61mm according to Hammer (2010) but this is well within the measurements of this variety as found during the present study.
[3]This includes measurements of all the former recognised varieties of *Lithops karasmontana.*
[4]The *Lithops optica* 'maculata' form has smaller seeds at 0.55mm according to Hammer (2010).
[5]The eastern populations of *Lithops pseudotruncatella* known as the *mundtii-type have larger seeds of up to 1.04mm.
[6]The 'Prince Albert' form of *Lithops terricolor* has smaller seeds at 0.51mm according to Hammer (2010).

Table 2. Features used to describe SEM images of *Lithops* seeds.

Term	Higher magnification image	Example
Smooth surface		*L. hookeri* var. *hookeri* (Figure 8C)
Wave like rugose surface	Figure 2A	*L. hallii* var. *hallii* (Figure 7D)
Flat tubercles	Figure 2B	*L. dorotheae* (Figure 5G)
Interlocking tubercles	Figure 2C	*L. bella* (Figure 3F)
Small individual tubercles	Figure 2D	*L. naureeniae* (Figure 10G)
Large individual tubercles	Figure 2E	*L. lesliei* var. *lesliei* (Figure 9G)
Uniform rugosity pattern		*L. viridis* (Figure 13H)
Bi-rugosity pattern		*L. karasmontana* (Figure 9D)
Rounded globe		*L. amicorum* (Figure 3A)
Rounded/marginally flattened		*L. hookeri* var. *susannae* (Figure 8G)
Flattened globe		*L. aucampiae* (Figure 3B)
Indented globe		*L. lesliei* var. *lesliei* (Figure 9G)

***Lithops vallis-mariae* (Dinter & Schwantes) N.E.Br. (1925):** The seeds of *Lithops vallis-mariae* have a rounded globe with a very smooth surface. The long and straight rostrum is covered in rows of ill-defined flat tubercles towards the tip of the rostrum where the papilla is often present (Figure 13B). The seeds are 0.72mm long. A relationship between *L. vallis-mariae* and *L. dendritica* subsp. *groendrayensis* has been suggested in the past mainly based on the fine pitted appearance of the leaf surface of some individual subsp. *groendrayensis* plants that resemble that of *L. vallis-mariae* (Cole & Cole, 2005). Although the seeds of these two taxa are somewhat alike, the seeds of *L. vallis-mariae* are larger with the globe being very

Table 3. Taxonomic changes in *Lithops* N.E.Br.

Reinstated Taxon/New Taxon	Previous classification[1]
L. bella N.E.Br.(1922)	*L. karasmontana* (Dinter & Schwantes) N.E.Br. subsp. *bella* (N.E.Br.) D.T. Cole (1988)
L. dendritica Nel subsp. *dendritica* (1946)	*L. pseudotruncatella* (A. Berger) N.E.Br. subsp. *dendritica* (Nel) D.T. Cole (1988)
L. dendritica Nel subsp. *archerae* (de Boer) Earlé & Young. **comb. nov.** Basionym: *L. archerae* de Boer, *Succulenta* **46**: 122. 1967.	*L. pseudotruncatella* (A. Berger) N.E.Br. subsp. *archerae* (de Boer) D.T. Cole (1988)
L. dendritica Nel subsp. *groendrayensis* (H.J. Jacobsen) Earlé & Young. **comb. nov.** Basionym: *L. pseudotruncatella* var. *groendrayensis* H.Jacobsen, *Kakt.and.Sukk.* **12**: 169. 1961.	*L. pseudotruncatella* (A. Berger) N.E.Br. subsp. *groendrayensis* (H.J. Jacobsen) D.T. Cole (1988)
L. dendritica Nel subsp. *schoemanii* (Earlé & Uijs) Earlé & Young. **comb. nov.** Basionym: *L. pseudotruncatella* subsp. *schoemanii* Earlé & Uijs, *CactusWorld* **37**(3): 198. 2019.	*L. pseudotruncatella* (A. Berger) N.E.Br. subsp. *schoemanii* Earlé & Uijs (2019)
L. dinteri Schwantes subsp. *dinteri* (1927)	*L. dinteri* Schwantes var. *brevis* (L. Bolus) Fearn (1970)
L. eberlanzii (Dinter & Schwantes) N.E.Br. (1926) var. *eberlanzii* (1925).	*L. karasmontana* (Dinter & Schwantes) N.E.Br. subsp. *eberlanzii* (Dinter & Schwantes) D.T. Cole (1988)
L. eberlanzii (Dinter & Schwantes) N.E.Br. (1926) var. *aiaisensis* (de Boer) Earlé & Young. **comb. nov.** Basionym: *L. erniana* var. *aiaisensis* de Boer, *Succulenta* **43**(1): 6–7. 1964.	*L. karasmontana* (Dinter & Schwantes) N.E.Br. subsp. *karasmontana* var. *aiaisensis* (de Boer) D.T. Cole (1987)
L. divergens L. Bolus subsp. *divergens*.	*L. divergens* L. Bolus var. *divergens*
L. divergens L. Bolus subsp. *amethystina* (de Boer) Earlé & Young (1955) **stat. nov.** Basionym: *L. divergens* var. *amethystina* de Boer, *Succulenta* **40**(4): 40. 1961.	*L. divergens* L. Bolus var. *amethystina* de Boer(1961)
L. gesinae de Boer subsp. *gesinae*	*L. gesinae* de Boer var. *gesinae*
L. gesinae de Boer subsp. *annae* Earlé & Young (1956) **comb. nov.** Basionym: *L. annae* de Boer, *Succulenta* **35**(6): 90. 1956.	*L. gesinae* De Boer var. *annae* (de Boer) de Boer & Boom (1964).
L. julii (Dinter & Schwantes) N.E.Br. subsp. *rouxii* (de Boer) Earlé & Young **stat nov.** Basionym: *L. julii* var. *rouxii* de Boer, *Succulenta* **43**(10): 139. 1964.	*L. julii* (Dinter & Schwantes) N.E.Br. subsp. *fulleri* (N.E.Br.) B. Fearn var. *rouxii* (de Boer) D.T. Cole (1964)
L. karasmontana (Dinter & Schwantes) N.E.Br. (1920)	*L. karasmontana* (Dinter & Schwantes) N.E.Br. subsp. *karasmontana* var. *immaculata* D.T. Cole (2012)
	L. karasmontana (Dinter & Schwantes) N.E.Br. subsp. *karasmontana* var. *lericheana* (Dinter & Schwantes) D.T. Cole (1988)
	L. karasmontana (Dinter & Schwantes) N.E.Br. subsp. *karasmontana* var. *tischeri* D.T. Cole (1973)

[1]Classification according to Cole & Cole (2005) and Earlé & Uijs (2019).

much smoother than those of subsp. *groendrayensis* (c.f. Figures 4H & 13B).

***Lithops verruculosa* Nel (1943):** In this species two varieties are currently recognised, var. *verruculosa* and var. *glabra*. The seeds of these varieties are similar in shape with both having a rounded globe with a long rostrum. However, the seeds of var. *verruculosa* are uniformly covered in medium sized individual tubercles (Figure 13D) while in var. *glabra* de Boer (1966) the seed surface is bi-rugose with the globe having a smooth to slightly wave-like rugose surface and the crest and rostrum being covered in rows of medium sized tubercles (Figure 13C). On the strength of the marked differences in the seeds and the clear differences in both colour and leaf surface appearance between the adult plants of these two varieties (var. *glabra* being much greyer with few or absent raised dots on the surface of the leaves), the varieties are retained. The seeds of var. *verruculosa* are 0.47mm long but can be as small as 0.40mm (Hammer, 2010). By comparison, var. *glabra* has larger seeds at 0.54mm (Table 1).

***Lithops villetii* L. Bolus (1950):** At present three subspecies are recognised in this species, subsp. *villetii,* subsp. *deboeri* (Schwantes) Cole (1952) and subsp. *kennedyi* (de Boer) Cole (1967). The seeds of all three subspecies are similar having a rounded to minimally flattened globe and a long rostrum (Figures 13E–G). The globe of the seeds shows a wave-like rugosity merging into more prominent small tubercles on the crest and rostrum of the seeds. The seeds are all light brown to yellow brown with a darker brown rostrum. The mean measurement of the seeds of subsp. *villetii* is 0.65mm but unlike most other *Lithops* taxa the size of the seeds varies widely between 0.58–0.72mm (Table 1). The mean length of individual seeds of subsp. *deboeri* is 0.50mm and again these seeds show a wide range (0.44–0.53mm) but do not overlap in size with the seeds of subsp. *villetii.* Subsp. *kennedyi* has seeds measuring 0.55mm with a smaller range than the other subspecies (0.54–0.56mm) which does not overlap with subsp. *villetii.* The wide variation in the seed size within this species has also been observed by Hammer (2010). In summary, although these three taxa possess morphologically similar seeds, their sizes do not overlap, and the plants are usually easily identified by leaf surface patterns as described by Cole & Cole (2005). Furthermore, the subspecies all have slightly different patterns of tanniniferous idioblasts (Cole & Cole, 2005) and as a result, it is proposed that these subspecies should be retained.

***Lithops viridis* H. Lückhoff (1958):** Seeds of *L. viridis* have a rounded to slightly anteriorly flattened globe uniformly covered in small to medium sized individual tubercles (Figure 13H). On the anterior distension of the globe the tubercles merge to form parallel ridges. The seeds are yellow brown and relatively large at 0.82mm when compared with the seeds of other similarly sized plants.

***Lithops werneri* Schwantes & Jacobsen (1950):** The seeds of this species have a rounded globe with a medium length rostrum. The globe and crest surfaces are smooth with some large, widespread waves present on some seeds. This merges into a wave-like rugosity towards the tip of the rostrum where flat tubercles are arranged in rows (Figure 14A). The seeds are yellow brown with a darker brown rostrum and measure 0.89mm which is much larger than the value given by Hammer (2010) at 0.64mm.

Conclusion

Studying the seeds of all the *Lithops* taxa through a combination of light and scanning electron microscopy has provided valuable information about the relationships of many taxa within the genus. It has proven to be most useful when used alongside other morphological features (leaf and flower structure) and the scant molecular information available rather than in isolation. Considerable variation in both the size and structure of *Lithops* seeds has been observed across the genus with some being immediately recognisable (e.g., *L. lesliei*). A summary of the proposed changes to the classification of taxa within the genus *Lithops* arising from this study is given in Table 3 and we believe that these changes will improve the understanding of the genus and provide the best possible classification of these plants at the present time.

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