New World species of the genus *Crassula*

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Summary. The New World taxa of *Crassula* are revised; 13 native species are recognized plus one adventive. The following taxonomic changes are made: *C. saginoides* (Maxim.) Bywater & Wickens, *C. venezuelensis* (Steyermark) Bywater & Wickens, *C. minutissima* (Skottsberg) Bywater & Wickens, *C. longipes* (Rose) Bywater & Wickens and *C. viridis* (S. Watson) Bywater & Wickens are all transferred from *Tillaea*. *C. connata* (Ruiz & Pav.) Berger is divided into 5 varieties, var. *connata*, var. *erectoides* Bywater & Wickens, var. *eremica* (Jepson) Bywater & Wickens, var. *subsimplex* (S. Watson) Bywater & Wickens and var. *muscoides* Bywater & Wickens.

INTRODUCTION

The known New World native taxa of *Crassula* all belong to the subgenus *Disporocarpa*. Traditionally many American botanists have tended to maintain these taxa in the genus *Tillaea*, which is here treated as a synonym of *Crassula* in accordance with practice in the Old World.

There are over 60 names that have been applied to these taxa of which we recognize 13 native species. The excessive number of names and their various combinations is largely due to a lack of communication between taxonomists in the various countries where the genus occurs. In South America the proliferation of names can also be attributed to unexpected disjunct distributions. Bird dispersal could account for the distribution but the plants are under-collected and further collections may reveal a more consistent pattern.

There is a general lack of good morphological characters for distinguishing between the various taxa; this has been accentuated by the failure to recognize possible morphological variability within the species due to dry land and aquatic habitats as well as developmental changes from aestivation to maturity. Early and late lengthening of the pedicel varies from species to species.

The most reliable character that we have discovered is undoubtedly the surface structure of mature seed as seen under the scanning electron microscope (SEM). For non-research purposes × 50 magnification by normal light microscopy (LM) is sufficient for routine determinations. Descriptions are given, of the seed, using both methods of microscopy. Because of the late development of the surface structures in some seed, care must be taken to use mature seed from fruiting specimens.

Although helpful, the provenance of a specimen should be used with care because of the risk, due to under-collecting, of finding a species outside its known distribution area.

We would like to stress that although we believe advances have been made regarding the internal taxonomic status of the New World taxa, the relationship with the Old World taxa still requires further study. Further good collections are also required from Central and South America.

A full list of all specimens, identified during the course of this study, is available from Kew upon request.

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TABLE 1. Distribution of New World species of *Crassula*

	1. *moschata*	2. *aquatica*	3. *saginoides*	4. *venezuelensis*	5. *minutissima*	6. *solierii*	7. *longipes*	8. *peduncularis*	9. *drummondii*	10. *viridis*	11. *decumbens*	12. *closiana*	13. *connata*	14. *tillaea*
Alsaka		×	×											
N. W. Territories		×												
Quebec		×												
Newfoundland		×												
New Brunswick		×												
Nova Scotia			×											
Prince Edward Is.		×												
Maine		×												
Massachusetts		×	×											
Connecticut		×												
New York		×												
Maryland		×												
Florida							×							
Louisiana							×							
Colorado									×					
Wyoming			×			×								
Idaho										×				
Nevada			×			×								
Arizona			×						×				×	
Texas						×	×		×					
Washington			×											
Oregon		×	×			×								
California		×	×			×							×	×
Mexico			×				×			×		×	×	
Guatemala													×	
Brazil								×					×	
Paraguay							×	×	×	×				
Colombia				×									×	
Venezuela				×										
Ecuador				×									×	
Peru				×								×	×	
Bolivia				×								×	×	
Argentina	×				×		×	×	×				×	
Chile	×					×		×	×		×	×	×	
Uruguay								×	×					
Falklands	×													
Antarctica	×													

DISTRIBUTION

The distribution of the 13 native species (Table 1) follows well recognized patterns common to other families.

Two species are confined to North America. The circumpolar distribution of *C. aquatica* is well documented (Hultén 1958, Komarov 1971). The greater concentration of records in northern Europe and eastern North America is possibly a reflection on the intensity of collecting rather than an indication of long-distance bird dispersal across the Atlantic. With our present state of knowledge it would be wrong to dismiss a connection across the Bering Sea.

The second species, *C. saginoides*, also occurs in Mongolia and central Asia, where it is undercollected. It has been referred to *C. vaillantii* (Komarov 1971) but appears to be distinct. Its distribution in North America and Asia would certainly suggest a connection across the Bering Sea.

Of the remaining 11, 5 are restricted to South America and 6 occur in both

sub-continents, being concentrated towards the west in North America and more widely scattered within the temperate regions of South America. It is generally accepted that these disjunct distribution patterns can be attributed to long-distance bird dispersal. Cruden (1966) has, by a process of elimination, suggested 5 species of migrant birds frequenting wet and marshy habitats in the western region of North America with widespread overwintering areas in the south, which could be held responsible for such dispersal patterns. Since the migrants probably spend 2 months in travelling, external carriage of the propagules must be assumed. It is yet to be demonstrated that such a method actually works.

Cruden also argues in favour of the propagules' being carried during the northward migration. Although the genus *Crassula* is cosmopolitan in its distribution, the greater number of species are concentrated in the southern hemisphere, suggestive of a former Gondwanaland distribution. This would fit with Cruden's hypothesis. However, Raven & Axelrod (1974) believe that the *Crassulaceae* may not have reached South America prior to the late Miocene or Pliocene and to have spread there from North America.

As Raven (1963) rightly pointed out, with disjunct distributions it is virtually impossible to judge on present-day distribution evidence whether a species is native to only one or to both of the two areas. Raven continues with the suggestion that species that exhibit parallel series of variation in both continents are hardly likely to be of recent introduction; *C. connata* would appear to belong to this category.

The circum-antarctic distribution of *C. moschata* is obviously post ice-age in origin. Thorne (1972) suggested that oceanic birds from southern South America and New Zealand would presumably be responsible for the long-distance dispersal of such a distribution pattern.

There is a somewhat similar but clearly more temperate distribution of *C. closiana*, *C. peduncularis* and *C. decumbens*. *C. closiana* extends from Mexico to Chile and also occurs in Australia. The second species is widespread in the southern region of South America, and also occurs in Australia and New Zealand. The third is restricted to Chile but also extends to South Africa and Australia. Tölken (1981) considers these three species to be native in Australia. It is possible to evoke a former Gondwanaland distribution to account for these present-day patterns. However the possibility of an early introduction into South America as wool aliens cannot be discounted.

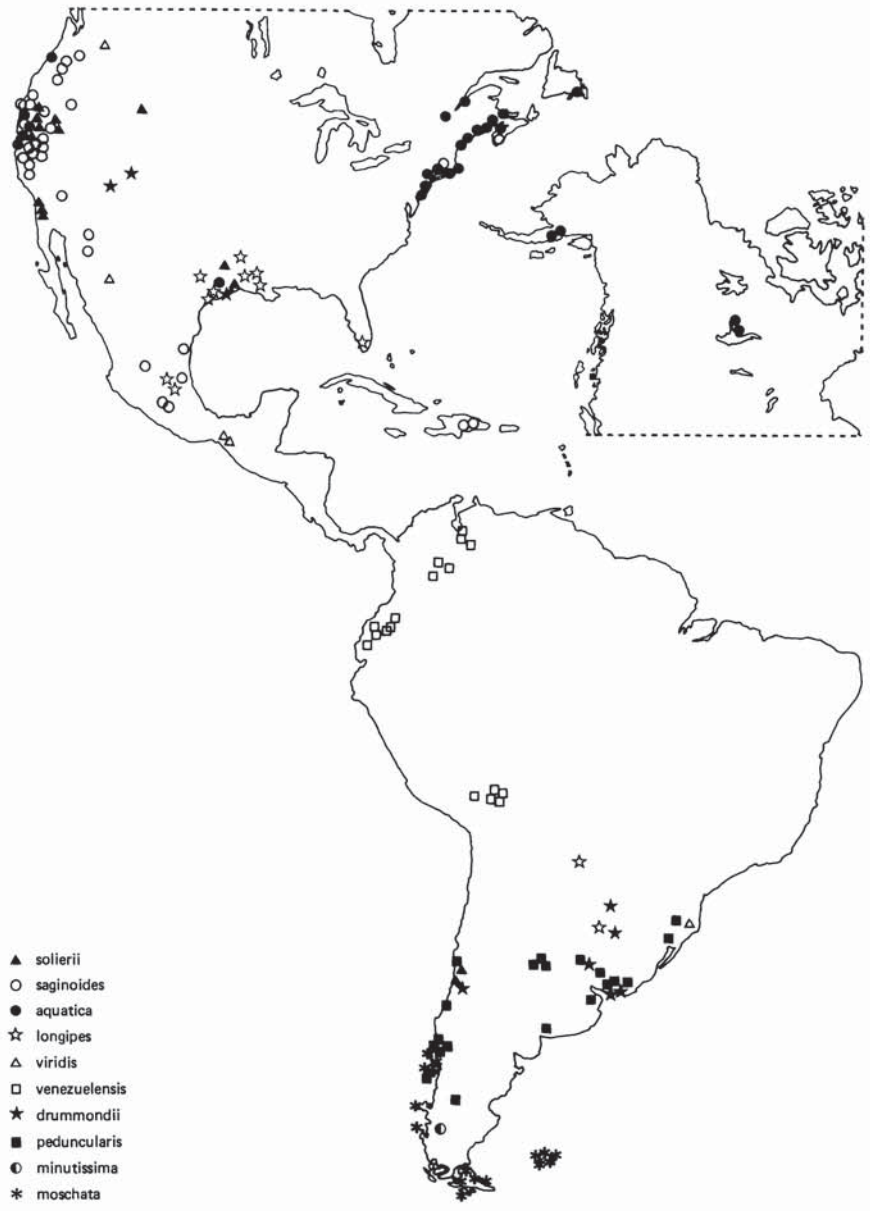
The remaining species, *C. tillaea* has a Mediterranean distribution and is clearly adventive in California.

From the above discussions it is clear that there is considerable difficulty in interpreting the distribution of the genus *Crassula*. A critical cyto-taxonomic study of subgenus *Disporocarpa* could help towards a solution of this problem.

Crassula *L.*, Sp. Pl. ed. 1: 282 (1753) subgen. **Disporocarpa** *Fischer & C. A. Mey.* Ind. Sem. Petropol. 8: 56 (1841).

Sect. **Helophytum** (*Eckl. & Zeyh.*) *Tölken* in Contrib. Bolus Herb. 8: 84 (1977).

Annual herbs. Inflorescences thyrsoid, terminal and often axillary with mainly monochasial branches; flowers 1(–3) in the leaf axils, peduncle absent. Calyx up to $\frac{2}{3}$ the length of the corolla, lobes usually obtuse. Carpels with obovoid ovaries abruptly constricted into short styles. Species 1–10. Map 1.



MAP 1. Distribution of New World species of *Crassula* sect. *Helophytum*.

DISTRIBUTION. Cosmopolitan but individual species usually restricted.

Sect. **Glomeratae** *Haw.*, Rev. Pl. Succ.: 12 (1821).

Annual herbs, rarely perennials. Inflorescences thyrsoid, terminal and/or axillary with 1–many dichasia. Calyx as long as or longer than corolla, acute

MAP 2. Distribution of New World species of *Crassula* sect. *Glomeratae*.

or pointed. Carpels with elongate ovaries gradually tapering into slender styles. Species 11–14. Map 2.

DISTRIBUTION. Cosmopolitan with most species in South Africa.

KEY TO SPECIES OF CRASSULA IN THE NEW WORLD

1. Flowers large 2·3–3 × 2·5–3 mm; plants robust; seeds large 0·6–0·7 mm long; coast of southern S. America . . . . . **1. moschata**

1. Flowers smaller, not exceeding 2 mm; plants delicate; seeds rarely exceeding 0·5 mm in length
 2. Carpels (1–)2-seeded
  3. Sepals up to ½ the length of the petals; flowers 1 per node . . . . . **5. minutissima**
  3. Sepals equal to or exceeding petals; flowers (1-)2 per node
   4. Flowers 3–4-merous
    5. Flowers subsessile, 3(–4)-merous . . . . . **14. tillaea**
    5. Flowers pedicellate, (3–)4-merous . . **13. connata** var. **eremica**
   4. Flowers 4–5-merous . . . . . **13. connata**
 2. Carpels 3–or more-seeded
  6. Sepals equal to or longer than the petals; flowers (1–)2 per node
   7. Leaf-margins papillate-ciliate; sepals papillate . . **12. closiana**
   7. Leaf margins entire; sepals not papillate . . . . **11. decumbens**
  6. Sepals half the length of the petals; flowers 1 per node
   8. Seeds papillate
    9. Leaves small, linear-lanceolate, 1·5–3 mm long, apex obtuse; seeds small (0·27–)0·29–0·39(–0·48) mm long with 1 papilla per cell . . . . . **9. drummondii**
    9. Leaves large, narrowly triangular, (2·5–)3–9(–10) mm long, apex acute
     10. Leaves (4–)6–9(–10) mm long; seeds (0·46–)0·5–0·54 mm long with 1 papilla per cell . . . . . **10. viridis**
     10. Leaves (2·5–)3–5 mm long; seeds (0·29–)0·37–0·44 mm long with 4–8 papillae per cell . . . . . **8. peduncularis**
   8. Seeds not papillate
    11. Seeds surface rugulose, dull
     12. Seeds small, 0·24–0·33 mm long, lobes of surface cells triangular; carpels 12–14 seeded; plants delicate . . . . . **7. longipes**
     12. Seeds larger, (0·34–)0·39–0·65(–0·68) mm long, lobes of surface cells broadly spathulate; carpels usually 9-seeded; plants not notably delicate
      13. Fruiting pedicels < 1 mm; habitat saline, near sea level . . . . . **2. aquatica**
      13. Fruiting pedicels > 1 mm; habitat fresh water lakes and rivers, reaching higher altitudes
       14. Leaves elliptic to oblanceolate; petals exceeding carpels by c. 0·2 mm . . . . . **3. saginoides**
       14. Leaves narrowly triangular-lanceolate; petals not exceeding carpels . . . . . **4. venezuelensis**
    11. Seed surface smooth, shiny . . . . . **6. solierii**

1. Crassula moschata *Forst. f.* in Comm. Soc. Sci. Gotting. II, 9: 16 (1787). Type: Tierra del Fuego, Isla de los Estados, *J. R. & G. Forster* (whereabouts unknown).

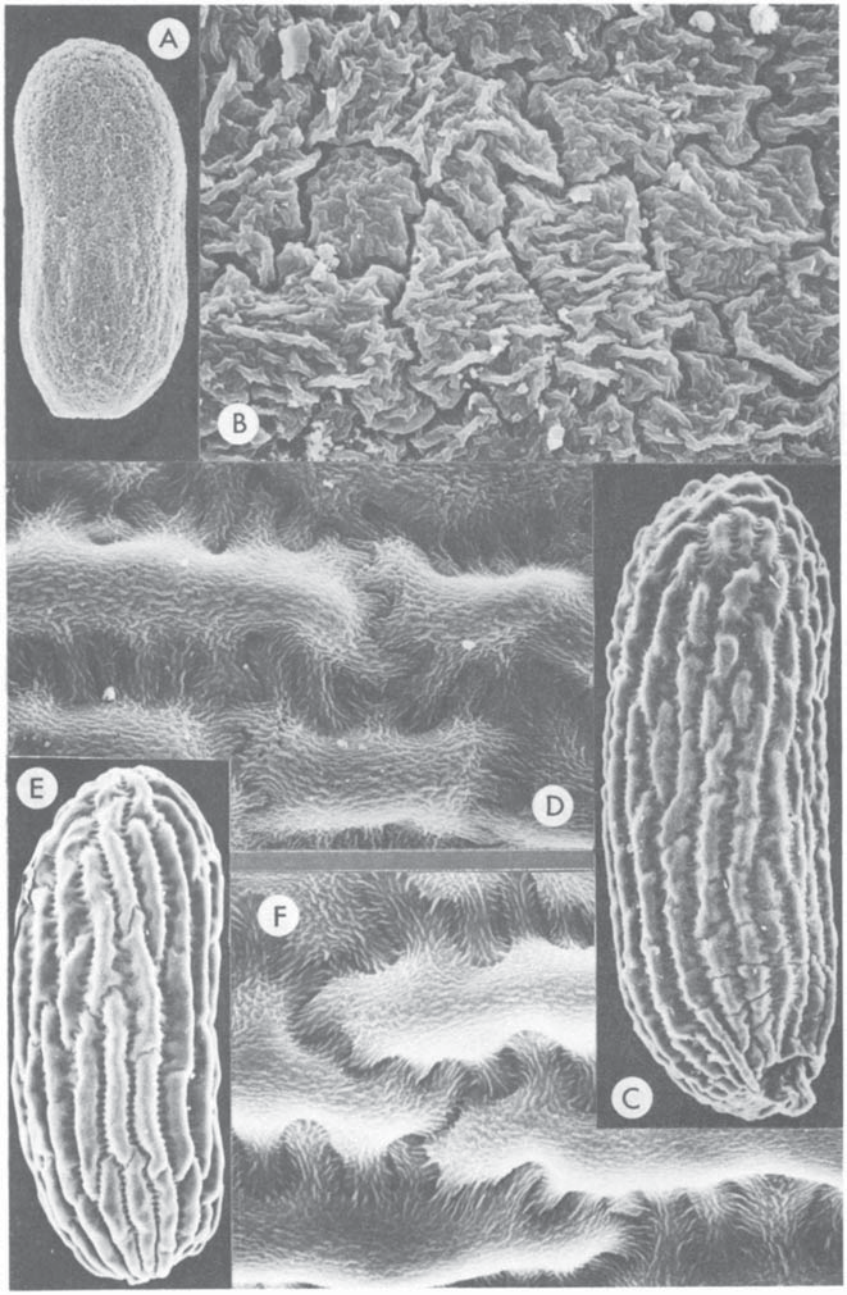
Bulliarda magellanica DC. in Bull. Sci. Soc. Philom. 3, No. 49: 2 (1801), nom. nud., based on a specimen collected by *Commerson.*

B. moschata (Forst. f.) D'Urv., Fl. Is. Mal.: 53 (1825).

Tillaea magellanica Willd. ex Schultes, Mantissa in L. Syst. Veg, 3: 345 (1827). Type: Magellan's Str., (*collector unknown*) (holotype B microfiche!).

FIG. 1. **A–E** *C. moschata*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Moore* 1621. **F–K** *C. aquatica*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26, from *Fernald & Svenson* 911. Drawn by author (M.B.).

PLATE 29



A–B *C. moschata*: **A** seed × 73; **B** surface × 725, from *Reed s.n.*; **C–D** *C. aquatica*: **C** seed × 145; **D** surface × 725, from *Blake 5626*; **E–F** *C. saginoides*: **E** seed × 145; **F** surface × 725, from *Orcutt s.n.*

Tillaea moschata (Forst. f.) DC., Prodr. 3: 382 (1828).

T. chiloensis Gay, Fl. Chil. 2: 532 (1847). Type: Chile, Chiloe, San Carlos, *Gay* s.n. (holotype P!).

Crassula magellanica (Willd. ex Schultes) Macloskie in Scott, Rep. Princeton Univ. Exped. Patag. 8: 456 (1905).

Erect, leafy, reddish, robust herb up to 50 mm high. Stems thick (c. 1 mm), leaves elliptic (2·4–)3·3–5 mm long, often with conspicuous round gland dots abaxially. Pedicels 2–3 mm long. Flowers 1 per node, 4-merous, 2·3–3 × 2·5–3 mm. Sepals triangular to obtuse, 1·5–1·7 × 0·9–1 mm with gland dots on dorsal side. Petals oblong-lanceolate, 2–2·3 × 1 mm, exceeding sepals. Scales large, oblong, 1 × 0·5 mm with rounded apex. Carpels 2–4(–8) seeded. (Fig. 1 A–E).

SEEDS. [LM]: oblong-ellipsoid, 0·6–0·71 × (0·31–)0·35–0·44 mm, reddish brown, unridged, minutely rugulose, ends rounded, [SEM]: divisions apparent between irregularly shaped cells, surface rugose; cell lobes irregular, angular. Possible small amount of wax debris on surface. (Plate 29 A–B). Of the 34 specimens of *C. moschata* examined, SEM studies were carried out on the seed from 6. Further investigations were considered unnecessary with such a large, distinctive seed, which is easily identified using the LM, but measurements given are from those 6 collections only and may not cover the complete range of seed size.

HABITAT. Rock crevices in upper tidal and splash zones of ocean, usually just above high-water mark; 0–45 m.

DISTRIBUTION. Argentina, Chile, Falkland Is., Marion, Crozet & Kerguelen Is., Auckland Is., Australia, Tasmania, New Zealand, Chatham Is., Stewart Is. (Map 1).

The largest of the S. American species, *C. moschata* is easily distinguished from all others. It is a sturdy plant with large flowers containing usually 2–4 large oblong seeds which could not be confused with those of any other species. The range of this taxon is well defined, being restricted in S. America to the southern coasts of Argentina and Chile and the neighbouring islands.

2. Crassula aquatica (*L.*) *Schönl.* in Engl. & Prantl, Pflanzenfam. 3, 2a: 37 (1890). Type: 'Habitat in Europae inundatis.' (holotype BM! (Hort. Cliff.)).

Tillaea aquatica L., Sp. Pl.: 128 (1753).
Bulliarda aquatica (L.) DC. in Bull. Sci. Soc. Philom. 3, No. 49: 2 (1801).
Tillaea simplex Nuttall in Journ. Acad. Philod. 1: 114 (1817), non Phil. (1872). Type: Pennsylvania, Kensington, Philadelphia, banks of Delaware River, *Nuttall* s.n. (syntypes BM!, K!); Connecticut, Newhaven, *Ives* s.n. (syntype ?).
T. ascendens Eaton, Man. Bot. N. States ed. 2: 465 (1818). Type: Connecticut, R. Housatanic, *Ives* s.n. (holotype ? YU).
T. angustifolia Nuttall ex Torr. & Gray, Fl. N. Amer. 1: 558 (1840). Type: Oregon, Oregon River, *Nuttalll* s.n. (syntype K!), Wahlamet River, *Nuttall* s.n. (syntype BM!).
Tillaeastrum aquaticum (L.) Britton in Bull. N.Y. Bot. Gard, 3: 1 (1903).
Hydrophila aquatica (L.) House in Amer. Mid. Nat. 6: 203 (1920).

Erect to decumbent herb. Aquatic stems up to 100 mm long. Leaves elliptic-oblanceolate, 3–6·5 mm long, acute to obtuse. Pedicels not exceeding 1 mm. Flowers 1 per node, 4-merous, 1·3–2 × 1–1·7 mm. Sepals triangular to obtuse, 0·6–0·9 × 0·7–0·8 mm wide with occasional black gland dots. Petals

rhomboid-ovate, 1·4–1·7 × 0·8–0·9 mm, twice as long as sepals. Scales filamentous, spathulate, 0·8 mm long. Carpels (5–)9–12-seeded. (Fig. 1 F–K).

SEEDS. [LM]: oblong-elliptic, (0·36–)0·43–0·49(–0·6) × (0·16–) 0·18–0·22 mm, reddish-brown, longitudinally striate, minutely rugulose; [SEM]: striations consisting of long rugulose cells joined by rounded, interlinking lobes. (Plate 29 C–D). Of 37 specimens seen, seeds examined from 16 collections proved to be uniform and were taken as representative. They could not be distinguished from those of *C. saginoides*.

HABITAT. Subaquatic. Saline, estuarine or coastal; brackish mud flats, intertidal zones.

DISTRIBUTION. Alaska, North West Territories, Quebec, Newfoundland, New Brunswick, Prince Edward Is., Maine, Massachusetts, Connecticut, New York, Maryland, Oregon, California; also northern Europe and Asia. (Map 1).

C. aquatica is found in North America where it is likely to be confused with *C. saginoides* and *C. solierii*. Whereas the pedicels on *C. saginoides* tend to elongate in fruit those of *C. aquatica* remain less than 1 mm. *C. aquatica* in North America is also restricted to low altitude, usually near sea level, coastal conditions, often within tidal and splash zones. The pedicels of *C. solierii* also tend to elongate in fruit but the seeds retain a shiny wax coating into maturity unlike either *C. aquatica* or *C. saginoides*.

3. Crassula saginoides (*Maxim.*) *Bywater & Wickens* comb. nov.

Tillaea simplex Phil. in Anal. Univ. Chil.: 719 (1872) non Nutt. (1817). Type: Chile, Catapilco, *Philippi* s.n. (holotype SGO!).

T. angustifolia Nuttall var. *bolanderi* S. Watson in Watson, Gray & Brewer, Fl. Calif. 1: 209 (1876), Type: California, San Francisco, *Bolander* s.n. (holotype GH, n.v.).

T. saginoides Maxim. in Bull. Acad. Petersb. 26: 473 (1880). Type: Mongolia, Irtysch, *Potanin* s.n. (holotype LE; isotype K!).

T. bolanderi (S. Watson) Greene, Fl. Francisco: 183 (1891).

T. drummondii Torr. & Gray var. *bolanderi* (S. Watson) Jepson, Fl. W. Mid. Calif.: 265 (1901).

Tillaeastrum pringlei Rose in Bull. N.Y. Bot. Gard. 3: 2 (1903). Type: Mexico, Serrania de Ajusco, *Pringle* 6517 (holotype US; isotype BM! K! UC!).

[*Tillaea vaillantii* sensu Gray, New Man. Bot. ed. 7: 442 (1908), non Willd.]

[*Hydrophila vaillantii* sensu House in Amer. Mid. Nat. 6: 203 (1920), non (Willd.) Roth.]

Erect to decumbent herb. Stems up to 135 mm long. Leaves elliptic-oblanceolate, 2–5 mm long, acute. Pedicels extending in fruit, (0·5–)2–19 mm long. Flowers 1 per node, 4-merous, 2–2·1 × 1·5–2 mm. Sepals triangular to obtuse, 0·9–1·3 × 0·4–0·9 mm wide with occasional black gland dots. Petals oblong to ovate 1·3–1·9 × 0·5–0·7 mm, exceeding sepals. Scales filamentous, spathulate 0·9 mm long. Carpels (6–)8–10(–17)-seeded. (Fig. 2 A–E).

SEED. [LM]: oblong-ellipsoid, (0·34–)0·39–0·42(–0·57) × 0·14–0·2 (–0·22) mm, reddish brown, longitudinally striate, minutely rugulose. [SEM]: cells oblong, longitudinally striate, joined by rounded, interlinking lobes. Wax debris may be present. (Plate 29 E–F). Of the 72 specimens examined, seeds were studied from 38 and were all of similar form to those of *C. aquatica*.

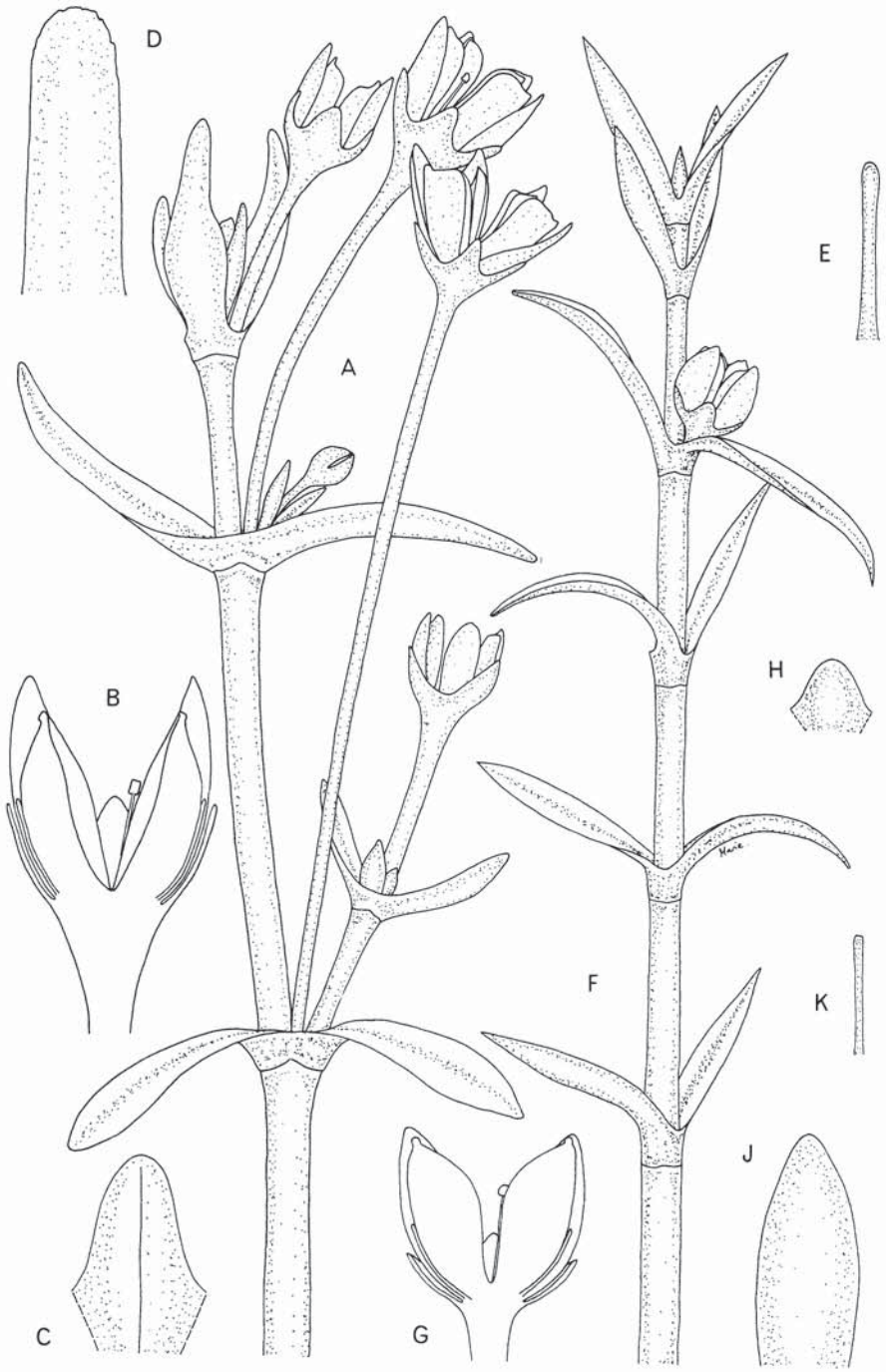


FIG. 2. **A–E** *C. saginoides*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Hoover* 2016. **F–K** *C. venezuelensis*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26, from *Beck* 1865. Drawn by author (M.B.).

HABITAT. Terrestrial to subaquatic; inland, wet and muddy places; ditch banks, seasonal pools, lake and river shores, fresh-water marshes. Reaching high altitudes <3000 m.

DISTRIBUTION. Alaska, Nova Scotia, Massachusetts, Wyoming, Nevada, Arizona, Washington, Oregon, California, Hispaniola, Mexico (Map 1); also Mongolia, central Asia; naturalised in Portugal (*C. bonariensis* sensu Webb in Fl. Europ. 1: 351 (1964) non (DC.) Camb. (1829)).

C. saginoides can easily be confused with *C. aquatica* or *C. solierii* in North America. In *C. saginoides*, however, the pedicels tend to elongate in fruit, while those of *C. aquatica* are subsessile. When dealing with immature or depauperate specimens this distinction may not always be apparent. From *C. solierii*, *C. saginoides* differs in its rugulose seed and long pedicels. *C. solierii* has smooth, shiny seed and shorter pedicels.

This species has been referred to *C. vaillantii* (Willd.) Roth which has pedicels of c. 4 mm compared with those of *C. saginoides* which may reach 19 mm at maturity. It is possible that the two species merge in central Asia and extensive field studies would be needed to show the true range of these taxa.

4. Crassula venezuelensis (*Steyermark*) *Bywater & Wickens* comb. nov.

Tillaea venezuelensis Steyermark in Fieldiana Bot. 28: 914 (1957). Type: Venezuela between Chachopo and Los Apartaderos, near El Aguila, *Steyermark* 55906 (holotype F!; isotype K! NY!).

Erect to decumbent herb. Aquatic stems up to 100 mm long. Leaves narrowly triangular-lanceolate 3·5–5 mm long, submucronate, forming an acute angle to the stem. Pedicels up to 15 mm long. Flowers 1 per node, 4-merous 1·2–2·3 × 1–1·9 mm. Sepals triangular-ovate 1 × 0·8 mm. Petals 1·4 × 0·7 mm, exceeding sepals. Scales filamentous 0·6 mm long. Carpels 6–8 seeded. (Fig. 2 F–K).

SEED. [LM]: large, oblong, (0·43–)0·54–0·63(–0·68) × 0·2–0·25 (–0·34) mm, reddish-brown, longitudinally striate, minutely rugulose. [SEM]: striations consisting of long rugose cells joined by rounded, interlinking lobes. (Plate 30 A–B). Of the 22 specimens examined, seeds were studied from 19, some of which were immature but the surface structure is consistent and the seeds large.

HABITAT. Mainly aquatic; inland lakes and lakesides, at high altitudes, 3000–4500 m.

DISTRIBUTION. Colombia, Venezuela, Ecuador, Peru, Bolivia, ? Chile (Map 1).

As the flowers of the type of *C. venezuelensis* are immature, seed characters cannot be used. Habit and gross morphology, particularly the narrowly triangular, sharply pointed leaves, place this specimen within a taxon found in the north and west of South America which has large, broadly oblong, striate seeds.

C. venezuelensis can be separated from *C. peduncularis* and *C. viridis*, which are similar in outward appearance, by the relatively large, non-papillate, seeds. It differs from *C. saginoides* in its leaf shape, larger seed and predominantly aquatic habitat. It is frequently found at high altitudes, between 3000 and 4500 m, unlike *C. peduncularis* which is rarely found over 1000 m.

FIG. 3. **A–E** *C. minutissima*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Skottsberg* 710. **F–K** *C. solierii*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26, from *Philippi* s.n. **L–R** *C. longipes*: **L** habit × 8; **M** ½ young flower × 16; **N** sepal × 20; **P** petal × 20; **Q** scale × 26, from *Pringle* 13407. Drawn by author (M.B.).

5. Crassula minutissima (*Skottsberg*) *Bywater & Wickens* comb. nov.

Tillaea minutissima Skottsberg in Kungl. Svensk. Vet.-Akad. Handl. n.s. 56, 5: 237, t. 22, fig. 19 (1916). Type: *Skottsberg* 710 (holotype UPS!).

Small erect herb c. 15 mm high. Leaves lanceolate, 2–3·5 mm long, acute. Pedicels c. 0·2 mm long. Flowers 1 per node, 4-merous, 0·9 × 0·7 mm. Sepals triangular, obtuse, 0·3 × 0·4 mm. Petals ovate, 0·8 × 0·4 mm. Scales filamentous, 0·4 mm long. Carpels 2-seeded. (Fig. 3 A–E).

SEED. [LM]: large, oblong, 0·58 × 0·23 mm, reddish-brown, striate, longitudinally ridged, rugose. [SEM]: cell differentiation clear, cells long and narrow joined by interlinking rounded lobes. (Plate 30 C–D).

HABITAT. In damp places.

DISTRIBUTION. Argentina (Map 1).

This species has been identified only from the type collection but is sufficiently distinct from other plants in the locality to be maintained in its own right. It is similar to *C. aquatica* and *C. saginoides* from which it differs in its small size and its large seed of which there are only 2 per carpel. It is also found a great distance from any representatives of these species. It is possible that the range of *C. peduncularis* could extend this far south but the seed of *C. minutissima* show no sign of latent papillae and are significantly larger than any yet recorded for *C. peduncularis*. The size of the seed and morphology of the plant are closest to terrestrial forms of *C. venezuelensis*. The later species is not known

to contain only 2 seeds per carpel, and the inclusion of this specimen would extend the range of the species further south than previously recorded.

Further collections of *Crassula* in southern Argentina may provide further indications of the affinities of this collection.

6. Crassula solierii (*Gay*) *Meigen* in Engl., Bot. Jahrb. 17: 239 (1893).

Tillaea solierii Gay, Fl. Chil. 2: 530 (1847). Type: Chile, Santiago, *Gay* 178 (holotype P!).

T. andicola Phil. in Anal. Univ. Chil. 41: 720 (1872). Type: Chile, Cord. Santiago, Valle del Yeso, *Philippi* 775 (holotype SGO!; isotype K!).

Crassula andicola (Phil.) Meigen in Engl., Bot. Jahrb. 17: 239 (1893).

Erect to decumbent herb. Stems up to 55 mm long. Leaves lanceolate, 2·4–3·3 mm long. Pedicels (0·6–)1·2–2·5 mm long. Flowers 1 per node, 4-merous, 1·5 × 2 mm. Sepals triangular, 0·6–0·9 × 0·5–0·8 mm. Petals triangular, 0·9–1·3 × 0·5–0·6 mm, exceeding sepals. Scales filamentous, spathulate, 0·65 mm long. Carpels 9–14 seeded. (Fig. 3 F–K).

SEED. [LM]: oblong-ellipsoid, 0·32–0·42(–0·55) × (0·14–)0·15–0·19 (–0·21) mm, reddish brown, smooth and shiny with possible longitudinal ridges. [SEM]: cell differentiation clear, individual cells smooth, shiny, wax covered; cells joined by triangular lobes. (Plate 30 E–F). Throughout the 19 specimens examined within this species the seed type was consistent. Micrographs were taken of 14 of these.

HABITAT. Terrestrial or subaquatic; shores of lakes and rivers, seasonal pools, open prairie.

DISTRIBUTION. Wyoming, Nevada, Texas, Oregon, California, Chile (Map 1).

This taxon is very similar in form to both *C. aquatica* and *C. saginoides* in N America. The main difference lies in the seed of *C. solierii* which retain a complete wax sheath through into maturity, giving the seed a smooth shiny surface, easily seen with a light microscope. These seeds are generally smaller than those of *C. aquatica* and *C. saginoides* and under SEM the surface cells are shown to be linked together by triangular lobes rather than the more usual rounded ones.

7. Crassula longipes (*Rose*) *Bywater & Wickens* comb. nov.

[*Tillaea drummondii* sensu Torrey & Gray, Fl. N. Am. 1: 558 (1840) pro specim. Louisiana, *Carpenter* s.n. (BM!, GH!, NY!).]

[*Tillaeastrum drummondii* sensu (Torrey & Gray) Brit. in Bull. N.Y. Bot. Gard. 13: 1 (1903) pro parte.]

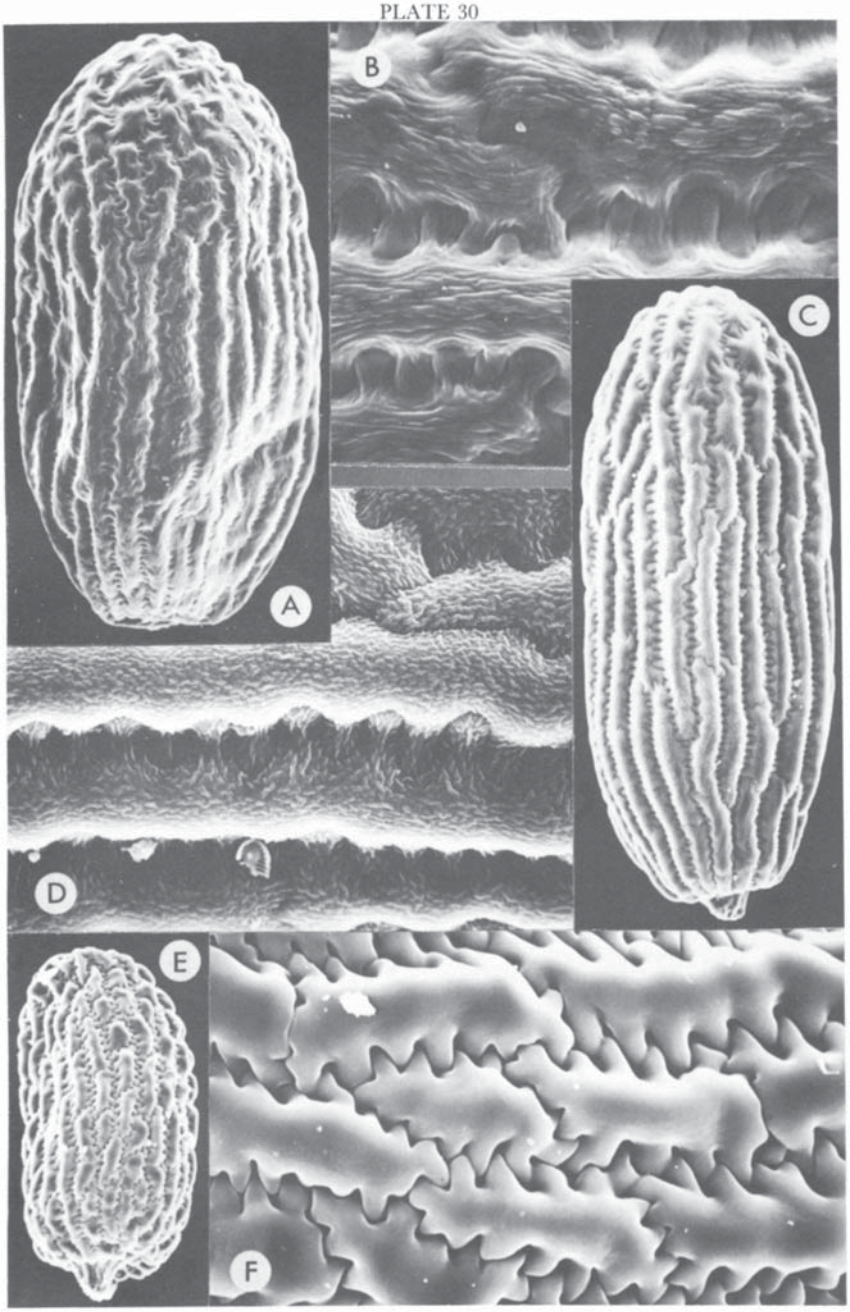
[*Crassula drummondii* sensu (Torrey & Gray) Fedde in Just., Bot. Jahrb. 31: 829 (1904) pro parte.]

Tillaeastrum longipes Rose in Contrib. US Nat. Herb. 13: 301 (1911). Type: Mexico, Hidalgo, Trinidad, *Pringle* 13407 (holotype US!).

[*Hydrophila drummondii* sensu (Torrey & Gray) House in Amer. Mid. Nat. 6: 203 (1920) pro parte.]

[*Tillaea aquatica* L. var. *drummondii* sensu (Torrey & Gray) Jepson, Man. Fl. Pl. Calif.: 449 (1925) pro parte.]

PLATE 30



A–B *C. venezuelensis*: **A** seed × 145; **B** surface × 725, from *Cazalet & Pennington 5476*; **C–D** *C. minutissima*: **C** seed × 145; **D** surface × 725, from *Skottsberg 710*; **E–F** *C. solierii*: **E** seed × 145; **F** surface × 725, from *Wheeler 3389*.

Erect herb up to 25 mm high. Leaves lanceolate to oblanceolate (0·3–)2–4·5(–5·2) mm long, acute to obtuse. Pedicels (1·2–)1·5–3(–8) mm long. Flowers 1 per node, 4-merous, (1·2–)1·7–1·8(–2) × (1·3–)1·4–1·6

(–1·8) mm. Sepals ± triangular, 0·4–0·7 × 0·3–0·6 mm, obtuse. Petals triangular, 1·1–1·7 × 0·4–0·6 mm, acute, exceeding sepals. Scales filamentous, 0·4 mm long. Carpels 12–14-seeded (Fig. 3 L–R).

SEED. [LM]: small, oblong, (0·24–)0·27–0·31(–0·33) × (0·13–)0·15 (–0·16) mm, reddish-brown, apparently slightly ridged, ends rounded. [SEM]: cell differentiation clear, cells in rows giving the possible ridged appearance seen under LM; cell lobes triangular, surface rugulose. Remains of wax sheath may be evident. (Plate 31 A–B). Seed from 11 of the 12 specimens seen were scanned and revealed consistent surface patterns and size.

HABITAT. Terrestrial to sub-aquatic; in wet places, on wet bare clay to half-submerged river ledges.

DISTRIBUTION. Florida, Louisiana, Texas, Mexico, Paraguay, Argentina (Map 1).

C. longipes is a small plant which can easily be confused with other small Crassulas. In North America it was considered conspecific with *C. drummondii*, which also has many small seeds, and in Paraguay it has been separated in a mixed collection (*Balansa* 2350) from *C. peduncularis*. It differs from *C. drummondii* and the small-seeded *peduncularis* specimens in that these have papillate seed. From small plants of *C. saginoides* and immature *C. peduncularis* it can be distinguished by its virtually unridged seed consisting of short surface cells with triangular lobes.

8. Crassula peduncularis (*Sm.*) *Meigen* in Engl., Bot. Jahrb. 17: 239 (1893) & 18: 417 (1894). Type: Uruguay, Montevideo, *Commerson* s.n. (holotype LINN!, photo. K!).

Bulliarda bonariensis DC. in Bull. Sci. Soc. Philom. 3, No. 49: 2 (1801), nom. nud.

Tillaea peduncularis Sm. in Rees, Cyclop. 35: Tillaea 4 (1819).

Crassula bonariensis Cambess. in St. Hil., Fl. Bras. Mer. 2: 195 (1830), nom. illegit., superfl., type as for *C. peduncularis*.

Tillaea paludosa Schldl. in Lechl., Berber. Amer. austr.: 54 (1857) nom. nud. Specimen: Chile, *Lechler* 472 (K! P, SGO).

Tillaea simplex Phil. in Anal. Univ. Chile 719–720 (1872), non Nutt (1817). Type: *R. A. Philippi* 780 (holotype SGO!).

Crassula paludosa (Schldl.) Reiche, Fl. Chile 2, 369 (1898). Type: Chile, *Lechler* 472 (holotype SGO; isotypes K! P).

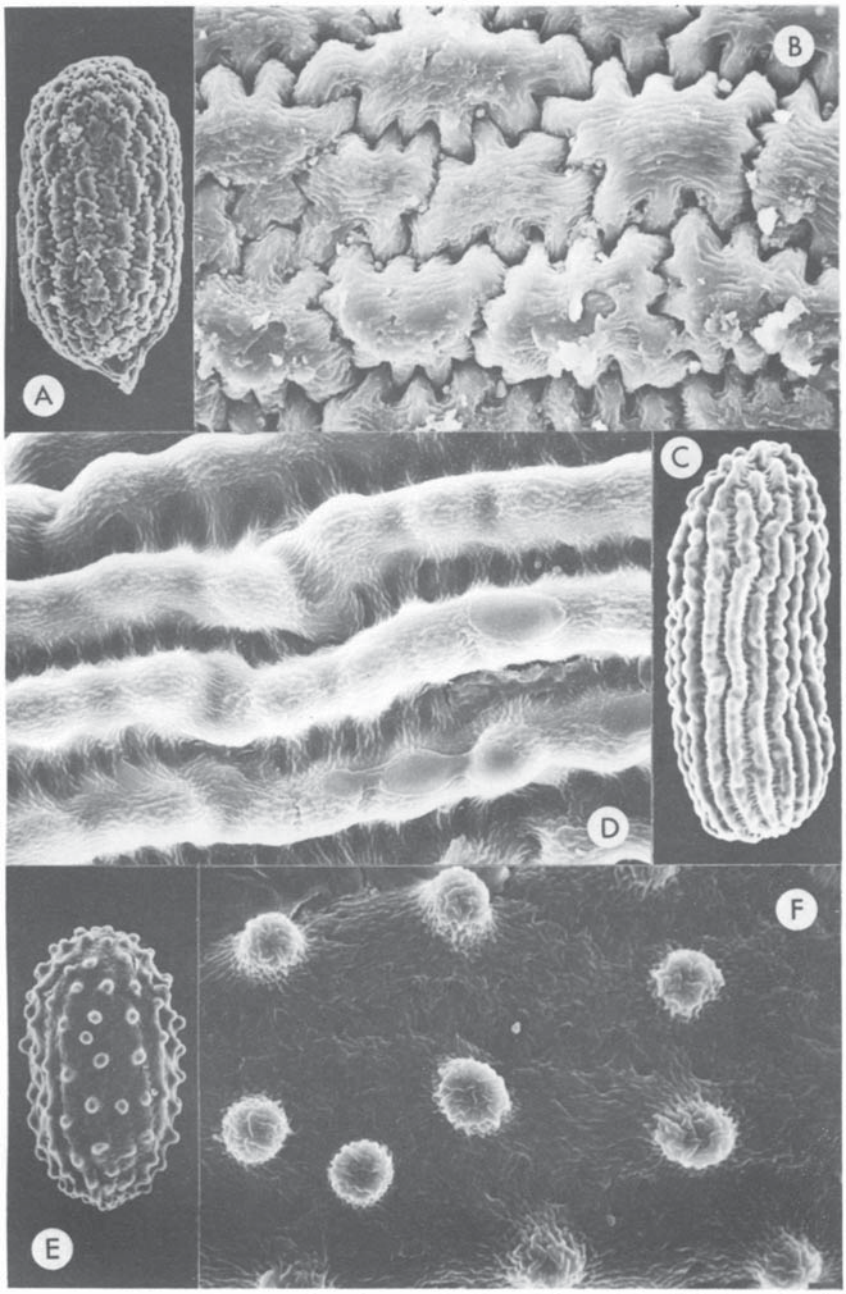
Crassula paludosa (Schldl.) P. Dusén in Rep. Princetown Univ. Exped. Patag. 8: 22 (1903) comb. illegit.

Tillaea bonariensis (DC.) Britt. in Herter, Est. Bot. Rég. Uruguaya 4: 65 (1930), comb. illegit.

Crassula caudiculata Bacigalupo & Rossow in Hickenia 2: 3 (1983). Type: Argentina, *Troncoso, Bacigalupo & Guaglianone* 2212 (holotype SI).

Erect or decumbent herb up to 55 mm high. Leaves lanceolate to narrowly triangular, (2·5–)3–5 mm long, acute. Pedicels, extending in fruit, (0·5–)5·5–9 (–11) mm long. flowers 1 per node, 4-merous, 2–2·3 × (1·3–)1·4–2(–2·3) mm. Sepals triangular, 1–1·5 × 0·5–0·7 mm, acute. Petals triangular-ovate, 1·3–1·7 × 0·5 mm, acute, exceeding sepals. Scales filamentous, spathulate, 0·6 mm

PLATE 31



A–B *C. longipes*: **A** seed × 145; **B** surface × 725, from *Pringle 13407*; **C–D** *C. peduncularis*: **C** seed × 145; **D** surface × 725, from *Felippone 5075*; **E–F** *C. drummondii*: **E** seed × 145; **F** surface × 725, from *Drummond III 95*.

long. Carpels (6–)8–9(–16)-seeded. (Fig. 4 A–E).

SEED. [LM]: small, oblong, (0·33–)0·39–0·44(–0·46) × (0·14–)0·16–0·19

(–0·21) mm, reddish brown, longitudinally striate, papillate. [SEM]: longitudinally striate with (4–)5–6(–8) papillae along the length of each cell, cells forming ridges, cell differentiation occasionally obscure, cells joining by interlinking rounded lobes, surface rugulose. Remnants of wax may persist into maturity. (Plate 31 C–D). Of the 38 specimens seen of this species seed was scanned from 36. Whereas the mature seeds show clear rows of papillae, quite distinct from any other species, immature material may lack these features or show them as low undulating ridges.

HABITAT. Terrestrial, in wet mud on banks of streams and rivers, at sea level and altitudes < c. 1500 m.

DISTRIBUTION. S Brazil, Paraguay, Argentina, Chile, Uruguay (Map 1); also in Australia and New Zealand.

Mature specimens, from fruiting material, of *C. peduncularis* can easily be distinguished by the long rows of papillae on the seed. It is morphologically similar to *C. viridis* which also has papillate seed but the papillae on *C. viridis* occur always as one per cell and the cells are shorter than in *C. peduncularis*. The seed of *C. viridis* are also much larger and, although poorly known at present, distribution of the two species seems distinct. Immature seed of *C. peduncularis* do not always show signs of the late-developing papillae and such specimens could be confused with *C. venezuelensis* or *C. saginoides*. These species have not, however, been found within the seemingly limited distribution range of *C. peduncularis*.

9. Crassula drummondii (*Torrey & Gray*) *Fedde* in Just., Bot. Jahrb. 31: 829 (1904) pro parte excl. specim. typ. *Carpenter*. Type: Texas, Galveston Bay, *Drummond* III, 95 (lectotype GH!, selected here; isolectotype BM! GOET! K!).

Tillaea drummondii Torrey & Gray, Fl. N. Amer. 1: 558 (1840) pro parte.
Tillaeastrum drummondii (Torrey & Gray) Brit. in Bull. N.Y. Bot. Gard. 3: 1 (1903) pro parte.
Hydrophila drummondii (Torrey & Gray) House in Amer. Mid. Nat. 6: 203 (1920) pro parte.
Tillaea aquatica L. var. *drummondii* (Torrey & Gray) Jepson, Man. Fl. Pl. Calif.: 449 (1925) pro parte.

Erect or decumbent herb. Aquatic stems reaching 40 mm long. Leaves linear-lanceolate, 1·5–3 mm long, apex obtuse. Pedicels (0·5–)1–1·3(–2) mm long. Flowers 1 per node, 4-merous, 1·2 × 0·4–1·1 mm. Sepals triangular, 0·4 × 0·3 mm. Petals lanceolate, 1·3 × 0·3 mm. Scales not seen. Carpels (9–)13–15-seeded. (Fig. 4 F–K).

SEED. [LM]: small, oblong to ellipsoid (0·27–)0·29–0·39(–0·48) × 0·14–0·18 (–0·21) mm, reddish brown, papillate. [SEM]: cells small, one papilla per cell, joined by interlinking triangular lobes, surface smooth to minutely rugulose. Some wax may remain at maturity. (Plate 31 E–F). Seed from the 12 specimens seen varied in size and surface texture, but showed the same distinctive surface structure.

HABITAT. Terrestrial or subaquatic, along margins of pools and rivers and seasonally damp areas.

DISTRIBUTION. Colorado, Arizona, Texas, Paraguay, Argentina, Chile, Uruguay (Map 1).

The original description of *C. drummondii* was based on the two specimens,

FIG. 4. **A–E** *C. peduncularis*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20, from *Felippone* 5075. **E** scale × 26, from *Philippi* s.n. **F–K** *C. drummondii*: **F** habit × 8; **G** ½ flower × 16; **H** ½ fruit × 16; **J** sepal × 20; **K** petal × 20, from *Drummond* III 95. **L–Q** *C. viridis*: **L** habit × 8; **M** ½ young flower × 16; **N** sepal × 20; **P** petal × 20; **Q** scale × 26, from *Breedlove* 22864. Drawn by author (M.B.).

Drummond III, 95 from Galveston, Texas and *Carpenter* s.n. from Feliciana, Louisiana. Although outwardly similar, these plants contain seed of different forms. The seed surface cells of the Drummond specimen are clearly papillate whereas those of *Carpenter* s.n. are unraised. The selection of *Drummond* III, 95, as lectotype, is based on the statement, 'pedicels at length as long as the leaves', from the original description. The Carpenter specimen, in which the pedicels exceed the leaves, is now referred to *C. longipes* (Rose) Bywater & Wickens.

C. drummondii may be distinguished from other Crassulas by its small, numerous, papillate seeds with one papilla per cell. The seed of *C. viridis* is also of this form but the surface cells in the seed of *C. drummondii* are joined by triangular lobes; those of *C. viridis* are rounded. *C. pedunculatis* has several papillae per cell. Seed of *C. drummondii* are also consistently smaller than those of *C. viridis*. These species can be distinguished on outward morphology, *C. viridis* and *C. pedunculatis* being larger plants with acutely pointed triangular leaves. Those of *C. drummondii* are small, broadly lanceolate and ± obtuse.

10. Crassula viridis (*S. Watson*) *Bywater & Wickens* comb. nov.

Tillaea viridis S. Watson in Proc. Am. Acad. 23: 272 (1888). Type: Mexico, Sierra Madre, Chihuahua, *Pringle* 1366 (holotype VT!; isotypes K! MA! NY!).

Tillaeastrum viride (S. Watson) Britten in Bull. N.Y. Bot. Gard. 3: 1 (1903).

Decumbent herb, 50–70 mm high. Leaves narrowly triangular, (4–)6–9 (–10) mm long, apex acute. Pedicels (0·4–)0·6–1(–4) mm long. Flowers 1 per node, 4-merous, 1·4–1·5 × 1·3–1·7 mm. Sepals broadly triangular, 0·7–0·8 × 0·5–0·7 mm, obtuse. Petals triangular, 1·3 × 0·6 mm, acute. Scales filamentous, 0·6 mm long. Carpels 6–12-seeded. (Fig. 4 L–Q).

SEED. [LM]: relatively large, oblong to narrowly reniform, (0·46–)0·5–0·54 × (0·18–)0·2(–0·23) mm, reddish brown, longitudinally striate, papillate. [SEM]: cells in long rows forming longitudinal striations, developing one papilla per cell in mature specimens, cells joined by interlinking rounded lobes, cell divisions apparent, surface rugose. Some wax debris may be present. (Plate 32 A–B). Seed from the 7 specimens examined were uniform in mature samples. Immature seed showed partly developed papillae.

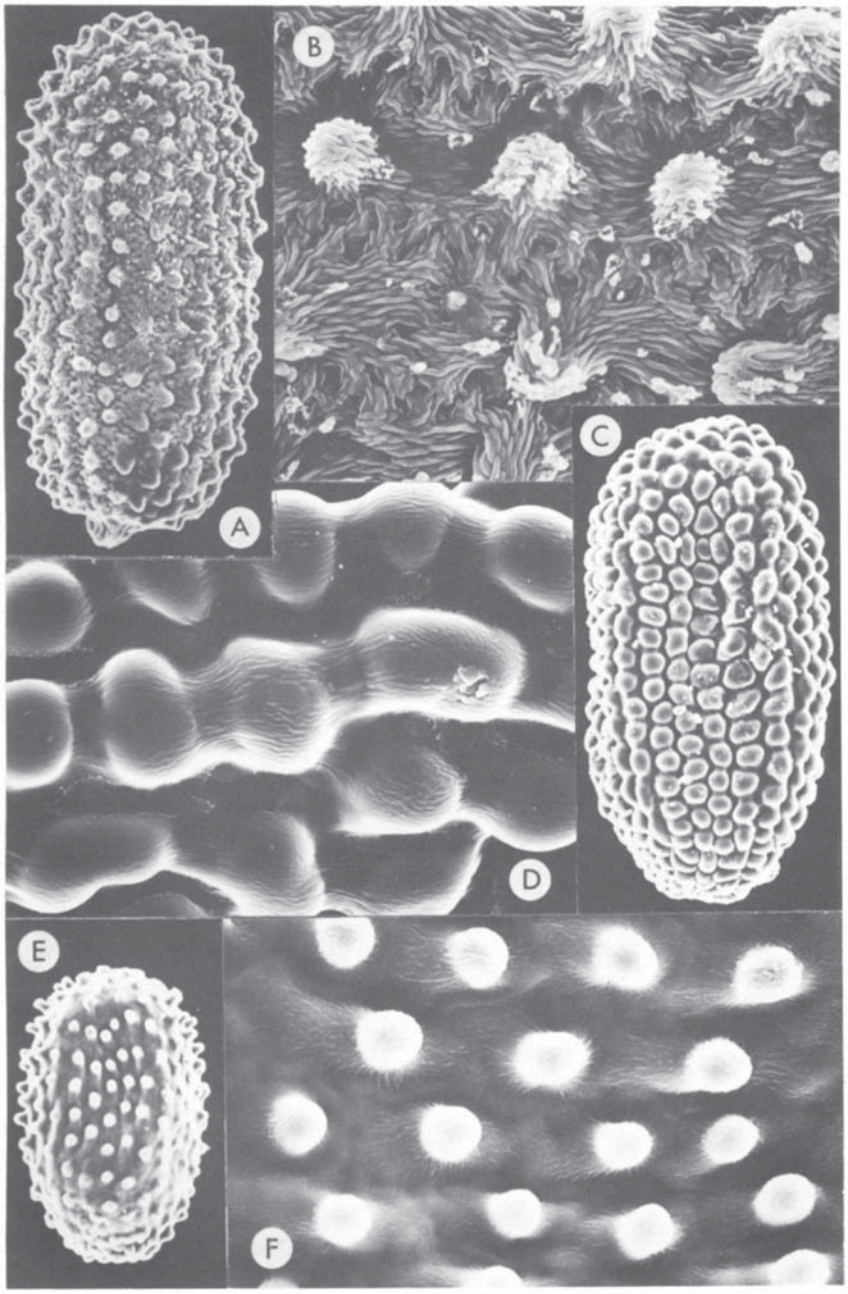
HABITAT. Terrestrial or aquatic, on margins of pools and rivers, in shallow water and damp places.

DISTRIBUTION. Idaho, Mexico, Brazil (Map 1).

Outwardly *C. viridis* most resembles *C. venezuelensis* and *C. pedunculatis* with its relatively large, triangular leaves. It can be distinguished from these by the form of the seed; seed of *C. venezuelensis* are also large but do not have any papillae; those of *C. pedunculatis* are smaller and have a number of papillae to each cell. *C. drummondii* also has one papilla per cell but the cell lobes are triangular and the seed and plant are smaller, the leaves short and obtuse. The papillae of *C. viridis* are late-developing and immature specimens could be mistaken for similar species. Further collections in both North and South America are needed to clarify the distribution of this species.

The original description cites *Pringle* 1561 in error, this being a collection of *Ceanothus fendleri* Gray. Details of Pringle's collection of number 1366 are found in H. B. Davis (1936).

PLATE 32



A–B *C. viridis*: **A** seed × 145; **B** surface × 725, from *Pringle 1366*; **C–D** *C. decumbens*: **C** seed × 145; **D** surface × 725, from *Philippi s.n.*; **E–F** *C. closiana*: **E** seed × 145; **B** surface × 725, from *Gay s.n.*

11. Crassula decumbens *Thunb.*, Prodr.: 54 (1794). Type: South Africa, near Cape Town, *Thunberg* in UPS 7751 (lectotype UPS, desig. Tölken in

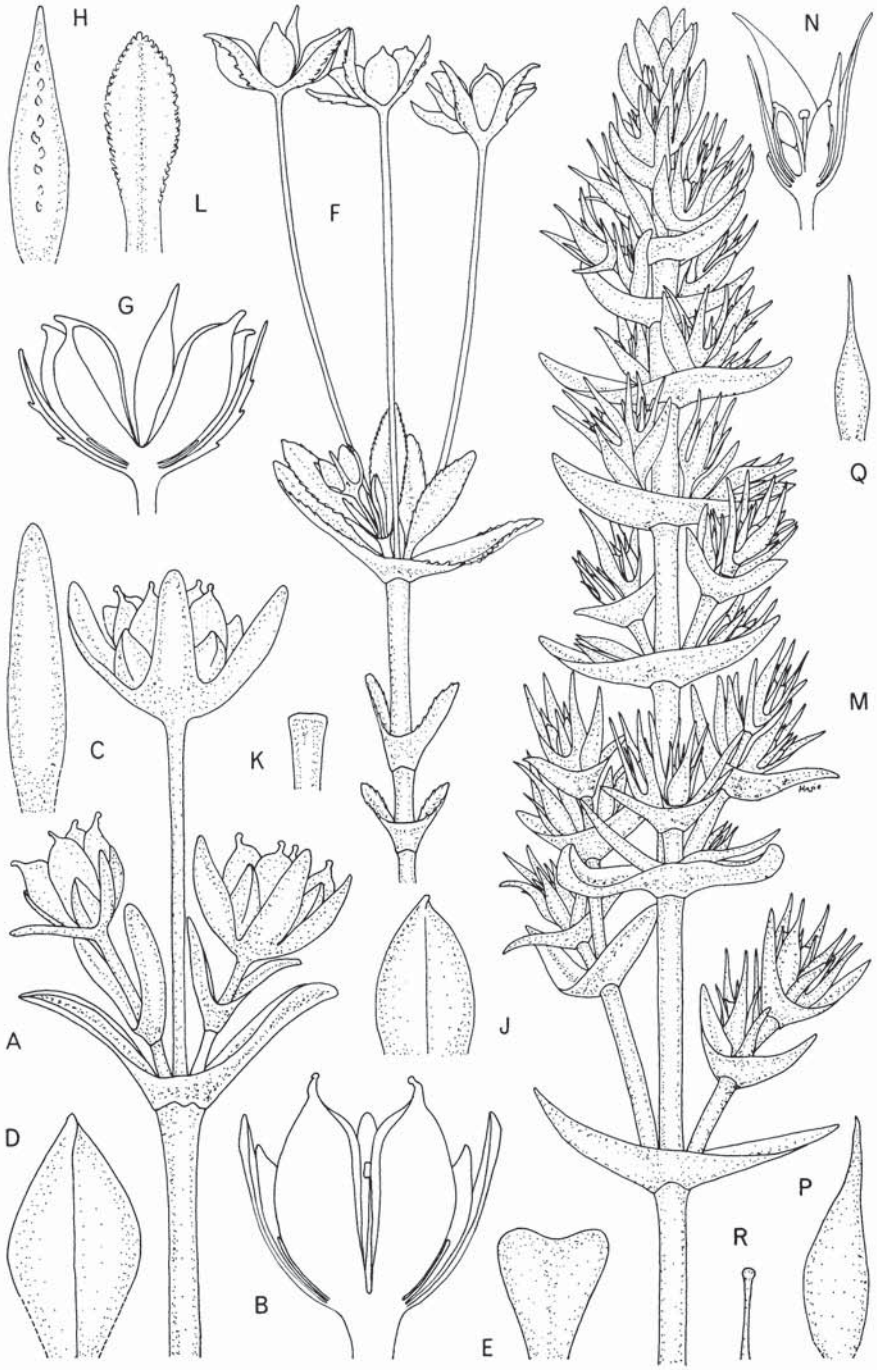


FIG. 5. **A–E** *C. decumbens*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Philippi* s.n. **F–L** *C. closiana*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26; **L** leaf × 12, from *Gay* s.n. **M–R** *C. tillaea*: **M** habit × 8; **N** ½ flower × 16; **P** sepal × 20; **Q** petal × 20; **R** scale × 26, from *Sharsmith* 4454. Drawn by author (M.B.).

Contrib. Bolus Herb. 8: 120 (1977); isolectotype BM! STB).

Bulliarda trichotoma Eckl. & Zeyh., Enum.: 290 (1837). Type: South Africa, Table Mountain, *Ecklon & Zeyher* 1851 (holotype S; isotype SAM).

Tillaea macrantha Hook.f. in Hook., Icon. Pl. 4: t. 310 (1841). Type: Australia, Van Diemen's Land, *Gunn* s.n. (holotype K!).

Tillaea trichotoma (Eckl. & Zeyh.) Walp., Rep. 2: 251 (1843).

T. radicans Phil. in Anal. Univ. Chile 41: 718 (1872). Type: Chile, rio Tinguiririca, San Fernando, *Philippi* s.n. (holotype SGO!).

T. ovallei Phil. in Anal. Univ. Chile 41: 719 (1872). Type: Chile, Aconcagua Prov., Catapilco Hacienda, *Philippi* s.n. (holotype SGO!; isotype K!).

Crassula mongolica Franch. in Nouv. Arch. Mus. Paris II, 5: pl. 16, fig. 1 (1882–3), 6: 7 (1883). Type: Mongolia, Géhol, *Abbé David* s.n. (holotype P!); **synon. nov.**

Tillaea rencana Phil. in Anal. Univ. Chile 85: 324 (1894). Type: Chile, Santiago, hill at Rencana, *Philippi* s.n. (holotype SGO).

Crassula radicans (Phil.) Reiche, Fl. Chile 2: 370 (1897).

C. ovallei (Phil.) Reiche, Fl. Chile 2: 370 (1897).

C. leipoldtii Schönl. & Bak.f. in Journ. Bot. 40: 288 (1902). Type: South Africa, Clanwilliam, *Leipoldt* 392 (holotype GRA; isotype PRE).

C. macrantha (Hook.f.) Diels & Pritzel in Engl., Bot. Jahrb. 35: 210 (1904).

C. longebergensis Schönl. in Trans. Roy. Soc. S. Afr. 17: 184 (1929). Type: South Africa, Longeberg, *Muir* 3354 (holotype GRA).

Tillaea mongolica (Franch.) Fu in Acta Phytotax. Sin. Addit. 1: 112 (1965).

Erect to decumbent herb 20–25mm high, branched from near the base. Leaves oblanceolate, 2·1–3 × 0·5–1 mm, obtuse. Pedicels 3–7 mm long. Flowers 1–2 per node, 4-merous(–5-merous in S Africa), 0·9–2·4 × 2·1–3·6 mm. Sepals ovate, (1·3–)1·9–2·4 × 0·3–0·8 mm, equal to or exceeding petals, rarely with one which is shorter. Petals ovate, (1–)1·5–1·9 × 0·6–0·9 mm. Scales obtriangular, 0·4 × 0·3 mm. (Fig. 5 A–E).

SEED. [LM]: oblong, 0·44–0·5 × 0·22–0·24 mm, reddish brown, densely papillate. [SEM]: papillae wide, rounded, in longitudinal rows; cell differentiation obscure but c. 3–6 papillae per oblong cell, surface rugulose, minutely striate. (Plate 32 C–D). Seeds were scanned from 3 of the 4 specimens examined. The distinctive oblong shape and low rounded papillae are also discernible under LM.

HABITAT. Terrestrial, inland, damp places.

DISTRIBUTION. Chile, S Africa, Australia, Mongolia (Map 2).

C. decumbens is easily recognized by its relatively large flowers with long, non-papillate sepals and its large, densely papillate seed. *C. closiana* and *C. connata* also have long sepals but in *C. closiana* the sepals are papillate and the leaves ciliate; *C. connata* has two ellipsoid, slightly ridged seeds per carpel. Although the distribution of *C. decumbens* seems strange, there is no doubt as to the identity of the Mongolian material. It is probable that further collections will extend the range and so clarify the overall pattern.

12. Crassula closiana *(Gay) Reiche,* Fl. Chile 2: 369 (1897). Type: Chile, Santiago, *Gay* s.n. (holotype P!).

Tillaea closiana Gay, Fl. Chile 2: 531 (1847).

T. macrantha Hook.f. var. *pedicellosa* F. Muell., Fragm. 11: 118 (1881). Type: Western Australia, Sterling Mountains, *Mueller* in MEL 88451 (lectotype MEL!).
T. pedicellosa (F. Muell.) F. Muell., Second Cens. 1: 84 (1889).
Tillaeastrum latifolium Rose in Contrib. U.S. Nat. Herb. 13: 301 (1911). Type: Mexico, Nevada de Toluca, *Rose & Painter* 7891 (holotype US!).
Crassula pedicellosa (F. Muell.) Ostenf., Dansk bot. Ark. 2, 8: 42 (1918).
Crassula macbridei Steyerm. in Publ. Field Mus. Nat. Hist. Bot. 13, 2: 1009 (1938). Type: Peru, Lima, Lurin, *Macbride* 5971 (holotype F!).
Tillaea latifolia (Rose) Calderón in Bol. Soc. Bot. Mex. 33: 61 (1974).

Erect herb, 20–45 mm high, simple or sparsely branched from mid stem. Leaves oblanceolate to obovate, 2–9 × 1–2·5 mm ± acute. Pedicels (1–)6–8 (−11) mm long. Flowers 1–2 per node, 3–4-merous, 1·3–1·4 × 1·4–2 mm. Sepals lanceolate, 1·4–2·4 × 0·2–0·5 mm, papillate on dorsal side of midrib. Petals ovate, 1·1–1·3 × 0·5–0·7 mm, slightly hooded. Scales oblong 0·4 × 0·2 mm. (Fig. 5 F–L).

SEED. [LM]: small, oblong, (0·25–)0·27–0·32 × (0·14–)0·16–0·19 mm, reddish brown, papillate, minutely rugulose. [SEM]: surface cells small with one small central papilla, cell differentiation often obscure, cells apparently linked by bluntly triangular lobes, surface rugulose. (Plate 32 E–F). 6 specimens of *C. closiana* were examined. Seed were scanned from 5 of these and showed distinctive size and structure.

HABITAT. Terrestrial; damp places, coastal and inland.

DISTRIBUTION. Mexico, Peru, Bolivia, Chile, Australia, Tasmania (Map 2).

C. closiana is easily distinguished from all other American *Crassula* by its papillate sepals, ciliate leaves and long pedicels.

C. pedicellosa is included here after studying the type specimen; the description by Tölken (1981) could be misleading.

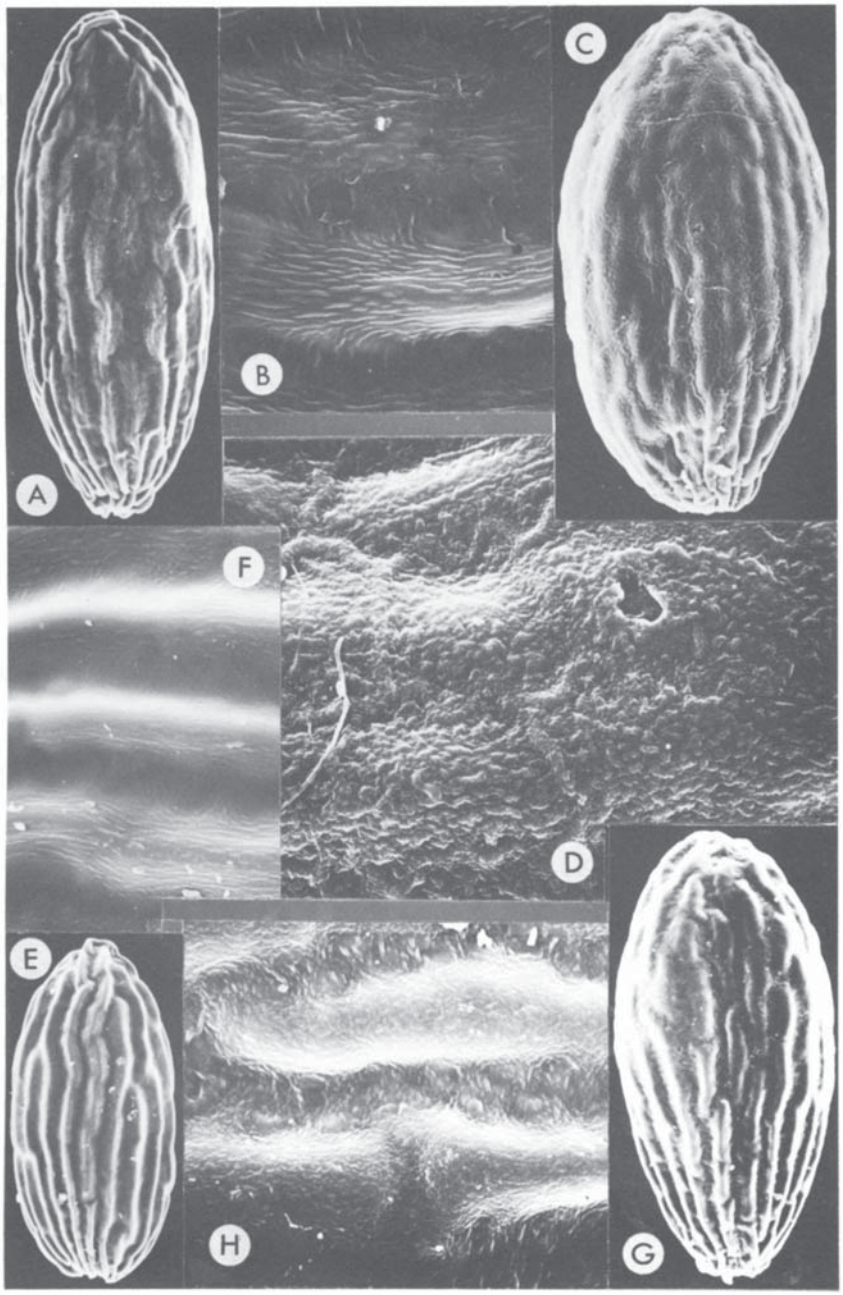
13. Crassula connata *(Ruiz & Pav.) Berger* in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 18a: 389 (1930); non Donn (1804) nomen nud. of uncertain application.

Tillaea connata Ruiz & Pav., Fl. Peru 1: 70, t. 106 (1798). Type: Peru, Chancay, *Ruiz & Pavón* 10/89 (holotype MA!; isotypes FI, OXF).
? T. erecta Hook. & Arn., Bot. Beechey's Voy.: 24 (1830). Type: Chile, Concepcion, *Lay & Collie* s.n. (holotype not located).
Crassula erecta (Hook. & Arn.) Berger in Engl. & Prantl, Pflazenfam. ed. 2, 18a: 289 (1930).

Erect herb up to 65 mm high, simple or sparingly branched from the base. Leaves lanceolate-triangular, (0·8–)1·8–3(–6·5) × (0·4–)0·7–1(–1·4) mm, obtuse or acute. Pedicels (0·2–)1–3(–6) mm. Flowers (1–)2 per node, 3–5-merous, (0·6–)0·9–1·5(–2·3) × (0·5–)0·8–1·3(–1·6) mm. Sepals triangular, (0·6–)0·8–1·4(–2·3) × (0·2–)0·3–0·5(–0·7) mm, acute to aristate. Petals narrowly triangular, (0·6–)0·8–1·1(–1·2) × (0·1–)0·2–0·3(–0·4) mm, acute to attenuate. Scales filamentous, narrowly spathulate, 0·3–0·6 mm long. Carpels (1–)2-seeded.

SEED. [LM]: small, ellipsoid (0·3–)0·34–0·47(–0·57) × (0·15–)0·17–0·25 (–0·28) mm, reddish brown, smooth, often irregularly, longitudinally ridged. [SEM]: cell differentiation often obscure, best seen in var. *muscoides*; cells

PLATE 33



A–F *C. connata*: **A–B** *var. connata*: **A** seed × 145; **B** surface × 725; from *Ugent 4633*; **C–D** *var. muscoides*: **C** seed × 145; **D** surface × 725, from *Gay 52*; **E–F** *var. erectoides*: **E** seed × 145; **F** surface × 725, from *Nuttall 143*; **G–H** *C. tillaea*: **G** seed × 145; **H** surface × 725, from *Sharsmith 4454*.

oblong, linked by rounded lobes, surface smooth to minutely rugulose. (Plate 33 A–F). Of the 271 specimens identified as *C. connata,* seeds were examined

under SEM from 65 collections. These proved to be of the same form as those of *C. tillaea*, and showed little variation.

HABITAT. Terrestrial; on sandy soil and rocks, wet or dry places, from sea level to 2700 m.

DISTRIBUTION. Species (as a whole) Oregon to Argentina (Map 2).

KEY TO VARIETIES OF CRASSULA CONNATA

1. Flowers pedicellate
   2. Plants robust; subtending leaf (2·5–)3–4·5(–5·4) × (0·8–)1·5 mm, exceeding pedicels; flowers 4–5-merous (1–)1·5–2 mm long; pedicels up to 3·5 mm long; sepals 1·5–2 × length of carpels; leaf size ± uniform
      3. Internodes often exceeding leaves, plants simple or little-branched, erect; flowers 4-merous, longer than wide. (Fig. 7 A–E). . a. var. **connata**
      3. Internodes shorter than leaves, plants branched, 'bushy'; flowers 4–5-merous, ± equidimensional (Fig. 7 F–K) . e. var. **muscoides**
   2. Plants delicate; subtending leaf (1·6–)2–2·3(–2·8) × (0·6–)0·8–1·1(–1·4) mm, not exceeding the longer pedicels; flowers 3–4-merous, 0·6–1·5 mm long; pedicels up to 6 mm long; sepals 1–1·5 × length of carpels; upper leaves much reduced
      4. Sepals barely exceeding carpels; flowers 0·6–1(–1·5) mm long, pedicels (1–)2–4 mm long. (Fig. 6 A–E). . . . . b. var. **erectoides**
      4. Sepals 1·5 × length of carpels; flowers 1–1·5 mm long, pedicels (1–)3–6 mm long. (Fig. 6 F–K). . . . . .c. var. **eremica**
1. Flowers ± subsessile
   5. Leaves 1·5–2·5 × 1 mm; basal leaf axils sterile; flowers small, 0·8–1·2 × 0·8–1 mm, 4-merous; pedicels 0·2–0·5(–1·5) mm long; plants erect, simple, little branched up to 40 mm high, internodes exceeding leaves; N America (Fig. 6 L–R) . . . . . .d. var. **subsimplex**
   5. Leaves 2–3·5 × 1 mm, basal leaf axils fertile; flowers 1·5 × 1 mm, 4–5-merous; pedicels 0·2–1·5(–2·5) mm long; plants erect to decumbent with branched ascending stems up to 60 mm; internodes shorter than leaves; S America (Fig. 7 F–K) . . . . . e. var. **muscoides**

a. var. **connata**

Tillaea rubescens Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. 6: 43 (1823). Type: Ecuador, Alausi, 1802 *Humboldt & Bonpland* s.n. (holotype P!).

T. minima Miers, Trav. Chile & La Plata 2: 530 (1826) nom. nud.

T. minima Miers ex Hook. & Arn., Bot. Misc. 3: 338 (1833), nom. illegit., superfl. Type as for *T. erecta*.

T. minima Gay, Fl. Chil. 2: 529 (1847). Type: Chile, Santiago, *Gay* s.n. (holotype P!).

DISTRIBUTION. California, Mexico, Guatemala, Colombia, Ecuador, Peru, Bolivia, Argentina, Chile (Map 2, Fig. 7 A–E).

b. var. **erectoides** *Bywater & Wickens* var. nov.

A var. *eremica* sepalis carpellis aequilongis, floribus parvis et pedicellis brevibus differt. Type: California, Santa Catalina Island, *Nuttall* 143 (holotype K!). (Plate 33 E–F, Fig. 6 A–E).

DISTRIBUTION. Arizona, California, Mexico, Chile (Map 2).

FIG. 6. *C. connata*: **A–E** *var. erectoides*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Nuttall* 143. **F–K** *var. eremica*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26, from *Jepson* 8636. **L–R** *var. subsimplex*: **L** habit × 8; **M** ½ flower × 16; **N** sepal × 20; **P** petal × 20; **Q** scale × 26, from *Hartweg* 1734. Drawn by author (M.B.).

c. var. **eremica** *(Jepson) Bywater & Wickens* comb. nov.

Tillaea erecta Hook. & Arn. var. *eremica* Jepson, Man. Fl. Pl. Calif.: 450 (1925). Type: California, Vallecito, *Jepson* 8636 (holotype JEPS!).
T. erecta Hook. & Arn. subsp. *eremica* (Jepson) Wiggins in Shreve & Wiggins, Veg. & Fl. Sonoran Desert 1: 572 (1964).

DISTRIBUTION. Arizona, California, Mexico, Peru (Map 2, Fig. 6 F–K).

d. var. **subsimplex** *(S. Watson) Bywater & Wickens* comb. nov.

Tillaea leptopetala Benth., Pl. Hartw.: 310 (1849). Type: California, San Francisco, *Hartweg* 1734 (holotype K!; isotype NY!).
T. minima Miers ex Hook. & Arn. var. *subsimplex* S. Watson in Brewer, Watson & Gray, Bot. Calif. 1: 208 (1876). Type as for *T. leptopetala*.

DISTRIBUTION. Arizona, Oregon, California, Mexico (Map 2, Fig. 6 L–Q).

e. var. **muscoides** *Bywater & Wickens* var. nov.

Tillaea muscosa Gay, Fl. Chil. 2: 529 (1847) non L. (1753). Type: Chile, Chiloe, *Gay* s.n. (holotype P!).

A var. *connata* floribus sessilibus usque brevipedicellatis, longioribus quam latis, interdum 5-meris, foliis internodia superantibus et caulibus ramosissimis differt. Type: as for *Tillaea muscosa* Gay, above. (Plate 33 C–D, Fig. 7 F–K).

DISTRIBUTION Argentina, Chile (Map 2).

While we have endeavoured to take a wide view of the *Crassula connata* complex throughout its New World distribution, relationships between Australian and South African species of Sect. *Glomeratae* cannot be discounted. A world-wide revision of this section is needed to establish the true specific limits.

14. Crassula tillaea Lester-Garland, Fl. Jersey: 87 (1903); Wickens & Bywater in Kew Bull. 34; 634 (1980).

Tillaea muscosa L., Sp. Pl.: 129 (1953). Type: 'Habitat in Italiae, Siciliae, Galliae muscosis' (holotype LINN!).
Crassula muscosa (L.) Roth, Enum. Pl. Phan. Germ. 1: 994 (1827) non *C. muscosa* L., Pl. Afr.: 10 (1760).

Erect herb up to 40 mm high, little branched from base. Leaves lanceolate-triangular, 1–2 mm long, acute. Pedicels 0·2–0·5(–1·5) mm long, not exceeding leaves. Flowers (1–)2 per node, 3(–4)-merous, 1·3–1·6 × 0·7–1·2 mm. Sepals triangular, c. 1·5 × petals, 1·2–1·6 × 0·4–0·6 mm, aristate. Petals narrowly triangular, 0·8–1 × 0·2–0·3 mm, aristate. Scales filamentous, narrowly spathulate, 0·5 mm long. Carpels 2-seeded. (Fig. 5 M–R).

SEED. [LM]: small, ellipsoid, 0·32 × 0·15 mm, reddish brown, smooth with irregular longitudinal ridges apparent towards apices. [SEM]: cell divisions obscure, cell lobes rounded, surface smooth to minutely rugulose. (Plate 33 G–H). Of the 12 Californian specimens seen, seeds were examined under SEM of 2 collections. These were indistinguishable from seeds previously examined from European specimens and of the same form as those of *C. connata*.

HABITAT. Terrestrial, sides of roads and ditches, generally on dry, well-drained sites.

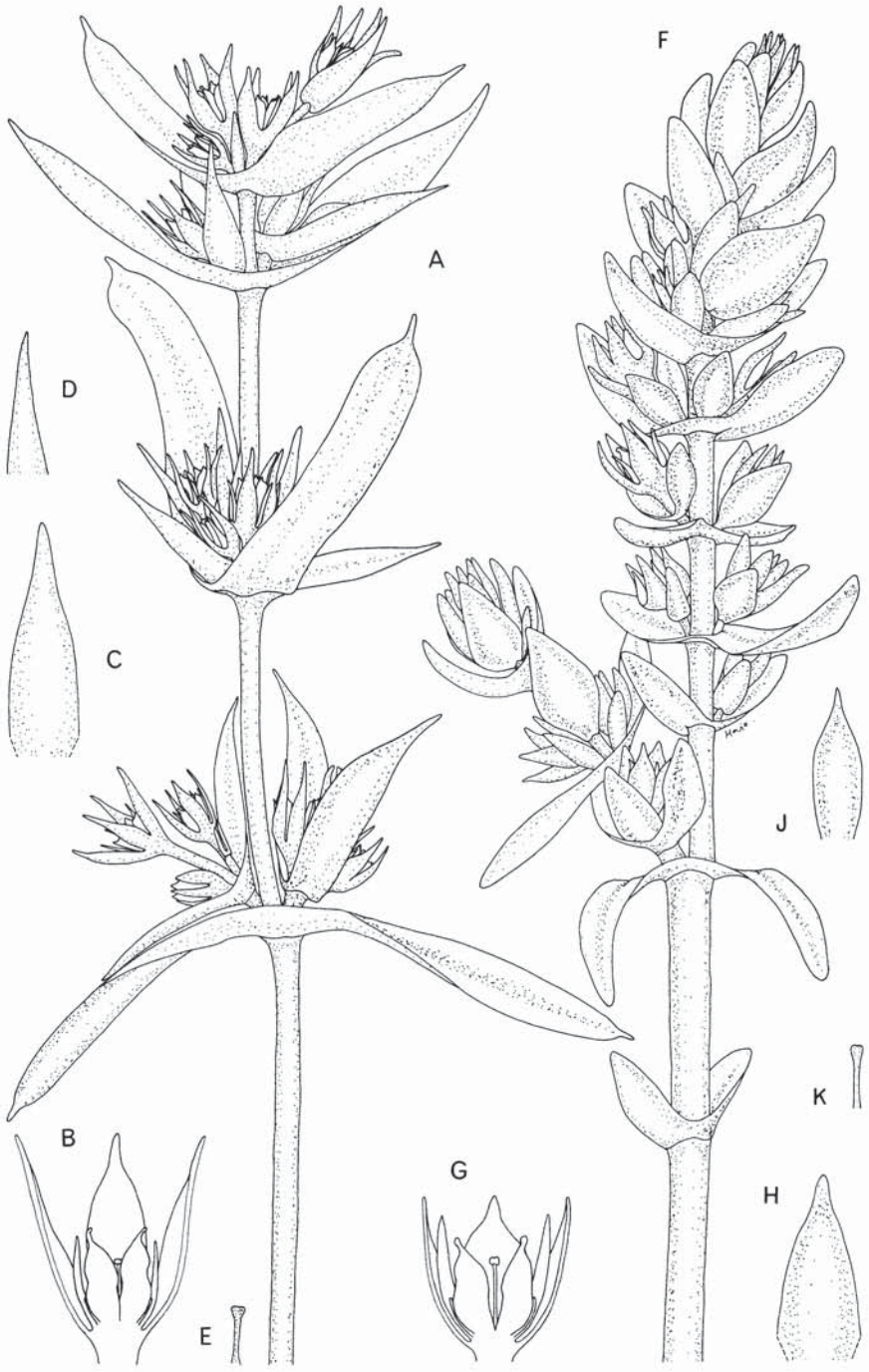


FIG. 7. *C. connata*: **A–E** *var. connata*: **A** habit × 8; **B** ½ flower × 16; **C** sepal × 20; **D** petal × 20; **E** scale × 26, from *Eyerdam* 24958. **F–K** *var. muscoides*: **F** habit × 8; **G** ½ flower × 16; **H** sepal × 20; **J** petal × 20; **K** scale × 26, from *Gay* s.n. Drawn by author (M.B.).

DISTRIBUTION. California (introduced and naturalized), W & S Europe, Turkey, Morocco to Tunisia, Madeira and Canary Is. (Map 2).

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2. aquatica	7. longipes	12. closiana	c. eremica
3. saginoides	8. peduncularis	12/1. phascoides	d. subsimplex
4. venezuelensis	9. drummondii	13. connata	e. muscoides
5. minutissima	10. viridis	var.a. connata	14. tillaea

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