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## A new subfamily Calasterelloideae and new genus *Calasterella* for a phylogenetically and morphologically distinct member of the Aytoniaceae

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### Abstract

Based on a phylogenetically and morphologically distinct species, a new genus *Calasterella* is established. A new subfamily, Calasterelloideae, is also proposed to contain this genus.

### Introduction

Since the introduction of molecular approaches to studies on the genus *Asterella* Palisot de Beauvois (1805: 257), the current morphology-based classification and specific treatment of this genus have been partly challenged (Schill *et al.* 2010; Xiang *et al.* 2022), and these issues require further careful review. *Asterella californica* (Hampe ex Austin 1873: 33) Underwood (1895: 60) is one such controversial species, which was originally published as “*Fimbriaria californica*” Hampe ex Austin (Austin 1873) and transferred to *Asterella* by Underwood in 1895 (Fig. 1). The latter treatment has been widely adopted since then (Long 2005, 2006; Söderström *et al.* 2016). However, recent molecular studies seem to suggest a different view, in which *A. californica* is resolved in its own separate clade sister to a *Asterella*-*Mannia* Corda (1829: 646)-*Plagiochasma* Lehmann (1832: 13)-*Reboulia* Raddi (1818: 357) clade (Long *et al.* 2000) or *Mannia* clade (Borovichev *et al.* 2015) rather than nested within *Asterella*. In 2016, Villarreal *et al.* conducted a multi-locus phylogenetic study and resolved Aytoniaceae into three major clades, *Asterella californica*, *Asterella* (s.str.)-*Mannia*-*Plagiochasma*-*Reboulia* and *Asterellopsis* Zhu & Xiang (2022: 659)-*Cryptomitrium* Austin ex Underwood (1884: 36). A more extensive molecular study now nearing completion should further reinforce this conclusion (Long *et al.*, unpublished). All of the above studies seem to consistently support an independent generic status for *A. californica* rather than as a member of *Asterella*.

Morphologically, *Asterella californica* has been regarded as a highly distinctive taxon in *Asterella* (Howe 1899; Evans 1920; Haupt 1929; Long 1999, 2005). This species is distinguished from all other taxa of Aytoniaceae by the following morphological combination: (1) dioicous sexuality, (2) strictly dichotomous branching, (3) ventral scales with up to four subulate appendages, (4) an ovoid deeply lobed female receptacle with pseudoperianths, (5) an involucre cleft to base, and (6) lemon-yellow spores with conspicuous trilete ridges, prominent equatorial wing, similar ornamentation on proximal and distal surfaces, lacking large areolae but with fine network of alveolae (Fig. 1, 2, 3). Based on the collective phylogenetic and morphological evidence noted above, we here propose to establish a new genus, *Calasterella*, to contain this species. Due to the unique combination of morpho-phylogenetic characters, a new subfamily, Calasterelloideae, is also proposed to contain this genus. The following treatment is thus necessary:

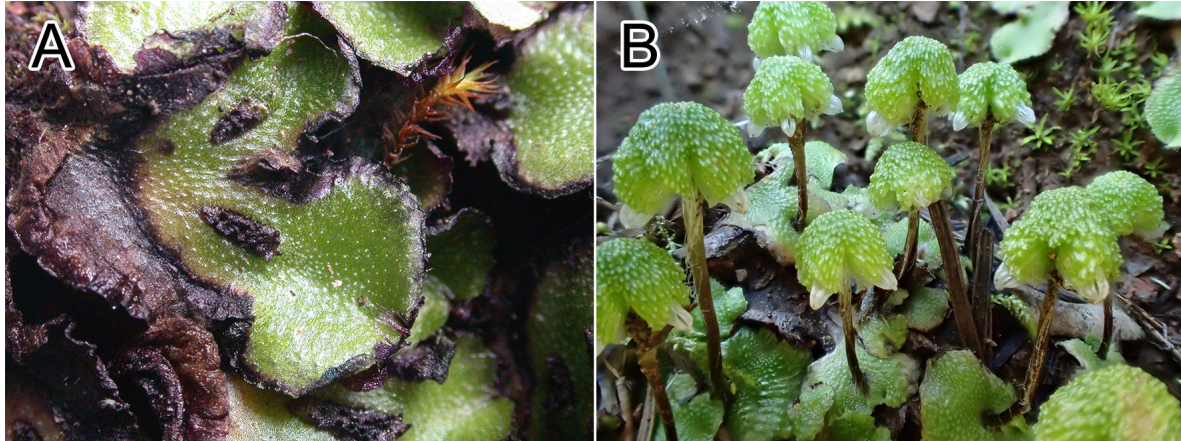
### Taxonomy

#### 1. Calasterelloideae T.X.Zheng & D.G.Long, *subfam. nov.*

Calasterelloideae T.X.Zheng & D.G.Long *subfam. nov.* includes one genus, *Calasterella* D.G.Long & T.X.Zheng, *gen. nov.*

**Diagnosis:** Differs from Aytonioideae and Reboulioideae by the following combination: dioicous sexuality; strictly dichotomous branching pattern; ventral tissue with mucilage cavities; up to four appendages of ventral scale; deeply-lobed female receptacle with pseudoperianths and involucre cleft to base; lemon-yellow spores with conspicuous trilete ridges, prominent equatorial wing, similar ornamentation on proximal and distal surfaces, lacking large areolae but with fine network of alveolae.

**Type:** *Calasterella* D.G.Long & T.X.Zheng, *gen. nov.*



**FIGURE 1.** *Calasterella californica* (Hampe ex Austin) D.G.Long & T.X.Zheng ( $\equiv$  *Asterella californica* (Hampe ex Austin) Underw.). A. Male plant (*W. T. Doyle 11445-b*, E). B. Female plant (*D.G. Long & J. Shevock 45892*, E).

## 2. *Calasterella* D.G.Long & T.X.Zheng, *gen. nov.*

Type species: *Calasterella californica* (Hampe ex Austin) D.G.Long & T.X.Zheng *comb. nov.* ( $\equiv$  *Fimbraria californica* Hampe ex Austin, *Hepat. bor.-amer.* 33, 1873).

### Fig. 1, 2, 3

**Description:** Dioicous; thallus lacking odour when crushed, branching strictly dichotomous, differentiated into upper photosynthetic aerenchyma with irregular air chambers in up to 5 layers and ventral compact tissue with mucilage cavities, epidermis with simple air pores; ventral scales in two rows, each with 1–4 subulate appendages; gemma cups absent; rhizoids dimorphic; androecium cushioned, dorsal, not terminating vegetative growth; female receptacle ovoid, deeply 4(5)-lobed, with stout, longitudinally ridged stalk, terminal on main thallus, not terminating vegetative growth which continues as innovations from both apical lobes; involucre deeply cleft to base, sporophyte enclosed in pseudoperianth; spores lemon-yellow with conspicuous trilete ridges, prominent equatorial wing, similar ornamentation on proximal and distal surfaces, lacking large areolae but with fine network of alveolae.

**Etymology:** The genus is named by the combination of the abbreviation of its main distribution region “California”, and the previous placement “*Asterella*”.

**Distribution:** North America (Mexico and United States).

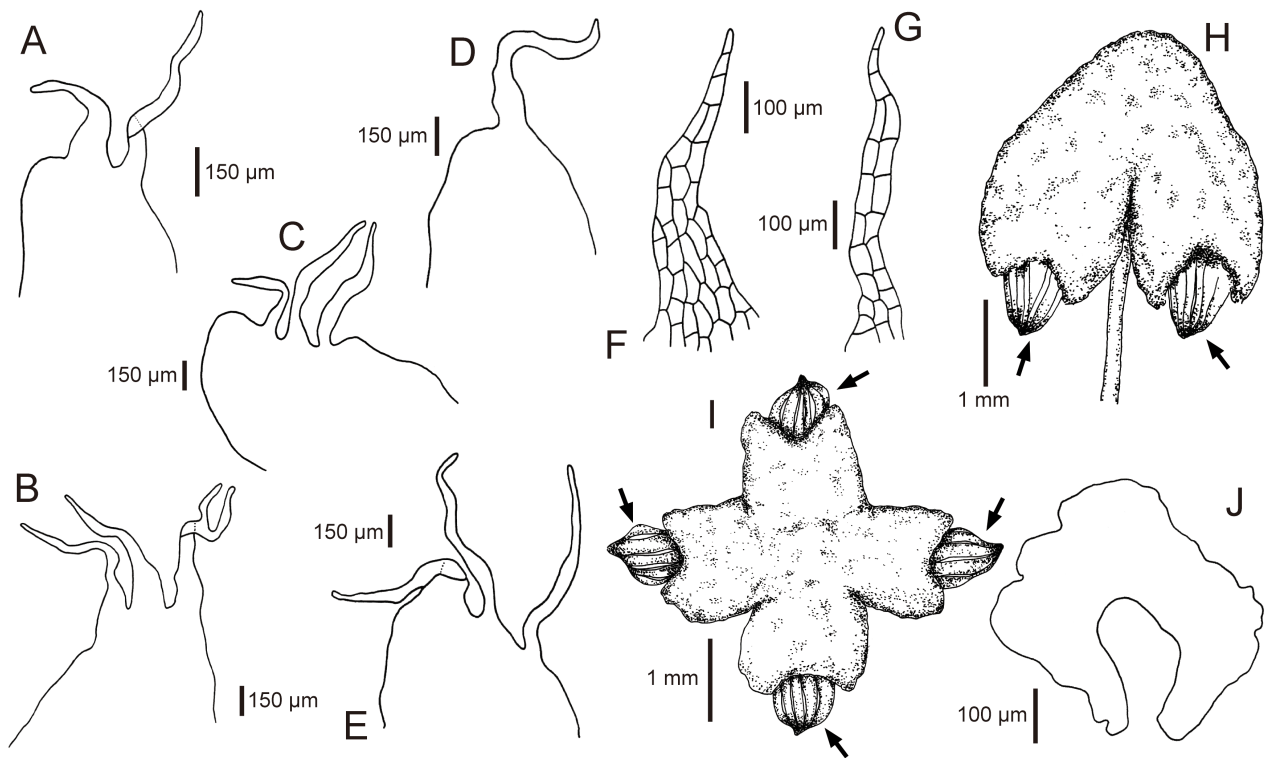
## 3. *Calasterella californica* (Hampe ex Austin) D.G.Long & T.X.Zheng, *comb. nov.*

Basionym: *Fimbraria californica* Hampe ex Austin, *Hepat. bor.-amer.* 33, 1873.

$\equiv$  *Asterella californica* (Hampe ex Austin) Underw., *Bot. Gaz.* 20: 60, 1895.

**Representative specimens examined:** MEXICO. Baja California: Cedros Island, 27 March 1952, *G. Lindsay 17559* (HIRO). UNITED STATES. California: El Dorado County, American River at Folsom Lake, 290 m, 31 March 1998, *D.G. Long 27540* (CAS, E00995790); Fresno Co., Sunnyside Road, west end of Pine Flat Lake, 310 m, 2 April 1998, *D.G. Long 27552* (CAS, E00995793); Lake Co., Route 20 east of Clearlake Oaks, 660 m, 30 March 1998, *D.G. Long 27533* (E00995789); Los Angeles Co., Angels Crest Highway above La Canada, 780 m, 7 April 1998, *D.G. Long 27614* (E00995163); Marin Co., Cataract Creek, above Alpine Lake, 220 m, 16 March 2019, *D.G. Long & J. Shevock 45892* (E01004900); Mariposa Co., Merced River Canyon at Slate Creek Bridge east of Briceburg, 390 m, 20 April 2017, *D.G. Long & J. Shevock 44775* (E00997959); Napa Co., Wooden Valley Grade, 18 Mar. 1934, *A. Carter 444* (NICH 201792); Nevada Co., north of Bridgeport on Pleasant Valley Road, 12 Apr. 1965, *E. G. McLaughlin s.n.*

(NICH 262543); Riverside Co., Dripping Springs, Agua Tibia Wilderness, 460 m, 9 April 1998, *D.G. Long 27651* (E00995160); San Benito Co., Pinnacles National Monument, between parking area and caves, 350 m, 27 April 2006, *W. T. Doyle 11445-b* (E01004302). Western foothills of the Gabian Range, San Juan Grade Road, County Road 3, just west of the 1.21 mileage marker, 154 m, 19 March 2010, *W. T. Doyle 11553* (CAS, TNS); San Bernardino Co., San Gabriel Mountains, near Lytle Creek, 740 m, 8 April 1998, *D.G. Long 27624* (E00995162); San Luis Obispo Co., Los Padres National Forest West Cuesta Ridge on TV Tower Road, 640 m, 30 March 2019, *D.G. Long & J. Shevock 45940* (E); Santa Clara Co., Los Altos Hills, 31 Aug. 1971, *W. B. Schofield s.n.* (NICH 306406), *do.*, 10 Mar. 1993, *W. B. Schofield 98595* (NICH 428742); Sonoma Co., route 128 NW of Cloverdale, 200 m, 27 March 1998, *D.G. Long 27481* (E00995788); Tulare Co., east side of Lake Kaweah near Three Rivers, 219 m, 7 March 2017, *D.G. Long, J. Shevock & W.-Z. Ma 44666* (E00997960); Tuolumne Co., Columbia, 1.0 mile above Parrott's Ferry Bridge over the Stanislaus River, 2 July 1966, *D. M. J. Mueller 6703* (NICH 298550); Ventura Co., Creek Road, Ojai, 23 Mar. 1927, *N. B. Kimber 2894* (NICH 216581). Oregon: Josephine Co., south side of Rogue River along trail to Raine Falls below Grave Creek Bridge, 205 m, 25 March 2018, *D.G. Long & J. Shevock 45333* (E00997086).

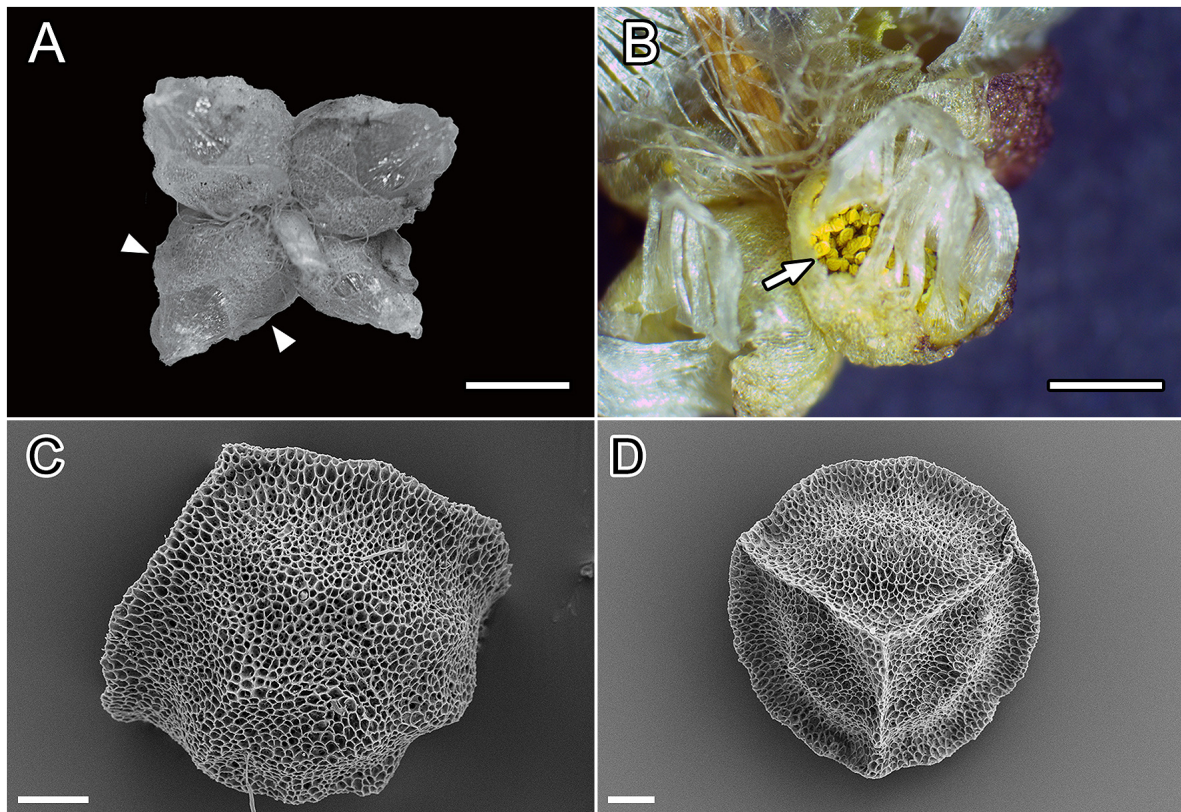


**FIGURE 2.** *Calasterella californica* (Hampe ex Austin) D.G.Long & T.X.Zheng. A–E. Ventral scales; F, G. Appendages of ventral scales; H. Carpocephalum showing pseudoperianths (lateral view); I. Carpocephalum showing pseudoperianths (dorsal view); J. Transverse section of stalk of archegoniophore. Arrow: pseudoperianths.

[A: *N. B. Kimber 2894* (NICH). B, G, H: *E. G. McLaughlin s.n.* (NICH). C, F: *A. Carter 444* (NICH). D, I, J: *W. B. Schofield 98595* (NICH). E: *W. B. Schofield s.n.* (NICH).]

**Taxonomic notes:** Based on the morphological and phylogenetic evidence, we here establish *Calasterella* D.G.Long & T.X.Zheng as the seventh genus of the family Aytoniaceae. This genus may be confused with *Mannia* and *Reboulia* given that they share a similar appearance and female receptacle, respectively (Bischler 1998; Bischler-Causse *et al.* 2005). However, both *Mannia* and *Reboulia* show absence of a pseudoperianth (except *Mannia gracilis* (Weber 1815: 105) Schill & Long (2010: 173)) but display dichotomous, ventral or terminal innovative thallus branching while *Calasterella* has dichotomous branching only. In addition, *Mannia* possesses (1) aromatic plants, (2) depressed hemispherical or subglobose female receptacles, and (3) cup-shaped involucre (Schill 2006). *Reboulia* has (1) bilabiate involucre, (2) ventral scales with 2–3(4) filiform appendages, (3) 4–7-lobed receptacles and (4) yellowish brown coarsely areolate spores (Bischler 1998; Bischler-Causse 2005). *Calasterella* can be confused with *Asterellopsis* because both taxa have dichotomously branching thalli. The latter, however, is distinguished by (1) fewer (1–2) and sometimes unequally bifid ventral scale appendages, (2) spherical female receptacles, and (3) dark brown or black spores with germinal apertures. When sterile, *Calasterella* is more or less similar to *Preissia* Corda (1829: 647)

and *Bucegia* Radian (1903: 3) (Marchantiaceae). However, the latter two genera can be readily differentiated by their compound air pores (Zheng & Shimamura 2022). The only other dioicous species traditionally placed in *Asterella* is the Asiatic *A. wallichiana* (Lehmann & Lindenbergh 1832: 4) Grolle (1966: 262), but as pointed out by Long (2006) the latter is readily distinguished by the complete cessation of vegetative growth at the apex of the thallus of female plants, whereas in *C. californica* vegetative growth continues from the lateral lobes at the thallus apex (Haupt 1929: Fig. 9).



**FIGURE 3.** *Calasterella californica* (Hampe ex Austin) D.G.Long & T.X.Zheng. A: Immature carpocephalum from below showing deeply cleft involucre with overlapping margins of cleft. B: Mature carpocephalum from below showing pseudoperianths and dehiscid sporophyte with lemon-yellow spores. C: Scanning Electron Micrographs of the spores, distal face. D: Scanning Electron Micrographs of the spores, proximal face. Arrow heads: involucre. Arrow: spores. Scale bars: A, 2 mm; B, 1 mm; C, D: 20 µm.

[A: D.G. Long 45940 (E). B: D.G. Long 45333 (E). C, D: D. G. Long *et al.* 44666 (E)]

Traditionally, Aytoniaceae was divided into two subfamilies (Grolle 1983; Grolle & Long 2000), Aytonioideae (*Plagiochasma*) and Reboulioideae (*Asterella* s. lat., *Cryptomitrium*, *Mannia*, and *Reboulia*). However, recent phylogenetic studies on complex thalloid liverworts have proposed a different conclusion (Villarreal *et al.* 2016; Xiang *et al.* 2022), in which Aytoniaceae is resolved into five major clades, namely *Asterella* s. str., *Asterellopsis-Cryptomitrium*, *Calasterella*, *Mannia* and *Reboulia-Plagiochasma*, and this grouping is inconsistent with the traditional bipartite classification of the family. Previously, the presence of pseudoperianths was regarded as a unique character that distinguished *Asterella* s. lat. from other genera of the family (Long 2006). However, the recent studies by Schill *et al.* (2010) transferred *A. gracilis* to *Mannia*, and Xiang *et al.* (2022) established a new genus *Asterellopsis* based on the species *Asterella grollei* Long (1999: 102), indicating that the pseudoperianth is probably a plesiomorphic feature, and the morphology of spores might be used as a more informative character to underpin the classification within Aytoniaceae (Long 1998; Schill 2006; Schill *et al.* 2010). To solve this problem and propose an amended classification of Aytoniaceae at subfamily level, phylogenetic studies involving more samples from a wide geographical range are now nearing completion.

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