

Review of the fossil record of *Passiflora*, with a description of new seeds from the  
Pliocene Gray Fossil Site, Tennessee, U.S.A.

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16

## Abstract

17

18       *Premise of the research.* Passifloroideae (over 700 species), which include the  
19 large genus *Passiflora* (over 550 species), are distributed pantropically today. The fossil  
20 record of the group is, nevertheless, small and poorly understood. In this study, I  
21 provide a critical review of the fossil record of *Passiflora* and Passifloroideae, with a  
22 description of a new fossil species based on seeds.

23       *Methodology.* I examined thirteen specimens of *Passiflora*-like seeds from the  
24 Pliocene Gray Fossil Site, eastern Tennessee, U.S.A. In order to evaluate their  
25 affinities, I reviewed the available literature on Passifloroideae with emphasis on  
26 *Passiflora*, including images of seeds of over 200 species of *Passiflora*. I also reviewed  
27 the literature on the fossil record of Passifloroideae and obtained supplementary images  
28 of some fossil taxa.

29       *Pivotal results.* Several subgeneric groups within *Passiflora* can be distinguished  
30 on the basis of isolated seeds. As a result, I emend the diagnosis of  
31 *Passifloroidesperma* Martínez-A.—a fossil genus encompassing seeds assignable to  
32 Passifloroideae but not an extant genus therein—to eliminate characters diagnostic for  
33 subgeneric taxa within *Passiflora*. Two Miocene fossil seed species from Europe,  
34 *Passiflora kirchheimeri* Mai and *P. heizmannii* H.-J. Gregor, are reassigned to  
35 *Passifloroidesperma*. Two additional fossil seed species are assigned to *Passiflora*:  
36 *Passiflora bulgarica* (Palam.) Hermsen, stat. nov., from the middle Miocene of Bulgaria  
37 and *P. appalachiana* Hermsen, sp. nov., from Gray Fossil Site.

38           *Conclusions.* The presence of fossil passifloroid seeds in Europe shows that  
39 Passifloroideae once occurred in that region, although they are no longer found there  
40 today. *Passiflora bulgarica* has characteristics consistent with placement in  
41 supersection *Cieca*, a group today confined to the Americas. *Passiflora appalachiana* is  
42 similar to modern *Passiflora incarnata*, which is widespread in the eastern United  
43 States. *Passiflora appalachiana* is the first plant macrofossil taxon described from Gray  
44 Fossil Site that shows a neotropical rather than Laurasian biogeographic connection.

45

## 46           **Introduction**

47

48           The genus *Passiflora* L. (Passifloraceae Juss. ex. Roussel, subfamily  
49 Passifloroideae Burnett), the passionflowers, includes over 550 species of vines, lianas,  
50 shrubs, and small trees (MacDougal and Feuillet 2004; Ulmer and MacDougal 2004;  
51 Feuillet and MacDougal 2007; Hilgenhof 2013; Krosnick et al. 2013a). Passionflowers  
52 are known for their unusual flowers, which often have a conspicuous corona made up of  
53 one or more series of sterile appendages, as well as stamens and carpels that are  
54 fused into an androgynophore (Jørgensen et al. 1984; Ulmer and MacDougal 2004;  
55 Feuillet and MacDougal 2007; Bonilla Morales et al. 2015); some species are cultivated  
56 as ornamentals, for their edible fruits, or for medicinal purposes (Ulmer and MacDougal  
57 2004; Ocampo Pérez 2007; Yockteng et al. 2011). *Passiflora* is primarily distributed in  
58 the Americas—especially the Neotropics—although a small number of species (ca. 25)  
59 are native to the Old World tropics in South Asia to China, southeast Asia, and Oceania  
60 (Fig. 1; Krosnick and Freudenstein 2005; Ocampo Pérez 2007; Wang et al. 2007;

61 Krosnick et al. 2009, 2013a, 2013b; Ma et al. 2019). The taxonomy of the genus is  
62 complex, with species presently divided into five subgenera: *Astrophea* (DC.) Mast. (66  
63 species), *Decaloba* (DC.) Rchb. (ca. 230 species), *Deidamiooides* (Harms) Killip (13  
64 species), *Passiflora* (ca. 250 species), and *Tetrapathea* (DC.) P.S. Green (3 species)  
65 (Feuillet and MacDougal 2003; MacDougal and Feuillet 2004; Krosnick et al. 2009,  
66 2013a; Hilgenhof 2013); four of the subgenera are further subdivided in supersections,  
67 sections, and/or series (Feuillet and MacDougal 2003; MacDougal and Feuillet 2004).  
68 Despite the modern diversity of the genus, few reports of *Passiflora* macrofossils exist,  
69 and the majority of these are considered dubious (reviewed by Kozak 2015; Martínez  
70 2017; see also the discussion below). The most credible reports are typically considered  
71 to be of selected fossil *Passiflora* seeds from the Miocene of Germany (one of these  
72 seeds was used as a fossil calibration by Hearn 2006 and Muschner et al. 2012; see  
73 also reviews by Kozak 2015 and Martínez 2017). However, Martínez (2017) argued that  
74 *Passiflora* seeds cannot be distinguished from those of other extant genera in subfamily  
75 Passifloroideae, and thus that isolated fossil "Passiflora" seeds should be referred to the  
76 subfamily using the fossil genus *Passifloroidesperma* Martínez-A.

77 Passifloroideae (16 genera, over 700 species, mostly neotropics and  
78 paleotropics; Fig. 1) are the largest subfamily of Passifloraceae, a family that includes  
79 about 27 genera and over 1000 species of plants primarily distributed in the tropics  
80 (Stevens 2001 onwards). The family is divided into four subfamilies: Malesherbioideae  
81 Burnett, Turneroideae Eaton, Passifloroideae, and Pibirioideae M.W.Chase &  
82 Christenh. (Stevens 2001 onwards; APG III 2009; Maas et al. 2019). Passifloraceae are  
83 characterized by the presence of cyclopentenoid cyanogenic glycosides (Stevens 2001

84 onwards; APG II 2003; Maas et al. 2019). Distinctive morphological characteristics  
85 shared by some or all subfamilies of Passifloraceae include extrafloral glands (i.e., leaf  
86 glands/nectaries or glandular hairs), a floral tube formed by the perianth, a corona, an  
87 androgynophore, a tricarpellate ovary with parietal placentation, and arillate seeds (APG  
88 II 2003; Arbo 2007; Feuillet and MacDougal 2007; Kubitzki 2007; Maas et al. 2019). All  
89 three subfamilies of Passifloraceae for which seeds are known  
90 (*Malesherbioideae/Malesherbia* Ruiz & Pav., Passifloroideae, Turneroideae) have a  
91 seed coat with a layer of elongated, sclerified cells (palisade/radial in *Malesherbia* and  
92 Passifloroideae, oblique in Turneroideae) and often foveolate or reticulate sculpture  
93 (Johri et al. 1992; Arbo 2007; Feuillet and MacDougal 2007; Kubitzki 2007; Gonzalez  
94 and Arbo, 2013; Martínez 2017). Notably, seeds of Passifloroideae can easily be  
95 distinguished from seeds of other subfamilies of Passifloraceae because passifloroid  
96 seeds are usually compressed (Stevens 2001 onwards; Martínez 2017). They also have  
97 ruminate endosperm (Dathan and Singh, 1973; Johri et al. 1992; Feuillet and  
98 MacDougal 2007; Gurski 2015; Martínez 2017), which is absent (Turneroideae: Johri et  
99 al. 1992) or not reported and here presumed absent (*Malesherbioideae*) in the other  
100 subfamilies. For a discussion of other differentiating seed characteristics at the  
101 subfamily level in Passifloraceae, see Martínez (2017).

102 For this study, I reassessed the morphological variation among seeds of taxa  
103 within Passifloroideae—with particular focus on subgroups within the genus  
104 *Passiflora*—primarily on the basis of published images and descriptions. Based on my  
105 findings, I emend the circumscription of *Passifloroidesperma* and provide updated  
106 classifications for fossil seed species and subspecies from Europe. I also describe a

107 new species of fossil *Passiflora* seeds from the early Pliocene Gray Fossil Site (GFS),  
108 eastern Tennessee, U.S.A. The GFS seeds are similar to the seeds of the eastern  
109 North American native species *Passiflora incarnata* L. (purple passionflower/maypop)  
110 and provide a new, neotropical biogeographic connection for the Gray Fossil Site  
111 macroflora.

112

113 *Fossil record of Passifloroideae*

114

115 The fossil record of Passifloroideae has been reviewed recently by Kozak (2015,  
116 who also covered Turneroideae) and Martínez (2017). Each provided evaluations of  
117 pollen, leaf, and seed records, although their treatments overlap only partially in  
118 taxonomic coverage and occurrences. They considered most fossil pollen reports  
119 dubious (Table A3), including pollen from the Paleogene (*Spirosyncolpites spiralis*  
120 González-Guzmán) and Neogene (*Stephanocolpites* sp. Hammen) of northern South  
121 America and the Neogene of Mexico (*Passiflora*) (for original reports, see Graham  
122 1976; Hoorn 1994; Jaramillo et al. 2010a, b). Martínez (2017: 1858) rated only one—  
123 *Syncolpites* sp. Hammen from the late Miocene of Patagonia, Argentina (Palazzi et  
124 al. 2014)—to be of “medium” reliability. Palazzi et al. (2014, see their supplementary  
125 information) compared this pollen to pollen of extant *Passiflora caerulea* L. (as  
126 “*Passiflora coerulea*”). Examination of published images of a Patagonian *Syncolpites*  
127 grain (see supp. fig. 3C, F in Palazzi et al. 2014), however, shows that it has more  
128 apertures than a *P. caerulea* pollen grain (cf. *P. caerulea* pollen, fig. 35 in Amela García  
129 et al. 2002); furthermore, the apertures (holes) in the *Syncolpites* grain are distributed

130 over the entire surface of the grain rather than equatorially, as in *P. caerulea* (cf. *P.*  
131 *caerulea* pollen, fig. 35 in Amela García et al. 2002; see also Table A3). Thus, the  
132 assignment of the Patagonian fossil pollen to *Passiflora* based on similarity to *P.*  
133 *caerulea* pollen is not supported. A final fossil pollen report not covered in prior reviews  
134 is *Retistephanocolpites "passionis"* (ined., name proposed in a thesis) from the Miocene  
135 of Brazil; this pollen type was considered to have affinities to *Passiflora* or possibly  
136 Bignoniacae Juss. (D'Apolito 2016; see also Table A3).

137 Both Kozak (2015) and Martínez (2017) considered reports of passifloroid  
138 macrofossils from the Late Cretaceous—including the seed *Carpolithus passifloriformis*  
139 K.I.M.Chesters from Nigeria (Chesters 1955) and the leaf *Passiflora antiqua* Newb. from  
140 the northeastern U.S.A. (Newberry 1895)—to be unreliable. *Carpolithus passifloriformis*  
141 is represented by one seed (Chesters 1955). Chesters (1955; see also Martínez 2017)  
142 noted that the seed differs from modern passifloroid seeds in size and seed coat  
143 sculpture (i.e., presence of a vertical furrow, number of pits), and thus indicated  
144 uncertainty about its affinities. The holotype of *Passiflora antiqua* is a bilobed leaf from  
145 Woodbridge, New Jersey (Fig. 2A; Newberry 1895; Berry 1911). While bilobed leaves  
146 occur in extant *Passiflora* (Fig. 2B; MacDougal and Feuillet 2004; Ulmer and  
147 MacDougal 2004; Milward-de-Azevedo et al. 2012; Krosnick et al. 2013a; Boza  
148 Espinoza et al. 2018), it seems more likely that *P. antiqua* is a poorly preserved  
149 example of similar leaves from Woodbridge assigned to *Bauhinia cretacea* Newb. (Fig.  
150 2C; Newberry 1886, 1895; Berry 1911). Newberry (1895) separated *P. antiqua* and *B.*  
151 *cretacea* based on overall size, apex angle, and venation pattern. Newberry's  
152 "Bauhinia" leaves have been linked to *Liriophyllum* Lesq. (Herendeen et al. 1992) and

153    *Liriodendrites* Johnson (Wang et al. 2014, see their additional file 4; Fig. 2D).  
154    *Liriophyllum* (Albian–Cenomanian, North America) and *Liriodendrites* (Cretaceous–  
155    Paleocene, Eurasia and North America) are bilobed leaf types with probable  
156    (*Liriophyllum*) or possible (*Liriodendrites*) affinities to Magnoliaceae (cf. *Liriodendron* L.)  
157    (Dilcher and Crane 1984; Johnson 1996; Alekseev 2009; Wang and Dilcher 2009, 2018;  
158    Romanov and Dilcher 2013; Wang et al. 2014; Harris and Arens 2016).

159           Cenozoic fossil leaves have been reported from deposits in Europe, the  
160    Americas, and Antarctica (Table A4). The first published fossil passifloroid leaves were  
161    from Italy and were originally assigned to *Granadilla* Mill. (synonym of *Passiflora*)  
162    (Massalongo 1850; IFPNI International Editorial Board 2014–2020); they have all since  
163    been reassigned to unrelated genera (Massalongo 1859). Many remaining reports of  
164    fossil *Passiflora* leaves from the nineteenth to mid-twentieth centuries are each based  
165    on few (ca. one to four) specimens of unlobed or trilobed leaves (Table A4; Friedrich  
166    1883a, b; Britton 1893; Berry 1919, 1939; Hollick 1927; Hunger 1939; Fischer 1950);  
167    the reliability of these reports is questionable, and they have been omitted from recent  
168    reviews of fossil Passifloroideae (Kozak 2015; Martínez 2017). Another genus,  
169    *Passifloraephyllum* Rásky, with the sole species *Passifloraephyllum kraeuselii* Rásky  
170    (Rásky 1960), is based on a single partial leaf specimen from the Oligocene of Hungary  
171    (Rásky 1960; revised age after Hably and Fernandez Marron 1998); Rásky (1960)  
172    compared the fossil leaf to leaves of several extant species of *Passiflora* (e.g.,  
173    *Passiflora sexflora* Juss.). *Passifloraephyllum* was used as a calibration in a study by  
174    Kozak (2015), who accepted it as a reliable record. In contrast, it was called  
175    “unconfirmed” by Krošnick et al. (2013a: 704, as *Passiflora*) and considered dubious by

176 Martínez (2017). Its relationship to Passifloroideae is equivocal. Pole (1994) described  
177 one partial leaf specimen from the Eocene of New Zealand with morphology similar to  
178 leaves of *Passiflora edulis* Sims; the relationships of this specimen are uncertain (Pole  
179 1994; Kozak 2015).

180 Fossil *Passiflora* leaf species based on larger suites of specimens (ca. 10 or  
181 more) include *Passiflora nikolaevii* Budantsev (likely including *Passiflora feilletii* Torres,  
182 nom. nud.), *Passiflora braunii* R.Ludw., and *Passiflora basiloba* Smiley. Of these, the  
183 oldest is *P. nikolaevii*, which is based on about 10 leaves from the Paleogene of King  
184 George Island, Antarctica (Budantsev 2012); these leaves are broad and bilobed with a  
185 truncate apex (Torres 2003; Budantsev 2012). Notably, *Passiflora* species with bilobed  
186 leaves tend to occur in the large monophyletic supersection *Decaloba* (DC.) Rchb.  
187 (MacDougal and Feuillet 2004; Ulmer and MacDougal 2004; Krosnick et al. 2013a;  
188 Boza Espinoza et al. 2018), and Budantsev (2012) compared *P. nikolaevii* leaves to  
189 bilobed leaves of the extant species *Passiflora biflora* Lam. of supersection *Decaloba*  
190 (Fig. 2B). While the bilobed-truncate morphology of *P. nikolaevii* is suggestive of a  
191 relationship to *Passiflora*, illustrations of the material do not show much architectural  
192 detail; thus, further investigation is necessary. *Passiflora braunii* was originally  
193 described on the basis of leaves, fruits, and seeds from the Miocene of Germany  
194 (Ludwig 1859–1860; IFPNI International Editorial Board 2014–2020). The illustrated *P.*  
195 *braunii* leaves (Ludwig 1859–1860: pl. 48, figs. 1–10) are simple, unlobed dicot leaves  
196 and are apparently not from the same plant as the reproductive material, which has  
197 been reassigned to *Spirematospermum* M.Chandler ex Kirchh. (discussed further  
198 below; see also Fischer et al. 2009 for leaf taxa associated with *Spirematospermum*);

199 the connection of the leaves to *Passiflora* is equivocal (Kirchheimer 1957). *Passiflora*  
200 *basiloba* is based on 15 specimens of 3–5-lobed leaves from the Miocene of the  
201 Ellensburg flora of Washington, U.S.A. (Smiley 1963; Gross 2021); the leaves have a  
202 long middle lobe, shorter lateral lobes, a cordate base, and no teeth (Smiley 1963).  
203 Smiley (1963) compared *P. basiloba* to leaves of the modern species *Passiflora foetida*  
204 L., a widespread New World species that is today found as far north as Texas (Smiley  
205 1963; Goldman and MacDougal 2015). As with *P. braunii*, *P. basiloba* is in need of  
206 reinvestigation.

207 The remainder of the macrofossil record of Passifloroideae comprises  
208 reproductive material, mostly Cenozoic seeds from Europe (Tables A1, A5; Fig. 3A–D).  
209 The first published fruits and seeds attributed to *Passiflora*, material assigned to  
210 *Passiflora braunii* (Ludwig 1859–1860) and *Passiflora pomeria* (Schloth.) Poppe (Poppe  
211 1866), have since been moved to *Spirematospermum wetzleri* (Heer) M.Chandler ex.  
212 Kirchh., an extinct monocot species (Kirchheimer 1957; Koch and Friedrich 1971;  
213 Fischer et al. 2009). The remaining fossil passifloroid seed reports include  
214 *Passifloroidesperma sogamosense* Martínez-A. from the Eocene of Colombia (Martínez  
215 2017), *Passiflora* cf. *kirchheimeri* Mai from the Eocene of Germany (Henniger et al.  
216 2011), *Passiflora heizmannii* H.-J.Gregor and *Passiflora* spec. from the Miocene of  
217 Germany (Gregor 1982), *Passiflora kirchheimeri* Mai from the Miocene of Germany and  
218 Poland (Mai 1960, 1967, 2000; Czeczott & Skirgielło 1967; Gregor 1978), and  
219 *Passiflora kirchheimeri* Mai subspecies *bulgarica* Palam. from the Miocene of Bulgaria  
220 (Palamarev 1971; Palamarev et al. 1999, 2005). All of these taxa are based on small  
221 seeds with reticulate-foveolate (or reticulate-foveate) surface sculpture and, where

222 described, a palisade seed coat (Tables A2, A5). Kozak (2015) and Martínez (2017)  
223 differed somewhat in their assessments of the reliability of these reports, although both  
224 agreed that at least some occurrences of *Passiflora kirchheimeri* credibly represent  
225 Passifloroideae (for details, see Table A5). Martínez (2017) recommended transferring  
226 the fossil taxa *Passiflora heizmannii*, *Passiflora kirchheimeri*, and *Passiflora*  
227 *kirchheimeri* subspecies *bulgarica* to the fossil genus *Passifloroidesperma*, which  
228 encompasses fossil seeds with characteristics of Passifloroideae.

229

230 **Materials and Methods**

231

232 *Fossil Passifloroideae*

233

234 The thirteen fossil seeds representing a new species of *Passiflora* studied for this  
235 project come from Gray Fossil Site (GFS), Gray, eastern Tennessee, U.S.A. The  
236 deposits at the site represent sediments from sinkholes that developed in carbonate  
237 bedrock (Shunk et al. 2006, 2009; Whitelaw et al. 2008). The GFS sinkhole sediments  
238 are divided into three facies; plant and vertebrate macrofossils occur in the laminated  
239 (middle) facies and the underlying transition zone between the laminated and graded  
240 (lower) facies, with well-preserved plant macrofossils occurring from about 505–500 m  
241 above sea level (Shunk et al. 2006; Gong et al. 2010; Liu and Jacques 2010). While  
242 there is some debate as to whether the site includes palynomorph-bearing Paleogene  
243 deposits (Zobaa et al. 2011; Odom et al. 2019), the macrofossil-bearing sediments are  
244 interpreted as being from a Neogene lake or pond thought to be near the Miocene-

245 Pliocene boundary in age (Parmalee et al. 2002; Wallace and Wang 2004; Shunk et al.  
246 2006, 2009; Gong et al. 2010; Liu and Jacques 2010). Recent age estimates from two  
247 independent sources—overlap in stratigraphic ranges of selected mammal taxa and  
248 cosmogenic nuclide burial dating—indicate a likely early Pliocene (Blancan) age of at  
249 least 4.5 Ma (Samuels et al. 2018; Odom et al. 2019). The Neogene GFS paleobiota  
250 includes large and small vertebrates (e.g., Parmalee et al. 2002; Wallace and Wang  
251 2004; Mead et al. 2012; Bourque and Schubert 2015; Czaplewski 2017; Jasinski and  
252 Moscato 2017; Doughty et al. 2018; Samuels et al. 2018; Short et al. 2019), plant  
253 macrofossils (Gong et al. 2010; Liu and Jacques 2010; Brandon 2013; Noll 2013;  
254 Huang et al. 2014, 2015; Quirk and Hermsen 2020; Siegert and Hermsen 2020), pollen  
255 and spores (Wallace and Wang 2004; Ochoa et al. 2012; Worobiec et al. 2013; Liu and  
256 Quan 2020), and fungi (Worobiec et al. 2018).

257 All Gray Fossil Site *Passiflora* seeds included in this study are permanently  
258 curated in the collections of the East Tennessee State University Museum of Natural  
259 History (ETMNH) at Gray Fossil Site, Gray, Tennessee, U.S.A. They include a total of  
260 13 seeds: two whole seeds (ETMNH 22625, 22627), nine half seeds (i.e., seeds that  
261 split longitudinally so that only one face or the other is preserved: ETMNH 21283,  
262 22626, 22630–22636), and two seeds broken irregularly (ETMNH 22628, 22629).  
263 Specimens were examined with a Nikon SMZ18 stereomicroscope and images were  
264 captured with a Nikon DS-Ri2 camera using NIS Elements Br software (1991–2018,  
265 Laboratory Imaging). Lighting was lateral, with specimens oriented longitudinally or  
266 transversely. NIS Elements was used to take measurements. Reported seed

267 dimensions (other than seed coat thickness) are based on measurements taken on the  
268 outer surface of each seed for the sake of consistency.

269 Other fossil Passifloroideae were investigated using the published literature and  
270 online databases (i.e., IFPNI International Editorial Board 2014–2020; GBIF.org 2020d).

271 New images of *Passiflora kirchheimeri* subspecies *bulgarica* were obtained courtesy of  
272 the Paleobotanical Collection, Institute of Biodiversity and Ecosystem Research,  
273 Bulgarian Academy of Sciences (IBER-PB), Sofia, Bulgaria; these include images of  
274 four seeds on a slide labelled “*Passiflora*” and “III/13 Чукурово [Chukurovo] *P. suberosa*  
275 L.” New combinations and changes in status for other fossil seed species from Europe  
276 are based entirely on published descriptions and illustrations, as cited below. *Passiflora*  
277 *antiqua*, *Bauhinia cretacea*, and *Liriodendrites* are illustrated here (Fig. 2A, C, D) using  
278 images captured by the Division of Paleobotany, Peabody Museum of Natural History  
279 (YPM), Yale University, New Haven, Connecticut, U.S.A. (Gall 2020a–c).

280

#### 281 *Classification system*

282

283 Circumscription of Passifloraceae herein follows APG IV (2016; see also APG II  
284 2003; APG III 2009; Stevens 2001 onwards). The family includes four subfamilies  
285 (Stevens 2001 onwards), three of which (Malesherbioideae, Turneroideae, and  
286 Passifloroideae) were previously recognized as distinct families (APG 1998; APG II  
287 2003; APG III 2009); the fourth (Pibirioideae) has only recently been described (Maas et  
288 al. 2019). Thus, subfamily Passifloroideae in this study is equivalent to Passifloraceae

289 as recognized in much of the older literature (e.g., APG 1998; Feuillet and MacDougal  
290 2007; Goldman and MacDougal 2015).

291 Passifloroideae include 16 extant genera; although 17 were previously  
292 recognized (Feuillet and MacDougal 2007; Tokuoka 2012; Martínez 2017), *Hollrungia*  
293 K.Schum. is now included in *Passiflora* (Krosnick et al. 2009). Within *Passiflora*, the  
294 infrageneric classification system of Feuillet and MacDougal (2003) and MacDougal and  
295 Feuillet (2004) has been followed to the extent possible. Because this system did not  
296 include a species list for *Passiflora*, most species were attributed to infrageneric taxa  
297 following other sources (Table A6; Jørgensen [no date]; Cervi 2003; Feuillet and  
298 MacDougal 2003, 2008; Ulmer and MacDougal 2004; Vanderplank 2004, 2013; Hansen  
299 et al. 2006; Feuillet 2007; Jørgensen and Vásquez 2009; Krosnick et al. 2009, 2013a;  
300 Vanderplank and Zappi 2011; Yockteng et al. 2011; Bernacci and Souza 2012;  
301 Hilgenhof 2013; Koch et al. 2013; Bonilla Morales 2014; Porter-Utley 2014; Nardin et al.  
302 2015; Ocampo et al. 2015; Ocampo Pérez and Molinari 2017; Rome and Coppens  
303 d'Eeckenbrugge 2017; Boza Espinoza et al. 2018; Ocampo Pérez et al. 2018; Silva et  
304 al. 2018; Svoboda and Harris 2018; Esquerre-Ibañez 2019; Ma et al. 2019). The small  
305 genera *Hollrungia* and *Tetrapathea* (DC.) Rchb. were included in *Passiflora* subgenus  
306 *Tetrapathea*—which was not part of the Feuillet and MacDougal (2003) and MacDougal  
307 and Feuillet (2004) system—following Krosnick et al. (2009). Authorship of species  
308 names in extant *Passiflora* and other extant taxa follows Feuillet and MacDougal (2002)  
309 and/or IPNI (2020) to the extent possible.

310

311 *Comparison to modern species*

312

313       The seeds from Gray Fossil Site were compared to seeds of Passifloroideae  
314 primarily using published photographs and descriptions. Seeds of over 200 extant  
315 species of *Passiflora* (not including hybrids) have been illustrated in photographs and/or  
316 scanning electron micrographs in publications or theses; these species represent all five  
317 subgenera, all supersections, and many of the sections and series of *Passiflora* (Tables  
318 A6, A7; Mai 1960; Czeczott and Skirgiel&oacute; 1967; MacDougal 1994; Gilbert and  
319 MacDougal 2000; Deginani 2001; Pérez-Cortéz et al. 1995, 2002, 2009; Vanderplank  
320 2004; Pérez-Cortéz 2007; González-Benito et al. 2009; Cárdenas-Hernández et al.  
321 2011; Mondin et al. 2011; Vanderplank and Zappi 2011; Bernacci and Souza 2012;  
322 Milani 2014; Gurski 2015; Ocampo et al. 2015; Silva et al. 2016, 2020; Mezzonato-Pires  
323 et al. 2017; Martínez 2017; Ocampo Pérez and Molinari 2017; Boza Espinoza et al.  
324 2018; Ocampo Pérez et al. 2018; Esquerre-Ibañez 2019; Ma et al. 2019; Silveira et al.  
325 2019). Some additional photographs were available in online databases (Kirkbride et al.  
326 2006; USDA, NRCS 2019–2020). Seeds of three species (*Passiflora caerulea*,  
327 *Passiflora edulis* Sims, and *Passiflora incarnata*) were obtained from Sheffield's Seed  
328 Company (Locke, New York) and examined, but provided no novel information  
329 (however, the *P. caerulea* seeds were morphologically similar to seeds of *P. edulis*, in  
330 contrast to *P. caerulea* seeds figured in other publications). Species with figured seeds  
331 were sorted into infrageneric taxa (subgenera, supersections, sections, and series) to  
332 look for patterns in seed characteristics that might be phylogenetically significant and/or  
333 diagnostic at the infrageneric level (Tables A6, A7).

334 Seed characteristics of non-*Passiflora* Passifloroideae were primarily  
335 investigated based on a table of morphological characteristics compiled by Martínez  
336 (see appendix S2 in Martínez 2017), supplemented with published descriptions and  
337 drawings (Masters 1871; Sleumer 1970; de Wilde 1971, 1972, 1973, 1974, 1976;  
338 Robyns 1989, 1995; Gentry 1992; Verdcourt 1998; Breteler 1999, 2003; Hearn 2007; de  
339 Vos and Breteler 2009; Feuillet 2009, 2010, 2011, 2020; MacDougal 2011; Ngumbau et  
340 al. 2017). Photographs of two to three species of *Adenia* Forssk. (*Adenia* sp.: Martínez  
341 2017; *Adenia angulosa* G.W.Hu & Q.F.Wang and *Adenia gummifera* Harms: Ngumbau  
342 et al. 2017), one species of *Dilkea* Mast. (*Dilkea ovalis* Feuillet, as part of an herbarium  
343 sheet: Feuillet 2009), and one species of *Ancistrothrysus* Harms (*Ancistrothrysus*  
344 *scopae* Feuillet, as part of an herbarium sheet: Feuillet 2020) were located in  
345 publications; a photograph of an *Adenia huillensis* (Welw.) A.Fern & R.Fern seed was  
346 found in an online database (Kirkbride et al. 2006). For the most part, seed  
347 characteristics of non-*Passiflora* Passifloroideae were found to be similar to the  
348 characteristics reported by Martínez (2017), although the characteristics of *Dilkea*  
349 differed substantially. This discrepancy appears to have occurred because an  
350 herbarium specimen (Herbario Universidad de Antioquia HUA0008478, identified as  
351 *Dilkea acuminata* Mast., image and data from JSTOR 2015) consulted for Martínez's  
352 study may be misidentified. The seeds of HUA0008478, which are obovate and  
353 coarsely foveate (Martínez 2017), do not match the seed characteristics reported for  
354 *Dilkea* in publications (discussed below, and also see Feuillet 2009, 2010, 2011;  
355 MacDougal 2011).  
356

## Results

357

358

359 Order—Malpighiales Juss. ex Bercht. & J.Presl

360 Family—Passifloraceae Juss. ex Roussel

361 Subfamily—*Passifloroideae* Burnett

## 362 Genus—*Passifloroides* *desperma* Martínez-A., emend. Hermsen

363

Original generic diagnosis (Martínez 2017: 1860). "Seeds compressed; shape ovoid, obovoid or elliptic, bilaterally symmetrical or slightly asymmetrical; apex with a prominent to inconspicuous apical appendage, with or without lateral protrusions; base acute, obtuse, truncated or rounded; length less than 20 mm; length to width ratio around 1:1 to 2:1; seed surface foveolate, coarsely foveolate, reticulate-foveolate or transversally grooved; seed endosperm ruminate; seed coat with prismatic palisade cells."

371        *Emended generic diagnosis.* Seeds compressed; shape obovate, oblong, or  
372        elliptical, bilaterally symmetrical to slightly asymmetrical; apical appendage present or  
373        absent, solitary when present (i.e., lateral protrusions absent and apex not tridentate);  
374        base variable (pointed, rounded, truncate); length typically 10 mm or less, sometimes  
375        up to 15 mm; length-to-width ratio 1:1 to 2.5:1; surface reticulate-foveate to reticulate-  
376        foveolate, size and number of foveae/foveolae variable; endosperm ruminant (i.e.,  
377        interior of seed coat with projections); seed coat with radially oriented palisade cells.

378 *Type species. Passifloroidesperma sogamosense* Martínez-A.

379

380        *Other included species.* See Tables A1, A5.  
381        *Distribution.* See Tables A1, A5; Fig. 3A, B, D.  
382        *Remarks.* Martínez (2017) summarized the seed characteristics for each genus  
383        of Passifloroideae (see appendix S2 in Martínez 2017) and concluded that the genera  
384        could not be reliably distinguished from one another on the basis of seed characteristics  
385        alone. Thus, Martínez (2017) erected the genus *Passifloroidesperma* to encompass  
386        fossil seeds attributable to Passifloroideae. A review of the literature for the current  
387        study also failed to find seed characters that distinguish amongst most genera of  
388        Passifloroideae, with the caveat that seeds of most genera are poorly documented  
389        (Tables A6, A7). The typical passifloroid seed is small (usually 10 mm or less in length);  
390        often elliptical, obovate, or oblong; compressed; with or without an apical appendage;  
391        and has a pitted surface (for references, see Materials and Methods, as well as Tables  
392        A6, A7). The single passifloroid genus that can be consistently distinguished on the  
393        basis of its seeds is the New World genus *Dilkea*. Seeds of *Dilkea* (ca. 12 species) differ  
394        from those of other Passifloroideae in being relatively large (13–20 mm in length),  
395        uncompressed to slightly compressed, and ovate, elongated, or medially constricted;  
396        their ornamentation is smooth to pustulate (Feuillet 2009, 2010, 2011; McDougal 2011).

397        Notably, the combination of ruminate endosperm and palisade seed coat that  
398        characterizes passifloroid seeds is rare among angiosperms as a whole; a review by  
399        Martínez (see tables 2, 3 in Martínez 2017) indicated that this character combination is  
400        only known in Passifloraceae (equivalent to Passifloroideae in this study),  
401        Dipterocarpaceae Blume, and Myristicaceae R.Br. In seeds of Dipterocarpaceae and  
402        Myristicaceae, ruminations in the endosperm (or embryo) often form at least in part from

403 the chalazal region, are not created by the palisade layer, and may project far into the  
404 seed, appearing convoluted in section (Corner 1976; Johri et al. 1992). In contrast, the  
405 ruminate endosperm of seeds of Passifloroideae is caused by differential growth of the  
406 palisade cells in the seed coat, causing the inner surface to appear uneven, i.e., bumpy  
407 or, in cross or longitudinal section, undulate (Dathan and Singh 1973; Corner 1976;  
408 Johri et al. 1992; Feuillet and MacDougal 2007; Milani 2014; Gurski 2015; Martínez  
409 2017). Thus, identification of fossil passifloroid seeds to the subfamily level should be  
410 reliable if the most diagnostic features—particularly overall size and form,  
411 ornamentation, compression, seed coat structure, and inner wall surface—are  
412 preserved.

413 Two characteristics included in the original diagnosis of *Passifloroidesperma*, a  
414 tridentate seed apex and transversely sulcate (grooved) seed coat ornamentation, are  
415 restricted mostly to specific subgroups within *Passiflora*. The tridentate seed apex is  
416 found in supersections *Laurifolia* (Cervi) Feuillet & J.M.MacDougal, *Passiflora*, and  
417 *Stipulata* Feuillet & J.M.MacDougal (especially section *Dysosmia* DC.) of subgenus  
418 *Passiflora*, although it is not consistently present in any of these supersections (Table  
419 A7). In some cases, the tridentate apex consists of a prominent central appendage  
420 flanked by two less prominent lateral appendages (as in *Passiflora foetida* in  
421 supersection *Stipulata*: Deginani 2001; Pérez-Cortéz et al. 2002, 2009; Ulmer and  
422 MacDougal 2004; Vanderplank 2004, 2013; Pérez-Cortéz 2007; Mondin et al. 2011;  
423 Gurski 2015; USDA, NRCS 2019–2020). In other cases, the base of the central apical  
424 appendage appears to be sunken between lateral shoulders (see Pérez-Cortéz et al.  
425 2002; for specific examples, see *Passiflora cacao* Bernacci & M.M.Souza and *Passiflora*

426 *edulis* in supersection *Passiflora*: Deginani 2001; Pérez-Cortéz et al. 2002; Vanderplank  
427 2004; Pérez-Cortéz 2007; Mondin et al. 2011; Bernacci & Souza 2012; USDA, NRCS  
428 2019–2020; *Passiflora seemannii* Griseb. in supersection *Laurifolia*: Vanderplank 2004;  
429 Pérez-Cortéz 2007). While Martínez (see appendix S2 in Martínez 2017) also  
430 documented “protrusions” in *Dilkea* and *Efullesia* C.H.Wright seeds, these are absent  
431 in *Dilkea* (Feuillet 2009, 2010, 2011; McDougal, 2011) and could not be confirmed in  
432 *Efullesia* (de Wilde 1974; Robyns 1995). Thus, the tridentate apex tentatively provides  
433 justification for assignment to *Passiflora* subgenus *Passiflora*.

434 The sulcate seed coat has a phylogenetically significant distribution within  
435 *Passiflora*, although it has originated more than once. The largest sulcate-seeded group  
436 is the monophyletic *Passiflora* supersection *Decaloba* (ca. 130 species, New World),  
437 which includes sections *Decaloba* DC. and *Xerogona* (Raf.) Killip (Krosnick et al.  
438 2013a). Seeds of members of supersection *Decaloba* are usually relatively small (about  
439 1.3–6 mm long x 1.1–6 mm wide) and have a transversely sulcate seed coat with about  
440 4–12 grooves (MacDougal 1994; MacDougal and Feuillet 2004; Ulmer and McDougal  
441 2004; Milward-de-Azevedo et al. 2012; Krosnick et al. 2013a; Milani 2014; Boza  
442 Espinoza et al. 2018; Ocampo Pérez et al. 2018; Esquerre-Ibañez 2019; see also  
443 selected images in Deginani 2001; Pérez-Cortéz et al. 2002; Vanderplank 2004; Pérez-  
444 Cortéz 2007; Mondin et al. 2011; USDA, NRCS 2019–2020; Silva et al. 2020).  
445 Transversely sulcate seed coats are also known in two smaller groups: supersection  
446 *Auriculata* J.M.MacDougal & Feuillet (8 species) and several species of subgenus  
447 *Deidamiooides* (Ulmer and MacDougal 2004; see also selected images in Pérez-Cortéz  
448 et al. 2002; Vanderplank 2004; Pérez-Cortéz 2007; Silva et al. 2020). Notably, neither

449 supersection *Auriculata* or subgenus *Deidamiooides* is monophyletic (Krosnick et al.  
450 2013a).

451 The emended diagnosis above is based on Martínez's (2017) original diagnosis,  
452 modified to incorporate the results of the literature review performed for this study (see  
453 references in Materials and Methods, as well as Tables A6, A7). I have removed  
454 diagnostic characteristics that can be used to conclusively refer isolated seeds to  
455 existing genera of Passifloroideae; these include seeds over 15 mm in length (the upper  
456 limit once *Dilkea* is removed), seeds with a transversely sulcate seed coat, and seeds  
457 with a tridentate apex. It should be noted that the sulcate seed coat and tridentate apex  
458 are not necessarily the only features that can be used to distinguish *Passiflora* seeds  
459 from those of other genera of Passifloroideae, they are simply the features relevant to  
460 the diagnosis of *Passifloroidesperma*. For other potential diagnostic characters for  
461 subgroups of *Passiflora* (e.g., winged seeds in supersection *Pterosperma* (L.E.Gilbert &  
462 J.M.MacDougal) J.M.MacDougal & Feuillet: Gilbert and MacDougal 2000; MacDougal  
463 and Hansen 2003; Ulmer and MacDougal 2004; Krosnick et al. 2013a; also, selected  
464 images in Vanderplank 2004), see Table A7.

465

466 Species—*Passifloroidesperma kirchheimeri* (*Mai*) Hermsen, comb. nov.

467 Basionym—*Passiflora kirchheimeri* *Mai* 1960, *Paläont Z* 34: 82–83, pl. 5, figs. 5–  
468 8.

469 Synonyms—*Passiflora kirchheimeri* *Mai*. *Mai* 1967: pl. II, fig. 16. Czeczott and  
470 Skirgielło 1967: 156, pl. VII, figs. 4, 5. Gregor 1978: 57, pl. 12, figs. 4, 5. *Mai* 2000: 41,  
471 pl. 10, figs. 21, 22.

472

473       Species—*Passifloroidesperma heizmannii* (H.-J. Gregor) Hermsen, comb. nov.

474       Basionym—*Passiflora heizmannii* H.-J. Gregor 1982, *Die jungtertiären Floren*

475       Süddeutschlands: Paläokarpologie, Phytostratigraphie, Paläoökologie,

476       Paläoklimatologie: 115–116, pl. 11, figs. 24–26.

477

478       Occurrences. *Passifloroidesperma kirchheimeri*: Early–middle Miocene, Bavaria

479       and Saxony, Germany, and Lower Silesia Vovoideship, Poland (Fig. 3A, B; Mai 1960,

480       1967, 2000; Czeczott and Skirgielło 1967; Czeczott 1970; Gregor 1978).

481       *Passifloroidesperma heizmannii*: Early Miocene, Baden-Württemberg, Germany (Fig.

482       3A, B; Gregor 1982).

483       Remarks. Martínez (2017: 1858, footnote b beneath table) recommended

484       transfer of *Passiflora heizmannii* and *Passiflora kirchheimeri* to *Passifloroidesperma*, but

485       did not formally create the new combinations. I have here created the new combinations

486       based on both Martínez's (2017) recommendation as well as my own assessment of

487       published descriptions of the species.

488       *Passifloroidesperma kirchheimeri* has the characteristics of subfamily

489       Passifloroideae but lacks diagnostic characteristics that could be used to place it within

490       *Passiflora*. Specifically, seeds are compressed, obovate, have a palisade seed coat, an

491       apical appendage with no lateral appendages, and reticulate-foveolate ornamentation

492       (Mai 1960, 1967, 2000); one specimen figured by Mai (1960, 2000) shows wall

493       ingrowths, indicating the presence of ruminant endosperm. The species was originally

494       described by Mai (1960; see also Mai 1967, 2000) based on seeds from lower Miocene

495 deposits of Wiesa (near Kamenz), Saxony, Germany. Later, Czeczott and Skirgiel&lsquo;  
496 (1967) figured a *P. kirchheimeri* seed from the Lower Silesia region of Poland, and  
497 Gregor (1978) figured two seeds from Bavaria, Germany. The specimens figured by  
498 Gregor (1978) appear, however, poorly preserved and lack the prominent apical  
499 appendage characteristic of *P. kirchheimeri*. Both Kozak (2015) and Martínez (2017)  
500 considered the German occurrences of *P. kirchheimeri* to be reliably assigned to  
501 Passifloroideae (for further details, see Table A5). In my opinion, the type material from  
502 Wiesa is well documented enough to be considered a reliable report of Passifloroideae;  
503 other Miocene occurrences (Czeczott and Skirgiel&lsquo; 1967; Gregor 1978) are likely  
504 reliable by assignment to the species. Notably, de Wilde (1971) suggested that seeds of  
505 this species could belong to *Adenia*, although did not provide supporting details for this  
506 opinion.

507 *Passifloroidesperma heizmannii* is based on three specimens from Langenau  
508 (near Ulm), Baden-Württemberg, Germany (Gregor 1982). The seeds are small and  
509 elliptical to somewhat obovate. Unlike *Passifloroidesperma kirchheimeri*, *P. heizmannii*  
510 does not have a clearly defined apical extension (see plate 11, figs. 25, 26 in Gregor  
511 1982). The seed surface appears finely reticulate-foveolate (Gregor 1982). Both Kozak  
512 (2015) and Martínez (2017) indicated uncertainty as to whether this taxon represents  
513 Passifloroideae. According to Gregor (1982), the seeds do have a palisade seed coat,  
514 which would support an assignment to Passifloroideae. No published figures illustrate  
515 the seed coat structure or the inner seed coat surface, however, and the endosperm  
516 type (i.e., inner seed coat surface) was not described. Thus, some ambiguity remains  
517 about the assignment of this material.

Two additional reports of *Passiflora* seeds that potentially belong within  
*Passifloroidesperma* are not included in the formal taxonomy here because they were  
not formally described. Henniger et al. (2011) illustrated two seed fragments from the  
Eocene of Karsdorf, Saxony-Anhalt, Germany (Fig. 3A, B), as *Passiflora* cf.  
*kirchheimeri*. The fragments have finer pits than the Miocene material and the fragment  
showing a putative apex (pl. 2, fig. 11 in Henniger et al. 2011) lacks an extended  
appendage; the structure of the seed coat (i.e., presence of palisade cells and/or  
ruminant endosperm) was not described. Thus, the affiliation of these specimens with  
the otherwise Neogene species *Passifloroidesperma kirchheimeri* is uncertain. Gregor  
(1982) described a *Passiflora* seed based on an impression from the upper Miocene at  
Derching in Bavaria, Germany (Fig. 3A, B), and indicated that it has a palisade seed  
coat (the seed coat structure was not figured).

Finally, a single seed from Bulgaria (Fig. 4A)—found in the same locality (Fig. 530  
3A, C, D) as *Passiflora bulgarica* (stat. nov., below)—has morphology consistent with  
531 *Passifloroidesperma*, although its wall structure and details of its internal surface are  
532 unknown.  
533

534

535 Genus—Passiflora L.

536 Subgenus—Decaloba (DC.) Rchb.

537 Supersection—Cieca (Medic.) J.M. MacDougal & Feuillet

538 Species—*Passiflora bulgarica* (*Palam.*) Hermsen, stat. nov. (Fig. 4B, C)

539 Basionym—*Passiflora kirchheimeri* Mai subspecies *bulgarica* Palam. 1971,

540 *Palaeontographica Abt. B* 132: 156–157; pl. 22, figs. 5, 7; pl. 24, figs. 16–18.

541      *Synonyms*—*Passiflora kirchheimeri Mai subspecies bulgarica Palam.* *Palamarev et al.*  
542                          1999: *pl. 3, fig. 5.*

543

544      *Original species diagnosis* (*Palamarev 1971: 157*). “Samen eiförmig, beidseitig  
545      schwach konvex, 4,5 mm lang; 3—3,5 mm breit; 1,5 mm dick. Aufgesetzte Spitze mit  
546      kurzem „Schnäbelchen“ mit Mikropyle. Sklerotesta mit polygonalen Vertiefungen. Die  
547      Testa 150—200 $\mu$  dick, aus langen, radial gestreckten Palisadenzellen.”

548      *Emended species diagnosis*. Seed slightly falcate (tapering at both ends and  
549      slightly asymmetrical) with convex sides, 4.5 mm long, 3–3.5 mm wide, and 1.5 mm  
550      thick; apical appendage short to absent; base of seed rounded-acute, somewhat  
551      beaked; seed surface coarsely reticulate-foveate, with overlying, longitudinally oriented,  
552      shallow striations; margin slightly undulate.

553      *Holotype*. *Palamarev (1971)*, *pl. 22, figs. 5, 7*; *Palamarev et al. (1999)*, *pl. 3, fig.*  
554      *5*; *Fig. 4B, C*. Held in the Paleobotanical Collection of the Institute of Biodiversity and  
555      Ecosystem Research, Bulgarian Academy of Sciences (IBER-PB), Sofia, Bulgaria  
556      (National Museum of Natural History, Bulgarian Academy of Sciences 2020)

557      *Type locality and age*. Middle Miocene brown coal, “Čukurovo-West” open-pit  
558      mine (Choukourovo), Bulgaria (Fig. 3C, D; *Palamarev 1971*; *Palamarev et al. 2005*).

559

560      *Remarks*. *Passiflora bulgarica* is from the middle Miocene of Bulgaria (*Palamarev*  
561      1971; *Palamarev et al. 2005*). The emended diagnosis above is based on *Palamarev’s*  
562      (1971) diagnosis and published illustrations, as well as additional images of three seeds  
563      provided to me for this study. *Palamarev (1971)* figured two complete seeds with the

564 original description of *P. bulgarica*; the one designated as the holotype was also figured  
565 by Palamarev et al. (1999). Based on comparison between new images made in 2020  
566 to Palamarev's (1971) original figures, the image designated as the holotype  
567 (Palamarev 1971: pl. 22, fig. 7; Palamarev et al. 1999: pl. 3, fig. 5) appears to be the  
568 same specimen and same surface shown here in Figure 4B. I believe that the other  
569 published image of a complete seed is the opposite side of the holotype rather than a  
570 second specimen (cf. Fig. 4C and pl. 22, fig. 5 in Palamarev 1971). Palamarev (1971)  
571 indicated that one illustration of the palisade seed coat (Palamarev 1971: pl. 24, fig. 17)  
572 also came from the holotype, although this is not possible if the holotype is still fully  
573 intact. Two other specimens clearly belong to *Passiflora bulgarica* based on shape and  
574 ornamentation pattern. A fourth seed (Fig. 4A) from the same locality is distinct in  
575 morphology and likely represents a different species with characteristics that link it to  
576 *Passifloroidesperma* (see above). New images of the seed cross sections and  
577 macerations illustrated by Palamarev (1971: pl. 24, figs. 16–18) were not obtained for  
578 this study, and they are here assumed to belong to *P. bulgarica*.

579 Palamarev (1971) originally described *Passiflora bulgarica* as a subspecies of  
580 *Passiflora kirchheimeri*. The holotype of *Passiflora bulgarica* is, however, distinct  
581 enough in form and ornamentation from *Passifloroidesperma kirchheimeri* to justify  
582 raising it to species rank. *Passifloroidesperma kirchheimeri* seeds are smaller than  
583 *Passiflora bulgarica* seeds, obovate rather than falcate in shape, have finer  
584 reticulations, and have an extended triangular apical appendage (see Mai 1960, 1967,  
585 2000; Czeczott and Skirgielło 1967). Palamarev (1971) highlighted the similarity of  
586 *Passiflora bulgarica* to seeds of modern *Passiflora suberosa* L. (subgenus *Decaloba*,

587 supersection *Cieca*: Porter-Utley 2014; see Fig. 4D), while comparing  
588 *Passifloroidesperma kirchheimeri* to *Passiflora alba* Link & Otto (synonym of *Passiflora*  
589 *subpeltata* Ortega, subgenus *Passiflora*, supersection *Stipulata*: Ulmer and MacDougal  
590 2004) and “*Passiflora aurantiaca* Forst.,” apparently meaning the Australasian species  
591 *Passiflora aurantia* G.Forst. (subgenus *Decaloba*, supersection *Disemma* (Labill.)  
592 J.M.MacDougal & Feuillet: Ulmer and MacDougal 2004).

593 Although not noted by Palamarev (1971), the reticulations on the seed coat of  
594 *Passiflora bulgarica* are overlain by shallow longitudinal striations, rendering the seeds  
595 coarsely reticulate and striate (Fig. 4B, C). The shape and ornamentation of *Passiflora*  
596 *bulgarica* are similar to seeds of members of *Passiflora* supersection *Cieca*. Seeds of  
597 members of supersection *Cieca* are distinguished by their fusiform to slightly falcate  
598 shape; they have coarsely reticulate sculpture with foveae, often with longitudinally  
599 oriented, shallow striations (see fig. 3ñ of *Passiflora suberosa* in Pérez-Cortéz et al.  
600 2002; see also published images of *Passiflora coriacea* Juss., *Passiflora juliana*  
601 J.M.MacDougal, *Passiflora obtusifolia* Sessé & Moc., *Passiflora pallida* L., *P. suberosa*,  
602 *Passiflora viridiflora* Cav., and *Passiflora xiikzodz* J.M.MacDougal: Mai 1960; Deginani  
603 2001; Pérez-Cortéz et al. 2002; Vanderplank 2004; Pérez-Cortéz 2007; Mondin et al.  
604 2011; USDA, NRCS 2019–2020). As originally noted by Palamarev (1971), *Passiflora*  
605 *bulgarica* is especially similar in form and ornamentation to modern *Passiflora suberosa*  
606 (Fig. 4D; see also the figures of *P. suberosa* seeds in references cited above), although  
607 the fossil seeds are slightly larger (*Passiflora suberosa* = 2–4 mm long x 1.5–2.5 mm  
608 wide: Deginani 2001; Porter-Utley 2014). Seeds produced by some members of  
609 supersection *Bryoniooides* (Harms) J.M.MacDougal & Feuillet also have coarsely

reticulate-foveate sculpture and a tapering (beaked) base (MacDougal 1994); however, they tend to lack the distinctive curvature present in *P. bulgarica* and modern members of *Cieca*, and also lack the striations overlying the reticulations (see published images of *Passiflora dioscoreifolia* Killip, *Passiflora gracilis* J.Jacq. ex Link, *Passiflora lobata* (Killip) Hutch. ex J.M.MacDougal, and *Passiflora morifolia* Mast.: MacDougal 1994; Deginani 2001; Pérez-Cortéz et al. 2002; Vanderplank 2004; Pérez-Cortéz 2007; Mondin et al. 2011; Gurski 2015).

617

618 Subgenus—Passiflora

619 Supersection—Passiflora?

620 Series—Passiflora?

621 *Species—Passiflora appalachiana* Hermans, sp. nov. (Fig. 5A-L)

622

623           *Species diagnosis.* Seed obovate, slightly asymmetrical, 5.7–6.3 mm long, 3.9–  
624        4.3 mm wide, and 2.6–2.9 mm thick; apical appendage conspicuous and triangular,  
625        base of appendage encircled by a collar; base of seed truncate, oblique, unlobed, often  
626        with central mucro; seed surface reticulate-foveolate; margin entire.

627 Holotype. ETMNH 22625 (Fig. 5A, B). Held at the East Tennessee State

## 628 University Museum of Natural History (ETMNH) collections, Gray Fossil Site, Gray,

629 Tennessee, U.S.A.

630 Paratypes. ETMNH 21283, 22626–22636 (Fig. 5C–L).

631           *Etymology.* The species epithet refers to the occurrence of this species in the  
632       Appalachian region of the United States.

633        *Type locality and age.* Gray Fossil Site, Tennessee, U.S.A. (Fig. 3E); sinkhole  
634 sediments, lower Pliocene (Samuels et al. 2018; Odom et al. 2019).

635        *Species description.* Seed compressed (Fig. 5A), obovate, slightly asymmetrical  
636 (Fig. 5B–D), 5.7–6.3 mm long, 3.9–4.3 mm wide, 2.6–2.9 mm thick; length:width ratio  
637 1.4:1–1.6:1. Apex with conspicuous, triangular apical appendage; slightly thickened  
638 collar (rim) encircling the base of the apical appendage (Fig. 5B–E). Apical appendage  
639 0.6–1.0 mm high from tip of appendage to top edge of collar. Base truncate and oblique,  
640 often with central mucro (Fig. 5B–D, F). Seed margin entire, surface reticulate-  
641 foveolate; foveolae on each seed face numerous (~45 or more, from 5 seeds) (Fig. 5B–  
642 D, G). Seed coat with palisade structure made up of elongated, radially aligned cells,  
643 270–580 µm thick, thickest in the region of the rim at the base of the apical appendage  
644 and near the base of the seed (Fig. 5H–L). Canals through the seed coat traverse the  
645 interior of the apical appendage and the base of the seed (Fig. 5H, I). Endosperm  
646 reticulate, i.e., inner surface of the seed coat with projections (Fig. K, L).

647

648        *Remarks.* *Passiflora appalachiana* has the essential characteristics that support  
649 placement in Passifloroideae; the seeds are obovate (Fig. 5B–D), compressed (Fig.  
650 5A), and less than 10 mm long with a triangular apical appendage (Fig. 5B–E),  
651 reticulate-foveolate ornamentation (Fig. 5B–D, G), reticulate endosperm (Fig. 5K, L),  
652 and palisade seed coat (Fig. 5H–L). *Passiflora appalachiana* is larger than passifloroid  
653 seeds from European deposits and additionally differs from *Passiflora bulgarica* in  
654 shape and ornamentation (Table A2; cf. Fig. 4B, C and Fig. 5B–D). *Passifloroidesperma*  
655 *sogamosense* (length:width ratio of about 1.7:1: Martínez 2017) is slightly more

656 elongated than *Passiflora appalachiana*. *Passifloroidesperma sogamosense* also differs  
657 in being centrally reticulate-foveolate with radiating costae (narrow ridges) toward the  
658 margin (see fig. 3 of Martínez 2017).

659         Although not conspicuously tridentate, *Passiflora appalachiana* seeds have a  
660 collar encircling the apex of the seed, which forms very short lateral projections (Fig.  
661 5B–E). For this reason, it is my opinion that the species may belong to *Passiflora*  
662 subgenus *Passiflora*. *Passiflora appalachiana* is very similar in form and ornamentation  
663 to the extant species *Passiflora incarnata* (subgenus *Passiflora*, supersection  
664 *Passiflora*: Ulmer and MacDougal 2004; see Fig. 5M and images of *P. incarnata* in  
665 Pérez-Cortéz et al. 2002; Vanderplank 2004; Pérez-Cortéz et al. 2009; USDA, NRCS  
666 2019–2020), which is native to and widespread in eastern North America today (Fig. 3E;  
667 Goldman and MacDougal 2015). Notably, the apex structure of *P. incarnata* is  
668 somewhat variable; the apical appendage may be inconspicuous (with the apex  
669 appearing truncate) or conspicuous, and may or may not be surrounded by a basal  
670 ridge (Fig. 5M; see also descriptions and/or images of *P. incarnata* in Pérez-Cortéz et  
671 al. 2002, 2009; Ulmer and MacDougal 2004; Vanderplank 2004; USDA, NRCS 2019–  
672 2020).

673

## 674                      Discussion

675

676         This study confirms Martínez's (2017) conclusion that seed morphology is often  
677 not diagnostic at the genus level in Passifloroideae. There are important exceptions,  
678 however, including seeds of *Dilkea* and seeds of some groups within the well-studied

679 genus *Passiflora* (e.g., supersection *Decaloba*). Thus, most reports of fossil *Passiflora*  
680 seeds are best referred to *Passifloroidesperma*, including *Passifloroidesperma*  
681 *sogamosense* from South America and *Passifloroidesperma kirchheimeri*,  
682 *Passifloroidesperma heizmannii*, and most other *Passiflora*-like seeds reported from  
683 Europe. Two species, *Passiflora bulgarica* from the Miocene of Bulgaria and *Passiflora*  
684 *appalachiana* from the Pliocene of eastern North America, can be assigned to  
685 *Passiflora* based on their morphology. Because relatively little is known about the seed  
686 morphology of most genera of Passifloroideae, further investigations may yield  
687 additional differentiating characters that allow for more precise placement of seeds  
688 currently referred to *Passifloroidesperma*.

689 Subfamily Passifloroideae is highly structured in its present geographic  
690 distribution. A mostly New World or American clade including *Passiflora* and three other  
691 genera—*Ancistrothyrsus*, *Dilkea*, and *Mitostemma* Mast.—is nested within the  
692 paraphyletic Old World genera of Passifloroideae (Muschner et al. 2012; Tokuoka 2012;  
693 Kozak 2015). The extant Old World genera of Passifloroideae (12 genera, over 150  
694 species) occur in the paleotropics, with most of their diversity in continental Africa and  
695 Madagascar; only about 15 species in two genera (*Adenia* and *Paropsia* Noronha ex  
696 Thouars) occur in Asia and Oceania (Fig. 1; Sleumer 1970; de Wilde 1971, 1972;  
697 Feuillet and MacDougal 2007; Martínez 2017). Within the American clade, only about  
698 25 species in two groups of *Passiflora* (supersection *Disemma*, 22 species, Asia to  
699 Oceania; subgenus *Tetrapathea*, 3 species, Oceania) are native to the Old World  
700 (Krosnick and Freudenstein 2005; Wang et al. 2007; Krosnick et al. 2009, 2013b; Ma et  
701 al. 2019). No members of Passifloroideae are native to Europe today.

702       The presence of *Passifloroidesperma sogamosense* in Colombia indicates that  
703 Passifloroideae were present in South America by the late Eocene (Martínez 2017);  
704 solely considering the biogeographic evidence (Fig. 1, 3A), *P. sogamosense* likely has  
705 affinities with the New World clade, and the fossil species resembles seeds of some  
706 species of *Passiflora* subgenus *Astrophea* in sculpture and form (e.g., *Passiflora*  
707 *macrophylla* Spruce ex Mast.: see images in Vanderplank 2004; Mezzonato-Pires et al.  
708 2017). No unique diagnostic characters were identified for *Astrophea* seeds in this  
709 study, however, so the fossil species cannot be attributed to the subgenus. The affinities  
710 of the European *Passifloroidesperma* occurrences (Fig. 3A, B, D; Mai 1960, 1967, 2000;  
711 Czeczott & Skirgielło 1967; Gregor 1978, 1982; Henniger et al. 2011) within  
712 Passifloroideae are unclear. They could plausibly have links to the African  
713 Passifloroideae or to the American genera, the latter via the North Atlantic Land Bridge  
714 (NALB) that once connected Europe to North America (McKenna 1975; Tiffney 1985;  
715 Tiffney and Manchester 2001; Milne 2006).

716       *Passiflora bulgarica* (Fig. 4B, C), from the Miocene of Bulgaria, is most similar to  
717 seeds of members of *Passiflora* supersection *Cieca* (Fig. 4D). All 19 species of *Cieca*  
718 are native to the Americas today, with the northernmost-ranging species occurring as  
719 far north as northern Mexico, Texas, Florida, and the West Indies (Fig. 3C; Porter-Utley  
720 2014). Monophyly of *Cieca* is supported by molecular phylogenetic analyses as well as  
721 morphological data (Krosnick et al., 2013a; Porter-Utley 2014; Kozak 2015). *Cieca* is  
722 not closely related to either of the modern Old World *Passiflora* clades (Krosnick et al.,  
723 2013a), and the supersection has no other known fossil occurrences in Eurasia.

724           The presence of *Passiflora bulgarica* in Europe is plausibly explained by an  
725 ancient connection through the NALB, which operated as a link between eastern North  
726 America and Europe in the Paleogene (McKenna 1975; Tiffney 1985; Tiffney and  
727 Manchester 2001; Milne 2006), with some arguing for at least an intermittent connection  
728 into the Miocene for temperate taxa (Tiffney and Manchester 2001; Grímsson and Denk  
729 2007; Tiffney 2008; Denk et al. 2010). Long-distance dispersal is, of course, another  
730 possibility. The complete absence of *Passiflora* in Europe today is not entirely surprising  
731 given the Cenozoic history of the European flora. Many warm temperate to subtropical  
732 plant genera found in the European fossil record disappeared from Europe in the later  
733 Neogene to the Pleistocene but are still present elsewhere today, perhaps best  
734 represented in the modern floras of North America and especially Asia (Manchester  
735 1999; Manchester et al. 2009; Martinetto et al. 2017, 2020).

736           *Passiflora appalachiana*, from Gray Fossil Site, Tennessee, U.S.A., is the first  
737 credible report of a fossil *Passiflora* from eastern North America. The GFS macroflora is  
738 best known for yielding genera that have northern hemisphere distributions; these  
739 genera typically have connections to modern genera or species found today primarily in  
740 eastern North America and/or eastern Asia, and fossil records that are Laurasian in  
741 distribution (Gong et al. 2010; Liu and Jacques 2010; Brandon 2013; Noll 2013; Huang  
742 et al. 2014, 2015; Quirk and Hermsen 2020). Most genera so far described from the  
743 GFS fruit and seed flora are extant and presently occur in eastern North America (Gong  
744 et al. 2010; Brandon 2013; Noll 2013; Baumgartner 2014; Huang et al. 2014, 2015).  
745 Several GFS macrofossil plant genera, like *Corylopsis* Siebold & Zucc. and *Sinomenium*  
746 Diels, are currently endemic to Asia but have more widespread northern hemisphere

747 fossil records (Liu and Jacques 2010; Jacques et al. 2011; Quirk and Hermsen 2020);  
748 one genus, *Cavilignum* Siegert & Hermsen, is entirely extinct (Siegert and Hermsen  
749 2020). The fauna shows at least some parallels to the flora; the herptiles are largely  
750 from groups found in southeastern North America today, whereas the mammals include  
751 some taxa with connections to present-day eastern Asia and Eurasia (Bourque and  
752 Schubert 2015; see also Wallace and Wang 2004; Mead et al. 2012). Thus far, extinct  
753 groups—e.g., saber-toothed cats (cf. *Machairodus* Kaup), North American rhinos  
754 (*Teleoceras aepysoma* Short et al.)—are a more significant element of the fauna than  
755 the flora (Bourque and Schubert 2015; Short et al. 2019).

756 *Passiflora* includes a small number of extant species native to eastern Asia and  
757 to the Americas north of the Neotropics. All Asian species of *Passiflora* belong to  
758 section *Octandranthus* Harms, which includes about 18 of the 22 species in  
759 supersection *Disemma* (Krosnick and Freudenstein 2005; Krosnick et al. 2013a, b; Ma  
760 et al. 2019). For *Octandranthus*, only a photo of a *Passiflora menghaiensis* X.D.Ma et  
761 al. seed was located for this study (fig. 1F in Ma et al. 2019). The seed of *P.*  
762 *menghaiensis* is dissimilar from *Passiflora appalachiana*; it is small (4 mm long x 3 mm  
763 wide) and broadly obovate, with a tapering, beaked base and 25–35 foveolae on each  
764 side (Ma et al. 2019). Based on the limited evidence available, seed morphology does  
765 not support a close relationship between *P. appalachiana* and the modern Asian  
766 passifloras.

767 About 18 species of *Passiflora* occur in the continental United States today, 13 of  
768 which are native (Goldman and MacDougal 2015). Of the native species, most reach  
769 the northern limits of their ranges in Arizona, Florida, or Texas; only two, *Passiflora*

770 *incarnata* and *Passiflora lutea* L., are currently widespread in the eastern United States  
771 (*Goldman and MacDougal 2015*). *Passiflora appalachiana* seeds are dissimilar from  
772 seeds of *P. lutea*, which have the sulcate seed coat typical for members of supersection  
773 *Decaloba* (*Ulmer and MacDougal 2004*; see also images of *P. lutea* in *Vanderplank*  
774 2004; *USDA-NRCS 2019–2020*). As noted above, *P. appalachiana* is similar in  
775 morphology to *P. incarnata* (cf. Fig. 5B–D to Fig. 5M), and Gray Fossil Site is within the  
776 native range of the modern species (Fig. 3E; *Goldman and MacDougal 2015*).  
777 *Passiflora incarnata* is in subgenus *Passiflora* (250 species), series *Passiflora* (14  
778 species) (*Ulmer and MacDougal 2004*; *Krosnick et al. 2013a*; *Bernacci and Souza*  
779 2012). Other members of series *Passiflora* and subgenus *Passiflora* are native to the  
780 Americas, with the greatest number of species in subgenus *Passiflora* occurring in  
781 northern South America (*Ulmer and MacDougal 2004*). Thus, it is reasonable to  
782 conclude that *P. appalachiana* represents the first Neotropical connection identified from  
783 the Gray Fossil Site macroflora. Notably, Neotropical connections are also rare in the  
784 fauna; one Neotropical animal genus, *Heloderma* (*Wiegmann*) (beaded lizard), has  
785 been described from the site (*Mead et al. 2012*; *Noll 2013*). It is possible that *Passiflora*  
786 may have dispersed to GFS from south to north, as hypothesized for *Heloderma* (*Mead*  
787 *et al. 2012*).

788

789

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790

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- 1563

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1565

1566 **Figure 1.** Approximate distribution of modern Passifloroideae, based on the

1567 distributions of the two largest genera, *Adenia* and *Passiflora* (these genera encompass

1568 most or all of the native range of the subfamily); some outlying islands have been

1569 circled to provide a sense of the complete range of the subfamily. Of the three major

1570 regions of distribution, no genera are shared between the Americas and

1571 Africa/Madagascar. Three genera are found in Asia and Oceania: *Passiflora* (ca. 25

1572 species: Krosnick and Freudenstein 2005; Wang et al. 2007; Krosnick et al. 2009,

1573 2013b; Ma et al. 2019) from the New World group and *Adenia* (ca. 14 species: de Wilde

1574 1971, 1972) and *Paropsia* (1 species: Sleumer 1970) from the Africa/Madagascar

1575 group. Sources: Reiche (1898), de Wilde (1971, 1972), Deginani (2001), Stevens (2001

1576 onwards), Ocampo-Pérez (2007), Krosnick et al. (2009, 2013b), Milward-de-Azevedo et

1577 al. (2012), Porter-Utley (2014), Goldman and MacDougal (2015), Boza Espinoza et al.

1578 (2018), GBIF.org (2020a, b, c). GBIF occurrence datasets were checked against other

1579 sources to exclude occurrences outside of the documented native range for a given

1580 taxon or group of taxa.

1581

1582 **Figure 2.** Fossil and modern leaves. A. Holotype of *Passiflora antiqua* (YPM PB

1583 011087, Late Cretaceous, Woodbridge, New Jersey, U.S.A.), previously figured by

1584 Newberry (1895), Berry (1911), and Kozak (2015). B. Leaf of *Passiflora biflora* Lam.

1585 (US 01245631, Ortiz, O.O. 503, Panama); scale bar = 2 cm. C. *Bauhinia cretacea* (YPM

1586 PB 011289, Late Cretaceous, Woodbridge, New Jersey, U.S.A.), previously figured by

1587 Newberry (1895). D. Leaf of *Liriodendrites bradacii* Johnson (YPM PB 006361, Late  
1588 Cretaceous, North Dakota, U.S.A.), previously figured by Johnson (1996). Image  
1589 credits: A, C, D. Photos by Division of Paleobotany (YPM PB), courtesy of the Peabody  
1590 Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A. (Gall  
1591 2020a–c). B. Photo by I. Lin, courtesy of United States National Herbarium (US) (Orrell  
1592 2020).

1593

1594 **Figure 3.** Distribution of fossil *Passifloroidesperma* and *Passiflora* seed species. A–B,  
1595 D. Distribution of *Passifloroidesperma* as recognized in this study (for references, see  
1596 Tables A1, A5). Worldwide distribution (A), distribution in Central Europe (B), and  
1597 distribution in Bulgaria (D). 1. *Passifloroidesperma sogamosense* (Eocene, Santander,  
1598 Colombia). 2. *Passifloroidesperma?* sp. (Eocene, Saxony-Anhalt, Germany). 3.  
1599 *Passifloroidesperma* sp. (Miocene, Bavaria, Germany). 4. *Passifloroidesperma*  
1600 *heizmannii* (Miocene, Baden-Württemberg, Germany). 5. *Passifloroidesperma*  
1601 *kirchheimeri* (Miocene: 5a = Saxony, Germany; 5b = Lower Silesia Vovoideship,  
1602 Poland; 5c = Bavaria, Germany). 6. *Passifloroidesperma* sp. (Miocene, Sofia, Bulgaria).  
1603 C–D. Distribution of modern and fossil members of *Passiflora* supersection *Cieca*. C.  
1604 *Passiflora bulgarica* (Miocene, Sofia, Bulgaria: Palamarev 1971; Palamarev et al. 1999,  
1605 2005) and modern distribution of *Passiflora* supersection *Cieca* (after maps in Porter-  
1606 Utley 2014). D. Approximate location of Čukurovo open-pit mine (6), type locality of  
1607 *Passiflora bulgarica*. E. *Passiflora appalachiana* (Pliocene, Tennessee, U.S.A.: this  
1608 paper) and distribution of extant *Passiflora incarnata* (after Goldman and MacDougal  
1609 2015; GBIF.org 2020c). Note: Ranges for extant taxa (*Cieca*, *P. incarnata*) include only

1610 their native distributions. Maps created with Simplemappr (Shorthouse 2010), modified  
1611 in Photoshop. Scale bars: A, C = 3300 km; B, D = 222 km; E = 870 km.

1612

1613 **Figure 4.** A–C. Fossil seeds from Čukurovo open-pit mine, Miocene, Bulgaria. A. Seed  
1614 here attributed to *Passifloroidesperma*. B–C. *Passiflora bulgarica* (Palam.) Hermsen,  
1615 stat. nov. B. Holotype (cf. Palamarev 1971: pl. 22, fig. 7; Palamarev et al. 1999: pl. 3,  
1616 fig. 5). C. Opposite surface of holotype (cf. Palamarev 1971: pl. 22, fig. 5). D. Modern  
1617 seeds of *Passiflora suberosa*. Scale bars: A–C = approximately 1 mm (estimated from  
1618 rulers in background); D = 1 mm. Image credits: A–C. Photos of specimens held at  
1619 IBER-PB by Dr. Mila Andonova. D. Photo by Steve Hurst, hosted by USDA-NRCS  
1620 PLANTS Database (USDA, NRCS 2019–2020).

1621

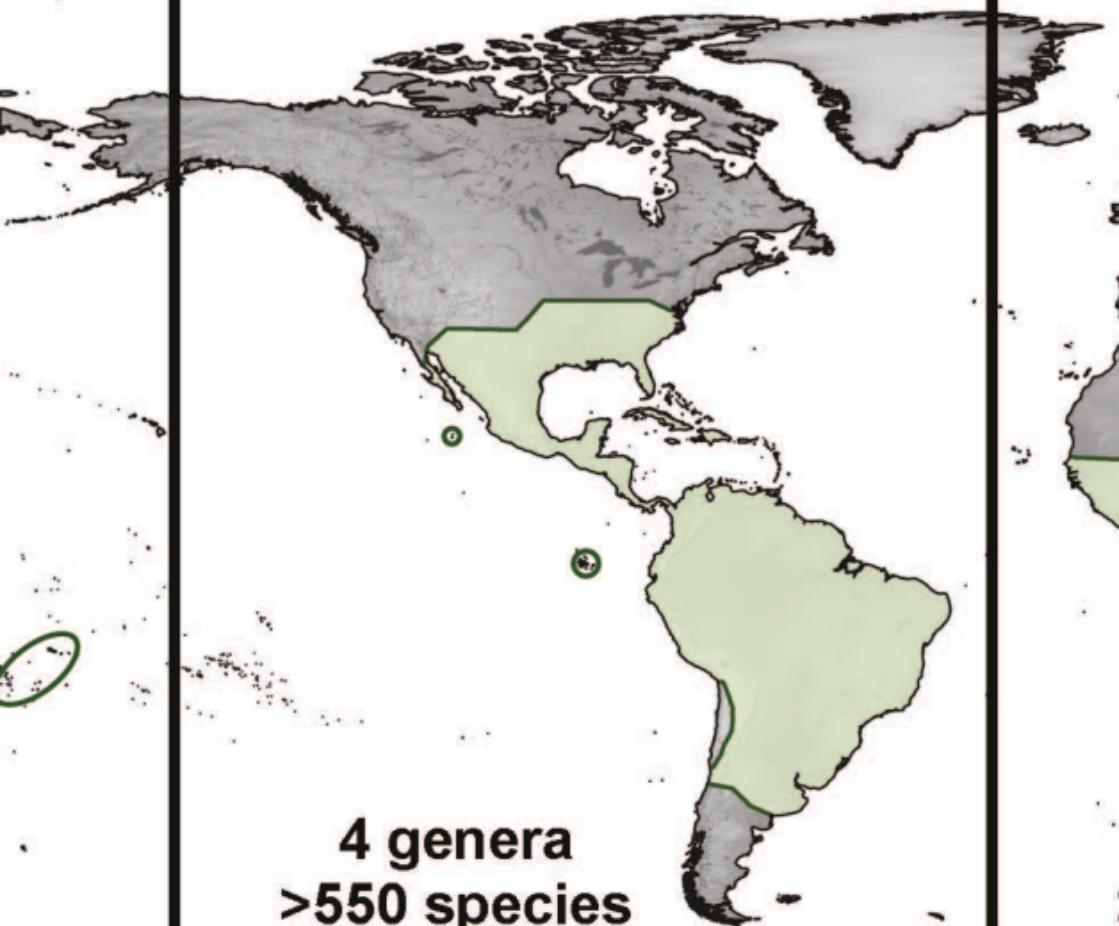
1622 **Figure 5.** A–L. *Passiflora appalachiana* Hermsen, sp. nov. A. Edge of seed showing  
1623 compression. ETMNH 22625 (holotype). B–D. Lateral views of complete seeds showing  
1624 overall form, apical appendage, base, and sculpture. B. ETMNH 22625 (holotype). C.  
1625 ETMNH 22627. D. ETMNH 22626. E. Detail of apical appendage. ETMNH 22631. F.  
1626 Detail of base with mucro. ETMNH 22635. G. Detail of outer surface with foveolae.  
1627 ETMNH 22631. H. Inner surface of apical appendage with canal and radiating palisade  
1628 cells. ETMNH 22632. I. Inner surface of base with canal and radiating palisade cells.  
1629 ETMNH 22632. J. Detail of seed coat showing radiating palisade cells. ETMNH 22633.  
1630 K–L. Details of inner surface showing rounded projections (= ruminant endosperm). J.  
1631 ETMNH 22633. L. ETMNH 22635. M. *Passiflora incarnata* (extant). Scale bars: A–D, K–  
1632 M = 1 mm; E, G, H = 0.5 mm; F, I = 0.2 mm; J = 0.1 mm.

1633

- 1634                   **Description of Supplementary Tables A3–A7**
- 1635
- 1636   **Tables A3–A5.** Summary of the fossil record of Passifloroideae. All tables are  
1637   organized first by age (oldest to youngest by period and epoch), then alphabetically, first  
1638   by generic name, then by species epithet.
- 1639   **Table A3.** Fossil pollen reports of *Passiflora* and Passifloroideae, with assessments of  
1640   their reliability.
- 1641   **Table A4.** Fossil leaf reports of *Passiflora* and Passifloroideae, with notes.
- 1642   **Table A5.** Fossil seed reports of *Passiflora* and *Passifloroidesperma*, with assessments  
1643   of their reliability.
- 1644   **References, Tables A3–A5.** Reference list for Tables A1–A3.
- 1645
- 1646   **Tables A6, A7.** Morphology of modern seeds of Passifloroideae.
- 1647   **Table A6.** Summary of figured seeds of Passifloroideae (only photographic figures or  
1648   SEM photomicrographs included).
- 1649   **Table A7.** Summary of differentiating seed characteristics of groups within  
1650   Passifloroideae.
- 1651   **References, Tables A6, A7.** Reference list for Tables A4–A5.
- 1652
- 1653



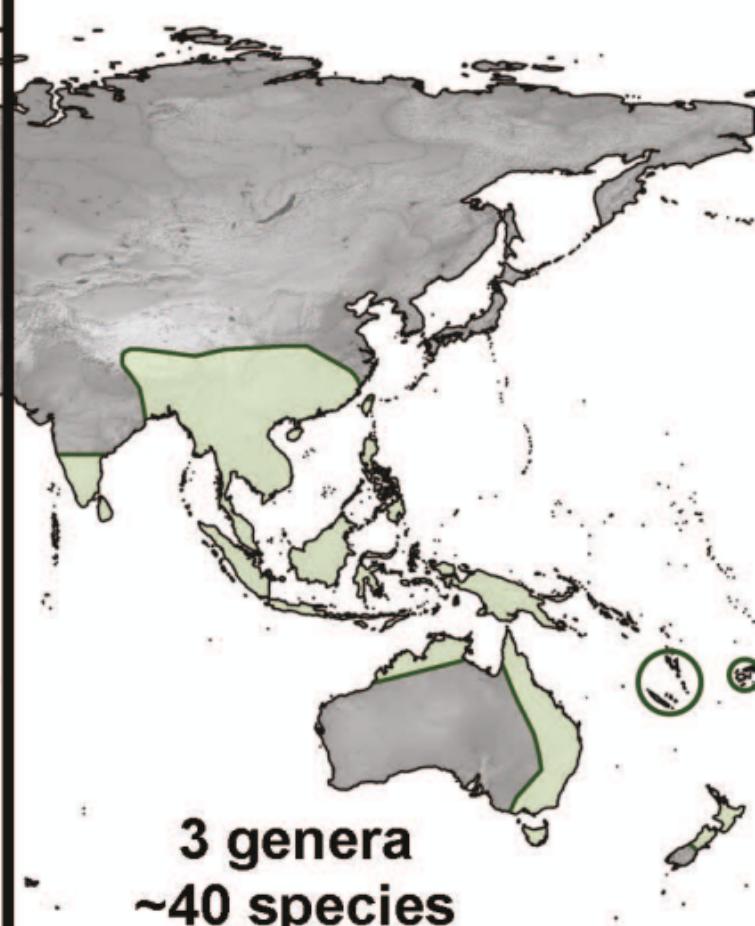
## North & South America



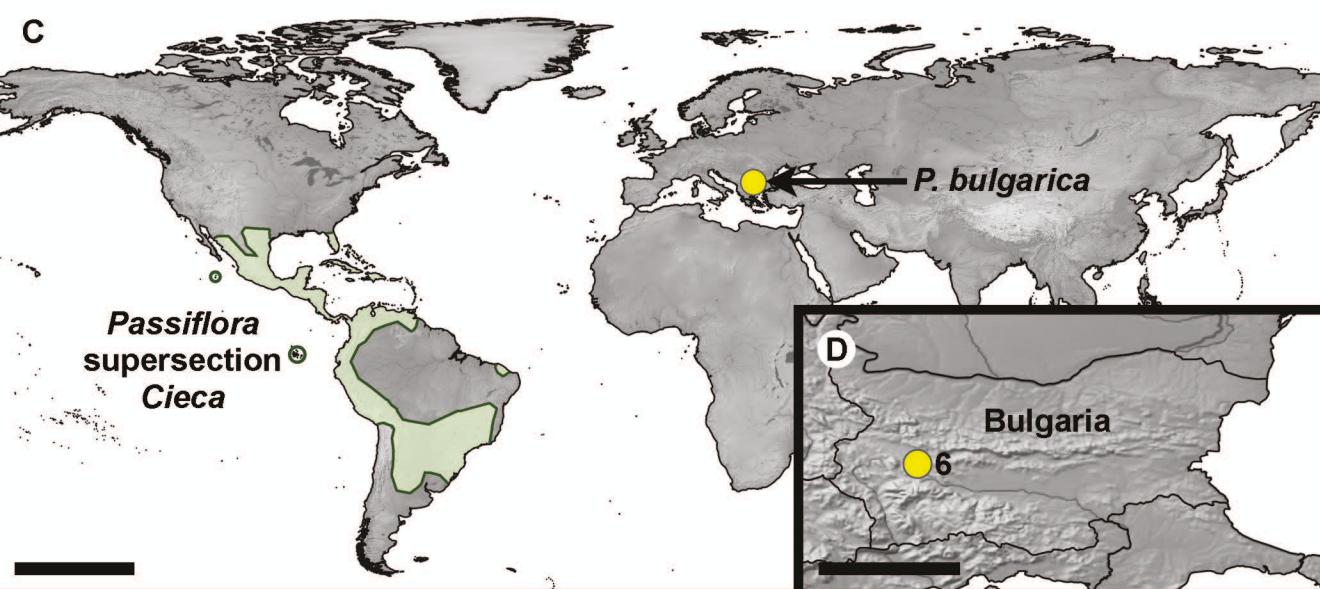
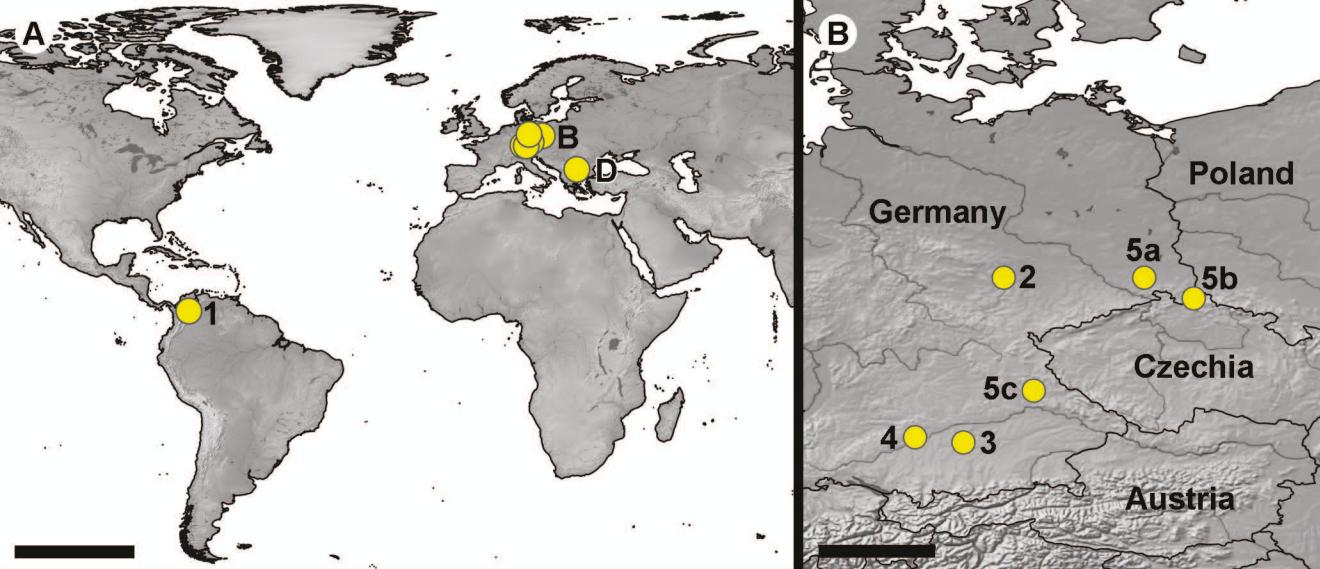
## Africa & Madagascar

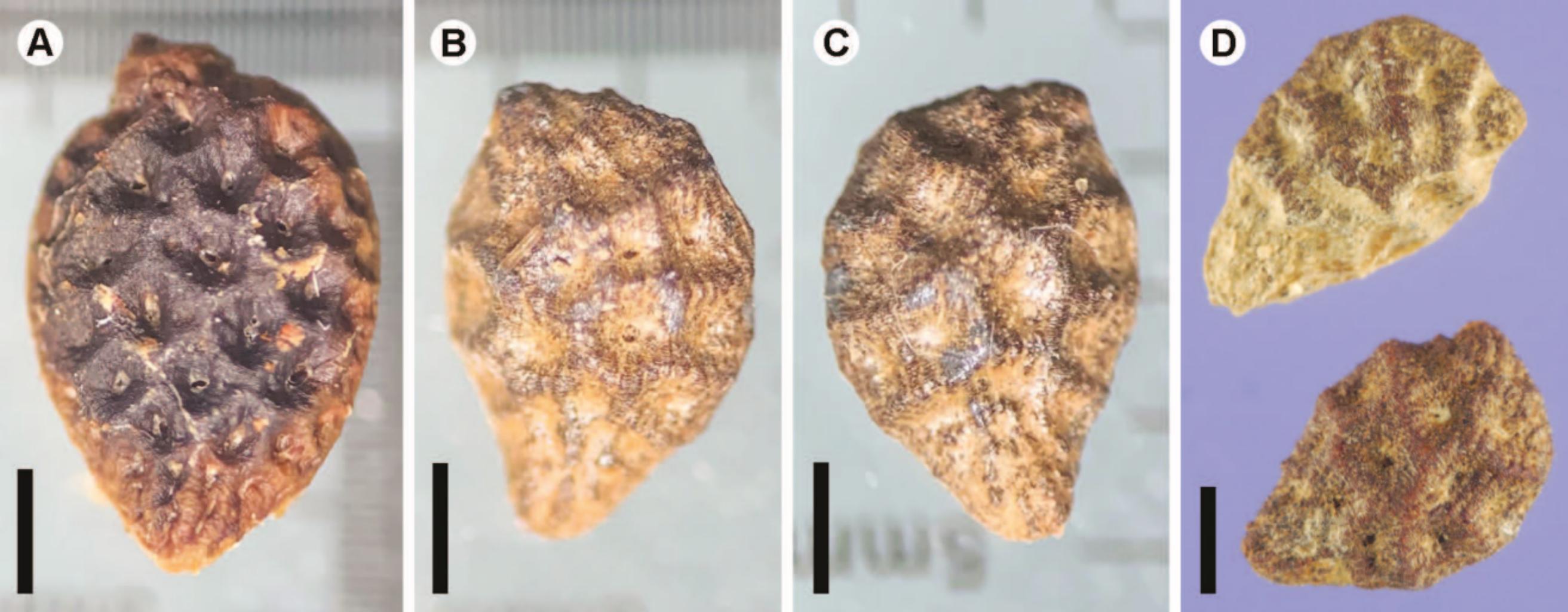


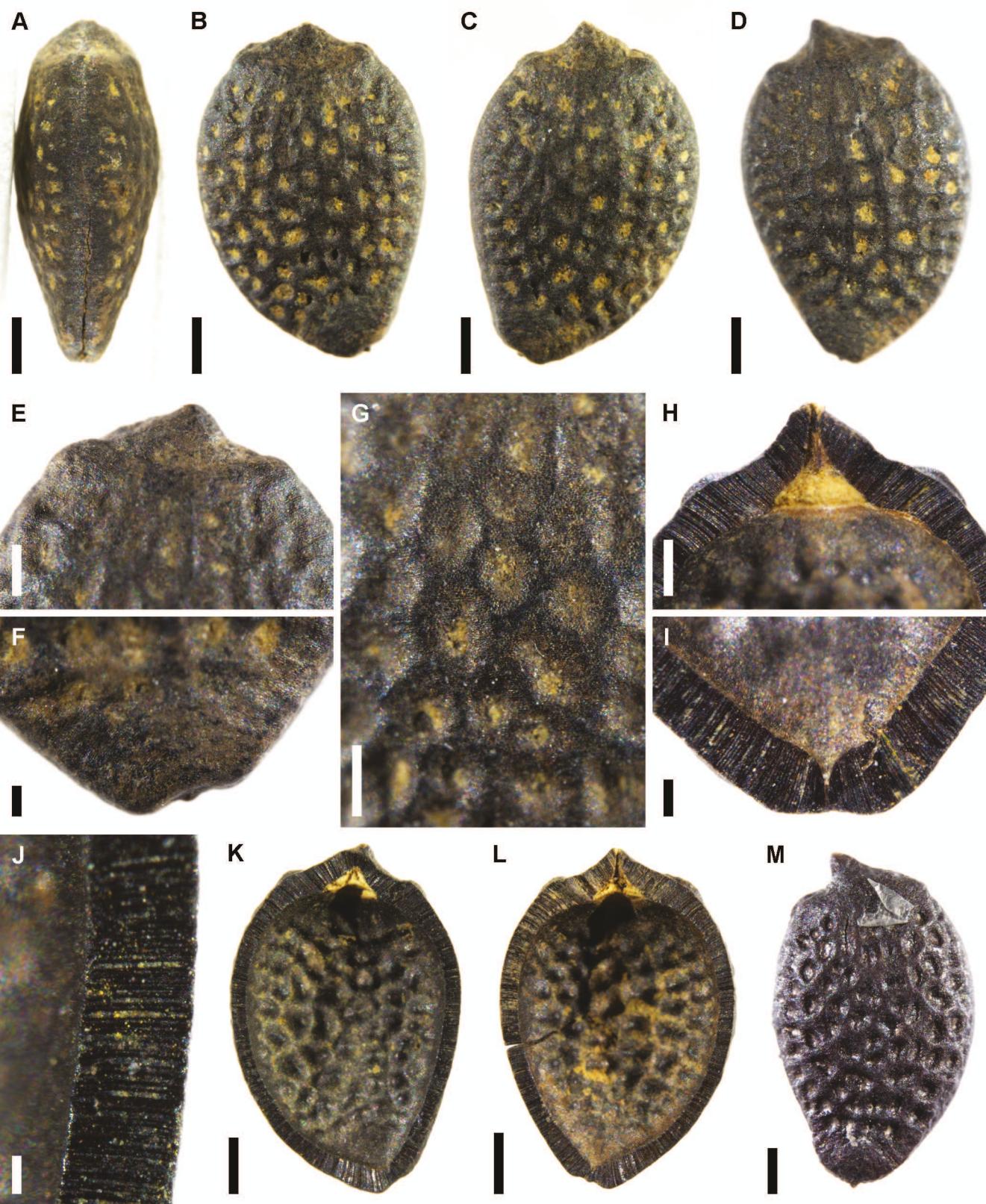
## Asia & Oceania











**Table A1.**  
**Fossil Record of Seeds Attributed to Passifloroideae**

Original name	Age	Location <sup>1</sup>	References	Revised status
<i>Passifloroidesperma sogamosense</i>	Eocene	Colombia	Martínez (2017)	Unchanged
Martínez-A.				
<i>Passiflora</i> cf. <i>kirchheimeri</i> Mai	Eocene	Germany	Henninger et al. (2011)	<i>Passifloroidesperma</i> ? sp.
<i>Passiflora</i> spec.	Miocene	Germany	Gregor (1982)	<i>Passifloroidesperma</i> sp.
<i>Passiflora heizmannii</i> H.-J. Gregor	Miocene	Germany	Gregor (1982)	<i>Passifloroidesperma</i> <i>heizmannii</i> (H.-J. Gregor) Hermsen, comb. nov.
<i>Passiflora kirchheimeri</i> Mai	Miocene	Germany, Poland	Mai (1960, 1967, 2000), Czeczott & Skirgiel&oacute; (1967), Gregor (1978)	<i>Passifloroidesperma</i> <i>kirchheimeri</i> (Mai) Hermsen, comb. nov.

<i>Passiflora kirchheimeri</i> Mai subspecies <i>bulgarica</i> Palam.	Miocene	Bulgaria	Palamarev (1971), Palamarev et al. (1999, 2005), this study	<i>Passiflora bulgarica</i> (Palam.) Hermsen, stat. nov., and <i>Passifloroidesperma</i> sp.
<i>Passiflora appalachiana</i> Hermsen, sp. nov.	Pliocene	U.S.A.	This study	Not applicable

<sup>1</sup> Localities are mapped in Fig. 3.

**Table A2.**  
**Comparison of fossil passifloroid seed species<sup>1</sup>**

Taxon	Shape	Length (mm)	Width (mm)	Thickness (mm)	Seed coat thickness (μm)	Surface sculpture	Apical appendage
<i>Passiflora</i> <i>appalachiana</i>	Obovate	5.7–6.3	3.9–4.3	2.6–2.9	270–580	Reticulate-foveolate	Triangular with basal collar
<i>Passiflora bulgarica</i>	Slightly falcate	4.5	3–3.5	1.5	150–200	Coarsely reticulate-foveate with shallow longitudinal striations	None to very short triangular
<i>Passifloroidesperma</i> <i>heizmannii</i>	Elliptical to obovate	1.7–2.3	1.1–1.6	—	200	Reticulate-foveolate	Short triangular

<i>Passifloroidesperma</i>	Obovate	3–4	1.5–3	0.5–1	200–400	Reticulate-	Triangular
<i>kirchheimeri</i>						foveolate	
<i>Passifloroidesperma</i>	Obovate	4–9	2.5–4.5	–	300	Reticulate-	Triangular
<i>sogamosense</i>						foveolate, radiating marginal costae	

<sup>1</sup> Sources: *Passiflora appalachiana* (this study), *Passiflora bulgarica* (Palamarev 1971, this study), *Passifloroidesperma heizmannii* (Gregor 1982), *Passifloroidesperma kirchheimeri* (Mai 1960, 1967, 2000; Czeczott and Skirgielło 1967; Gregor 1978), *Passifloroidesperma sogamosense* (Martínez 2017). Descriptive terminology standardized for this study.

Taxon	Proposed affinities in original study	Figures	Period	Epoch	State/province
<i>Spirosyncolpites spiralis</i> González-Guzmán	Passifloraceae (probably equivalent to Passifloroideae of this study)	None	Paleogene	Paleocene–Eocene	Norte de Santander Department (Colombia), Zulia (Venezuela)
<i>Passiflora</i>	<i>Passiflora</i>	Graham (1976), figs. 177, 178	Neogene	Miocene	Veracruz
<i>Retistephanocolpites "passionis"</i> D'Apolito, ined. (thesis name)	Bignoniaceae?, <i>Passiflora</i>	D'Apolito (2016), pl. 23, figs. 7–9	Neogene	Miocene	
<i>Stephanocolpites</i> sp. Hammen	Passifloraceae? (probably equivalent to Passifloroideae of this study)	Hoorn (1994), pl. 1, fig. 4	Neogene	Miocene	
<i>Syncolpites</i> sp. Hammen	<i>Passiflora</i> -type, <i>Passiflora</i> spp.	Palazzi et al. (2014), suppl. fig. 3C, F	Neogene	Miocene	Chubut, Rio Negro

Taxon	Country/continent/region	Key references (descriptions, figures)	Additional references (supplementary information on status of name, synonyms, age, locality, etc.)	Kozak (2015, table 3.1).	Martínez (2017, table 1).
				Assessment of fossil Passifloraceae (equivalent to Passifloroideae + Passifloroideae + Turneroideae of this study). Reliability ratings = low, medium, high.	Assessment of fossil Passifloroideae. Reliability ratings = low, medium, high.
<i>Spirosyncolpites spiralis</i> González-Guzmán	Colombia, Venezuela	Jaramillo et al. (2010b)		Not treated	"Not Passifloraceae"
<i>Passiflora</i>	Mexico	Graham (1976)		Low	Low
<i>Retistephanocolpites "passionis"</i> D'Apolito, ined. (thesis name)	Brazil	D'Apolito (2016)		Not treated	Not treated
<i>Stephanocolpites</i> sp. Hammen	NW Amazon region (Brazil-Colombia-Peru)	Hoorn (1994)	Jaramillo et al. (2010a)	Low (citing only Jaramillo et al. 2010a)	Not treated
<i>Syncolpites</i> sp. Hammen	Argentina	Palazzi et al. (2014)		Not treated	Medium

**Taxon**

**This study.** Assessment of fossil Passiflora and Passifloroideae. Reasoning provided based on figures and descriptions in published sources.

*Spirosyncolpites spiralis*  
González-Guzmán

Ambiguous. Not figured, assignment to Passifloraceae not discussed in Jaramillo et al. (2010b, see esp. supporting online material). Martínez (2017) provided no discussion for unambiguously concluding that this report is not Passifloraceae.

*Passiflora*

Ambiguous. Assignment to *Passiflora* not discussed in Graham (1976). Muller (1981) considered figures inadequate.

*Retistephanocolpites "passionis"*  
D'Apolito, ined. (thesis name)

Ambiguous. Possible assignment to *Passiflora* not discussed in D'Apolito (2016). A comparison of images of *Retistephanocolpites "passionis"* (D'Apolito 2016) to images of *Passiflora* pollen (Amela García et al. 2002; Roubik and Moreno Patiño 2003; Milward-de-Azevedo et al. 2004; Mezzonato-Pires et al. 2015) and Bignonaceae Juss. pollen (Roubik and Moreno Patiño 2003; Souza et al. 2019) for this study shows that the fossil pollen has similarities to at least some modern pollen forms in both groups (e.g., *Passiflora misera* Kunth, *Passiflora suberosa* L., *Anemopaegma chamberlainii* (Sims) Bureau & K.Schum.).

*Stephanocolpites* sp. Hammen

Ambiguous. Assignment to Passifloraceae not discussed in Hoorn (1994) or Jaramillo et al. (2010a).

*Syncolpites* sp. Hammen

Dubious. Palazzesi et al. (2014, see their supplementary information) compared this pollen to pollen of extant *Passiflora caerulea* L. (as "*Passiflora coerulea*") in size, wall characteristics, and aperture type. The illustrated *Syncolpites* grain (see supp. fig. 3C, F in Palazzesi et al. 2014) has, in my interpretation, ca. seven holes (fenestrae), whereas a similarly preserved *P. caerulea* grain would have three (see fig. 35 in Amela García et al. 2002). Furthermore, in the *Syncolpites* grain, the holes occur all over the grain, whereas they would be equatorial in *P. caerulea* (see fig. 35 in Amela García et al. 2002 and discussion in main text).

Taxon	Synonyms	Figures	Period	Epoch	State/province
<i>Passiflora antiqua</i> Newb.		Newberry (1895), pl. 23, fig. 7; Berry (1911), pl. 23, fig. 5; Kozak (2015), fig. 3.1; this study, Fig. 2A [Note: Figures in Berry (1911) and Kozak (2015) are reprints of the illustration in Newberry (1895).]	Cretaceous	Late Cretaceous	New Jersey
<i>Passiflora feuilletii</i> Torres, nom. nud.		Torres (2003), fig. 24.4	Paleogene	Paleocene-Eocene	King George Island
<i>Passiflora nikolaevii</i> Budantsev		Budantsev (2012), pl. 16, figs. 2–9	Paleogene	Paleocene-Eocene	King George Island
Parataxon TARA-6 (?Proteaceae, ?Passifloraceae)		Pole (1994), fig. 25	Paleogene	Eocene	North Otago
<i>Passiflora</i> sp.		Hunger (1939), pl. 4, fig. 57	Paleogene	Eocene	Saxony-Anhalt
<i>Passiflora</i> spec.?		Fischer (1950), pl. 8, fig. 3	Paleogene	Eocene	Saxony
<i>Passiflora hauchecornei</i> Friedrich		Friedrich (1883b), pl. 31, figs. 1, 2	Paleogene	Oligocene	Saxony-Anhalt
<i>Passiflora tenuiloba</i> Friedrich, non Engelm.		Friedrich (1883b), pl. 25, fig. 20	Paleogene	Oligocene	Saxony-Anhalt
<i>Passifloraephyllum kraeusei</i> Rásky, originally 'kraeusei'		Rásky (1960), pl. 4, fig. 16	Paleogene	Oligocene	Budapest
<i>Passiflora basiloba</i> Smiley		Smiley (1963), pl. 15, figs. 1, 6	Neogene	Miocene	Washington
<i>Passiflora braunii</i> R. Ludw., originally 'brauni' [name published 1860]	<i>Calycanthus braunii</i> Brongn., nom. nud.	Ludwig (1859–1860), pl. 48, figs. 1–10 (leaves) & figs. 11–16 (fruits & seeds)	Neogene	Miocene	Hesse
<i>Passiflora canadensis</i> Hollick		Hollick (1927), pl. 37, fig. 2	Neogene	Miocene	British Columbia
<i>Passiflora canfieldii</i> Britton, originally 'canfieldi'	<i>Passiflora</i> (?) <i>canfieldii</i> Britton, originally 'canfieldi'	Britton (1893), figs. 12, 13; Berry (1919), pl. 18, figs. 4, 5	Neogene	Miocene	Potosí Department

Taxon	Country/continent	Key references (descriptions, figures)	Additional references (supplementary information on status of name, synonyms, age, locality, etc.)
<i>Passiflora antiqua</i> Newb.	USA	Newberry (1895), Berry (1911)	Newberry (1886), Herendeen et al. (1992), Wang et al. (2014), Kozak (2015), Martínez (2017), Gall (2020a, b), GBIF.org (2020)
<i>Passiflora feuilletii</i> Torres, nom. nud.	Antarctica	Torres (2003)	GBIF.org (2020)
<i>Passiflora nikolaevii</i> Budantsev	Antarctica	Budantsev (2012)	
Parataxon TARA-6 (?Proteaceae, ?Passifloraceae)	New Zealand	Pole (1994)	Kozak (2015)
<i>Passiflora</i> sp.	Germany	Hunger (1939)	
<i>Passiflora</i> spec.?	Germany	Fischer (1950)	
<i>Passiflora hauchecornei</i> Friedrich	Germany	Friedrich (1883a, b)	IFPNI International Editorial Board (2014–2020), GBIF.org (2020)
<i>Passiflora tenuiloba</i> Friedrich, non Engelm.	Germany	Friedrich (1883a, b)	IFPNI International Editorial Board (2014–2020)
<i>Passifloraephyllum kraeuselii</i> Rásky, originally 'kraeuseli'	Hungary	Rásky (1960)	Hably & Fernandez Marron (1998), Krosnick et al. (2013), Kozak (2015), Martínez (2017)
<i>Passiflora basiloba</i> Smiley	USA	Smiley (1963)	GBIF.org (2020)
<i>Passiflora braunii</i> R.Ludw., originally 'brauni' [name published 1860]	Germany	Brongniart (1849), Ludwig (1859–1860)	Kirchheimer (1957), Koch & Friedrich (1971), IFPNI International Editorial Board (2014–2020), GBIF.org (2020)
<i>Passiflora canadensis</i> Hollick	Canada	Hollick (1927)	LaMotte (1952), Clague (1974)
<i>Passiflora canfieldii</i> Britton, originally 'canfieldi'	Bolivia	Britton (1893), Berry (1919)	Berry (1939), Gregory-Wodzicki et al. (1998), Gall (2020c, d), GBIF.org (2020)

TAXON	NOTES	Species discussed in main text of this paper?
<i>Passiflora antiqua</i> Newb.	Bilobed leaf, 1 figured specimen (Newberry 1895; Berry 1911; Kozak 2015); 2 specimens held at Yale Peabody Museum (YPM PB 011087, 152005), New Haven, Connecticut, USA (GBIF.org 2020). Images of one specimen available online (Gall 2020a). Considered a low-reliability record by Kozak (2015) and Martínez (2017). Probably the same species as <i>Bauhinia cretacea</i> Newb. (1886, 1895; see Gall 2020b and main text for images of a comparable <i>B. cretacea</i> specimen from the same locality), which may belong to <i>Liriophyllum</i> Lesq. or <i>Liriodendrites</i> Johnson (Herendeen et al. 1992; Wang et al. 2014).	Yes
<i>Passiflora feijuetii</i> Torres, nom. nud.	Obdeltoid leaf, 1 figured specimen (Torres 2013). Nomen nudum, specimen figured with no diagnosis or description. Probably a specimen of <i>Passiflora nikolaevii</i> .	Yes (with <i>P. nikolaevii</i> )
<i>Passiflora nikolaevii</i> Budantsev	Bilobed, roughly obdeltoid leaves, about 10 specimens (Budantsev 2012).	Yes
Parataxon TARA-6 (?Proteaceae, ?Passifloraceae)	One partial lobed leaf (Pole 1994). Kozak (2015) considered it a low-reliability report of Passifloraceae.	Yes
<i>Passiflora</i> sp.	One partial trilobed leaf (Hunger 1939).	No
<i>Passiflora</i> spec.?	One unlobed leaf (Fischer 1950). Fischer (1950) compared this leaf to two species of <i>Passiflora</i> and to <i>Miquelia cumingii</i> Baill. (Icacinaceae).	No
<i>Passiflora hauchecornei</i> Friedrich	Unlobed and trilobed leaves, 2 specimens figured (Friedrich 1883a, b).	No
<i>Passiflora tenuiloba</i> Friedrich, non Engelm.	Trilobed leaf, 1 specimen figured (Friedrich 1883a, b). Nomen illegitimum, later homonym of <i>Passiflora tenuiloba</i> Engelm. (IFPNI International Editorial Board, 2014–2020).	No
<i>Passifloraephillum kraeusei</i> Rásky, originally 'kraeusei'	One partial leaf (Rásky 1960). Accepted as a record of Passifloraceae by Kozak (2015), but considered dubious by Krošnick et al. (2013, as <i>Passiflora</i> ) and Martínez (2017).	Yes
<i>Passiflora basiloba</i> Smiley	15 total specimens, two specimens figured; 3–5-lobed leaves with no teeth (Smiley 1963). This taxon includes leaves, fruits, and seeds. The basionym for this species ( <i>Calycanthus braunii</i> ) is a nomen nudum (IFPNI International Editorial Board, 2014–2020, and confirmed for this study by examining Brongniart 1849). The leaves appear to be simple dicot leaves, apparently at least 10 specimens (see plate 48 in Ludwig 1859–1860). Associated fruits and seeds of <i>Passiflora braunii</i> have been referred to <i>Spirematospermum wetzleri</i> (Heer) M.Chandler (Kirchheimer 1957; Koch & Friedrich 1971). The holotype is unclear, although Ludwig (1859–1860) indicated that Brongniart based the species on fruit. This was confirmed in Brongniart (1849). Kirchheimer (1957) indicated that the relationship of <i>P. braunii</i> leaves to <i>Passiflora</i> was equivocal.	Yes
<i>Passiflora braunii</i> R.Ludw., originally 'braunii' [name published 1860]	One partial trilobed leaf (Hollick 1927).	No
<i>Passiflora canadensis</i> Hollick	Trilobed leaves, 2 figured specimens (Britton 1893); 4 specimens total (YPM PB 027922, 028175, 152698, 152699), held at Yale Peabody Museum (YPM), New Haven, Connecticut, USA (GBIF.org 2020). Images of two specimens available online (Gall 2020c, d).	No
<i>Passiflora canfieldii</i> Britton, originally 'canfieldii'		

Taxon (this study)	Original name (if name revised)	Figure	Period	Epoch	Locality	Latitude	Longitude
<b><i>Passiflora</i> L.</b>							
<i>Passiflora bulgarica</i> (Palam.) Hermsen	<i>Passiflora kirchheimeri</i> Mai subsp. <i>bulgarica</i> Palam.	Palamarev (1971), pl. 22, fig. 5, 7; pl. 24, figs. 16–18; Palamarev et al. (1999), pl. 3, fig. 5; this study, Fig. 4B, C	Neogene	Miocene	Tagebau "Čukurovo-West"	42.53	23.61
<i>Passiflora appalachiana</i> Hermsen		This study, Fig. 5A–L	Neogene	Pliocene	Gray Fossil Site	36.39	-82.50
<b><i>Passifloroidesperma</i> Martínez-A.</b>							
<i>Passifloroidesperma</i> ? sp.	<i>Passiflora</i> cf. <i>kirchheimeri</i> Mai	Henniger et al. (2011), pl. 2, figs. 11, 17	Paleogene	Eocene	Karsdorf	51.27	11.66
<i>Passifloroidesperma sogamosense</i> Martínez-A.		Martínez (2017), figs. 3A–D	Paleogene	Eocene	Topocoro Dam	7.11	-73.42
<i>Passifloroidesperma</i> sp.	<i>Passiflora</i> spec.	Gregor (1982) pl. 7, fig. 15	Neogene	Miocene	Derching (near Augsburg)	48.41	10.96
<i>Passifloroidesperma</i> sp.	<i>Passiflora kirchheimeri</i> Mai subsp. <i>bulgarica</i> Palam.? (inferred, specimen not figured in previous publications)	This study, Fig. 4A	Neogene	Miocene	Tagebau "Čukurovo-West"	42.53	23.61
<i>Passifloroidesperma heizmannii</i> (H.-J.Gregor) Hermsen	<i>Passiflora heizmannii</i> H.-J.Gregor	Gregor (1982), pl. 11, figs. 24–26	Neogene	Miocene	Langenau (near Ulm)	48.50	10.12
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	<i>Passiflora kirchheimeri</i> Mai	Mai (1960), pl. 5, figs. 5–8; Mai (1967), pl. 2, fig. 16; Mai (2000), pl. 10, figs. 21, 22 [Note: Figures in Mai (1967, 2000) appear to be reprints of figures from Mai (1960).]	Neogene	Miocene	Wiesa (near Kamenz)	51.27	14.10
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	<i>Passiflora kirchheimeri</i> Mai	Czeczott & Skirgiello (1967), pl. 7, figs. 4, 5	Neogene	Miocene	Turów (near Bogatynia)	50.91	14.96
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	<i>Passiflora kirchheimeri</i> Mai	Gregor (1978), pl. 12, figs. 4, 5	Neogene	Miocene	Oder II	49.31	12.18

Taxon (this study)	Distribution map (this paper)	Coordinate Source	State/province	Country/continent	Main references	Kozak (2015, table 3.1). Assessment of fossil Passifloraceae (equivalent to Passifloroideae + Turneroideae of this study). Reliability ratings = low, high.
<b><i>Passiflora</i> L.</b>						
<i>Passiflora bulgarica</i> (Palam.) Hermsen	Fig. 3C, D (6)	Estimated	Sofia	Bulgaria	Palamarev (1971), Palamarev et al. (1999, 2005)	Low (listed as <i>Passiflora kirchheimeri</i> , with organ type listed as "pollen (?)")
<b><i>Passifloroidesperma</i> Martínez-A.</b>						
<i>Passifloroidesperma</i> ? sp.	Fig. 3A, B (2)	Estimated	Saxony-Anhalt	Germany	Henniger et al. (2011)	Not treated
<i>Passifloroidesperma sogamosense</i> Martínez-A.	Fig. 3A (1)	Converted from coordinates reported in Martínez (2017).	Santander	Colombia	Martínez (2017)	Not treated
<i>Passifloroidesperma</i> sp.	Fig. 3A, B (3)	Estimated	Bavaria	Germany	Gregor (1982)	Not treated
<i>Passifloroidesperma</i> sp.	Fig. 3A, D (6)	Estimated	Sofia	Bulgaria	Palamarev (1971), Palamarev et al. (2005)	Not treated
<i>Passifloroidesperma heizmannii</i> (H.-J.Gregor) Hermsen	Fig. 3A, B (4)	Estimated	Baden-Württemberg	Germany	Gregor (1982)	Low (organ type listed as "?")
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	Fig. 3A, 3B (5a)	Estimated	Saxony	Germany	Mai (1960, 1967, 2000), GBIF.org (2020)	High (listed as " <i>Passiflora</i> OR <i>Turnera</i> "; only Mai 1967 reference cited)
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	Fig. 3A, 3B (5b)	Estimated	Lower Silesia Voivodeship	Poland	Czeczkott & Skirgiello (1967), Czeczkott (1970)-age	Low (listed as <i>Passiflora</i> sp.; organ type listed as "?")
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	Fig. 3A, 3B (5c)	Estimated	Bavaria	Germany	Gregor (1978)	High (organ type listed as "fruit and seed")

Taxon (this study)	Martínez (2017, table 1). Assessment of fossil Passifloroideae. Reliability ratings = low, medium, high.	This study. Assessment of fossil <i>Passiflora</i> and Passifloroideae. Reasoning provided based on figures and descriptions in original sources and/or personal observations, where applicable.
<b><i>Passiflora</i> L.</b>		
<i>Passiflora bulgarica</i> (Palam.) Hermsen	High	Reliable. Three seeds consistent with <i>Passiflora</i> supersection <i>Cieca</i> in shape and ornamentation (see Palamarev 1971; this study, Fig. 4B, C). Palamarev (1971, plate 24, figs. 17, 18) shows palisade seed coat structure. Ruminant endosperm not documented.
<i>Passiflora appalachiana</i> Hermsen	Not treated	Reliable. Seeds similar to <i>Passiflora incarnata</i> in shape and ornamentation. Compression, palisade seed coat, and ruminant endosperm documented (this study).
<b><i>Passifloroidesperma</i> Martínez-A.</b>		
<i>Passifloroidesperma</i> ? sp.	Not treated	Ambiguous. Two partial seeds figured. Seed coat structure and ruminant endosperm not documented.
<i>Passifloroidesperma sogamosense</i> Martínez-A.	High (not in table, rating inferred)	Reliable. Size, shape, and ornamentation consistent with Passifloroideae. Martínez (2017) described and illustrated the palisade seed coat (Martínez 2017, fig. 3C) and ruminant endosperm (Martínez 2017, fig. 3A).
<i>Passifloroidesperma</i> sp.	Not treated	Somewhat ambiguous. Low quality image. Described as having palisade seed coat (Gregor 1982, pg. 116), but no figure of seed coat structure provided.
<i>Passifloroidesperma</i> sp.	Not treated	Probably reliable. This seed was not figured by Palamarev (1971, 1999), but it was on a slide with three <i>Passiflora bulgarica</i> seeds. Size, shape, and ornamentation are consistent with Passifloroideae. Seed coat structure and ruminant endosperm not documented.
<i>Passifloroidesperma heizmannii</i> (H.-J.Gregor) Hermsen	Medium	Somewhat ambiguous. Seeds small, shape and ornamentation consistent with Passifloroideae. Described as having palisade seed coat (Gregor 1982, pg. 115), but no figure of seed coat structure provided. Ruminant endosperm not documented.
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	High (only Mai 1960 and Mai 2000 references cited)	Reliable. Size, shape, ornamentation, and palisade seed coat consistent with subfamily. Palisade seed coat figured (Mai 1960, pl. 5, figs. 6, 8; Mai 2000, pl. 10, fig. 22). Figure showing inner seed surface indicates ruminant endosperm (Mai 1960, pl. 5, fig. 6; Mai 2000, pl. 10, fig. 22).
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	Not treated	Probably reliable. Images show that it is similar to German material figured by Mai (1960, 1967, 2000). Seed coat structure and ruminant endosperm not documented.
<i>Passifloroidesperma kirchheimeri</i> (Mai) Hermsen	High	Probably reliable. Seeds appear similar to material figured by Mai (1960, 1967, 2000), but preservation is not as good and apical appendage is small and blunt rather than extended and triangular. Seed coat structure and ruminant endosperm not documented.

Author(s)	Year	Title	Book/Journal, volume, pages, etc.	DOI or URL
Amela Garcia MT, BG Galati, AM Anton	2002	Microsporogenesis, microgametogenesis and pollen morphology of <i>Passiflora</i> spp. (Passifloraceae)	<i>Botanical Journal of the Linnean Society</i> 139: 383–394.	<a href="https://doi.org/10.1046/j.1095-8339.2002.00072.x">https://doi.org/10.1046/j.1095-8339.2002.00072.x</a>
Berry EW	1911	The flora of the Raritan Formation	Geological Survey of New Jersey Bulletin 3. MacCrellich & Quigley, State Printers, Trenton, New Jersey.	<a href="https://doi.org/10.5962/bhl.title.7725">https://doi.org/10.5962/bhl.title.7725</a>
Berry EW	1919	Fossil plants from Bolivia and their bearing upon the age of uplift of the eastern Andes	<i>Proceedings of the United States National Museum</i> 54: 103–164.	<a href="https://doi.org/10.5479/si.00963801.54-2229.103">https://doi.org/10.5479/si.00963801.54-2229.103</a>
Berry EW Britton NL	1939 1893	The fossil flora of Potosí, Bolivia Note on a collection of Tertiary fossil plants from Potosí, Bolivia	<i>The Johns Hopkins University Studies in Geology</i> 13: 9–67. <i>Transactions of the American Institute of Mining Engineers</i> 21: 250–259. Pages 52–173 in C. D'Orbigny, ed. <i>Dictionnaire universel d'histoire naturelle</i> . Tome Treizième. MM. Renard, Martinet et C. Paris.	<a href="https://books.google.com/books?id=DcxMAAAAYAAJ&amp;printsec=frontcover&amp;v=onepage&amp;q=f=false">https://books.google.com/books?id=DcxMAAAAYAAJ&amp;printsec=frontcover&amp;v=onepage&amp;q=f=false</a>
Bronniart AT	1849	Végétaux fossiles	Továřiščestvo nauchnykh izdanií KMK, St. Petersburg, Moscow. [In Russian with English summary, e-book published 2018]	<a href="https://doi.org/10.5962/bhl.title.23115">https://doi.org/10.5962/bhl.title.23115</a>
Budantsev LYU	2012	Tertiary flora of the King George Island (Antarctica)	<i>Canadian Journal of Earth Sciences</i> 11: 916–938.	<a href="https://doi.org/10.1139/e74-091">https://doi.org/10.1139/e74-091</a>
Clague JJ	1974	The St. Eugene Formation and the development of the southern Rocky Mountain Trench	<i>Kwartalnik Geologiczny</i> 14: 778–801.	<a href="https://doi.org/10.2307/20100202">https://doi.org/10.2307/20100202</a>
Czeczkott H	1970	O wieku trzeciorzędowej flory Turowa k. Bogatyni (Góra Luzyce)	<i>Prace Muzeum Ziemi</i> 10: 97–166.	
Czeczkott H, A Skirgiello	1967	Flora Kopalna Turowa Kolo Bogatyni, Część Druga: Systematyczny opis szczątków roślinnych (3). Praca Zbiorowa	Landscape evolution in western Amazonia: Palynostratigraphy, palaeoenvironments and diversity of the Miocene Selimões Formation, Ph.D. thesis. University of Birmingham, Birmingham, U.K.	<a href="http://etheses.bham.ac.uk/id/eprint/6781">http://etheses.bham.ac.uk/id/eprint/6781</a>
D'Apolito C	2016	Paleoenvironments and diversity of the Miocene Selimões Formation	<i>Abhandlungen des Geologischen Dienstes Berlin, Neue Folge</i> 221: 1–28.	<a href="https://books.google.com/books?id=IJeDwAAQBAJ&amp;pg=PP1&amp;pg=PP1#v=onepage&amp;q=f=false">https://books.google.com/books?id=IJeDwAAQBAJ&amp;pg=PP1&amp;pg=PP1#v=onepage&amp;q=f=false</a>
Fischer E	1950	Pflanzenabdrücke aus dem Alttertiär von Mosel bei Zwickau in Sachsen	<i>Abhandlungen zur geologischen Spezialkarte von Preussen und den Thüringischen Staaten</i> 4: 1–305 [159–463].	<a href="https://www.biodiversitylibrary.org/page/35796233">https://www.biodiversitylibrary.org/page/35796233</a>
Friedrich P	1883a	Beiträge zur Kenntniss der Tertiärfloren der Provinz Sachsen	<i>Abhandlungen zur geologischen Spezialkarte von Preussen und den Thüringischen Staaten</i> 4: 1–305 [159–463].	<a href="https://www.biodiversitylibrary.org/page/57917841">https://www.biodiversitylibrary.org/page/57917841</a>
Friedrich P	1883b	Atlas von einunddreißig Lichtdrucktafeln zu der Abhandlung: Beiträge zur Kenntniss der Tertiärfloren der Provinz Sachsen	<i>Abhandlungen zur geologischen Spezialkarte von Preussen und den Thüringischen Staaten</i> 4 (Atlas); plates 1–31.	<a href="https://doi.org/10.15468/dl.juzerk">https://doi.org/10.15468/dl.juzerk</a>
GBIF.org	2020	GBIF Occurrence Download (8 September 2020). <a href="https://doi.org/10.15468/dl.juzerk">https://doi.org/10.15468/dl.juzerk</a>		
Gall L	2020a	<i>Passiflora antiqua</i> Newberry, GBIF occurrence 1039330373	Paleobotany Division, Yale Peabody Museum. <a href="https://doi.org/10.15468/hpasyo">https://doi.org/10.15468/hpasyo</a>	<a href="https://www.gbif.org/occurrence/1039330373">https://www.gbif.org/occurrence/1039330373</a>
Gall L	2020b	<i>Bauhinia cretacea</i> Newberry, GBIF occurrence 1039291629	Paleobotany Division, Yale Peabody Museum. <a href="https://doi.org/10.15468/hpasyo">https://doi.org/10.15468/hpasyo</a>	<a href="https://www.gbif.org/occurrence/1039291629">https://www.gbif.org/occurrence/1039291629</a>
Gall L	2020c	<i>Passiflora canfieldii</i> , GBIF occurrence 1039292037	Paleobotany Division, Yale Peabody Museum. <a href="https://doi.org/10.15468/hpasyo">https://doi.org/10.15468/hpasyo</a>	<a href="https://www.gbif.org/occurrence/1039292037">https://www.gbif.org/occurrence/1039292037</a>
Gall L	2020d	<i>Passiflora canfieldii</i> , GBIF occurrence 1039371229	Paleobotany Division, Yale Peabody Museum. <a href="https://doi.org/10.15468/hpasyo">https://doi.org/10.15468/hpasyo</a>	<a href="https://www.gbif.org/occurrence/1039371229">https://www.gbif.org/occurrence/1039371229</a>
Graham A	1976	Studies in Neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico	<i>Annals of the Missouri Botanical Garden</i> 63: 787–842.	<a href="https://doi.org/10.2307/2395250">https://doi.org/10.2307/2395250</a>
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Number, Feuillet & MacDougal	Genus	Subgenus	Supersection	Section	Series	Species in published photos	Species author (ref: Feuillet & MacDougal 2002 and/or IPNI 2020)	Reference for figure (light photograph, light photomicrograph, or SEM photomicrograph)	Reference for classification within Passiflora (if applicable)
NA	<i>Ancistrothrysus</i>	<i>Ancistrothrysus</i>				<i>A. scopae</i>	Feuillet	Feuillet (2020)	
NA	<i>Adenia</i>	<i>Adenia</i>				<i>Adenia</i> sp.		Martínez (2017)	
	<i>Adenia</i>					<i>A. angulosa</i>	G.W.Hu & Q.F.Wang	Ngumbau et al. (2017)	
	<i>Adenia</i>					<i>A. gummifera</i>	Harms	Ngumbau et al. (2017)	
	<i>Adenia</i>					<i>A. huilensis</i>	(Welw.) A.Fern & R.Fern	Kirkbride et al. (2006)	
NA	<i>Androsiphonia</i>	<i>Androsiphonia</i>				None found			
NA	<i>Barteria</i>	<i>Barteria</i>				None found			
NA	<i>Basananthe</i>	<i>Basananthe</i>				None found			
NA	<i>Crossostemma</i>	<i>Crossostemma</i>				None found			
NA	<i>Deidamia</i>	<i>Deidamia</i>				None found			
NA	<i>Dilkea</i>	<i>Dilkea</i>				<i>D. ovalis</i>	Feuillet	Feuillet (2009)	
NA	<i>Efullesia</i>	<i>Efullesia</i>				None found			
NA	<i>Mitostemma</i>	<i>Mitostemma</i>				None found			
NA	<i>Paropsia</i>	<i>Paropsia</i>				None found			
NA	<i>Paropsiopsis</i>	<i>Paropsiopsis</i>				None found			
NA	<i>Schlechterina</i>	<i>Schlechterina</i>				None found			
NA	<i>Smeathmannia</i>	<i>Smeathmannia</i>				None found			
NA	<i>Vindivia</i>	<i>Vindivia</i>				None found			
<b>Passiflora</b>									
	Passiflora	?	?	?	?	<i>Passiflora</i> sp.		Czeczott & Skirgiello (1967)	
	Passiflora	?	?	?	?	<i>P. brevifilla</i>	Killip	Vanderplank (2004)	
	Passiflora	?	?	?	?	<i>P. comte</i>	ined.	Vanderplank (2004)	
	Passiflora	?	?	?	?	<i>P. cyanea</i>	Mast.	Pérez-Cortéz (2007)	
	Passiflora	?	?	?	?	<i>P. luismanvillii</i>	ined.	Vanderplank (2004)	
	Passiflora	?	?	?	?	<i>P. spectabilis</i>	Killip	Pérez-Cortéz et al. (2002, 2009). One of these is mislabeled (mixed up with <i>P. sidifolia</i> ).	
	Passiflora	?	?	?	?	<i>P. tikillii</i>	ined.	Vanderplank (2004)	
1	Passiflora	<i>Astrophea</i>							
1.1	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>					
1.1.1	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. araguensis</i>	L.K. Escobar	Pérez-Cortéz (2007)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. engleriana</i>	Harms	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. lindeniana</i>	Planch. ex Triana & Planch.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. macrophylla</i>	Spruce ex Mast.	Vanderplank (2004), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. sphærocarpa</i>	Triana & Planch.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>P. tica</i>	Gómez-Laur. & L.D. Gómez	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
1.1.2	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>					
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>	<i>NA</i>	<i>P. ceratocarpa</i>	F.Silveira	Vanderplank (2004), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>	<i>NA</i>	<i>P. faroana</i>	Harms	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>	<i>NA</i>	<i>P. hexagonocarpa</i>	Barb.Rodr.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>	<i>NA</i>	<i>P. maguirei</i>	Killip	Pérez-Cortéz (2007)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>	<i>NA</i>	<i>P. pittieri</i>	Mast.	Vanderplank (2004)	Hilgenhof (2013)
1.1.3	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Leptopoda</i>					
	Passiflora	<i>Astrophea</i>	<i>Astrophea</i>	<i>Leptopoda</i>	<i>NA</i>	None found			
1.2	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>						
1.2.1	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>					
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. candida</i>	(Poepp. & Endl.) Mast.	Vanderplank (2004), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. costata</i>	Mast.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. elliptica</i>	Gardner	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. haematostigma</i>	Mast. ex. Mast.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. mansoi</i>	Mast.	Pérez-Cortéz et al. (2002) as " <i>P. mansii</i> ", Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
	Passiflora	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>	<i>NA</i>	<i>P. ovata</i>	Jos.Martin ex DC.	Vanderplank (2004), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)

Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. pentagona</i>	Mast.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. rhamnifolia</i>	Mast.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. sclerophylla</i>	Harms	Pérez-Cortéz (2007)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. skiantha</i>	Huber	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. tessmannii</i>	Harms	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Pseudoastrophea	NA	<i>P. venosa</i>	Rusby	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea					
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea					
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea					
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea		<i>P. pyrrhantha</i>	Harms	Pérez-Cortéz (2007), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea		<i>P. rusbyi</i>	Mast.	Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea		<i>P. securicata</i>	Mast.	Pérez-Cortéz (2007), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea		<i>P. spinosa</i>	Mast.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Botryastrophea					
Passiflora	Astrophea	Pseudoastrophea	Carnaee					
Passiflora	Astrophea	Pseudoastrophea	Carnaee		<i>P. amoena</i>	L.K.Escobar	Vanderplank (2004)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Carnaee		<i>P. fuchsiflora</i>	Hemsl.	Pérez-Cortéz (2007)	Hilgenhof (2013)
Passiflora	Astrophea	Pseudoastrophea	Carnaee		<i>P. longiracemosa</i>	Ducke	Pérez-Cortéz (2007), Mezzonato-Pires et al. (2017)	Hilgenhof (2013)
Passiflora	Deidamiooides							
Passiflora	Deidamiooides	NA	Polyanthea					
Passiflora	Deidamiooides	NA	Polyanthea	NA	<i>P. cirrhiflora</i>	Juss.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Deidamiooides	NA	Deidamiooides					
Passiflora	Deidamiooides	NA	Deidamiooides	NA				
Passiflora	Deidamiooides	NA	Tetrasylis					
Passiflora	Deidamiooides	NA	Tetrasylis	NA	<i>P. ovalis</i>	Vell.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Deidamiooides	NA	Mayapathanthus					
Passiflora	Deidamiooides	NA	Mayapathanthus	NA				
Passiflora	Deidamiooides	NA	Tryphostemmatoides					
Passiflora	Deidamiooides	NA	Tryphostemmatoides	NA	<i>P. disciphora</i>	P.Jørg. & Lawesson	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Tryphostemmatoides	NA		<i>P. gracillima</i>	Killip	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Pterosperma						
Passiflora	Decaloba	Pterosperma	NA	NA	<i>P. lancetillensis</i>	J.M.MacDougal	Vanderplank (2004) as " <i>P. lanceolensis</i> "	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Pterosperma	NA	NA	<i>P. microstipula</i>	L.E.Gilbert & J.M.MacDougal	Gilbert & MacDougal (2000), Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Hahnianopathanthus						
Passiflora	Decaloba	Hahnianopathanthus	NA	NA	<i>P. guatemalensis</i>	S.Watson	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Hahnianopathanthus	NA	NA	<i>P. hahnii</i>	Mast.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Disemma						
Passiflora	Decaloba	Disemma	Octandranthus					
Passiflora	Decaloba	Disemma	Octandranthus	NA	<i>P. menghaiensis</i>	X.D.Ma, L.C.Yan & J.Y.Shen	Ma et al. (2019)	Ma et al. (2019)
Passiflora	Decaloba	Disemma	Disemma					
Passiflora	Decaloba	Disemma	Disemma	NA	<i>P. aurantia</i>	G.Forst.	Czeczkott & Skirgjello (1967) as " <i>P. aurantiaca</i> ", Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Disemma	Disemma	NA	<i>P. cinnabarinia</i>	Lindl.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Disemma	Disemma	NA	<i>P. herbertiana</i>	Ker Gawl.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Hollrungiella						
Passiflora	Decaloba	Hollrungiella	Hollrungiella	NA				
Passiflora	Decaloba	Multiflora						
Passiflora	Decaloba	Multiflora	NA	NA	<i>P. holosericea</i>	L.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Auriculata						
Passiflora	Decaloba	Auriculata	NA	NA	<i>P. auriculata</i>	Kunth	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007), Silva et al. (2020)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Auriculata	NA	NA	<i>P. fanchonae</i>	Feuillet	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Auriculata	NA	NA	<i>P. rufa</i>	Feuillet & J.M.MacDougal	Vanderplank (2004)	Feuillet & MacDougal (2008)
Passiflora	Decaloba	Cieca						
Passiflora	Decaloba	Cieca	NA	NA	<i>P. coriacea</i>	Juss.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. juliana</i>	J.M.MacDougal	Vanderplank (2004)	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. obtusifolia</i>	Sessé & Moc.	Vanderplank (2004)	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. pallida</i>	L.	USDA, NRCS (2019–2020)	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. suberosa</i> (incl. subsp.)	L.	Mai (1960), Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), USDA, NRCS (2019–2020)	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. viridiflora</i>	Cav.	Vanderplank (2004) as " <i>P. viridiflora</i> "	Porter-Utley (2014)
Passiflora	Decaloba	Cieca	NA	NA	<i>P. xikzodz</i>	J.M.MacDougal	Vanderplank (2004) as " <i>P. xikzodz</i> "	Porter-Utley (2014)
Passiflora	Decaloba	Bryoniooides						
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. adenopoda</i>	DC.	MacDougal (1994), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. bryoniooides</i>	Kunth	MacDougal (1994), Vanderplank (2004) as " <i>P. bryoniooides</i> "	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. colimensis</i>	Mast. & Rose	MacDougal (1994)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. dioscoreifolia</i>	Killip	MacDougal (1994)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. dolichocarpa</i>	Killip	MacDougal (1994)	Krosnick et al. (2013a)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. exudans</i>	Zucc.	MacDougal (1994)	Jørgensen (no date)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. gracilis</i>	J.Jacq. ex Link	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. karwinskii</i>	Mast.	MacDougal (1994), Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. lobata</i>	(Killip) Hutch. ex J.M.MacDougal	MacDougal (1994), Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryoniooides	NA	NA	<i>P. morifolia</i>	Mast.	MacDougal (1994), Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Gurski (2015)	Ulmer & MacDougal (2004)

Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. oaxacensis</i>	J.M.MacDougal	MacDougal (1994)	Jørgensen (no date)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. pendens</i>	J.M.MacDougal	MacDougal (1994)	Krosnick et al. (2013a)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. pilosa</i> subsp. <i>dimidiata</i>	Ruiz & Pav. ex DC.	MacDougal (1994)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. podadenia</i>	Killip	MacDougal (1994)	Jørgensen (no date)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. pterocarpa</i>	J.M.MacDougal	MacDougal (1994)	Jørgensen (no date)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. queretorum</i>	Killip	MacDougal (1994)	Jørgensen (no date)
Passiflora	Decaloba	Bryonioides	NA	NA	<i>P. sicyoides</i>	Cham. & Schtdl.	MacDougal (1994)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	?	NA	<i>P. lyra</i> (misidentified?)	Planch. & Linden ex Killip	Pérez-Cortéz (2007)	Jørgensen (no date); imaged seed not consistent with supersection.
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. affinis</i>	Engelm.	Vanderplank (2004), USDA, NRCS (2019–2020)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. allantophylla</i>	Mast.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. alnifolia</i>	Kunth	Vanderplank (2004), Pérez-Cortéz (2007) as <i>P. cf. alnifolia</i> and <i>P. bauhinifolia</i>	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. amabacarpa</i>	Barb.Rodr.	Vanderplank (2004)	Vanderplank (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. andicola</i>	Esquerre	Esquerre-Ibañez (2019)	Esquerre-Ibañez (2019)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. apetala</i>	Killip	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. bicornis</i>	Mill.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007) as <i>P. pulchella</i> . Image in Pérez-Cortéz (2007) probably incorrect (same image as <i>P. aff. tiliacea</i> in same publication).	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. biflora</i>	Lam.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), USDA, NRCS (2019–2020)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. boenderi</i>	J.M.MacDougal	Vanderplank (2004) as " <i>P. boenderii</i> "	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. candollei</i>	Triana & Planch.	Pérez-Cortéz et al. (2002), Vanderplank (2004)	Vanderplank (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. colinvauxii</i>	Wiggins	Vanderplank (2004)	Vanderplank (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. cuneata</i>	Willd.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. filipes</i>	Benth.	Pérez-Cortéz (2007)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. gilbertiana</i>	J.M.MacDougal	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. helleri</i>	Peyr.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. jorullensis</i>	Kunth	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. lancearia</i>	Mast.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. lutea</i>	L.	Vanderplank (2004), USDA, NRCS (2019–2020)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. misera</i>	Kunth	Deginani (2001), Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007), Mondin et al. (2011)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. mollis</i>	Kunth	Pérez-Cortéz (2007)	Supersection: Jørgensen (no date). Section: this study, based on seed sculpture.
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. murucuja</i> (misidentified?)	L.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. organensis</i>	Gardn.	Mondin et al. (2011)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. ornithoura</i>	Mast.	Vanderplank (2004)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. pardifolia</i>	Vanderpl.	Vanderplank (2004)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. punctata</i>	L.	Pérez-Cortéz et al. (2002), Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. quimbayensis</i>	Ocampo & Forero	Ocampo Pérez et al. (2018)	Ocampo Pérez et al. (2018)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. sexflora</i>	Juss.	Pérez-Cortéz et al. (2002)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. standleyi</i>	Killip	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. tricuspis</i>	Mast.	Vanderplank (2004)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. tuberosa</i>	Jacq.	Pérez-Cortéz et al. (2002) as <i>P. aff. tuberosa</i> , Pérez-Cortéz (2007)	Krosnick et al. (2013a)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. tulae</i>	Urb.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. urnaefolia</i>	Rusby	Deginani (2001), Mondin et al. (2011) as " <i>P. urnifolia</i> "	Supersection: Jørgensen (no date). Section: this study, based on seed sculpture.
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. vespertilio</i>	L.	Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Decaloba	Decaloba	Decaloba	<i>P. yucatanensis</i>	Killip ex Standl.	Vanderplank (2004)	Ulmer & MacDougal (2004)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. capsularis</i>	L.	Deginani (2001), Pérez-Cortéz (2002), Vanderplank (2004), Pérez-Cortéz (2007), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. cissana</i>	Harms	Boza Espinoza et al. (2018), Silva et al. (2020)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. citrina</i>	J.M.MacDougal	Vanderplank (2004), Milani (2014), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. cobanensis</i> subsp.	Killip	Vanderplank (2004) as <i>P. brevipes</i> , Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. conzattiana</i>	Killip	Vanderplank (2004), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. costaricensis</i>	Killip	Pérez-Cortéz et al. (2002), Vanderplank (2004), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. goniosperma</i>	Killip	Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. pusilla</i>	J.M.MacDougal	Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. quinquangularis</i>	S.Calderón ex J.M.MacDougal	Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. rovirosae</i>	Killip	Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. rubra</i>	L.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Milani (2014), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. sanguinolenta</i>	Mast. & Linden	Vanderplank (2004), Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Decaloba	Xerogona	Xerogona	NA	<i>P. tenella</i>	Killip	Boza Espinoza et al. (2018)	Boza Espinoza et al. (2018)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. guazumaefolia</i>	Juss.	Pérez-Cortéz (2007)	Rome & Coppens d'Eeckenbrugge (2017)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. maliformis</i>	L.	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. nephrodes</i>	Mast.	Vanderplank (2004)	Vanderplank (2004)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. pallens</i>	Poep. ex Mast.	Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004)	Hansen et al. (2006)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. cf. picturata</i>	Ker Gawl.	Pérez-Cortéz (2007)	Silva et al. (2018)
Passiflora	Passiflora	Passiflora	Passiflora	?	<i>P. stipulata</i>	Aubl.	Vanderplank (2004)	Vanderplank (2004)
Passiflora	Passiflora	Passiflora	Passiflora	NA	<i>P. cacao</i>	Bernacci & M.M.Souza	Bernacci & Souza (2012)	Bernacci & Souza (2012)

	Passiflora	Passiflora	Passiflora	NA	Passiflora	<i>P. cincinnata</i>	Mast.	Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Gurski (2015)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Passiflora	NA	Passiflora	<i>P. edulis</i> (incl. forms)	Sims	Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), USDA, NRCS (2019-2020)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Passiflora	NA	Passiflora	<i>P. incarnata</i>	L.	Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004), USDA, NRCS (2019-2020), this study	Ulmer & MacDougal (2004)
4.1.2	Passiflora	Passiflora	Passiflora	NA	Passiflora	<i>P. mayarum</i>	J.M.MacDougal	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Passiflora	NA	Passiflora	<i>P. serratifolia</i>	L.	Vanderplank (2004)	Ulmer & MacDougal (2004)
4.1.3	Passiflora	Passiflora	Passiflora	NA	<b>Palmatisectae</b>		<i>P. palmatisecta</i>	Mast.	Deginani (2001)-only apex figured
4.1.4	Passiflora	Passiflora	Passiflora	NA	<b>Pedatae</b>		<i>P. pedata</i>	L.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007), Silva et al. (2016)
4.2	Passiflora	Passiflora	Passiflora	NA	<b>Setaceae</b>		<i>P. setacea</i>	None found	Feuillet & MacDougal (2003)
4.2.1	Passiflora	Passiflora	Stipulata	Stipulata	<b>Granadillastrum</b>				Feuillet & MacDougal (2003)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. actinia</i>	Hook.	Vanderplank (2004), Mondin et al. (2011)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. amethystina</i>	J.C.Mikan	Deginani (2001), Vanderplank (2004), Mondin et al. (2011)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. caerulea</i>	L.	Deginani (2001), Vanderplank (2004), Mondin et al. (2011)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. danielii</i>	Killip	Ocampo et al. (2015)	Ocampo et al. (2015)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. eichleriana</i>	Mast.	Gurski (2015), Mondin et al. (2011). Images in these two sources are dissimilar (different species?).	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. elegans</i>	Mast.	Deginani (2001), Vanderplank (2004), Mondin et al. (2011)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. exura</i>	Feuillet	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. garckei</i>	Mast.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. gibertii</i>	N.E.Br.	Deginani (2001) as " <i>P. giberti</i> ", Vanderplank (2004), Gurski (2015). Vanderplank (2004) may be misidentified (very different in morphology from other sources).	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. gritensis</i>	H.Karst.	Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. menispermifolia</i>	Kunth	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. mooreana</i>	Hook.f.	Deginani (2001), Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. mucronata</i>	Lam.	Vanderplank (2004), Gurski (2015)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. oerstedii</i> (incl. varieties)	Mast.	Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. reticulata</i>	Mast. & André	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. retipetala</i>	Mast.	Vanderplank (2004), Pérez-Cortéz (2007)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. sidifolia</i>	M.Roem.	Pérez-Cortéz et al. (2002) as " <i>P. sidifolia</i> ", Pérez-Cortéz et al. (2009) as " <i>P. sidifolia</i> ". Nardin et al. (2015)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. sprucei</i>	Mast.	One of these is mislabeled (mixed up with <i>P. spectabilis</i> ). Vanderplank (2004) as " <i>P. sprucei</i> ".	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. subpetiata</i>	Ortega	Mai (1960) as <i>P. alba</i> , Vanderplank (2004), Pérez-Cortéz (2007), Pérez-Cortéz et al. (2009). Seed in Pérez-Cortéz (2007) and Pérez-Cortéz et al. (2009) is different than those in other sources.	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. tenuifila</i>	Killip	Deginani (2001), Vanderplank (2004) as " <i>P. tenuifila</i> ", Mondin et al. (2011)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. tucumanensis</i>	Hook.	Deginani (2001), Vanderplank (2004) as " <i>P. naviculata</i> "	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Granadillastrum	NA	<i>P. urubiciensis</i>	Cervi	Mondin et al. (2011)	Cervi (2003)
4.2.2	Passiflora	Passiflora	Stipulata	<b>Calopathanthus</b>		<i>P. racemosa</i>	Brot.	Vanderplank (2004)	Ulmer & MacDougal (2004)
4.2.3	Passiflora	Passiflora	Stipulata	<b>Tacsonioides</b>					
	Passiflora	Passiflora	Stipulata	Tacsonioides	NA	<i>P. reflexiflora</i>	Cav.	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Tacsonioides	NA	<i>P. tarapotina</i>	Harms	Pérez-Cortéz et al. (2002)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Tacsonioides	NA	<i>P. umbilicata</i>	Harms	Deginani (2001)-only apex figured, Vanderplank (2004)	Ulmer & MacDougal (2004)
4.2.4	Passiflora	Passiflora	Stipulata	<b>Kermesinae</b>					
4.2.5	Passiflora	Passiflora	Stipulata	<b>Dyosomia</b>		<i>P. kermesina</i>	Link & Otto	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. ciliata</i> (incl. varieties)	Aiton	Vanderplank (2004) as <i>P. foetida</i> var. <i>hirsutissima</i> , <i>P. foetida</i> var. <i>lanuginosa</i> , <i>P. foetida</i> var. <i>maxoni</i> , <i>P. foetida</i> var. <i>orinocensis</i> , <i>P. foetida</i> var. <i>parvifolia</i>	Vanderplank (2013)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. chrysophylla</i>	Chodat.	Deginani (2001)	Vanderplank (2013)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. foetida</i> (incl. varieties)	L.	Deginani (2001), Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Gurski (2015), USDA, NRCS (2019-2020)	Vanderplank (2013)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. pentaschista</i>	(Killip) H.T.Svoboda	Vanderplank (2004) as <i>P. arida</i> var. "pentachista"	Svoboda & Harris (2018)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. sub lanceolata</i>	(Killip) J.M.MacDougal	Vanderplank (2004) as <i>P. palmeria</i> var. "sub lanceolate"	Vanderplank (2013)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. urbaniana</i>	Killip	Vanderplank (2004)	Vanderplank (2013)
	Passiflora	Passiflora	Stipulata	Dyosomia	NA	<i>P. vesicaria</i> var.	L.	Vanderplank (2004) as <i>P. foetida</i> var. <i>galapagensis</i>	Vanderplank (2013)
4.3	Passiflora	Passiflora	Laurifolia						
4.3.1	Passiflora	Passiflora	Laurifolia	NA	<b>Laurifoliae</b>				
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. acuminata</i>	DC.	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. ambigua</i>	Hemsl.	Vanderplank (2004), Pérez-Cortéz (2007)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. capparidifolia</i>	Killip	Pérez-Cortéz (2007)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. cerasina</i>	Annonay & Feuillet	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. crenata</i>	Feuillet & Cremers	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. gabrielliana</i>	Vanderpl.	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. gleasonii</i>	Killip	Pérez-Cortéz (2007) as " <i>P. gleasonii</i> "	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. gustaviana</i>	Ocampo & Molinari	Ocampo Pérez & Molinari (2017)	Ocampo Pérez & Molinari (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. laurifolia</i>	L.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), USDA, NRCS (2019-2020)	Rome & Coppens d'Eeckenbrugge (2017)	
	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. nigra</i>	Rusby	Vanderplank (2004)	Rome & Coppens d'Eeckenbrugge (2017)	

	Passiflora	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. nitida</i>	Kunth	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Rome & Coppens d'Eckenbrugge (2017)
	Passiflora	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. pergrandis</i>	Holm-Nielsen & Lawesson	Vanderplank (2004)	Rome & Coppens d'Eckenbrugge (2017)
4.3.2	Passiflora	Passiflora	Laurifolia	NA	Laurifoliae	<i>P. riparia</i>	Mart. ex Mast.	Pérez-Cortéz et al. (2002), Pérez-Cortéz (2007)	Rome & Coppens d'Eckenbrugge (2017)
	Passiflora	Passiflora	Laurifolia	NA	Quadrangulares	<i>P. alata</i>	Curtis	Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Mondin et al. (2011), Gurski (2015). Seed in Gurski (2015) misidentified? (does not match images in other sources).	Koch et al. (2013)
	Passiflora	Passiflora	Laurifolia	NA	Quadrangulares	<i>P. phoenicea</i>	Lindl.	Vanderplank (2004) as " <i>P. phoenicia</i> "	Koch et al. (2013)
	Passiflora	Passiflora	Laurifolia	NA	Quadrangulares	<i>P. quadrangularis</i>	L.	Pérez-Cortéz et al. (1995, 2002), Vanderplank (2004), Pérez-Cortéz (2007)	Koch et al. (2013)
	Passiflora	Passiflora	Laurifolia	NA	Quadrangulares	<i>P. triatula</i>	Feuillet & J.M.MacDougal	Vanderplank (2004)	Koch et al. (2013)
4.3.3	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. ligularis</i>	Juss.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Kirkbride et al. (2006), Pérez-Cortéz (2007), Cárdenas-Hernández et al. (2011), USDA, NRCS (2019–2020)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. magnifica</i>	L.K.Escobar	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. multiformis</i>	Jacq.	Pérez-Cortéz (2007)	Yockteng et al. (2011)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. platyloba</i>	Killip	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. seemannii</i>	Griseb.	Vanderplank (2004) as " <i>P. seemannii</i> ", Pérez-Cortéz (2007) as " <i>P. seemanni</i> "	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. serratodigitata</i>	L.	Vanderplank (2004)	Ulmer & MacDougal (2004)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. serrulata</i>	Jacq.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Yockteng et al. (2011)
	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. aff. tiliifolia</i>	L.	Pérez-Cortéz et al. (2002) as " <i>P. sp. n. aff. tiliifolia</i> ", Pérez-Cortéz (2007) as " <i>P. aff. tiliæfolia</i> "	Feuillet & MacDougal (2003)
4.3.4	Passiflora	Passiflora	Laurifolia	NA	Tiliifolia	<i>P. triloba</i>	Ruiz & Pav. ex DC.	Vanderplank (2004)	Ulmer & MacDougal (2004)
4.4	Passiflora	Passiflora	Laurifolia	NA	Marginatae	None found			
	Passiflora	Passiflora	Coccinea	NA		<i>P. aimae</i>	Annonay & Feuillet	Vanderplank (2004) as " <i>P. aimae</i> "	Feuillet (2007)
	Passiflora	Passiflora	Coccinea	NA		<i>P. coccinea</i> (incl. subspp.)	Aubl.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Vanderplank & Zappi (2011), Gurski (2015)	Feuillet (2007)
	Passiflora	Passiflora	Coccinea	NA		<i>P. quadrifaria</i>	Vanderpl.	Vanderplank (2004)	Feuillet (2007)
	Passiflora	Passiflora	Coccinea	NA		<i>P. quadriglandulosa</i>	Rodsched	Pérez-Cortéz (2007)	Feuillet (2007)
	Passiflora	Passiflora	Coccinea	NA		<i>P. vitifolia</i>	Kunth	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)	Feuillet (2007)
4.5	Passiflora	Passiflora	Distephana						
	Passiflora	Passiflora	Distephana	NA	NA	<i>P. amicorum</i>	Wurdack	Pérez-Cortéz (2007)	Vanderplank & Zappi (2011)
	Passiflora	Passiflora	Distephana	NA	NA	<i>P. cristalina</i>	Vanderpl. & Zappi	Vanderplank & Zappi (2011), Silveira et al. (2019)	Vanderplank & Zappi (2011)
	Passiflora	Passiflora	Distephana	NA	NA	<i>P. glandulosa</i>	Cav.	Vanderplank (2004), Pérez-Cortéz (2007), Vanderplank & Zappi (2011)	Vanderplank & Zappi (2011)
	Passiflora	Passiflora	Distephana	NA	NA	<i>P. variolata</i>	Poepp. & Endl.	Vanderplank (2004), Pérez-Cortéz (2007)	Vanderplank & Zappi (2011)
4.6	Passiflora	Passiflora	Tacsonia						
4.6.1	Passiflora	Passiflora	Tacsonia		Rathea				
	Passiflora	Passiflora	Tacsonia		Rathea	None found			
4.6.2	Passiflora	Passiflora	Tacsonia		Insignes				
	Passiflora	Passiflora	Tacsonia		Insignes	NA	Sacco	Vanderplank (2004) as " <i>P. piloscorona</i> "	Jorgensen & Vásquez (2009)
	Passiflora	Passiflora	Tacsonia		Insignes	NA	Cav.	Vanderplank (2004), González-Benito et al. (2009)	Jorgensen & Vásquez (2009)
4.6.3	Passiflora	Passiflora	Tacsonia		Colombiana				
4.6.3.1	Passiflora	Passiflora	Tacsonia		Colombiana	Colombianae			
	Passiflora	Passiflora	Tacsonia		Colombiana	Colombianae	<i>P. rugosa</i>	Planch. & Triana	Bonilla Morales (2014)
	Passiflora	Passiflora	Tacsonia		Colombiana	Colombianae	<i>P. truxillensis</i>	Planch. & Lind. ex Triana & Planch.	Bonilla Morales (2014)
4.6.3.2	Passiflora	Passiflora	Tacsonia		Leptomischae				
	Passiflora	Passiflora	Tacsonia		Leptomischae	<i>P. antioquiensis</i>	H.Karst.	Vanderplank (2004)	Bonilla Morales (2014)
4.6.3.3	Passiflora	Passiflora	Tacsonia		Colombiana	Quindiensæ			
	Passiflora	Passiflora	Tacsonia		Colombiana	Quindiensæ	None found		
4.6.4	Passiflora	Passiflora	Tacsonia		Parritana				
	Passiflora	Passiflora	Tacsonia		Parritana	NA	None found		
4.6.5	Passiflora	Passiflora	Tacsonia		Fimbriatistipula				
	Passiflora	Passiflora	Tacsonia		Fimbriatistipula	NA	None found		
4.6.6	Passiflora	Passiflora	Tacsonia		Tacsoniopsis				
	Passiflora	Passiflora	Tacsonia		Tacsoniopsis	NA	None found		
4.6.7	Passiflora	Passiflora	Tacsonia		Elkea				
	Passiflora	Passiflora	Tacsonia		Elkea	NA	<i>P. tarminiana</i>	Coppens & V.E.Barney	Bonilla Morales (2014)
	Passiflora	Passiflora	Tacsonia		Elkea	NA	<i>P. tripartita</i>	Breiter	Pérez-Cortéz et al. (2002) as <i>P. mollissima</i> , Pérez-Cortéz (2007) as <i>P. mollissima</i> , González-Benito et al. (2009) as <i>P. mollissima</i> , Martínez (2017), USDA, NRCS (2019–2020)
4.6.8	Passiflora	Passiflora	Tacsonia		Tacsonia				
	Passiflora	Passiflora	Tacsonia		Tacsonia	NA	<i>P. matthewsii</i>	(Mast.) Killip	Bonilla Morales (2014)
	Passiflora	Passiflora	Tacsonia		Tacsonia	NA	<i>P. mixta</i> (incl. varieties)	L.f.	Bonilla Morales (2014)
4.6.9	Passiflora	Passiflora	Tacsonia		Boliviiana				
	Passiflora	Passiflora	Tacsonia		Boliviiana	NA	None found		
4.6.10	Passiflora	Passiflora	Tacsonia		Trifoliata				
	Passiflora	Passiflora	Tacsonia		Trifoliata	NA	None found		
4.6.11	Passiflora	Passiflora	Tacsonia		Manicata				
	Passiflora	Passiflora	Tacsonia		Manicata	NA	<i>P. manicata</i>	Pers.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007)
									Bonilla Morales (2014)

NA	<b>Passiflora</b> Passiflora	<b>Tetrapathea</b> Tetrapathea	NA	NA	NA	<i>P. tetrandra</i>	Banks ex DC.	Vanderplank (2004)	Krosnick et al. (2009)
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Number, Feuillet & MacDougal	Genus	Subgenus	Supersection	Section	Series	Estimated number of species	Citation for number of species	Number of species with figured seeds (from Table S4)	Possible differentiating (unique or rare) seed features (vs. other Passifloroideae)	References consulted (only listed when features suggested; also see Table S4)	Notes
NA	<i>Ancistrothyrsus</i>					3	Feuillet (2020)	1	Seeds relatively large (12–14 mm in length).	Gentry (1992), Martínez (2017), Feuillet (2020)	
NA	<i>Adenia</i>					100	Feuillet & MacDougal (2007), Hearn (2006)	3–4			
NA	<i>Androsiphonia</i>					1	Feuillet & MacDougal (2007)	0			
NA	<i>Barteria</i>					4	Feuillet & MacDougal (2007)	0			
NA	<i>Basananthe</i>					30	Feuillet & MacDougal (2007)	0			
NA	<i>Crossostemma</i>					1	Feuillet & MacDougal (2007)	0			
NA	<i>Deidamia</i>					5	Feuillet & MacDougal (2007)	0			
NA	<i>Dilkea</i>					12	Feuillet (2011)	1	Seeds relatively large (13–20 mm long), not compressed to slightly compressed; shape ovoid, elongate, or centrally constricted; surface smooth to pustulate.	Feuillet (2009, 2010, 2011), MacDougal (2011)	These characteristics differ from those reported by Martínez (2017) for <i>Dilkea</i> . See text for details.
NA	<i>Efullesia</i>					2	Feuillet & MacDougal (2007)	0			
NA	<i>Mitostemma</i>					3	Feuillet & MacDougal (2007)	0			
NA	<i>Paropsia</i>					12	de Vos & Breteler (2009)	0			
NA	<i>Paropsiopsis</i>					2	de Vos & Breteler (2009)	0			
NA	<i>Schlechterina</i>					1	Feuillet & MacDougal (2007)	0			
NA	<i>Smeathmannia</i>					2	de Vos & Breteler (2009)	0			
NA	<i>Viridivia</i>					1	Feuillet & MacDougal (2007)	0			
<hr/>											
	<i>Passiflora</i>					562	Sum of subgenus estimates	218	None for the genus as a whole. Some subgroups have distinctive features (discussed below).		
	<i>Passiflora</i>	Unknown				NA		6			Number of species could be 7 (one seed not identified to species).
1	<i>Passiflora</i>	<i>Astrophea</i>				66	Hilgenhof (2013)	30			Subgenus <i>Astrophea</i> is monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a).
1.1	<i>Passiflora</i>	<i>Astrophea</i>	<i>Astrophea</i>			33	Hilgenhof (2013)	11			
1.1.1	<i>Passiflora</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Astrophea</i>		15	Hilgenhof (2013)	6			
1.1.2	<i>Passiflora</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Capreolata</i>		16	Hilgenhof (2013)	5			
1.1.3	<i>Passiflora</i>	<i>Astrophea</i>	<i>Astrophea</i>	<i>Leptopoda</i>		2	Hilgenhof (2013)	0			
1.2	<i>Passiflora</i>	<i>Astrophea</i>	<i>Pseudoastrophea</i>			33	Hilgenhof (2013)	19			
1.2.1	<i>Passiflora</i>	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Pseudoastrophea</i>		20	Hilgenhof (2013)	12			
1.2.2	<i>Passiflora</i>	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Botryastrophea</i>		13	Hilgenhof (2013)	7			
1.2.2.1	<i>Passiflora</i>	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Botryastrophea</i>	<i>Botryastrophea</i>	6	Hilgenhof (2013)	4			
1.2.2.2	<i>Passiflora</i>	<i>Astrophea</i>	<i>Pseudoastrophea</i>	<i>Botryastrophea</i>	<i>Carnae</i>	7	Hilgenhof (2013)	3			
2	<i>Passiflora</i>	<i>Deidamiooides</i>				13	MacDougal & Feuillet (2004)	4			Subgenus <i>Deidamiooides</i> is polyphyletic. The sections are in three separate clades: 1) <i>Polyantha</i> + <i>Deidamiooides</i> + <i>Tetraphylis</i> ; 2) <i>Mayapathanthus</i> ; 3) <i>Tryptostemmatoides</i> (Krosnick et al. 2013a).
2.1	<i>Passiflora</i>	<i>Deidamiooides</i>	NA	<i>Polyantha</i>		1	Krosnick et al. (2013a)	1	<i>P. cincinnata</i> has transversely sulcate seed sculpture similar to section <i>Xerogona</i> ; image in Vanderplank (2004) shows that central sulcus is x-shaped.	Ulmer & MacDougal (2004), Vanderplank (2004)	The <i>Polyantha</i> + <i>Deidamiooides</i> + <i>Tetraphylis</i> clade is monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a).
2.2	<i>Passiflora</i>	<i>Deidamiooides</i>	NA	<i>Deidamiooides</i>		1	Krosnick et al. (2013a)	0			The <i>Polyantha</i> + <i>Deidamiooides</i> + <i>Tetraphylis</i> clade is monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a).
2.3	<i>Passiflora</i>	<i>Deidamiooides</i>	NA	<i>Tetraphylis</i>		2	Krosnick et al. (2013a)	1			The <i>Polyantha</i> + <i>Deidamiooides</i> + <i>Tetraphylis</i> clade is monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a).
2.4	<i>Passiflora</i>	<i>Deidamiooides</i>	NA	<i>Mayapathanthus</i>		2	MacDougal & Feuillet (2004)	0	Sculpture of <i>P. obovata</i> Kilip "irregularly deeply rugose with 5–7 radial and transverse ridges."	Ulmer & MacDougal (2004, pg. 103)	This section is within subgenus <i>Decaloba</i> (Krosnick et al. 2013a).
2.5	<i>Passiflora</i>	<i>Deidamiooides</i>	NA	<i>Tryptostemmatoides</i>		7	MacDougal & Feuillet (2004)	2	Sculpture sometimes sulcate ( <i>P. arborea</i> Urive).	Ulmer & MacDougal (2004)	This section is sister to subgenus <i>Astrophea</i> (Muschler et al. 2012; Krosnick et al. 2013a).
3	<i>Passiflora</i>	<i>Decaloba</i>				230	Krosnick et al. (2013a)	84	None consistent for entire subgenus; however, some subgroups have distinctive features (discussed below).	See references for supersections and sections.	Subgenus <i>Decaloba</i> is likely monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a). However, see notes for supersection <i>Pterosperma</i> below.
3.1	<i>Passiflora</i>	<i>Decaloba</i>	<i>Pterosperma</i>			4	Krosnick et al. (2013a)	2	Seeds relatively large (ca. 7.5–12 mm long x 7–11 mm wide), overall shape bilobed, having lateral striate wings with irregular margins.	Gibert & MacDougal (2000), MacDougal & Hansen (2003), Ulmer & MacDougal (2004), Vanderplank (2004), Krosnick et al. (2013a)	Krosnick et al. (2013a) found supersection <i>Pterosperma</i> to be monophyletic, whereas Sader et al. (2019) found supersection <i>Pterosperma</i> to be polyphyletic.
3.2	<i>Passiflora</i>	<i>Decaloba</i>	<i>Hahniopanthus</i>			5	Krosnick et al. (2013a)	2			Supersection <i>Hahniopanthus</i> is monophyletic (Krosnick et al. 2013a).
3.3	<i>Passiflora</i>	<i>Decaloba</i>	<i>Disemma</i>			22	Krosnick et al. (2013b), Ma et al. (2019)	4			Supersection <i>Disemma</i> is monophyletic (Krosnick et al. 2013a, b).
3.3.1	<i>Passiflora</i>	<i>Decaloba</i>	<i>Disemma</i>	<i>Octandranthus</i>		18	Krosnick et al. (2013b), Ma et al. (2019)	1			Section <i>Octandranthus</i> is monophyletic (Krosnick et al. 2013a, b).
3.3.2	<i>Passiflora</i>	<i>Decaloba</i>	<i>Disemma</i>	<i>Disemma</i>		3	Krosnick et al. (2013b)	3			Section <i>Disemma</i> is monophyletic (Krosnick et al. 2013a, b).
3.3.3	<i>Passiflora</i>	<i>Decaloba</i>	<i>Disemma</i>	<i>Hollringiella</i>		1	Krosnick et al. (2013b)	0			

3.4	<i>Passiflora</i>	<i>Decaloba</i>	<i>Multiflora</i>		22 Krosnick et al. (2013a)	1		<p><i>P. multiflora</i> L. is not closely related to the remainder of supersection <i>Multiflora</i>. Supersection <i>Multiflora</i> is paraphyletic, with subsection <i>Auriculata</i> embedded within it (Krosnick et al. 2013a).</p>	
3.5	<i>Passiflora</i>	<i>Decaloba</i>	<i>Auriculata</i>		8 Krosnick et al. (2013a)	3	Sculpture transversely sulcate with rugulose ridges.	<p>Pérez-Cortéz et al. (2002), Ulmer &amp; MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Silva et al. (2020)</p>	
3.6	<i>Passiflora</i>	<i>Decaloba</i>	<i>Cieca</i>		19 Krosnick et al. (2013a), Porter-Utley (2014)	7	Seeds often fusiform to falcate, ornamentation coarsely reticulate-foveate, often with shallow longitudinal striations overlying reticulations.	<p>Mai (1960), Deginani (2001), Pérez-Cortéz et al. (2002), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), USDA, NRCS (2019–2020)</p>	
3.7	<i>Passiflora</i>	<i>Decaloba</i>	<i>Bryonioides</i>		22 Krosnick et al. (2013a)	17		<p>Supersection <i>Bryonioides</i> is monophyletic (Krosnick et al. 2013a).</p>	
3.8	<i>Passiflora</i>	<i>Decaloba</i>	<i>Decaloba</i>		130 Krosnick et al. (2013a)	48	Sculpture transversely sulcate.	<p>In addition to the references for sections <i>Decaloba</i> and <i>Xerogona</i> below, see MacDougal (1994), Krosnick et al. (2013a).</p>	
NA	3.8.1	<i>Passiflora</i>	<i>Decaloba</i>	<i>Decaloba</i>	<i>Unknown Decaloba</i>	115 Krosnick et al. (2013a)	1	34 Sculpture transversely sulcate with rugulose ridges.	<p>Deginani (2001), Pérez-Cortéz et al. (2002), Ulmer &amp; MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Ocampo Pérez et al. (2018), Esquerre-Ibáñez (2019), USDA, NRCS (2019–2020)</p>
3.8.2	<i>Passiflora</i>	<i>Decaloba</i>	<i>Decaloba</i>		<i>Xerogona</i>	15 Krosnick et al. (2013a), Boza Espinoza (2018)	13	Sculpture transversely sulcate, typically with smooth ridges (ridges sometimes rugulose). Notable exception: <i>P. goniosperma</i> , which has toothed longitudinal ridges (see Boza Espinoza et al. 2018.)	<p>Deginani (2001), Pérez-Cortéz et al. (2002), Ulmer &amp; MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Milani (2014), Krosnick et al. (2013a), Boza Espinoza et al. (2018), Silva et al. (2020)</p>
4	<i>Passiflora</i>	<i>Passiflora</i>			250 Krosnick et al. (2013a)	93	None consistent for entire subgenus; however, seed apex sometimes tridentate or shallowly tridentate in	<p>See references for sections and series.</p>	
NA	<i>Passiflora</i>	<i>Passiflora</i>	Unknown		NA	6	supersections <i>Laurifolia</i> , <i>Passiflora</i> , and <i>Stipulata</i> .	<p>Subgenus <i>Passiflora</i> is monophyletic (Hansen et al. 2006; Muscher et al. 2012; Krosnick et al. 2013a; Sader et al. 2019).</p>	
4.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Passiflora</i>		20 Sum of series values (below)	8	Apex sometimes tridentate.	<p>See references for series.</p>	
4.1.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Passiflora</i>	NA	<i>Passiflora</i>	14 Bernacci & Souza (2012)	6	Apex sometimes tridentate.	<p>Deginani (2001), Pérez-Cortéz et al. (2002, 2009) Ulmer &amp; MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Bernacci &amp; Souza (2012), Gurski (2015), USDA, NRCS (2019–2020), this study</p>
4.1.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Passiflora</i>	NA	<i>Palmatisectae</i>	1 MacDougal & Feuillet (2004)	1	Apex tridentate.	<p>Deginani (2001)</p>
4.1.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Passiflora</i>	NA	<i>Pedatae</i>	1 MacDougal & Feuillet (2004)	1		
4.1.4	<i>Passiflora</i>	<i>Passiflora</i>	<i>Passiflora</i>	NA	<i>Setaceae</i>	4 MacDougal & Feuillet (2004)	0		
4.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		98 Sum of section values (below)	34	Apex sometimes tridentate (esp. section <i>Dysosmia</i> ).	<p>See references for sections.</p>	
4.2.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		<i>Granadillastrum</i>	66 MacDougal & Feuillet (2004)	22	Apex sometimes tridentate? Unambiguously tridentate forms— <i>P. gibertii</i> in Vanderplank (2004), <i>P. eichleriana</i> in Gurski (2015), and <i>P. subpelata</i> in Pérez-Cortéz (2007) and Pérez-Cortéz et al. (2009)—do not match images of seeds of the same species in other sources.	<p>Mai (1960), Deginani (2001), Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Gurski (2015), Ocampo et al. (2015)</p>
4.2.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		<i>Calopathanthus</i>	1 MacDougal & Feuillet (2004)	1		
4.2.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		<i>Tacsonioides</i>	4 MacDougal & Feuillet (2004)	3	Apex sometimes tridentate? Ulmer and MacDougal (2004) reported tridentate seeds in <i>P. reflexiflora</i> and <i>P. umbilicata</i> , but published images do not support this. Similarly, Pérez-Cortéz et al. (2002) described <i>P. tarapotina</i> as tridentate, but published image is open to interpretation.	<p>Deginani (2001), Pérez-Cortéz et al. (2002), Ulmer &amp; MacDougal (2004), Vanderplank (2004)</p>
4.2.4	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		<i>Kermesinae</i>	4 MacDougal & Feuillet (2004)	1		
4.2.5	<i>Passiflora</i>	<i>Passiflora</i>	<i>Stipulata</i>		<i>Dysosmia</i>	23 Vanderplank (2013), Svoboda & Harris (2018), Svoboda (2019)	7	Seed shape cuneate, oblong, rectangular, or scutiform; apex often tridentate (prominence of lateral appendages variable); base sometimes bilobed (winged).	<p>Deginani (2001), Pérez-Cortéz et al. (2002, 2009), Vanderplank (2004, 2013), angular/rectangular or scutiform when compared to seeds of Pérez-Cortéz (2007), Ulmer &amp; MacDougal (2004), Mondin et al. (2011), Gurski (2015), Svoboda &amp; Harris (2018), USDA, NRCS (2019–2020)</p>
4.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Laurifolia</i>		44 Sum of series values (below)	26	Apex sometimes tridentate.	<p>See references for series.</p>	
4.3.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Laurifolia</i>	NA	<i>Laurifoliae</i>	24 Rome & Coppens d'Eeckenbrugge (2017)	13	Apex sometimes tridentate.	<p>Pérez-Cortéz et al. (2002), Ulmer &amp; MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Ocampo Pérez &amp; Molinari (2017), USDA, NRCS (2019–2020)</p>

4.3.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Laurifolia</i>	NA	<b>Quadrangulares</b>	5 Koch et al. (2013)	4 Seeds relatively large (5–10 mm long x 4–8 mm wide), apex often tridentate, margin striate; base sometimes bilobed.	Deginani (2001), Pérez-Cortéz et al. (1995, 2002), Ulmer & MacDougal (2004), Vanderplank (2004), Pérez-Cortéz (2007), Mondin et al. (2011), Gurski (2015)	Some (e.g., <i>P. quadrangularis</i> ) have seeds very similar to seeds of supersection <i>Pterosperma</i> (see Vanderplank 2004, pl. 33).
4.3.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Laurifolia</i>	NA	<b>Tiliifolia</b>	14 MacDougal & Feuillet (2004)	9 Apex sometimes tridentate.	Pérez-Cortéz et al. (2002), Vanderplank (2004), Kirkbride et al. (2006), Pérez-Cortéz (2007), Cárdenas-Hernández et al. (2011), USDA, NRCS (2019–2020)	
4.3.4	<i>Passiflora</i>	<i>Passiflora</i>	<i>Laurifolia</i>	NA	<b>Marginatae</b>	1 MacDougal & Feuillet (2004)	0		
4.4	<i>Passiflora</i>	<i>Passiflora</i>	<i>Coccinea</i>			18 Feuillet (2007)	5		
4.5	<i>Passiflora</i>	<i>Passiflora</i>	<i>Distephana</i>			6 Vanderplank & Zappi (2011)	4		
4.6	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>			65 Ocampo et al. (2017)	10		Supersection <i>Tacsonia</i> is monophyletic (Abrahamczyk et al. 2014).
4.6.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Rathea</i>		4 Bonilla Morales (2014)	0		
4.6.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Insignes</i>		6 Jørgensen & Vásquez (2009)	2		
4.6.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Colombiana</i>		19 MacDougal & Feuillet (2004)	3		
4.6.3.1	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Colombianae</i>		9 MacDougal & Feuillet (2004)	2		
4.6.3.2	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Leptomischae</i>		8 MacDougal & Feuillet (2004)	1		
4.6.3.3	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Quindiensae</i>		2 MacDougal & Feuillet (2004)	0		
4.6.4	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Parritana</i>		2 MacDougal & Feuillet (2004)	0		
4.6.5	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Fimbriatistipula</i>		2 MacDougal & Feuillet (2004)	0		
4.6.6	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Tacsoniopsis</i>		2 MacDougal & Feuillet (2004)	0		
4.6.7	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Eikea</i>		15 MacDougal & Feuillet (2004)	2		
4.6.8	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Tacsonia</i>		6 Bonilla Morales (2014)	2		
4.6.9	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Boliviiana</i>		2 MacDougal & Feuillet (2004)	0		
4.6.10	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Trifoliata</i>		1 MacDougal & Feuillet (2004)	0		
4.6.11	<i>Passiflora</i>	<i>Passiflora</i>	<i>Tacsonia</i>	<i>Manicata</i>		5 MacDougal & Feuillet (2004)	1		
NA	<i>Passiflora</i>	<i>Tetrapathea</i>				3 Krosnick et al. (2009)	1 Sculpture rugose in <i>P. kuranda</i> and <i>P. tetrandra</i> . (Note: Seeds not transversely sulcate as in supersection <i>Decaloba</i> .) Seeds winged in <i>P. kuranda</i> .	Vanderplank (2004), Krosnick et al. (2009)	Subgenus <i>Tetrapathea</i> is monophyletic (Krosnick et al. 2013a). Includes the formerly independent genera <i>Holrrungia</i> and <i>Tetrapathea</i> (Krosnick et al. 2009).

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Bernacci LC, MM Souza	2012	<i>Passiflora cacaoe</i> (Passifloraceae), a new species from southern Bahia, Brazil	<i>Novon</i> 22 :1–7. <a href="https://doi.org/10.3417/2010043">https://doi.org/10.3417/2010043</a>	
Bonilla Morales MM	2014	Biogeografía y morfología de las Passifloraceae (subg. <i>Tacsonia</i> , <i>Rathea</i> y <i>Manicata</i> ) del trópico andino como estrategia de conservación.	Magister en Ciencias Biológicas thesis. Universidad Nacional de Colombia, Palmira, Colombia. <a href="http://www.bdigital.unal.edu.co/47460/">http://www.bdigital.unal.edu.co/47460/</a>	
Boza Espinoza TE, PM Jørgensen, JM MacDougal	2018	A taxonomic revision of <i>Passiflora</i> sect. <i>Xerogona</i> (Passifloraceae) using principal component analysis	<i>Annals of the Missouri Botanical Garden</i> 103: 258–313. <a href="https://doi.org/10.3417/2017055">https://doi.org/10.3417/2017055</a>	
Cárdenas-Hernández J, D Miranda L., S Magnitskiy, C Carranza	2011	Morphological and anatomical analyses of the seed coats of sweet granadilla ( <i>Passiflora ligularis</i> Juss.) seeds	<i>Agronomía Colombiana</i> 29: 377–385. <a href="https://revistas.unal.edu.co/index.php/agrocol/article/view/21650">https://revistas.unal.edu.co/index.php/agrocol/article/view/21650</a>	
Cervi AC	2003	Estudo das Passifloraceae brasileiras. Uma nova espécie de <i>Passiflora</i> L. para Santa Catarina	<i>Sellowia</i> 53–55: 9–14.	
Czeczkott H, A Skirgiello	1967	Flora Kopala Turowa Kolo Bogatyni, Część Druga: Systematyczny opis szczątków roślinnych (3), Praca Zbiorowa	<i>Prace Muzeum Ziemi</i> 10: 97–166. <a href="http://www.redalyc.org/articulo.oa?id=66939206">http://www.redalyc.org/articulo.oa?id=66939206</a>	
Deginani NB	2001	Las especies Argentinas del género <i>Passiflora</i> (Passifloraceae). A revision of the African genera <i>Paropsisopsis</i> and <i>Smeathmannia</i> (Passifloraceae-Paropsidiae), including a new species of <i>Paropsisopsis</i> from Cameroon	<i>Darwiniana</i> 39: 43–129. <a href="https://doi.org/10.1017/S0960428609005174">https://doi.org/10.1017/S0960428609005174</a>	
de Vos JM, FJ Breteler	2009	Una nueva especie de Passiflora sección Decaloba (Passifloraceae) de Perú	<i>Edinburgh Journal of Botany</i> 66: 27–49. <a href="https://doi.org/10.1080/0960428609005174">https://doi.org/10.1080/0960428609005174</a>	
Esquerre-Ibañez B	2019	Folia taxonomica 2. New species of <i>Passiflora</i> subgenus <i>Passiflora</i> (Passifloraceae) from the Guianas	<i>Darwiniana, nueva serie</i> 7: 279–288. <a href="https://doi.org/10.14522/darwiniana.2019.72.842">https://doi.org/10.14522/darwiniana.2019.72.842</a>	
Feuillet C	2007	Folia taxonomica 16. <i>Dilkea</i> (Passifloraceae) 1. <i>Epkia</i> , a new subgenus and five new species from western Amazonia and the Guianas	<i>Journal of the Botanical Research Institute of Texas</i> 1: 819–825. <a href="https://www.biodiversitylibrary.org/page/34483095">https://www.biodiversitylibrary.org/page/34483095</a>	
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Feuillet C	2010	Two new species of <i>Dilkea</i> subgenus <i>Dilkea</i> (Passifloraceae) from Loreto, Peru	<i>Journal of the Botanical Research Institute of Texas</i> 4: 55–62. <a href="https://www.biodiversitylibrary.org/page/48586057">https://www.biodiversitylibrary.org/page/48586057</a>	
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Feuillet C, JM MacDougal	2020	Checklist of recognized species names of passion flowers	<i>Phytotaxa</i> 438: 207–212. <a href="https://doi.org/10.11646/phytotaxa.438.3.5">https://doi.org/10.11646/phytotaxa.438.3.5</a>	
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Feuillet C, JM MacDougal	2003		<i>Passiflora</i> 13: 34–38. <a href="https://doi.org/10.1007/978-3-540-32219-1_35">https://doi.org/10.1007/978-3-540-32219-1_35</a>	
Feuillet C, JM MacDougal	2007	Passifloraceae	<i>Journal of the Botanical Research Institute of Texas</i> 2: 817–824. <a href="https://www.biodiversitylibrary.org/page/41536046">https://www.biodiversitylibrary.org/page/41536046</a>	
Feuillet C, JM MacDougal	2008	Folia Taxonomica 9. New species of <i>Passiflora</i> subg. <i>Decaloba</i> (Passifloraceae) from northern South America	<i>Novon</i> 2: 333–338. <a href="https://doi.org/10.2307/3391490">https://doi.org/10.2307/3391490</a>	
Gentry AH	1992	New species of woody plants from Amazonian Peru	<i>Lundellia</i> 3: 1–5. <a href="https://doi.org/10.25224/1097-993X-3.1.1">https://doi.org/10.25224/1097-993X-3.1.1</a>	
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González-Benito ME, N Aguilar, T Ávila	2009	Germination and embryo rescue from <i>Passiflora</i> species seeds post cryopreservation	<i>Cryo Letters</i> 30:142–147. <a href="https://doi.org/10.1080/01612370902850011">https://doi.org/10.1080/01612370902850011</a>	
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