Notes on Early Land Plants Today. 69. Circumscription of Plagiochilaceae (Marchantiophyta) with a preliminary infrageneric subdivision of Plagiochila

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Abstract

Plagiochilaceae is here circumscribed to include 10 genera, Acrochila, Chiastocaulon, Dinckleria, Pedinophyllopsis, Pedinophyllum, Plagiochila, Plagiochilidium, Plagiochilion, Pseudolophocolea and Xenochila. For the forthcoming world checklist of hornworts and liverworts we here summarize the current knowledge and identify the sections of Plagiochila that are currently recognized by morphological and molecular studies. Plagiochila is provisionally divided into 28 sections based on recent morphological and molecular studies. Plagiochila ecuadorica and Plagiochila sciophila subsp. ciliigera are new combinations, Plagiochila umbrosioides is a nomen novum.

Circumscription of Plagiochilaceae

The family Plagiochilaceae Müller (1956: 877) was originally circumscribed to include the genera Mylia Gray (1821: 693), Pedinophyllum (Lindberg 1874: 366) Lindberg (1875: 504) and Plagiochila (Dumortier 1831: 42) Dumortier (1835: 14). Mylia was transferred to Jungermanniaceae by Grolle (1962) forming a new subfamily, subfam. Mylioideae Grolle (1962: 15), which was later elevated to its own family, Myliaceae Schliakov (1975: 308). Later, several genera, mostly segregates from Plagiochila were established and referred to the family. Crandall-Stotler et al. (2009) included Acrochila Schuster (1963: 285), Chiastocaulon Carl (1931a: 58), Dinckleria Trevisan (1877: 421), Pedinophyllopsis R.M.Schust. et Inoue in Schuster & Engel (1981: 311), Pedinophyllum, Plagiochila, Plagiochilidium Herzog (1931: 186), Plagiochilion Hattori (1947: 7) and Xenochila Schuster (1959a: 15). Söderström et al. (2013) moved the genus Pseudolophocolea R.M.Schust. et Inoue in Schuster & Engel (1982: 71) from Lophocoleaceae Vanden Berghen (1956: 208) to Plagiochilaceae. Plagiochilaceae is related to Lophocoleaceae and several genera have shifted positions between the families. Other genera that have been included in Plagiochilaceae in various publications are either synonyms with any of the mentioned genera, or now included in other families. In addition to Plagiochila, the following genera are now recognized within the family.

Acrochila was established to accommodate Acrochila simpsonii (W.Martin & E.A.Hodgs. in Martin 1950: 497) Schuster (1963: 285) [= Acrochila biserialis (Lehm. et Lindenb. in Lindenberg 1843: 126) Grolle (1964a: 236)] and Acrochila etesseana (Stephani 1908: 152) Schuster (1963: 285) [= Acrochila caledonica (Stephani 1908: 32) Inoue 1967: 182], two segregates from Plagiochila. The genus was included in the molecular study of Groth (2005) with conflicting results. One marker placed it in Plagiochilaceae and another marker as a sister to Adelanthus Mitten (1864: 243). However, we here retain it in Plagiochilaceae until further studied.

Chiastocaulon was established to accommodate Chiastocaulon dendroides (Nees 1830: 77) Carl (1931a: 59), Chiastocaulon flagelliferum Stephani (1918: 155) Carl (1931a: 60) and Chiastocaulon minutifolium Stephani (1921: 185) Carl (1931a: 60). All three species were united to one species by Dugas (1929) who considered it a Plagiochila species. This view was followed by most authors until Groth & Heinrichs (2003) in a molecular study showed it to be distinct from Plagiochila.
Dinckleria was established to include only one species, Dinckleria pleurata (Hooker & Taylor 1844a: 372) Trevisan (1877: 421). This name had generally been synonymized with Plagiochila until the new genus Proskauera Heinrichs et J.J.Engel in Heinrichs et al. (2006: 235) was described with two species, Proskauera pleurata (Hook. f. et Taylor) Heinrichs et J.J.Engel in Heinrichs et al. (2006: 235) and Proskauera fruticella (Hooker & Taylor 1844c: 565) Heinrichs et J.J.Engel (2006: 237) overlooking the older name Dinckleria. This was corrected in Engel & Heinrichs (2008). The close relationship to Plagiochila and inclusion in Plagiochilaceae has never been challenged.

Pedinophyllopsis was established to accommodate Pedinophyllopsis abdita (Sullivant 1850: 317) R.M.Schust. et Inoue in Schuster & Engel (1981: 311). It was originally placed in Geocalycaceae, but it was noted to be a very isolated in the family and He-Nygrén & Piippo (2003) showed that it is better placed in Plagiochilaceae.

Pedinophyllum was established to accommodate Pedinophyllum pyrenaicum (Spruce 1847: no. 9) Lindberg (1875: 504) [= Pedinophyllum interruptum (Nees 1833: 165) Kaalaas (1893: 190)] and now includes four species (although some not universally recognized). Although recognized as close to Plagiochila its position within Plagiochilaceae has sometimes been questioned, but Feldberg et al. (2010b) showed it belongs there.

Plagiochilidium was described with one species, Plagiochilidium borneensis Herzog (1931: 186) [= Plagiochilidium bidentulum (Stephani 1905e: 1134) Grolle (1988: 408)]. It was described as closely related to Jamesoniella (Spruce 1876: 230) Carrington (1881: 25) and originally placed in Lophoziaceae Cavers (1910: 293) together with Plagiochila. Buch et al. (1937) then transferred it to Plagiochilaceae.

Plagiochilion was originally established to include two species, Plagiochilion oppositum (Reinwardt et al. 1824: 226) Hattori (1947: 7) and Plagiochilion braunianum (Nees 1830: 80) Hattori (1947: 7) in the Plagiochilaceae. Later, several other species have been referred to the genus. Fourteen species are recognized at present.

Pseudolophocolea was established to accommodate Pseudolophocolea denticulata Schuster & Engel (1982: 73). It was originally described as being closely related to Pedinophyllopsis. The authors even speculated that the two genera might be regarded as subgenera of a single genus. Although both genera were placed in Geocalycaceae subfam. Leptoscyphoideae Schuster (1980: 267), an affinity with the plagiochiloid Pedinophyllum was also noted. He-Nygrén & Piippo (2003) showed that Pedinophyllopsis is best placed in Plagiochilaceae, a hypothesis further supported by the molecular studies of Groth (2005). Based on the morphological similarities of Pseudolophocolea with Pedinophyllopsis and Pedinophyllum detailed in Schuster & Engel (1982), Pseudolophocolea was placed in Plagiochilaceae by Söderström et al. (2013).

Xenochila was established to accommodate Xenochila paradoxa (Stephani 1921: 197) Schuster (1959a: 15) [= Xenochila integrifolia (Mitten 1861: 96) Inoue (1963: 373)]. It was assumed to be related to Plagiochilidium by Inoue (1963).

Infrageneric structure of Plagiochila

Plagiochila is a large genus with almost 3,000 names out of which some 700 species are recognized today (ELPT database). Over one hundred subdivisions (mostly sections) have also been described. The genus has never been completely monographed although several regional revisions exist. Lindenberg (1839, 1840, 1844) was the first to publish a study including a considerable number of species. He was also the first to classify them into sections. Spruce (1885) described a large number of species, but only South American taxa. He divided them in two main groups, “Divisio I” Cauliflorae Spruce (1885: 453) and “Divisio II” Ramiflorae Spruce (1885: 460). Those groups were further divided into 5 subgroups (both levels unranked). Schiffner (1900a) recognized seven sections among the 23 taxa he recognized on Java. Stephani (1902a, b, c, 1903a, b, c, d, e, f, g, 1904a, b, c, d, e, f, 1905a, b, c, d, e) was the first to include all species he knew from all around the world, but apart from the two main categories recognised by him, Patulae and Ampliatae, he separated them further on geographical basis only. He recognized almost 800 species. Dugas (1929) mentioned just over 400 species in her study of the genus mainly from the Paris herbarium. Carl (1931b) also presented a classification that in large part was geographically based.
During the past 50–60 years some important revisions trying to classify the genus into subgenera and sections have appeared. It is worth mentioning the works by Schuster (1959a, b, 1960, 1980) for North America, Jones (1962) for Africa, Inoue & Schuster (1971) for Tasmania and New Zealand, Inoue (1986) for mainland Australia, Hässel (2004, 2006, 2008a, b, 2009) for southern South America and So (2001a) for China, in addition to the series of studies by H. Inoue spanning over 25 years leading to his summary of the genus in southeast Asia (Inoue 1984). All these studies are morphological and the subdivisions of the genus have mostly been done based on the taxa in the region under study.

The first study also including molecular methods appeared early this century (Heinrichs et al. 2002a). Subsequent molecular studies have used a broader spectrum of taxa from various parts of the world, although southeast Asia and Australasia are still under-represented compared to Europe, North America, South America and Africa. All taxa have been revised for Africa (Heinrichs et al. 2005a), North America (Heinrichs et al. 2004a) and Europe (although there is no synopsis published for the European taxa). All these studies, and several more, have shown that there are several subdivisions that should be recognized. However, a global synthesis of the genus has not been undertaken including information from any molecular study or recent morphological studies.

For the forthcoming world checklist of hornworts and liverworts (Söderström et al. in press) we here summarize the current knowledge and identify the sections that are currently recognized by morphological and molecular studies. The format of this note follows Söderström et al. (2012) and a series of notes directly associated with the worldwide checklist, most recently He et al. (2014), Long et al. (2014), Qui et al. (2014), Shu & Zhu (2014) and Váňa et al. (2014).


Note:—Plagiochila sect. Adiantoideae has been included in molecular studies and was recognized by Heinrichs et al. (2003) and subsequent studies. The type species of all three sections have also been included in molecular studies and proved to belong here.


Note:—The section was first recognized in the molecular and morphological study by Heinrichs et al. (2005a).


Note:—Recognition of the section is supported by several molecular studies, e.g. Groth (2005) and Heinrichs et al. (2006).


Note:—The single species of the section has never been included in any molecular study, but the section was recognized by Engel & Smith Merrill (2013) on morphological evidence.


Note:—Inoue (1965b) stated that the section is close to *Plagiochila*. *Ciliatae* (= *Plagiochila sect. Cucullatae*). No species has been included in any molecular study, but the section was recognized by So (2001a).


Note:—The section was recognized by Inoue (1984) and So (2001b), which also included *Plagiochila sect. Trabeculatae*, the latter with species included in molecular studies. However, since *Plagiochila cobana* is so poorly known and not included in any molecular study, Groth et al. (2004) and Heinrichs et al. (2004a) kept them separate.


= *Plagiochila sect. Ciliatae Schiffn.,* Hep. Fl. Buitenzorg: 107, 1900 (Schiffner 1900a), syn. nov. Type (ICN Art. 22.6):—*Plagiochila ciliata* Gottsch. (1857: 334) [= *Plagiochila sciophila* Lindenberg (1840: 100), cf. Inoue (1984)]. Note:—Heinrichs et al. (2004a) showed that the type of the section belongs to *Plagiochila sect. Cucullatae*.


= *Plagiochila sect. Acanthophyllae Carl,* Ann. Bryol., Suppl. 2: 104, 1931 (Carl 1931b), syn. nov. Type (ICN Art. 22.6):—*Plagiochila acanthophylla* Gottsch. (1868: 38) [= *Plagiochila sciophila* Lindenberg (1840: 100), cf. Inoue (1984)]. Note:—Heinrichs et al. (2004a) showed that the type of the section belongs to *Plagiochila sect. Cucullatae*.


Note:—Recognition of *Plagiochila sect. Cucullatae* is supported by several molecular studies, e.g. Groth (2005) and Heinrichs et al. (2006). The types of all synonyms have been included in molecular studies confirming their position.


= *Plagiochila sect. Alternantes Carl,* Ann. Bryol., Suppl. 2: 75, 1931 (Carl 1931b). Type (ICN Art. 22.6):—*Plagiochila alternans* Gottsch. et al. (1847: 648). Note:—Groth (2005) and Heinrichs et al. (2006) showed that the section should be placed in synonymy with *Plagiochila sect. Denticulatae* although they used the later name *Alternantes*.

= *Plagiochila sect. Minutidentes Carl,* Ann. Bryol., Suppl. 2: 72, 1931 (Carl 1931b), syn. nov. Type (ICN Art. 22.6):—*Plagiochila minutidens* Stephani (1916: 205) [= *Plagiochila ovata* Gottsch. et al. 1847:656], cf. Müller et al. 1999]. Note:—Groth (2005) and Heinrichs et al. (2006) showed that the section should be placed in synonymy with *Plagiochila sect. Alternantes* which is a later synonym of *Plagiochila sect. Denticulatae*.


Plagiochila sect. Giganteae Carl, Ann. Bryol., Suppl. 2: 143, 1931 (Carl 1931b). Type:—Plagiochila gigantea Lindenberg (1840: 115). Note:—Engel & Smith Merrill (2013) did not describe the section, but apparently tried to validate it with a reference to Plagiochila sect. Gigantea subsect. 2 Carl (1931b: 145). However, the latter does not have any description either. In addition, they included two sections as synonyms that were available as names. They considered Plagiochila sect. Deltoidae to be illegitimate as Hodgson (1944) included the type of the older Plagiochila sect. Banksianae in it. However, as Engel &
Smith Merrill (2013) deliberately excluded that element, the name became available. However, *Plagiochila* sect. *Deltoidea* is not validly published as Hodgson failed to provide a Latin description. Engel & Smith Merrill’s (2013) “typification” of *Plagiochila sect. Deltoidea* with *Plagiochila banksiana* must also be rejected as the section should be automatically typified with *Plagiochila deltoidea* (ICN Art. 22.6). The other older section name included as a synonym is *Plagiochila* sect. *Fragmentissimae*, a section we provisionally treat as a synonym of *Plagiochila sect. Denticulatae*.

Note:—Recognition of *Plagiochila sect. Durae* is supported by several molecular studies (Groth 2005, Heinrichs et al. 2005a, 2006). The types of all synonymized sections, except *Plagiochila sect. Angulatae* have been included in molecular studies confirming their position.


Note:—Recognition of the section is supported by the study by Groth (2005) and Heinrichs et al. (2006).


Note:—No species of this section has been included in any molecular study, but the section was recognized by Hässel (2008b).


Note:—Recognition of the section is supported by several molecular studies (e.g. Groth 2005, Heinrichs et al. 2006).


Note:—Recognition of *Plagiochila sect. Fuscoluteae* including its synonyms is supported by several molecular studies (e.g. Heinrichs et al. 2005a, Groth 2005).


Note:—The section was identified by Heinrichs et al. (2000) and was supported by the molecular studies by Heinrichs et al. (2002a) and later authors.


Note:—The types of all synonyms of Plagiochila sect. Hylacoetes have been included in molecular studies and the recognition of Plagiochila sect. Hylacoetes as circumscribed by Heinrichs (2002) is well supported by several studies.


Note:—The section was recognized morphologically by Hässel (2009).


Note:—The section was recognized by Inoue (1984), but no species has been included in any molecular study.


Note:—The section was recognized by Hässel (2008b), but no species has been included in any molecular study.


Note:—The section was recognized by Hässel (2008b), but the sole species has not been included in any molecular study.


Plagiochila sect. Zonatae Carl, Ann. Bryol., Suppl. 2: 97, 1931 (Carl 1931b), syn. nov. Type (ICN Art. 22.6):—Plagiochila zonata Stephani (1894: 225). Note:—Species of the section were resolved within Plagiochila sect. Peculiares by Heinrichs et al. (2006), but the type was not included in the study. However, Heinrichs et al. (2004c) placed the type as sister to Plagiochila magna Inoue (1965a: 216) which was included and shown to belong to Plagiochila sect. Peceliares in the 2006 study.

Plagiochila sect. Renitentes Carl, Ann. Bryol., Suppl. 2: 114, 1931 (Carl 1931b), syn. nov. Type (ICN Art. 22.6):—Plagiochila renitens (Nees 1830) Lindenberg (1840: 90). Note:—The type of the section was resolved within Plagiochila sect. Peculiares by Heinrichs et al. (2005a) but its position in the study by Groth (2005) was unclear. The synonymization here is thus preliminary.

Note:—The type of the section has not been included in any molecular study, but Grolle & So (1999b) placed it in synonymy with Plagiochila sect. Zonatae.


Note:—The type species of both sections have been included in molecular studies (e.g. Groth et al. 2004, Heinrichs et al. 2004a) and the section Poeltiae is well supported.


Note:—The type species of both sections have been included in molecular studies supporting the synonymy and recognition of Plagiochila sect. Rutilantes.


Type:—Plagiochila strombifolia Lehmann (1844: 5).

Note:—The type species has not been included in any molecular study, but Engel & Smith Merrill (2013) recognized the section.


= Plagiochila sect. Capillares Carl, Ann. Bryol., Suppl. 2: 90, 1931 (Carl 1931b). Type (ICN Art. 22.6):—Plagiochila capillaris Stephani (1918: 137) [= Plagiochila corticola Stephani (1894: 224), cf. So & Grolle 2000b]. Note:—The type has not been included in any molecular study, but So (2001a) included the type in Plagiochila sect. Firmae.


Note:—Groth (2005) recognized Plagiochila sect. Tayloriae, but did not include the type species in the study.


Note:—The section is recognized since the type and two other species of the section have been included in molecular studies (e.g. Groth 2005, Heinrichs et al. 2006). Some authors (Inoue 1984, So 2001b) have synonymized it with Plagiochila sect. Cobanae, but Groth et al. (2004) and Heinrichs et al. (2004a) abstained from combining the two until Plagiochila sect. Cobanae has been studied closer.


Plagiochila sect. Abietinae Schiffner, Hep. Fl. Buitenzorg: 106, 1900 (Schiffner 1900a), syn. nov. Type (ICN Art. 22.6):—Plagiochila abietina (Nees 1830: 76) Montagne (1839: 81). Note:—Groth (2005) included the type in his study and showed that it should be included in Plagiochila sect. Vagae.


= Plagiochila subsect. Belangeriaeae (Carl) Inoue, J. Hattori Bot. Lab. 20: 67, 1958 (Inoue 1958). Note:—The type species has been included in several molecular studies confirming the placement in Plagiochila sect. Vagae.

= Plagiochila sect. Latifoliae Carl, Ann. Bryol., Suppl. 2: 108, 1931 (Carl 1931b). Type (ICN Art. 22.6):—Plagiochila latifolia Stephani (1905b: 742). Note:—No species from the section has been included in any molecular study, but Grolle & So (1999a) placed the section in synonymy with Plagiochila sect. Contiguae.


Nomenclatural novelties

Plagiochila ecuadorica (Inoue) L.Söderstr., comb. nov. Basionym:—Steereochila ecuadorica Inoue, Mem. New York Bot. Gard. 45: 279, 1987 (Inoue 1987). Type:—ECUADOR. Carchi: Cordillera Occidental, Tulcán-Maldonado road, 1983, Steere 26580. (NY, holotype; TNS, isotype). = Plagiochila dimorpha var. ecuadorica (Inoue) Heinrichs, Bryophyt. Biblioth. 58: 87, 2002 (Heinrichs 2002). Note:—Heinrichs (2002) showed that Steereochila ecuadorica is a Plagiochila close to Plagiochila dimorpha Lindenh. et Gottsche in Gottsche et al. (1847: 327) and treated it as a variety. However, in Heinrichs (2002) Plagiochila dimorpha and Plagiochila ecuadorica do not form a monophyletic lineage, but a polytomy including also Plagiochila turgida Herzog (1932: 196), or a paraphyletic group with the latter nested in the group. Although there are some morphological similarities between Plagiochila dimorpha and Plagiochila ecuadorica, we prefer to treat it on the same level as Plagiochila turgida until studied further, and as Plagiochila ecuadorica was previously recognized as a separate genus, we prefer to keep them apart at species level instead of variety level.

Plagiochila sciophila subsp. ciliigera (R.M.Schust.) L.Söderstr., comb. nov. Basionym:—Plagiochila japonica subsp. ciliigera R.M.Schust., Amer. Midl. Naturalist. 62: 354, 1959 (Schuster 1959b). Type:—USA. Arkansas: Stone Co., Sylamore National Forest, Anderson (DUKE, holotype). Note:—Inoue (1982) synonymized Plagiochila japonica Sande Lacoste (1864: 290) with Plagiochila sciophila Nees ex Lindenberg (1840: 100) without transferring or synonymizing the American subspecies. Schuster (1959b) described the subspecies with minor but clear differences from Plagiochila japonica subsp. japonica. Until further studied, given the morphological differences and the wide geographical separation of the two taxa we prefer to recognize them at subspecific level for now, although Plagiochila sciophila subsp. ciliigera may warrant recognition at specific level.

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