Resurrection of the genus *Aphyllon* for New World broomrapes (*Orobanche* s.l., *Orobanchaceae*)

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Abstract

Recent phylogenetic studies support a monophyletic clade of New World broomrapes (*Orobanche* sects. *Gymnocaulis* and *Nothaphyllon*) sister to the Old World genus *Phelipanche*. I place the New World taxa in the genus *Aphyllon*, propose 21 new combinations, and provide a list of currently accepted taxa.

Keywords

*Aphyllon*, broomrape, *Gymnocaulis*, *Myzorrhiza*, *Nothaphyllon*, nomenclature, *Orobanche*, *Orobanchaceae*

Introduction

Phylogenetic analysis of broomrapes and related holoparasites using nuclear DNA have found that the small eastern Mediterranean genus *Diphelypaea* Nicolson is nested within *Orobanche* sensu lato (s.l.) as circumscribed by Beck (1890) (Schneeweiss et al. 2004a). Morphological and cytological differences between groups of taxa within *Orobanche* s.l. have led some botanists to adopt a narrower generic circumscription. In this taxonomic concept, *Orobanche* sensu stricto is limited to Old World species that lack bracteoles and have a base chromosome number of \( x = 19 \), a calyx divided to the base, and generally unbranched stems (Holub 1977, 1990). Other Old World broomrapes are treated as *Phelipanche* Pomel or the monotypic genus *Boulardia* F.W. Schultz...
Broomrape species native to the New World constitute two well-supported clades that together form a clade sister to *Phelipanche* (Schneider et al. 2016). Taxonomically, these clades have been recognized as two separate genera *Aphyllon* (= *Orobanche* sect. *Gymnocaulis* Nutt.) and *Myzorrhiza* Phil. (= *O. sect. Nothaphyllon* (A. Gray) Heckard) by Holub (1977, 1990) and others (Schneweiss 2013), or more rarely, together as *Aphyllon* s.l. (Gray 1876). However, neither of these generic taxonomies has been widely adopted among American botanists, in part because of the lack of available names for many taxa. Providing evidence to support the treatment of all New World broomrapes as *Aphyllon* and a providing list of recognized species (with homotypic synonymns) is the purpose of this paper. New combinations are made where appropriate.

**Methods**

In order to compare molecular branch lengths of major clades of *Orobanche* s.l., a maximum likelihood (ML) phylogram of *Aphyllon* and related holoparasites was inferred from 3 nuclear DNA loci (ITS, phytochrome A, and phytochrome B). All sequences were downloaded from Genbank, aligned, and concatenated into a supermatrix using SUMAC (Freyman 2015). The ML phylogeny was estimated using RAxML (Stamatakis 2014) with a GTR+Γ nucleotide substitution model and 1000 rapid bootstrapping replicates.

Information about type specimens, basionyms, and synonomy of these new combinations was gathered by examining protologues and images of type specimens using major databases, including Tropicos (http://www.tropicos.org), JSTOR Global Plants (http://plants.jstor.org), and the International Plant Names Index (http://www.ipni.org). Types for all North American taxa and *O. weberbaueri* Mattf. have been designated by previous authors and are presented here. For three of the four South American taxa, typification would require more careful efforts beyond the scope of this article. No repository is given in the protologue for two syntypes of *Orobanche tacnaensis* Mattf. (Woitschach 71 and F. J. F. Meyen s.n.). The current existence of these specimens could not be verified, although a photograph of the Woitscach 71 (possibly from a specimen at B) is available at F. No specimens are cited by Rodolfo Phillipi in the protologues of the two taxa that he described.

**Discussion**

Molecular phylogenetic analyses have consistently supported a sister-group relationship between two strongly supported two American clades, representing *O. sect. Gymnocaulis* and *O. sect. Nothaphyllon* (McNeal et al. 2013; Schneider et al. 2016; Fig. 1). This relationship is supported by biogeography and synapomorphies such as a calyx with five fully developed lobes and a base chromosome number of $x = 12$, with polyploidy in most
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Figure 1. Maximum likelihood (ML) phylogram of *Aphyllon* and related holoparasite species inferred from 3 nuclear DNA loci (ITS, phytochrome A and phytochrome B). Bootstrap support values >70% are labeled. Due to space constraints, several clades have been collapsed. For a more detailed and thorough study of phylogenetic relationships within *Aphyllon*, see Schneider et al. (2016).

The genus *Aphyllon* was described by Mitchell (1769), although it was not until nearly 80 years later that Asa Gray made a combination for *A. uniflorum* A. Gray. This species was the only broomrape included in his *Manual of the Botany of the Northern United States* (1848), though in the second edition (1856) Gray recognized two additional species. Gray limited his generic concept for *Aphyllon* to taxa assignable to *O. sect. Gymnocaulis*, instead recognizing *O. ludoviciana* Nutt. in *Phelipaea* Tourn. ex Desf. However, after a study of the Californian flora, Gray amended his generic concept of *Aphyllon* to include two sections, *Aphyllon* and *Nothaphyllon*, together containing all taxa native to the New World (Gray 1876). Though expanded from Gray’s initial circumscription, it was appropriate given Michell’s original diagnosis of *Aphyllon* as having a five-toothed calyx (“semiquinquefllum”), a synapomorphy of New World broomrapes. A generation later, Rydberg (1906) proposed elevating Gray’s *Aphyllon* sect. *Nothaphyllon* to genus rank on the basis of differences in habit and placentation using the available name *Myzorrhiza* Phil. However, the broader generic concept of *Orobanche* used by Beck (1890) has prevailed, particularly among American botanists.

Due to the biogeographical, morphological, cytological, and phylogenetic affinities of the New World broomrapes, I recommend treating them in a single genus, *Aphyllon*, composed of sections *Aphyllon* (= *O. sect. Gymnocaulis*) and *Nothaphyllon* (= *O. sect. Nothaphyllon*). Below, I present a key to sections and a list of recognized taxa in
Aphyllon, proposing new combinations as necessary. Combinations are made at the most recently treated rank for the taxon in Orobanche, with the exception of Orobanche uniflora subsp. occidentale Greene, which is recognized at species rank under the available name Aphyllon purpureum (A. Heller) Holub due to its unique hosts, long molecular branch lengths, and recent discovery of sympatric populations of A. purpureum and A. uniflorum in southwestern British Columbia (Schneider et al. 2016). The treatment of Aphyllon sect. Aphyllon should be considered tentative; further taxonomic study is underway which will result in the recognition of several additional taxa.

Key to sections of Aphyllon

1 Bracteoles subtending the calyx absent; pedicels much longer than flower (2-8× length); stems subterranean or rising to about ground level ...................... Aphyllon sect. Aphyllon (syn.: O. sect. Gymnocaulis)
1′ Bracteoles subtending the calyx 2; pedicels equal to or shorter than flower, occasionally 2x length; stems usually rising above ground level ...................... Aphyllon sect. Nothaphyllon (syn.: O. sect. Nothaphyllon)

Taxonomic treatment

Aphyllon Mitch., Diss. Brevis. Princ. Bot. 43. 1769.

Loxanthes Raf. Neogenyton 3. 1825. [Type: Loxanthes fasciculatus (Nutt.) Raf.]
Anoplanthus Endl., nom. superfl., Gen. Pl. [Endlicher] pr. 10: 727. 1839.
Thalesia Raf. ex Britton, nom. superfl., Mem. Torrey Bot. Club 5: 298. 1894.

Type. Aphyllon uniflorum (L.) Torr. & A. Gray, Manual 290. 1848.

Description. Herb, annual or rarely perennial, achlorophyllous, holoparasitic. Stems fleshy. Leaves reduced to scale-like bracts. Inflorescences terminal racemes, spikes, corymbs, or panicles. Calyx 5-toothed. Corolla sympetalous, bilabiate to regular, tubular and often curved. Style long, stigma crateriform and peltate, or bilamellar. Fruit loculicidal capsules.

About 22 species: 18 in North America, 4 in South America.

Aphyllon sect. Aphyllon

Orobanche sect. Gymnocaulis Nutt., Gen. N. Amer. Pl. [Nuttall]. 2: 59. 1818.

Description. Stems subterranean or rising to about ground level. Pedicels long and slender, much longer than flower. Bracteoles subtending the calyx absent.
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*Aphyllon fasciculatum* (Nutt.) Torr & A. Gray, *Manual* (ed. 2) 281. 1848.

*Orobanche fasciculata* Nutt., *Gen. N. Amer. Pl.* 2: 59. 1818.

*Phelipaea fasciculata* (Nutt.) Spreng., *Syst. Veg.* [Sprengel] 2: 818. 1825.

*Loxanthes fasciculatus* (Nutt.) Raf., *Neogenyt.* 3. 1825.

*Anoplon fasciculatum* (Nutt.) G. Don., *Gen. Hist.* 4: 633. 1838.

*Anoplanthus fasciculatus* (Nutt.) Walp., *Repert. Bot. Syst.* 3: 480. 1844.

*Thalesia fasciculata* (Nutt.) Britton, *Mem. Torrey Bot. Club* 5: 298. 1894.

**Type.** USA: “Missouri”, ca. 1811, *Nuttal s.n.*, (holotype, PH).

*Aphyllon purpureum* (A. Heller) Holub, *Preslia* 70: 100. 1998.

*Thalesia purpurea* A. Heller, *Bull. Torrey Bot. Club* 24: 313. 1896.

*Orobanche porphyrantha* Beck, *Pflanzenr.* 96[IV,261]: 49. 1930.

*Orobanche uniflora* var. *purpurea* (A. Heller) Achey, *Bull. Torrey Bot. Club* 60: 445. 1933.

**Type.** USA: Idaho: Nez Perce Co.: near mouth of the Potlatch, 20 May 1896, *Heller 3099*. (no holotype designated; isotypes, CAS, DAO, K, MIN, MO, MSC, NDG, PH, US).

*Aphyllon uniflorum* (L.) Torr & A. Gray, *Manual* (Gray) 290. 1848

*Orobanche uniflora* L., *Sp. Pl.* 2: 633. 1753.

*Anoplanthus uniflorus* (L.) Endl., *Gen. Pl.* [Endlicher] 727. 1839.

*Thalesia uniflora* (L.) Britton, *Mem. Torrey Bot. Club* 5: 298. 1894.

**Type locality.** USA: Virginia (lectotype, *Clayton 387*, BM).

*Aphyllon sect. Nothaphyllon* A. Gray, *Bot. California* [W.H. Brewer] 1: 584. 1876

*Myzorrhiza* Phil., *Linnea* 29: 36. 1858. [Type: *Myzorrhiza chilensis* Phil.]

*Orobanche sect. Myzorrhiza* Beck, *Bibliotheca Botanica* 4(19): 78. 1890.

*Orobanche sect. Nothaphyllon* (A. Gray) Heckard, *Madroño* 22: 41. 1973.

**Type.** *Aphyllon californicum* (Cham. & Schltdl.) A. Gray, lectotype designated by Heckard, *Madroño* 22: 41. 1973.

**Description.** Stems clearly rising above ground. Pedicels equal to or shorter than flower. Bracteoles subtending the calyx 1 or 2.
Aphyllon arizonicum (L.T. Collins) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77158997-1

Orobanche arizonica L.T. Collins, Phytoneuron 2015–48: 16, f. 1, 2, 4, 5, 6A, 7. 2015.

Type. USA: Arizona, Coconino Co.: near Tuba City, 1539 m, 27 September 1935, Kearney & Peebles 12867 (holotype, ARIZ; isotype, US).

Aphyllon californicum (Cham. & Schltdl.) A. Gray, Bot. California 1: 584. 1876.

Orobanche californica Cham. & Schltdl., Linnea 3: 134–136. 1828.  
Phelypaea californica (Cham. & Schltdl.) G. Don, Gen. Hist. 4: 632. 1838.  
Myzorrhiza californica (Cham. & Schltdl.) Rydb., Bull. Torrey Bot. Club 36: 696. 1909.

Type. USA: California: Near Port of San Francisco, Aug 1816, Chamisso s.n (holotype, LE).

Aphyllon californicum subsp. condensum (Heckard) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77159010-1

Orobanche californica subsp. condensa Heckard, Madroño 22: 59–60, f. 11-L, 5. 1973.

Type. USA: California: San Luis Obispo Co.: Yaro Creek, 25 May 1955, Bacigalupi, Ferris & Robbins 5242 (holotype, JEPS; isotypes, NY, RSA, US, WTU).

Aphyllon californicum subsp. feudgei (Munz) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77159005-1

Orobanche grayana var. feudgei Munz, Bull. Torrey Bot. Club 57: 616–617, pl. 38, f. 8. 1930.  
Orobanche californica subsp. feudgei (Munz) Heckard, Madroño 22: 62. 1973.

Type. USA: California: San Bernardino Co.: Baldwin Lake, 2 June 1924, Munz 8177 (holotype, POM).

Aphyllon californicum subsp. grande (Heckard) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77159011-1

Orobanche californica subsp. grandis Heckard, Madroño 22: 60–62, f. 1P-R, 3A, 4E, 5. 1973.
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**Type.** USA: California: Santa Barbara Co.: dunes at Surf, 22 July 1954, *H. M. Pollard* (holotype, UC; isotype, CAS).

*Aphyllon californicum* subsp. *grayanum* (Beck) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77159006-1

*Orobanche grayana* Beck, *Biblioth. Bot.* 4: 79. 1890.  
*Myzorrhiza grayana* (Beck) Rydb., *Bull. Torrey Bot. Club* 36: 695. 1909.  
*Orobanche californica* subsp. *grayana* (Beck) Heckard, *Madroño* 22: 54. 1973.

**Type.** USA: Oregon: banks of the Columbia River, 1825, *Douglas s.n.* (lectotype, K).

*Aphyllon californicum* subsp. *jepsonii* (Munz) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77159007-1

*Orobanche grayana* var. *jepsonii* Munz, *Bull. Torrey Bot. Club* 57: 617, pl. 38, f. 10. 1930.  
*Orobanche californica* subsp. *jepsonii* (Munz) Heckard, *Madroño* 22: 57. 1973.

**Type.** USA: California: Colusa Co.: Princeton, October 1905, *H. P. Chandler s.n.* (holotype: POM, isotype: UC).

*Aphyllon chilense* (Phil.) A.C. Schneid., comb. nov.  
urn:lsid:ipni.org:names:77158998-1

*Myzorrhiza chilensis* Phil., *Linnea* 29: 36–37. 1857.  
*Orobanche chilensis* (Phil.) Beck, *Biblioth. Bot.* 4: 82–83. 1890.

*Aphyllon cooperi* A. Gray, *Proc. Amer. Acad. Arts* 20: 307. 1885.

*Orobanche ludoviciana* var. *cooperi* (A. Gray) Beck, *Biblioth. Bot.* 4(Heft 19): 81. 1890.  
*Orobanche cooperi* (A. Gray) A. Heller, *Cat. N. Amer. Pl.* 7. 1898.  
*Myzorrhiza cooperi* (A. Gray) Rydb. *Bull. Torrey Bot. Club* 36: 695. 1909.

**Type locality.** USA: Arizona: Fort Mojave (lectotype designated by Munz, *Bull. Torrey Bot. Club* 57: 620-21, *Cooper s.n.* in 1860-61, GH).
**Aphyllon cooperi subsp. latilobum** (Munz) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77159008-1

*Doroebanche* ludoviciana var. *latiloba* Munz, *Bull. Torrey Bot. Club* 57: 621–622, pl. 39, f. 18. 1930.

*Doroebanche cooperi* subsp. *latiloba* (Munz) L.T. Collins, *Phytoneuron* 2015–48: 15. 2015.

**Type.** USA: California: Riverside Co.: Colorado Desert, 22 April 1922, *Munz & Keck* 4960 (holotype: POM, isotype, US).

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**Aphyllon cooperi subsp. palmeri** (Munz) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77159009-1

*Doroebanche* multicaulis var. *palmeri* Munz, *Bull. Torrey Bot. Club* 57: 613, pl. 38, f. 2. 1930.

*Doroebanche cooperi* subsp. *palmeri* (Munz) L.T. Collins, *Phytoneuron* 2015–48: 16. 2015.

**Type.** Mexico, Durango, April-November 1896, *Palmer* 7 (holotype: GH, isotypes, MO, UC).

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**Aphyllon corymbosum** (Rydb.) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77158999-1

*Myzorrhiza corymbosa* Rydb., *Bull Torrey Bot. Club* 36: 696. 1909.

*Doroebanche corymbosa* (Rydb.) Ferris, *Contr. Dudley Herb.* 5: 99. 1958.

**Type.** USA: Reynold’s Creek, 2 July 1892, *Isabel Mulford* s.n. (holotype, NY; isotype, MO).

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**Aphyllon corymbosum subsp. mutabile** (Heckard) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77159012-1

*Doroebanche corymbosa* subsp. *mutabilis* Heckard, *Canad. J. Bot.* 56: 187–188. 1978.

**Type.** USA: Washington: Grant Co.: O’Sullivan Dam, 11 July 1950, *S. W. Harris* 97 (holotype, WS).

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**Aphyllon dugesii** S. Watson, *Proc. Amer. Acad. Arts* 18: 132. 1883.

*Doroebanche dugesii* (S. Watson) Munz, *Bull. Torrey Bot. Club* 57: 613, t. 38, f. 3. 1931.

**Type.** Mexico: Gueanajataoo, *Dugès* s.n. (holotype, GH).
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*Aphyllon ludovicianum* (Nutt) A. Gray. *Bot. California* [W.H.Brewer] 1. 585.

*Orobanche ludoviciana* Nutt. Gen. N. Amer. Pl. 2: 58–59. 1818.

*Phelypaea ludoviciana* (Nutt) Walp. *Repert. Bot. Syst.* 3: 461. 1844.

*Myzorrhiza ludovicana* (Nutt) Rydb. *Fl. S.E. U.S* 1338. 1903.

**Type.** USA: Fort Mandan, 1810-1811, *Nuttall s.n.* (holotype, PH).

*Aphyllon multiflorum* (Nutt) A. Gray. *Bot. California* [W.H.Brewer] 1. 585.

*Orobanche multiflora* Nutt., *J. Acad. Nat. Sci. Philadelphia*, ser. 2 1: 179. 1848.

**Type.** USA: Rio Grande, 1845, *Gambel s.n.* (neotype designated by White & Holmes, *Sida* 19: 623, USA: Texas: Jim Wells Co., 19 April 1944, *Lundell & Lundell* 12809, LL; isoneotype, LL).

*Aphyllon parishii* (Jeps.) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77159001-1

*Orobanche californica* var. *parishii* Jeps. *Man. Fl. Pl. Calif.* 952. 1925.

*Orobanche parishii* (Jeps.) Heckard. *Madroño* 22: 66. 1973.

**Type.** USA: California: San Bernardino Co.: Bear Valley, 1894, *S. B. Parish s.n.* (holotype, JEPS).

*Aphyllon parishii* subsp. *brachylobum* (Heckard) A.C. Schneid., comb. nov.

urn:lsid:ipni.org:names:77159013-1

*Orobanche parishii* subsp. *brachyloba* Heckard, *Madroño* 22: 68–70, 2J, 3N, 5. 1973.

**Type.** USA: California: Ventura Co.: Dutch Harbor, San Nicolas Island, 23 April 1966, *Raven & Thompson* 20794 (holotype, JEPS; isotypes, MO, RSA, SBBG).

*Aphyllon pinorum* (Geyer ex Hook.) A. Gray, *Bot. California* 1: 585. 1876.

*Orobanche pinorum* Geyer ex Hook., *Hooker’s J. Bot. Kew Gard.* 3:297–298. 1851.

**Type.** USA: Idaho/Washington border, *Geyer 445* (holotype, K).
**Aphyllon riparium** (L.T. Collins) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159002-1

*Orobanche riparia* L.T. Collins, *J. Bot. Res. Inst. Texas* 3: 7–10, f. 1A-B, 2. 2009.

**Type.** USA: Indiana, Gibson Co.: Griffin, 16 August 1931, *Deam 50941* (holotype, IND; isotypes, A, F, GH, IND, MINN, WIS).

**Aphyllon robbinsii** (Heckard ex Colwell & Yatsk.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159015-1

*Orobanche robbinsii* Heckard ex Colwell & Yatsk., *Phytoneuron* 2016-58: 2. 2016.

**Type.** USA: California: San Francisco Co.: Lands End, 13 August 1956, *Robbins 3707* (holotype, JEPS; isotypes, CAS, GH, NY).

**Aphyllon tacnaense** (Mattf.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159016-1

*Orobanche tacnaensis* Mattf., *Notizbl. Bot Gart. Berlin-Dahlem* 8: 185–186. 1922.

**Syntypes.** Peru: Tacna, 1890, *Woitschach 71* (photograph of type: F); Peru: Tacna, 1833, *F. J. F. Meyen s.n.*

**Aphyllon tarapacanum** (Phil.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159003-1

*Orobanche tarapacana* Phil., *Anales Mus. Nac. Santiago de Chile* 1891: 69. 1891.

**Aphyllon tuberosum** (A. Gray) A. Gray, *Bot. California* 1: 585. 1876.

*Phelopaea tuberosa* A. Gray, *Proc. Amer. Acad. Arts* 7: 371. 1868.
*Orobanche bulbosa* Beck, *Biblioth. Bot.* 4: 83–84. 1890.

**Type.** USA: California: Monterey Co: Gavilan Mountains, 1860-1862, *Brewer 743* (holotype, GH; isotype K).
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*Aphyllon validum* (Jeps.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159017-1

*Orobancha valida* Jeps., *Madroño* 1: 255–256. 1929.
*Orobancha ludoviciana* var. *valida* (Jeps.) Munz, *Bull. Torrey Bot. Club* 57: 621. 1930.

**Type.** USA: California: Rock Creek, San Gabriel Mountains, 2 June 1923, *F. W. Peirson* 7937 (holotype: JEPS, isotype: RSA).

*Aphyllon validum* subsp. *howellii* (Heckard & L.T Collins) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159018-1

*Orobancha valida* subsp. *howellii* Heckard & L.T Collins, *Madroño* 29: 98–100, f. 1A–E. 1982.

**Type.** USA: California: Mendocino Co.: Impassable Rock, 14 July 1951, *Donald V. Hemphill s.n.* (holotype: UC).

*Aphyllon vallicolum* (Jeps.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159004-1

*Orobancha comosa* var. *vallicola* Jeps., *Man. Fl. Pl. Calif.* 952. 1925.
*Orobancha vallicola* (Jeps.) Heckard, *Madroño* 22: 64. 1973.

**Type.** USA: California: Santa Clara Co.: Coyote, 14 October 1914, *W. L. Jepson* 6196 (holotype: JEPS, isotypes: GH, MO).

*Aphyllon weberbaueri* (Mattf.) A.C. Schneid., comb. nov.
urn:lsid:ipni.org:names:77159019-1

*Orobancha weberbaueri* Mattf., *Notizbl. Bot Gart. Berlin-Dahlem* 8: 185. 1922.

**Type.** Peru: Camaná: Arequipa, Hafen Chala, 26 November 1915, *A. Weberbauer* 7185 (isotypes: GH, US).

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