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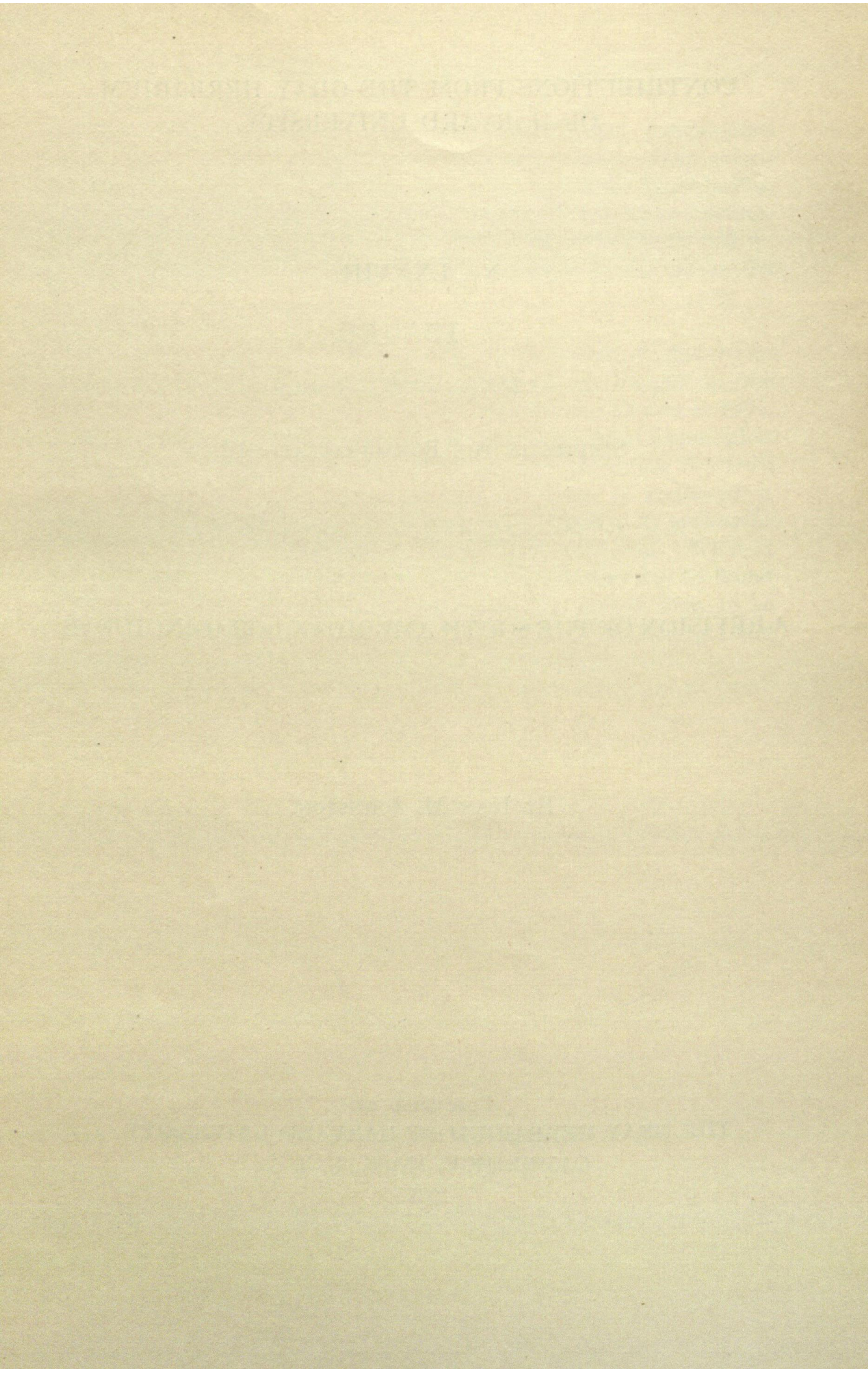
STUDIES IN THE BORAGINACEAE.—VI.

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A REVISION OF THE SOUTH AMERICAN BORAGINOIDEAE.

BY IVAN M. JOHNSTON.

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A REVISION OF THE SOUTH AMERICAN BORAGINOIDEAE.

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IN the present paper an attempt has been made to give a critical descriptive account of the American species of the subfamily *Boraginoideae* now known from south of Panama. The species of this group were last brought together in the general account of the whole subfamily published in 1846 in the 10th volume of DeCandolle's *Prodromus*. Since the appearance of this scholarly treatment great changes have come about, the generic classification has been well nigh remade and the great abundance of the group in the Chilean flora has become known, the recognized species being much more than doubled. The subfamily having the South American distributional center in Chile, the recent work dealing most extensively with these plants is Reiche's account of the family published serially in the *Anales de la Universidad de Chile* (vol. cxxi) in 1907 and 1908 and as part of his *Flora de Chile* (vol. v) in 1910. This treatment is very disappointing, for through the author's careless and often manifestly inaccurate interpretations of the Philippian species, the types of which he might have studied, he has only added to that confusion in the literature on the Chilean flora that first arose from R. A. Philippi's over zealous multiplication of species.

The classification here presented has developed from a fairly detailed account of the Chilean species which I prepared in 1926 while studying in the Philippi herbarium at the Museo Nacional in Santiago. After my return from Chile I was loaned the South American material of the group from the collections of the United States National Herbarium, the New York Botanical Garden and the Field Museum of Chicago. With this extensive material to supplement the rich collections of the Gray Herbarium the extra-Chilean species were also studied, the account of the Chilean species thoroughly revised and the present paper written. Though as thorough and critical as the materials and facilities available permitted, the following treatment makes no pretense at finality, but is believed to afford a consistent and logical summary of our present knowledge, thus providing a sound foundation for the work still to be done in further elucidation of the complexities of this interesting group.

Without opportunity to study the extensive and fundamental collections of Philippi in the Museo Nacional at Santiago the subjoined account of the South American *Boraginoideae* could never have been written. I am, therefore, under particular obligation to the Committee on Sheldon Fellowships at Harvard University for the privilege

of visiting Chile as a Sheldon Traveling Fellow. I am also extremely indebted for the very courteous treatment which I received from the staff of the Museo Nacional de Chile at Santiago. Prof. Carlos Porter, Prof. Marcial R. Espinoza, Sr. Luis Moreira, Sr. Gualterio Looser and Sr. Gilberto Montero were very friendly and helpful and did much to make my work in the museum both pleasant and profitable. I am particularly indebted, however, to Prof. Francisco Fuentes, Curator of the Phanerogamic Herbarium, through whose friendliness and courtesy I was afforded every facility for studying the famous collection which is in his charge. While at Santiago I also received very courteous treatment from Prof. Victor M. Baeza, of the Instituto Pedagógico de Chile, being through his kindness permitted to study the fine herbarium of recent collections brought together by his efforts and those of Prof. Federico Johow and their students.

Various persons have assisted me in important details. Dr. H. M. Hall of the Carnegie Institution and Mr. E. P. Killip of the United States National Museum generously procured for me photographs of various essential types in the European herbaria. Prof. H. Lecomte of the Muséum d'Histoire Naturelle, Paris, most kindly sent for my examination, fragments of certain obscure species of Clos and Weddell. Dr. A. Brand, the well known monographer of the family, in generous coöperation has provided me with fragments of and notes concerning his recently published South American species. I have also been much aided by notes and specimens received from Dr. A. W. Hill, Director of the Royal Gardens at Kew, Prof. Carl Skottsberg of the Göteborgs Botaniska Trädgård, Prof. C. C. Hosseus, of the Universidad Nacional de Córdoba, Prof. Lucien Hauman, formerly of the Universidad de Buenos Aires, Dr. Alberto Castellanos of the Museo Nacional of Buenos Aires, Prof. L. R. Parodi of the Universidad de Buenos Aires, and the late Carlos Spegazzini of La Plate. Of great aid in the present work, have been the large loans received from the United States National Herbarium through Dr. W. R. Maxon, from the New York Botanical Garden through Dr. N. L. Britton and from the Field Museum of Natural History of Chicago through Mr. D. C. Davies and Mr. J. F. Macbride. In preparation of this paper, as well as in the previous ones of the series, I have profited much from the suggestions and the able editorial assistance of Prof. B. L. Robinson as well as from the help in bibliographic matters received from the librarian of the Gray Herbarium, Miss Ruth D. Sanderson. Greatly appreciating the aid of all these persons, who have so courteously responded to my needs, I would here express my hearty thanks for their generous assistance.

In the systematic account, which follows, I have cited all the material which I have examined. I have tried to arrange the collections listed in geographical sequence grouping them under the countries and the major subdivisions (Provinces or Departments) of the countries. Following the citation of each collection, I have appended in parenthesis initials indicating the herbarium in which I have seen material of the particular collection. The initials used and the herbaria they indicate are as follows—"G" for Gray Herbarium, "NY" for New York Botanical Garden, "US" for United States National Herbarium, "FM" for Field Museum of Chicago, "MS" for the Museo Nacional of Santiago and "IP" for the Instituto Pedagógico of Santiago.

ARTIFICIAL KEY TO SOUTH AMERICAN GENERA.

- Nutlet wing-margined or appendaged dorsally.
- Nutlets with appendages or teeth of the margin tipped with stout unciniate bristles, the body usually with unciniate pubescence; slender herbs with the lowermost leaves opposite. 17. *Pectocarya*.
 - Nutlets with glochidiate appendages; leaves all alternate.
 - Nutlets equalling the subulate gynobase to which they are affixed for nearly their whole length along the ventral keel. 13. *Lappula*.
 - Nutlets much longer than the pyramidal gynobase to which they are affixed by a broad areola.
 - Nutlets spreading or divergent, not keeled ventrally; areola apical or lateral and extending down from the apex of the nutlet. 16. *Cynoglossum*.
 - Nutlets ascending, keeled ventrally above the medial areola.
 - Pedicels recurving in fruit; inflorescence paniculate, sparsely bracted or naked; herbs. 14. *Hackelia*.
 - Pedicels erect in fruit; inflorescence corymbose, bractless; shrub. 15. *Selkirkia*.
- Nutlets neither wing-margined nor appendaged dorsally.
- Attachment-surface of nutlet plug-shaped, strophiolate, surrounded by a tumid rim.
 - Corolla subrotate, suggesting that of a *Solanum*; stamens conspicuously exserted, appendaged dorsally. 7. *Borago*.
 - Corolla salverform; stamens included, unappendaged. 6. *Anchusa*.
 - Attachment-surface of nutlets flat, convex or annulate, simple or carunculate, not surrounded by a tumid rim.
 - Stamens very unequal, some exserted; corolla irregular. 5. *Echium*.
 - Stamens equal, usually included; corolla regular.
 - Corolla-lobes contorted in the bud. 8. *Myosotis*.
 - Corolla-lobes imbricated in the bud.
 - Calyx or bracts with unciniate hairs.
 - Inflorescence bracted; nutlets stipitate. 3. *Thaumatocaryon*.
 - Inflorescence bractless; nutlets sessile. 4. *Moritzia*.
 - Calyx or bracts completely lacking unciniate hairs.
 - Nutlets with a broad basal attachment; leaves all alternate. 1. *Lithospermum*.

- Nutlets attached laterally; at least lower leaves opposite.
- Corolla blue; stigmas geminate.....2. *Antiphytum*.
- Corolla not blue; stigmas solitary and simple.
- Corolla yellow or orange, throat unappendaged. 12. *Amsinckia*.
- Corolla white, throat appendaged.
- Nutlets with pericarpial wall fused above middle to form a definite medial ventral keel. 11. *Plagiobothrys*.
- Nutlets with a medial ventral groove formed by the non-fusion of the pericarpial wall.
- Calyx cut to base, distinct from the bracts. 9. *Cryptantha*.
- Calyx cylindrical, merely toothed, with floral bracts decurrent on its lower part.....10. *Nesocaryum*.

I. TRIBE LITHOSFERMEAE.

Nutlets erect, straight or rarely bent, smooth or rough, unmarginated; areola basal or occasionally suprabaasal, near tip of cotyledon, unmarginated, flat or nearly so, not at all strophiolate, usually sessile but occasionally stipitate; gynobase flat or low-pyramidal, not excavated; style cleft or entire; stigmas 2 or exceptionally 4, distinct or proximate or rarely fused, capitate or obscurely thickened; corolla yellow or orange or occasionally white or somewhat purplish.—Johnston, Contr. Gray Herb. lxxiii. 43 (1924).

KEY TO GENERA.

- Corolla with conspicuously oblique limb and unequal stamens...5. *Echium*.
- Corolla with horizontal limb and equal stamens.
- Mature calyx cut to near base, the elongate lobes erect or spreading; nutlets usually 4, falling individually; calyx and bracts lacking uncinata hairs.
- Nutlet-areola basal, sessile; leaves all alternate.....1. *Lithospermum*.
- Nutlet-areola suprabaasal, sessile or stipitate, at least the lower leaves opposite.....2. *Antiphytum*.
- Mature calyx cylindrical or ellipsoid, merely toothed with the teeth connivent over the fruit; nutlets solitary, falling away tightly invested by the calyx; calyx or bracts with uncinata pubescence.
- Inflorescence bracted; calyx lacking uncinata hairs; corolla-throat pubescent along obscure horizontal plaits; nutlet with stipitate areola.....3. *Thaumatocaryon*.
- Inflorescence bractless; calyx with uncinata hairs; corolla-throat with circular villous spots or intruded appendages; nutlet with sessile basal areola.....4. *Moritzia*.

1. *Lithospermum* L.

Calyx usually divided. Corolla tubular or salverform; tube cylindrical; lobes spreading, imbricate; throat with intruded appendages or

PLAGIOBOTHRYS MURICATUS (R. & P.) Johnston, Contr. Gray Herb. lxxviii. 79 (1923). *Lithospermum muricatum* R. & P. Fl. Peruv. ii. 4 (1799); Lehm. Asperif. ii. 327 (1818). *Eritrichium muricatum* A. DC. Prodr. x. 132 (1846); Ph. Anal. Univ. Chile xc. 540 (1895). *Allocarya muricata* Reiche, Anal. Univ. Chile cxxi. 809 (1908) and Fl. Chile v. 215 (1910).—The type of *L. muricatum* is said to have come from Concepcion, Chile. It is described as a prostrate annual herb with opposite leaves, small inconspicuous corollas and muricate nutlets. Possibly it is the same as *P. polycaulis* which has been collected near Concepcion. That species is an inconspicuously flowered plant but its nutlets are certainly not muricate.

12. *Amsinckia* Lehm.

Calyx cut to base into erect lanceolate or oblong lobes. Corolla tubular or salverform; tube cylindrical, glabrous, unappendaged; lobes spreading, rounded, imbricate; throat unappendaged; stamens included, affixed in the tube; filaments very short; anthers oblong, obtuse. Style filiform, included; stigma capitate, emarginate. Ovules 4. Cotyledons 2-parted. Nutlets 4, erect, angulate-ovoid, smooth or rough, unmarginated, strongly keeled ventrally; areola infra-medial, small, carunculate. Gynobase frustate, about half the height of the nutlets.—Annual herbs. Leaves alternate, linear to ovate, usually veinless. Racemes usually bractless.—Del. Sem. Hort. Hamburg 7 (1831). *Benthamia* Lindl. Nat. Syst. 241 (1830), nomen.

A genus of considerable technical difficulty which centers in western North America and has only two South American representatives.

KEY TO SPECIES.

- Nutlets tessellate, 3–3.5 mm. long; corolla 6.5–7.5 mm. long; plants rather coarse.....1. *A. tessellata*.
 Nutlets verrucose, 2–2.8 mm. long; corolla 3–7 mm. long; plants usually slender.....2. *A. hispida*.

1. ***Amsinckia tessellata*** Gray. Rather coarse plants, 8–20 cm. tall, with loosely or strictly ascending stems, shaggy-hirsute with the younger parts also somewhat hispid-villous; leaves firm, obtuse, appressed-hispid, usually densely pustulate; lower leaves somewhat crowded, oblanceolate, 4–6 cm. long, 7–9 mm. broad; middle cauline leaves gradually reduced, oblong to oblong-ovate; racemes usually short and densely flowered, 1–3 cm. long, solitary, bractless or bracted only at base; calyx densely appressed tawny-hirsute as well as short appressed white-villous, at maturity 6–8 mm. long with erect coarse lance-linear obtuse lobes; pedicels ca. 1 mm. long; corolla yellowish, 6.5–

7.5 mm. long, subtubular, limb ca. 2 mm. broad, throat weakly flaring, tube ca. 1 mm. thick; nutlets triangular, angulate, 3–3.5 mm. long, tessellate with flattened very crowded tuberculations, frequently with short transverse rugae along the medial line, the back very broadly obtuse, almost flat, with a weakly developed medial ridge.—Proc. Am. Acad. x. 54 (1875); Macbr. Contr. Gray Herb. xlix. 6 (1917).

ARGENTINA. CHABUT: along Rio Carren-leufú, March 1, 1900, *Spegazzini* (G).

CHILE. SANTIAGO: Las Arañas silver mines, Nov. 1861, *Philippi* (MS).

This species, frequent in the deserts of southwestern United States and now first reported from South America, was long ago known and distinguished by Spegazzini, Anal. Soc. Cient. Argentina liii. 137 (1902), who treated it as *A. pseudolycopsicoides* under the supposition that it was Clos's *A. angustifolia*, var. *pseudolycopsioides*. He reported the plant from Rio Carren-leufú and Lago Nahuel-huapi. Although apparently indistinguishable from some of the low spreading forms from North America, the two South American collections studied are not so tall nor so erect as the common forms of the species in the deserts of United States.

2. **A. hispida** (R. & P.) Johnston. Erect annual, 2–7 dm. tall, simple or loosely branched, conspicuously shaggy-hirsute and with the upper parts frequently finely villous-hispid as well; leaves hirsute, acute, gradually reduced up the stem; lower leaves usually crowded, oblanceolate, 5–15(–18) cm. long, 5–15(–24) mm. broad; cauline leaves linear to lanceolate, usually strictly ascending; racemes solitary or geminate, bractless or bracted only at base, much elongating, becoming very loosely flowered and 1–2.5 dm. long; calyx somewhat tawny, hirsute and more or less hispid-villous, becoming 4–6 mm. long with acuminate-linear or lance-linear lobes; pedicels ascending, 1–3 mm. long; nutlets triangular-ovate or triangular, angulate, incurved, 2–2.8 mm. long, granulate-tuberculate, commonly with strong irregular transverse crests, back definitely obtuse, the medial ridge frequently longitudinally cristate.—Johnston, Contr. Gray Herb. lxxiii. 75 (1924). *Lithospermum hispidum* R. & P. Fl. Peruv. ii. 5 (1799); Lehm. Asperif. ii. 328 (1818). *A. angustifolia* Lehm. Del. Sem. Hort. Hamburg 7 (1831) and Linnaea vi. Litt. 74 (1831); F. & M. Ind. Sem. Hort Petrop. ii. 26 (1835); DC. Prodr. x. 118 (1846); Clos in Gay, Fl. Chile iv. 473 (1849); Reiche, Anal. Univ. Chile cxxi. 833 (1908) and Fl. Chile v. 238 (1910); Johnston, Contr. Gray Herb. lxx. 44 (1924). *Benthamia angustifolia* Druce, List Brit. Pl. 103 (1908). *A. parviflora* Bernh. Del. Sem. Hort. Erf. (1833) and Linnaea x. Litt.

73 (1836). *L. calycinum* Moris, "Enum. Sem. Hort. (1831)" and Mem. Acad. Torino xxxvii. 98, t. 22 (1833). *L. chilense* Colla, Mem. Acad. Torino xxxviii. 127, t. 40 (1834). *A. angustifolia*, var. *pseudolycopsioides* Clos in Gay, Fl. Chile iv. 473 (1849). *A. pseudolycopsioides* Speg. Anal. Soc. Cient. Argentina liii. 137 (1902). *Eritrichium pachnophilum* Wedd. Chlor. Andina ii. 87 (1859). *A. basistaminea* Cesati, Atti Acc. Sc. Nap. ser. 5, vii. 14 (1873). *B. basistaminea* Druce, Rep. Exch. Cl. Brit. Isl. iv. 298 (1916). *E. Mandonii* Ball, Jour. Linn. Soc. Bot. xxii. 51 (1885). *A. angustifolia*, var. *microcarpa* Speg. Anal. Soc. Cient. Argentina liii. 136 (1902). *Cryptantha Spegazzinii* Johnston, Contr. Gray Herb. lxxviii. 54 (1923). *Plagiobothrys aurantiacus* Brand in Fedde, Repert. xx. 46 (1924).

ARGENTINA. SANTA CRUZ: vicinity of Lago Argentina, 1907-08, *Furlong 120* (G, NY); Patagonia, lat. 50°-53°, *Moreno & Tonini 106, 309 and 531* (NY). CHABUT: very dry slope near Cabo Raso, Feb. 15, 1900, *Spegazzini* (G); no locality given, 1898, *Kowbowky* (G). RIO NEGRO: vicinity of General Roca, 250-360 m. alt., Sept. 25, 1914, *Fischer 81* (G, US, FM); dry gravelly place at junction of Rio Neuquen and Rio Negro, Jan. 21, 1898, *Spegazzini* (G).

CHILE. MEGALLANES: Cabo Negro, Nov. 1867, *Cunningham* (G); Packet Harbor, Nov., *Lechler 1133* (MS); Oazy Harbor, Nov. 1852, *Lechler 1133* (MS); Fuegia, Feb. 1879, *O.* (MS). ÑUBLE: Chillan, *Man. Ant. de Solis* (MS). OHIGGINS: Rancagua, July 1878, *collector not given* (MS); Rancagua, *Bertero 379* (G). SANTIAGO: Santiago, Aug. 1830, *Gay 1628* (MS); Santiago, Nov. 1860, *no collector given* (MS); Santiago, Oct. 1858, *no collector given* (MS); Santiago, Nov. 1918, *Claude-Joseph 706* (US); Santiago, *Gay 48* (G, photo of TYPE of *A. angustif.* var. *pseudolycopsioides*); Cerro San Cristobal, Oct. 1886, *Gigoux* (G); San Cristobal, Nov. 1900, *Hastings 114* (US); San Cristobal, 1917, *Baeza* (IP); Cerro de San Bernardo, *Reed* (G); San Bernardo, 1923, *Baeza* (IP); Quinta Normal, Nov. 1877, *no collector given* (MS); Peñaflor, 1921, *Baeza* (IP); Talagante, 1916, *Baeza* (IP); San Juan de Pirque, 1914, *Baeza* (IP). VALPARAISO: Limache, [*Bertero*] (US); hills, Quillota, 1829, *Bertero* (G); Valparaiso, *Cumings 512* (G). ACONCAGUA: Zapallar, 1908 and 1909, *Johow* (IP); Las Astas, Oct. 1914, *Rose 19358* (US, NY). COQUIMBO: Frai Jorge Estancia, Aug. 15, 1917, *Skottsberg 804* (G); sand, Heradura near Coquimbo, Sept. 27, 1917, *Skottsberg 1060* (G); Punta de Teatinos, Nov. 1925, *Werdermann 878* (G); Coquimbo, Oct. 1878, *Ortega* (MS); Coquimbo, 1889-90, *Geisse* (MS); Coquimbo, 1856, *Harvey* (G). ANTOFAGASTA: Tocopilla, 1918, *Gülland* (IP); Tocopilla, Oct. 1925, *Johnston 3576* (G). TARAPACÁ: Quebrada Huantajaya, Iquique, ca. 700 m. alt., *Werdermann 761* (G). INDEFINITE: costa, Nov. 4, 1920, *Claude-Joseph 1210* (US); no locality given, *Gay* (G) and *Gilles* (G).

BOLIVIA. POTOSI: Quebrada de las lagunas, March, *D'Orbigny 1448* (G, frag. TYPE of *E. pachnophilum*). ORURO: Pazna, 3900 m. alt., Apr. 3, 1921, *Asplund 5893* (US). LA PAZ: General Campero, 4200 m. alt., March 4, 1921, *Asplund 5892* (US); Calavaya near Sorata, 2700-2900 m. alt., *Mandon 378* (G, NY; ISOTYPES of *E. Mandonii*).

PERU. CUSCO: Paucartambo, 3500-3700 m. alt., *Herrera 1006a* (US). LIMA: abandoned field, Rio Blanco, 4500 m. alt., March, 1923, *Macbride 2968* (G, FM); grassy canyon slope, Rio Blanco, 3600 m. alt., May 1922, *Macbride & Featherstone 729* (G, FM); Chicla, 3600-3900 m. alt., April 1882, *Ball* (NY). HUANUCO: edge of alfalfa-field, Llata, 2100 m. alt., *Macbride & Featherstone 2288* (G, FM).

ECUADOR. CAÑAR: vicinity of Cañar, Sept. 16, 1918, *Rose 22728* (G, NY). PICHINCHA: plains of Chillagallo, Sept. 1856, *Remy* (G, fragment). INDEFINITE: without data but probably Ecuadoran, *André 662* (NY).

Considering the extent of its range, this species is quite constant and shows very little of that capacity for bewildering variation which is so characteristic of its immediate relatives in North America. In habit and corolla-structures and -form, the plant is not unusually variable. The most striking variations are those of nutlet-size. The majority of the specimens studied had nutlets about 2.5 mm. long. In Asplund's Bolivian collections, and in that cited from extreme northern Chile, the nutlets are slightly larger, becoming 2.8 mm. long. On the other hand in the material sent me by Spegazzini from the confluence of the Rio Negro and Rio Neuquen as representing *A. angustifolia*, var. *microcarpa*, the nutlets are about 2 mm. long. While worthy of note these variations in size of nutlets scarcely merit nomenclatorial recognition.

13. *Lappula* Moench.

Calyx 5-parted into spreading lanceolate lobes. Corolla with a rather short tube; lobes rounded, ascending, imbricate; throat closed by intruded appendages; stamens affixed in the tube, included; filaments slender, short; anthers oblong, obtuse. Style short surmounting the subulate-columnar gynobase, commonly surpassing the mature nutlets; stigma subcapitate. Ovules 4. Nutlets 4, erect, smooth or verrucose, narrowly but firmly attached to the gynobase along the length of the well developed ventral keel, back angulate or margined by a single or double row of prickles which by confluence frequently form a wing-like or cupulate border.—Annual or rarely perennial herbs. Leaves alternate, usually narrow, firm and veinless. Flowers small, blue or white, on usually erect pedicels or rarely sessile, in bracted racemes.—Meth. 416 (1794); Johnston, Contr. Gray Herb. lxxiii. 60 (1924). *Echinosperrum* Sw. ex Lehm. Asperif. i. 113 (1818). *Staurina* Nutt. Jour. Acad. Philad. i. 182 (1848).

A very difficult genus, the South American forms of which are very imperfectly known. The species are mainly critical ones, being largely separated by technical characters of the fruit, such as size and form of the nutlets, their surface and the characters of the dorsal-margin.

KEY TO SPECIES.

- Nutlet-margin armed with a row of stout flattened glochidiate subulate appendages.....1. *L. Redowskii*.
Nutlet-margin bearing an up-turned cupulate wing.....2. *L. texana*.