REVISION OF PECTIS SECTION PECTIDIUM (COMPOSITAE: TAGETEAE)

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Pectis L. sect. Pectidium (Less.) A. Gray is a small but very wide-ranging group of taxa. The geographic range of this section includes both insular distribution patterns and broad disjunctions. In an effort to clarify the systematic relationships and to provide a possible explanation for the interesting distribution patterns, I undertook an investigation of this section.

TAXONOMIC HISTORY

Pectis linifolia L. was the first representative of Pectis to be recognized. Sloane (1707) described and illustrated this species from West Indian material as "Hieracium fruticosum angustissimis gramineis foliis capitulis parvis." Linnaeus (1759) published alternate names for Sloane's plant under both Pectis and Verbesina.

The history of sect. *Pectidium* is closely intertwined with a long-standing misapplication of the name *Pectis linifolia*. Only a year after Linnaeus described *P. linifolia*, Jacquin (1760) published *Pectis punctata*. Although *P. punctata* is now known to be tax-onomically synonymous with *P. linifolia*, this situation was not recognized by early botanists. The name *Pectis punctata* soon gained wide acceptance while *P. linifolia* slipped into obscurity and disuse. In 1831 Lessing described the genus *Pectidium*, based upon *P. punctata*. In the same publication, he misapplied *Pectis linifolia* to a plant now correctly known as *P. leptocephala* (Cass.) Urban. Lessing's misapplication of *P. linifolia* was widely followed, and most 19th century literature mentioning *P. linifolia* actually pertains to *P. leptocephala*.

Gray (1852) reduced *Pectidium* from generic to sectional status. In 1853, Gray described *Pectis imberbis*, and in 1883 he included this species, *P. punctata*, and two species previously assigned to sect. *Heteropectis*, *P. multiseta* Benth. and *P. coulteri* Harv. & Gray, in a broadened concept of sect. *Pectidium*. Fernald (1897) removed *P. coulteri* and *P. multiseta* from sect. *Pectidium* and raised the section to subgeneric status. Fernald also finally corrected the misapplication of *P. linifolia* and properly relegated *P.*

punctata to synonymy. The present circumscription of sect. Pectidium is based upon Fernald's treatment, but the sectional rather than subgeneric rank is used.

SECTIONAL RELATIONSHIPS

The species of sect. *Pectidium* are morphologically distinctive. In most sections of *Pectis*, plants are relatively low-growing and stems are very leafy. In sect. Pectidium the plants are usually tall and erect with elongated internodes. Section Pectidium does not appear to be closely related to any other section of the genus. The only taxa for which a possible relationship has been suggested probably represent evolutionary convergences in a few characteristics. Grav (1883) suggested a close relationship between the taxa of sects. Pectidium and Heteropectis. Keil (1975b) indicated that the relationship between these sections is probably remote. Wiggins (1950) proposed a close relationship between P. linifolia and his newly-described P. vollmeri. On the basis of overall morphology, Keil (1973) placed P. vollmeri in sect. Pectothrix A. Gray. In the cases of both sect. Heteropectis and P. vollmeri, undue emphasis has been placed upon similarities in the structure of the pappus, and important dissimilarities in other features have received less attention or have been ignored. At the present time, there do not seem to be any close relatives for sect. Pectidium.

CHROMOSOME STUDIES

Prior to this study, a chromosome count of n=12 for Pectis linifolia var. linifolia was the only published report for a taxon of sect. Pectidium (Pinkava & Keil, 1977). This and counts of n=12, from meiotic microsporocytes, reported here for P. imberbis (Table 1, Figure 2e), are consistent with the previously established base number for the genus, x=12 (Johnston & Turner, 1962; Keil, 1977). The regular formation of a quadrivalent in meiosis in one plant (Pinkava & Keil K11006D) indicates the presence of a heterozygous translocation, a condition not previously reported for any other Pectis species.

BIOGEOGRAPHY AND EVOLUTIONARY RELATIONSHIPS

The range of sect. Pectidium extends into a variety of different

geographical areas (Figure 1), and includes many different vegetational zones. This broad distribution is due almost entirely to the widespread occurrence of a single taxon, *Pectis linifolia* var. *linifolia*. The two remaining taxa occupy only limited ranges. Any explanation that accounts for the broad range of the section must, therefore, concentrate upon the distribution and establishment of *P. linifolia* var. *linifolia*.

Dispersal mechanisms and reproductive biology of *Pectis linifolia* var. *linifolia* are of major importance in its broad distribution. In the establishment of the present range of this taxon, numerous crossings of significant water barriers have occurred. Throughout the West Indies and in the Galapagos Islands, *P. linifolia* var. *linifolia* has become established on many islands. Additionally, its mainland distribution involves disjunctions of thousands of kilometers. The success of this taxon in crossing numerous barriers is indicative of a specialized dispersal mechanism and of reproductive adaptations favoring the establishment of founder populations.

Pectis linifolia var. linifolia has adaptations that appear to favor animal dispersal, with birds being the most likely carriers. The achenes of these plants characteristically bear stout, divaricately spreading awns that project from the fruiting heads (Figure 2a). The achenes readily cling to fabrics and presumably equally well to feathers. The plants commonly grow in open rocky coastal sites which in insular situations are favored by sea birds.

Plants of *Pectis linifolia* var. *linifolia* are apparently autogamous. Morphological evidence for autogamy includes the marked reduction in ligule size (only 1 mm. long), the low number of disc florets per head (1–3), and small anthers (less than 1 mm. long) with low pollen production. Other species of *Pectis* with reduced, inconspicuous heads and low pollen production (e.g., *P. cylindrica* (Fern.) Rydb., *P. prostrata* Cav.) are known to be self-fertile (Keil, 1975a). The establishment of the autogamous condition is of primary importance in a colonizing species (Baker, 1955). Such a condition is also a common adaptation to dry habitats (Davis & Heywood, 1965) or coastal situations (Eisikowitch, 1973).

Inland populations among members of sect. *Pectidium* are best developed in North America. The progenitor for sect. *Pectidium* probably developed in the Mexican highlands, a center of diversity for *Pectis* and various other genera of the Tageteae. This original



Figure 1. Geographical distribution of the taxa of Pectis sect. Pectidium.

Pectidium was probably a perennial and may have been similar to P. imberbis. Pectis linifolia, an annual, is probably a derived taxon that became adapted to dry lowland conditions and subsequently spread to similar habitats in other areas. With the only significant inland populations restricted to North America, the remaining range is probably attributable to the high dispersibility of achenes of P. linifolia var. linifolia.

TAXONOMY

Pectis L. sect. Pectidium (Less.) A. Gray, Smithsonian Contr. Knowl. 3(5): 83. 1852.

Pectidium Less. Linnaea 6: 706. 1831. Pectis L. subg. Pectidium (Less.) A. Gray ex Fern. Proc. Am. Acad. 33: 85. 1897. Type Species: Pectis punctata Jacq.
Tetracanthus A. Rich. in Sagra, Hist. Fis. Polit. Nat. Cuba 11: 60. 1850. Type Species: T. linearifolius A. Rich.

Annual or perennial, non-aromatic herbs. Stems erect or ascending, 1–12 dm. tall, with internodes usually equalling or longer than the adjacent leaves, usually simple below, much-branched above. Leaves linear to linear-elliptic, punctate on the undersur-

face with circular glands. Heads solitary or in diffuse cymose clusters, slender-peduncled. Involucre cylindric; bracts 5, linear, very convex, indurate nearly to the apex, strongly glandular-punctate. Ray florets 5; ligules often glandular-punctate. Disc florets 1–7; corollas regular, 5-lobed, some or all of the teeth glandular-punctate just below the apex. Achenes cylindric, puberulent. Pappus of 1–4 stout, spreading, smooth or minutely antrorsely barbed awns, or sometimes reduced to a crown, or absent in some of the achenes. Chromosome base number: x = 12.

KEY TO THE TAXA OF PECTIS SECT. PECTIDIUM

- 1. Annual herbs from a slender to stout taproot; ray corollas 2-4 mm. long. . . 2.
- 1. Pectis linifolia L., Syst. Nat. ed. 10. 1221. 1759.

TYPE: without data (LINN, holotype; IDC microfiche 177: 601: III:4!).

Verbesina linifolia L., Syst. Nat. ed. 10. 1226. 1759, nom superfl.

Pectis punctata Jacq., Enum. Syst. Pl. 28. 1760. LECTOTYPE: Select. Stirp. Am. Hist. t. 128. 1763.

Pectidium punctatum (Jacq.) Less., Linnaea 6: 706. 1831.

Tetracanthus linearifolius A. Rich. in Sagra, Hist. Fis. Polit. Nat. Cuba 11: 60. 1850. Type: Cuba, juxta Santiago de Cuba, Linden 1714 (P, holotype!).

Pectis linifolia L. var. marginalis Fern., Proc. Am. Acad. 33: 85. 1897. SYNTYPES: United States. ARIZONA: "Southern Arizona," Palmer 129 (GH. syntype!; MO. isosyntype!); Tuscan (Tucson?), Smart 382 (GH!); Santa Catalina, Lemmon 3031 (GH. snytype!; UC, isosyntype!); Malpais Mts., 31 Aug. 1881, Pringle s.n. (GH. syntype!; MICH, MO, US, isosyntypes!). Mexico. SONORA: Guaymas, Palmer 224 (GH. 2 syntypes!; UC, US, isosyntypes!). LECTOTYPE (here designated): Pringle s.n. (GH).

¹Authentic type specimens have not been located. Stafleu (1967) indicated that few of Jacquin's West Indian material are known to exist, and that Jacquin's 1760 publication represents a prodromus for his larger illustrated work. The illustration of *Pectis punctata* from the latter publication is selected here as the lectotype.

Erect or ascending annual herbs 1-10 dm. tall. Stems solitary or few, pseudodichotomously branched above, sharply 6-angled (at least above), purplish or stramineous. Principal leaves linear to linear-elliptic, 1-6 cm. long, 1-8 mm. wide, apically acute, often revolute-margined, punctate on the undersurface with marginal or scattered glands. Peduncles filiform, 1-3 cm. long, bearing 1-5 scale-like bractlets ca. 1 mm. long. Heads solitary in the axils or forks of the stem, or in diffuse cymose clusters at the ends of the branchlets. Involucre green or more commonly dark purplishbrown; bracts 4.5-7 mm. long, ca. 0.5 mm. wide, apically obtuse or acutish, hyaline-margined, punctate submarginally with one or more rows of linear-elongate to elliptic glands and subapically with one to several elliptic glands. Ray corollas yellow, commonly drying white to purple, 2-4 mm. long, often punctate on the ligule with 1 or 2 small glands, glabrous. Disc florets 1-6; corollas vellow, often drying white to purplish, 2-4 mm. long, 4 or all 5 of the lobes punctate with a solitary round gland, sometimes with a few additional glands on the throat; anthers 0.8 mm. long with tiny emarginate appendages. Achenes of ray and disc similar or disc achenes abortive, 3.5-5.0 mm. long, black or dark brown, strigillose or hirtellous with acute-tipped double hairs. Pappus of 1-4 awns 2-3 mm. long, or sometimes reduced to a low crown.

The range of *Pectis linifolia* (Figure 1) includes several major disjunctions. Populations are found in the Sonoran Desert region of the southwestern United States and adjacent Mexico, southern Mexico, the Caribbean region, the west coast of Ecuador and Peru, and the Galapagos Islands. Flowering time varies greatly depending upon the local seasonal patterns. In drier climates the species is mostly a summer- or fall-flowering ephemeral. In moister regions, the plants apparently flower through much of the year. *Pectis linifolia* is divisible into two varieties.

1a. **Pectis linifolia** L. Syst. Nat. ed. 10. 1221. 1759. var. **linifolia**. Stem glabrous or minutely roughened on the angles. Leaves 2–6 cm. long, 1.0–4.5 mm. wide, with a single pair of basal setae 1–2 mm. long or setae absent on some or all of the leaves, minutely roughened on the margin and midrib beneath, otherwise glabrous. Involucre green to purplish-brown, 4.5–7.5 mm. long, with bracts

minutely ciliolate at the apex, otherwise glabrous. Ray florets with the tube 1-2 mm. long, with the ligules ca. 1 mm. long and about as wide. Disc florets 1-3, fertile, with corollas 2-3.5 mm. long, with the ovary turgid. Achenes 3.5-5.0 mm. long. Ray and disc pappus similar, 1-4 aristate, rarely reduced to a crown or absent, the awns 2-3 mm. long, often divaricately spreading in age. Chromosome number: n=12. Figure 2a, b.

Throughout most of its broad range (Figure 1), *Pectis linifolia* var. *linifolia* grows below 200 m., but in southern Arizona and adjacent areas of Sonora, some populations occur at elevations up to 800 m.

Although *Pectis linifolia* var. *linifolia* occurs in many different vegetation zones, it does not appear to be divisible into recognizable subunits. Undoubtedly there are physiological differences among the populations adapted to different areas, but no recognizable morphological features have been found in var. *linifolia* which vary consistently on a geographical basis. Fernald (1897) described var. *marginalis* for the Sonoran Desert populations on the basis of a marginal rather than a scattered position of the foliar oil glands. Additional collections that were unavailable to Fernald, however, do not show this feature consistently.

REPRESENTATIVE SPECIMENS: Bahamas. Grand Turk Island, Millspaugh & Millspaugh 9038 (GH, NY). Colombia. BOLIVAR: Tierrabompa Island, Killip & Smith 14130 (GH, NY, US); MAGDALENA: Santa Marta, Smith 530 (GH, LL, MICH, MO, NY, TEX, US, USF, WIS). Cuba. Farallón, Wright 1630 (GH, MO). Dominican Republic. 3 mi E of Boca Chica, Liogier 17647 (NY, US). Ecuador. GUAYAS: Puntilla, Svenson 11128 (GH, NY, UC, US); GALAPAGOS ISLANDS: Isla Santa Cruz, Wiggins & Porter 711 (GH, NY). Guatemala: Zacapa, Standley 73633 (US). Haiti: St. Michel de l'Atalaye, Leonard 7334 (GH, NY, UC, US). Jamaica: Hope Grounds, Harris 12127 (GH, NY, US). Mexico. Baja California sur: El Llanito, Carter & Moran 5283 (MICH, MO, TEX, US); OAXACA: 38 mi W of Tehuantepec, Cronquist 9682 (MICH, MO, NY, TEX, US); SONORA: between Hermosillo and Tastiota, Wiggins & Rollins 269 (LL, MICH, MO, UC, US); YUCATÁN, without locality, Gaumer 887 (F, MO, NY, US). Netherlands Antilles. CURAÇÃO: Willemstad, Britton & Shafer 2910 (GH, NY, US). Peru. CAJAMARCA: Pucará, Hutchison & Wright 3578 (GH, MICH, NY, UC, US). United States. ARIZONA: Pima Co.: 4 mi W of Havanakya, Gould & Haskell 3196 (TEX, UC); PUERTO RICO: Ponce, Heller 6322 (GH, NY, US); VIRGIN ISLANDS: St. Croix, Ricksecker 12 (GH, NY, UC, US). Venezuela: Maracaibo, Moritz 473 (GH).

1b. Pectis linifolia L. var. hirtella Blake, Jour. Wash. Acad. Sci. 25: 322. 1935. Type: Mexico. Guerrero: Dist. Coyuca, Tanganhuato, *Hinton 6606* (US, holotype!; F, MO, US, isotypes!).

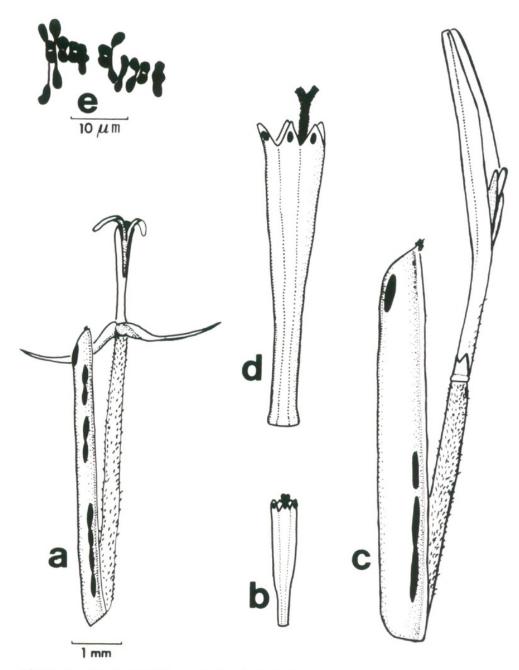


Figure 2. Pectis linifolia and Pectis imberbis. a, b, P. linifolia var. linifolia: a, ray floret with subtending involucral bract; b, disc corolla; a, b, Nash, Brown, MacIntyre, McGill & Pinkava P9907 (ASU). c, d, e, P. imberbis: c, ray floret with subtending involucral bract; d, disc corolla; e, chromosome complement at metaphase I (2n = 12 II); c, d, Pinkava & Keil K11006A (ASU); e, Pinkava & Keil K11006C (ASU).

Stems glabrous or hirtellous on the angles. Leaves 1.0–5.5 cm. long, 1–8 mm. wide, with 1–3 pairs of basal setae up to 7 mm. long, glabrous or hirtellous on the margins and midrib below. Involucre purple, 5.0–6.5 mm. long, glabrous or hirtellous. Ray florets with the tube 1.5 mm. long and the ligule 2.25–2.50 mm. long. Disc florets 5–6, sterile, with the corollas 3.5–4 mm. long; ovary shrunken, 3 mm. long. Ray achenes 4.5 mm. long. Ray pappus biaristate, 2.5 mm. long; disc pappus coroniform. Chromosome number unknown.

Pectis linifolia var. hirtella occupies a limited range in Michoacan and Guerrero, Mexico at 300-600 m. (Figure 1). Plants of var. hirtella are known to flower from August to December.

The varietal epithet of this taxon is somewhat of a misnomer. Most collections lack the pubescence of the type. The most easily recognizable characteristic for distinguishing this taxon from var. *linifolia* is the elongate basal setae of the leaves.

REPRESENTATIVE SPECIMENS: **Mexico.** GUERRERO: dist. Coyuca, Chacamerito, *Hinton 6440* (GH, US); MICHOACÁN: below Uruapan, *Lape 26* (MICH); above Apatzingán, *Leavenworth & Hoogstraal 1504* (F, MO); 9 mi SE of Apatzingán, *McVaugh 17987* (MICH, US); Las Juntas, *Rzedowski 26654* (ENCB).

2. **Pectis imberbis** A. Gray, Smithsonian Contr. Knowl. **5**(6): 70. 1853. TYPE: "Sonora, on the Sonoita" *Wright 1399* (GH, holotype!; F, GH, MO, US, isotypes!).²

Erect perennial herb 3–12 dm. tall, arising from a woody caudex 2–8 mm. diameter. Stems virgate, green, 6-angled above, becoming terete below, much-branched with ascending branches above, glabrous. Leaves narrowly linear, 1–5 cm. long, 1–2 mm. wide, sometimes much-reduced and bractlike above, apically acute, entire or bearing a single pair of basal setae 1–3 mm. long, usually revolute, punctate on the undersurface near each margin with a row of elliptical glands and on the upper surface with a single elongate medial subterminal gland, glabrous except for a minute axillary tuft of hairs. Heads solitary or in open cymose clusters at the tips of the branches. Peduncles 1–8 cm. long, slender, glabrous, bearing 2–4 slender alternate bracteoles 1–2 mm. long. Involucre green or

²Charles Wright collected the type of *Pectis imberbis* prior to the Gadsden Purchase (1853). Although his collection labels list the locality as Sonora, the collection site is now a part of Santa Cruz County, Arizona.

purplish; bracts oblong, 5.0-9.5 mm. long, 1.0-1.5 mm. wide, apically obtuse, narrowly hyaline-margined, punctate with 1-2 swollen subapical glands and a row of 2 or 3 linear submarginal glands on each side of the midrib, minutely ciliolate and bearing an apical tuft of hairs, otherwise glabrous. Ray corollas vellow, often drying pink or purple, 6-11 mm. long, with tubes 2-3 mm. long and ligules 4-8 mm. long and 1.0-2.5 mm. wide, often punctate near the margin with several inconspicuous glands, sparsely puberulent on the tube with multicellular trichomes less than 0.1 mm. long. Disc florets 4-7; corollas yellow, often drying purplish, 3.7-6.0 mm. long, the lobes triangular, ca. 0.5 mm. long, punctate just below the tip with a solitary gland, glabrous or sparsely puberulent; anthers ca. 2.5 mm. long. Achenes black, 3.5-5.0 mm. long, puberulent with ascending blunt-tipped double-hairs 0.1-0.2 mm. long. Pappus of ray and disc achenes similar, aristate with 1-3 stout awns 1-2 mm. long, or reduced to a low crown. Chromosome number: n = 12. Figure 2, c-e.

Pectis imberbis occurs over a relatively limited range in southern Arizona, western Chihuahua, and eastern Sonora at elevations of 1100–1700 m. Through most of its range, *P. imberbis* is uncommon. Each of the populations examined in the field during the present study consisted of less than ten individuals. No seedlings were found in these populations. Pectis imberbis has been recommended for inclusion on the list of threatened or endangered species (Mrs. Elinor Lehto, pers, comm.).

Fernald (1897) indicated that *Pectis imberbis* has a strong terebinthine odor but did not cite the source of his information. My own observations have indicated that plants from Arizona populations are non-aromatic, and none of the labels from plants of this species that I have examined mention any odor.

REPRESENTATIVE SPECIMENS: **Mexico.** CHIHUAHUA: Guasaremos, *Gentry 1857* (DES, LL, MO, UC, US); Batopillas, *Gentry 2617* (MO, US); **Sonora:** Cañon Saucito, *Gentry 705M* (MICH); Cañon de la Petaquilla, *White 3337* (MEXU, MICH). **United States.** ARIZONA: Cochise Co.: Huachuca Mts, *Lemmon 2783* (US); Ft Huachuca, *Wilcox 390* (US); Santa Cruz Co.: Patagonia Mts, *Kearney & Peebles 14826* (LL, US); Atacosa Mts, *Parker 7399* (UC); Peña Blanca Lake, *Pinkava & Keil K11006* (ASU).

Table 1. New chromosome counts from Pectis sect. Pectidium.

Pectis imberbis A. Gray

United States. ARIZONA: Santa Cruz Co.: Peña Blanca Lake Recreation Area, *Pinkava & Keil K11006B*, *C* (Figure 2e), $2n = 12_{II}$; *K11006D*, $2n = 10_{II} + 1_{IV}$. 3.7 mi W of Peña Blanca Lake, *Pinkava & Keil K11076A*, $2n = 12_{II}$.

Vouchers are deposited at ASU.

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