CHROMOSOME STUDIES IN NORTH AND CENTRAL AMERICAN SPECIES OF PECTIS L. (COMPOSITAE: TAGETEAE)

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Chromosomal modification is often a major factor in the evolutionary diversification of a large, rapidly evolving genus. *Pectis,* the largest and most widespread genus in the New World tribe Tageteae (Compositae), has radiated into a variety of habitats during its evolutionary history. Until relatively recently, however, little has been known of the role of chromosomal change in the evolution of the genus. *Pectis* was cytologically unknown until the studies of Raven and Kyhos (1961) and of Turner, Ellison, and King (1961). Subsequently, additional counts have been reported for several taxa (Table 1). To date, however, only a few of the species have been studied cytologically, and these only from a few populations. Of the four large genera of the Tageteae, *Pectis* has been the most poorly represented in cytological studies.

This investigation is one of a series of studies of the evolution and taxonomy of *Pectis.* The genus reaches its greatest diversity in the warmer areas of North America, and it is from this region that most of the collections upon which this study is based were made. Through an examination of the chromosomes of as many species as possible, and from numerous populations of wide-ranging species, information regarding the variability of chromosomes in *Pectis* can be better correlated with the evolutionary history and systematics of the genus.

MATERIALS AND METHODS

Immature capitula were killed and fixed in the field in modified Carnoy's fixative (4 chloroform : 3 ethanol : 1 glacial acetic acid), and were kept under refrigeration prior to examination. In a modification of the methods of Beeks (1955), whole floret buds were stained (usually without heat) for 2–48 hours in standard 1% acetocarmine or iron acetocarmine solution and were squashed without prior maceration in a drop of Hoyer's solution. Camera lucida drawings were prepared from meiotic microsporocytes to document each reported count.

Table 1. **Previously reported chromosome counts for Pectis.**

Reported count (*n*)	Taxon	Reference
	P. angustifolia Torr. var. *angustifolia*	
12	(*as P.* cf. *texana* Cory)	Powell & Turner (1963)
12	(as *P. angustifolia* Torr.)	Powell & Turner (1963)
	P. angustifolia Torr. var. *tenella* (DC.) Keil	
12	(as *P. tenella* DC.)	Powell & Turner (1963); Strother (1972); Urbatch in Löve (1974)
12	*P. coulteri* Harv. & Gray	Keil (1975B)
12	*P. depressa* Fern.	Powell & Turner (1963)
	P. filipes Harv. & Gray var. *subnuda* Fern	
12	(as *P. filipes* Harv. & Gray)	Powell & Sikes (1970); Fay in Löve (1974)
ca. 24	*P. latisquama* Sch. Bip. ex Greenm.	Powell & Turner (1963)
12	*P. multiseta* Benth. var. *ambigua* (Fern.) Keil	Keil (1975B)
12	*P. multiseta* Benth. var. *multiseta*	Keil (1975B)
	P. papposa Harv. & Gray var. *papposa*	
12	(as *P. papposa* Harv. & Gray)	Raven & Kyhos (1961); Watson (1973)
12	*P. papposa* Harv. & Gray var. *grandis* Keil	Keil (1974); Keil & Stuessy (1975)
12, 12 + fragment	(as *P. papposa* Harv. & Gray)	Powell & Sikes (1970)
12	*P. pringlei* Fern.	Fay in Löve (1974)
12	*P. purpurea* Brandeg. var. *sonorae* Keil	Keil (1974)
12	(as *P. palmeri* S. Wats.)	Turner & Flyr (1966)
	P. rusbyi Greene ex A. Gray	
12	(as *P. palmeri* S. Wats.)	Turner & Flyr (1966)
12	(as *P. puberula* Greenm.)	Turner & Flyr (1966)
12	*P. saturejaoides* (Mill.) Sch. Bip.	Turner, Ellison & King (1961); Powell & Turner (1963)
12	*P. sinaloensis* Fern.	Turner & Flyr (1966)
36	*P. subsquarrosa* (Hook. f.) Sch. Bip.	Kyhos in Wiggins & Porter (1971)

RESULTS AND DISCUSSION

Chromosome counts were obtained from 28 taxa and from five natural interspecific hybrids (Table 2; Figures 1–34). Of the taxa studied, 22 are diploids with $n = 12$, three are tetraploids with $n = 24$, one has both a diploid and a tetraploid race, and two are hexaploids with $n = 36$. Two of the hybrids are triploids with 8–12 bivalents and correspondingly 12–20 univalents at metaphase I and with very irregular meiotic behavior. The remaining hybrids are functional diploids with only sporadic incidence of meiotic irregularities. Supernumerary chromosomes were noted in three species and in some of the interspecific hybrids. Of the counts reported, 18 of the taxa and all of the interspecific hybrids are first reports.

Several evolutionary lines are represented in the newly reported counts. Some of these lines correspond to named sections of the genus. However, since sectional limits have never been applied to the entire genus, and in some cases, previously published sectional limits have been found to be in error (Keil, 1977), not all taxa are presently assignable to sections. Consequently, in the following discussion, taxa will be referred to section only when the affinities are well established.

Section *Pectothrix* A. Gray is easily the best-known portion of the genus cytologically. Counts are known for all except two species, *Pectis vollmeri* Wiggins and the newly described *P. peruviana* Keil (Keil, 1977), although varieties remain uncounted in two other species. First reports for this section are two western Mexican taxa, *P. filipes* var. *filipes* and *P. stenophylla* var. *biaristata,* a Chihuahuan Desert endemic, *P. incisifolia,* and a Texas endemic, *P. angustifolia* var. *fastigiata.* Numerous additional counts are reported for *P. angustifolia* vars. *angustifolia* and *tenella, P. filipes* var. *subnuda, P. papposa* vars. *papposa* and *grandis, P. pringlei, P. rusbyi,* and *P. sinaloensis.*

Section *Pectothrix* is interesting from the standpoint of chromosomal uniformity and the relative lack of sterility which characterize the known natural hybrids within the group. Of the various hybrid combinations which have been studied cytologically, only one, *Pectis angustifolia* var. *angustifolia* × *P. papposa* var. *grandis,* was found to possess individuals displaying meiotic irregularities. Inversion bridge-fragment formations and

Table 2. **New chromosome counts for taxa of Pectis.**

Chromosome number (n)	Taxon with location and voucher[a]
12	**Pectis angustifolia** Torr. var. **angustifolia** **México.** CHIHUAHUA: 13.6 mi S of Cd. Jiménez, *K & M 8387A;* 25.6 mi N of Janos, *K & M 8432A, B.* DURANGO: 1.8 mi E of Nazareno, *K & M 8014A.* **United States.** COLORADO: Fremont Co.: Indian Spring Campground, *K 7637A;* Canyon City, *K 7638* (Figure 1); Sedgwick Co.: 1.5 mi S of Ovid, *K 7634.* NEBRASKA: Keith Co.: 1 mi S of Ogallala at S Platte River, *Stuessy & Stuessy 1717;* Keith-Lincoln Co. line at S Platte River, *K 7635;* Lincoln Co.: S Platte River at Hershey Rd, *K 7603;* S Platte River at Sutherland, *K 7620A.* NEW MEXICO: Grant Co.: S of Sherman along Mimbres River, *K & M 8465A;* 6.5 mi E of Santa Rita, *K & M 8740;* 4 mi N of Silver City, *K & M 8481A*[b]*;* Hidalgo Co.: 7.2 mi NE of jctn. w/US 70 on NM 90, *K & M 8494A.* TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7795A;* 15.1 mi N of Castolon, *K & M 7798A;* Culberson Co.: 1.4 mi SE of Hudspeth Co. line on I-10, *K & M 7687;* Hudspeth Co.: SE of Ft Hancock, *K & M 7665A, B;* Presidio Co.: 18.5 mi S of Marfa, *K & M 7741;* 13.1 mi SE of Presidio, *K & M 7774A, B.*
12*	**Pectis angustifolia** Torr. var. **fastigiata** (A. Gray) Keil **United States.** TEXAS: Sutton Co.: Sonora, *Keil & Roberts 10074* pop. (Figure 2).
12	**Pectis angustifolia** Torr. var. **tenella** (DC.) Keil **México.** COAHUILA: 107 mi S of Piedras Negras, *K & M 7849A, B, C;* 114 mi S of Piedras Negras, *K & M 7860A;* between Nueva Rosita and Monclova, *K & M 7865A;* 11.4 mi S of Monclova, *K & M 7875;* 27 mi S of Monclova, *K & M 7879A, B* (Figure 3); 60 mi S of Monclova, *K & M 7911A;* 22.5 mi E of Paila, *K & M 7944A;* 16.7 mi E of Paila, *K & M 7950A, B;* 5.3 mi E of Paila, *K & M 7954A*[c]*;* 13 mi W of Paila, *K & M 7960A, B;* 8.6 mi E of Emiliano Zapata, *K & M 7996;* 4.2 mi S of Acatita, *K & M 8052A;* 2.1 mi N of Acatita, *K & M 8065A;* 7.8 mi N of Acatita, *K & M 8072A;* 1.1 mi S of Rancho El Cinco, *K & M 8102A;* 10.3 mi S of Rancho los Charcos, *K & M 8165A, B.* DURANGO: E of Mapimí, *K & M 8186A.* **United States.** TEXAS: Hidalgo Co.: 0.8 mi E of jctn. w/Texas FM rd 886 on US 83, *K & C 9247A, B;* Starr Co.: 1 mi W of jctn. w/Texas FM rd 1430 on US 83, *K & C 9248B;* 11.6 mi SE of jctn. w/Texas FM rd 2098 on US 83, *K & C 9249A.*

Table 2 — continued

Chromosome number (n)	Taxon with location and voucher
12*	**Pectis berlandieri** DC. **México.** TAMAULIPAS: just E of Magiscatzan, *K & C 9235 A, B, C;* 3 mi E of Mante, *K & C 9238B;* 8.9 mi W of Magiscatzan, *K & C 9240A* (Figure 4), *B.*
24*	**Pectis bonplandiana** H.B.K. **Guatemala.** SUCHITEPEQUEZ: Puente Siguacan, *K 9439A* (Figure 5); 5.4 km E of jctn. w/rd to Chicanoa on CA-2, *K 9442A;* 11.5 km E of Puente Siguacan on CA-2, *K9448A*[d].
12*	**Pectis capillipes** (Benth.) Hemsl. **Honduras.** CHOLUTECA: just S of San Antonio de Flores, *K 9505A* (Figure 6), *B,* pop.; 8.4 km W of Choluteca *K 9517* pop.
24*	**Pectis cylindrica** (Fern.) Rydb. **México.** COAHUILA: 9.4 mi S of Rancho los Charcos, *K & M 8161* pop. (Figure 7). SONORA: 28.5 mi W of Álamos, *K & C 8663* pop.
12*	**Pectis filipes** Harv. & Gray var. **filipes** **México.** SONORA: 28 mi S of Hermosillo, *K & C 8617A, B, C;* 3.8 mi E of jctn. w/Mexico 15 on rd to Álamos, *K & C 8659A, B;* 11.8 mi E of jctn. w/Mexico 15 on rd to Álamos, *K & C 8665A, B*[c]*, C;* 7.2 mi SE of Navojoa, *K & C 8725A* (Figure 8).
12	**Pectis filipes** Harv. & Gray var. **subnuda** Fern. **México.** CHIHUAHUA: 24 mi N of Nueva Casas Grandes, *K & M 8406A, B.* **United States.** ARIZONA: Cochise Co.: 0.5 mi S of Paradise, *K & M 8512A;* Chiricahua Natl Monument, *K & M 8528A* (Figure 9). TEXAS: Presidio Co.: 18.5 mi S of Marfa, *K & M 7742A, B;* 1.4 mi N of Cibola Creek on US 67, *K & M 7749A;* Brewster Co.: 15.1 mi N of Castolón, *K & M 7797A, B, C, D;* 12.5 mi N of Castolón, *K & M 7811A.*

Table 2 — continued

Chromosome number (n)	Taxon with location and voucher
12*	**Pectis haenkeana** (DC.) Sch. Bip. **México.** GUERRERO: 3.2 mi S of Iguala, *K & C 9144A, B;* 1.4 mi N of Sabina Grande, *K & C 9115A* (Figure 10), *B;* 22 mi S of Iguala, *K & C 9117A;* 22 mi N of Zumpango del Río, *K & C 9119A, B;* 4.5 mi N of Iguala on México 95-D, *K & C 9137A, B.* MORELOS: 25.7 mi N of Morelos-Guerrero boundary on México 95-D, *K & C 9140A.*
12*	**Pectis incisifolia** I. M. Johnston **México.** COAHUILA: S of Laguna del Rey, *K & M 8101A* (Figure 11), *B, D, E; 8102A; 8105A, B; 8109A, B, C.*
12*	**Pectis leavenworthii** Standl. **México.** MICHOACÁN: 5 mi E of Apatzingan, *Stuessy & Roberts 3744* pop. (Figure 12).
12*	**Pectis longipes** A. Gray **United States.** ARIZONA: Santa Cruz Co.: 2.5 mi N of Sonoita, *K & M 8566A* (Figure 13).
36*	**Pectis multiflosculosa** (DC.) Sch. Bip. **México.** SINALOA: Mazatlán, *Keil & Roberts 10160B;* Mazatlán, *Stuessy & Gardner 3040* pop. (Figure 14).
12*	**Pectis oerstediana** Rydb. **Guatemala.** JUTIAPA: 7.7 km E of jctn. w/rd to Quesada on CA-1, *K 9413B* (Figure 15).
12	**Pectis papposa** Harv. & Gray var. **papposa** **México.** SINALOA: Altata, *K & C 8785A, B, C.* SONORA: 72 mi S of Benjamin Hill on Mexico 15, *K & C 8609A, B;* 12 mi S of Hermosillo, *K & C 8616A, B;* 7 mi NW of Cd. Obregon, *Stuessy & Gardner 3015A, B, C.* **United States.** ARIZONA: Maricopa Co.: 12 mi N of Riggs Rd on I-10, *K & C 8576B;* Pima Co.: 13.6 mi NW of Cortaro Rd exit on I-10, *K & C 8579A;* Pinal Co.: 2.3 mi NW of jctn. w/Storey Rd on I-10, *K & C 8578A.* NEW MEXICO: Hidalgo Co.: 2.5 mi S of I-10 on US 80, *K & M 8496A, B* (Figure 16); Cienega Lake turnoff on US 80, *K & M 8500A.*

Table 2 — continued

Chromosome number (n)	Taxon with location and voucher
12	**Pectis papposa** Harv. & Gray var. **grandis** Keil **México.** CHIHUAHUA: 15.4 mi N of Cd Camargo, *K & M 8252-1A;* 20.2 mi N of Janos, *K & M 8429;* 25.6 mi N of Janos, *K & M 8433A*. **United States.** NEW MEXICO: Doña Ana Co.: 28 mi N of Las Cruces, *K 7654A, C* (Figure 17); 1 mi N of jctn. I-10 & I-25, *K 7655A, B.* TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7818A*[f]*:* El Paso Co.: Horizon City exit on I-10, *K & M 7659A, B;* 2.6 mi NW of Tornillo exit on I-10, *K & M 7664A;* Presidio Co.: 2.7 mi SE of Redford, *K & M 7778A*.
12	**Pectis pringlei** Fern. **México.** CHIHUAHUA: 0.6 mi N of jctn. w/rd to Escalón on México 49, *K & M 8206-2A, B, C;* 29.9 mi S of Jiménez, *K & M 8218A* (Figure 18). COAHUILA: 36.9 mi W of Paila, *K & M 7976A, B, C, D;* jctn. w/rd to San Pedro on México 40, *K & M 7988A, B;* 10.3 mi S of Rancho los Charcos, *K & M 8164A*. DURANGO: 17.5 mi S of Nazareno, *K & M 8033B, C;* 22 mi S of Nazareno, *K & M 8041A*.
12*	**Pectis prostrata** Cav. **El Salvador.** LA LIBERTAD: 1 km E of Santa Tecla, *K9400* pop. **Guatemala.** EL PROGRESSO: 43 km W of El Progresso, *K 9417A;* 23 km W of El Progresso, *K 9418A* (Figure 19). GUATEMALA: 30 km SE of Cd. Guatemala, *K 9398A*. JUTIAPA: 7.3 km W of jctn. w/dirt rd to Jalpatagua on CA-1, *K 9409A*. SANTA ROSA: 3.5 km NW of jctn. w/rd to Culiapa on CA-1, *K 9400A;* 11 km E of Puente Culiapa on CA-1, *K 9405A;* 2.1 km E of jctn. w/rd to Jalpatagua on CA-1, *K 9406A*. ZACAPA: 3.1 km E of Puente Palmilla on CA-1, *K 9424A*. **México.** CHIHUAHUA: 4.5 mi N of Galeana, *K & M 8388*. COAHUILA: 47 mi S of Monclova, *K & M 7901A, C.* MEXICO: 20 mi SSE of Zitacuaro, *Stuessy & Gardner 3126A*. NAYARIT: 44 mi SE of Acaponeta, *K & C 8959A,* pop. SINALOA: 8.7 mi SE of Rosario, *K & C 8948A*. VERACRUZ: 1 mi SE of Tantoyuca, *K & C 9227B.* **United States.** NEW MEXICO: Grant Co.: 6½ mi E of Santa Rita, *K & M 8472* pop.
24*	**Pectis repens** Brandeg. **México.** JALISCO: 6.1 mi E of Nayarit-Jalisco boundary on Mexico 15, *K & C 8993* pop. (Figure 20).
12*	**México.** MÉXICO: 0.5 mi N of Guerrero-México boundary on Federal Rte 55, *K & C 9097* pop. (Figure 21).

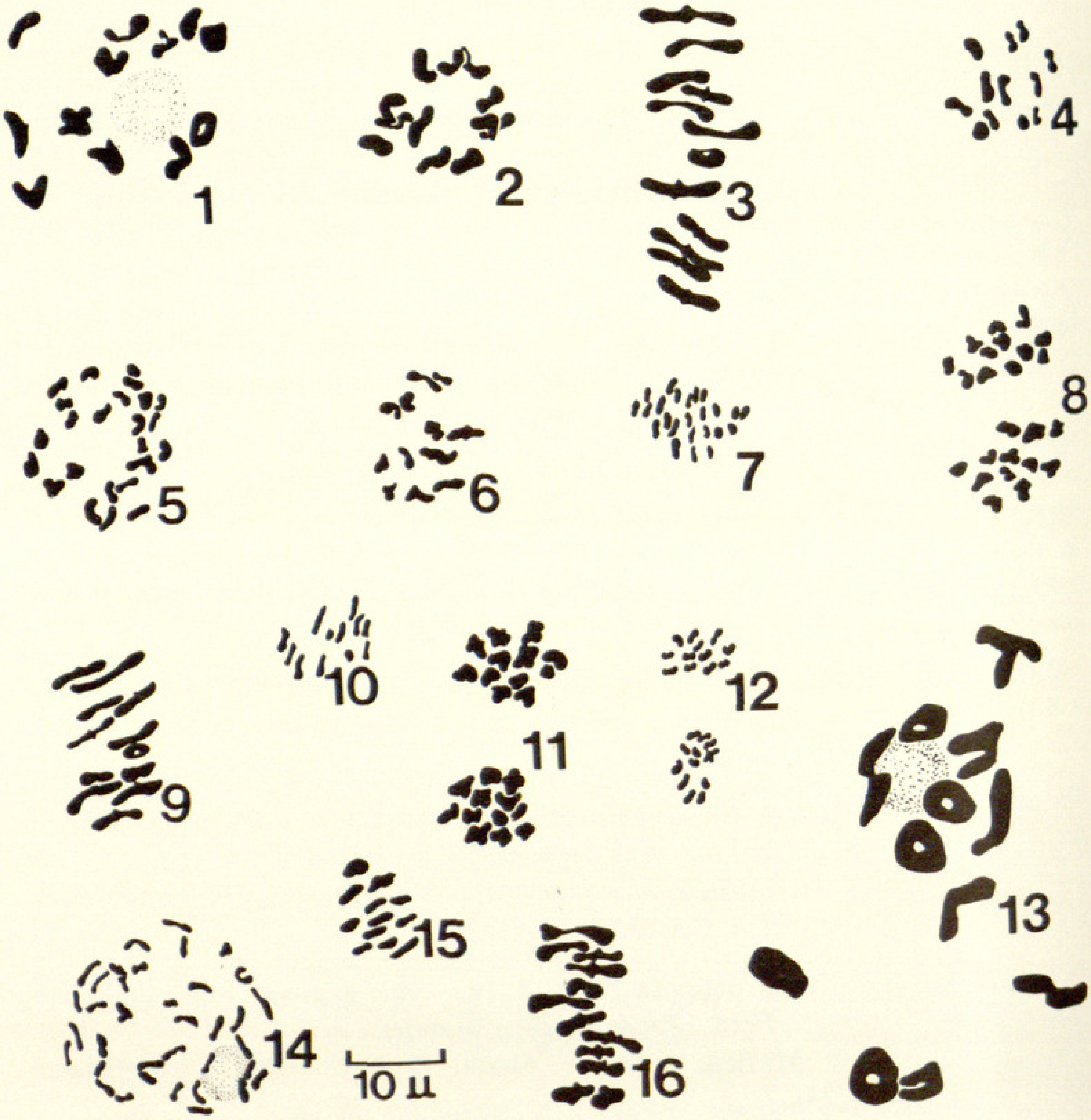
Table 2 — continued

Chromosome number (*n*)	Taxon with location and voucher
12	**Pectis rusbyi** Greene ex A. Gray **México.** SINALOA: 20.6 mi S of Sonora-Sinaloa boundary on México 15, *K & C 8738A, B;* 1.8 mi E of San Blas, *K & C 8744A, B, C.* SONORA: just S of Magdalena, *K & C 8594A, B, C*[b]*, D;* 7 mi S of Magdalena, *K & C 8595A;* 17 mi S of Hermosillo, *K & C 8614B;* 28 mi S of Hermosillo, *K & C 8621A;* 6.5 mi S of jctn. w/rd to Bahia Kino on Mexico 15, *K & C 8629A;* jctn. w/rd to Bahia San Carlos on Mexico 15, *K & C 8632A;* 0.7 mi S of jctn. w/Sonora 19 on Mexico 15, *K & C 8654* (Figure 22); 14.1 mi W of Álamos, *Stuessy & Gardner 3022* pop.; 29.3 mi W of Álamos, *Stuessy & Gardner 3024* pop. **United States.** ARIZONA: Maricopa Co.: White Tank Mountains, *K 8570* pop.; Yavapai Co.: 2.5 mi S of Beaver Creek Ranger Station, *K 8575AA, BB.*
12	**Pectis saturejaoides** (Mill.) Sch. Bip. **Guatemala.** EL PROGRESSO: 5.6 km E of turnoff to El Rancho on CA-9, *K 9423A* (Figure 23), *B, C;* 0.5 km W of turnoff to El Rancho on CA-9, *K 9427A, B.*
12	**Pectis sinaloensis** Fern. **México.** SINALOA: Altata, *K & C 8786G;* Mazatlán, *K & C 8810A, B, C, D* (Figure 24), *E.*
12*	**Pectis stenophylla** A. Gray var. **biaristata** (Rydb.) Keil **México.** SINALOA: 16.8 mi W of El Fuerte, *K & C 8752A, B, C* (Figure 25).
36	**Pectis subsquarrosa** (Hook. f.) Sch. Bip. **Galapagos Islands:** Hood Island, *C. H. Racine s.n.* (Figure 26).
24*	**Pectis swartziana** Less. **Honduras.** VALLE: 1.9 km S of jctn. w/CA-5 on CA-1, *K 9510A* (Figure 27), pop.
12*	**Pectis uniaristata** DC. var. **holostema** A. Gray **El Salvador.** LA LIBERTAD: 10.1 km N of Quetzaltepeque exit on El Salvador 1, *K 9452A, B.* **Honduras.** CHOLUTECA: 24 km W of Choluteca, *K 9512A* (Figure 28); 20 km W of Choluteca, *K 9515A.*

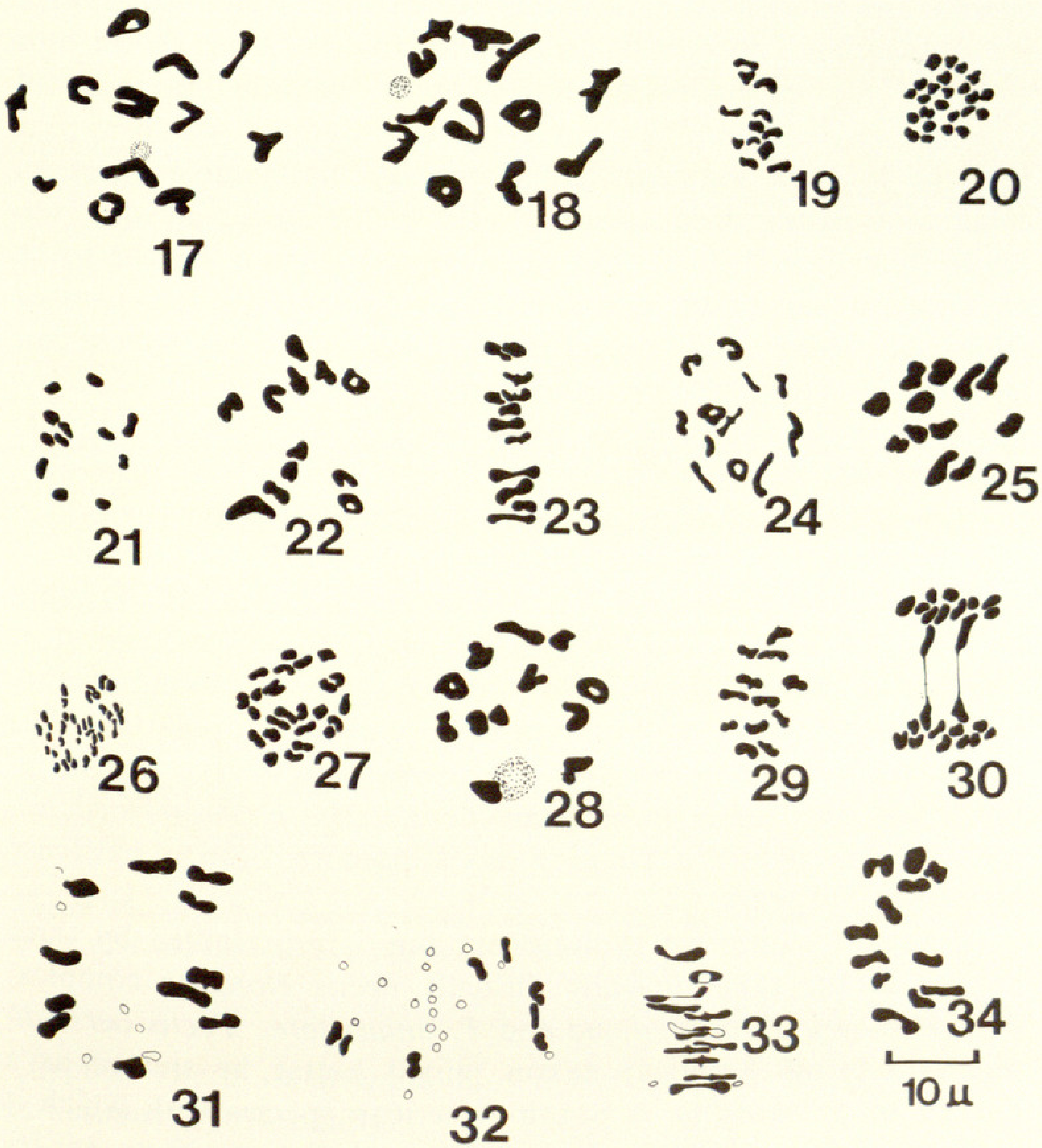
Table 2 — continued

Chromosome number (n)	Taxon with location and voucher
12*	**Pectis uniaristata** DC. var. **jangadensis** (S. Moore) Keil **México.** GUERRERO: 12 mi S of Chilpancingo, *K & C 9127* pop. JALISCO: 2.1 mi NW of Magdalena airport, *K & C 9004A, B;* 1.7 mi NW of jctn. w/México 70 on Mexico 15, *K & C 9024* pop. NAYARIT: 18 mi SE of Tepic, *K & C 8971-1* pop.; 16.3 mi W of Nayarit-Jalisco boundary on México 15, *K & C 8997A* (Figure 29), *B, D.*
12*	**Pectis angustifolia** Torr. var. **angustifolia** × **P. papposa** Harv. & Gray var. **grandis** Keil **United States.** TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7797;* Presidio Co.: 10 mi S of Cibola Creek, *K & M 7756 K*[f] (Figure 30), *U*[g] (Figure 31).
12 II + 12 I*; 8 II + 20 I*	**Pectis bonplandiana** H. B. K. × **P. prostrata** Cav. **Guatemala.** SUCHITEPEQUEZ: Puente Siguacan *K & C 9438A, B* (Figure 32).
12*	**Pectis filipes** Harv. & Gray var. **filipes** × **P. papposa** Harv. & Gray var. **papposa** **México.** SONORA: 72 mi S of Benjamin Hill on Mexico 15. *K & C 8611D*[b] (Figure 33).
12*	**Pectis papposa** Harv. & Gray var. **papposa** × **P. sinaloensis** Fern. (*Pectis* × *salina* Brandeg.) **México.** SINALOA: Altata, *K & C 8786B, C, D* (Figure 34), *F.*
ca. 9 II + 18 I*	**Pectis swartziana** Less. × **P. uniaristata** DC. var. **holostema** A. Gray **Honduras.** CHOLUTECA: 20 km W of Choluteca, *K 9514B.*

*Previously unreported taxon or hybrid combination.
[a]Abbreviations of collectors' names: *K* = David Keil; *K & M* = Keil & Lyle A. McGill; *K & C* = Keil & Judith M. Canne. Voucher specimens are deposited at the Ohio State University Herbarium (OS).
[b]$2n$ = 12 II + 2 small supernumeraries.
[c]Anaphase I bridge observed in some cells.
[d]Some cells contain one or two anaphase I bridges and associated fragments.
[e]$2n$ = 12 II + 1 small supernumerary.
[f]Some cells contained one or two anaphase I bridges and associated fragments. Synapsis in some cells resulted in formation of 10 II + 1 IV.
[g]$2n$ = 12 II + 6 small supernumeraries which synapsed irregularly; one pair of regular-sized chromosomes occasionally failed to synapse.



Figures 1–16. **Camera lucida drawings of meiotic chromosomes of Pectis taxa and hybrids.** Voucher specimens are cited in Table 2. All figures are the same scale. 1, *P. angustifolia* var. *angustifolia*, diakinesis, $2n = 12$ II. 2, *P. angustifolia* var. *fastigiata*, diakinesis, $2n = 12$ II. 3, *P. angustifolia* var. *tenella*, metaphase I, $2n = 12$ II. 4, *P. berlandieri*, metaphase I, $2n = 12$ II. 5, *P. bonplandiana*, diakinesis, $2n = 24$ II. 6, *P. capillipes*, metaphase I, $2n = 12$ II. 7, *P. cylindrica*, metaphase I, $2n = 24$ II. 8, *P. filipes* var. *filipes*, anaphase I, $n = 12$. 9, *P. filipes* var. *subnuda*, metaphase I, $2n = 12$ II. 10, *P. haenkeana*, metaphase I, $2n = 12$ II. 11, *P. incisifolia*, anaphase I, $n = 12$. 12, *P. leavenworthii*, telophase I, $n = 12$. 13, *P. longipes*, diakinesis, $2n = 12$ II. 14, *P. multiflosculosa*, diakinesis, $2n = 36$ II. 15, *P. oerstediana*, metaphase I, $2n = 12$ II. 16, *P. papposa* var. *papposa*, metaphase I, $2n = 12$ II.



Figures 17–34. **Camera lucida drawings of meiotic chromosomes of Pectis taxa and hybrids.** 17, *P. papposa* var. *grandis*, diakinesis, $2n$ = 12 II. 18, *P. pringlei*, diakinesis, $2n$ = 12 II. 19, *P. prostrata*, metaphase I, $2n$ = 12 II. 20, *P. repens* metaphase I (polar view), $2n$ = 24 II. 21, *P. repens*, diakinesis, $2n$ = 12 II. 22, *P. rusbyi*, metaphase I, $2n$ = 12 II. 23, *P. saturejaoides*, metaphase I, $2n$ = 12 II. 24, *P. sinaloensis*, diakinesis, $2n$ = 12 II. 25, *P. stenophylla* var. *biaristata*, metaphase I, $2n$ = 12 II. 26, *P. subsquarrosa*, metaphase I, $2n$ = 36 II. 27, *P. swartziana*, diakinesis, $2n$ = 24 II. 28, *P. uniaristata* var. *holostema*, diakinesis, $2n$ = 12 II. 29, *P. uniaristata* var. *jangadensis*, metaphase I, $2n$ = 12 II. 30, *P. angustifolia* var. *angustifolia* × *P. papposa* var. *grandis*, anaphase I, n = 12, double inversion bridge plus fragments. 31, *P. angustifolia* var. *angustifolia* ×*P. papposa* var. *grandis*, metaphase I, $2n$ = 11 II + 2 I + 6 supernumeraries. 32, *P. bonplandiana* × *P. prostrata*, metaphase I, $3n$ = 8 II + 20 I (triploid). 33, *P. filipes* var. *filipes* × *P. papposa* var. *papposa*, metaphase I, $2n$ = 12 II + 2 supernumeraries. 34, *P.* × *salina*, metaphase I, $2n$ = 12 II.

possible translocation multivalent formations were found in a few individuals, but even in these individuals, not nearly all cells exhibited the irregularities. Based upon the low frequency of microsporocytes containing anaphase I bridges, it would appear that the inverted segments are relatively small and are not an effective isolating mechanism. Multivalents occur at an even lower frequency than bridges and likewise do not appear to be an effective barrier to hybrid fertility. Some hybrids possessed from one to six small supernumerary chromosomes which pair irregularly. These extra chromosomes were not limited to hybrids, however, as they occasionally appeared in non-hybrid plants as well.

Perhaps the most striking hybrid in sect. *Pectothrix* is *Pectis* × *salina,* a fertile hybrid between *P. papposa* var. *papposa* and *P. sinaloensis,* morphologically two very diverse parents. A well-developed hybrid swarm has formed where these two taxa grow together at Altata, Sinaloa. No evidence of chromosomal sterility barriers has been found in any members of this population. The two parents in this population are probably not very closely related, but apparently have retained ancestral chromosomal homology. The hybrid population has apparently been in existence for at least 70 years.

A distinctly different evolutionary line is represented by three species of the taxonomically difficult *Pectis elongata* complex: *P. berlandieri, P. oerstediana* and *P. uniaristata. Pectis oerstediana,* a Central American taxon, might better be treated as a variety of *P. elongata,* a South American species with which it has often been confused. Two varieties of *P. uniaristata* are reported here. One, var. *holostema* (*P. dichotoma* Klatt), is a predominantly Central American taxon. The other variety is one of those unusual taxa with an amphitropical distribution, with populations in west-central Mexico and in Southern Brazil. All the counts are from the Mexican range of the taxon. Recognition of the conspecificity of the Mexican and Brazilian population systems has necessitated the following new combination:

Pectis uniaristata DC. Prodr. **5:** 99. 1836. var. **jangadensis** (S. Moore) Keil, comb. nov. (Figure 35). BASIONYM: *Pectis jangadensis* S. Moore, Trans. Linn. Soc. London Bot. **4:** 389. 1895. TYPE: **Brazil.** MATO GROSSO: near Jangada, Sep 1891, *S. Moore 256* (Holotype: BM, not seen; isotypes, B, photo US!, K!, NY!).

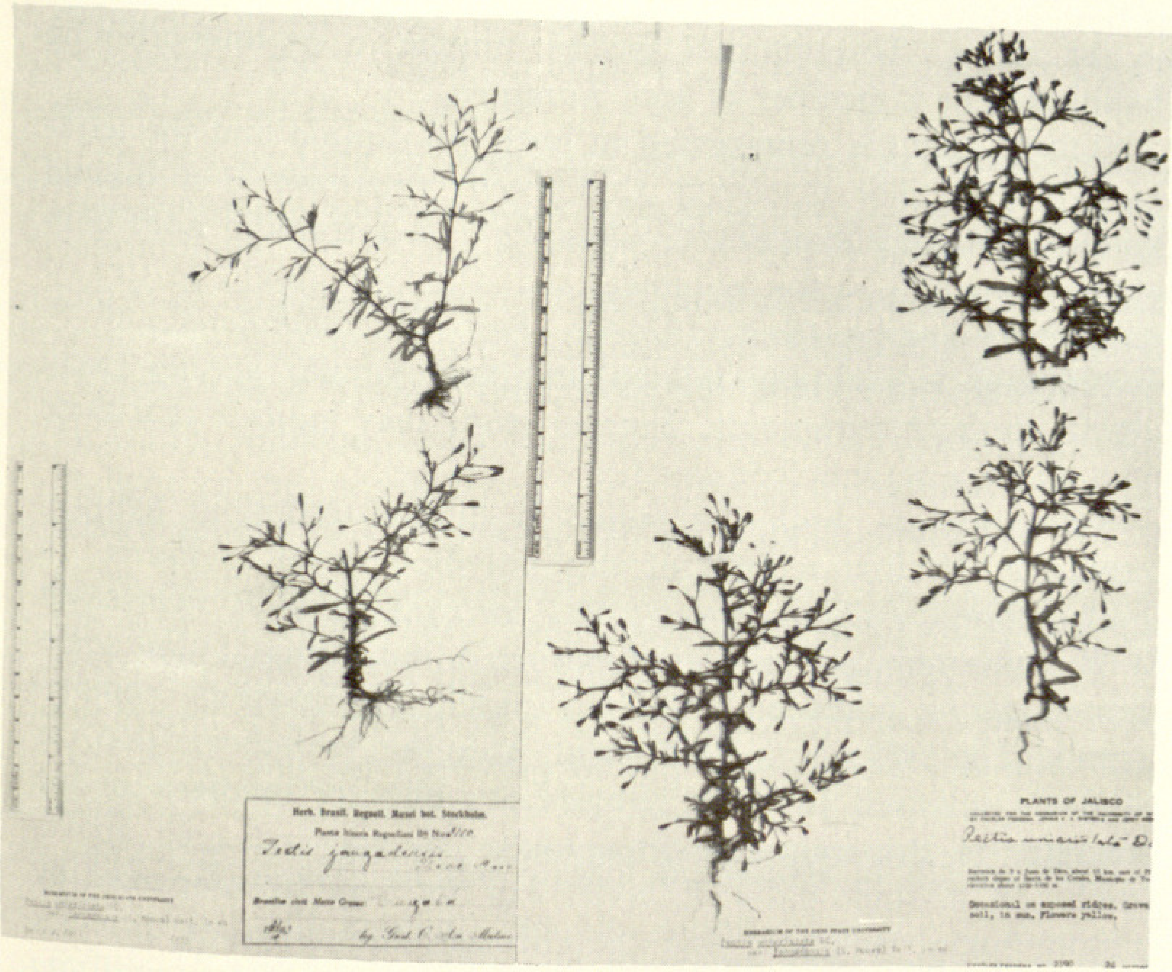


Figure 35. Brazilian and Mexican collections of *Pectis uniaristata* var. *jangadensis*, *Malme 3110* (GH) and *Feddema 2190* (MICH).

Typical *Pectis uniaristata*, also a Mexican taxon, has not yet been studied cytologically.

Stable polyploids have arisen in at least three different evolutionary lines in *Pectis*. Section *Lorentea* A. Gray, perhaps the most primitive of the genus, contains both diploids and polyploids. Three species from the section, *P. haenkeana*, *P. leavenworthii* and *P. saturejaoides*, are known only as diploids, and one, *P. latisquama*, has been reported only at the tetraploid level. *Pectis repens*, also a member of sect. *Lorentea*, apparently has both diploid and tetraploid races. Further study of additional populations will be necessary for an understanding of the basis for these different races. The two levels may eventually prove to represent cryptically differing species. *Pectis multiflosculosa*, a widespread perennial species which occurs on Pacific Ocean beaches from Sinaloa to Peru, is one of the two known hexaploids in the genus. This unusual species, unique in its long-creeping habit, may be a member of sect. *Lorentea.*

Section *Pectis* is represented at both the diploid and the tetraploid levels. The discovery that *Pectis prostrata* is a diploid whereas the very similar *P. cylindrica* is a tetraploid adds considerable weight to the argument that the two should be treated as distinct species (Keil, 1975A). *Pectis bonplandiana* and *P. swartziana,* two closely related and very similar species (Keil, 1974), are both tetraploids. Further study may indicate that these two taxa are actually conspecific.

Two triploids, both the result of diploid-tetraploid hybrids, represent the first reports of this polyploid level in *Pectis.* In both hybrids, *P. bonplandiana* × *P. prostrata* and *P. swartziana* × *P. uniaristata,* partial pairing occurred, indicating at least some homology or homoeology of the parent chromosome complements. The evidence is insufficient, however, to indicate that the diploids involved in these hybrids are directly involved in the ancestry of the respective tetraploids. As was indicated above, evolution in some parts of *Pectis* has not been accompanied by chromosomal isolation, and the chromosomes of quite different species may be capable of full pairing. The ability of *P. uniaristata* var. *holostema* to hybridize with a member of sect. *Pectis* suggests that there may be a fairly close relationship between the *P. elongata* complex and sect. *Pectis.*

The only species known cytologically from the South American region is *Pectis subsquarrosa,* a hexaploid endemic of the Galapagos Islands. The hexaploid level suggests that this species has had a complex evolutionary history. Current research (Keil, unpubl.) suggests that a pattern of adaptive radiation and subsequent migration may have played a part in the evolution of both *P. subsquarrosa* and *P. tenuifolia* (DC.) Sch. Bip., also endemic to the Galapagos Islands. Further samples of these species from additional islands may provide more information regarding the evolution of these species. Both Galapagos Islands species are members of an unnamed South American section of *Pectis.*

Diploid counts are reported here for the first time for two perennial species of uncertain affinities. *Pectis longipes* appears to be most closely related to sect. *Pectothrix* but also possesses features in common with some members of sect. *Lorentea. Pectis* *capillipes* (*P. erecta* Fern.) appears to be most closely related to members of the *P. elongata* complex, perhaps through the perennial *P. diffusa* Hook. & Arn.

Thirty-four taxa in *Pectis* are now known cytologically, some from many populations, some from only one. Thus far, only one base number, $x = 12$, has been reported for the genus. This situation is in strong contrast to that found in the other large genera of the Tageteae, which are all multibasic: *Dyssodia,* $x = 7,8,(12?), 13$ (Johnston & Turner, 1962; Strother, 1969); *Porophyllum,* $x = 11, 12, 15$ (Johnson, 1969); and *Tagetes,* $x = 11,12$ (Strother, 1969). In light of the variability of the chromosome numbers of these related genera, it is surprising that such a widespread and diverse genus as *Pectis* has remained monobasic. Certainly not all of the taxa of *Pectis* have been examined cytologically, and the possibility still exists that additional base numbers may yet be discovered. The probability of such an event is lessened, however, by the broad spectrum of the genus which has now been sampled.

The largest gaps in the present knowledge of the cytology of *Pectis* lie in the West Indian and South American range of the genus. Of particular value will be counts from additional members of sect. *Pectis,* particularly from the Caribbean region.

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