

Electrophoretic characterization of the American sections of *Prosopis* L. (Leguminosae: Mimosoideae)

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ABSTRACT

The genus *Prosopis* was divided into five sections by Burkart (1976), but previously, several authors had treated the genus differently, by modifying of the intrageneric or generic limits. Three of Burkart's sections are present in America. With the aim of characterizing and confirming the sections in Burkart's system, polyacrylamide gel electrophoresis of seed proteins was carried out in sixteen species of the genus. A total of 89 different bands were identified. Some of the bands are characteristic and constant "markers" of the sections. The electrophoretic patterns of sections *Algarobia* and *Monilicarpa* display bands 9 and 89 which are not present in the *Strombocarpa* protein profiles. *Prosopis argentina* (sect. *Monilicarpa*) shows bands 15, 18 and 19 which are "markers" of this section. Protein profiles of all the species of sect. *Strombocarpa* present band 7 which is diagnostic of the section. Moreover, variation in presence/absence of other bands also confirm Burkart's system, considering the American sections as natural and clearly different groups. So, the different species of *Prosopis* may be easily placed into their respective groups, in the presently accepted taxonomic system, by analyzing their electrophoretic profiles of seed proteins. The results of this paper point out the usefulness of the seed proteins electrophoretic pattern analysis in taxonomic studies of *Prosopis*.

INTRODUCTION

The genus *Prosopis* L. includes about 45 species distributed in south-western Asia, Africa and predominantly in America (Burkart 1976, Hunziker *et al.* 1986). Three sections of the genus are represented on the latter continent: *Algarobia*, *Monilicarpa* and *Strombocarpa*.

Sect. *Algarobia* is the largest section of the genus and is comprised of spiny or rarely unarmed trees, shrubs or subshrubs with caulinar spines. Plants are distributed in warmer and drier parts of America.

Sect. *Strombocarpa* includes species commonly called "screwbeans" or "tornillos" due to their fruits which are coiled into a dense spiral. These species are spiny shrubs or trees, with stipular spines, and are distributed in the southwestern United States, Mexico and South America.

The monotypic sect. *Monilicarpa* is restricted to western Argentina.

Only partial analysis of some species has been carried out by various techniques. These studies are not always in agreement with the morphological taxonomic system of Burkart (1976).

Cytological and biochemical studies show some differences with the morphological ones (Hunziker *et al.* 1986).

Seed protein electrophoretic patterns are highly stable and conspicuously species-specific. Seed protein electrophoresis has been employed in more than 45 genera belonging to 13 plant families (Ladizinsky and Hymowitz 1979).

The peptidic map (through partial hydrolysis of proteins) is useful for addressing a variety of specific questions in plant systematics (Crawford 1990).

Seed protein profiles may be composed of 20 or more bands. The complexity of patterns can cause problems of interpretation (Crawford 1990). Even so, the use of banding patterns of seed proteins is utilized with classificatory and systematic purposes with the aim to evaluate divergence among taxa, due principally to its low cost and technical simplicity (Fontdevila 1987). Moreover, an additional and fundamental feature characterizes this technique: the results are repeatable.

González Aguilera *et al.* (1986) consider that the seed protein patterns constitute less variable and more precise markers than isozymes to determine affinities among related taxa.

Moreover, if the electrophoretic conditions are uniform, the banding profile of storage proteins is less affected than most of the exomorphological quantitative characteristics, by the ambient conditions (Hunziker 1969).

Relationships inferred by seed protein electrophoretic patterns are, generally, congruent with the morphological classification when all or mostly all the species of a genus are analyzed (e.g. species of *Bulnesia* (Zygophyllaceae) (Comas *et al.* 1979, 1984) and *Zea* (Maydeae, Poaceae) (Harborne and Turner 1984). Results of investigations on several leguminous plants have shown electrophoretic analysis of crude protein extracts obtained at low pH to be a powerful tool in revealing interspecific differences (Przybylska 1995, Przybylska and Zimniak-Przybylska 1995).

The electrophoretic analysis of four species from the sect. *Algarobia*, of the genus *Prosopis*, had showed that these species displayed a high protein similarity; consequently, it is difficult to identify them by this method (Burghardt and Palacios 1991a and 1991b, Burghardt 1992).

To determine if it is possible to identify the electrophoretic seed protein profiles of different sections occurring in America and to verify whether this might be a useful technique to place different species into their proper sections, an extensive analysis of 16 species belonging to the three American sections was made and the results are presented in the present paper.

Scientific and common names of the species and their taxonomic position, *sensu* Burkart 1976, are shown in Table 1.

MATERIAL AND METHODS

The mobility of seed proteins was studied in 16 species of the genus. Collection data of the main material examined in this study and the herbaria where it is deposited (abbreviations according to Holmgren *et al.* 1981) are indicated in Table 2.

Figure 1 displays the genus distribution in America and indicates the origin of the samples analyzed.

Electrophoretic techniques

Extraction of total seed proteins:

Seed proteins were extracted from single mature seeds in the case of the species of the sect. *Algarobia* and *Monilicarpa*. Due to the small seed size in species of sect. *Strombocarpa*, generally 3-4 seeds were used.

Seeds were subjected to grinding with mortar and pestle. To the resultant powder, 0.5 ml of aluminum lactate buffer pH 3.6 and 3 M urea was added. After 30 minutes the extracts were centrifuged at 10000 RPM for 30 minutes at 4°C, and the supernatant was directly used for electrophoresis.

Polyacrylamide gel electrophoresis (PAGE):

PAGE was performed in a 7% polyacrylamide gel made in water. The gel was equilibrated in the extraction buffer for at least 48 hrs., at 4°C. Using aluminum lactate buffer (pH 3.6) in both reservoirs, electrophoresis was conducted for c. 6 hrs. at 400-600 V. The gel was stained with 0.005% w/v Coomassie Brilliant Blue (SIGMA) in a solution of MeOH-HOAc-H₂O, 4:1:10 for 18 hrs. and destained with the same solution without the dye.

RESULTS

Seed protein profiles of samples from 16 species of *Prosopis* L. belonging to the three American sections of the genus were analyzed. (Figure 1, Table 2)

Altogether, 89 bands have been identified and were named according to their cathodic mobility. The occurrence of the bands in the electrophoretic patterns of different species is shown in Table 3.

All the *Algarobia* species show a striking degree of electrophoretic similarity as has been indicated in previous studies of several species of the same section (Burghardt 1982 and 1992, Burghardt and Palacios 1981, 1984, 1991a and 1991b). All of them display the marker bands (constant and exclusive bands) 9 and 89. In various species, bands 5, 12, 13, 14, 20, 21, 22, 24, 25, 26, 28, 33, 35, 36, 38, 42, 43, 44, 45, 46, 48, 49, 51, 58, 59, 64, 67, 68, 71, 73, 74, 79, 80, 82, 83, 84, 85, 86 and 87 may be present (Table 3).

Prosopis argentina Burkart, the only species of the sect. Monilicarpa, shows differences with respect to the species belonging to both sections Algarobia and Strombocarpa. The *P. argentina* electrophoretic pattern presents the band 9, as the fast migrating fraction (band 89) which appear in the Algarobia species too, and possess four proper bands: 15, 18, 19 and 88 (Table 3). The presence of bands 15, 18, and 19, which are present neither in Algarobia nor in Strombocarpa species, as well as the absence of an intermediate migrating band (17), that is present in all other species analyzed, constitute the most important evidence and diagnostic feature to characterize the sect. Monilicarpa.

To characterize the species of the sect. Strombocarpa, two features are relevant: first, the presence of a band slower than band 9 (band 7) which appears in all the species of the section; and second, the absence of the fastest bands which are present in Algarobia (bands 82 to 89) and Monilicarpa species (bands 88 and 89). Furthermore, protein profiles of species of this section exhibit exclusive but not constant bands (6, 8, 10, 11, 16, 23, 27, 29, 37, 41, 50, 52, 54, 63, 70, 72, 75, 76, 77, 78 and 81).

The presence of bands 9, 17 and 89 together, in an individual pattern is characteristic of the Algarobia protein profiles. Sect. Monilicarpa is characterized by the simultaneous presence of bands 9, 15, 18, 19, 88 and 89. The specimens of Sect. Strombocarpa are individualized by the presence of the bands 7 and 17, simultaneously, with the absence of the two fastest bands (82 to 89) (Figure 2).

DISCUSSION

It is possible, indubitably, to place any American *Prosopis* specimen in one of the three sections analyzed through the electrophoretic pattern of seed proteins.

All Algarobia species show a striking degree of electrophoretic similarity as has been indicated previously for several species of the same section (Burghardt and Palacios 1991a and 1991b, Burghardt 1982 and 1992). This result agrees with those of enzymatic proteins (Saidman and Vilardi 1987, Saidman 1993), foliar architecture (Martínez 1984) and woody anatomy (Castro 1989).

The differences in seed protein electrophoretic patterns found between species of sect. Algarobia and sect. Strombocarpa are in agreement with the great divergence reported by Saidman (1985, 1993) for enzymatic proteins. Moreover, Caccavari de Filice (1972) in her study of pollen grain morphology found variation between sections Strombocarpa and Algarobia. Differences in foliar architecture (Martínez 1984) and wood anatomy (Castro 1989) have also been reported.

On the other hand, the segregation of *P. argentina* in a different section (sect. Monilicarpa) (Burkart 1976) is supported by the present study, because of its protein profile which is clearly different from those of the species belonging to the other sections. Variation in four bands is a high degree of difference when contrasted with the great similarity existing among Algarobia species.

The evidence here presented, together with those of (Saidman, 1985, 1993) and the other authors mentioned above, have brought valuable information which support the proposal of

Hunziker *et al.* (1986), about the elevation of the sections from Burkart's system (Burkart 1976) to subgenera.

Seed protein profiles allow the identification of the three American sections of *Prosopis* by the electrophoretic study of the characteristic and constant (diagnostic) bands. This method is therefore a valuable tool to be considered when supraspecific studies are carried out in the genus *Prosopis*.

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Figure 1: Map showing provenances of *Prosopis* species analysed.

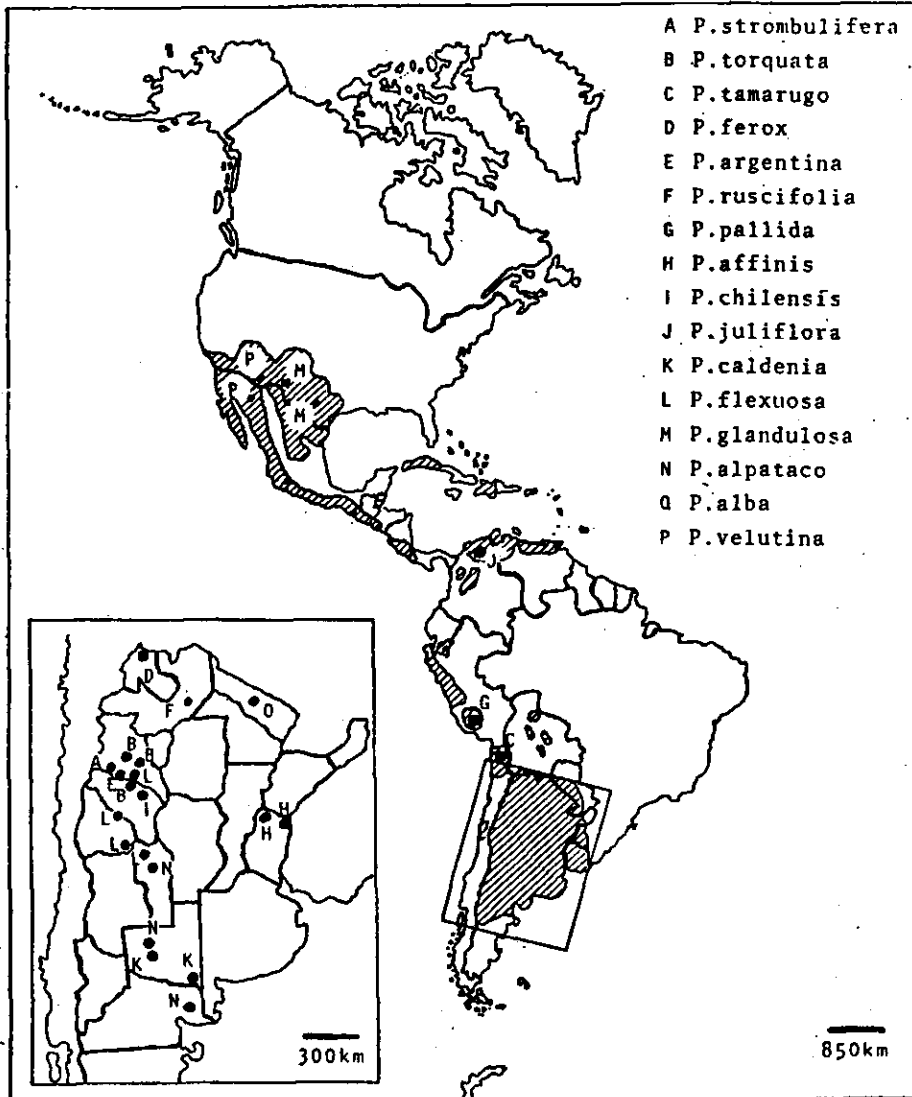
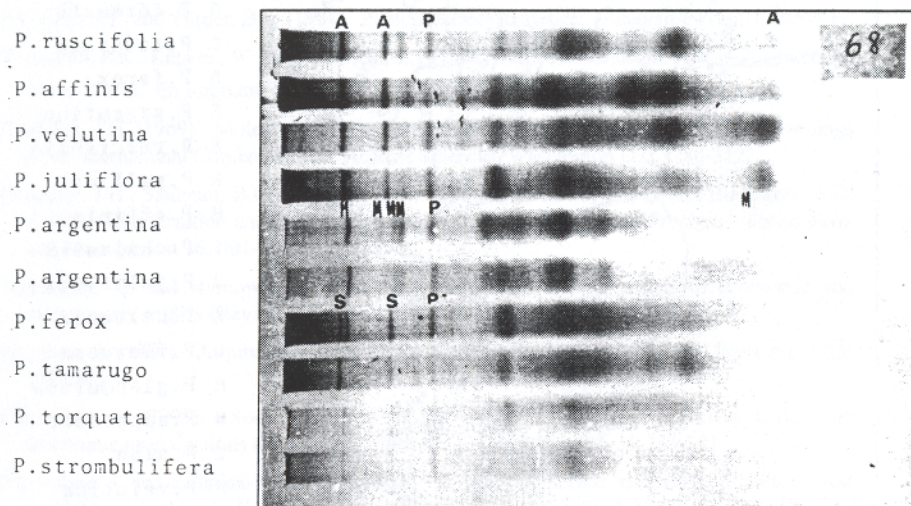


Figure 2: Polipeptidic patterns obtained by Coomassie Brilliant Blue (Sigma) of species belonging to three American sections of the genus *Prosopis*.



- A** characteristic bands of sect. Algarobia
- S** characteristic bands of sect. Strombocarpa
- M** characteristic bands of sect. Monilicarpa
- P** characteristic bands of genus *Prosopis*

Vertical lines join samples from the same section thus (from top to bottom): Algarobia, Monilicarpa and Strombocarpa.

Table 1. Taxonomic classification (*sensu* Burkart 1976) and common names of the *Prosopis* species analyzed.

Section	Series	Binomial	Common names
Strombocarpa	Strombocarpae	<i>P. strombulifera</i>	"retortuño", "mastuerzo"
		<i>P. torquata</i>	"tintinaco", "tusca"
	Cavenicarpae	<i>P. tamarugo</i>	"tamarugo"
		<i>P. ferox</i>	"churqui"
Monilicarpa		<i>P. argentina</i>	"algarrobilla"
Algarobia	Ruscifoliae	<i>P. ruscifolia</i>	"vinal"
	Pallidae	<i>P. pallida</i>	"huarango"
		<i>P. affinis</i>	"ñandubay"
	Chilenses	<i>P. chilensis</i>	"algarrobo de Chile"
		<i>P. juliflora</i>	"mesquite", "algarrobo"
		<i>P. caldenia</i>	"caldén"
		<i>P. flexuosa</i>	"algarrobo dulce"
		<i>P. glandulosa</i>	"honey mesquite"
		<i>P. alpataco</i>	"alpataco"
		<i>P. alba</i>	"algarrobo blanco"
<i>P. velutina</i>		"velvet mesquite"	

Table 2. Origin of the material analyzed in seed electrophoretic studies of the species of *Prosopis*. Collector abbreviations: Juan H. Hunziker (JHH), Carlos A. Naranjo (CAN), Ramón A. Palacios (RAP), Silvia Enus Zeiger (SEZ), Otto T. Solbrig (OTS) and Beryl B. Simpson (BS).

Species	Collector	Herbarium Number	Herbarium	Locality
<i>P. strombulifera</i> (Lam.) Bentham.	JHH	9563	BAFC	ARGENTINA: Prov. Catamarca, Dep. Tinogasta, Copacabana
<i>P. torquata</i> (Cavanilles ex Lagasca)	JHH	9571	BAFC	ARGENTINA: Prov. Catamarca, Dep. Belén, 34 km of Belén to Andalgalá
<i>P. torquata</i> (Cavanilles ex Lagasca)	JHH,CAN,RAP	9191	BAFC	ARGENTINA: Prov. Catamarca, Dep. Andalgalá, near Andalgalá
<i>P. torquata</i> (Cavanilles ex Lagasca)	JHH	III-1980	BAFC	ARGENTINA: Prov. La Rioja, Dep. Famatina, Famatina
<i>P. tamarugo</i> F. Philippi	C. Muñoz	XII-1966	SI	CHILE: Prov. Tarapacá, Pampa del Tamarugal
<i>P. tamarugo</i> F. Philippi	JHH	9839	BAFC	CHILE: Prov. Tarapacá, between Salar de Pintados and Quillagua
<i>P. ferox</i> Grisebach	C. y Bacigalupo	s/n°	SI	ARGENTINA: Prov. Jujuy, Dep. Humahuaca, Humahuaca
<i>P. argentina</i> Burkart	JHH	9564	BAFC	ARGENTINA: Prov. Catamarca, Dep. Tinogasta, 11 km S. of Copacabana
<i>P. ruscifolia</i> Grisebach	RAP	937	BAFC	ARGENTINA: Prov. Salta, Dep. Anta, Joaquín V. González
<i>P. pallida</i> (Humboldt & Bonpland ex Willd.) HBK	JHH	10008	BAFC	PERU. Majoro, 400 m of Hotel de la Borda, 4 km. of Nazca
<i>P. affinis</i> Sprengel	CAN	288	BAFC	ARGENTINA: Prov. Entre Ríos, Dep. La Paz, 10 km E of La Paz
<i>P. affinis</i> Sprengel	CAN	364	BAFC	ARGENTINA: Prov. Entre Ríos, Dep. La Paz, 10 km E of La Paz
<i>P. affinis</i> Sprengel	CAN	365	BAFC	ARGENTINA: Prov. Entre Ríos, Dep. La Paz, 10 km E of La Paz
<i>P. affinis</i> Sprengel	CAN	272	BAFC	ARGENTINA: Prov. Entre Ríos, Dep. Federación, 5 km N of Federación
<i>P. chilensis</i> (Molina) Stuntz emend Burkart	JHH	9737	BAFC	ARGENTINA: Prov. La Rioja, Dep. Famatina, Famatina
<i>P. juliflora</i> (Swartz) DC	JHH	10048	BAFC	COLOMBIA: Dep. Magdalena, Rodadero, 7 km of Santa Marta

Table 2 (cont.)

Species	Collector	Herbarium Number	Herbarium	Locality
<i>P. juliflora</i> (Swartz) DC	JHH	10046	BAFC	COLOMBIA: Dep. Magdalena, 20 km of Santa Marta
<i>P. caldenia</i> Burkart	JHH	9758	BAFC	ARGENTINA: Prov. La Pampa, Dep. Caleu Caleu, 55 km N of Rio Colorado
<i>P. caldenia</i> Burkart	SEZ	115	BAFC	ARGENTINA. Prov. La Pampa. Utracán. Chacharramendi to Limay Mahuida
<i>P. flexuosa</i> DC	JHH	9808	BAFC	ARGENTINA. Prov. San Juan. Dep. Valle Fértil. Between Los Baldecitos and Balde del Rosario
<i>P. flexuosa</i> DC	JHH,CAN,RAP	9199	BAFC	ARGENTINA. Prov. Catamarca. Dep. Andalgalá. Cuesta de la Chilca
<i>P. flexuosa</i> DC	JHH,CAN,RAP	9107	BAFC	ARGENTINA. Prov. San Juan. Dep. Caucete. Route 20.13 Km W of Marayes
<i>P. flexuosa</i> DC	JHH,CAN,RAP	9054	BAFC	ARGENTINA. Prov. San Luis. Dep. Pringles. Between Liborio Luna and Fraga
<i>P. glandulosa</i> Torrey	BS	2215/1	GH	U.S.A. New Mexico. Las Cruces. Luna Co.
<i>P. glandulosa</i> Torrey	BS	2216/1	GH	U.S.A. New Mexico. Las Cruces. Luna Co.
<i>P. glandulosa</i> Torrey	BS	2218/1	GH	U.S.A. Texas. Handspeth. Co. Mc. Nary
<i>P. glandulosa</i> Torrey	BS	2219/1	GH	U.S.A. Texas. Handspeth. Co. Mc. Nary
<i>P. alpataco</i> R.A. Philippi	JHH,CAN,RAP	8663	BAFC	ARGENTINA. Prov. Rio Negro. Dep. Conesa. 25 Km N of Gral. Conesa
<i>P. alpataco</i> R.A. Philippi	JHH,CAN,RAP	9053	BAFC	ARGENTINA. Prov. San Luis. Dep. Pringles. Between Liborio Luna and Pringles
<i>P. alpataco</i> R.A. Philippi	SEZ	108	BAFC	ARGENTINA. Prov. La Pampa. Dep. Utracán. Chacharramendi
<i>P. alba</i> Grisebach	OTS	4247	GH	ARGENTINA. Prov. Formosa. Dep. Patiffo. Bartolomé de las Casas
<i>P. velutina</i> Wootton	BS	2227/1	GH	U.S.A. Arizona Bune Co. Ajo way near Tucson
<i>P. velutina</i> Wootton	BS	2229/1	GH	U.S.A. Arizona Bune Co. Ajo way near Tucson
<i>P. velutina</i> Wootton	BS	2211/1	GH	MEXICO. Sonora. Km 557. Santa Ana

Table 3. Occurrence of seed protein fractions in 16 species of the genus *Prosopis* (+ = presence; - = absence; / = presence or absence).

Species	10									20												
	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2		
<i>P. ruscifolia</i>	-	+	/	-	/	-	-	-	+	-	-	/	-	-	-	-	+	-	-	-	/	-
<i>P. affinis</i>	-	/	/	-	-	-	-	-	+	-	-	/	-	-	-	-	+	-	-	-	-	-
<i>P. velutina</i>	-	/	/	-	-	-	-	-	+	-	-	-	/	/	-	-	+	-	-	-	-	-
<i>P. juliflora</i>	-	/	/	-	/	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>P. alba</i>	-	/	/	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>P. pallida</i>	/	/	/	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	/	-
<i>P. alpataco</i>	-	/	/	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	/	/	-
<i>P. flexuosa</i>	/	/	/	/	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	/	/	-
<i>P. caldenia</i>	-	/	/	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	/	+	-
<i>P. glandulosa</i>	-	/	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	/	-
<i>P. chilensis</i>	-	/	/	/	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	+
<i>P. argentina</i>	/	/	/	/	-	-	-	-	+	-	-	-	-	-	+	-	-	+	+	-	-	-
<i>P. ferox</i>	-	/	-	-	-	/	+	-	/	-	-	-	-	-	-	/	+	-	-	-	-	-
<i>P. tamarugo</i>	/	/	-	-	-	/	+	/	-	/	/	-	-	-	-	/	+	-	-	-	-	-
<i>P. torquata</i>	-	/	-	-	-	/	+	-	-	-	-	-	-	-	-	/	+	-	-	-	-	-
<i>P. strombulifera</i>	-	/	-	-	-	/	+	-	-	-	-	-	-	-	-	/	+	-	-	-	-	-

Species	30									40													
	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4			
<i>P. ruscifolia</i>	-	-	-	/	-	/	-	+	+	+	-	/	-	-	-	-	-	-	/	/	+		
<i>P. affinis</i>	-	-	+	-	-	-	-	+	/	-	/	+	-	-	-	-	-	-	-	/	+		
<i>P. velutina</i>	-	+	-	-	-	-	-	+	/	-	/	/	-	-	-	-	-	-	-	-	+	/	
<i>P. juliflora</i>	-	-	-	-	-	-	-	+	/	/	/	/	-	/	-	-	-	-	-	-	/	+	
<i>P. alba</i>	-	-	-	-	-	-	-	+	-	/	/	-	/	-	-	-	-	-	-	-	/	+	
<i>P. pallida</i>	-	-	/	-	-	/	-	+	/	/	/	+	-	-	-	/	-	-	-	-	+	+	
<i>P. alpataco</i>	-	-	-	/	-	-	-	+	/	-	/	/	-	-	-	-	-	-	-	-	+	+	
<i>P. flexuosa</i>	-	-	-	-	-	-	-	+	/	-	/	/	-	-	-	-	-	-	-	-	/	/	
<i>P. caldenia</i>	-	-	-	-	-	-	-	+	/	-	+	/	-	+	-	-	-	-	-	-	-	/	/
<i>P. glandulosa</i>	-	/	-	-	-	-	-	+	/	-	/	/	-	-	-	-	-	-	-	-	-	+	+
<i>P. chilensis</i>	-	-	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	+	+
<i>P. argentina</i>	-	-	-	-	-	-	-	+	/	/	-	-	-	-	-	-	+	/	-	-	-	-	
<i>P. ferox</i>	/	-	-	-	/	-	-	+	/	-	-	/	-	-	-	-	/	/	-	-	-	-	
<i>P. tamarugo</i>	-	-	-	-	/	-	/	+	-	/	-	+	-	-	-	-	+	/	-	-	-	-	
<i>P. torquata</i>	-	-	-	-	/	-	-	+	/	-	-	-	-	-	-	-	/	-	/	-	-	-	
<i>P. strombulifera</i>	/	-	-	-	/	-	/	+	/	-	-	+	-	-	/	-	/	-	/	-	-	-	

