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A PHYLOGENETIC ANALYSIS OF THE ARISTOLOCHIOIDEAE (ARISTOLOCHIACEAE)

By

FAVIO GONZALEZ

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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Abstract

A PHYLOGENETIC ANALYSIS OF THE SUBFAMILY ARISTOLOCHIOIDEAE (ARISTOLOCHIACEAE)

by

Favio González

Advisor: Dennis W. Stevenson, Ph.D.

A cladistic analysis of the subfamily Aristolochioideae (Aristolochiaceae) is presented, along with the results on studies on inflorescences and floral morphology and development, and pollen morphology in the subfamily. In chapter one, the history of the classification of the subfamily is reviewed. In chapter two, a comparative morphological study of the inflorescences throughout the family Aristolochiaceae is presented. In chapter three the studies on floral development and morphology are presented; these studies were foccussed on the perianth and the gynostemium, the two floral structures that have been crucial for the classification of the subfamily. The results support the interpretation of the perianth of *Aristolochia, Euglypha* and *Holostylis* as a trimerous calyx. Five main types of perianth development were found, which differ in the degree of fusion between the perianth lobes, the direction of the floral curvature, and the symmetry of the perianth limb. The results also show that carpellary tissue participates in the formation of the gynostemium. Complementary studies on floral morphology of the remaining members of the Aristolochiaceae, *Saruma*, *Asarum* and *Thottea*, are included. Chapter four deals with the results of a survey on pollen morphology, which was carried out in order to search for additional characters. In chapter five, a cladistic analysis based on morphological characters is presented. The analysis includes 65 taxa within the in-group, which represent all the tribes, subtribes, genera and infrageneric taxa formally described within the subfamily Aristolochioideae *sensu* Schmidt (1935). The analysis shows that *Aristolochia* s. l. is paraphyletic, and that *Euglypha* and *Holostylis* are not different lineages from *Aristolochia*. Two of the three subgenera traditionally recognized within *Aristolochia* are shown to be monophyletic. The third subgenus is paraphyletic. Taxa at lower rank levels (sections, subsections, series and subseries) are shown to be poly- or paraphyletic. The characters traditionally used for the recognition of these taxa are evaluated, and new characters are introduced. Finally, a new system of classification of the Aristolochioideae consisting of four genera and a number of lower rank taxa is proposed on the basis of the monophyletic groups obtained from the analysis.

To my son, my wife and my mother.

To the memory of my father.

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CHAPTER ONE

Systematics of the Aristolochiaceae

I. Introduction

The family Aristolochiaceae consists of ca. 500 species, 75% of which inhabit the tropics and subtropics of both hemispheres. The plants are aromatic (containing ethereal oils and benzilisoquinolic alkaloids) with alternate, distichous, usually palmately veined leaves, and adaxial prophylls; the flowers are essentially trimerous, with one or two perianth series, 5-46 stamens, and 4-6 carpels (Figs. 1, 2) generally forming a syncarpous, inferior ovary; the fruits are generally capsular. The family is included in the pharmacopeia of numerous cultures worldwide. Its medicinal values are considered to be abortifacient, antiinflamatory, antiophidic, hypotensive and hypotonic, and more recently, antitumoral and antimicrobial properties have been reported (Chen & Zhu, 1987). The ecology of the Aristolochiaceae has been studied with respect to its relationships with butterflies of the family Papilionidae in both the New and Old World. The butterflies lay their eggs on plants of Aristolochiaceae and the larvae feed exclusively upon these plants (see e.g. Weintraub, 1995). The sparse fossil records of the family date back to the early Tertiary and perhaps the late

Figure 1. Floral diagrams of members of the Aristolochiaceae. A. *Saruma henryi*, black circles, first initiated stamens; hatched crescent, petals. B. *Asarum caudatum*, black circles, first initiated (i.e. innermost, longest) stamens; hatched crescent, vestigial structures in petal position. C. *Thottea siliquosa*, hatched crescent, vestigial structures in petal position. D. *Aristolochia acutifolia*; the floral diagrams of *Euglypha rojasiana* and *Holostylis reniformis* are similar to this species.

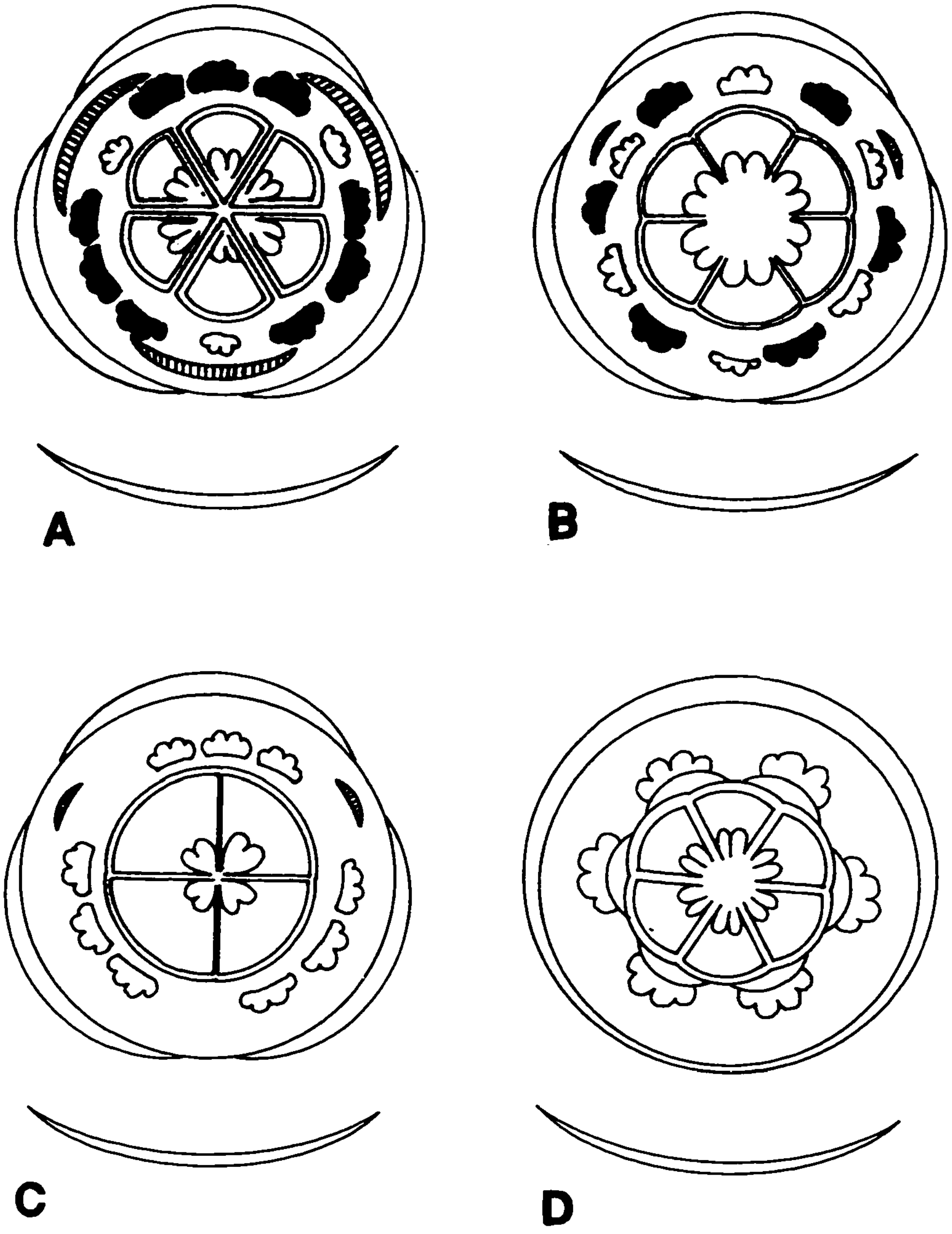
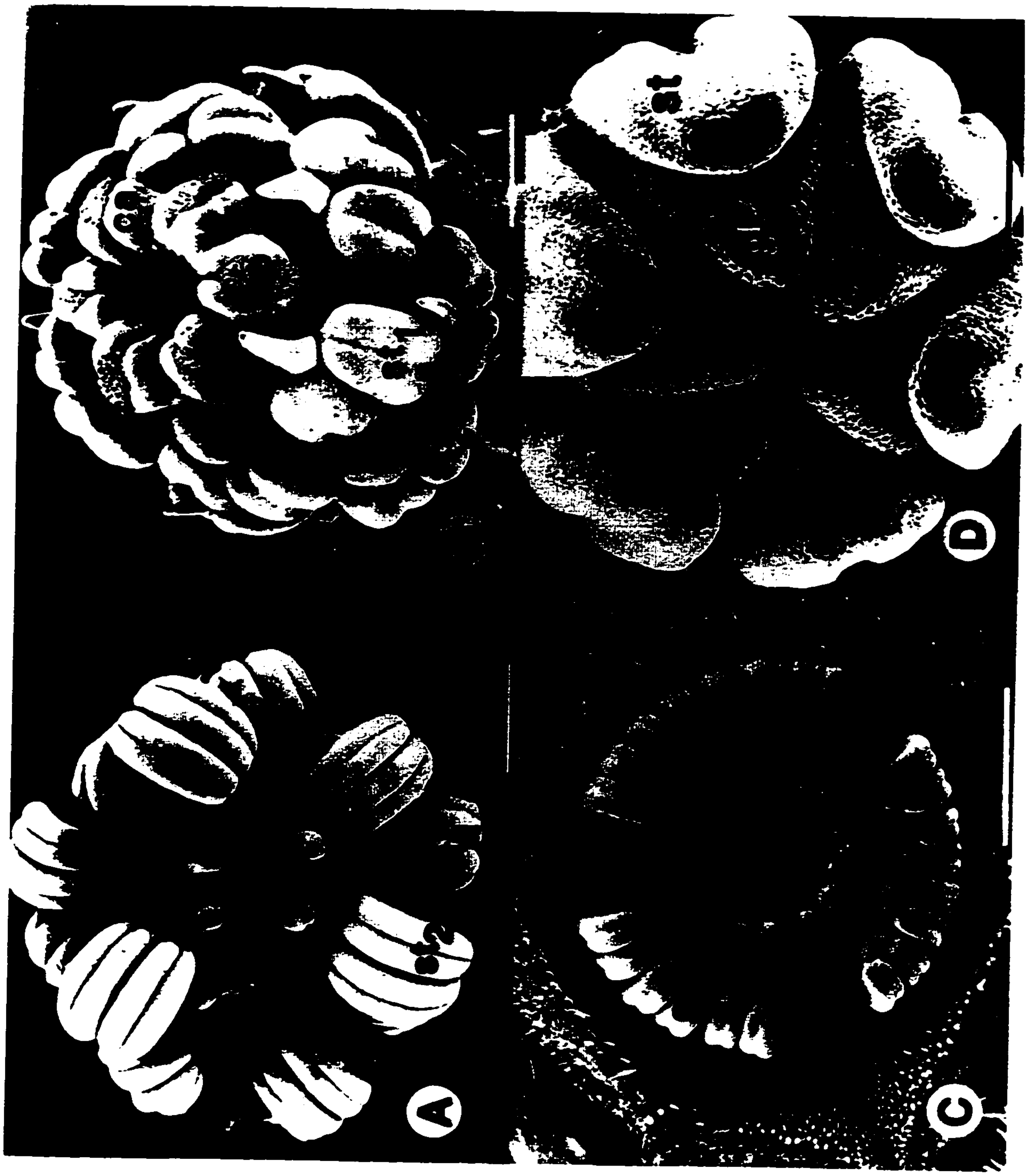

A
B
C
D

Figure 2. A. Flower of *Saruma henryi* (*Pruski 3748*), two whorls of six alternating stamens are present, the outer stamens (st_2) are alternate with the six free carpels; sepals, petals and one stamen removed. Bar = 1 mm. B. Flower of *Asarum canadense* (*González 3420*), two whorls of six alternate stamens are present, the inner stamens (st_1) are the first to be initiated and alternate with the six partially fused carpels; sepals removed. Bar = 0.5 mm. C. Flower of *Thottea siliquosa* (*Bot. Gard. Univ. Bonn,* acc. 0937), stamens are arranged in three groups of 3-4 each, around the 'secondary organs' (arrowheads); the open tips of the four carpels are seen towards the center; sepals removed. Bar = 0.5 mm. D. *Aristolochia pilosa* (*González 3571*), gynostemium from above, stamens are opposite the six gynostemium lobes. Bar = 0.1 mm. *ca*, carpels, *gl*, gynostemium lobe; *sp*, stigmatic papillae; *st*, stamen.


A
C
D
st

Cretaceous of India (Kulkarni & Patil, 1977), Europe (Kolakovski, 1957, 1964) and North America (MacGinitie, 1953, 1969, 1974).

Although generic circumscription in the family is currently in dispute, the majority of the classical and recent taxonomic treatments of the family recognize six genera in two subfamilies; the Asaroideae (*Asarum*, *Saruma* and *Thottea)*, with actinomorphic flowers (Fig. 1A-C), and the Aristolochiodeae (*Aristolochia*, *Euglypha*, and *Holostylis)* with a monosymmetric perianth (Fig. 1D). The Asaroideae, restricted to the Northern Hemisphere, consist of about 130 herbaceous species; *Asarum*, with ca. 100 species, is distributed in temperate areas of North America, Europe, and Asia; the monotypic *Saruma* is endemic from central China; and *Thottea*, with ca. 30 species, is restricted to tropical Asia. The Aristolochioideae, with a much wider distribution, are primarily climbing plants, but there are also herbs, treelets and shrubs. *Aristolochia*, with ca. 350 species, is principally tropical, but some species reach subtropical and temperate areas of both hemispheres. *Euglypha* and *Holostylis* are monotypic genera, both endemic to South America.

The taxonomic position of the Aristolochiaceae has changed drastically over the years, and still remains controversial. Currently, there are three competing hypotheses about their closest relatives. Aristolochiaceae has been variously allied with each of the following taxa:

1. Members of the order Magnoliales, especially Annonaceae, Myristicaceae and Canellaceae (Cronquist, 1981; Dahlgren, 1983; Leins & Erbar, 1995; Takhtajan, 1996; Thorne, 1992). This hypothesis is based on

the presence in Aristolochiaceae, as in many families of the order Magnoliales, of the general condition of P-type sieve-element plastids (Behnke, 1971), ethereal oil cells, aporphine alkaloids, and several carpels that are apocarpous and pluriovulate. Additional embryological (see Cocucci, 1983), karyological (Morawetz, 1985) and ultrastructural (Hennig & al. 1994) evidence has been presented.

2. The Rafflesiales (Baillon, 1888; Baldacci, 1894; Bartling, 1830; Brown, 1821; Delpino, 1893; Duchartre, 1877; Endress, 1990b, 1994; Hutchinson, 1969; Kubitzki, 1993; Solereder, 1889b). This hypothesis has been proposed on the basis of similarities in floral structure, particularly the presence of a simple, fleshy, sapromyophilous perianth, with connate pieces and a ring-like structure at the perianth entrance, the extrorse anthers, the fusion of the stamens and the style/stigma into a gynostemium, the ring-like, uninterrupted stigmas, and the inferior, pluriovulate ovary.

3. The so-called paleoherbs, especially the Piperales (Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Tucker & Douglas, 1996; Nandi et al. 1998). Among the paleoherbs, two sister-group relationships have been proposed for the Aristolochiaceae. One possibility is the piperalean Lactoridaceae, a relationship already anticipated by Dahlgren and Bremer (1985), and supported by wood anatomy (Carlquist, 1993), and molecular data (Qiu et al. 1993; Soltis et al. 1997); however, Lactoridaceae strongly differ in morphological, embryological, karyological and palynological characters (Lammers & al. 1986, Loconte & Stevenson, 1991; Sampson, 1995; Tobe et al. 1993; Tucker & Douglas, 1996). On the other hand, Stevenson and Loconte (1995) proposed that the Aristolochiaceae are the sister group of the whole monocot lineage,

since they share adaxial prophylls, trimerous flowers, monosulcate or inaperturate pollen, and sieve-element plastids of the specific type PIIc. Since Jussieu's (1789) placement of the Aristolochiaceae as the closest dicot member to the monocots, this relationship has been repeatedly emphasized over time (Bartling, 1830; Behnke, 1988, 1991; Blume, 1827; Dahlgren & Clifford, 1982; Erbar & Leins, 1994; Huber, 1977, 1985; Leins & Erbar, 1985; Lindley, 1853; Suessenguth, 1921; among others).

Most of the recent molecular studies are more or less concordant with the latter hypothesis, although some of them call into question the monophyly of the family, by separating *Saruma* and *Aristolochia* into two distinct clades (see e.g. Bharathan & Zimmer 1995). The relationship of Aristolochiaceae with Lactoridaceae results from the analysis of both rbcL (Qiu et al. 1993) and 18S ribosomal DNA sequence data (Soltis et al. 1997). In contrast, Bharathan and Zimmer (1995) have proposed a sister-group relationship between Aristolochiaceae and the monocots, also using 18S ribosomal DNA sequences. When molecular and morphological data are combined (Chase et al. 1995; Nandi et al. 1998), the analysis generates three possible sister groups for the Aristolochiaceae: the Lactoridaceae, the monocots, or the Nymphaeales-Piperales clade.

The most consistent synapomorphies of the family Aristolochiaceae are in the anatomy of the seed coat: cells of the inner layer of the outer integument have crystals, and the outer and inner layers of the inner integument are parallel to the seed axis, whereas the middle layer is transversely oriented, thus forming cross fibres (Corner, 1976; Huber, 1985, 1993; Kratzer, 1918; Mohana Rao, 1989; Periasamy, 1966). These traits are reported here for the first time in *Saruma*. Besides the aforementioned characters, the following assemblage of uniquely combined morphological characters suggests that *Aristolochia, Asarum, Euglypha, Holostylis, Saruma,* and *Thottea* form a monophyletic group: Alternate, distichous leaves with reticulate, palmate venation; adaxial prophylls; ethereal oil cells; perianth essentially trimerous; androecium and gynoecium essentially hexamerous; and pollen in monosulcate or inaperturate monads.

II. Systematics of the Aristolochiaceae

The family Aristolochiaceae was established by Jussieu (1789) as the only member of his Class "Dicotyledones Apetalae. Stamina epigyna". Jussieu's concept of the family included *Aristolochia, Asarum* and *Cytinus,* genera that had been kept separate in the Linnean system. The placement of *Aristolochia* and *Asarum* as close relatives, however, was proposed for the first time by Adanson (1763). Robert Brown (1821) added the genus *Thottea,* originally described by Rottboell (1783) as a member of his group " Contortae" . The inclusion of *Cytinus* in the Aristolochiaceae was questioned by Brown (1821), and Lindley (1832), who transferred that genus to the Rafflesiaceae. At the same time, Lindley (1832) assigned *Trichopus* to the Aristolochiaceae; however, Klotzsch (1859) presented evidence in favor of a closer relationship of *Trichopus* to the Dioscoreaceae. By the middle of the 19th century, the core of the family, comprised of three appearently diverse genera (and some of their segregates), *Aristolochia, Asarum,* and *Thottea,* was established. Since then, three more genera, all monotypic, have been added to the family, *Holostylis* Duchartre (1854a, b), *Saruma* Oliv. (1889), and *Euglypha* Chodat and Hassler (1906).

Six systems of classification have been proposed at the infrafamilial level based primarily on floral and fruit morphology and habit:

1. Klotzsch (1859) divided the family into two main groups (Fig. 3B; Table I): the Cleistostigmata (*Asarum* and *Thottea)*, with free anthers (Figs. 1B, C, 2B, C), a solid style, and discoidal or radiate stigmas which are closed at the middle; and the Aristolochieae (*Aristolochia*), with anthers fused to the hollow styles and stigmas (Figs. 1D, 2D).

2. Duchartre (1864) divided the family into three groups (Fig. 3A; Table I), the Asareae (*Asarum*), the Bragantieae (*Thottea*), and the Aristolochieae (*Aristolochia* and *Holostylis*). This system was followed by Solereder (1889b), Engler (1912), Hoehne (1927), and Gregory (1956; Fig. 3F).

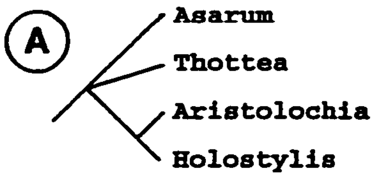
3. Baldacci (1894) proposed two major groups, one that keeps apart *Thottea*, and the other that connects *Aristolochia*, *Asarum* and *Holostylis* (Fig. 3C; Table I). The latter group was proposed because of the shape of the perianth of *Holostylis*, which seems intermediate between that of *Asarum* and *Aristolochia*.

4. Schmidt (1935) formally proposed the subfamilies Asaroideae and Aristolochioideae based strictly on perianth symmetry. The Asaroideae included the members with actinomorphic flowers (*Asarum*, *Saruma*, and *Thottea*); and the Aristolochioideae included the members with a monosymmetric perianth (*Aristolochia*, *Euglypha* and *Holostylis*). This

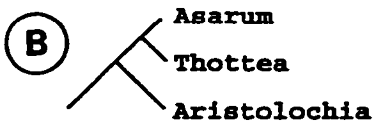
Table I. Comparison of five different classification systems of the Aristolochiaceae.

Authority	Subfamily (or equivalent)	Tribe (or equivalent)	Subtribe	Genus
Klotzsch, 1859	Cleistostigmata	Asarineae		*Asarum* *Heterotropa*
		Bragantieae		*Bragantia* *Thottea*
		Cyclodiscineae		*Cyclodiscus*
	Aristolochieae			*Aristolochia* *Endodeca* *Einomeia* *Howardia* *Siphisia*
Duchartre, 1864	Asareae			*Asarum* *Saruma*
	Bragantieae			*Bragantia* *Thottea*
	Aristolochieae			*Aristolochia* *Holostylis*
Baldacci, 1894	unnamed			*Aristolochia* *Asarum* *Holostylis*
	unnamed			*Bragantia* *Lobbia* *Thottea*
Schmidt, 1935	Asaroideae	Sarumeae		*Saruma*
		Asareae		*Asarum*
		Bragantieae		*Apama* *Thottea*
	Aristolochiodeae	Aristolochieae		*Aristolochia* *Holostylis*
		Euglypheae		*Euglypha*
Nakai, 1936				*Apama* *Aristolochia* *Bragantia* *Cyclodiscus* *Euglypha* *Hocquartia* *Holostylis* *Pararistolochia* *Thottea*
Huber, 1993	Asaroideae			*Asarum* *Saruma*
	Aristolochioideae	Bragantieae		*Asiphonia* *Thottea*
		Aristolochieae	Isotremantinae	*Endodeca* *Isotrema*
			Aristolochiinae	*Aristolochia* *Einomeia* *Euglypha* *Holostylis* "*Howardia*" *Pararistolochia*

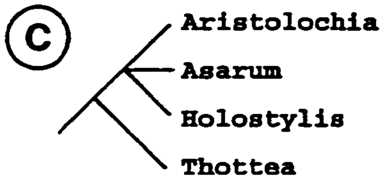
Figure 3. A-G. Implicit generic relationships in seven different systems of classification of the Aristolochiaceae. H. Published cladogram of the Aristolochiaceae by Weintraub (1995), redrawn.



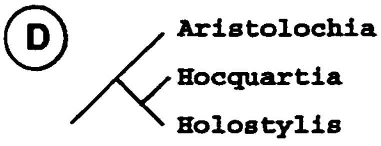
DUCHARTRE (1864)



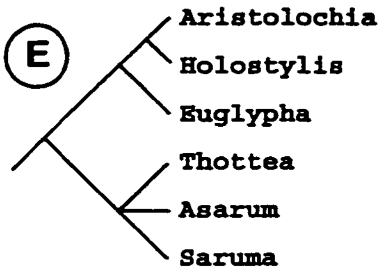
KLOTZSCH (1859)



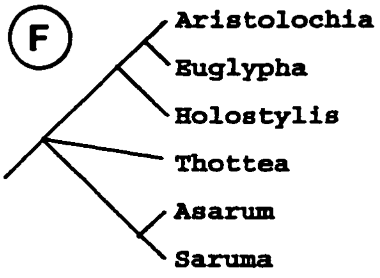
BALDACCI (1894)



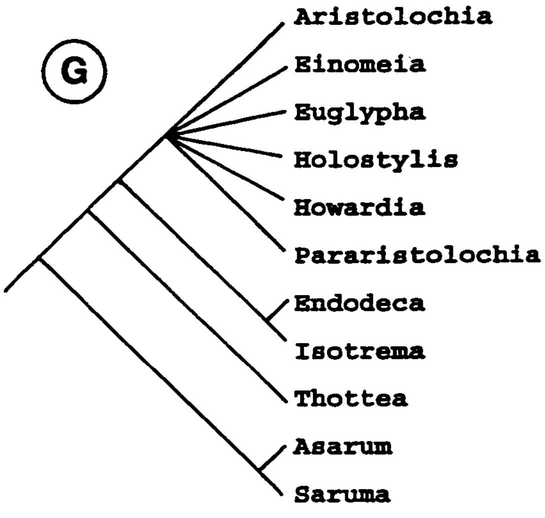
VAN TIEGHEM (1900)



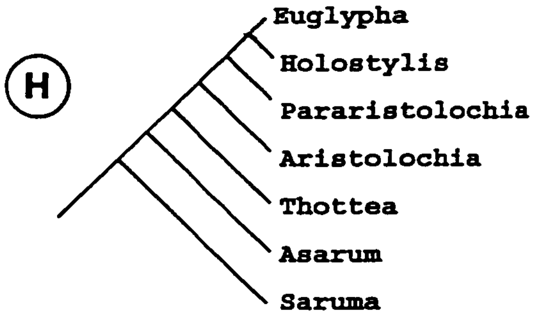
SCHMIDT (1935)



GREGORY (1956)



HUBER (1985, 1993)



WEINTRAUB (1995)

system (Fig. 3E; Table I), essentially similar to that proposed by Klotzsch (1859), has been adopted by Cheng and Yang (1988), Hoehne (1942), Hwang (1988), and Ma (1990).

5. Nakai (1936) placed *Aristolochia* and *Thottea*, and their segregates, along with *Euglypha* and *Holostylis* in the family Aristolochiaceae (Table I), and raised *Asarum* and *Saruma* to the family level, the Asaraceae and the Sarumataceae, respectively.

6. Huber (1985, 1993) recognized the two subfamilies proposed by Schmidt (1935) but transferred *Thottea* to the Aristolochioideae (Fig. 3G; Table I), because it shares with *Aristolochia*, *Euglypha*, and *Holostylis* the presence of hooked hairs, epigynous flowers, a constriction between perianth and ovary, a perianth shedding after anthesis, stamens frequently 6, and fruits usually dehiscent. This system was followed by Takhtajan (1996) and Thorne (1992).

Saruma was originally described as closely related to *Asarum* (Oliver, 1889), and most of the recent literature follows this placement (see e.g. Cheng & Yang, 1988; Dickison, 1992; Leins & Erbar, 1995). However, Loconte and Stevenson (1991) favor the placement of *Saruma* into its own family, the Sarumaceae. The cladistic analyses by Loconte and Stevenson (1991) and Weintraub (1995; Fig. 3H) do not support the monophyly of the subfamily Asaroideae either sensu Schmidt (1935) or sensu Huber (1985, 1993). Unfortunately, Weintraub (1995) did not explicitly mention any of the morphological or caryological data used. Furthermore, the parameters of the cladistic analysis were ommitted, thus preventing further testing of the analysis.

III. The subfamily Aristolochioideae

The subfamily Aristolochioideae (equivalent to the tribe Aristolochiineae sensu Huber, 1985, 1993) was formally proposed by Schmidt (1935) following Klotzsch (1859). It consists of the genera *Aristolochia, Euglypha* and *Holostylis*. The subfamily is well supported by the following set of synapomorphies (González, 1997): monosymmetric, tubular perianth differentiated into utricle, tube and limb (Fig. 4); stamens 6, uniseriate (Figs. 1D, 2D); and the formation of the so-called gynostemium (Figs. 1D, 2D, 4, 5).

With about 380 species, the Aristolochioideae is the most diverse subfamily. Most species grow in tropical rain forests, gallery forests, savannas, or dry forests. The perianth exhibits a remarkable variation in shape (1-6-lobed) and size (from 2 cm long in *Aristolochia nummularifolia*, to 1.5 m long in *A. grandiflora*). The number of anthers ranges from 5 to 24, whereas the number of carpels is 5 or 6. Within the Aristolochioideae, the large and complex genus *Aristolochia* stands in contrast with the monotypic *Euglypha* originally described by Chodat and Hassler (1906), and *Holostylis*, first described by Duchartre (1854a). *Euglypha* and *Holostylis* have been recognized by various authors since then (see e.g. Ahumada, 1967; Hoehne, 1927, 1942; Huber, 1993; Malme, 1904; Masters, 1875a; Schmidt, 1935; Solereder, 1889a, b; Wyatt, 1955a). However, the taxonomic placement of these two endemic genera from central South America has been controversial (Fig. 3; Table I). Van Tieghem (1900) proposed a closer relationship between *Holostylis* and the segregate *Hocquartia* (i.e. the species of *Aristolochia* with a 3-lobed

Figure 4. Schematic representation of a flower of *Aristolochia acutifolia* and corresponding transverse sections. Arrows indicate the middle vein of the perianth, which extends directly from the pedicel.

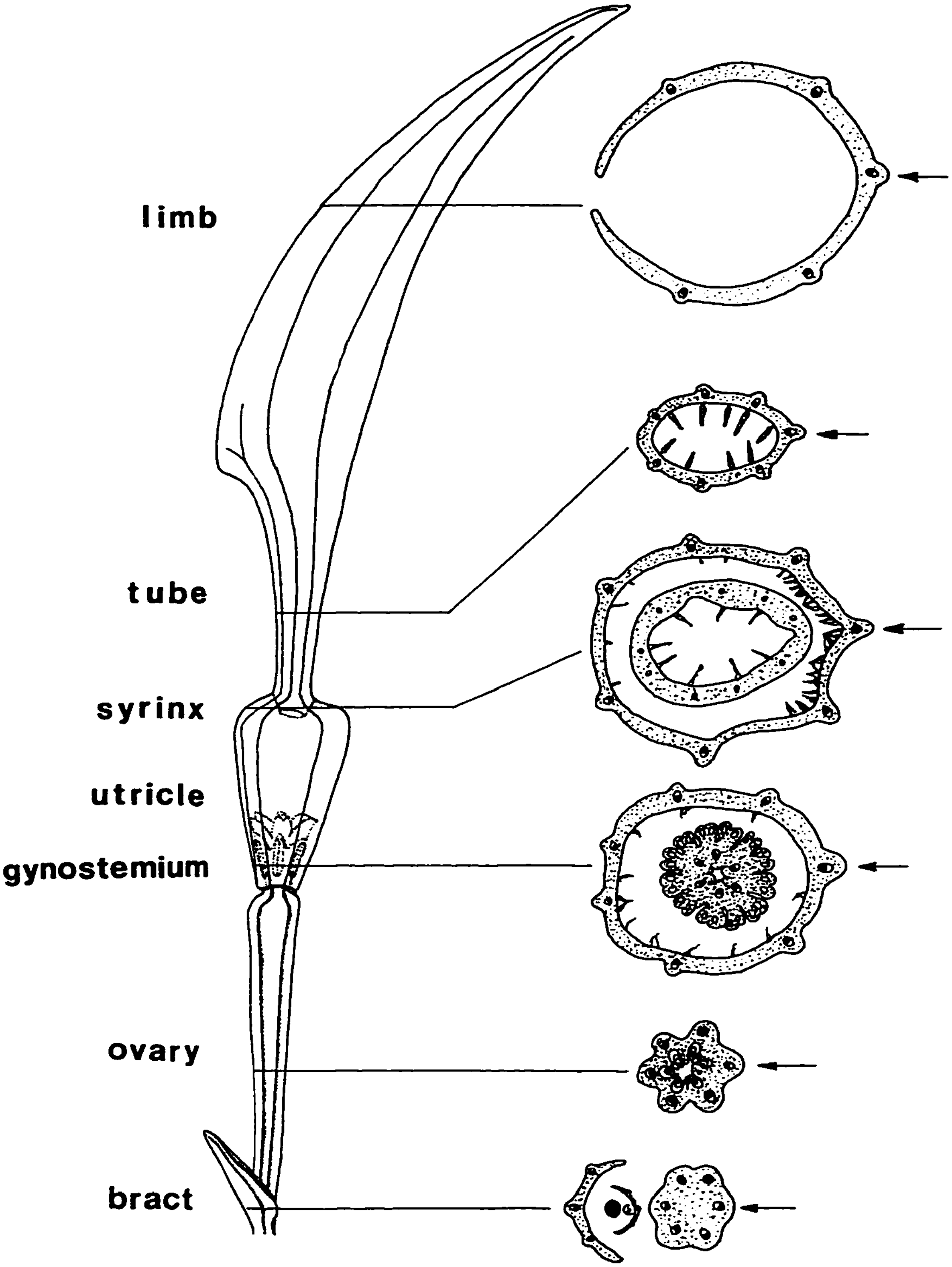

limb
tube
syrinx
utricle
gynostemium
ovary
bract

Figure 5. Gynostemia in *Aristolochia*. A. *A. stevensii* (*González 3416*), a member of subgenus *Siphisia*. Bar = 0.5 mm. B. *A. promissa* (*Bot. Gard. Univ. Bonn, acc. 13014*), a member of subgenus *Pararistolochia*. Bar = 0.1 mm. C. *A. erecta* (*González 3593*), a member of subgenus *Orthoaristolochia* section *Gymnolobus*; arrow indicates stigmatic papillae. Bar = 0.5 mm. D. *A. zollingeriana* (*Tsou 1175*), a member of subgenus *Orthoaristolochia* section *Diplolobus*; arrow indicates stigmatic papillae. Bar = 0.1 mm. *gl*, gynostemium lobe; *st*, stamen.


st
st
st
A
C
D

gynostemium) than with the other species of *Aristolochia* (Fig. 3D). Schmidt (1935) considered *Aristolochia* and *Holostylis* as closely related (Fig. 3E), and placed *Euglypha* in its own tribe, whereas Gregory (1956) proposed a closer relationship between *Aristolochia* and *Euglypha* (Fig. 3F). Weintraub (1995) proposed a sister-group relationship between *Euglypha* and *Holostylis* (Fig. 3H). Huber (1985, 1993) mentioned neither more precise relationships of these two monotypic genera with one another nor with *Aristolochia* and its segregates *Einomeia*, *Howardia* and *Pararistolochia* (Fig. 3G; Table I).

IV. The genus *Aristolochia*

Despite the fact that the majority of monographers treat *Aristolochia* in its broad sense (Davis & Khan 1961; Duchartre, 1854a, 1864; Hoehne, 1927, 1942; Hou, 1984; Ma, 1989; Nardi, 1984, 1991; Pfeifer, 1966, 1970; Phuphathanaphong 1985, 1987), several generic segregates have been proposed since the beginning of the 19th century (Tables II, III).

Dumortier (1822) segregated the species with a 3-lobed gynostemium into the genus *Hocquartia*. Rafinesque (1828, 1836) segregated as many as 12 genera, primarily on the basis of the perianth morphology; for example, *Glossula* included species with unilabiate and ligular flowers, such as *Aristolochia rotunda*; *Pistolochia* included species with " bilabiate" flowers, such as *A. bilabiata* and *A. ringens*; and *Siphisia* included species with flowers not labiate, with the limb " equal trilobe" , such as *A. sipho* and *A. tomentosa*. On the other hand, Klotzsch (1854) divided *Aristolochia* into five genera, using perianth and gynostemium morphology (Tables II, III).

Table II. Segregate genera from *Aristolochia* sensu lato.

Dumortier, 1822	**Rafinesque, 1828, 1836**	**Klotzsch, 1859**	**Hutchinson & Dalziel, 1927; Poncy, 1978; Parsons, 1996**	**Huber, 1985, 1993**
Aristolochia *Hocquartia*	*Ambuya* *Aristolochia* *Dasyphonion* *Dictyanthes* *Diglosselis* *Einomeia* *Endodeca* *Hexaplectris* *Isiphia* *Isotrema* *Pistolochia* *Plagistra* *Psophiza* *Pteriphis* *Siphisia* *Tropexa*	*Aristolochia* *Einomeia* *Endodeca* *Howardia* *Siphisia*	*Aristolochia* *Pararistolochia*	*Aristolochia* *Einomeia* *Endodeca* *Howardia* *Isotrema* *Pararistolochia*

Table III. Systems of classification of *Aristolochia* by Duchartre (1854, 1864), Bentham and Hooker (1880), and Schmidt (1935), and the corresponding segregates (capital letters) by Klotzsch (1859).

DUCHARTRE, 1854, 1864	**KLOTZSCH, 1859**	**BENTHAM & HOOKER, 1880**	**SCHMIDT, 1935**
ARISTOLOCHIA		**ARISTOLOCHIA**	**ARISTOLOCHIA**
Group I		Sect. *Siphisia*	Subgen. *Siphisia*
Sect. *Asterolytes*	**ENDODECA**		Sect. *Asterolytes*
Sect. *Siphisia*	**SIPHISIA**		Sect. *Siphisia*
Sect. *Hexodon*			Sect. *Hexodon*
Group II		Sect. *Gymnolobus*	Subgen. *Orthoaristolochia*
Sect. *Gymnolobus*			Sect. *Gymnolobus*
Subsect. *Pentandrae*	**EINOMEIA**		Subsect. *Pentandrae*
Subsect. *Hexandrae*	**HOWARDIA**		Subsect. *Hexandrae*
Ser. *Unilabiatae*			Ser. Unilabiatae
Ser. *Bilabiatae*			Ser. Ecaudata
Ser. *Peltiflorae*			Ser. *Alatae*
			Ser. *Bilabiatae*
			Ser. *Peltiflorae*
Sect. *Diplolobus*	**ARISTOLOCHIA**	Sect. *Diplolobus*	Sect. *Diplolobus*
Subsect. " Calyx sessile"	*Euaristolochia*		Subsect. *Euaristolochia*
Subsect. " Calyx stipitate"	*Podanthemum*		Subsect. *Podanthemum*
Sect. *Acerostylis*			
		Sect. *Polyanthera*	Subgen. *Pararistolochia*

Later, Bentham & Hooker (1880) divided the genus *Aristolochia* into four sections, including the new section *Polyanthera* (Table III). The latter section, which included most of the West african species, was raised to a generic level, *Pararistolochia*, by Hutchinson & Dalziel (1927).

Huber (1960, 1985, 1993) reestablished some of the segregates by Rafinesque (1836), Klotzsch (1859), and Hutchinson and Dalziel (1927) in splitting *Aristolochia* into six genera (Tables I, II). First, Huber (1960) supported the segregation of the genera *Endodeca*, *Isotrema*, and *Pararistolochia*, by using characters of the anatomy of the leaves, morphology of the gynostemium, inner surface of the flower, morphology of the fruit and the seeds, and to some extent, chromosome numbers. Later, Huber (1985) presented additional data on seed anatomy and morphology, that supported the recognition of two tribes (Table I), the Isotremantinae, with the genera *Endodeca* and *Isotrema*, and the Aristolochiinae, with the genera *Aristolochia* s. str., *Einomeia*, *Euglypha*, *Holostylis*, " *Howardia*" , and *Pararistolochia*. However, the detailed observations on seed anatomy presented by Huber (1985), did not provide clear evidence for the recognition of relationships within the segregates, nor unique features for the segregates. This is obvious in his recent treatment of the Aristolochiaceae (Huber, 1993), in which the segregates are retained, but are defined mostly on the basis on floral morphology. Moreover, no further hypothesis on the relationships between the six members of the Aristolochiinae is presented there.

The three subgenera of *Aristolochia* sensu lato, *Orthoaristolochia*, *Pararistolochia*, and *Siphisia*, were formally proposed by Schmidt (1935; Table III), based on the perianth morphology and the number of gynostemium lobes. The subgenus *Siphisia*, with a 3-lobed perianth and 3-lobed gynostemium (Fig. 5A), is essentially Group I in the system proposed by Duchartre (1854a, b, 1864). The subgenus *Pararistolochia*, with a 3-lobed perianth, and 6-12-lobed gynostemium (Fig. 5B), was based on the genus proposed by Hutchinson and Dalziel (1927). The subgenus *Orthoaristolochia*, with a 1-2-lobed perianth and 5-6-lobed gynostemium (Fig. 5C,D), equals group II of Duchartre (1854a, b, 1864).

Most of the taxa within each subgenus were first described by Duchartre (1854a, b; Tables III, IV). Klotzsch (1859) independently proposed a classification which is essentially the same as that proposed by Duchartre (1854a, b), but Klotzsch recognized most of the groups as distinct genera (Table III). Duchartre (1864), rather than use Klotzsch's generic segregates, kept his previous system intact. Duchartre's system has been the most widely used system since then, having undergone practically no substantial changes (see e.g. Ahumada, 1979; Bentham & Hooker, 1880; Hoehne, 1942; Masters, 1875a; Schmidt, 1927, 1930, 1932, 1935, 1938; Wyatt, 1955a).

The characters that define sections, subsections, series and subseries are based mainly on the morphology of the perianth and the gynostemium. For example, Duchartre (1854a, 1864) divided his 'Group II' (equivalent to subgenus *Orthoaristolochia*) into 2 sectional level taxa, *Gymnolobus*, in which the gynostemium lobes lack a ring-like structure (Fig. 5C), and *Diplolobus*, in which the gynostemium displays a ring-like structure on top of the stamens (Fig. 5D) that is formed by stigmatic papillae. Two further groups were recognized within the section *Gymnolobus*: *Pentandrae* (5 stamens and 5 carpels; Fig. 5C); and *Hexandrae* (6 stamens and 6 carpels; Figs. 2D, 4). Subsection *Hexandrae* in turn was further

Table IV. Summary of the infrageneric systems of classification of *Aristolochia* sensu lato. Taxonomic levels were not specified by Hoehne (1942).

Authority	Subgenus	Section	Subsection	Series	Subseries
Duchartre, 1854a, 1864; Schmidt, 1935; Ma, 1989, 1992	Siphisia	Asterolytes Siphisia Hexodon Pentodon Odontosiphisia Leptosiphisia Nepenthesia Obliquosiphisia			
	Orthoaristolochia	Gymnolobus	Hexandrae	Unilabiatae	Adenoracus Ancyclanthemum Stenanthemum Schismotus Macrotelus Cyphomanthemum Pedinochilus Cercanthemum Brachychilus
				Alatae Bilabiatae Peltiflorae unnamed group	
			Pentandrae		
		Diplolobus			
	Pararistolochia	Pararistolochioides Pararistolochia Aristolochioides			

Table IV. Continued.

Authority	Subgenus	Section	Subsection	Series	Subseries
Masters, 1875a		Peltiflorae	'Flores racemose' 'Flores solitarii vel gemini'		
		Unilabiatae	Caudatae Ecaudatae		
		Bilabiatae	'Perianthii labia subequilonga' Perianthii labium superior longisimum'		
Hoehne, 1942			Pseudostipulosae	Peltiflorae	Macranthae Mediocriflorae Parviflorae
				Bilabiatae	Parviflorae Macranthae Caudatae Alatae
				Caudatae	Trilobatae Integrifolia
			Exstipulosae	Volubilis	Subpeltiflorae Euunilabiatae Hiantiflorae Alatilobae Ciliatilobae
				Fruticulosae	

divided into species with a unilobed (*Unilabiatae*), bilobed (*Bilabiatae*), or 'peltate' (*Peltiflorae*) perianth (Table III).

Additional taxa based on the perianth morphology (e.g. *Alatae* or *Obliquosiphisia*), have been added by other authors such as Schmidt (1935; Table III) or Ma (1989; Table IV). Schmidt (1935) also used the indument of the inner surface of the perianth limb as an additional criterion for classification.

Hoehne (1942; Table IV) in his " ordem natural das espécies sul-americanas... baseada nos orgãos vegetativos e morfologia externa das inflorescências e flores" used the presence or absence of the so-called pseudostipules (Duchartre, 1854c) as the primary criterion of classification. In his system, Hoehne (1942) recommended abandoning Duchartre's scheme of classification because it " não representa um sistema de afinidades baseado nos orgãos em geral" . However, Hoehne's secondary set of characters is also strongly based on the shape and the size of the perianth.

González (1990, 1991) suggested that the perianth shape has been over-emphasized in the recognition of infrageneric taxa, resulting in a single character taxonomy. Instead, he has surveyed comparative morphological data from various parts of the plant to reevaluate the systematics of *Aristolochia* subsect. *Hexandrae*, and to propose an alternative classification for this taxon. As a result, some diagnostic characters, such as the presence of abscission zones on the petiole and peduncle, the architecture of inflorescences, and the morphology of fruits and seeds, were utilized in the recognition of species groups in the Neotropics.

After this brief introduction to the family Aristolochiaceae and the subfamily Aristolochioideae sensu Schmidt (1935), the following chapters present the morphological and systematic studies carried out on the members of this subfamily. In chapter two, I present a comparative survey of the inflorescence morphology of the Aristolochiaceae, in order to understand the type of growth forms within the family, the architecture of the flowering branches, and the relative position of the flowers. In chapter three, developmental and anatomical studies of flowers of *Aristolochia* are presented, in order to contribute to the discussion about structural homologies of the perianth and the so-called gynostemium, traditionally the most crucial structures for the classification of the subfamily. In chapter four the results of a survey on pollen morphology are presented. This study was carried out in order to search for additional characters to be used in the cladistic analysis of the Aristolochioideae. In chapter five a cladistic analysis of the tribes, subtribes, genera and infrageneric taxa formally described within the subfamily Aristolochioideae is presented, characters traditionally used for subfamilial classification are evaluated, and new characters are introduced; finally, a revised system of classification of the subfamily Aristolochioideae, based on the cladistic analysis, is proposed.

CHAPTER TWO

Inflorescence morphology

I. Introduction

Inflorescence morphology of the Aristolochiaceae has not been well studied, and its utility in classification has been overlooked. Although Bravais and Bravais (1837), Wydler (1857), Eichler (1878), Velenovsky (1905), Sandt (1925), and Troll (1969) included observations on inflorescences of some species of *Aristolochia* and *Asarum*, it was Weisse (1927) who presented a more comprehensive analysis of the inflorescence morphology of the family.

The inflorescences of Aristolochiaceae have been described in the taxonomic literature as 'fascicles', 'racemes', 'bundles', 'aggregates', or more often as consisting of 'axillary, solitary flowers' (e.g., Schmidt, 1935; Hoehne, 1942; Pfeifer, 1966, 1970; Poncy, 1978; Hou, 1984; Nardi, 1984; Parsons, 1996). In addition, Masters (1875a) and Hoehne (1942) used inflorescence characters to key out several groups of neotropical species, such as " flores racemose dispositi" , " flores solitarii vel gemini" , " flores cymoso-racemosi" , " ramuliflorae" or " axilliflorae" . Because of the ambiguity of these terms, and the absence of a thorough comparative framework, they have limited value in indicating relationships, and in suggesting homologies.

More recent studies of the neotropical members of *Aristolochia* have shown that inflorescence morphology is useful at an infrageneric level. González (1990, 1991) rearranged the taxa within *A.* subsect. *Hexandrae* by correlating of morphological characters of leaves, inflorescences, fruits, and seeds. Inflorescences were described as polytelic, being either thyrsic (in *A.* ser. *Thyrsicae*), or racemose (in *A.* ser. *Hexandrae*). Furthermore, two kinds of racemose inflorescences were described: those with leafy, elongated racemes located on the ultimate shoots, and those with extremely reduced, cauliflorous racemes.

In this chapter the results on the morphological studies of the inflorescences throughout the Aristolochiaceae are presented. In chapter five, the evolution of these characters is discussed along with the phylogenetic analysis of the subfamily Aristolochioideae.

II. Materials and methods

Living specimens and/or fixed material of *Saruma henryi*, *Thottea siliquosa*, four species of *Asarum*, and 55 species of *Aristolochia* were studied. The taxonomic scheme followed here is presented in Table VII. The studied species of *Aristolochia* represent a wide range of morphological variation within the three subgenera. Paraffin-embedded serial sections and SEM preparations were made by conventional methods. Data for additional species were taken from herbarium material.

The morphological terminology follows Troll (1964, 1969) as summarized in Weberling (1989). The partial florescence, defined by Weberling (1989) as a " cymosely branched element of a florescence," is taken as the comparative unit within the subfamily Aristolochioideae. In the Aristolochiaceae, a partial florescence (hereafter called PF) usually consists of a rhipidium or a helicoid cyme. The term prophyll is here used to refer to the first vegetative organ of a vegetative lateral shoot or a PF.

III. Results

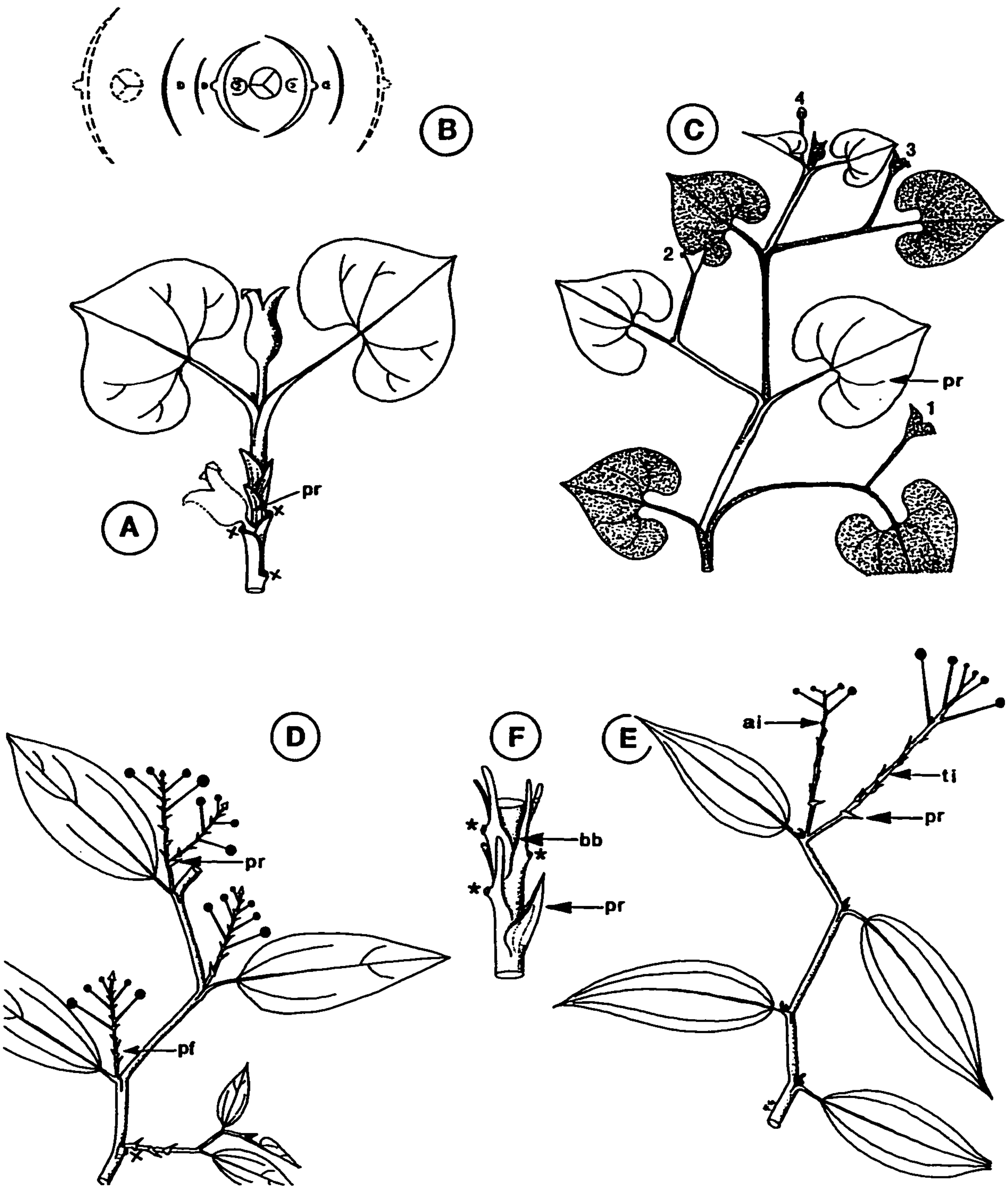
The Aristolochiaceae have distichous phyllotaxis. Prophylls on both vegetative shoots (Arber, 1925; Duchartre, 1854c) and PFs are adaxial. The prophyll of the PF may be empty (Figs. 6A, E, 8A, B, 9A, C), may be a bract directly subtending a flower (Figs. 8D-F, 9D, 10B, 11C), or may contain an axillary bud that develops into a lateral branch (Fig. 6C, D). The bracts within the PF also follow a distichous pattern, with minor variations. Furthermore, each bract is opposite to the median perianth part, which is the first to be formed (Figs. 10A-C, 14-17, 19, 24A, C, 48, 49, 50E, 51A, C; see also Payer, 1857; Leins & Erbar, 1995; Tucker & Douglas, 1996).

Subfamily Asaroideae

Saruma

Saruma is a herbaceous, erect plant that grows sympodially (see also

Figure 6. A, B. *Asarum canadense* (*González 3577*), drawing and corresponding diagram of a sympodial growth unit; dashed lines indicate the leaves and the flower of the previous growth season; solid lines in B are scale leaves. C. *Saruma henryi* (*Jiang & Jao 379*), drawing of five sympodial growth units, each ending in a flower; numbers indicate the order of flower development. D. *Thottea siliquosa* (*Sohmer & Waas 10338*), shoot with three partial florescences, the upper-most secondarily branched. E, F. *T. corymbosa* (*Boeea 5942*). E. Shoot with terminal and one accessory inflorescence. F. Detail of the inflorescence axis, showing the prophyll and three bilobed bracts on the sides of the peduncle scars. *ai*, accessory inflorescence; *bb*, bilobed bract; *pf*, partial florescence; *pr*, prophyll of the partial florescence; *ti*, terminal inflorescence; *x*, leaf scar; *, flower scar.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Wagner, 1907). Each sympodial growth unit consists of two leaves and a terminal flower (Fig. 6C), and in contrast to *Asarum* (see below), it lacks scale-leaves. Inflorescences in *Saruma* (Fig. 6C) are monotelic because each growth unit terminates in a flower. In some of the specimens examined, a vestigial axillary bud is present between the flower and the ultimate leaf.

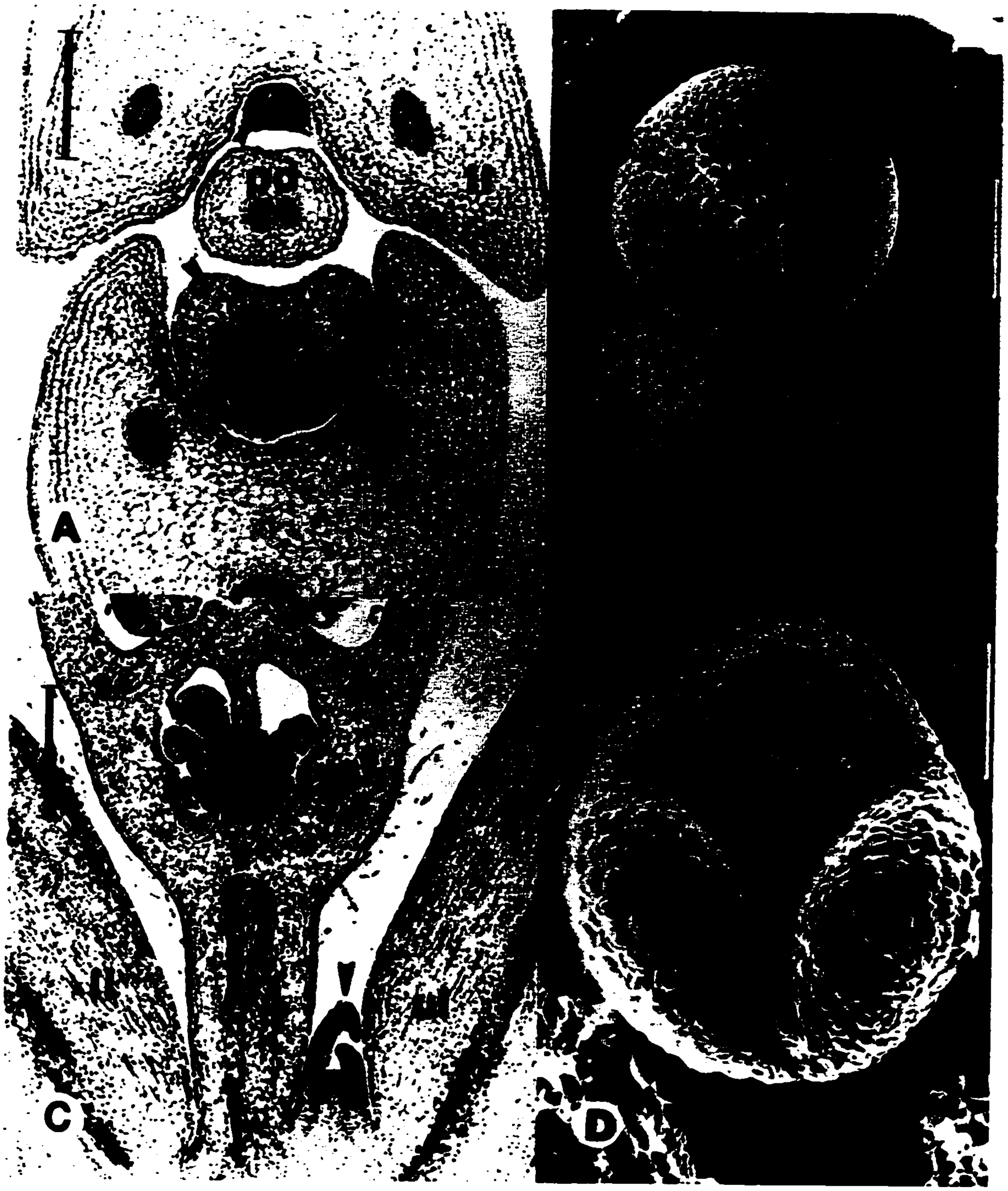
Asarum

Plants of *Asarum* are creeping herbs with sympodial growth. Each sympodial growth unit has 2-4 scale-leaves at the lower part, followed by 1-3 foliage leaves, and terminates in a flower (Figs. 6A, B, 7A-C). Therefore, inflorescences in *Asarum* (Figs. 6A, B, 7A-C) are monotelic. The axillary bud from the ultimate leaf usually develops (Figs. 6A, B, 7A); whereas, the axillary buds of the other leaf (or leaves) and the scale-leaves remain dormant and develop in subsequent seasons or are lacking. Prophylls of each axillary bud are adaxial, and the upper-most leaf and the median (first) sepal are distichous, as is characteristic of Aristolochiaceae (Fig. 7A-C).

Thottea

Plants of *Thottea* are uniaxial or slightly branched shrubs or subshrubs, usually with monopodial growth units. Inflorescences of *Thottea* are poorly known. Several species have been described as having flowers that are opposed to the bracts (Hou, 1984), which suggests that the PFs are cymose. *T. siliquosa* definitely develops cymes (Figs. 6D, 7D, 11A).

Figure 7. A. *Asarum canadense* (*González 3577*), transverse section showing the floral peduncle between two leaves and their corresponding axillary buds; arrowheads indicate the prophyll of each axillary bud. Bar = 500 µm. B. *Asarum canadense (González 3577)*, floral bud (top) and a vegetative bud (bottom). Bar = 100 µm. C. *Asarum europaeum* (*González 3419*), longitudinal section showing the terminal flower and the upper-most axillary bud (arrow). Bar = 500 µm. D. *Thottea siliquosa* (*Bot. Gard. Univ. Bonn, acc. # 09037*), floral bud at the time of initiation of perianth lobes; bract (bottom) has been removed. Bar = 50 µm. *ll*, lower-most leaf; *pd*, floral peduncle; *pl*, lateral perianth lobe; *pm*, median perianth lobe; *ul*, upper-most leaf.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D

In the other species this condition is not clear and the flowering shoots, which are usually cauliflorous, seem to be racemose.

Inflorescences of several species of *Thottea* have dimorphic bracts: the basal-most bract (i.e. the PF prophyll; *pr* in Fig. 6E, F) is entire, whereas the upper-most bracts, which subtend the flowers, are bilobed (*bb* in Fig. 6F). The axillary bud of the PF prophyll may develop into accessory flowering branches (Fig. 6D). Within the Aristolochiaceae, bilobed bracts are known to occur only in *Thottea*; all other taxa have entire bracts.

Interestingly, *Thottea corymbosa* does not exhibit cauliflory; conversely, several to many flowers are found along the distal portion of each branch (Fig. 6E). The flower-bearing portion has shortened internodes and extremely reduced vegetative elements. In addition, one or two accessory inflorescences (*ai* in Fig. 6E) commonly develop between the terminal inflorescence and the ultimate foliage leaf. This is the only known species in the Aristolochiaceae in which the terminal portion of the main axis is transformed (leaves and internodes are reduced) and specialized in the production of flowers (anthoblasts sensu Mora-Osejo, 1987).

Subfamily Aristolochiodeae

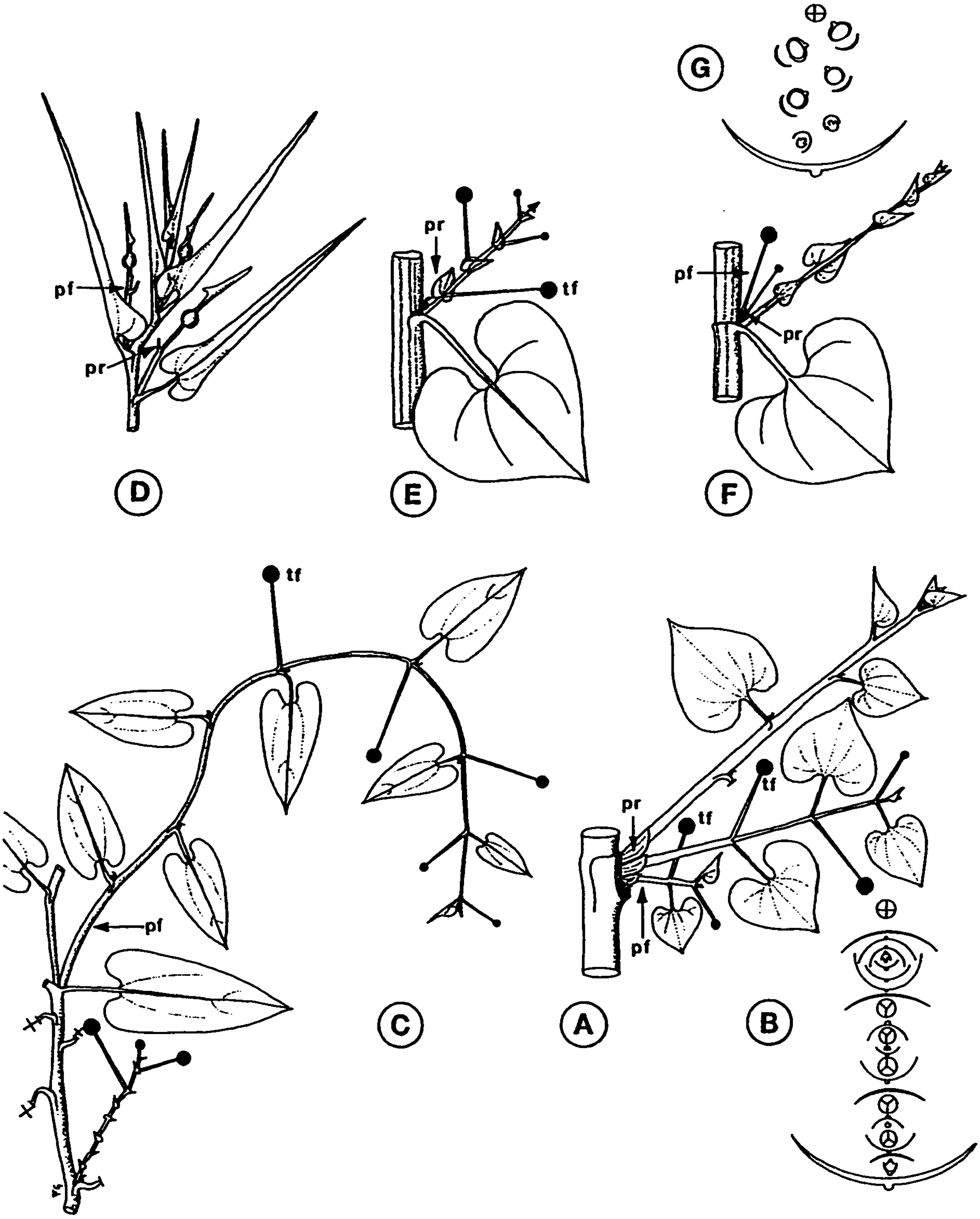
Inflorescences in the Aristolochioideae are mostly polytelic and thyrsic, because they have indeterminate main axes, with cymose PFs. The PFs are monochasial, usually rhipidia. When the PF is uniflorous and lacks a prophyll (the so-called non-bracteate, solitary flowers), a racemose type is formed (González, 1990, 1991).

Unlike *Asarum* and *Saruma*, where each growth unit has both vegetative and flowering functions (Fig. 6A-C), polytelic growth in the Aristolochioideae is associated with a separation of these functions into different axillary shoots (Figs. 8A, F, 9A, B). Vegetative renewal occurs from distinct axillary buds, and PFs seldom (e.g. *A. tomentosa*, Fig. 8A, B) develop expanded bracts that are similar to the leaves. In *Aristolochia* and *Euglypha* each flower or PF in an axil is usually located between the renewal shoot and the leaf (Figs. 9A, 10D, 21A).

Aristolochia* subgenus *Siphisia

This subgenus consists of ca. 50 species distributed in North and Central America, and temperate and tropical Asia. They are mostly climbing, highly branched plants. Temperate species of the subgenus (e.g. *A. californica, A. macrophylla, A. manshuriensis*, and *A. tomentosa*) have a single longitudinal row of axillary buds (Figs. 8A, B, 9A, 68A) that develop more or less simultaneously but differentially: the upper-most bud(s) develop into vegetative, long shoots, and the lower-most into PFs (Figs. 8A, B, 9A). Prophylls of both kinds of axillary buds are oblong, small, caducous, sessile, and more or less parallel-veined scale-leaves (cataphylls). Moreover, they differ in shape from the foliage leaves or the bracts. There is at least one bract always present, which may (e.g. in *A. tomentosa*, Fig. 8A, B), or may not (e.g. in *A. macrophylla*, Fig. 9A; see also Bravais & Bravais,

Figure 8. A, B. *Aristolochia tomentosa* (*Eggers* s.n.). A. Drawing of a leaf axil showing the upper vegetative shoot and the two lower buds that have developed into partial florescences. B. Corresponding diagram; solid lines indicate scale leaves. C. *A. deltantha* (*Smith 11566*), scheme showing one reduced (bottom) and one elongated (top) partial florescence. D. *A. thozetti* (*Clarkson* et al. *6725*), drawing showing one uniflorous partial florescence on each node. E. *A. albida* (*Chase 3651*), scheme of a partial florescence (rhipidium). F, G. *A. clematitis* (*Mullins* s.n.). F. Drawing of two uniflorous PFs; the lower-most bud has developed into a vegetative shoot. G. Diagram showing 4 adaxial uniflorous PFs, and 2 abaxial vegetative buds, arranged in 2 rows; bracts, solid lines. *pf*, partial florescence; *pr*, prophyll of the partial florescence; *tf*, terminal flower of a partial florescence.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1837; Wydler, 1857; Eichler, 1878; Sandt, 1925) have an axillary bud. As a result of the variable number of axillary buds within each PF, the number of flowers per PF varies from one, as in *A. macrophylla* (Fig. 9A) and *A. manshuriensis*, to several, as in *A. tomentosa* (Fig. 8A, B).

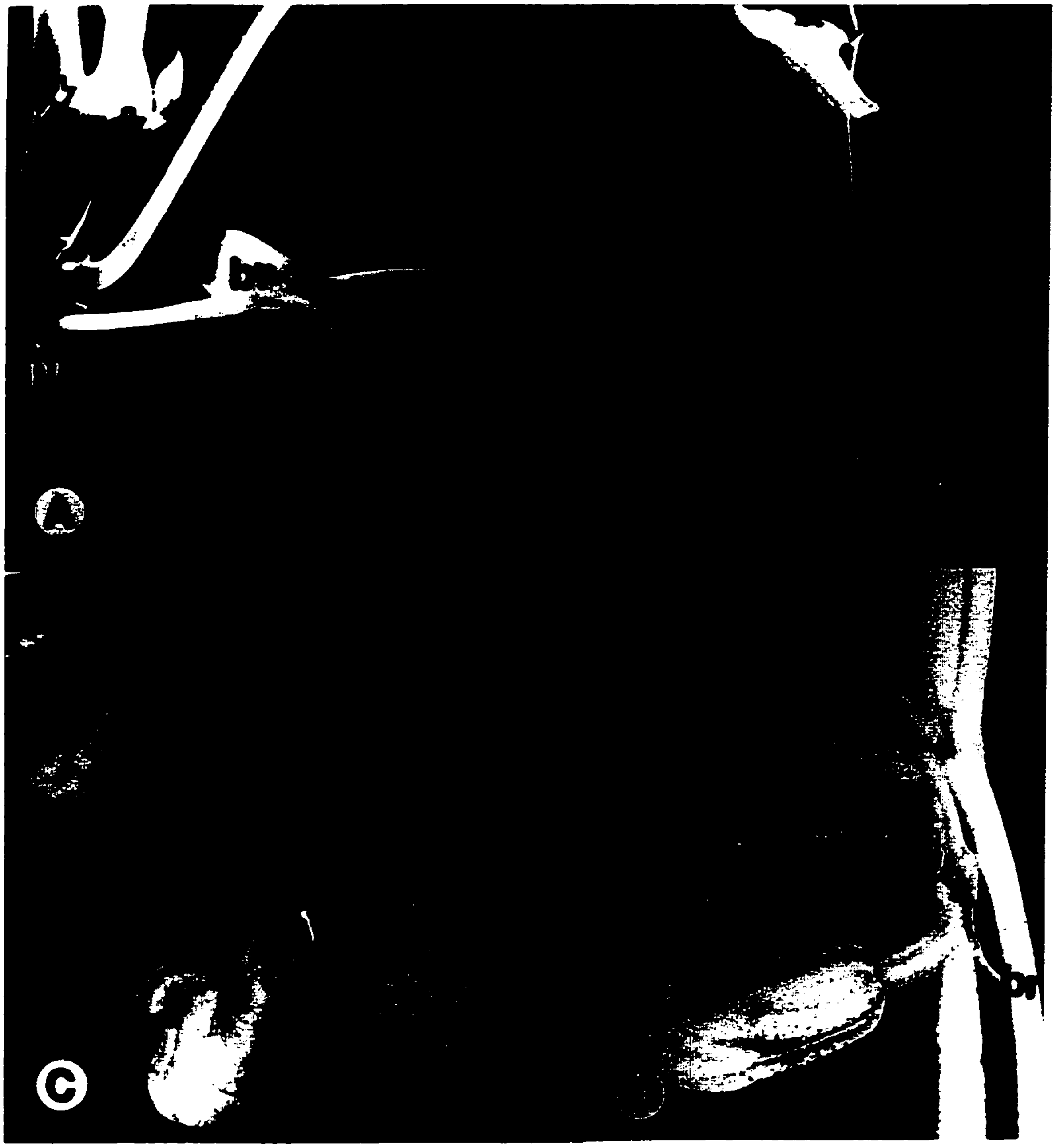
In the herbaceous North American *Aristolochia reticulata* and *A. serpentaria*, the upper nodes are entirely vegetative, and their axillary buds seldom grow out. PFs develop only from achlorophyllous, specialized branches that grow near the ground (Fig. 9B). While flowers of *A. reticulata* are subtended only by the prophyll (Fig. 14B, C), *in A. serpentaria* an additional, empty bract is formed between the prophyll and the flower (Fig. 11B).

In the tropical and subtropical species of *Aristolochia* subgenus *Siphisia*, the growth of vegetative and flowering axillary buds is not usually simultaneous (e. g. *A. panamensis*, and *A. tricaudata*). In some cases the PF develops very late, and is ramiflorous or cauliflorous (as e.g. in *A. stevensii*, Fig. 9C) and may be extremely branched (as e.g. in *A. arborea*). The prophyll of the PF is usually very small, does not subtend a flower (Fig. 9C), and its axillary buds are vestigial or lacking. The bracts are similar to the prophylls and are relatively small in comparison to those of temperate species.

Aristolochia subgenus *Pararistolochia*

Aristolochia subgenus *Pararistolochia* consists of ca. 10 African species, and about 23 species from Australia and New Guinea. The

Figure 9. A. *Aristolochia macrophylla* (*González 3578*), node with two upper vegetative buds (arrowheads), and a lower bud developed into a uniflorous partial florescence. B. A. *reticulata* (*González 3594*), several achlorophyllous flowering branches (arrow) have developed at the base of a single, leafy main axis. C. A. *stevensii* (*González 3416*), a cauliflorous partial florescence, with a reduced prophyll (arrowhead). D. A. *micrantha* (*González 3605*), uniflorous partial florescence. *br*, bract; *pr*, prophyll or prophyll scar.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inflorescence morphology is essentially different in these two geographically disjunct groups of species.

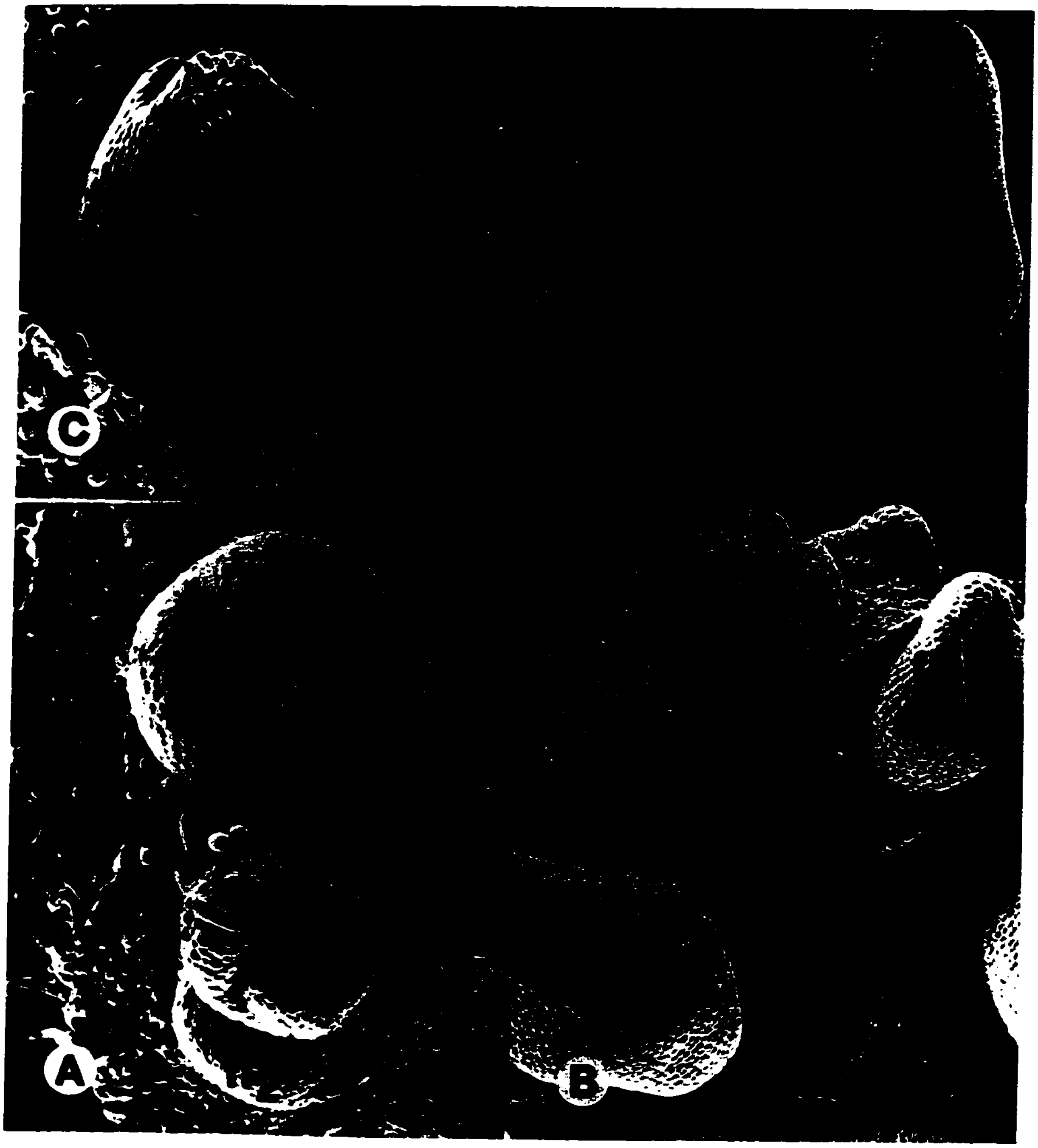
The African species and the Malesian A. *decandra* are characterized by the presence of cauliflorous inflorescences with reduced bracts. These inflorescences have been described in the literature as uniparous, helicoid (Poncy, 1978) or paniculiform cymes (Hou, 1984). My observations confirm that they are cymes, and that at least the PFs of A. *promissa* are helicoid cymes (Fig. 10A). They occur in the axils of old or fallen leaves; no development of PFs in the axils of the young leaves has been reported. As is frequent in other members of the Aristolochiaceae, the prophyll of the PF does not subtend a flower, but contains an axillary bud that sometimes grows out. The length of the PF internodes varies from 1-2 mm in A. *macrocarpa* up to 8 cm (or more) in A. *decandra* and A *goldieana*.

The species of *Aristolochia* subgenus *Pararistolochia* found in Australia and New Guinea exhibit a peculiar kind of inflorescence. Long, foliose shoots start growing as indeterminate shoots, but after developing a series of sterile nodes, the apical meristem produces a terminal flower. The growth becomes sympodial with a rhipidium being formed (Fig. 8C). Frequently both long, frondose, and short, bracteate flowering shoots are present on the same individual (Fig. 8C).

Aristolochia subgenus *Orthoaristolochia*

The subgenus *Orthoaristolochia*, widely distributed in both eastern and western hemispheres, includes about 330 species. The subgenus has been

Figure 10. A. *Aristolochia promissa* (*Bot. Gard. Univ. Bonn, acc. # 13014*), developing partial florescence (helicoid cyme); numbers indicate order of development of flowers and their corresponding bracts. B. *A. clematitis* (*Mullins* s.n.), apex of a flowering shoot showing the lateral arrangement of the partial florescences on each node; each PF is formed by a flower and its corresponding prophyll. C. A. *grandiflora* (*González 3443*), a floral bud subtended by a peltate prophyll. D. *A. nummularifolia* (*González 1258*), apex of a flowering shoot showing the development of a single, non-bracteate flower per node; the small buds on the adaxial side of each flower are vegetative buds. *br*, bract; *fl*, flower or floral bud.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traditionally divided into two sections. *Aristolochia* section *Diplolobus* consists of ca. 120 species, from Europe, N and E Africa, Asia, and N Australia. *Aristolochia* sect. *Gymnolobus* consists of ca. 210 species from the New World.

The majority of the species of *Aristolochia* sect. *Diplolobus* have PFs that are cymes. The cymes are usually rhipidia (as in e.g. *A. albida*, Fig. 8E) or helicoid cymes (as in e.g. *A. zollingeriana*), but can also be reduced to one, bracteate flower (as in e. g. *A. pistolochia*, Fig. 40C, and *A. thozetii*, Fig. 8D). Species having cymes with several to many flowers are mostly restricted to the tropics. Some of these species have large, round bracts, and 10 flowers or more per cyme (e.g., *A. albida*, Fig. 8E, and *A. jackii*); others have small, ovate bracts (as in e.g. *A. acuminata*, *A. indica*, *A. petersiana and A. zollingeriana*).

Within *Aristolochia* sect. *Diplolobus*, species of subsection *Euaristolochia* are usually described as having solitary, axillary flowers, implying the absence of a bract. However, some species, such as *A. clematitis* (Fig. 10B) and A. *pistolochia* (Fig. 40C) have bracteate flowers. In most of these species, the bract is usually reduced and located near the leaf axil, because the internode between the bract and the axil does not elongate (Fig. 10B). The axillary buds in species of A. subsect. *Euaristolochia* can be arranged either uniserially or biserially. In the latter, the prophyll is more or less lateral and located at the base of the pedicel; this is clearly visible in A. *clematitis* (Figs. 8F, G), as well as in A. *altissima*, A. *baetica*, A. *pistolochia* (Fig. 40C; see also Velenovsky, 1905), and A. *sempervirens*. In A. *clematitis* the lower-most buds on each axil become the renewal shoots (Figs. 8F, G, 10B; see also Bravais & Bravais, 1837; Wydler, 1857; Eichler, 1878; Goebel, 1905).

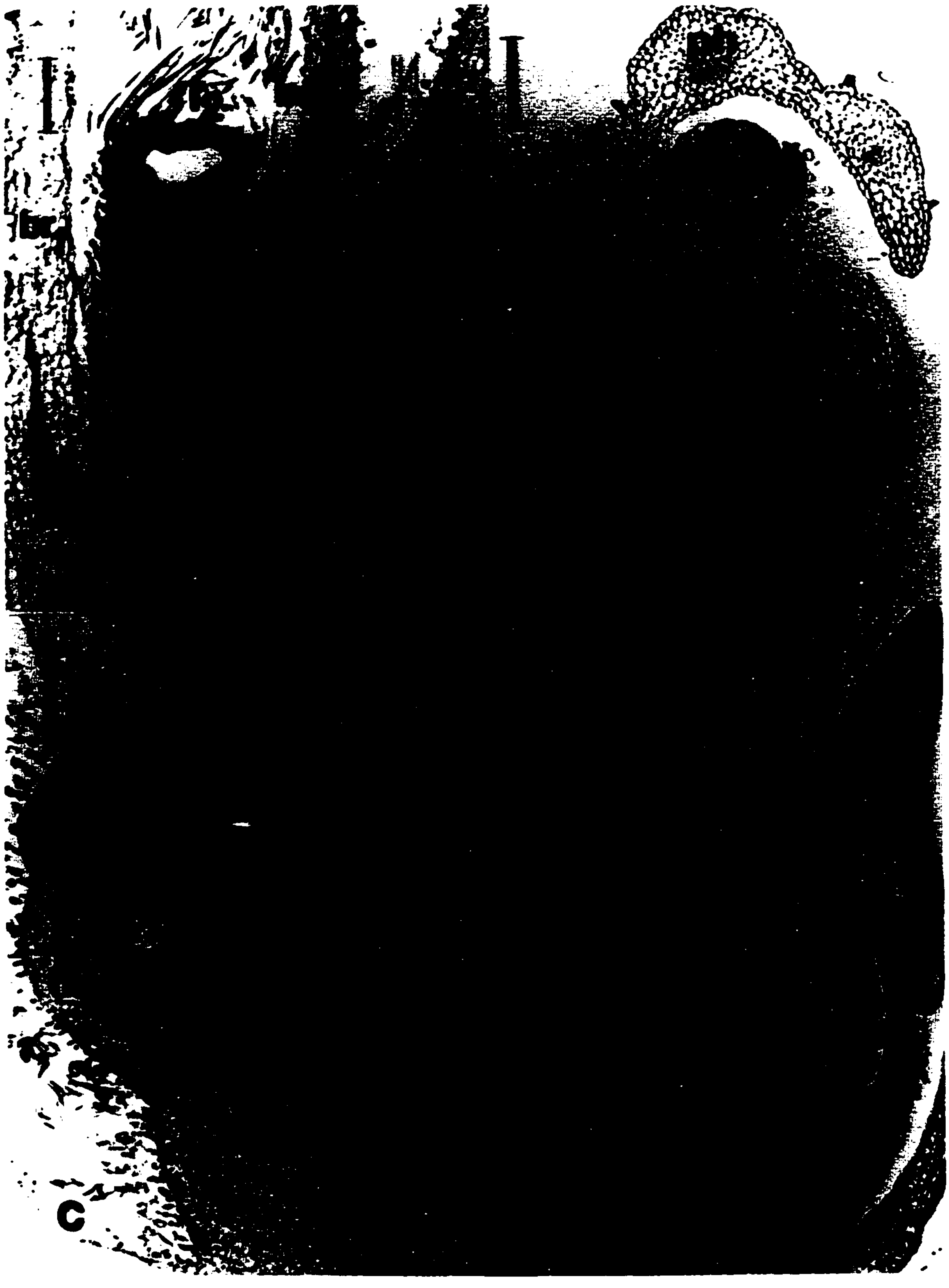
The remaining species of *Aristolochia* subgen. *Orthoaristolochia* form the section *Gymnolobus*. This section has been divided into two subsections, *Pentandrae* and *Hexandrae*. Whereas all the pentandrous species have bracteate, uniflorous PFs (Figs. 9D, 17), inflorescences in hexandrous species are more diverse. The latter, described in detail by González (1990, 1991), exhibit two types: thyrsic, with PFs in rhipidia in *A.* ser. *Thyrsicae* (Figs. 11C, 19D); and racemose, with non-bracteate, uniflowered PFs in *A.* ser. *Hexandrae* (Figs. 10D, 11D, 20-23, 28). Only five of the ca. 140 species of *A.* ser. *Hexandrae* have bracteate flowers; these are *A. burelae*, *A. grandiflora* (Figs. 16, 51C), *A. lindneri*, *A. stuckertii* and *A. urbaniana*.

Two additional groups are recognized within series *Hexandrae*: *Aristolochia* subseries *Hexandrae*, with leafy and elongated racemes (Fig. 20E); and *Aristolochia* subseries *Anthocaulicae*, with very shortened racemes that are usually cauliflorous and have extremely reduced leaves (Fig. 11D).

Euglypha* and *Holostylis

The remaining genera of the Aristolochioideae, the monotypic, South American endemic *Euglypha* and *Holostylis*, have racemose inflorescences. Flowers of *Euglypha* are located along the leafy, elongated, terminal branches, whereas flowers of *Holostylis* are produced in lateral racemes, with reduced leaves.

Figure 11. A. *Thottea siliquosa* (*Bot. Gard. Univ. Bonn, acc. # 09037*); longitudinal section showing a cymose partial florescence (rhipidium); numbers indicate the order of development of the flowers and their corresponding bracts (compare to Fig. 6D). Bar = 250 µm. B. *Aristolochia serpentaria* (*González 3604*, NY) transverse section showing the prophyll and the bract. Bar = 250 µm. C. *A. maxima* Jacq. (*González 3568*, NY), longitudinal section of a rhipidium. Bar = 100 µm. D. *A. leuconeura* Linden (*González 3569*, NY), longitudinal section of a short cauliflorous raceme, showing the non-bracteate, axillary flowers. Bar = 250 µm. *br*, bract; *fl*, flower or floral peduncle; *ph*, pherophyll.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Cauliflory

Cauliflory is frequent among members of Aristolochioideae, occurring in most species of *Thottea* and a number of species of *Aristolochia*. Flowering buds proliferate from the axils of old or fallen leaves. However, there are two structurally (and perhaps functionally) different types of cauliflory (or ramiflory).

The first type of cauliflory occurs when one or several PFs develop late from older woody stems. This occurs in many species of *Thottea* and *Aristolochia* subgenus *Pararistolochia* (Fig. 10A), as well as in some species of A. subgenus *Siphisia* (as in e.g. *A. arborea*, and *A. stevensii*, Fig. 9C) and in some of A. subgenus *Orthoaristolochia* (as in e.g. *A. maxima*, and *A. sprucei*; González, 1990).

The second type, only known in *Aristolochia* subseries *Anthocaulicae*, occurs when flowers are produced exclusively on extremely shortened, lateral racemes (Fig. 11D); in this case, no flowers are formed on the apical, leafy branches (González, 1990, 1991). In addition, pherophylls (flower-subtending leaves) are homogeneous and scaly.

As occurs in other cauliflorous plants (Thompson, 1944), the arrangement (sometimes chaotic) of the cauliflorous buds in *Aristolochia* is somewhat different from the buds in young shoots, which are uniserial. Also, they usually proliferate in number, up to 8-10 buds per node. Moreover, flowering within each cauliflorous raceme in the species of *Aristolochia* subseries *Anthocaulicae* is not acropetal, as is the norm in the genus, but irregular. This has been reported to occur in other taxa (Mora-Osejo, 1987; Weberling, 1989).

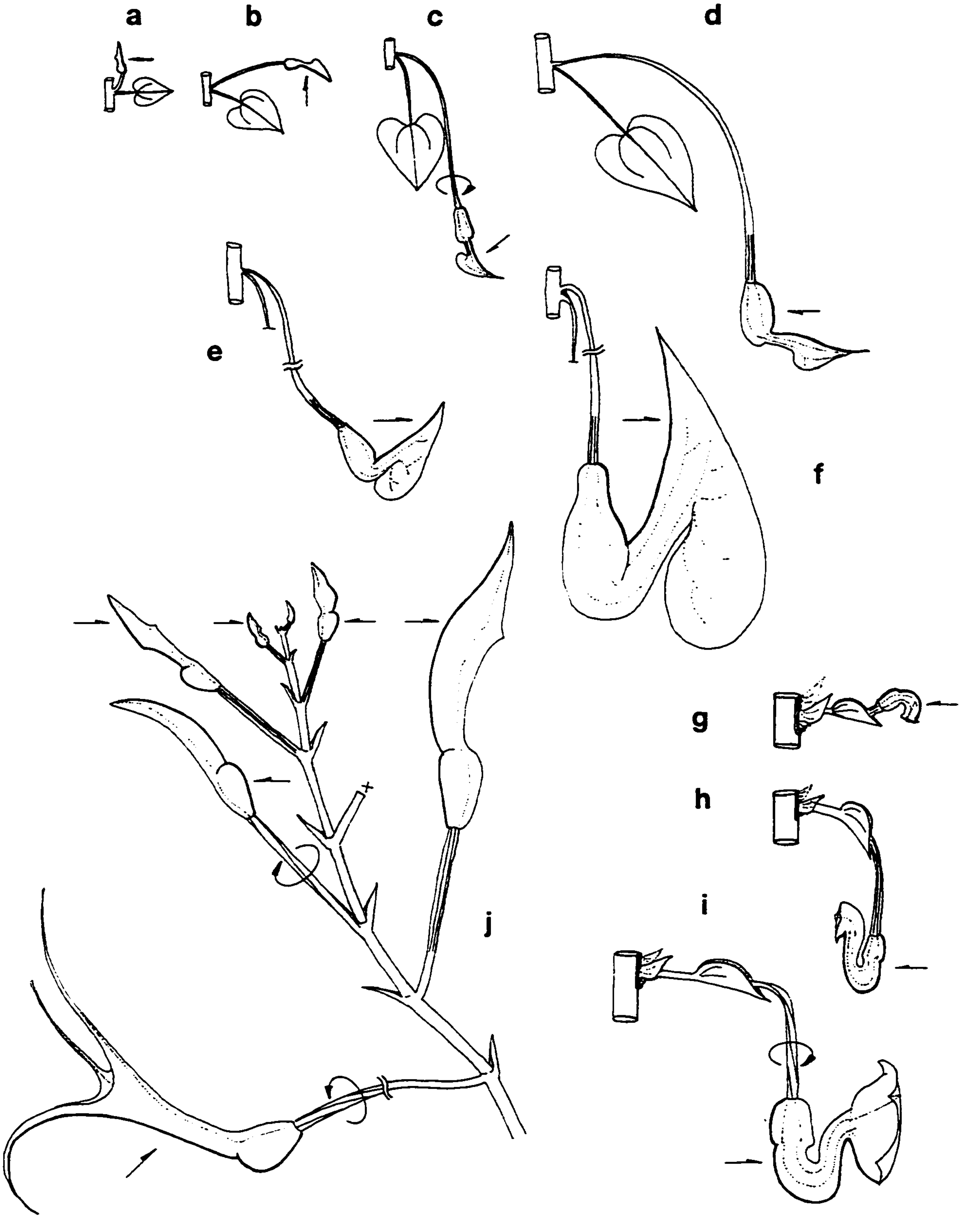
Resupination

Resupination essentially consists of a torsion of the peduncle and/or the ovary, that changes the initial position of the flower. It is known to occur in various families (Fabaceae, Acanthaceae, Lobeliaceae, Melianthaceae, Balsaminaceae, and Orchidaceae). Flowers of *Aristolochia*, *Euglypha* and *Holostylis* resupinate. Previous reports have been made in *Aristolochia* by Huber (1960), and Pfeifer (1966). In the floral bud, the median perianth primordium is found in abaxial position (Fig. 12A, B). Later, a torsion of the peduncle/ovary, turns the flower 180° (Fig. 12C, D), and consequently the median perianth part becomes located in adaxial position, opposite the suture through which the flower opens (Fig. 12E, F).

Resupination in *Aristolochia* occurs in uniflorous, non-bracteate (Figs. 12A-F, 20E), uniflorous, bracteate (Fig. 12G-I) or multiflorous (Fig. 12J) partial florescences. Two variants of this process occur in *Aristolochia*, one in species of the subgenera *Orthoaristolochia* (Fig. 12A-F) and *Pararistolochia* (Fig. 12J), and the other in species of subgenus *Siphisia* (Fig. 12G-I).

In the species of *Aristolochia* subgen. *Orthoaristolochia*, the peduncle and the ovary develop usually at an acute angle to the parental axis (Fig. 12A); later, in the species with long peduncles, they reflex to a right angle (Fig. 12 B). Then, the curvature of the perianth increases, and the peduncle becomes horizontal or pendent (Fig. 12C). Finally, the ovary turns 180°, and the abaxial side of the flower is placed adaxially

Figure 12. Resupination in *Aristolochia*. A-F. *A. gigantea* (*González 3445B*), floral buds at successive nodes of a branch. G-I. *A. macrophylla* (*González 3421*), floral buds at successive nodes of a branch. J. *A. preussii* (*Brenan 9484*, K), single partial florescence; the three oldest flowers are resupinate. Straight arrows indicate the morphological adaxial side of the flower. Curved arrows indicate the torsion of the flower.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(Fig. 12D), usually with the utricle and the gynostemium pendent or, sometimes, horizontal; simultaneously, the perianth acquires its final shape (Fig. 12E-F). Consequently, the inner side of the limb displays towards the outside at the time of anthesis. In the species of *Aristolochia* section *Diplolobus* with a short floral peduncle and lateral (not adaxial) bract, as in *A. clematitis* (Fig. 10B), resupination seems to be minor.

Although no field observations have been made in species of *Aristolochia* subgen. *Pararistolochia*, the ovaries or peduncles are usually twisted in herbarium specimens, which suggests that resupination also occurs in these species. Moreover, in two specimens examined of *A. decandra* and *A. preussii* the ovary has turned 360°, so that the perianth secondarily returns to its " original" position in relation to the axis of the PF (Fig. 12J).

Resupination occurs differently in the species of *Aristolochia* subgen. *Siphisia*. In young floral buds, the middle perianth lobe is placed in abaxial position relative to the bract; then, the lobe is pushed down, due to the stronger development of the abaxial side of the flower (Fig. 12G). In the species of this subgenus, the concave side of the flower is formed towards the morphologically adaxial side with respect to the bract (see chapter 3). The curvature formed is peculiarly strong in the species of this subgenus, and consequently the suture becomes oriented 'backwards" , towards the bract (Figs. 9C, 12H). Shortly after that, the ovary turns 180°. By the time of anthesis, the inner side of the limb is displayed opposite to the bract (Figs. 9A, C, 12I).

IV. Discussion

Flowers of *Saruma* were described as axillary by Ying and Boufford (1993), and Tucker and Douglas (1996). My observations, however, agree with the previous report by Wagner (1907), who interpreted the flower of *Saruma* as the terminal flower of a sympodium (Fig. 6C). Evidence of the terminal position of the flower is the formation of a vestigial axillary bud between the flower and the ultimate leaf, and the development of the first (median) sepal opposite to the ultimate leaf (Leins & Erbar, 1995; Tucker & Douglas, 1996). It may be recalled here that the median part of the perianth is opposite to the subtending bract in the other members of the Aristolochiaceae (Figs. 1, 6A-B, 7B, D, 8B, G, 9A,C, 10A-C, 12, 14-17, 19, 52).

Flowers of *Asarum* have often been described as " axillary" or " between two opposite leaves" (Cheng & Yang, 1983; Gaddy, 1987; Lubbock, 1895; Thorne, 1996). This erroneous interpretation has arisen because of the extremely shortened internodes between the alternate leaves. The specimens examined here show clearly that each growth unit terminates in a flower (Figs. 7A-C). Studies of vasculature (Dormer, 1955) and development support the interpretation of the terminal position of the flower (see also Eichler, 1878; Velenovsky, 1905).

With respect to *Thottea*, it appears that some metatopies due to partial coalescence of the peduncle and the inflorescence axis occur in this genus (A. Weber, personal communication; personal observation). This assumption is based on the presence of oblique ridges that run from the base of the bracts downwards to the flower below, on the opposite side of the axis (Fig. 6F). If this is the case, the bilobed bract on the side of each flower could be developmentally associated with the flower immediately below it, rather than with the flower located at its level; consequently the inflorescences would be cymose.

In *Aristolochia* subgen. *Siphisia*, the present results contradict the observations of Huber (1993), who described the prophylls of *Aristolochia macrophylla* (=*Isotrema macrophyllum* in Huber, 1993) as foliaceous. The prophylls of this species are cataphyllar, and the foliose bract (Fig. 9A) is not the prophyll. Also, Huber (1993) described the flowers of *A. tomentosa* (*I. tomentosum*) as leaf-opposed; this is due to the fact that in this species the bracts are leafy and similar in shape to the normal leaves (Fig. 8A).

The species of *Aristolochia* subgen. *Pararistolochia* from Australia and New Guinea seem to have a unique character within the genus, in terms of inflorescence morphology. In these species, the inflorescences seem to be monotelic, and the growth of the entire plant is sympodial. However, more field observations are necessary in order to precisely define whether the growth units on these plants are sympodial. My observations, based on herbarium specimens, demonstrate that flowers in these species are clearly opposite to scaly or foliose bracts, and form part of a rhipidium, rather than forming a raceme or being axillary, as described by Jebb (1993) and Parsons (1996).

Cauliflory does not support the concept of *Pararistolochia* as different from *Aristolochia*, contrary to the interpretations by Verdcourt (1986) and Parsons (1996), because the same type of cauliflorous inflorescences are present outside of subgenus *Pararistolochia* (e.g. in some species of *Aristolochia* subgen. *Siphisia*, and some species of *Aristolochia* ser.

Thyrsicae). On the other hand, the occurrence of cauliflory is not directly comparable in all members of the Aristolochioideae, because two different types of cauliflorous inflorescences are found, racemose and cymose. Similar finds have been reported before; for example, Thompson (1951) found that cauliflorous branches may be formed in various ways, and that they do not have the same structure; for instance cauliflorous buds in *Pleiocarpa* (Apocynaceae) and *Forsythia* (Oleaceae) form cymes whereas in *Swartzia* (Fabaceae) they form racemes (Thompson, 1951). My results show that both kinds occur in *Aristolochia*.

All species of *Aristolochia* subsect. *Podanthemum* studied have bracteate PFs, contradicting the key presented by Schmidt (1935), in which the majority of the species of this subsection were described as non-bracteate.

My observations also contradict the interpretation of the 'axillary complex' in *A. clematitis* either as a single (uniparous) scorpioid cyme (Payer, 1857; Delaigue, 1971) or as a raceme (Nardi, 1984). Payer (1857) and Delaigue (1971) described each 'axillary complex' as a uniparous scorpioid cyme. This interpretation requires several assumptions: (a) bracts are absent and bracteoles present, (b) development of the PF occurs in zig-zag, forming a scorpioid cyme; and (c) ultimate buds of the scorpioid cyme are completely vegetative. Evidence against these assumptions is (a) there is one, distinct bract per flower, and the development of flowers in the same axil is independent (Fig. 10B); (b) distichous phyllotaxis prevails as a general rule for both vegetative and reproductive axes; no scorpioid cymes occur in the Aristolochiaceae; (c) the development of renewal shoots from a PF is unknown in the family and very rare elsewhere. My interpretation also contradicts that of Nardi (1984), who described the axillary complex as formed by " short indeterminate inflorescences, referring ultimately to simple or even compound racemes, with bracteoles and internodes generally strongly reduced" . Rather, buds develop into PFs that are determinate (Fig. 10B), sometimes forming a vestigial bud in the axil of the bract. The only indeterminate buds in *A. clematitis* are the vegetative buds (Fig. 8F).

V. Conclusion

Within the Aristolochiaceae, two forms of inflorescences can be recognized: monotelic in *Asarum* and *Saruma*, associated with sympodial growth units (the truly terminal position of the flowers of *Asarum* and *Saruma* is here confirmed); and polytelic in *Aristolochia, Euglypha, Holostylis* and *Thottea*, associated with monopodial growth units. Within *Aristolochia*, however, some species of *Aristolochia* subgenus *Pararistolochia* from Australia and New Guinea might also have sympodial growth.

Cymose, distichous partial florescences and flowers with an adaxial bract (with respect to the parental axis) opposite to the middle lobe of the perianth are the rule within the Aristolochiaceae. However, variations consisting of helicoid cymes and lateral bracts are here reported. The number of flowers on each partial florescence is variable throughout *Aristolochia*, but it is often constant within the same species. Other characters that were thoroughly investigated are the shapes of the bracts, the presence of abscission zones at the base of the pedicel, and the position of the inflorescences. These characters have been included in the cladistic analysis (chapter five), after which a discussion of their evolution is presented.

Resupination in *Aristolochia*, *Euglypha* and *Holostylis* drastically changes the position of the flower. Two variants were detected, one in the species of the subgenera *Orthoaristolochia* and *Pararistolochia*, and the other in the subgenus *Siphisia*. In both, however, the abaxial side of the flower is placed adaxially, and the suture through which the flower opens becomes more or less opposite to the parental axis at the time of anthesis.

In *Aristolochia*, both thyrsic and racemose types of inflorescences occur. The first type occurs predominantly in temperate and paleotropical members of *Aristolochia*, whereas the second type is restricted to the Neotropics and a few Old World temperate species. Racemose inflorescences are formed only if the flowers lack a bract and there is only one flower per axil. Inflorescences of *Euglypha* and *Holostylis* do not differ from the racemose inflorescences found in many species of *Aristolochia*.

Finally, it should be mentioned that within *Aristolochia*, inflorescence morphology has also been crucial in terms of recognition of monophyletic groups of species (such as *Aristolochia* ser. *Thyrsicae*, or *A*. subser. *Anthocaulicae*; see González, 1990, 1991, 1994). Also, I have found in many species that structural characters of the PF, such as the number of flowers per PF, the length of the internodes, and the shape of the bracts, are also useful for species identification.

CHAPTER THREE

Floral development and morphology

I. INTRODUCTION

The flowers of the Aristolochiaceae are either actinomorphic (*Saruma, Asarum* and *Thottea*) or monosymmetric (*Aristolochia, Euglypha* and *Holostylis*). The perianth consists of three sepals and three petals in *Saruma* (Figs. 1A, 58A), three sepals in *Asarum* (Figs. 1B, 58B) and *Thottea* (Figs. 1C, 58C) or a tubular, 1-3(-6)-lobed and extremely modified structure in *Aristolochia* (Figs. 1D, 4, 58D), *Euglypha* (Fig. 49F) and *Holostylis* (Figs. 49H, 51A), that has been variously interpreted as a bract, a calyx or a corolla. Vestigial structures in petal positions have been reported in *Asarum* (Fig. 1B; Leins & Erbar, 1985; Maekawa, 1980) and *Thottea* (Fig. 1C; Leins et al. 1988). There are 5, 6, 8-10, 12, 24 or 36 stamens that are either free in *Saruma, Asarum* and *Thottea* (Figs. 1A-C, 2A-C, 58A-C) or form part of a massive structure, usually called a gynostemium, in *Aristolochia* (Figs. 1D, 2D, 4, 58D), *Euglypha* and *Holostylis* (Fig. 51B). The anthers are extrorse (functionally introrse in *Saruma;* Figs. 2A, 58A; Oliver, 1889; Dickison, 1992; Endress, 1995) and open by longitudinal slits. The number of carpels varies from 4 in *Thottea* to 6 in the remaining genera, and they form either a semi-superior and partially apocarpous gynoecium in *Saruma* (Figs. 1A, 2A, 58A) and *Asarum* (Figs. 1B, 2B, 58B) or an almost completely syncarpous and inferior ovary in *Thottea* (Figs.

2C, 57, 58C) and *Aristolochia* (Figs. 1C, D, 58C). The ovules, usually numerous, are arranged along submarginal placentae.

The flowers of the Aristolochiaceae, and particularly those of *Aristolochia*, have repeatedly been mentioned as among the most sophisticately adaptated for fly-pollination (Brues, 1928; Cammerloher, 1923; Costa & Hime, 1981; Hall & Brown, 1993; Endress, 1990b, 1994; Petch, 1924; Proctor & al. 1996; Razzak et al. 1992; Vogel, 1978). Flowers of *Aristolochia* display a remarkable mimicry of the flowers of *Ceropegia* (Asclepiadaceae) and the pseudanthia of *Cryptocoryne* (Troll, 1928) and other Araceae. Fungus mimicry by *Asarum* has also been reported (Vogel, 1978). Despite the extreme morphological variation in flowers of the Aristolochiaceae, fly-pollination seems to occur in many of its different members (Endress, 1990b; Proctor & al. 1996); however, self-pollination appears to occur commonly (Lu, 1982; Mesler & Lu, 1993; Petch, 1924; Razzak et al. 1992; Wildman, 1950), as a plesiomorphic condition at least in *Asarum* (Kelly, 1997).

Since the early 19th century, characters of the perianth and the gynostemium have been the most commonly used characters in the systematics of the Aristolochiaceae. This also applies to the classification within *Aristolochia*. Surprisingly, the morphology and ontogeny of the gynostemium (Leins & Erbar, 1985) and the perianth (Endress, 1994) remain controversial.

The trimerous condition of the perianth is clear in *Asarum*, *Saruma*, and *Thottea* (Fig. 1A-C), but is far from obvious in *Euglypha*, *Holostylis*, and most of *Aristolochia*. Usually, the number of lobes present in the mature flower of *Aristolochia* has been considered an *a priori* indication of the number of parts that form it (see e.g. Wyatt, 1955a). The few studies on floral ontogeny of *Aristolochia* have been restricted to *A. clematitis* and *A. gigantea*, both with an 'unilobed' perianth (Leins & Erbar, 1985; Payer, 1853, 1857).

The perianth of *Aristolochia* consists of a monosymmetric, apparently single structure, remarkably diverse in form and color. It is differentiated into three main regions: the utricle, an inflated structure at the base; the tube, a narrowed zone above the utricle; and the limb, an expanded, apical region (Fig. 4). Six different morphological interpretations exist for explaining the origin of the perianth of *Aristolochia*:

1. A structure that incorporates two alternating sets of three parts (Eichler, 1878; Mayoux, 1892). Based on the presence of three strong veins that alternate with three weak veins, Eichler (1878) proposed that the perianth of *Aristolochia* originates from a double set of three parts, fused together, the inner parts being suppressed.

2. A monosepalous calyx (van Tieghem, 1900, for most of the species of *Aristolochia*).

3. A trimerous calyx (Endress, 1994; Leins & Erbar, 1985; Pfeifer, 1966; Saunders, 1939; van Tieghem, 1900, for *Holostylis* and the segregate *Hocquartia*).

4. A corolla (Montemartini, 1902).

5. A *sui generis* tubular perianth, that is directly formed by the

irregular growth of the annular floral receptacle, and that is neither a calyx nor a corolla (Plantefol, 1948).

6. A bract or single leaf (Guédès, 1968; Hagerup, 1961; Lorch, 1959). Both Lorch (1959) and Hagerup (1961) interpreted the perianth of *Aristolochia* as homologous to a spathe-like leaf. Lorch (1959) found a teratological transition between a foliage leaf and a leaf that resembles the perianth in *A. maurorum*, and used this as evidence, along with the similarity of size, shape and venation of the leaves and the perianth to conclude that the perianth is leaf derived. Hagerup (1961) pointed out the absence of any developmental evidence for three fused primordia. Guédès (1968) compared leaf and perianth venation and claimed that the middle and the lateral veins of the perianth are homologous to the middle and lateral veins of the leaf.

The gynostemium, a structure often considered a result of fusion between the androecium and (usually) the upper part of the gynoecium (Endress, 1994; Weberling. 1989), is the most remarkable feature of the Aristolochioideae. Its morphology, however, is one of the most puzzling problems, because the gynostemium lobes are opposite the stamens rather than in the median planes of the adjacent carpels (Figs. 2D, 5, 13, 27-44, 52). Three interpretations have been proposed.

1. Duchartre (1854a, 1864) considered the "columna" (gynostemium) as built up from stamens fused with styles; since then, most authors (Baillon, 1888; Celakovský, 1877; Eichler, 1878; Henslow, 1888, 1891; Mayoux, 1892; Nair & Narayanan, 1962; Saunders, 1939; and Solereder, 1889b, among others) have supported Duchartre's interpretation.

Figure 13. Van Tieghem's alternative interpretations of the anther-ovary morphology in *Aristolochia*. A. Anthers with massive connectives, which are transformed into papillate structures (Van Tieghem, 1884, 1891). B. Anthers fused with the styles/stigmas (Van Tieghem, 1898, 1918).

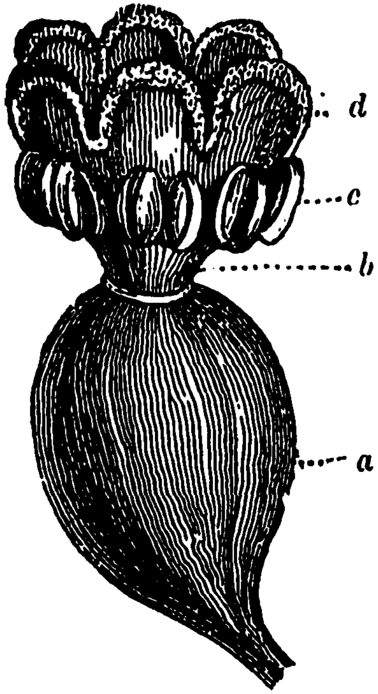

Fig. 260. — Fleur d'Aristoloche (*Aristolochia rotunda*), dont on a enlevé le calice. *a*, ovaire infère ; *b*, base apparente de la fleur; *c*, anthères soudées par leurs connectifs qui se développent au-dessus des sacs polliniques et se couvrent de papilles en *d*.

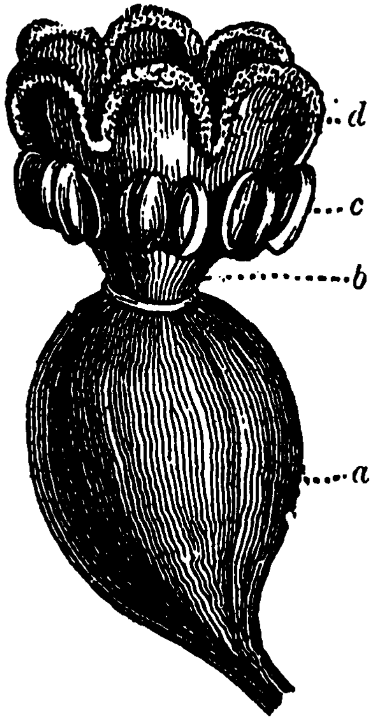

Fig. 178. — Fleur d'Aristoloche dont on a enlevé le calice en *b* ; *a*, ovaire infère ; *c*, anthères concrescentes dans toute leur longueur avec le gros style, qui se divise au sommet en six lobes stigmatiques superposés *d*.

Saunders (1939) interpreted the gynoecium morphology of *Aristolochia* as consisting of 6 sterile carpels and 6 fertile carpels, the latter forming the septae. She also described the stigmas as distinct and either centered over the sterile carpels in *Asarum*, centered over the fertile carpels (commissural) in *Aristolochia* spp., or as fused into three pairs in other *Aristolochia* spp. Moreover, Saunders (1940: 346-348) considered the inner whorl of stamens as absent in *Aristolochia,* and the outer stamens with "very short filaments, dividing into two as they separate from the style column; there is thus no connective, the two thecae of each anther being quite separate".

2. Other authors (Payer, 1857; Van Tieghem, 1884, 1891; Fig. 13) have interpreted the carpels of *Aristolochia* as reduced to their ovaries, the thickened connectives being the structures that take over the stigmatic and stylar functions. Under this interpretation, therefore, styles and stigmas are believed to be abortive. Van Tieghem himself abandoned this interpretation some years later (1898, 1900, 1918; Fig. 13) in favor of the presence of a true gynostemium, i. e. fused stigmas, styles and stamens. This change could have been prompted by studies on floral vascularization, particularly that of Mayoux (1892), who wrote in the introduction to her monograph (page 7): "Si l'analogie et la physiologie donnent des arguments en faveur de la primiere theorie; l'organogenie semble d'accord avec l'anatomie pour faire accepter la seconde".

More recently, Bowman (1973) described the gynostemium lobes sometimes as connectives (e.g. his Fig. 123 shows "connective tissue which becomes broadened and elongated... In some species studied, such as A.

ringens, the anthers become embedded completely in the broad connective tissue." p. 53), and sometimes as stigmas (e.g. Figs. 120-121 of the same series as Fig. 123 shows that "the stamens are adnate to the style and stigma, forming the gynostemium." p. 68). On the other hand, Leins and Erbar (1985) presented developmental data on two species of *Aristolochia,* both with 6-lobed gynostemia, that revive the view that the gynostemium lobes correspond to "secondary constructions belonging to the stamens only, on which the function of the reduced median carpel tips is transferred". This is based on the independent development of the lobes, which come from distinct primordia. Leins and Erbar (1985), however, did not arrive at a definite interpretation.

3. Solm-Laubach (1876) considered the reproductive structures of *Aristolochia* as formed from a single whorl of *sui generis* fertile leaves that produce ovules towards the base, and anthers and stigmas towards the apex.

This chapter deals with the floral development, anatomy and vascularization of 42 species of *Aristolochia,* which represent all the three subgenera, sections, and subsections formally proposed within this genus (Tables V, VII). Additional observations of floral buds of one species of *Thottea* and three of *Asarum* are included in order to cover most of the morphological variation within the family. The final part of the chapter discusses the observations with regard to the above-mentioned morphological interpretations of the perianth and the gynostemium and their use in the systematics of *Aristolochia.*

II. MATERIALS AND METHODS

Floral buds at different stages were initially fixed in FPA (formalin: propionic acid:ethanol in proportion 5:5:90). Dissections were made in 90% ethanol, then dehydrated in a series of absolute ethanol and acetone (90% ethanol, 30 min.; absolute ethanol, 30 min.; absolute ethanol: acetone in proportion 50:50, 10 min.; two steps of acetone, 10 min. each), critical point-dried in a Denton Vacuum DCP-1, using liquid CO2, mounted on aluminum stubs using colloidal graphite, and coated with gold-paladium in a Hummer 6.2 sputter coater.

Slides of floral buds at different stages of development and of flowers at anthesis were also prepared by conventional embedding in paraplast, serially sectioned (6-12.5 μm thickness), stained with safranin and counterstained with fast green or chlorazol black.

Clearings of flowers in relatively advanced development were also made by using 10% NaOH for 24-78 hours (depending on the texture of the flower), rinsing twice in water for 24-48 hours, staining with standard Schiff's reagent, and dehydrated with a series of 50%, 70%, 95%, absolute ethanol, 50:50 absolute ethanol:xylene, and xylene, 10 minutes each. The samples were stored in methyl salycilate.

III. RESULTS

Floral development

Perianth

All the early flower buds observed of *Aristolochia* are either slightly (Figs. 15A, 16A, 19A) or strongly monosymmetric, with a tangentially broad floral apex (Figs. 20A, 22A). Initially, the floral apex is flattened and obliquely dome-shaped (Figs. 10D, 15A, 16A, 19A, 20A, 21A, 22A); then it becomes slightly concave and three perianth primordia become more or less visible. The first primordium to be initiated is always located in the median plane opposite the subtending bract (Figs. 14A, 15B, 16A, B, 17A, 18A, 19A, B), or towards the parental axis if the bract is lacking. Subsequently, lateral perianth primordia begin to differentiate more or less simultaneously. These primordia are not well differentiated in some species (Fig. 20A). In others, they differentiate late (Figs. 22C, 23B).

The three primordia come into contact with each other and encircle the floral apex (Figs. 14A-B, 15B, 16B, 17A, 18A, 19B). At this stage, the floral apex appears to lose its meristematic appearance (no tunica-corpus is distinguishable; Figs. 31A, 36C) and becomes crateriform, and intercalary (zonal) growth below the insertion of the perianth primordia begins (Figs. 14C-D, 15C, 16C, 17C, 18B, 19C, 20B).

Figure 14. A-C. *Aristolochia reticulata* (*González 3594*). A. Young floral bud, showing the three perianth primordia. Bar = 50 µm. B. Mid-stage floral bud; median perianth lobe at top. Bar = 100 µm. C. Slightly older floral bud at the time of interlocking of the perianth margins; median perianth lobe at top. Bar = 100 µm. D. *A. serpentaria* (*González 3604*), perianth shortly before anthesis, frontal view. Bar = 0.5 mm. *pl*, lateral perianth lobe; *pm*, median perianth lobe.

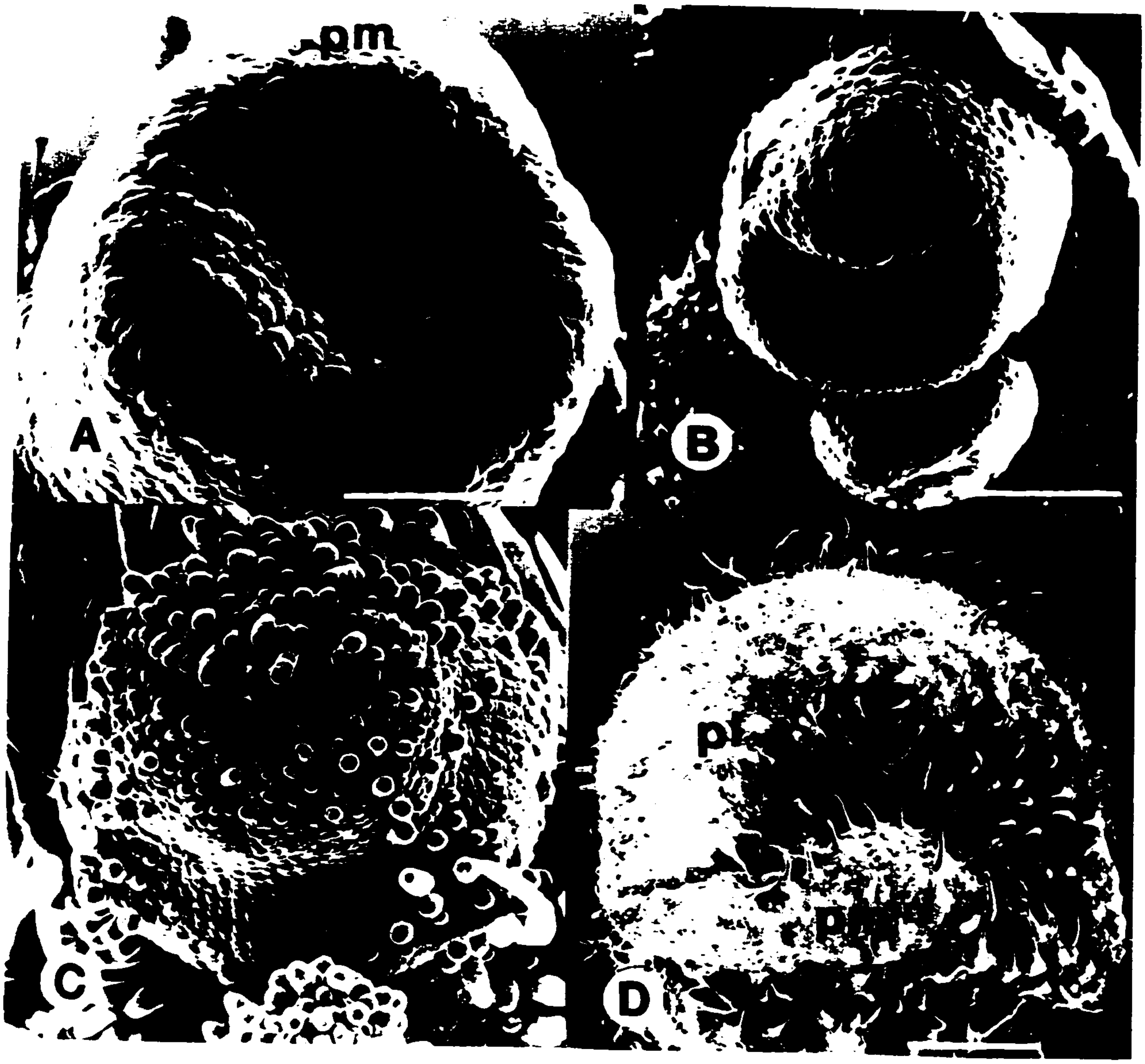
pm
A
B
C
D
pl
p

Figure 15. *Aristolochia arborea (González 3415)*. A. Floral apex, nearly lateral view; trichomes on the abaxial side are becoming evident. Bar = 50 µm. B. Perianth initiation. Bar = 50 µm. C. Floral bud, the three perianth lobes becoming apparent. Bar = 50 µm. D. Floral bud at the time of interlocking of the perianth lobes. Bar = 50 µm. E. Slightly older floral bud at the end of perianth interlocking. Bar = 0.1 mm. F. Flower at anthesis displaying a protrusion at the flower entrance (arrowhead); median perianth lobe at bottom. *pl,* lateral perianth lobe; *pm,* median perianth lobe.

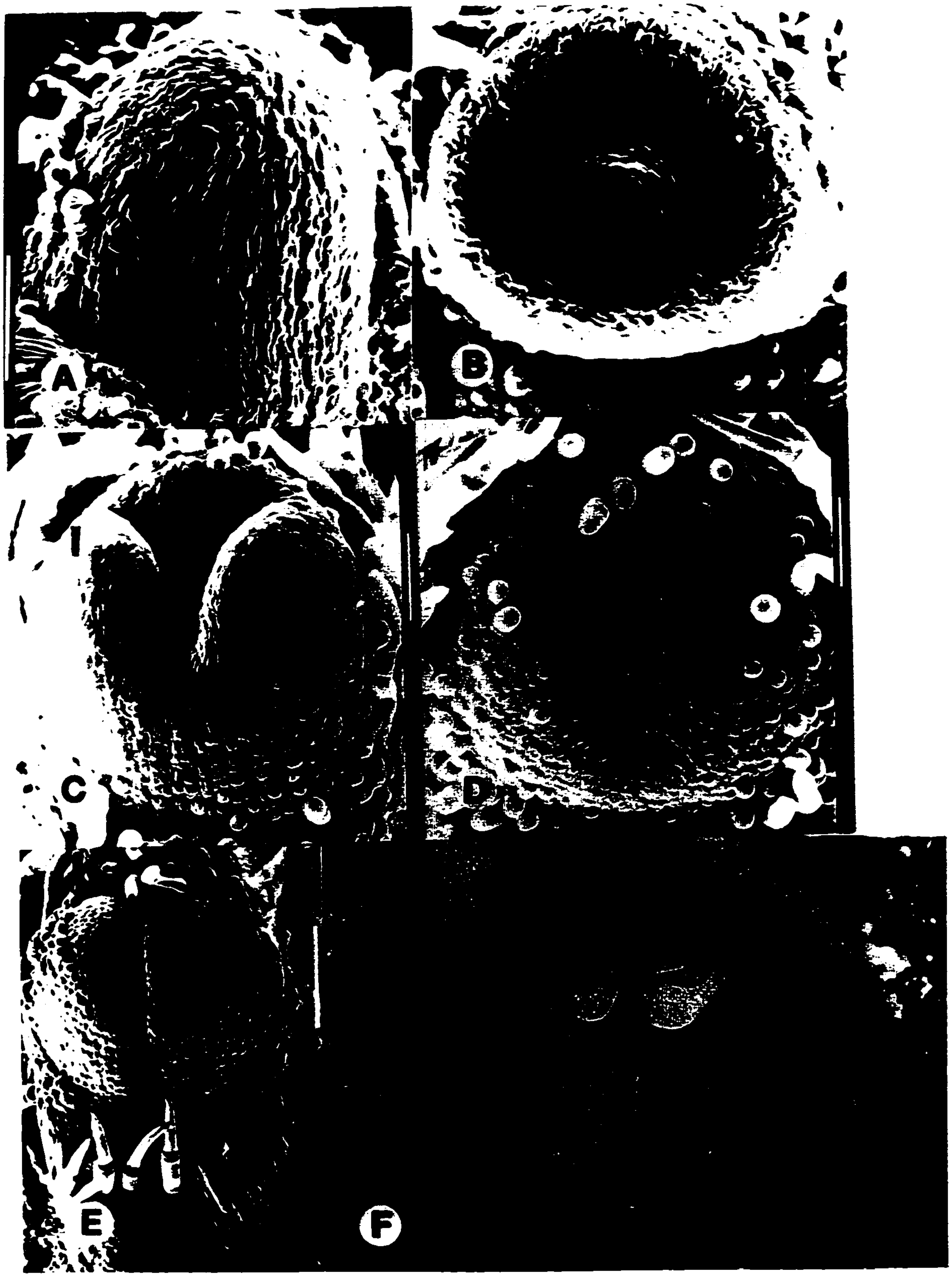
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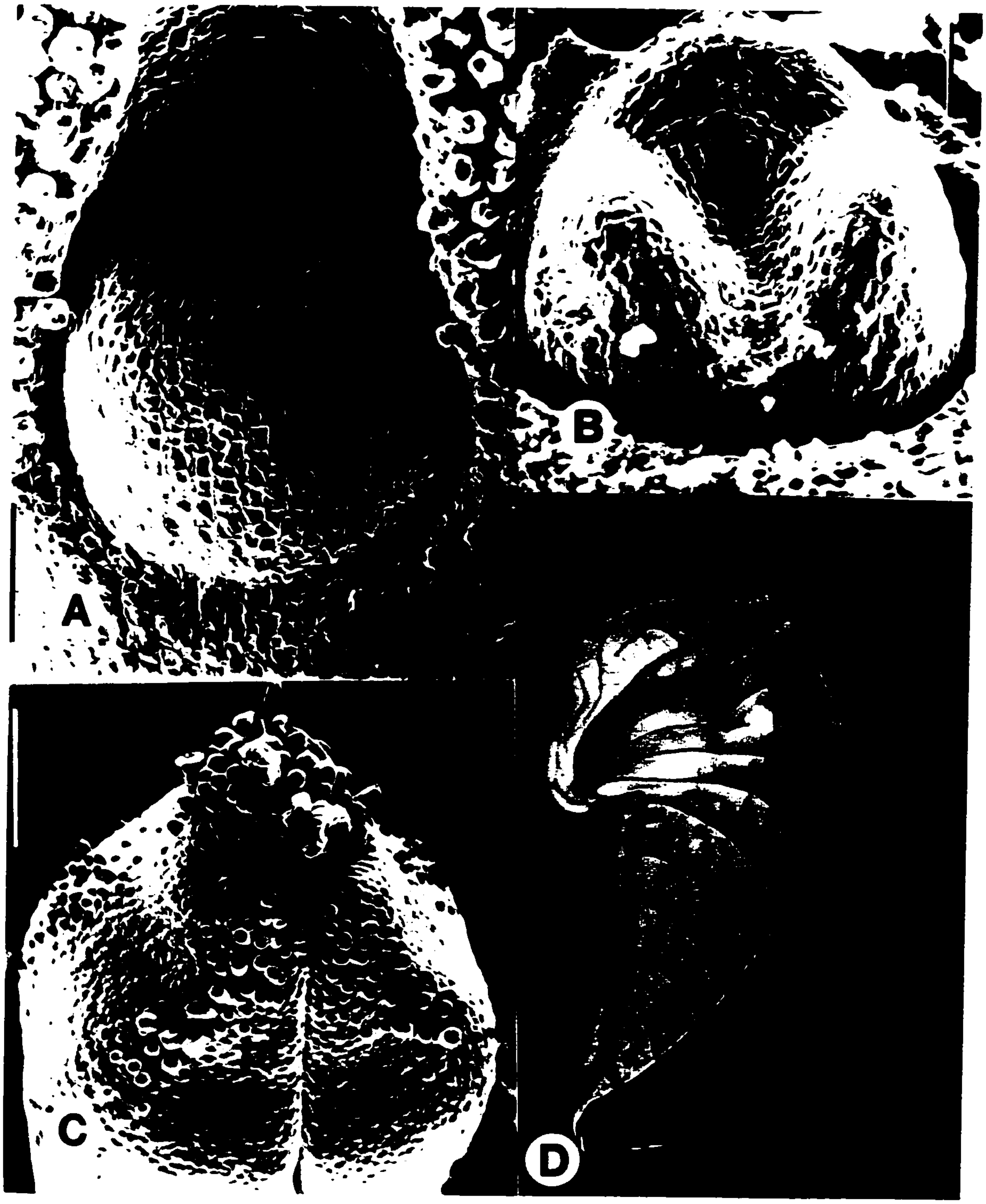
Figure 16. *Aristolochia grandiflora* (*González 3443*). A. Early floral bud, abaxial view, surrounded by a peltate bract. Bar = 50 µm. B. Floral bud with the perianth primordia becoming apparent, adaxial view; bract (bottom) removed. Bar = 50 µm. C. Mid-stage floral bud in adaxial and somewhat upper view, showing the beginning of perianth interlocking. Bar = 100 µm. D. Young flower in preanthesis. *pl*, lateral perianth lobe; *pm*, median perianth lobe.


A
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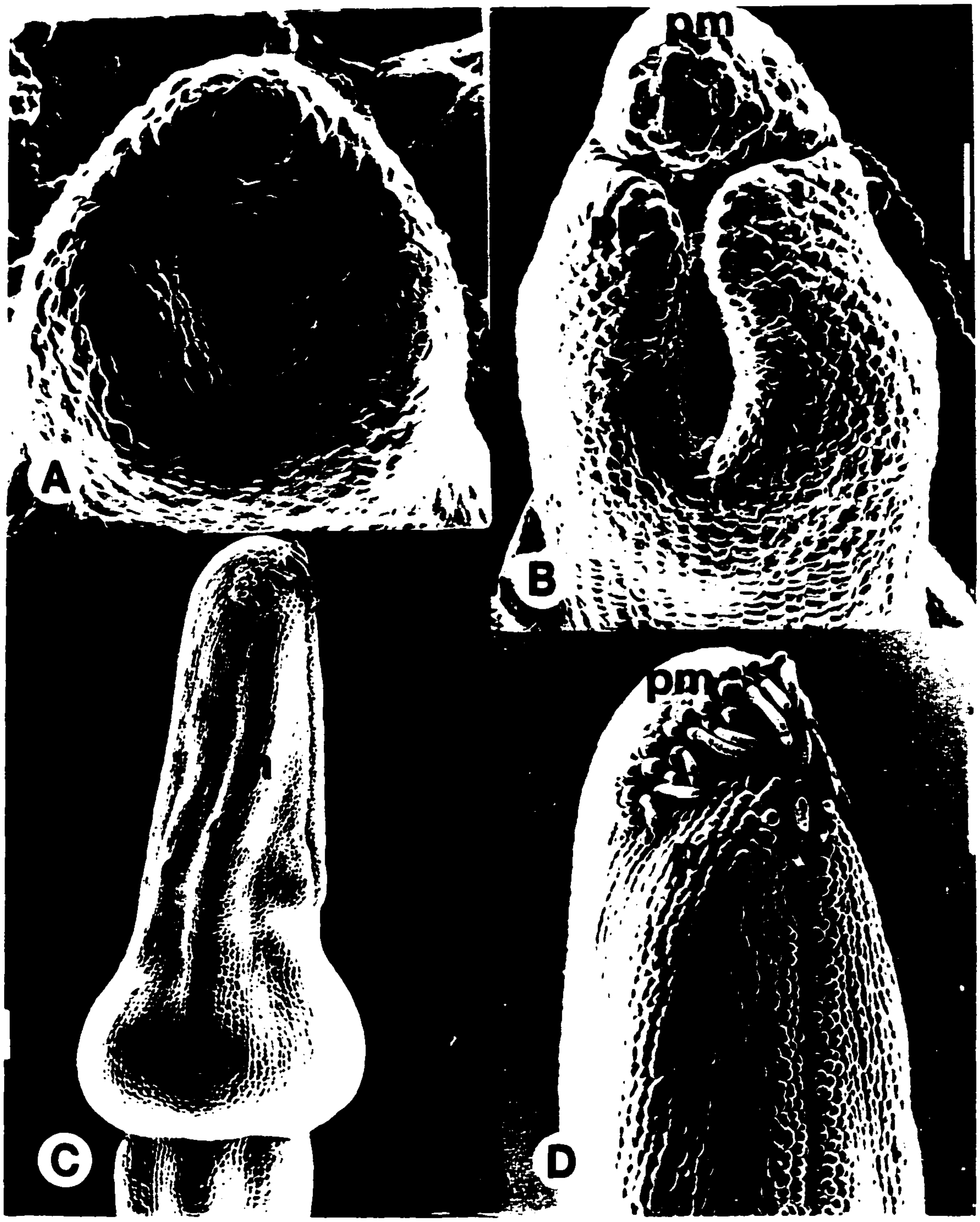
C
D

Figure 17. *Aristolochia pentandra* (*González 3603*). A. Early floral bud, abaxial and somewhat upper view, at the time of initiation of perianth lobes; the median lobe is facing the bract. Bar = 50 µm. B. Slightly older floral bud in lateral view. Bar = 50 µm. C. Floral bud completing interlocking of the perianth; a deep slit has formed between the lateral lobes. Bar = 50 µm. D. Flower at anthesis. *pl*, lateral perianth lobe; *pm*, median perianth lobe.


A
B
pm
C
pl
D

Figure 18. A-B. *Aristolochia zollingeriana* (*Tsou 1175*). A. Early floral bud showing the perianth primordia, top view. Bar = 50 µm. B. Floral bud at the beginning of perianth interlocking, adaxial view. Bar = 50 µm. C-E. *A. petersiana* (*NYBG acc. 151/97*). C. Floral bud at the beginning of perianth differentiation into utricle, tube and limb; the veins and the abscission zone between the ovary and the perianth have become apparent; note the lesser development of the veins in commissural position relative to the middle veins. Bar = 0.1 mm. D. Detail of the 3-lobed apex of the limb. Bar = 0.1 mm. E. Flower at anthesis, showing the stipe (arrow) at the base of the utricle. *c,* veins in commissural position; *m,* middle vein of a perianth lobe; *pl,* lateral perianth lobe; *pm,* median perianth lobe.


A
B
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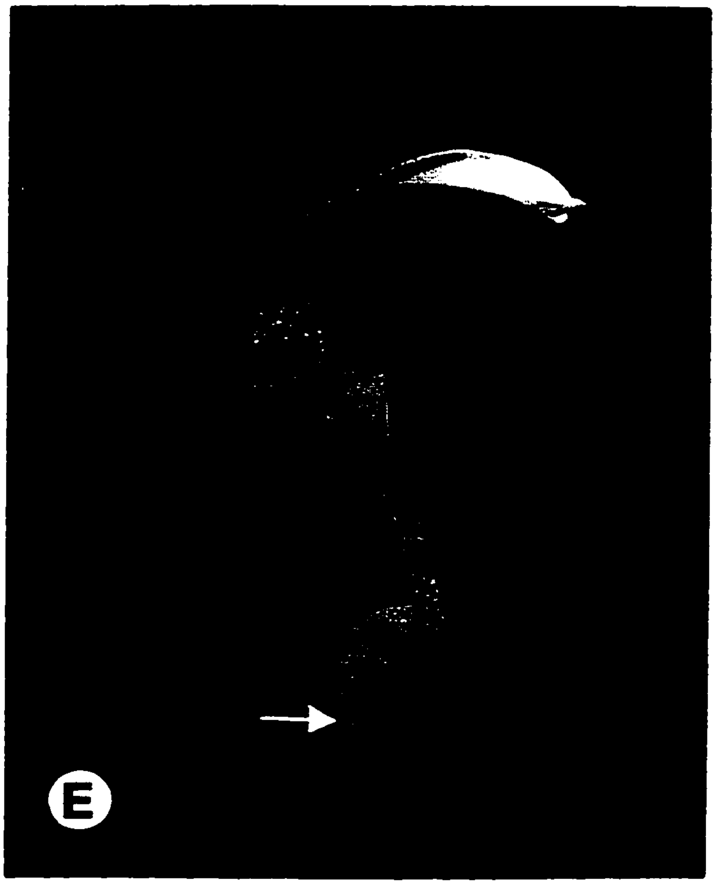
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Figure 19. *Aristolochia maxima* (*González 3289*). A. Early floral bud, from above. Bar = 50 µm. B. Initiation of the three perianth primordia; trichomes on the median primordium have started to develop. Bar = 50 µm. C. Mid-stage floral bud showing deep sinus between the two lateral perianth lobes. Bar = 50 µm. D. Partial florescence with a flower slightly before anthesis. In A-C, bract (bottom) removed. *pl*, lateral perianth lobe; *pm*, median perianth lobe.


A
B
pl
C
D

Figure 20. *Aristolochia elegans* (*González 3442*). A. Tangentially broad floral apex (top) opposite a vegetative bud (bottom). Bar = 50 µm. B. Early floral bud showing the slight differentiation of the perianth primordia. Bar = 50 µm. C. Floral bud at the time of ovary-perianth differentiation. Bar = 100 µm. D. Floral bud with the recently closed perianth. Bar = 100 µm. E. Flowers at preanthesis (left and center) and anthesis (right). Arrow indicates a pseudostipule.


A
B
C
D

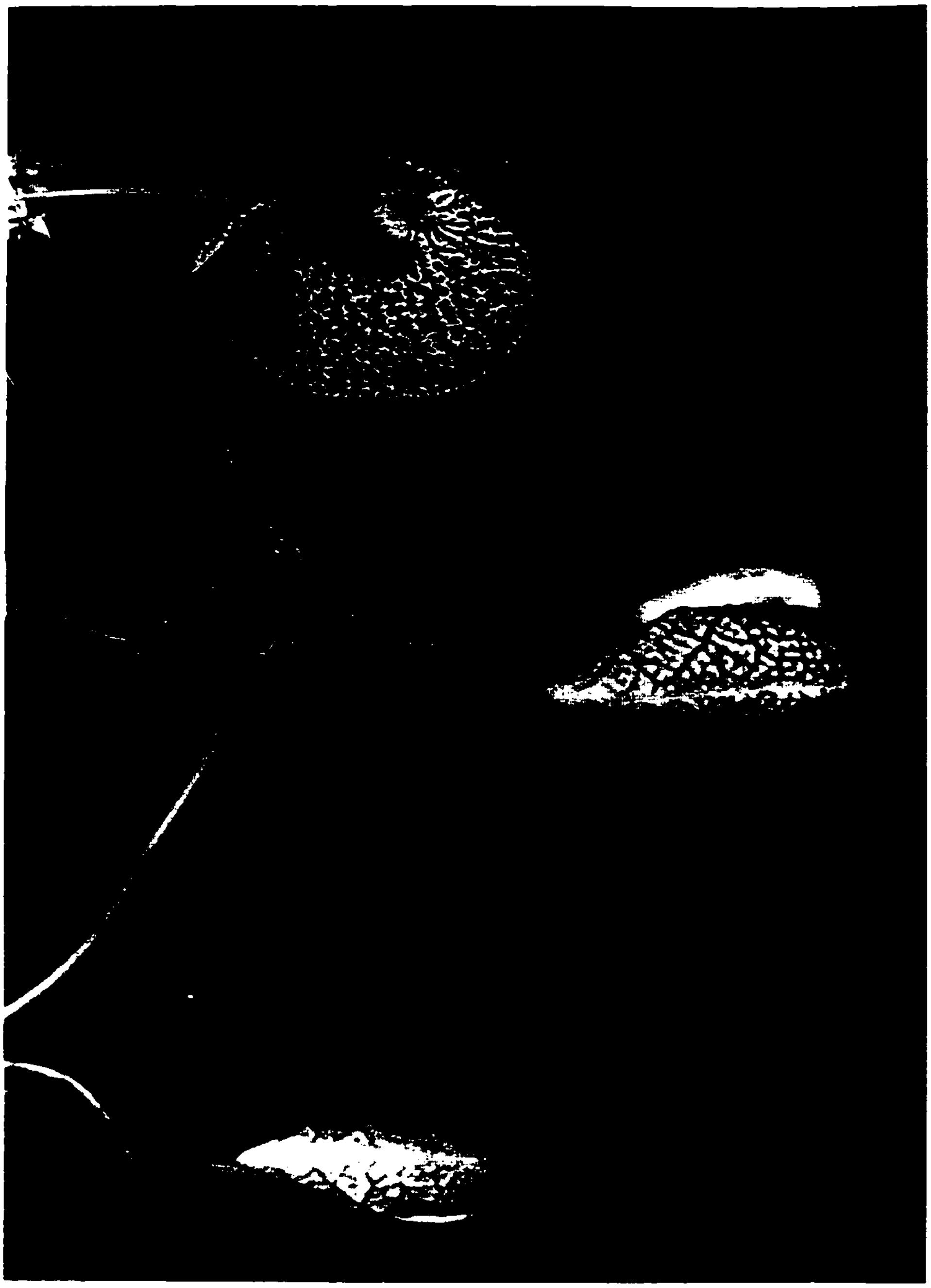


Figure 21. *Aristolochia ridicula* (KEW, acc. 1995-246). A. Plastochrones 1-6 displaying three successive stages of floral development (arrowheads). Bar = 0.1 mm. B. Floral bud at plastochrone 7. Bar = 0.1 mm. C. Longitudinal section of a late-stage floral bud that shows the late lateral expansion of the limb (arrow); conical trichomes in the inner surface of the tube have started differentiation. Bar = 0.5 mm. D. Flower at anthesis, middle perianth vein at top (arrowhead). *pm,* median perianth lobe.

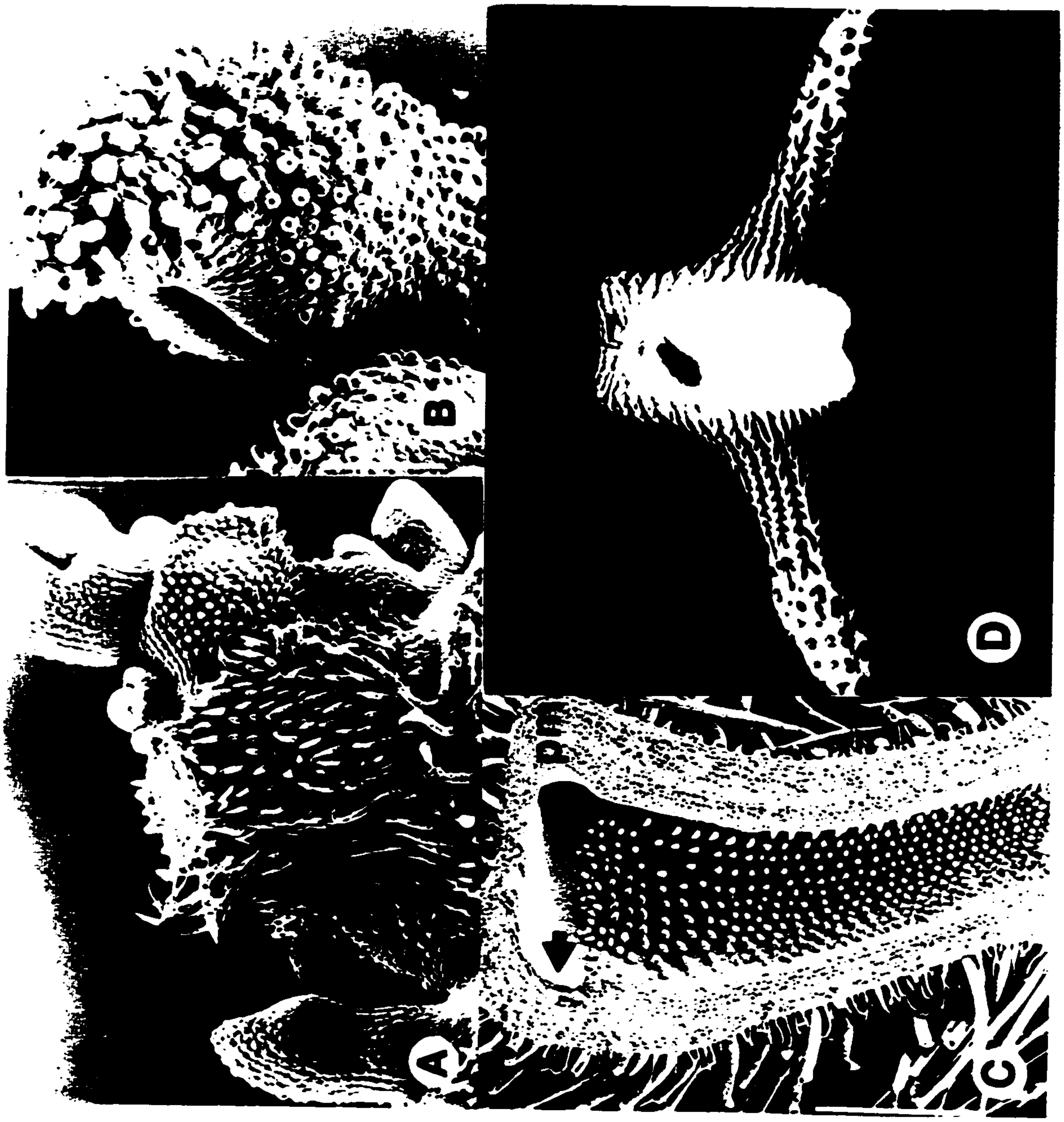

A
B
C
D

Figure 22. *Aristolochia labiata* (*González 3441*). A. Tangentially broad floral apex (top) opposite a vegetative bud (bottom). Bar = 50 µm. B. Early floral bud showing perianth initiation and the crateriform floral apex. Bar = 50 µm. C. Mid-stage floral bud showing initiation of the two lateral perianth primordia. Bar = 100 µm. D. Mid-stage floral bud (right). Bar = 100 µm. *pl*, lateral perianth lobe; *pm*, median perianth lobe.


A
B
C
D

Figure 23. *Aristolochia ringens* (*González 3575*). A. Mid-stage floral bud, from above, before initiation of the two lateral perianth primordia. Bar = 0.1 mm. B. Mid-stage floral bud, side view, showing the initiation of the lateral perianth primordia (arrowhead). Bar = 100 µm. C. Floral bud after postgenital fusion of the lateral primordia forming the lower lip (arrowhead) and interlocking of perianth margins; ovary has become visible. Bar = 0.5 mm. D. Flower at anthesis.


A
B
C
D

During the middle stage, enlargement and differentiation of the perianth takes place. Intercalary growth increases and the tubular portion of the flower becomes increasingly conspicuous (Figs. 18C, 20C, 22A-C, 23B, C). In species of *Aristolochia* with pubescent flowers, the trichomes along the middle plane of the median lobe begin to differentiate basipetally, followed by differentiation of trichomes of the lateral lobes (Figs. 14D, 15D, 16D, 19C-D).

The closure of the perianth occurs later in development by the interlocking of more or less papillate epidermal cells on the margins (Figs. 14D, 15D, 16D, 17C, 18C-D, 20D, 22C). The margins then remain tightly appressed until anthesis. Aestivation is valvate, and is concordant with the degree of symmetry of the flower. In the species with tail-like processes (e.g. *A. grandiflora*, Fig. 16), the valvate aestivation also extends to the tail. Closure of the perianth in *A. labiata* and *A. ringens* occurs partially by the interlocking of the margins of the median lobe, and partially by the interlocking of the lateral margins of the lateral lobes (Figs. 22C-D, 23C).

The formation of the tubular portion of the perianth and the expansion of the limb occurs mostly by intercalary growth and cell elongation. Elongation affects also the ovary, which in general ends up as a narrowly cylindrical structure (Figs. 4, 18C, 23C), vs. the globose or subglobose ovary of *Asarum* (Figs. 7C, 58B) and *Saruma* (Fig. 58A).

Differentiation of utricle, tube and limb (Fig. 4) begins more or less when perianth closure is completed (Figs. 18C, 20D, 23C). The portion that becomes the tube is relatively shorter than the portions corresponding to the utricle and the limb 18C, 20D). At the same stage, the abscission zone between the perianth-gynostemium and the ovary is formed, and the ovary becomes evident, as the dorsal carpellary veins increase in size (Figs. 18C, 20D, 23C, 25A, B, 34). Shortly after that, additional veins of the perianth begin to appear (Figs. 18C, 23C).

The strongly asymmetrical growth of the young floral bud produces the characteristic curvature of *Aristolochia*. Curvature forms earlier in *Aristolochia* subgenus *Siphisia*, than in the remaining species, in which it occurs more or less simultaneously with the beginning of resupination (see chapter 2, Fig. 12).

A clear-cut difference within *Aristolochia* occurs in the formation of the floral curvature (Table V). In all the species of *Aristolochia* subgenus *Siphisia* (Figs. 9A, C, 12G-I, 46B,D) and subgenus *Pararistolochia* (Figs. 12J, 46F), and in *A. grandiflora* (Figs. 16D, 48D), the concave side of the flower is formed away from the median perianth lobes, whereas in species of subgenus *Orthoaristolochia* (except *A. grandiflora*), and in *Euglypha* and *Holostylis* it is formed towards the median perianth lobe (Figs. 17, 18E, 19D, 20E, 23D, 47, 48B, F, 49).

All these different types of development can be sumarized in five categories, on the bases of distinctness and symmetry of the three lobes (Table V; Fig. 24).

In types I and II the three apical lobes remain distinct, and mature flowers have a clearly trilobed limb (Table V; Fig. 24). In type I zonal growth is more homogeneous and consequently sinuses between all

Table V. Types of perianth development, curvature, limb symmetry at anthesis, and number of gynostemium lobes and stamens in the studied species of *Aristolochia*.

Taxon	Type of perianth development*	Perianth curvature	Perianth limb at anthesis	No. of gynostemium lobes/ anthers
Subgenus *Siphisia*				
A. arborea	II	adaxial	3-lobed, monosymmetric	3/6
A. californica	I	adaxial	3-lobed, actinomorphic	3/6
A. cucurbitifolia	I	adaxial	3-lobed, actinomorphic	3/6
A. heterophylla	I	adaxial	3-lobed, actinomorphic	3/6
A. kaempferi	I	adaxial	3-lobed, actinomorphic	3/6
A. macrophylla	I	adaxial	3-lobed, actinomorphic	3/6
A. manshuriensis	I	adaxial	3-lobed, actinomorphic	3/6
A. reticulata	I	adaxial	3-lobed, actinomorphic	3-5/6
A. serpentaria	I	adaxial	3-lobed, actinomorphic	3-5/6
A. stevensii	II	adaxial	3-lobed, monosymmetric	3/6
A. tomentosa	I	adaxial	3-lobed, actinomorphic	3/6
A. tricaudata	II	adaxial	3-lobed, monosymmetric	3/6
Subgenus *Pararistolochia*				
A. promissa	II	adaxial	3-lobed, monosymmetric	9-10/9-10
Subgenus *Orthoaristolochia* Sect. *Gymnolobus* Subsect. *Pentandrae*				
A. coryi	III	abaxial	1-lobed, monosymmetric	5/5
A. erecta	IV	abaxial	1-lobed, monosymmetric	5/5
A. micrantha	III	abaxial	1-lobed, monosymmetric	5/5
A. pentandra	III	abaxial	1-lobed, monosymmetric	5/5

*For types see the text and Fig. 24.

Table V. Continued.

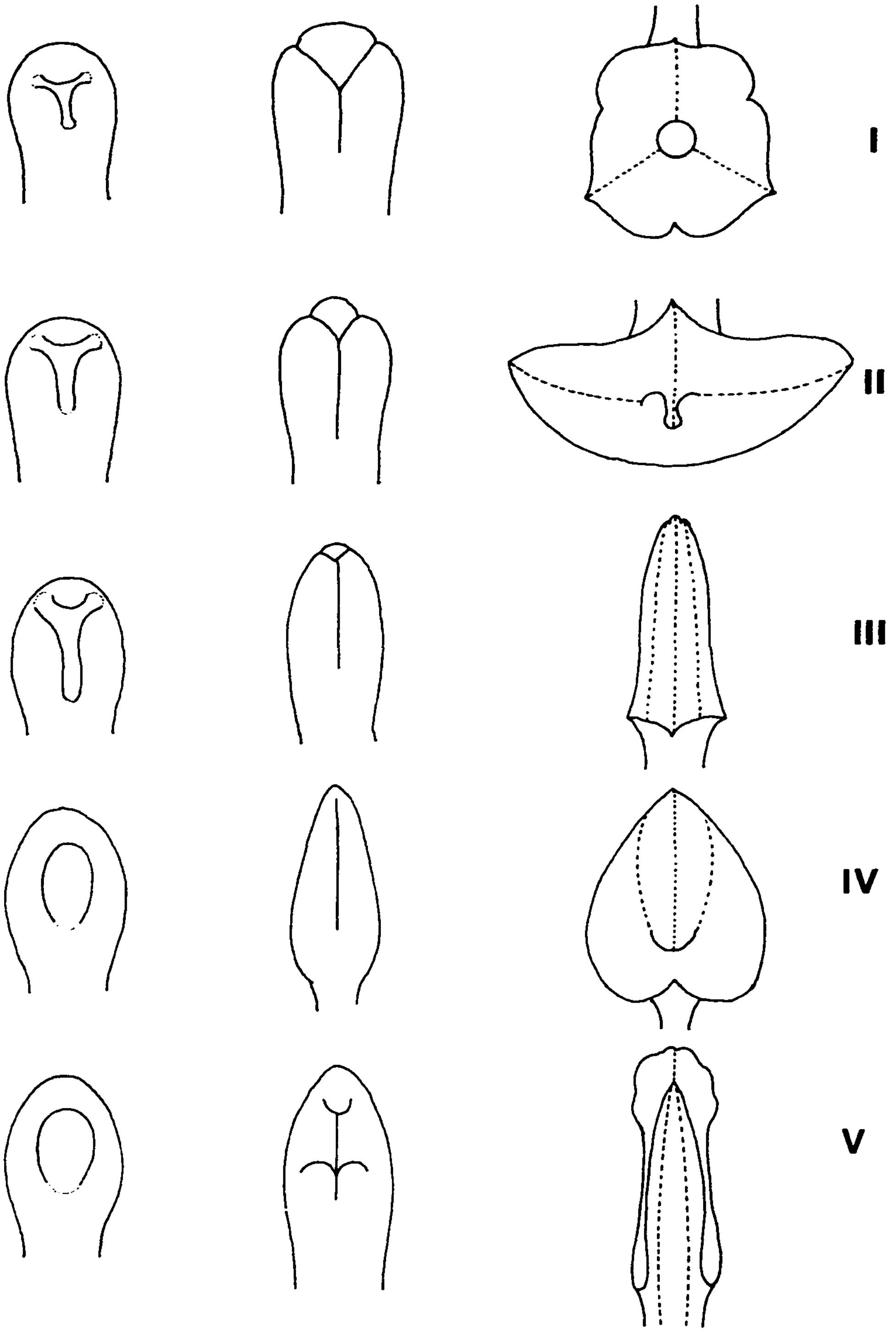
Taxon	Type of perianth development*	Perianth curvature	Perianth limb at anthesis	No. of gynostemium lobes/ anthers
Subgenus *Orthoaristolochia* Sect. *Gymnolobus* Subsect. *Hexandrae*				
A. acutifolia	III	abaxial	1-lobed, monosymmetric	6/6
A. anguicida	IV	abaxial	1-lobed, monosymmetric	6/6
A. arcuata	IV	abaxial	1-lobed, monosymmetric	6/6
A. elegans	IV	abaxial	1-lobed, monosymmetric	6/6
A. fimbriata	IV	abaxial	1-lobed, monosymmetric	6/6
A. gigantea	IV	abaxial	1-lobed, monosymmetric	6/6
A. grandiflora	III	adaxial	1-lobed, monosymmetric	6/6
A. labiata	V	abaxial	2-lobed, monosymmetric	6/6
A. leuconeura	IV	abaxial	1-lobed, monosymmetric	6/6
A. maxima	III	abaxial	1-lobed, monosymmetric	6/6
A. morae	IV	abaxial	1-lobed, monosymmetric	6/6
A. nummularifolia	IV	abaxial	1-lobed, monosymmetric	6/6
A. odoratissima	IV	abaxial	1-lobed, monosymmetric	6/6
A. pilosa	IV	abaxial	1-lobed, monosymmetric	6/6
A. ridicula	IV	abaxial	2-lobed, monosymmetric	6/6
A. ringens	V	abaxial	2-lobed, monosymmetric	6/6
A. trilobata	IV	abaxial	1-lobed, monosymmetric	6/6
Sect. *Diplolobus*				
A. acuminata	III	abaxial	1-lobed (slightly trilobed at the apex), monosymmetric	6/6
A. albida	III	abaxial	1-lobed (slightly trilobed at the apex), monosymmetric	6/6
A. clematitis	IV	abaxial	1-lobed, monosymmetric	6/6
A. cretica	IV	abaxial	1-lobed, monosymmetric	6/6
A. paucinervis	IV	abaxial	1-lobed, monosymmetric	6/6
A. petersiana	III	abaxial	1-lobed (slightly trilobed at the apex), monosymmetric	6/6
A. pontica	IV	abaxial	1-lobed, monosymmetric	6/6
A. zollingeriana	III	abaxial	1-lobed (slightly trilobed at the apex), monosymmetric	6/6

three perianth lobes are approximately the same depth; as a result, the perianth limb becomes actinomorphic, as in some species of *Aristolochia* subgenus *Siphisia* (Figs. 9A, 12I, 14, 46B) and subgenus *Pararistolochia* (Fig. 46F). In type II the two lateral perianth lobes are more completely fused to the median lobe; hence, the sinus that separates the two laterals is deeper (Figs. 9A, 15D, E), and the limb becomes monosymmetric (Figs. 15F, 46D), as in some species of *Aristolochia* subgenus *Siphisia* and subgenus *Pararistolochia*.

In types III and IV, there is a much stronger development of the abaxial side of the perianth (Figs. 16-21, 24; Table V). The median perianth primordium is fused to the laterals from early stages of development; the three primordia form a monosymmetric perianth (Table V). The lateral lobes remain well separated from each other, and form a deep sinus that becomes the suture through which the flower opens (Figs. 16C, 17C, 18B-D, 19C-D, 20C-D). Type III occurs in species where the lateral lobes remain easily distinguished at the mid-stage of development, as in *Aristolochia grandiflora* (Fig. 16), some species of *Aristolochia* subsect. *Pentandrae* (Fig. 17), the species of series *Podanthemum* (Fig. 18), and the species of series *Thyrsicae* (Fig. 19). In species of series *Podanthemum*, the lobes remain distinct in late stages (Fig. 18C-D). In *A. grandiflora* (Fig. 16), species of subsection *Pentandrae* (Fig. 17) and series *Thyrsicae* (Fig. 19), the lobes end up completely fused and indistinct shortly after the closure of the perianth margins.

Type IV occurs in most of the remaining species (Fig. 24, Table V). The connation between the median and two lateral lobes occurs during very early stages so that they are no longer distinguished as

Figure 24. Schematic representation of the five types of development of the perianth limb in *Aristolochia*. In type I, the three perianth lobes remain similar in size shape, and degree of fusion, forming a 3-lobed, actinomorphic limb (right). In type II, the three lobes develop as distinct lobes, but the median lobe is different from the lateral two, and the fusion between the lateral two is more complete, forming a 3-lobed, monosymmetric limb (right). In type III, the median lobe fuses more completely with the two lateral lobes, forming one large lobe with a slightly three-lobed tip. In type IV, the three lobes fuse completely early in development (left), forming a unilobed limb. In type V, the median lobe develops into a distinct lobe, and the two lateral lobes fused together late in development forming a lower lip. Dotted lines indicate the middle veins of the perianth parts.

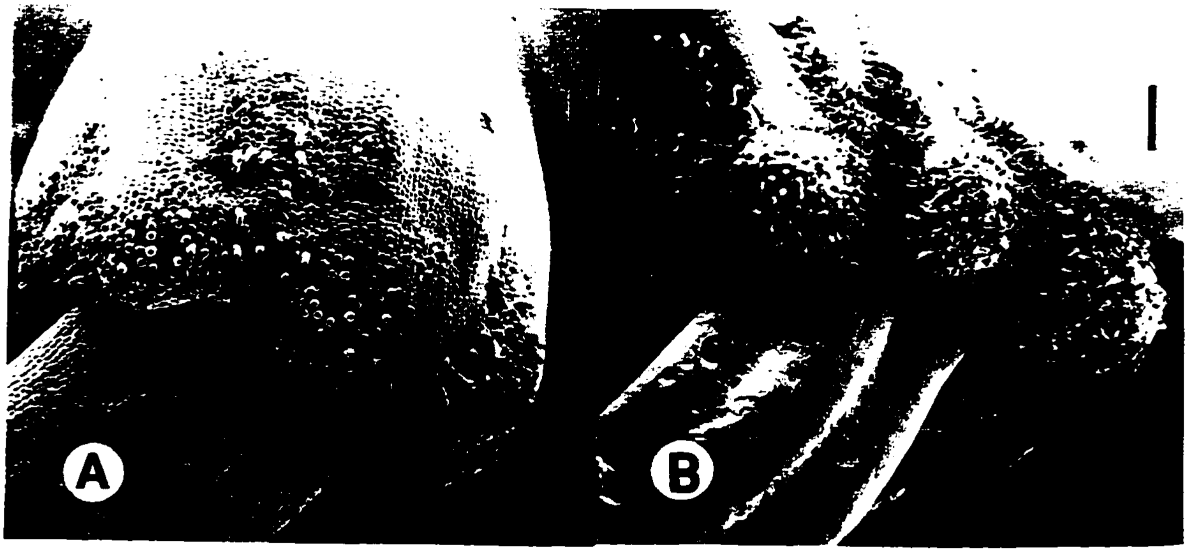

I
II
III
IV
V

individual primordia, and a rhomboidal border can be seen in frontal view (Fig. 20B) before the closure of the perianth. In *Aristolochia ridicula*, a species with two lateral lobes on mature flowers, the early stages are essentially similar. The lobes originate from a late lateral expansion of the flanks (Fig. 21B, C). Venation pattern confirms that these two lateral expansions correspond to the lateral lobes.

Type V occurs in species with a bilobed perianth (Table V). The mid-stages of floral development in these species are different from those in the other species of *Aristolochia*, because a rapid elongation of the median primordium occurs giving rise to the upper lip primordium (Figs. 22B-D, 23A-B). In frontal view, a rhomboidal border can be seen (Fig. 23A) that is formed mostly by the margins of the median primordium. Immediately after that, the two lateral primordia become confluent and fuse postgenitally (Figs. 22C-D, 23C), and start growing together as if they were a single structure. Thus the characteristic lower lip is formed (Fig. 23D).

In most of the species of *Aristolochia* the base of the utricle is more or less symmetrical, and does not have particular transformations. In some species, however, it undergoes some peculiar transformations. In all *Aristolochia* subsect. *Podanthemum* (Fig. 18E) and in *Euglypha*, the base of the utricle stretches up to 8 mm in length. In other species (e. g., *A. labiata* and *A. ringens*) the base becomes extremely asymmetrical due to a protuberance that develops towards the abaxial side (Fig. 23D). In *A. trilobata*, six calyculus-like, downward-pointing outgrowths are found at the base of the utricle, one in front of each median carpel ridge (Fig. 25). These outgrowths may become up

Figure 25. *Aristolochia trilobata* (*González 3445*). Successive stages of the initiation of the outgrowths at the base of the utricle. Bar = 0.1 mm. *ov*, ovary.

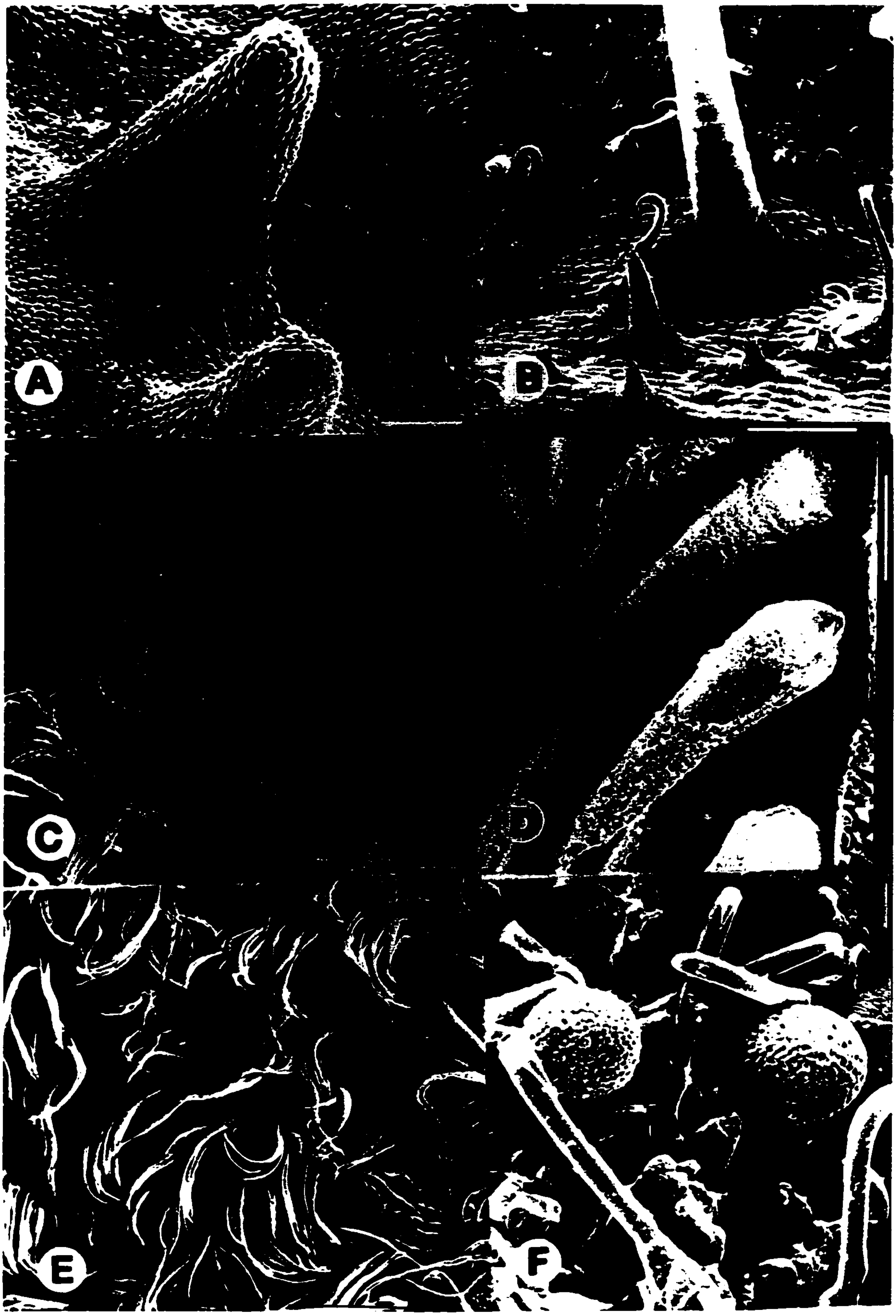

A
B

to 6 mm in length.

Formation of the different trichomes on the inner side of the perianth occurs late in the floral development, when the floral bud has become closed (see e.g. Fig. 21C). According to the species, up to five main types of trichomes or papillae can be found in a single flower (see also Correns, 1891; Solereder, 1889a): (1) nectariferous trichomes, usually located in one or two abaxial zones on the distal end of the utricle (Fig. 26B); (2) trichomes scattered on the utricle (Fig. 26C) that are essentially similar to those found in the nectariferous zones; (3) conical, white, or conspicuously colored trichomes in the tube and usually around the mouth and the proximal portion of the limb (Figs. 26 D, 31D); (4) papillae on the inner surface of the limb (Fig. 26 E); and (5) vascularized fimbriae usually located along the margin and/or on the inner surface of the limb (Fig. 21D). The first two, present in all the examined species, are mostly secretory and it is unlikely that they play an attraction role, because they are not visible from the outside. The conical trichomes, the papillae and the fimbriae, appear to play a mechanical and/or attraction role. Conical trichomes are missing in *Aristolochia* subgenus *Siphisia*. The outer indument of the perianth is similar to that found in the vegetative organs (Fig. 26 F).

Anthesis is associated with a set of changes in floral position due to resupination (see above under chapter 2), and changes in odors and colors especially of the inner surface. In species of *Aristolochia* from Australia and New Guinea such as *A. dielsiana, A. momandul, A. pithecurus*, and *A. schlechterii* (Jebb, 1993; Jones & Gray, 1977; Parsons, 1996), the 3 tapering, long and twisted lobes form three openings or windows similar to those found in *Ceropegia*

Figure 26. *Aristolochia pilosa* (*González 3571*). Trichomes and papillae in mature flowers. A. Papillae on the inner surface of the limb. Bar = 100 µm. B. Indument on the outer surface of the tube. Bar = 100 µm. C. Trichomes and papillae on the inner surface of the utricle. Bar = 100 µm. D. Conical trichomes on the inner surface of the tube. Bar = 100 µm. E. Nectarial trichomes on the inner surface of the utricle. Bar = 0.5 mm. F. Hooked trichomes and polen grains on the stigma. Bar = 10 µm.


A
B
C
D
E
F

(Asclepiadaceae), which typically occur in myophilous pitfall-trap flowers (Vogel, 1961). This happens also, at least temporarily, in the Central American *A. tricaudata* and the African *A. promissa*. Finally, during post-anthesis, the limb loses turgor and the perianth along with the gynostemium falls off.

Stamens and carpels

Stamen initiation of *Aristolochia* occurs on the border of the recently formed perianth tube (Figs. 27A, 28C, 29A, 31A, 35A, 37A, 41A), before the closure of the perianth. Two stamen primordia flank the median plane of the abaxial perianth part, two are lateral, and two flank the median plane of the adaxial perianth part (Fig. 1D). Initiation proceeds more or less simultaneously, but usually the two abaxial stamen primordia are formed slightly higher on the perianth tube than the others (Figs. 27A, 30A, 35A), which seems to be a result of the asymmetrical growth of the perianth. In the pentandrous species a single stamen primordium occupies the adaxial position (Figs. 35A, B, 36A), and no evidence of a vestigial stamen was detected. The presence of only 3 stamens reported by Pfeifer (1970) in *Aristolochia* was not observed in any of the studied species, nor has been reported elsewhere.

Shortly after stamen initiation, the developing anthers become progressively displaced towards the sides and separated from each other, due to the growth of a bulge on the upper part of the elongating ovary (Figs. 27B, 30B, 35B, 37B, 39A). The bulges are spatially and temporally connected to the carpellary septae below it (Figs. 29B, 30A,

Figure 27. *Aristolochia anguicida* (*González 3582*). A. Stamen initiation, side view; two stamen primordia removed. Bar = 50 µm. B. Stamens at the beginning of thecae differentiation, two of the gynostemium lobes become apparent towards the center; top view. Bar = 50 µm. C. Stamens with the thecae already differentiated, top view; the gynostemium lobes are beginning to overtop them. Bar = 0.1 mm. D. Late stage of development of the gynostemium lobes; top view. Bar = 0.1 mm. *gl*, gynostemium lobe; *st*, stamen.


A
st
B
C
D
gl

Figure 28. *Aristolochia pilosa* (*González 3571*). A, B. Transverse section of the same mid-stage floral bud through the gynostemium (A) and the ovary (B). A. Two lateral meristematic areas on the flanks of each gynostemium lobe (arrow) are distinct from the anther meristems; the vascular bundle of each lobe has become tangentially bifurcated (arrowheads). Bar = 100 µm. B. Ovary before the development of septae; each septum develops between the margins of two adjacent carpels (arrowheads). Bar = 50 µm. Bar = 100 µm. C. Longitudinal section of a floral bud at the time of the initiation of the gynostemium lobes (arrow). Bar = 100 µm. D. Longitudinal section of a floral bud showing the upwards growth of the primordia of the gynostemium lobes, the lateral displacement of stamen primordia, and the formation of the perianth-ovary abscission zone (arrow). Bar = 200 µm.


A
C
D

Figure 29. *Aristolochia trilobata* (*Gonzalez 3445*). A. Stamen initiation. Bar = 50 µm. B. Two stamen primordia at the time of the initiation of the gynostemium lobes (arrowhead). Bar = 50 µm. C. Slightly older stamen and gynostemium lobe primordium, with two distinct meristematic zones (arrows) forming the lobe. Bar = 50 µm. D. Stamens becoming overtopped by the gynostemium lobes; the two flanks at the top of one locule diverge towards two different gynostemium lobes (arrowheads). Bar = 0.1 mm. *gl,* gynostemium lobe; *se,* septum.

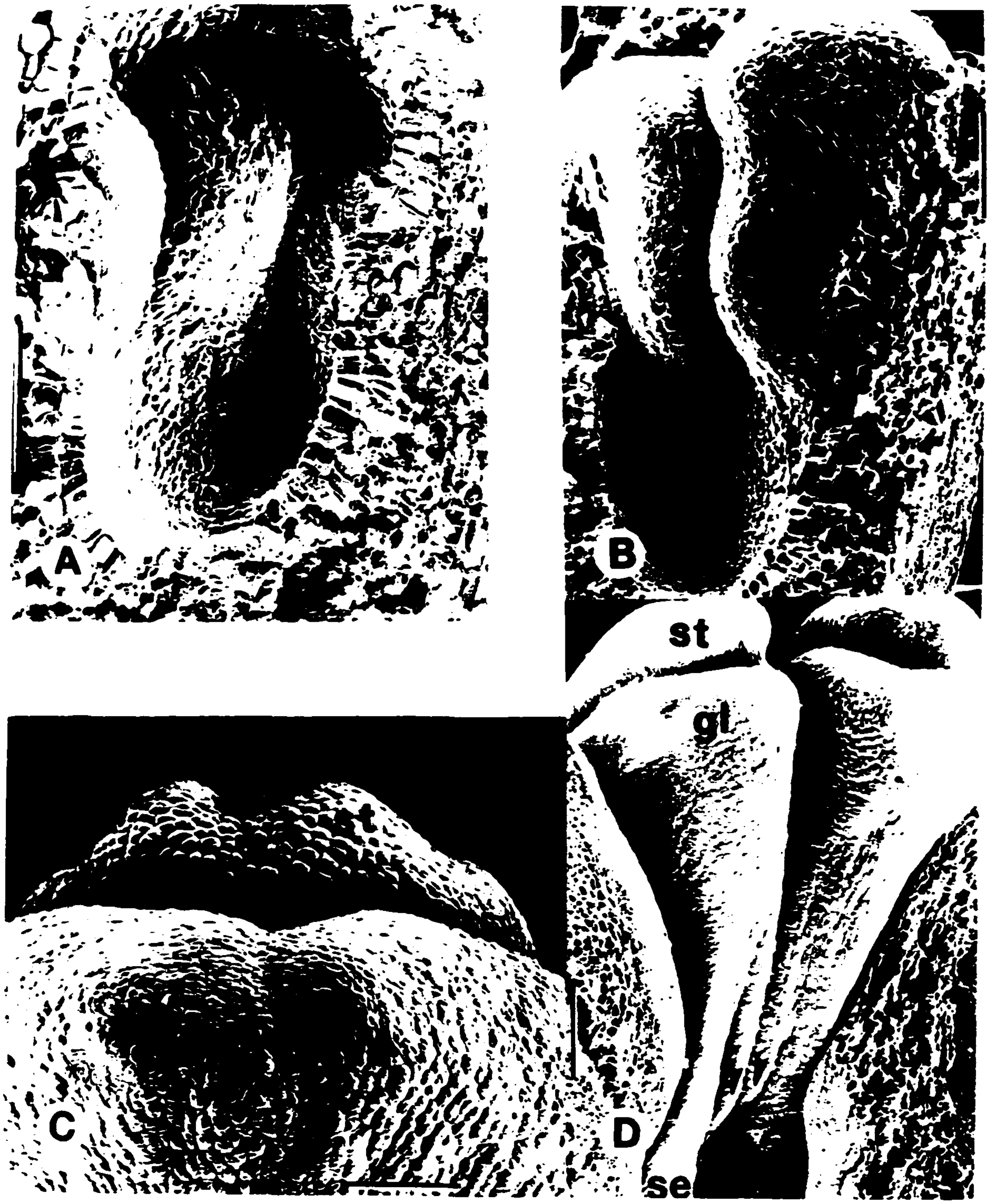
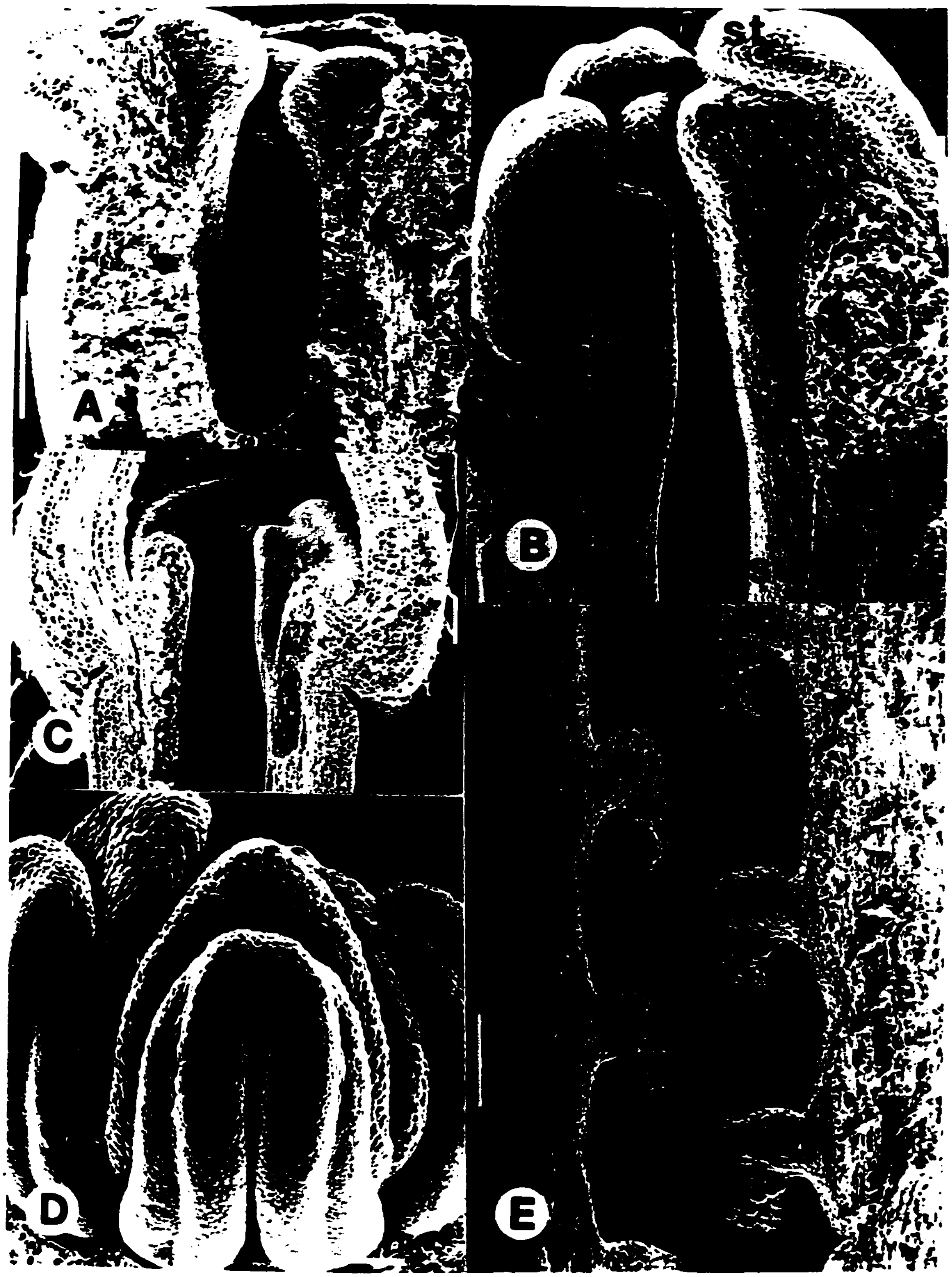

A
B
st
gl
C
D
se

Figure 30. *Aristolochia elegans* (*González 3442*). A. Longitudinal section of a young floral bud at the time of stamen initiation. B. Longitudinal section of a floral bud, showing the common development of the gynostemium lobes and the septae. C. A slightly older floral bud showing the anthers being overtopped by the gynostemium lobes. D. Gynostemium of a mid-stage floral bud; each stamen shows four pollen sacs. Bar = 0.1 mm. E. Longitudinal section of the ovary slightly before anthesis. In all, bar = 0.1 mm. *gl*, gynostemium lobe, *se*, septum; *st*, stamen.


A
B
st
C
D
E

B, 35C) but are in close contact with the adaxial side of the anther primordia because of the limited space on the narrowed floral bud. Beginning with early stages, each bulge appears to be formed by two different meristematic zones (Figs. 29C, D, 32 A, 35C, 37B, C, 39B). In transverse section, two meristematic areas on their flanks are visible (Figs. 28A, 44B).

The bulges begin to grow upwards and become the gynostemium lobes. The lobes reach the height of the anther primordia by the time the thecae are becoming apparent (Figs. 27C, 30B, 32A, 35B, 43A, C). Simultaneously, the septae along the developing ovary begin to grow inwards. Each septum develops exactly below each gynostemium lobe and form a continuous structure (Fig. 30B).

By the time the lobes overtop the anthers, four loculi are already visible on each anther (Figs. 30D, 37B, 43D). Usually the two abaxial stamens and their respective lobes are larger than the others (Figs. 27C, 30C, D). The sinuses between the gynostemium lobes are pushed upwards with ovary elongation and reach either the middle (e.g. *A. maxima*, Fig. 32B) or the upper level of the anthers (e.g. *A. anguicida*, Fig. 27D; *A. erecta*, Fig. 35D; *A. clematitis*, Fig. 39C; *A. zollingeariana*, Fig. 37 D-F). The ventral slits of the carpels end up between the gynostemium lobes (Figs. 28A, 29D, 30B, C, 35C, 37C).

In the flowers of *Aristolochia* subgenus *Siphisia* only three gynostemium lobes are formed (Figs. 5A, 41, 42C, 43A-C). The lobes are initiated at very early stages, and alternate with the three pairs of stamens (Figs. 41B, 42C, G, 43A). Each lobe incorporates, at least, the apical portion of each antesepalous carpel. Later on, the lobes overtop the anthers in height (Figs. 41D, 43C). Each of the anthers, however, bear its corresponding connective. The developing septae also form a continuous structure with the flanks of the lobes (Figs. 41C, D; 43B). As in the other subgenera, in the species of subgenus *Siphisia* the sinuses between the stigmatic lobes are pushed upwards with ovary elongation and reach the middle to the upper level of the anthers (Figs. 5A, 41E-F). By anthesis, the ventral slits of three alternating carpels end up between the gynostemium lobes, whereas the other three extend up near the top of each lobe (Figs. 41 D, F, 42C). In *A. reticulata* and *A. serpentaria*, some of the three lobes secondarily divide, forming a 4- or 5-lobed gynostemium (Fig. 43C, D), and the resulting lobes can also undergo minor, irregular divisions (Fig. 43D).

Shortly before anthesis, the stamens are oriented vertically or obliquely (Figs. 30D, 32B, 35D, 37D, E, 41E, F). Commonly, the anther epidermis develops hooked trichomes (Fig. 32B). Stamens bear a short connective extension above the microsporangia (Figs. 32B, 35D) which usually becomes partially covered by the flanks of the gynostemium lobe (Figs. 5C, 35D). The epidermis of the connective is different from that of the surrounding lobe, since the connective has a typical epidermis consisting of slightly stained, equilateral cells, with large vacuoles, and apparently no secretory function (Figs. 31C, 36G). The epidermis of the connective also develops hooked trichomes in some species (e.g. *A. acutifolia*).

By anthesis, the two flanks of each gynostemium lobe become clearly visible (Figs. 27D, 32B, 35D, 39B). The flanks form a continuous crest in which long, unicellular papillae develop (Figs. 32B, 33A, 37E, 39B, C). Papillae are secretory in all species examined. Most of the

Figure 31. *Aristolochia elegans* (*González 3442*). A. Longitudinal section of an early-stage floral bud (adaxial side to the right) showing the initiation of two stamen primordia (arrowhead). Bar = 50 µm. B, C. Transverse sections of a flower at the time of anthesis, through the upper (B, bar = 200 µm) and the lower levels of the gynostemium (C, bar = 250 µm); note the tangential branching of the vascular bundles (arrowheads). D. Conical trichome on the inner surface of the tube. Bar = 25 µm. *tt*, common pollen tube transmitting tissue.

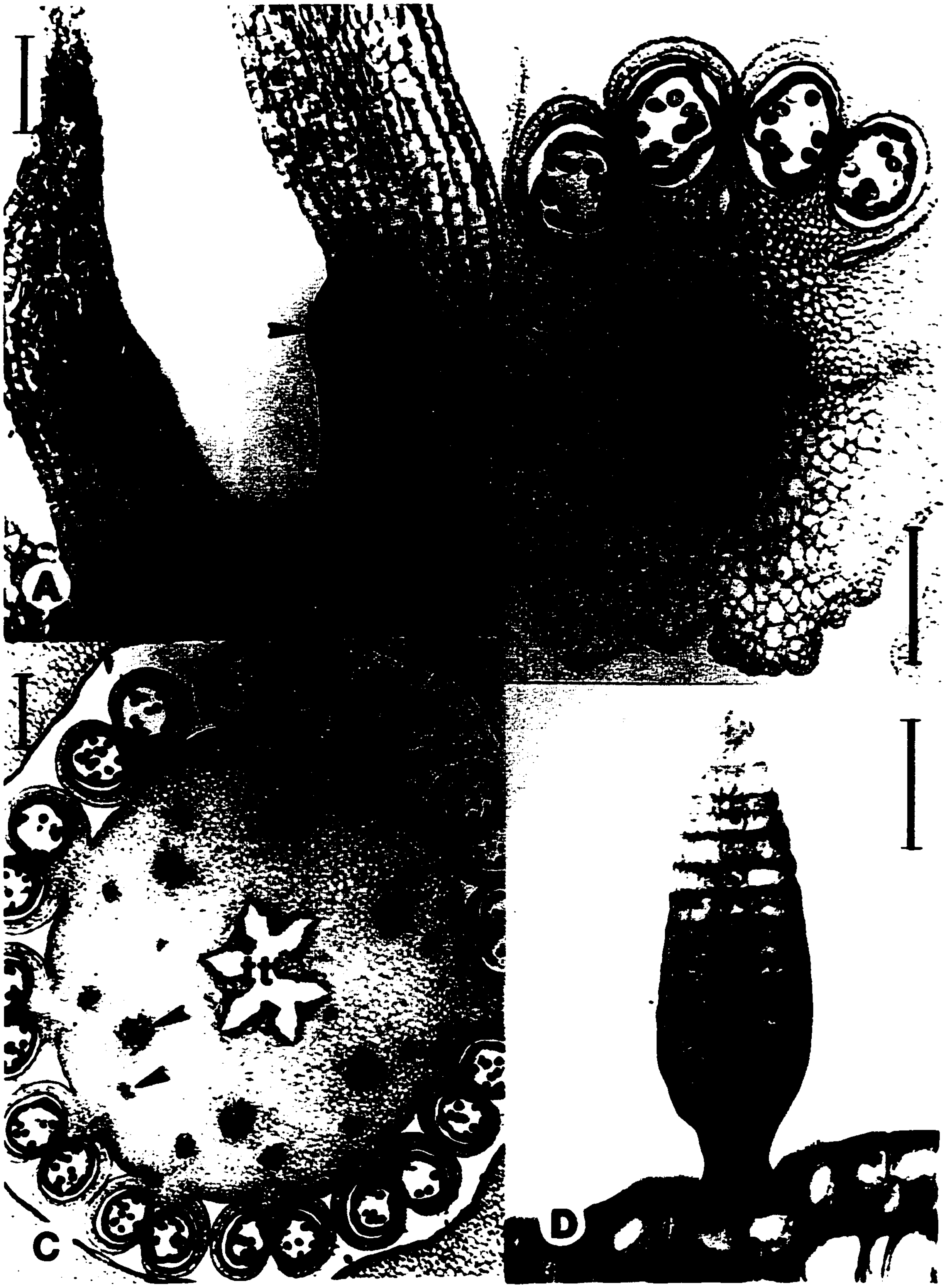
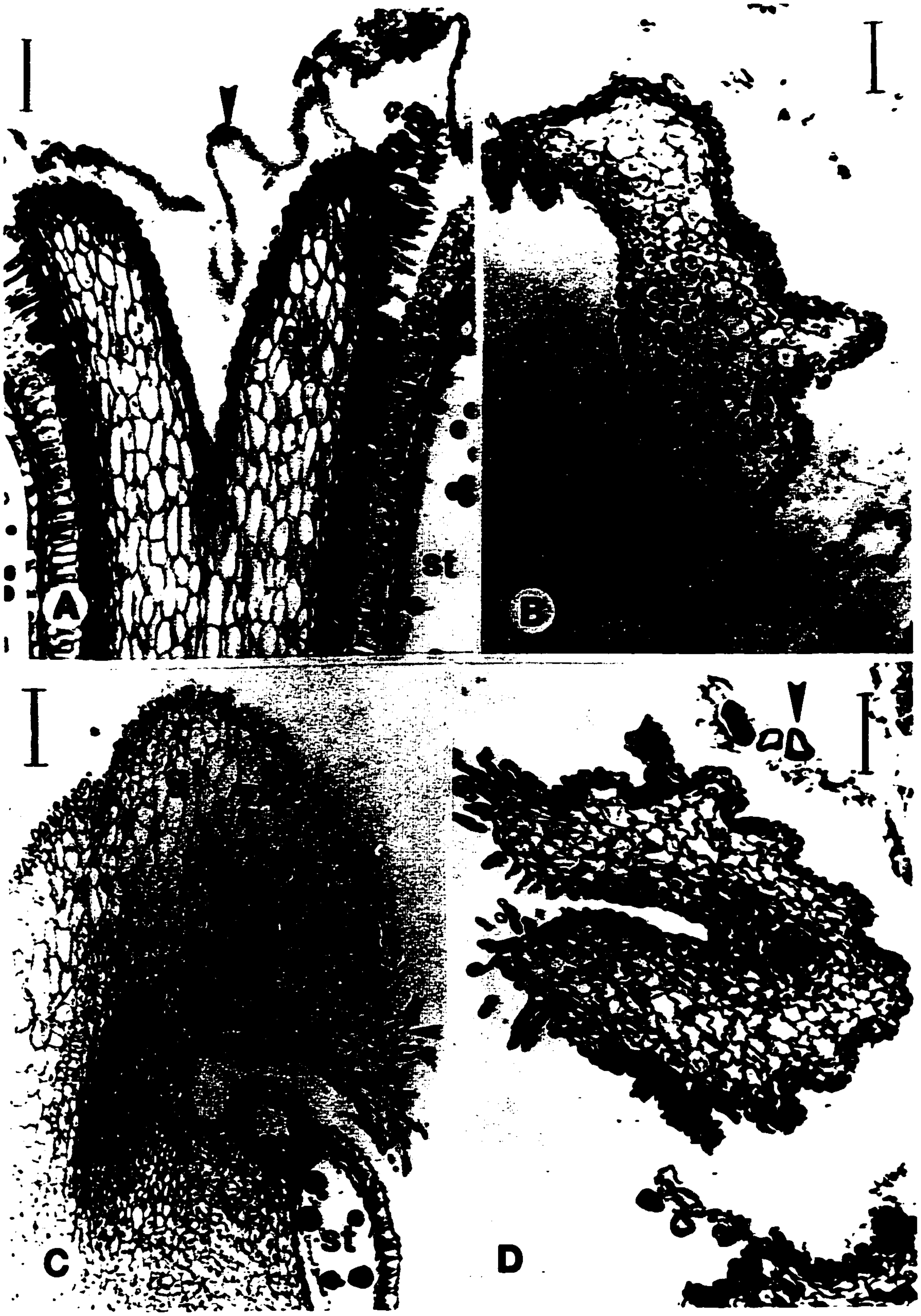

A
tt
C
D

Figure 32. *Aristolochia maxima* (*González 3289*). A. Gynostemium at the time the stamens are overtopped by the gynostemium lobes, top view. Bar = 0.1 mm. B. Gynostemium showing almost fully developed stamens, including a short connective extension (arrowhead); papillae at the flanks of each gynostemium lobe are becoming apparent. Bar = 0.1 mm. C. Multicellular, hooked trichomes 'floating' on the surface of the stigmatic secretion. Bar = 50 µm. D. Ovule at the time of anthesis, the micropyle facing the papillae along the placenta. Bar = 50 µm. *gl*, gynostemium lobe; *pl*, placenta; *st*, stamen.


A
st
B
g
C
D
pl

Figure 33. A, B. *A. maxima* (*González 3410*). A. Longitudinal section showing the region between two gynostemium lobes that are in close contact with the stamens; the lobes are covered with secretion (arrowhead). B. Transverse section of the tip of a gynostemium lobe covered with secretion; pieces of trichomes and pollen are visible on the surface of the secretion (arrowhead). C. *A. paucinervis (González 2551)*, longitudinal section of the tip of a gynostemium lobe; papillae are restricted to the base of the lobe (arrowhead). D. *A. pentandra (González 3603)*, transverse section through the tip of a gynostemium lobe covered with secretion; pieces of pollen are visible (arrowhead). In all, bar = 100 µm. *gl*, gynostemium lobe; *st*, stamen.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epidermal and subepidermal tissue of the stigmatic lobes seems to be also heavily secretory. By the time of anthesis, the top of the gynostemium is covered with a mucilaginous cap in which germinating pollen grains are often found (Figs. 33A, B, D, 37F, 39 C, D). The secretory epidermis is composed mainly of radially rectangular or papilliform thin-walled, heavily staining cells, rich in protoplasm (Figs. 33C, 36G, 42F-H). In some species (e.g. *A. acutifolia*; *A. pilosa*, Fig. 26F) hooked trichomes are also intermixed with the papillary surface of the gynostemium lobes. In *A. maxima*, multicellular trichomes with a hooked apical cell are found mostly on the inner surface of the gynostemium. These trichomes detach from the epidermis during the production of the mucilaginouos cap, and are found 'floating' on the surface of the secretion (Figs. 32C, 33A, B). From a functional viewpoint, the stigmas of *Aristolochia* can be considered as belong to the *W P* type (Heslop-Harrison, 1981), because they have receptive cells that are papillate and secretory. The present study provides further evidence that the receptive surface of the stigmas is papillate (Figs. 5C, 32B, 33, 37F, 39C, D); in a previous paper, Heslop-Harrison and Shivanna (1977) tentatively described the receptive surface in *Aristolochia* as non-papillate.

In the subgenera *Siphisia* and *Pararistolochia*, and especially in *Aristolochia* subsection *Diplolobus*, the innermost portion of the lobes forms a protrusion that overtops the papillate region at the time of anthesis (Figs. 33C, 37E, F, 39C, 42H). Consequently, the papillate region becomes situated towards the side and base of the gynostemium lobes. Hooker f. (1865) already noted this character in the stigmas of *A. goldieana*, a member of subgenus *Pararistolochia*. He described the stigmas of this species as being "swollen and apparently glandular apices of the stigmatic crura. The true position of the stigmatic surfaces is, in other species, marginal and decurrent on the lobes". In the species of subsection *Diplolobus* the papillae form a continuous roof-like rim above the stamens, and partially cover them (Figs. 33C, 37E, F; 38C, D, 39C; 40D). In the examined species of this series, most of the innermost parenchymatous cells of the tip of the gynostemium lobe appear to be densely secretory, as they become heavily stained (Figs. 38C, 40D).

The flanks and the inner surface of the gynostemium lobes form a common pollen tube transmitting tract, or compitum, that runs down to the locules (Figs. 28 C, D, 30B, C; 31C, C, 34E, F, 36E-G, 37C, E; 38B, C; 40D, 42E-G; 44B). The transmitting tissue is epidermal; the epidermal papillae and perhaps the subepidermal layer of this surface are highly secretory as revealed by their dense staining. Also a papillose epidermis is found through the inner sides of the placenta and around the funicles (Figs. 30E, 32D, 34F).

The development of the ovary proper occurs as follows. At very early stages, the ovary is circular at mid-level in cross section (Fig. 36B). Later, it becomes hexagonal (Fig. 40A) or (in the pentamerous species) pentagonal (Fig. 36D). Then, each side becomes slightly bilobed as a result of the first cell divisions of the placental regions at the carpellary margins (Figs. 28B, 34B, 44A). Shortly after that, basipetal initiation of the septae begins (see above; Figs. 29B, 30A, 34D, 35C, D, 36F, 39A, 41B). No evidence of a 3-4-carpellar gynoecium was found, contradicting previous reports by Wyatt (1955a) and Ortega (1987).

Figure 34. A, B. *Aristolochia maxima (González 3568)*, transverse section through the gynostemium (A, bar = 50 µm) and the ovary (B, bar = 100 µm) of one early-stage floral bud; note in A the tangential branching of the procambial strands (arrowheads), the outer branch supplying the stamen and the inner branch supplying the gynostemium lobe. Meristematic areas can also be seen on the flanks of the gynostemium lobes (arrow). C, D. *A. acutifolia (González 3358)*, transverse section through the gynostemium (C, bar = 100 µm) and the ovary (D, bar = 100 µm) of one floral bud; note in C the extension of the six locules (arrow) up to the level of the gynostemium. E. *A. maxima (González 3568)*, transverse section of the gynostemium at the time of anthesis; some veins are tangentially branched (arrowheads). Bar = 1 mm. F. *A. acutifolia (González 3358)*, transverse section through the ovary at the time of anthesis; the ventral carpellary slits remain open (arrowhead). Bar = 200 µm. *gl*, gynostemium lobe; *st*, stamen; *tt*, common pollen tube transmitting tract.

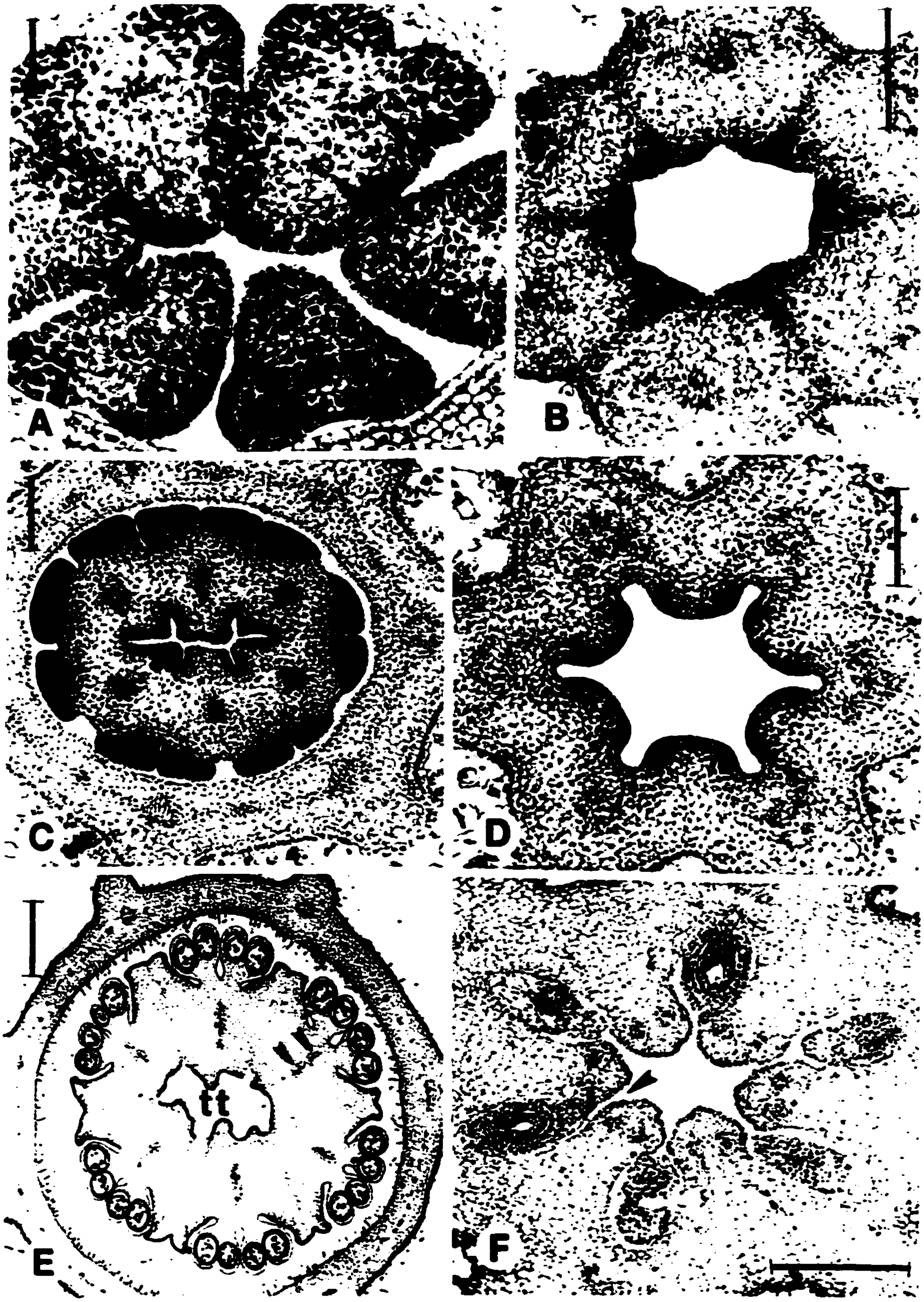
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Figure 35. *Aristolochia erecta* (*González 3593*). A. Stamen initiation, the primordium of the abaxial stamen is at the left. Bar = 50 µm. B. Gynostemium at the time the stamens are differentiated into two thecae; two gynostemium lobes are becoming apparent (arrowheads). Bar = 50 µm. C. Longitudinal section of a floral bud showing common development of each gynostemium lobe and its corresponding septum (arrow). D. Side view of the gynostemium showing the two flanks of a lobe overtopping the stamen, and the connective extending (arrowhead) above the anther. Bar = 0.1 mm. *gl*, half of a gynostemium lobe; *st*, stamen.

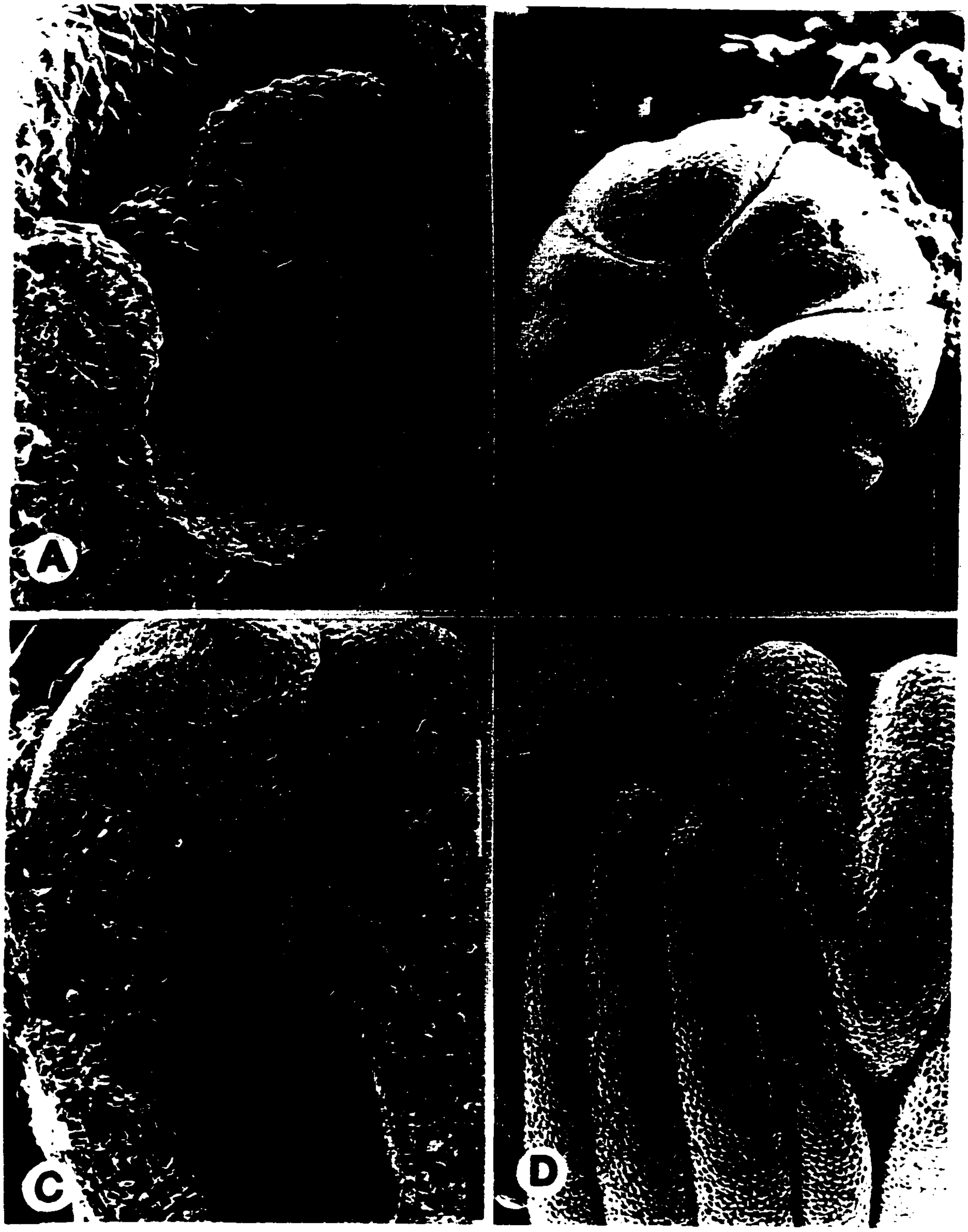
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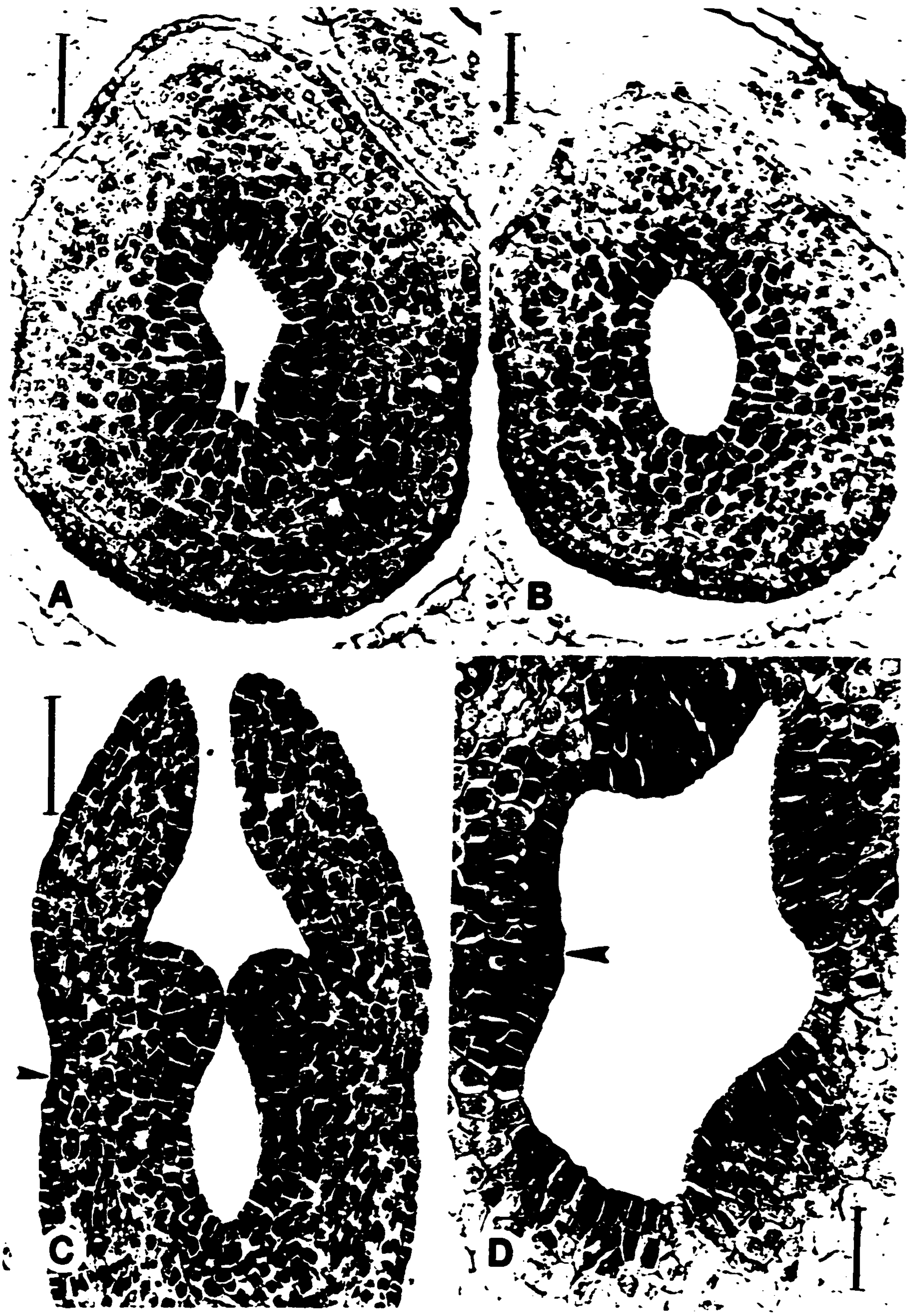
Figure 36. *Aristolochia erecta (González 3593)*. A, B. Transverse sections of one floral bud through the stamen primordia (A, bar = 50 µm) and the ovary (B, bar = 50 µm); only five stamens are initiated, the adaxial stamen primordium (arrowhead) occupies a median position. C. Longitudinal section of an early-stage floral bud showing the initiation of the stamens and the ovary-perianth abscission zone (arrowhead). Bar = 100 µm. D. Transverse section of the ovary at the time of septal initiation (arrowhead). Bar = 25 µm. E, F. Transverse sections of one floral bud through the gynostemium (E, bar = 100 µm) and the ovary (F, bar = 50 µm) at the beginning of septum ingrowth; the flank meristems (arrow in E) and the locules extend up to the gynostemium level. G, H. Transverse sections of one floral bud through the gynostemium (G, bar = 250 µm) and the ovary (H, bar = 100 µm); the vascular supply for each gynostemium lobe is tangentially bifurcated (arrowheads).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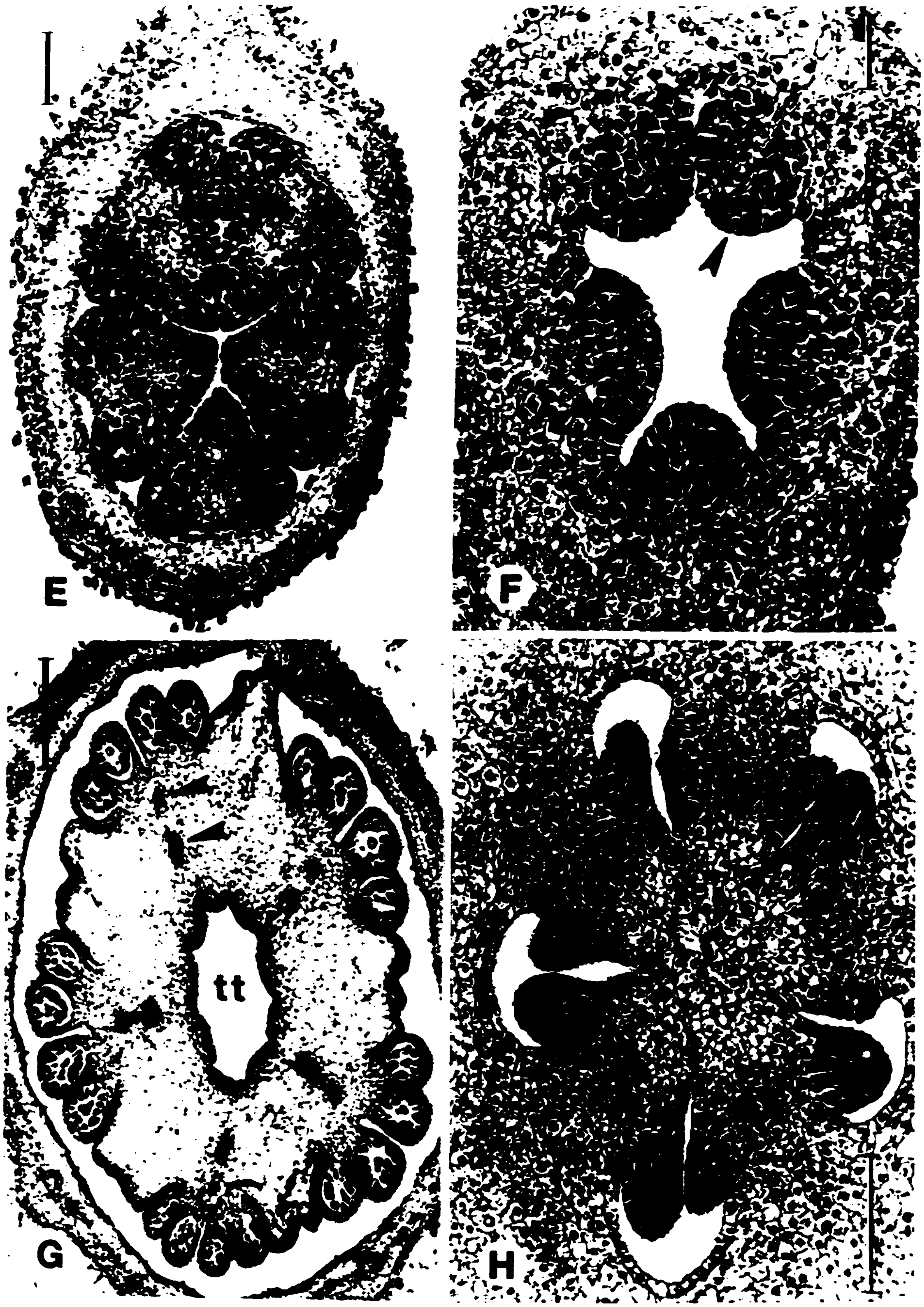
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Figure 37. *Aristolochia zollingeriana* (*Tsou 1175*). A. Early-stage floral bud, longitudinal section, showing stamen and ovary initiation. Bar = 50 µm. B. Gynostemium, top view, the lobes becoming apparent towards the center (circle). Bar = 0.1 mm. C. Mid-stage floral bud, longitudinal section, showing the connections between the septae (white arrow) at the level of the abscission zone (black arrows). Bar = 0.1 mm. D. Gynostemium, side view; the gynostemium lobes have overtopped the anthers. Bar = 0.1 mm. E. Gynostemium, longitudinal section, showing the papillose roof-like rim above the anthers (arrowhead). Bar = 0.1 mm. F. Gynostemium at late anthesis; the papillose rim appears as a continuous, distinct structure (arrowhead). Bar = 0.5 mm.

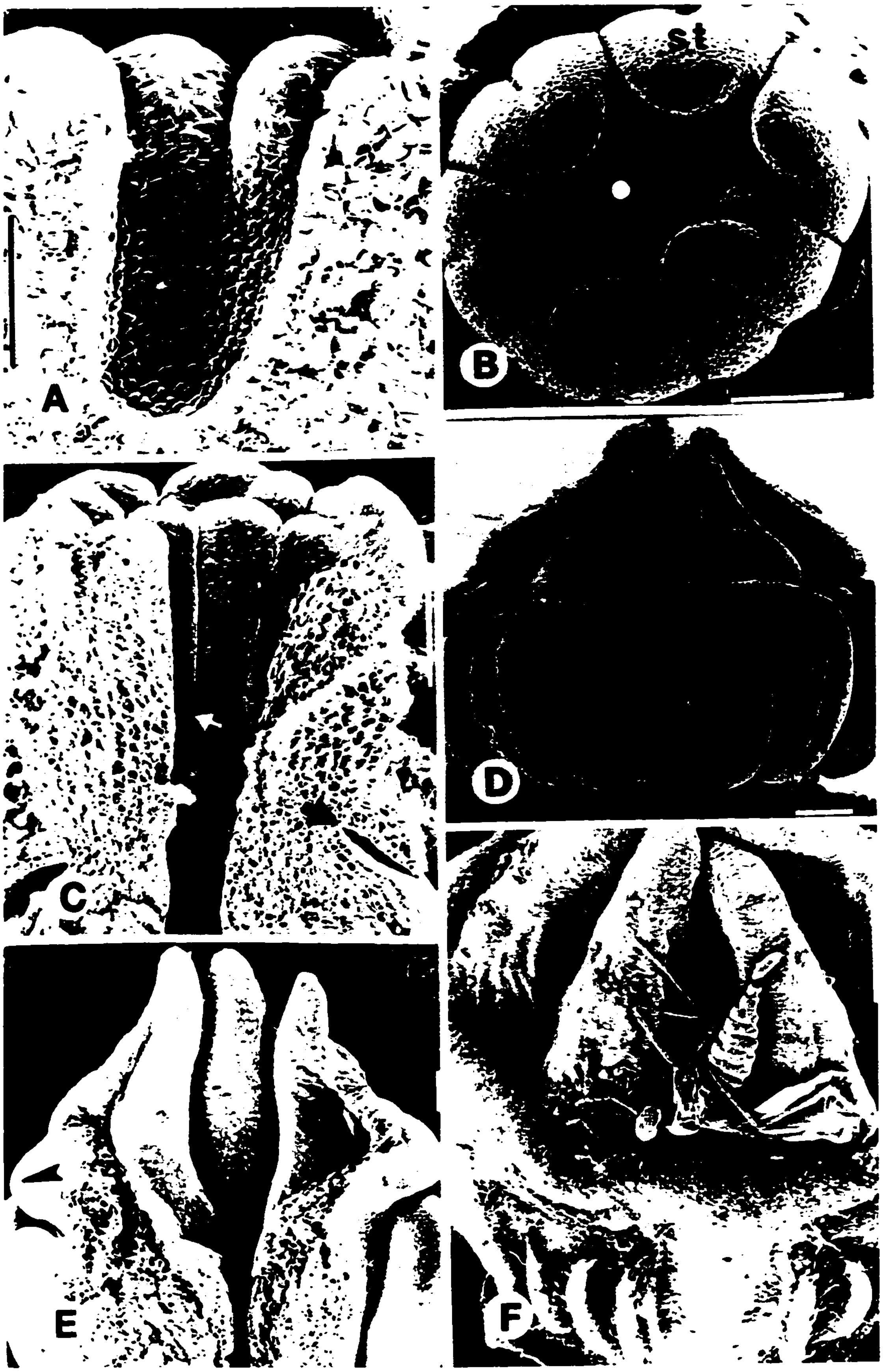
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Figure 38. *Aristolochia zollingeriana* (*Tsou 1175*). A. Transverse section through the ovary of a mid-stage flower. Bar = 100 µm. B-D. Transverse sections of a floral bud through the basal (B), middle (C) and apical (D) levels of the gynostemium; note the tangentially bifurcated veins (arrowhead in C), and the round common transmitting tract becoming 6-lobed towards the apex (D). The inner, massive structure in D corresponds to the roof-like rim above the anthers (compare to Fig. 39E). In all, bar = 250 µm. *tt*, common pollen tube transmitting tract.

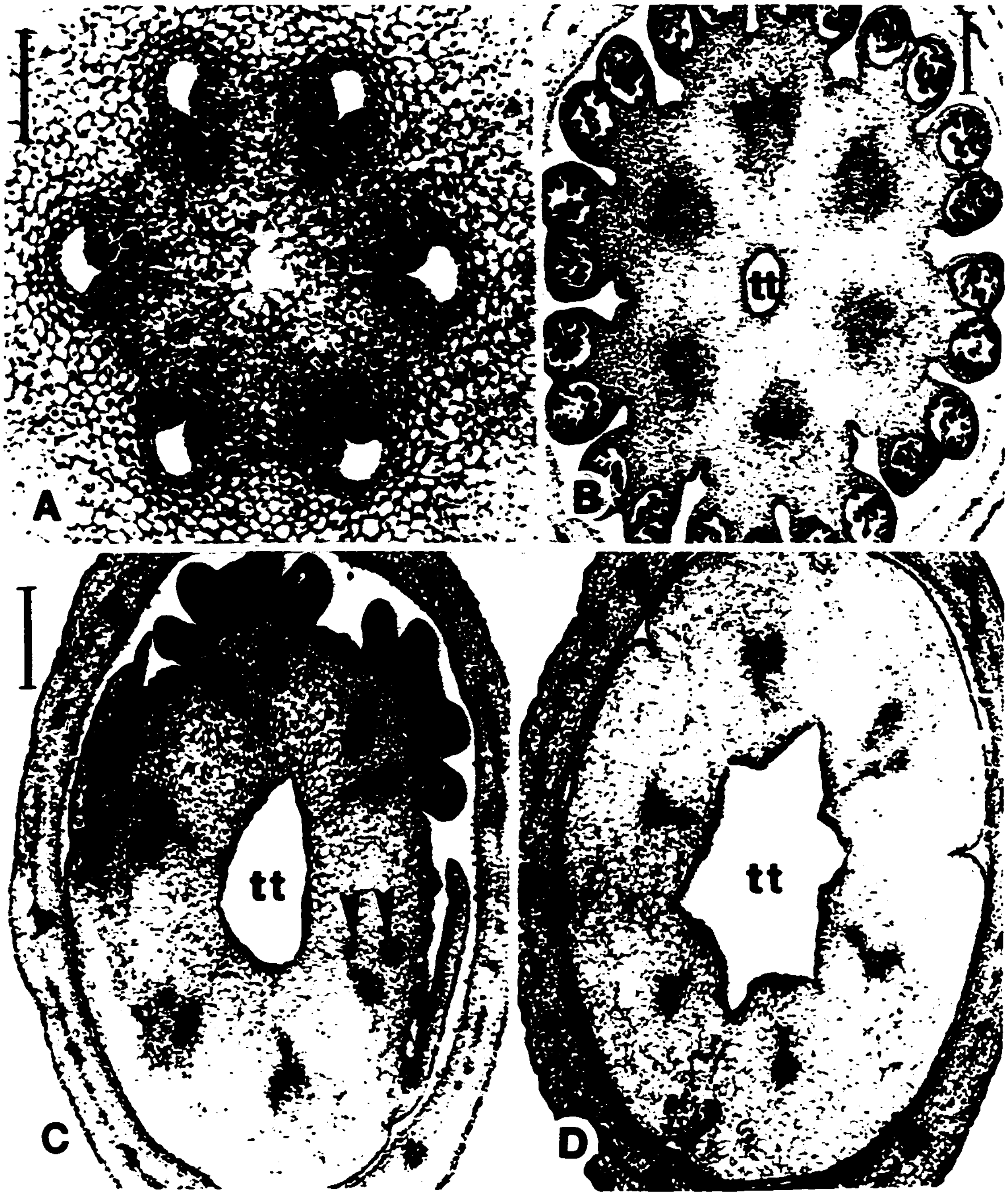
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Figure 39. *Aristolochia clematitis (González 3446)*. A. Mid-stage floral bud, longitudinal section, showing the continuous extension of the gynostemium lobes and the septae, and the transverse connections between the septae (arrowheads). Bar = 0.1 mm. B. Gynostemium shortly before anthesis; the stigmatic lobes have overtopped the anthers and the papillose roof-like rim is becoming apparent. Each lobe displays two flanks (arrowheads). Bar = 0.1 mm. C. Gynostemium at late anthesis; the papillose rim appears as a continuous, distinct structure. Bar = 0.5 mm. D. Detail of the papillose rim with germinating pollen grains. Bar = 50 µm.

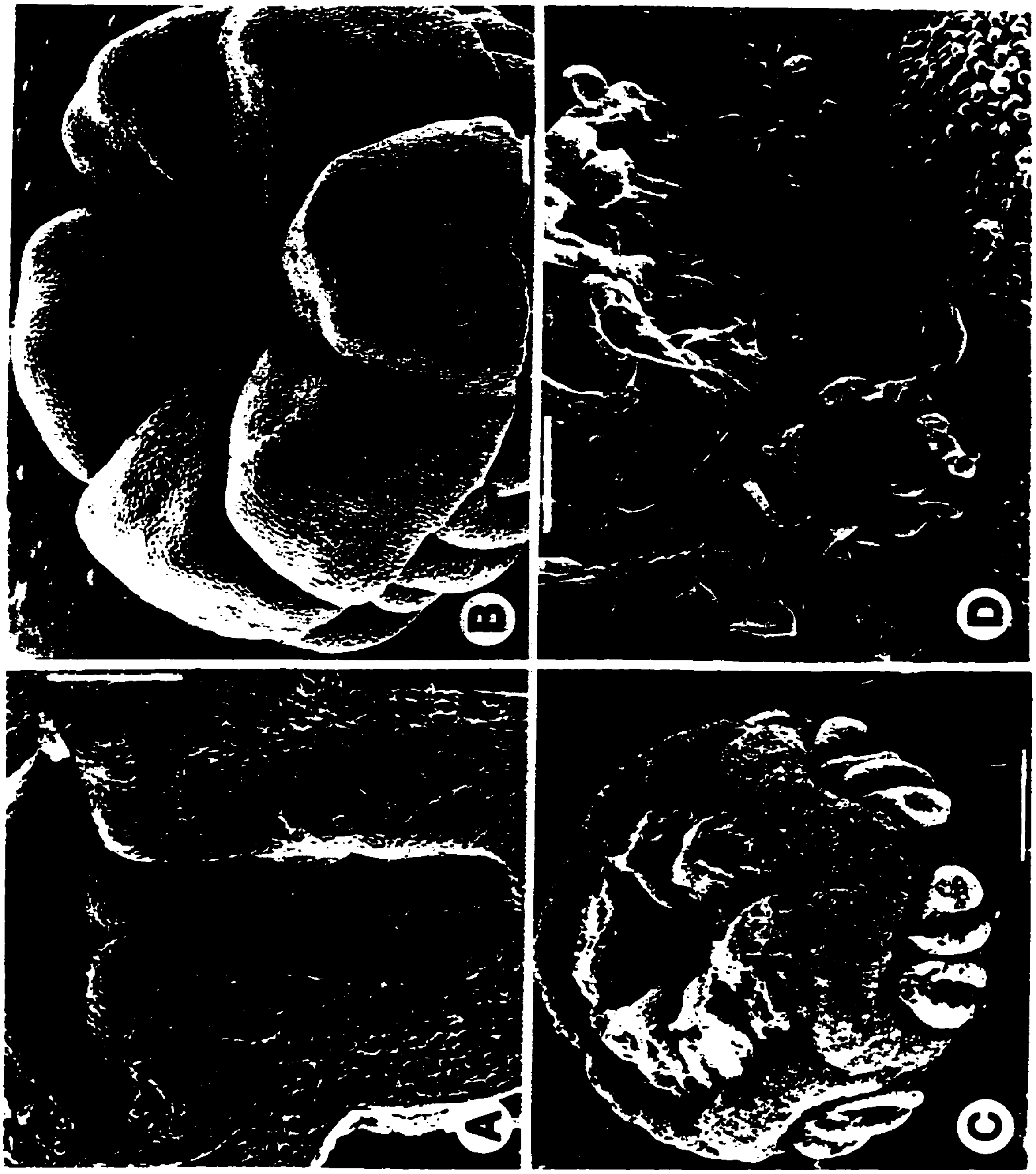
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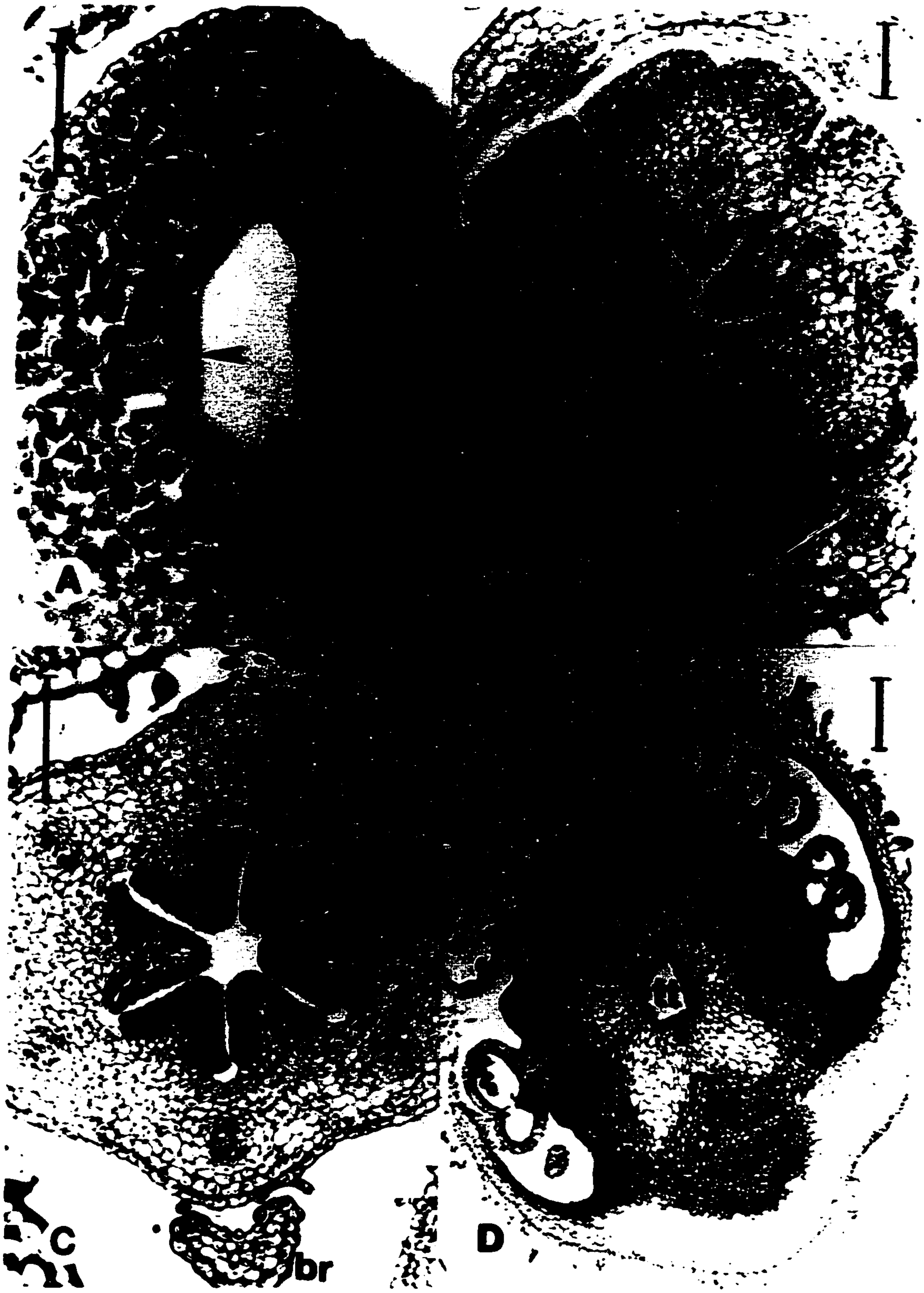
Figure 40. A-C. *Aristolochia pistolochia (Vargas* s.n.). A. Transverse section through an early floral bud, showing the ovary at the time of initiation of the septae (arrowhead). Bar = 50 µm. B, C. Transverse section of one middle-stage floral bud through the gynostemium (B, bar = 100 µm) and the ovary (C, bar = 200 µm); note in B the extension of the six locules and the flank meristems (arrow) above the level of the ovary (arrow). D. *A. paucinervis (González 2551)*, transverse section of a floral bud through the mid-level of the gynostemium, the papillose rim (arrowhead) surrounding the stamens. Bar = 250 µm. *br,* bract; *tt,* common pollen tube transmitting tract.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In all species studied, the ovary is completely syncarpous. The septae are formed from the fused margins of adjacent carpels. Carpels become plicate, as the septae develop inward (Figs. 30B, C, 34D, 36F, 37C, 40C, 41C, D, 42B, D, 43B, 44C). No evidence of carpel peltation was found at any developmental stage.

By the time the gynostemium lobes overtop the anthers, the septae become adjacent by inner proliferation. With the proliferation of the septae, the initially peripheral placentary areas are now located on the sides of the developing septae, and become secondarily submarginal (Figs. 34F, 36H, 42F, 44C). By anthesis, the inner carpellary epidermis along the placentae has become papillate (Fig. 32D). Crystals and oil cells are scattered throughout the ovary, and stomata are commonly found in the inner ovary wall.

In the majority of the species examined (Table VI), the ventral slit of each carpel is postgenitally fused prior to anthesis by means of interlocking through interdigitation of the marginal cells of the slits (Figs. 36H, 38A, 42F). Usually, the fusion is so complete that epidermal cells are no longer evident, and the ventral (placental) bundles may also anastomose (Fig. 42F). In some species, the parenchymatic cells towards the center of the fused carpels break down and become reabsorbed (e.g. *A. zollingeriana*, Fig. 38A). Open carpellary slits at the time of anthesis were detected only in *Aristolochia acutifolia* (Fig. 34F), *A. clematitis*, *A. maxima* and *A. paucinervis*.

The ovary of *Aristolochia* is open at the top; this resembles the ovary of *Thottea*, which is "not covered by a roof as usual, but is open

Figure 41. *Aristolochia arborea (González 3415)*. A. Longitudinal view of a floral bud showing stamen initiation. Bar = 50 µm. B. Slightly older floral bud showing the initiation of a gynostemium lobe between two stamen primordia. Bar = 50 µm. C. Longitudinal section showing two gynostemium lobes that are formed on top of the corresponding loculae. Bar = 0.1 mm. D. Longitudinal section showing the gynostemium lobes, postgenitally fused (arrowhead), at the time they overtop the anthers. E. Gynostemium, side view, showing two converging stamens. Bar = 0.1 mm. F. Gynostemium at the time of anthesis, showing the three main lobes and the six septal extensions (arrowhead) toward the center. Bar = 0.5 mm. gl, gynostemium lobe; se, septum; st, stamen.

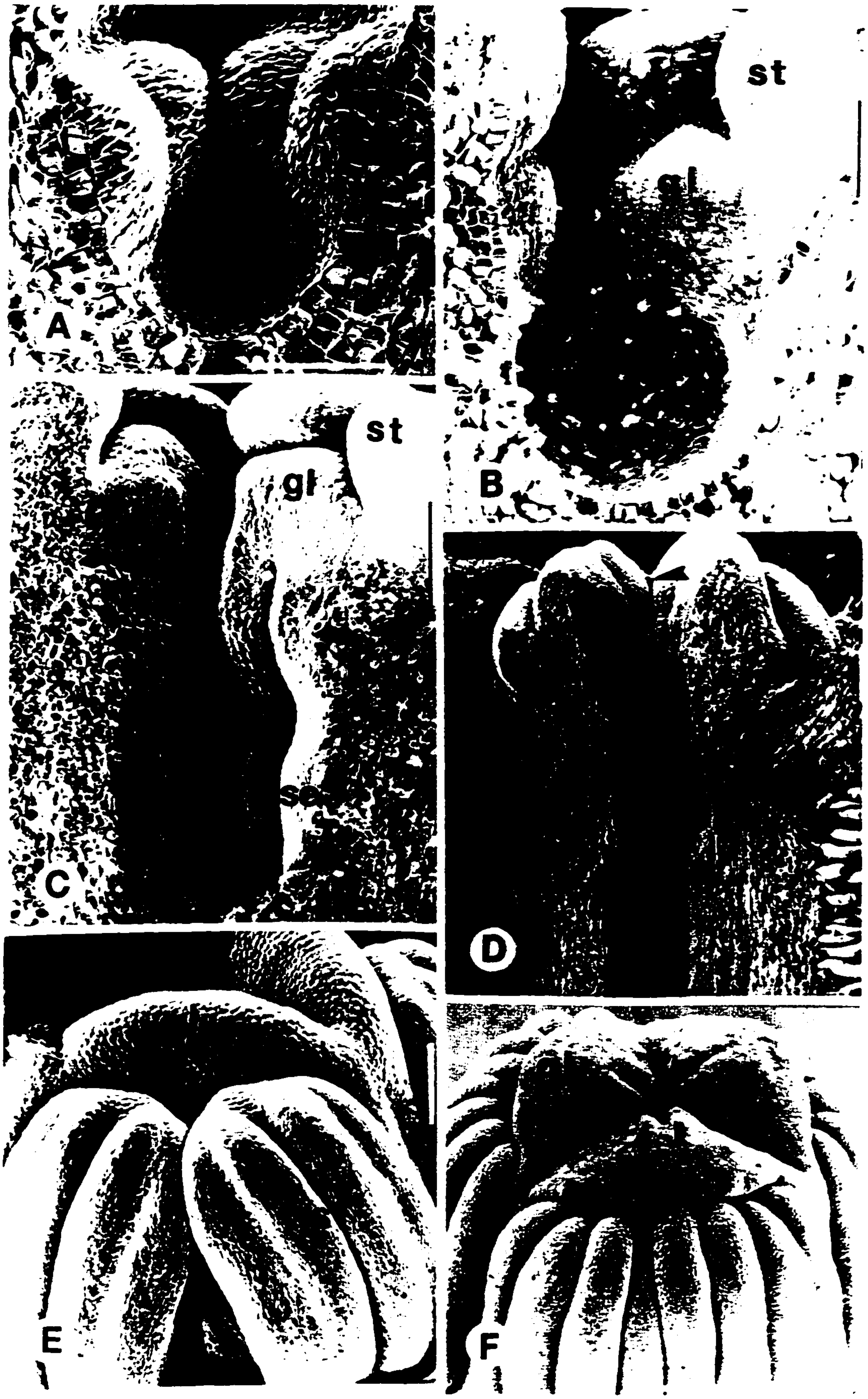
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Figure 42. *Aristolochia macrophylla (González 3421)*. A. Young floral bud, longitudinal section, showing the distinct stamen (upper arrow) and gynostemium (lower arrow) primordia. Bar = 100 µm. B, C. Transverse section of a floral bud through the ovary (B, bar = 50 µm) and the corresponding gynostemium (C, bar = 200 µm); note in C the gynostemium lobes alternating with the stamens, and the distinct vascular supply (arrowheads) for the lobes and the stamens. D. Transverse section of the mid-stage floral bud through the ovary at the beginning of the postgenital fusion of the septae (arrowhead). Bar = 100 µm. E, F. Transverse sections through the gynostemium and ovary of a late-stage floral bud (E, bar = 250 µm) (F, bar = 100 µm); note in F the complete postgenital fusion of the septae (arrowhead). G. Gynostemium at the time of anthesis, the vascular bundles tangentially bifurcated (arrowheads). Bar = 250 µm. H. Longitudinal section of the tip of the gynostemium lobe; papillae are apparent at the base of the lobe (arrowhead). Bar = 200 µm. *tt*, common pollen tube transmitting tissue.

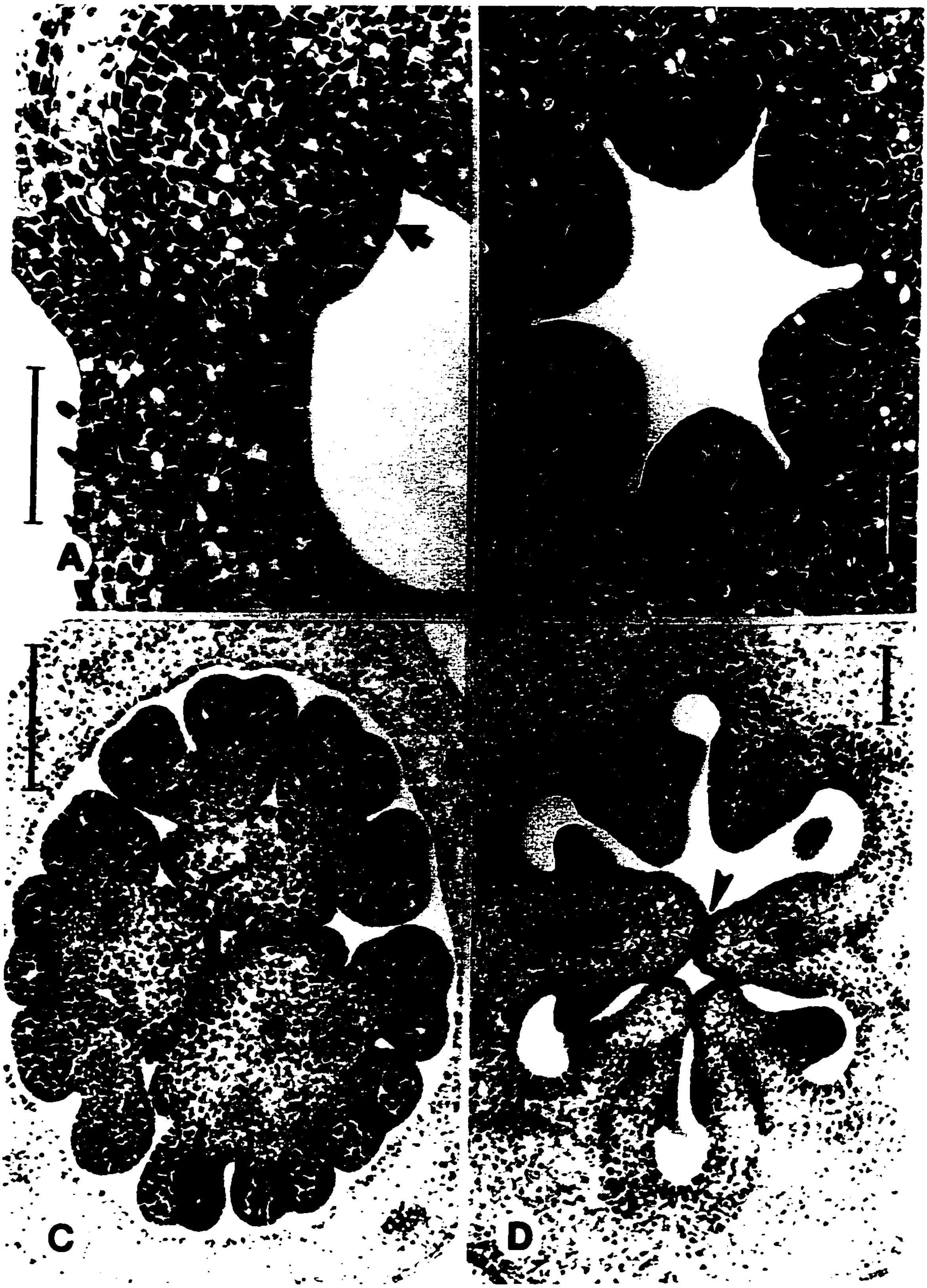
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Figure 43. *Aristolochia reticulata (González 3594)*. A. Stamens surrounding the three recently initiated gynostemium lobes (circle). Bar = 50 µm. B. Longitudinal section showing two gynostemium lobes alternating with the stamens; the gynostemium lobes are formed on top of the corresponding loculae. Bar = 0.1 mm. C. Gynostemium with one of the three stigmatic lobes secondarily divided (arrowhead), top view. Bar = 100 µm. D. Gynostemium shortly before anthesis, one of the three lobes displaying minor, irregular divisions (arrowhead), top view. Bar = 0.1 mm. *gl*, gynostemium lobe; *st*, stamen.

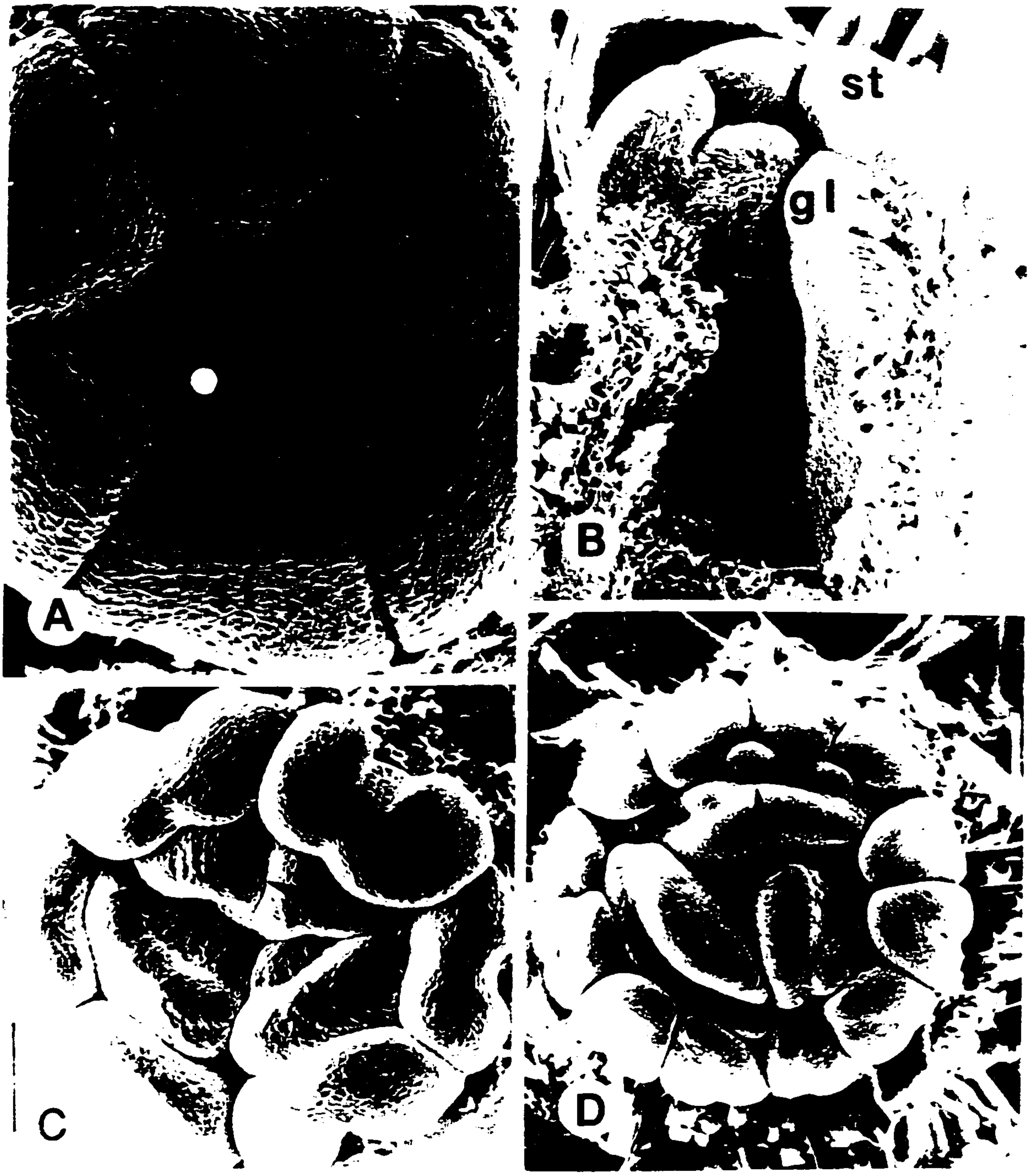
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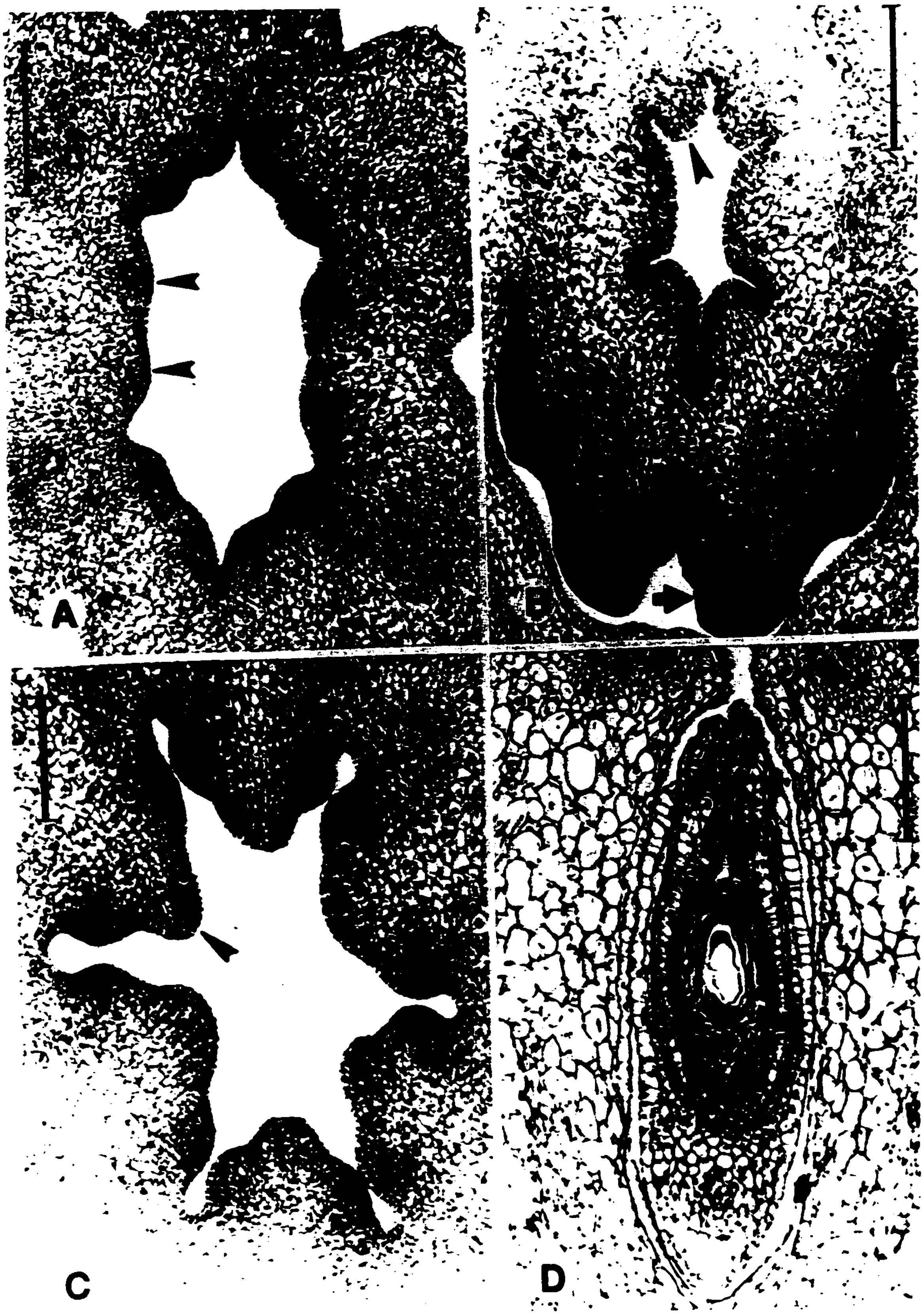
Figure 44. *Aristolochia ringens (González 3575)*. A. Transverse section through the ovary before septae initiation; carpellary margins are evident (arrowheads). B, C. Transverse section of one floral bud through the gynostemium (B) and the ovary (C); septae (arrowhead) develop as a continuous structure that reaches the level of the gynostemium (arrowhead in B; arrow indicates the stamen). D. Transverse section of an ovule at the time of anthesis. In all, bar = 100 µm.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above" (Leins & al., 1988:369). My observations of *T. siliquosa* confirm this interpretation (Fig. 2C). However, with the formation of the three gynostemium lobes in some species of *Aristolochia* subgen. *Siphisia*, a roof-like structure is formed on top of only three of the 6 carpels (Figs. 41B-D, 43B). Also, a slight transverse connection between the septa just above the locules was detected in *A. clematitis* (Fig. 39A), *A. leuconeura*, *A. trilobata*, and *A. zollingeriana* (Fig. 37C).

In many neotropical species of *Aristolochia*, the top of the ovary becomes strongly asymmetrical, thus displacing the perianth and the gynostemium to a sharp angle from the ovary (Fig. 23D). In that way, the flowers keep a position such that the utricle remains horizontal or pendulous, and the tube-limb portion remains ascending and more or less vertical in resupinate flowers.

Ovule development runs bidirectionally from the middle level of the ovary. Each carpel produces two rows of submarginal ovules (Figs. 30E, F, 34D, 36H, 38A, 40C, 42D, 44C), one at each side of the inner surface of each carpel; although there have been reports of ovules in one row (Bowman, 1973; Le Maout & Decaisne, 1873; Wyatt, 1955a), this was not found in any of the species examined in this study.

At anthesis, ovules in all species under study are anatropous, crassinucellate, bitegmic, and endostomic. The funicle is massive, and is fused to the ovule throughout its length (Figs. 30E, 32D). Each ovule is directly vascularized by a trace that comes from the ventral carpellary bundles. The ovular trace terminates near the chalaza. The micropyle faces the papillate epidermis of the adjacent placentae (Fig.

32D). The outer integument is more or less entire and formed by two cell layers; the inner by two or three cell layers (Fig. 44D), although in the micropylar region it can become 4-5-layered.

Floral vasculature

Peduncle and ovary

Six (five in pentandrous species) main vascular bundles are found in the floral peduncle of *Aristolochia, Euglypha* and *Holostylis*; just below the ovary, each of these bundles gives off two small lateral strands of phloem that converge toward the center, thus forming the two ventral (placentary) bundles of each carpel. The dorsal carpellary bundles run throughout the length of the ovary without splitting. The ventral bundles become inversely oriented and end blindly at the apex of the ovary, contrary to the report by Nair and Narayanan (1962) that the placental bundles anastomose with the dorsal carpellary bundles. In some species (as in *A. elegans,* Fig. 31B; see also Wyatt, 1955a) the ventral bundles continue up and reach the gynostemium. Pentandrous species present essentially the same basic pattern, but the basic number is five (Figs. 36A, 48A).

Perianth

The dorsal carpellary bundles that enter the perianth give off small, lateral strands that usually anastomose with adjacent bundles and form a plexus at the base of the perianth. The plexus may be complete, as

Figure 45. Floral vasculature. A-B. *Saruma henryi*. A. Plexus at the base of the perianth. B. Petal (arrowhead indicates abscission zone). C-D. *Asarum canadense*. C. Plexus at the base of the flower. D. Flower, side view. E-F. *Thottea siliquosa*. E. Plexus at the base of the flower. F. Flower, side view. *M*, middle vein of each sepal. In all, thin and dotted lines to the outside of the plexus indicate second and third order, longitudinal veins, respectively; thin lines to the inside indicate carpel (long, not present in *Thottea*) and stamen (short) vascular supply. *P*, petal traces. *C*, veins in commissural position (i.e. between the perianth parts).

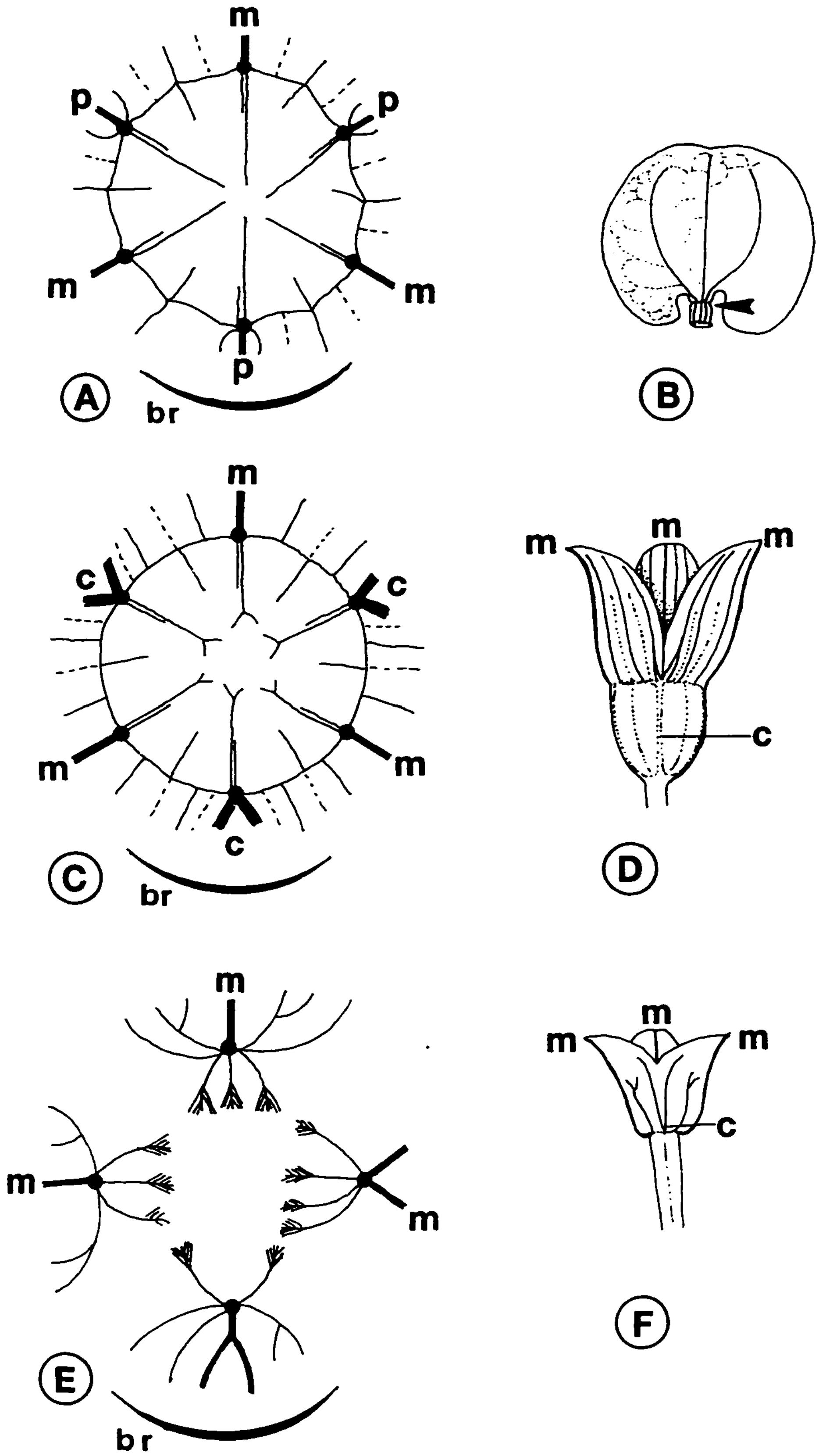
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Figure 46. Floral vasculature. A-B. *Aristolochia macrophylla*. C-D. *A. stevensii*. E-F. *A. deltantha*. In all, the plexus at the base of the perianth is to the left; thin lines to the outside of the plexus are second order, longitudinal veins; thin lines to the inside are the vascular supply of the gynostemium. The flowers in side view (right) show the extensions of the middle *(M)* and commissural *(C)* veins along the perianth. *br*, bract.

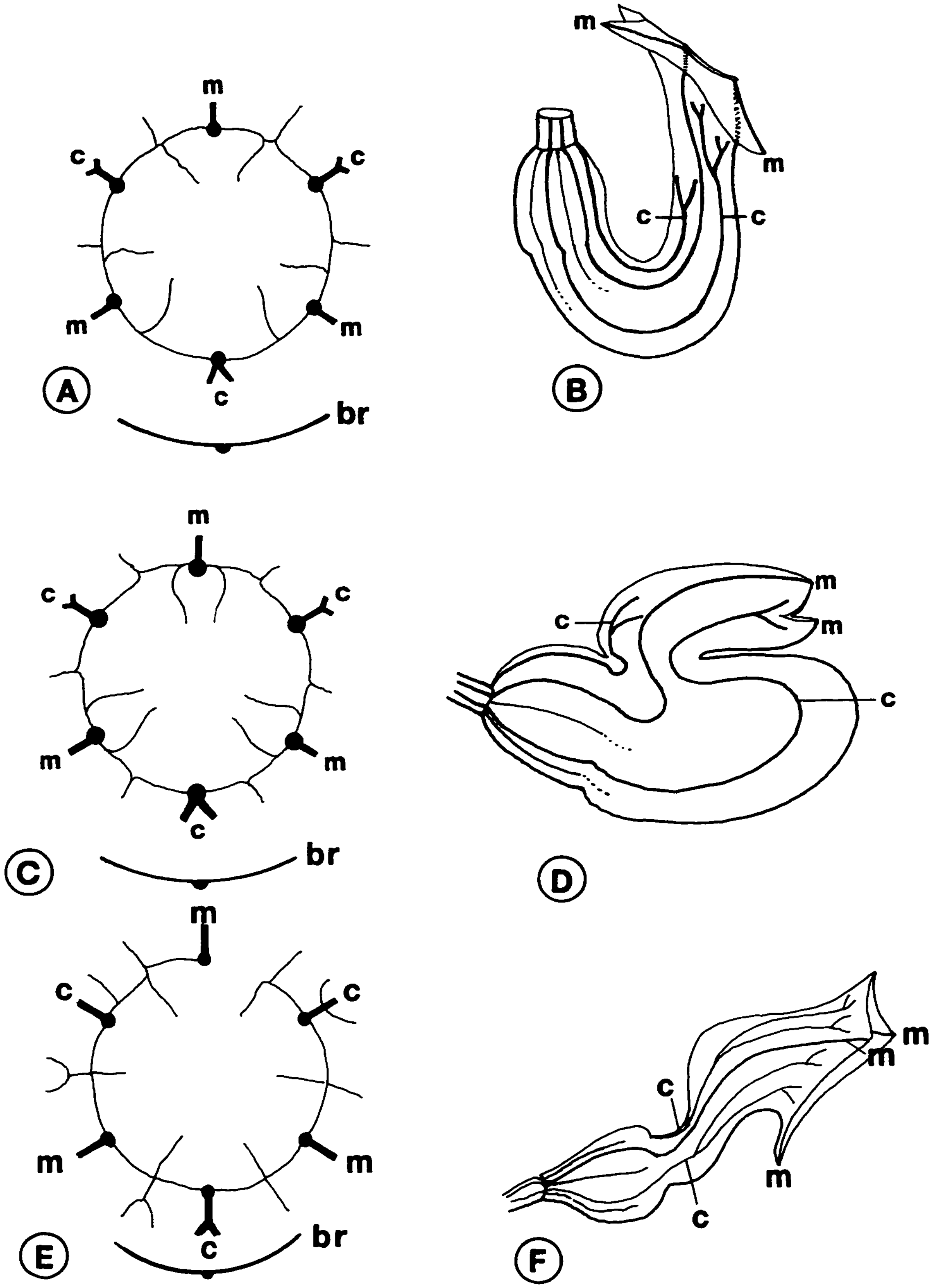
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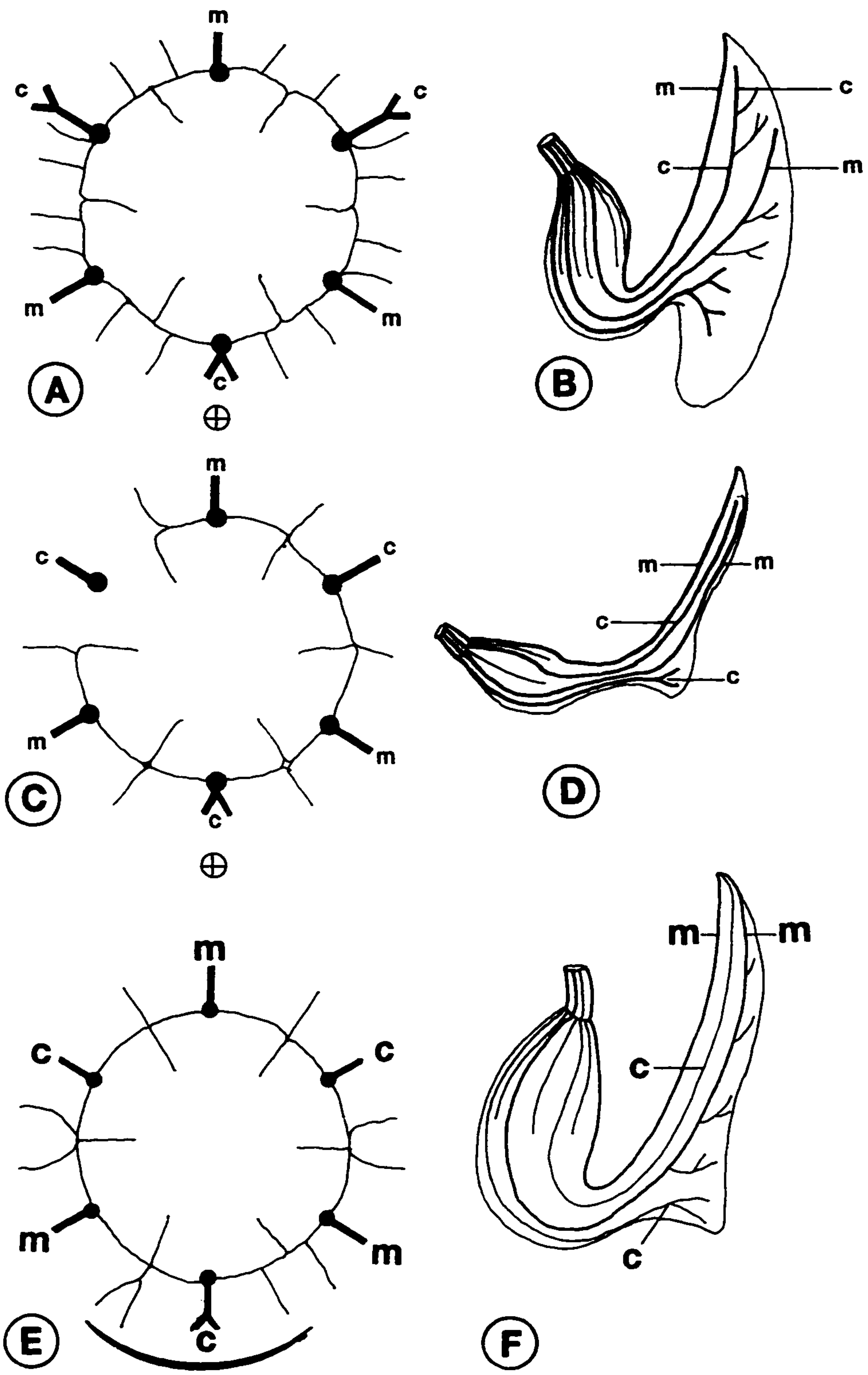
Figure 47. Floral vasculature. A-B. *Aristolochia odoratissima*. C-D. *A. pilosa*. E-F. *A. maxima*. In all, the plexus at the base of the perianth is to the left; thin lines to the outside of the plexus are second order, longitudinal veins; thin lines to the inside are the vascular supply of the gynostemium. The flowers in side view (right) show the extensions of the middle *(M)* and commissural *(C)* veins along the perianth. *br*, bract.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in most species of *Aristolochia* (Figs. 46A,C; 47A, E, 47C, E; Table VI), as well as in *Euglypha* (Fig. 49E) and *Holostylis* (Fig. 49G); or may be variously incomplete because some of the lateral strands do not form (Table VI; Figs. 46E, 47C, 48A, 49A,C). In most species, second order longitudinal veins that supply the base of the perianth depart as outer traces from the aforementioned plexus (Table VI). These veins depart more or less half-way between the dorsal bundles and opposite the inner branch that serves each of the gynostemium lobes (Figs. 46-49). The plexus is extremely poorly formed, and the second order, longitudinal, veins that supply the perianth base are lacking in the species of *Aristolochia* subsection *Diplolobus* examined (Table VI; Fig. 48A, C). Higher order venation, alike in all the species examined, is coarsely reticulate, with free vein endings.

The perianth in species of subgenera *Siphisia* and *Pararistolochia* has a common vascular pattern (Fig. 46). Each of the three main veins reaches the corresponding tip of the perianth parts. The middle vein runs longitudinally through the convex side of the perianth, to the apex of the median lobe. Three commissural veins alternate with them, and run longitudinally until a point near the commissures of the perianth lobes where they branch and anastomose with higher order veins.

In species of *Aristolochia* subgenus *Orthoaristolochia*, the middle vein is easily distinguished along the abaxial side of the flower (Figs. 47, 48A, B, E, F, 49A-D). The two veins corresponding to the mid-veins of the lateral perianth parts develop along the flanks of the floral bud, shortly before higher order veins develop. These two veins are less conspicuous, because their lobes are smaller and more completely fused

Figure 48. Floral vasculature. A-B. *Aristolochia pentandra*. C-D. *A. grandiflora*. E-F. *A. ringens*. In all, the plexus at the base of the perianth is to the left; thin lines to the outside of the plexus are second order, longitudinal veins; thin lines to the inside are the vascular supply of the gynostemium. The flowers in side view (right) show the extensions of the middle *(M)* and commissural *(C)* veins along the perianth. *br*, bract.

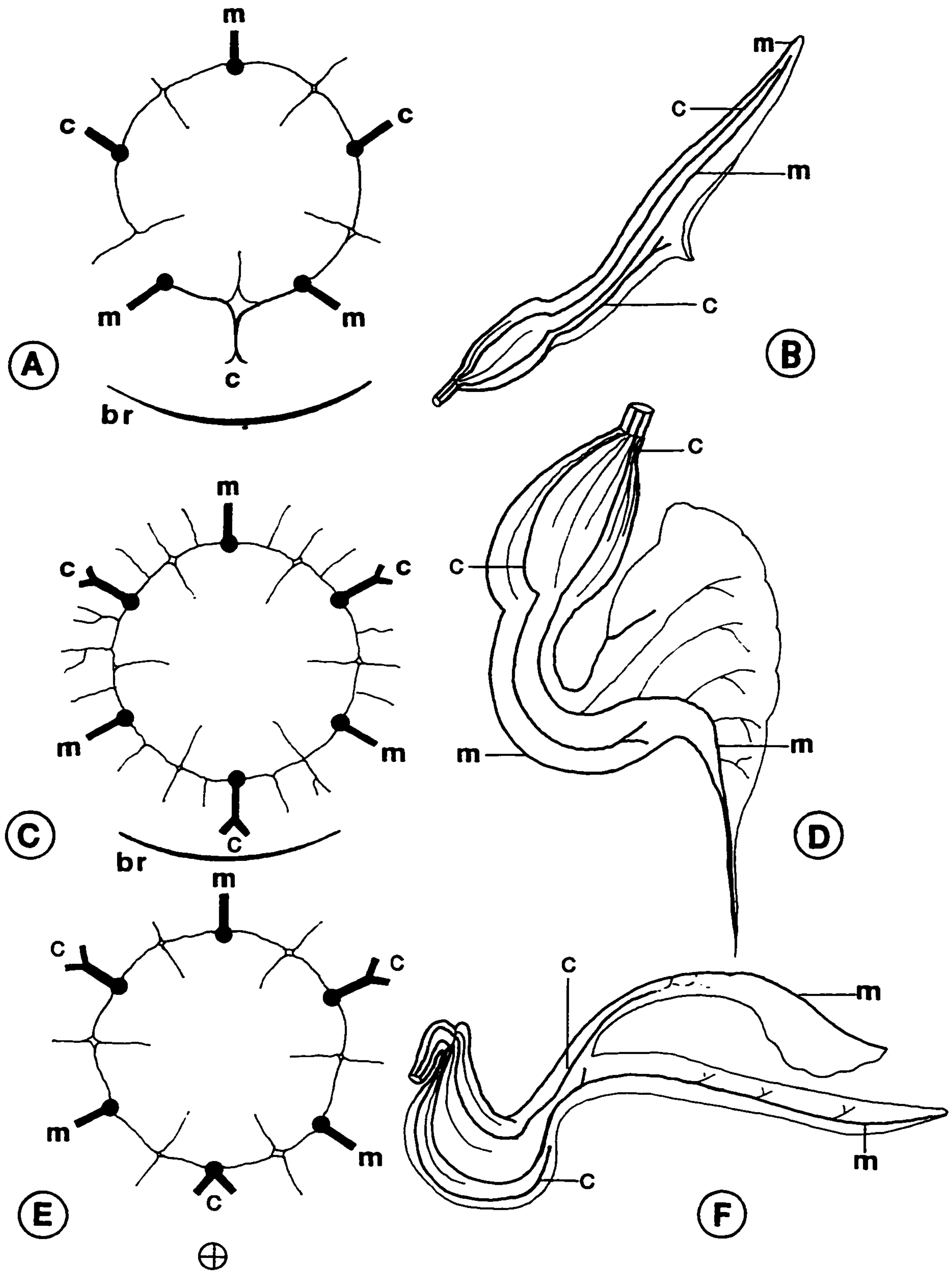
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Figure 49. Floral vasculature. A-B. *Aristolochia clematitis*. C-D. *Aristolochia zollingeriana*. E-F. *Euglypha rojasiana*. G-H. *Holostylis reniformis*. In all, the plexus at the base of the perianth is to the left; thin lines to the outside of the plexus are second order, longitudinal veins; thin lines to the inside are the vascular supply of the gynostemium. The flowers in side view (right) show the extensions of the middle *(M)* and commissural *(C)* veins along the perianth.

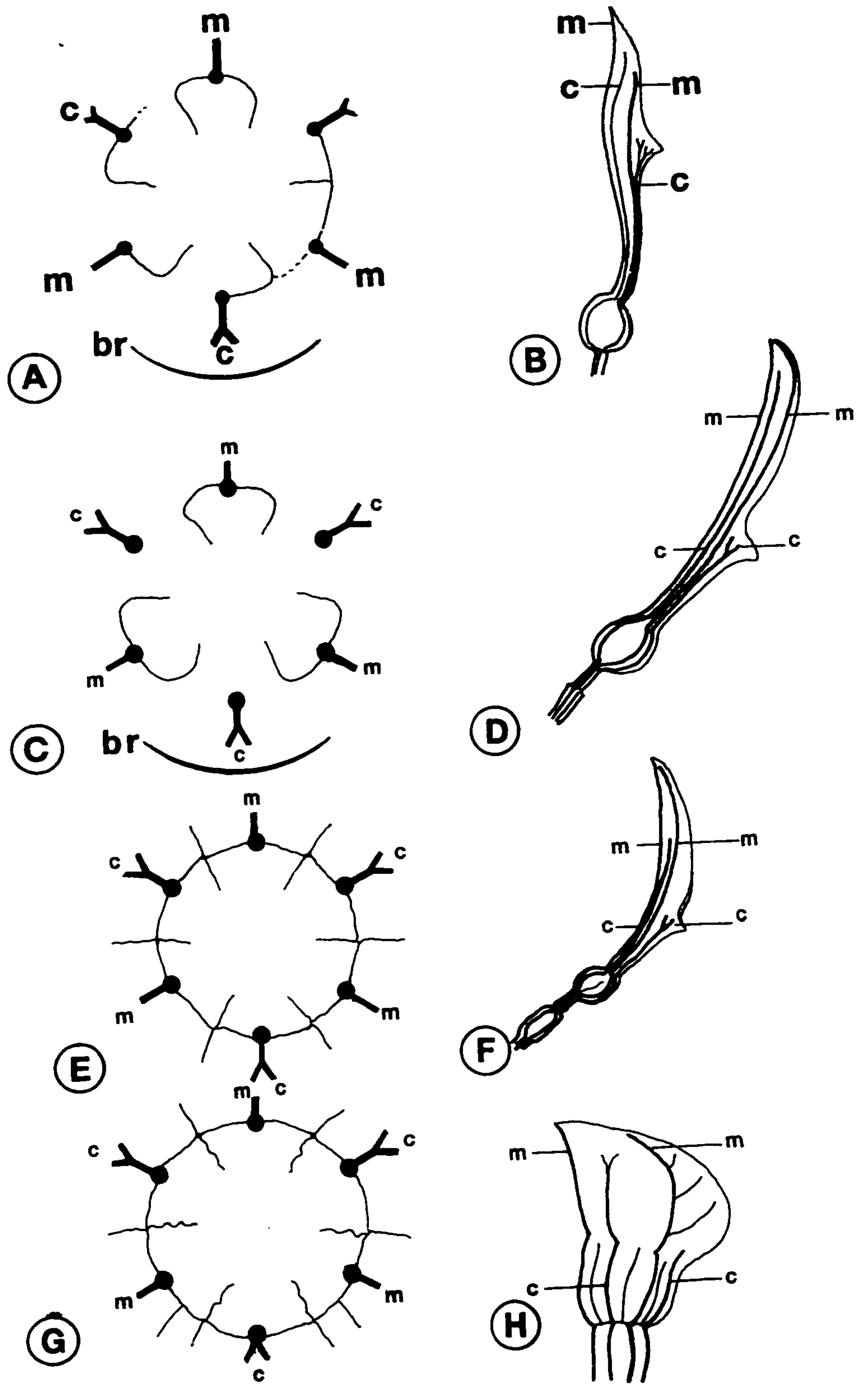
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Table VI. Vasculature and carpel closure in the the studied species of the subfamily Aristolochioideae.

Taxon	Basal plexus*	Gynostemium bundles	Carpels at anthesis	Second order, longitudinal veins in perianth
Subgenus *Siphisia*				
A. arborea	6/6	grouped	closed	present
A. californica	6/6	?	?	present
A. cucurbitifolia	6/6	grouped	closed	present
A. heterophylla	6/6	grouped	closed	present
A. kaempferi	6/6	grouped	closed	present
A. macrophylla	6/6	grouped	closed	present
A. manshuriensis	6/6	grouped	closed	present
A. reticulata	5/6	grouped	closed	present
A. serpentaria	6/6	grouped	closed	present
A. stevensii	6/6	grouped	closed	present
A. tomentosa	6/6	grouped	closed	present
A. tricaudata	6/6	grouped	closed	present
Subgenus *Pararistolochia*				
A. deltantha	5/6	?	?	present
A. promissa	?	equidistant	?	present
Subgenus *Orthoaristolochia* Sect. *Gymnolobus* Subsect. *Pentandrae*				
A. coryi	4/5	equidistant	closed	present
A. erecta	4/5	equidistant	closed	present
A. micrantha	4/5	equidistant	closed	present
A. pentandra	4/5	equidistant	closed	present

*Number of dorsal carpellary bundles connected/number total of bundles (see also Figs. 46-49).

Table VI. Continued.

Taxon	Basal plexus	Gynostemium bundles	Carpels at anthesis	Second order, longitudinal veins in perianth
Subgen. *Orthoaristolochia* Sect. *Gymnolobus* Subsect. *Hexandrae*				
A. *acutifolia*	5/6	equidistant	open	present
A. *anguicida*	3/6	equidistant	closed	present
A. *elegans*	6/6	equidistant	closed	present
A. *fimbriata*	5/6	equidistant	closed	present
A. *gigantea*	6/6	equidistant	closed	present
A. *grandiflora*	6/6	equidistant	closed	present
A. *labiata*	6/6	equidistant	closed	present
A. *leuconeura*	4/6	equidistant	closed	present
A. *maxima*	5/6	equidistant	open	present
A. *morae*	6/6	equidistant	closed	present
A. *nummularifolia*	6/6	equidistant	closed	present
A. *odoratissima*	6/6	equidistant	closed	present
A. *pilosa*	4/6	equidistant	closed	present
A. *ringens*	6/6	equidistant	closed	present
A. *trilobata*	6/6	equidistant	closed	present
Sect. *Diplolobus*				
A. *acuminata*	1-2/6	equidistant	closed	absent
A. *albida*	3/6	?	?	absent
A. *clematitis*	1-2/6	equidistant	open	absent
A. *cretica*	?	?	?	absent
A. *paucinervis*	3/6	equidistant	open	absent
A. *petersiana*	1-2/6	equidistant	closed	absent
A. *pontica*	?	?	?	absent
A. *zollingeriana*	1-2/6	equidistant	closed	absent

Euglypha rojasiana	5-6/6	equidistant	?	present
Holostylis reniformis	6/6	equidistant	?	present

with the median lobe. They continue up to near the limb apex, where they anastomose with the middle vein of the perianth. In mature flowers, they may become near each other (as in *A. maxima*, Figs. 19D, 47F) or not (as in *A. elegans*, Fig. 20E; *A. odoratissima*, Fig. 47B) according to the degree of lateral expansion of the limb. Three other longitudinal veins are developed in commissural positions, two laterals and one adaxial (Fig. 18C). The lateral veins ramify and anastomose to the main veins at the level of the limb. The adaxial vein bifurcates either at the base of the perianth (as in e.g. *A. odoratissima, A. pilosa*, and *A. maxima*; Fig. 47) or above (as in e.g. *A. clematitis* and *A. zollingeriana*; Fig. 49 A-D). This vein bifurcates and supplies the lower region of the limb (Figs. 47B, D, F; 49B,D). The perianth of the pentandrous species have essentially the same venation (Fig. 48B), except that the adaxial commissural vein which is missing at the level of the ovary, is formed from anastoming strands that depart from the two adaxial-most bundles (Fig. 48A). This adaxial commissural vein also bifurcates at the level of the utricle or the tube (Fig. 48B).

Aristolochia grandiflora is the only known species within subgenus *Orthoaristolochia* in which the middle vein runs longitudinally through the convex side of the perianth (Figs. 16D, 48C,D), as in species of the subgenera *Siphisia* and *Pararistolochia*. This vein converges with the mid-veins of the lateral perianth parts and runs parallel along the apical, tail-like appendix. The other three (i.e. commissural) veins end up branching and anastomosing with the higher order veins towards the base of the limb (Figs. 16D, 48D).

Perianth venation of *Aristolochia labiata* and *A. ringens* is different from the other species of subgenus *Orthoaristolochia*, because the two lateral main veins run along the adaxial side of the perianth and more or less parallel along the flanks of the lower lip. They do not converge towards the middle vein, which runs along the abaxial side of the flower, up to the tip of the upper lip (Fig. 48E, F).

Perianth venation of *Euglypha* and *Holostylis* is essentially similar to that of *Aristolochia* subgen. *Orthoaristolochia*. The adaxial commissural vein bifurcates at the base of the perianth in *Holostylis* (Fig. 49H) or above in *Euglypha* (Fig. 49F).

Gynostemium

The vascular bundles that supply the gynostemium of *Aristolochia* (Figs. 46A, C, E; 47A, C, E; 48A, C, E; 49A, C), *Euglypha* (Fig. 49E), and *Holostylis* (Fig. 49G) arise from the fusion of the lateral strands that depart from the dorsal carpellary bundles. Six (five in the pentandrous species of *Aristolochia*; Fig. 48A) vascular bundles enter the gynostemium. As mentioned before, some of the ventral carpellary bundles also reach the gynostemium in species such as e.g. *A. elegans* (Fig. 31B), *A. grandiflora,* and *A. gigantea.*

Gynostemium vasculature in *Aristolochia* subgenus *Siphisia* is essentially similar to that in the other hexamerous species, except that the six bundles are not equidistant but more or less grouped into three groups of 2 (Fig. 42E, G), corresponding to the formation of the three gynostemium lobes (Table VI). In *A. arborea,* the lateral strands that run along the septae in the ovary are uniquely numerous. The vascular bundles that enter the gynostemium divide into an outer, large trace and a small, inner trace that divides again into several smaller traces supplying the apex of the gynostemium lobe.

The bundles that enter the gynostemium of *Aristolochia* and *Euglypha* tangentially split into two bundles, at the level of the base of the anthers (Figs. 28A, 31B, 34E, 36G, 38C, 42C, G). The outer bundle remains as a single one and supplies the anther (as in e.g. *A. macrophylla*, Fig. 42G) or may split radially with each of the resulting traces supplying each individual theca (as in e.g. *A. elegans*, Fig. 31B). The inner bundles continue up to the gynostemium lobe (Figs. 33C, 38C, 40D, 42G, H).

In the species of *Aristolochia* sect. *Diplolobus* examined, the veins that supply the gynostemium either do not split radially (as e. g. in *A. clematitis*) or the inner bundles are reduced to short traces at the level of the anther apex (as in *A. paucinervis*, Fig. 33C, and *A. zollingeriana*).

IV. DISCUSSION

Perianth

Early ontogeny shows an obliquely dome-shaped floral apex (Figs. 10B, D; 14B, 15A, 16A, 20A, 21A, 22A), here interpreted as evidence of early monosymmetry preceding organ initiation. Organ initiation is centripetal, producing in succession perianth, androecium and gynoecium whorls. Perianth primordia develop unidirectionally, from the abaxial to the adaxial side of the floral apex, although this is less pronounced in the species of subgenera *Siphisia* (Figs. 14 A-C, 15A-C) and *Pararistolochia* (Fig. 10A). Intercalary growth of the perianth in *Aristolochia* prevails from early ontogeny, in contrast to its very late occurrence in development in the other members of the family. The strong intercalary growth in *Aristolochia* affects the shape of both perianth and ovary, the latter ending up as a lineariform (Figs. 9A, C,D, 16D, 18E, 19D, 23C, D) usually pluriovulate structure (Fig. 30E, F), in contrast to the globose or subglobose ovary in *Asarum* (Fig. 7A) and *Saruma* which also contains fewer ovules.

The present study supports the interpretation of the perianth of *Aristolochia* as basically trimerous. The three primordia that compose the perianth become apparent in early stages of development (Figs. 14A, 15B, 16B, 17A, 18A, 19B, 20B), and remain distinct to some extent during mid-stage floral buds of *Aristolochia* sect. *Podanthemum* (Fig. 18C,D), *A. grandiflora* (Fig. 16 C), and species of *Aristolochia* subsect. *Pentandrae* (Fig. 17C, D). In all the species of subgenera *Pararistolochia* and *Siphisia* the three lobes remain distinct until maturity (Figs. 9A, C, 12I, J, 14D, 15F, 46B,D,F). Moreover, the floral curvature in the latter two subgenera is entirely different to that found in subgenus *Orthoaristolochia,* because the convex side is formed towards the abaxial side (Figs. 9A, C, 12 I, J, 46B, D, F); the curvature pushes the median lobe farther from its insertion, and it becomes located towards the lower part of the flower. Eichler (1878) described this lobe as being in an upper position in *A. sipho (=A. macrophylla)*, which occurs only before the formation of the curvature (Fig. 12 G-I; see also chapter 2, resupination).

In the majority of *Aristolochia* (except the species of subgenus

Siphisia that have a radially symmetric limb, and in *A. labiata* and *A. ringens*), connation of the two lateral perianth lobes with the median lobe is more complete than that between the two laterals. This is especially noted in most of the species of *Aristolochia* sect. *Gymnolobus* where trimery is obscured by the more complete fusion of the perianth primordia during early (Figs. 20, 21) or middle-developmental (Figs. 16-19D) stages. Teratological development of three actinomorphic lobes in mature flowers of *A. floribunda*, a species usually with a monosymmetric unilobed perianth, was reported by Masters (1875b).

In flowers with two lateral lobes, such as *Aristolochia ridicula* (Fig. 21), the lobes form late in development by means of a lateral expansion of the flanks of the perianth limb. This expansion may be interpreted as an increased growth of the lateral perianth lobes, because the lateral main veins supply each of the lobes (Fig. 21D). This kind of floral development may also occur in other species with similar floral shape (as e.g. *A. birostris, A. cornuta, A. didyma, A. iquitensis*, and *A. klugii*), as suggested by the vasculature in mature flowers.

In the flowers of *Aristolochia labiata* and *A. ringens*, which have one upper and one lower lip at maturity, the upper lip is formed by the median perianth part, whereas the lower lip results from congenital fusion of the lateral perianth primordia (Figs. 22, 23), as predicted by Eichler (1878). However, no evidence was found of partition of the lower lip in mature flowers, as mentioned by Eichler (1878) in this type of floral construction. Conversely, at maturity the upper lip is often apically divided, as in *A. cymbifera, A. galeata*, and *A. labiata*. The type of floral development supports the monophyly of this group of species (described by Kloztsch, 1859, as a distinct section, *Dipharus*), which consists of approximately 25 neotropical species that also share similar vegetative prophylls (pseudostipules), leaves, perianth, and seeds.

The development of a bilobed perianth from three primordia in *Aristolochia labiata* and *A. ringens* (Type V) is the only known case in which the lateral lobes, which develop as strongly as the median lobe, become entirely fused. The presence of three perianth primordia (Figs. 22, 23), and the further development of three main veins that correspond in position to the lobes (Fig. 48F) contradicts the interpretation by Wyatt (1955a:99) that the two lobes are "simple modifications of the unilabiate condition".

Floral vascularization is consistent with the trimery of the perianth. It may be recalled here that in *Asarum*, *Saruma*, and *Thottea* each sepal is supplied by one main vein that comes from a dorsal carpellary bundle, and 2 or 3 pairs of lateral veins (Fig. 45). The veins that run near the margins of each sepal, i.e. the commissural veins, come from the bifurcations of three alternating dorsal carpellary bundles (Fig. 45A,C,E). Similarly, in *Aristolochia, Euglypha* and *Holostylis,* the perianth has three primary veins that alternate with three commissural veins (Figs. 46-49).

In the species of *Aristolochia* subgenus *Siphisia* and subgenus *Pararistolochia*, as in the genera of subfamily Asaroideae, each distinct perianth lobe has a main vein that reaches the lobe apex (Figs. 9A,C, 46B, D, F), and there are secondary, longitudinal veins that supply the base of the perianth (Fig. 46).

In the subgenus *Orthoaristolochia* where the perianth is strongly asymmetrical, the main veins of the two lateral perianth parts are not easily distinguished as a result of the differential development of the three perianth primordia. In the majority of the species of subgenus *Orthoaristolochia,* as well as in *Euglypha* (Fig. 49 E-F) and *Holostylis* (Figs. 49G,H, 51A), the main veins more or less converge toward the apex of the limb where the tips of the perianth parts are located (Figs. 16D, 17D, 18C,D, 19D, 47, 48A-D, 49A-D). In the remaining species, main lateral veins either diverge toward the lobes (in *A. ridicula* and other species with two lateral lobes; Fig. 21D), or symmetrically run along the lower lip in *A. labiata* and *A. ringens* (Figs. 22, 23, 48F).

The three alternating veins in a commissural position represent the lateral vascular bundles of the fused perianth lobes (see also Nair & Narayanan, 1962; Saunders, 1939). The commissural nature of the veins is supported by the fact that they ramify either at the base of the perianth or above. This is particularly conspicuous in the adaxial vein. None of the commissural veins reach the apex or the margins of the perianth. Also, these veins may develop later than the main veins in species such as *Aristolochia petersiana* (Fig. 18C).

Some species of *Aristolochia* have a floral limb that is almost circular (e.g. *A. deltantha*, Fig. 46F; *A. praevenosa; A. rigida*), or 6-lobed (e.g. *A. schlechterii*) and with three main and three alternating lobes (described as petals by Jebb, 1993). This may be the result of prolonged interprimordial growth as suggested by the perianth venation of these species. In *A. deltantha* and *A. praevenosa,* the venation is similar to that in other members of subgenera *Pararistolochia* and *Siphisia* where the three commissural veins do not reach either the margins or the three alternating lobes. With respect to *A. rigida*, Hutchinson (1969) paid special attention to what he considered to be actinomorphic flowers of this species as a criterion of primitiveness. This does not seem to be the case because the apparent actinomorphic limb is a result of a late interprimordial growth that superficially affects the gross floral shape, but does not affect venation (perianth venation of *A. rigida* is asymmetric as in all members of subgenus *Orthoaristolochia*). Moreover, the perianth of this species also develops the curvature characteristic of the subgenus *Orthoaristolochia*.

These results do not support the theories that consider the perianth in *Aristolochia* to be a bract or a single structure (Guédès, 1968; Hagerup, 1961; Lorch, 1959). The perianth in *Aristolochia* is formed by three primordia. Interpretations by Hagerup (1961) and Lorch (1959) considering the perianth to be homologous to the spathe of Araceae are not supported either anatomically or developmentally. Perianth development of *Aristolochia* is essentially different from that of the spathe in Araceae, in which a clearly single foliar structure (see e.g. Goebel, 1900:55; Lehmann & Sattler, 1992) prevails.

Guédès (1968) used the strong resemblance of venation and shape of leaves and mature perianth limb as a criterion for homology between them. Although in some species the shape and venation of the perianth limb resembles those of the leaf, in many others, especially those of the subgenera *Pararistolochia* and *Siphisia*, as well as in *Aristolochia labiata*, and *A. ringens*, they are completely different. Guédès (1968) did not study the vasculature at the ovary-perianth junction, which is crucial to understanding that perianth and gynostemium vasculature comes from 5 or 6 veins from below the level of the ovary. In contrast, the petiole of *Aristolochia* is usually 3-veined. Lorch (1959) argued that the distichous position of the flower with respect to the prophyll supported his interpretation that the perianth is the equivalent of a spathe such as that found in aroids. However, the distichous position is the norm in the whole family (see also chapter 2), and this positional relationship has no bearing on the interpretation of the perianth. Hagerup (1961), who followed Lorch's interpretation, studied only one species, *A. elegans*. He did not study material young enough to detect the three perianth primordia. This is critical in *A. elegans*, where perianth primordia are not readily apparent and become fused and asymmetrical very early in development (Fig. 20).

No ontogenetic evidence was found that indicates two alternating sets of three parts (that is, presence of sepals and petals) in the perianth of *Aristolochia*. Presence of six parts, stated by Eichler (1878) and Mayoux (1892), is based on the number of main vascular bundles that supply the perianth. This interpretation would imply that each perianth member is supplied by a single vascular bundle, and that these veins are equivalent. On the contrary, it has been demonstrated that each of the sepals of *Saruma* (Dickison, 1992) and each of the perianth members of *Asarum* and *Thottea* (Fig. 45) are supplied by 3 to 6 basal veins (Renuka & Swarupanandan, 1986; Sugawara, 1987), and not by a single vascular bundle. Furthermore, in *Aristolochia*, *Euglypha* and *Holostylis*, the six veins that enter the perianth are not equivalent; whereas three alternating veins usually reach the tips of the perianth parts, the other three (commissural) veins ramify and do not reach the perianth apex (Figs. 18C, 46-49). Moreover, members of the Aristolochiaceae with a two whorled perianth (Fig. 1A-C), either with well developed (in *Saruma*, Figs. 1A, 58A) or vestigial (in *Asarum* and *Thottea*; Fig. 1B, C) petals, show no evidence of fusion between members of these whorls.

The interpretation of the perianth of *Aristolochia* as a calyx is supported in terms of position (item 1, see below), morphology (items 2 and 3), development (items 2 and 4), and comparison to related taxa (item 5). This agrees with some of the general principles used to distinguish sepals from petals, summarized by Endress (1990a, 1994), and Weberling (1989) as given below.

1. The median lobe of a trimerous calyx is always opposite to the bract, following a prophyllate aestivation (as defined by Weberling, 1989). This is the case in all species of *Aristolochia* with bracteate flowers (Figs. 1, 4, 6B, 7C, D, 8B, G, 10A-C, 14B-D, 15B-E, 16A, B, 17A, B, 19, 45, 46, 47E, 48A, C, 49A, C).

2. Sepals often have a broad base, where they touch each other in the bud and may become postgenitally fused. Early stages of perianth development, nearly identical in *Asarum* (Leins & Erbar, 1985), *Thottea* (Fig. 7D; see also Leins & al. 1988) and *Aristolochia* (see especially Figs. 10A, C, 14, 15B, C, 16A, B, 17A, 18A, 19A,B) show wide primordia that touch each other. This does not occur in the petals of *Saruma*, whose narrow primordia are clearly separated from each other and do not show any sign of postgenital fusion (Leins & Erbar, 1995; Tucker & Douglas, 1996). Furthermore, petals of *Saruma* become stalked at the

base, and have a clear ring-like abscission zone slightly above their insertion (Fig. 45B; see also Dickison, 1992). In later stages, they become cochleariform (Leins & Erbar, 1995; Tucker & Douglas 1996), in contrast to the typical triangular shape of the sepals in *Asarum*, *Saruma*, and *Thottea*.

3. Petal development is delayed in the bud, and petals are initiated almost simultaneously. Petals of *Saruma* (see Figs. 3-17 in Leins & Erbar, 1995; and Fig. 7.2 E in Tucker & Douglas, 1996), and the vestigial organs in the petal position in *Asarum* (see Figs. 2-4 in Leins & Erbar, 1985) appear to initiate almost simultaneously, after the sepals have already formed a floral cup. In *Asarum europeum* the vestigial petals arise simultaneously with the stamens, apparently from the outer bulge of a "double primordium" that produces a stamen to the inside and a petal to the outside. In both genera, petals (or petal vestigials) are clearly located toward the inner side of the sepals and alternate with them.

4. Perianth aestivation is valvate throughout the family (including *Saruma*) whereas petal aestivation in *Saruma* is apert.

5. Petals of *Saruma* are uniformly yellow, glabrous, lack stomates, and their epidermal cells are papillate, striate, and with sinuous anticlinal walls (Fig. 54B). Sepals of *Saruma* (Fig. 54A) and the perianth of the remaining genera have stomates, and trichomes, and their epidermal cells have more or less straight anticlinal walls, resembling thus the epidermis of the vegetative organs.

Stamens

In most species, initiation and development of stamens of *Aristolochia* seem to be affected by the asymmetrical development of the perianth (Figs. 27A-C, 28D, 30A-C, 35A,B). Perianth monosymmetry affecting anther initiation has also been reported in Fabaceae (Tucker, 1984), Verbenaceae (Sattler, 1973) and Scrophulariaceae (Eichler, 1875; Ronse-Decraene & Smets, 1994).

Based on position, the single whorl of stamens of *Aristolochia* (Figs. 1D, 52) *Euglypha* and *Holostylis* (Fig. 51B) represents the inner whorl of the stamens in *Saruma* (Figs. 1A, 2A) and *Asarum* (Figs. 1B, 2B). The inner whorl of stamens is the first to be formed at least in *Asarum* (Leins & Erbar, 1985). When stamens are suppressed in *Asarum*, it is mostly the outer whorl that fails to form (Nakamura & al. 1982; Wyatt, 1955a). All this evidence contradicts the interpretation of Saunders (1940) that the inner whorl of stamens in *Aristolochia* is missing. It also contradicts this same interpretation by Masters (1875b), because he erred in describing the stamens of *Aristolochia* as opposite the carpels.

The presence of five carpels and five stamens in *Aristolochia* subsect. *Pentandrae* (Figs. 35, 36, 52F) or more than six stamens in some species of the subgenus *Pararistolochia* (Figs. 5B, 50, 52C) affects neither the basic trimery of the perianth nor suggests primitive pentamery or polymery in the genus. Cladistic analysis (chapter five) shows that both conditions are derived within the Aristolochiaceae. The plesiomorphic condition in the family is the two-whorled 12 stamen androecium and a six-carpellar gynoecium. For *Aristolochia*, the hexamerous androecium and gynoecium are plesiomorphic.

Several facts suggest that polyandry in *Aristolochia* subgenus *Pararistolochia* (Figs. 5B, 50) may be secondary due to lateral 'dédoublement' (as defined by Ronse-Decraene & Smets, 1993) of some of the six original stamen primordia. In cases where there are more than six stamens, some of them are atypically smaller than others (Figs. 5B, 50; see also Poncy, 1978). Unlike polyandry in *Asarum*, *Saruma*, and *Thottea*, where two or more whorls may be formed, additional stamens in species of subgenus *Pararistolochia* do not form an extra whorl (Figs. 5B, 50, 52C). Moreover, the number of stamens in these species of *Aristolochia* is not fixed, and commonly varies even within the same individual. For example, the specimen of *A. promissa* studied here shows 10 (Figs. 5B, 50A, B) or 9 stamens (Fig. 50C, D); this has also been reported elsewhere (Huber, 1960; Ma, 1992; Poncy, 1978). Additionally, the number of stamens does not always coincide with the number of gynostemium lobes (Poncy, 1978).

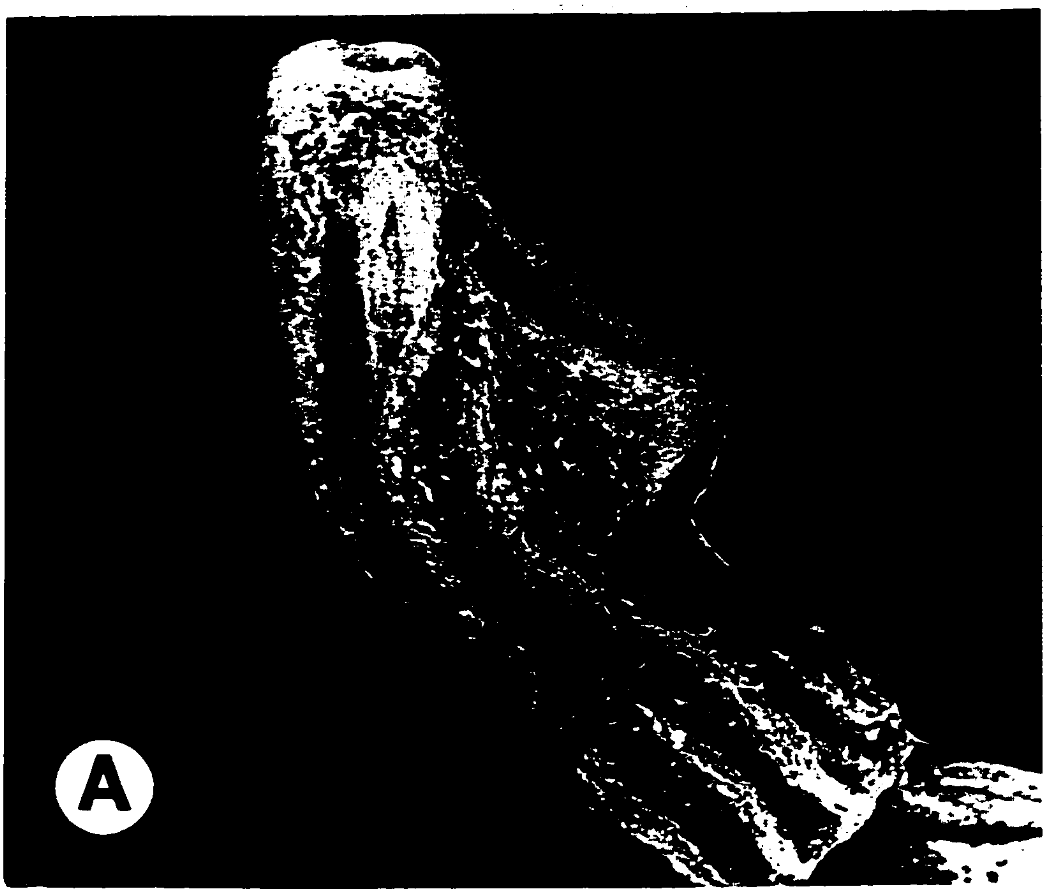
Polyandry in some species of *Aristolochia* subgenus *Pararistolochia* concomitantly occurs with a change of the number of gynostemium lobes suggesting connective origin of these lobes. However, the development of extra anthers could secondarily induce the corresponding gynostemium lobe to split because of their close contact during development from very early stages of development. In this subgenus the number of stamens and gynostemium lobes is not always the same, as Poncy (1978) pointed out; for example, *A. goldieana* has 24 stamens but only 12 gynostemium lobes (Hooker, 1865; Poncy, 1978; personal observation).

Figure 50. Gynostemium of *Aristolochia promissa (Bot. Gard. Univ. Bonn, acc. 13014)*. A, B. top (A) and side (B) views. Stamens are in a single whorl; four stigmatic lobes (arrowheads) appear smaller than the others. Bar = 0.1 mm. C, D. Transverse sections of the lower (C) and upper (D) levels of the gynostemium, showing the initiation of only 9 stamens, in contrast to the ten stamens in A and B. Bar = 50 µm. Bar = 50 µm.


C

Figure 51. *Holostylis reniformis*. A. Young floral bud showing the monosymmetric perianth. B. Apex of the gynostemium showing three (arrows) of the six vestigial lobes. *st*, stamens.


B


A

Moreover, in some species of *Asarum*, changes in the number of anthers occur simultaneously with changes in the number of styles (Nakamura et al. 1982). This suggests a close interrelation between the developmental pathways of androecium and gynoecium in other members of the family.

Some reports of the presence of 3 or 4 stamens, and/or 3 carpels or locules in members of the family exist (Gregory, 1956; Mayoux, 1892; Nakai, 1936; Ortega, 1987; Pfeifer, 1970), but no evidence that this occurs was found in this study. Also, all the species of *Aristolochia* subgen. *Pararistolochia* from Australia and New Guinea possess 6 anthers, not 6 pairs of anthers as stated by Parsons (1996) and this character seems to be intraspecifically variable only in the African species of this subgenus.

Gynostemium

Data from development support the interpretation that the gynostemium lobes are formed from carpellary tissue rather than from the connectives. Each lobe is built up by the flanks of two adjacent carpels (i.e. commissural), plus the corresponding septum (Figs. 29C, D). The bulges that form the gynostemium lobes form a clearly continuous structure with the septae at the level of the ovary, and grow together (Figs. 28C,D, 29 B, D, 30 A-C, 35C, 37C,E, 42A). Although the lobes grow towards the anther primordia, their initiation is temporally and spatially more related to the development of the carpels than to that of the anthers (Figs. 34A, B, 36E, F, 40B,C, 42A, 44A-C). Lobes initiate close to the stamens because the area available for insertion is reduced as a result of the narrowed floral tube. In *Asarum* and *Saruma*, the carpels also initiate in close contact to the base of the stamens, as shown in figures 6-9 and 13-14 by Leins and Erbar (1985, 1995, respectively), but they remain fused, which might be related to the broader insertion area in flowers of these genera.

The presence of two distinct primordia, one that forms the anther and other that form the gynostemium lobe, does not support the interpretation of these lobes as massive connectives. The connective appendages in stamens of *Aristolochia* (Figs. 32B, 35D, 41E, 42G) are formed from the same primordium that forms the anther distinct from the gynostemium lobes. Similarly, in *Asarum*, *Saruma* and *Thottea*, where the anthers and the connectives are more differentiated at maturity (Fig. 2A-C), they develop from the same primordium (see Leins & Erbar, 1985, 1995; Leins et al. 1988). Furthermore, the primordia that form the gynostemium lobes in the species of *Aristolochia* subgenus *Siphisia* are alternate (i.e. not in the same radius!) to the anther primordia (Figs. 41B-E, 42C).

Two other facts support the interpretation that the gynostemium lobes are distinct from the connectives. First, vascularization indicates that the gynostemium lobes in the Aristolochioideae are compound structures. Each of the bundles that enter the gynostemium almost always tangentially bifurcates, the outer bundle supplying the anther, and the inner bundle continuing to the stigmatic lobe (Figs. 28A, 31B, 34E, 36G, 38C, D, 42C, G; see also Henslow, 1891; Mayoux, 1892, Wyatt, 1955a). In members with free stamens (*Asarum* and *Thottea)*, the staminal bundle is unbranched, or splits either randomly in *Asarum* (Hufford, 1980) or tangentially and in a fan-like fashion in *Thottea*

(Figs. 45E, 57D; see also Wyatt, 1955a). Second, in some species of *Aristolochia (e.g. A. elegans*, Fig. 31B; *A. gigantea,* and *A. grandiflora*) there are direct extensions of the ventral carpellary bundles into the gynostemium.

The commissural origin of the gynostemium lobes is concordant with the fact that carpel tips are slightly (in *Saruma*; Fig. 55A) or strongly (in *Asarum*; Fig. 55B, C) bifurcated. Furthermore, the dorsal carpellary bundle in *Saruma* bifurcates for a short length at the level of separation of the carpels from the hypanthium. In *Asarum*, besides the bifurcation of the carpel tips, the flanks of adjacent carpels of several species undergo fusion (Figs. 2B, 57F; see also Cheng & Yang, 1983; Eichler, 1878; Kelly, 1997; Leins & Erbar, 1985; Mayoux, 1892; Nair & Narayanan, 1962; Payer, 1857; Sugawara, 1987; Wyatt, 1955a). These two processes result in the formation of commissural endings (Figs. 2B, 56C) that are structurally similar to the gynostemium lobes of *Aristolochia*.

Although in *Aristolochia clematitis* and a few other species (such as *A. zollingeriana*) there are roof-like ingrowths on top of the ovary, these are not sufficient evidence to consider these lobes solely as connectives, as suggested by Leins and Erbar (1985). These ingrowths might be a result of the constriction that the base of the perianth undergoes during the formation of the abscission zone (Figs. 37C, 39A). This constriction is very pronounced in species of *Aristolochia* section *Diplolobus* (including *A. clematitis* and *A. zollingeriana*), and narrows the common pollen tube transmitting tissue into a circular tract (Figs. 37E, 38B, 39A-B, 40D) on which is not possible to detect the six septal extensions. The latter, however, become apparent once again towards the tip of the gynostemium (Figs. 37E, 38D, 39B, 40B).

The gynostemium lobes display a 'two-flank' growth even from early stages (Figs. 28A, 29C,D, 32B, 35C-D, 39B), indicating their compound nature. This is also reflected in the formation of the stigmatic papillae along the flanks rather than on the middle part of the gynostemium lobes (Figs. 30D, 32B).

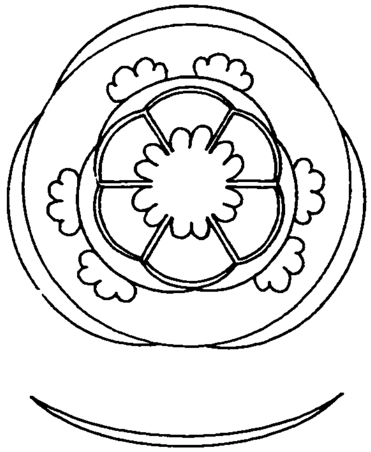
The extrorse position of the stigmatic papillae of *Aristolochia* is due to the late elongation of the gynostemium lobes upwards and outwards (Figs. 27C, D, 28A, 29D). In *Asarum*, elongation of the carpellary flanks also occurs late in development (Leins & Erbar, 1985), and the stigmatic papillae are located mainly on the bifurcation of each carpel (Figs. 2B, 55B, C, 56C).

There is no evidence in favor of Solm-Laubach's (1876) interpretation that each gynostemium lobe is a single *sui generis* fertile leaf that produces ovules at its base, and anthers and stigmae at its apex. Ontogeny and vascularization of flowers of *Aristolochia*, as well as comparisons with the related genera, demonstrate that stamens and carpels develop as distinct organs.

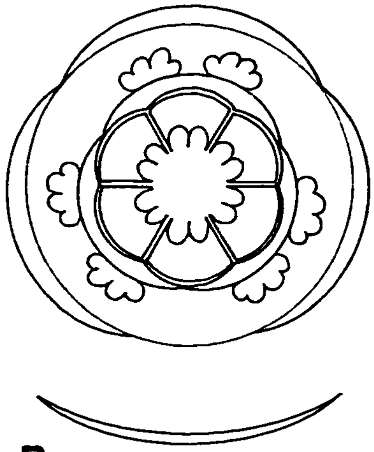
V. Conclusion: Floral morphology and the systematics of the Aristolochiaceae

In general, the floral groundplan of Aristolochiaceae follows Hofmeister's rule (as cited by Leins & Erbar, 1997). The median sepal is opposite the bract (Figs. 1, 52). Petals in *Saruma* and vestigial

Figure 52. Floral diagrams of *Aristolochia*. A-B. Subgenus *Siphisia*. A. Species with an actinomorphic perianth. B. Species with a monosymmetric perianth. C. Subgenus *Pararistolochia*. D. Subgenus *Orthoaristolochia*, flower bracteate. E. Subgenus *Orthoaristolochia*, flower ebracteate. F. Subsection *Pentandrae*.



A



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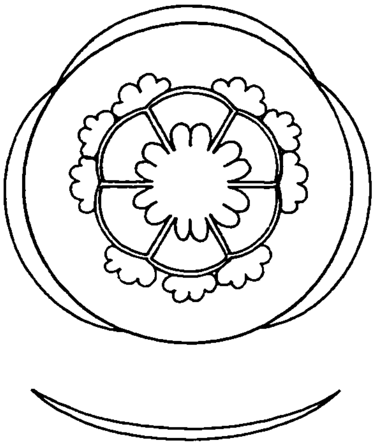

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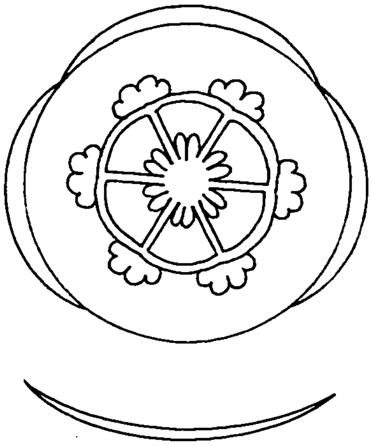
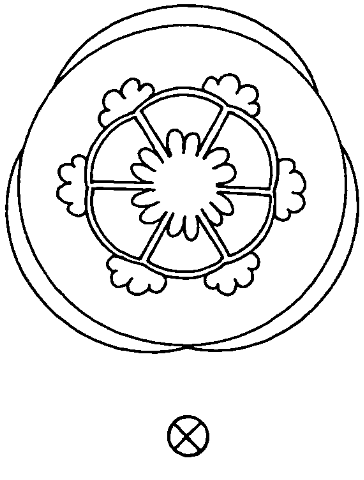
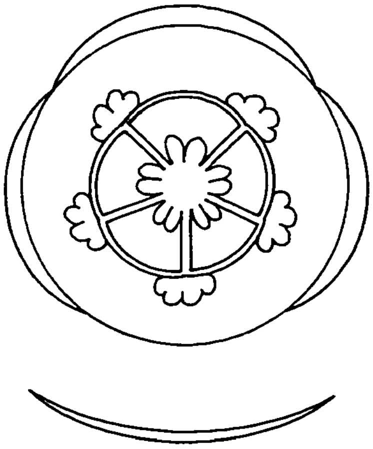


D



E



F

Figure 53. Diagram of the gynoecium of *Aristolochia* split longitudinally and spread open, illustrating the commissural nature of the gynostemium. Numbers indicating the 6 carpels are placed below each dorsal carpellary bundle. The edge of each carpel is between the two placentary bundles that supply the ovules. Stamens, dotted lines.

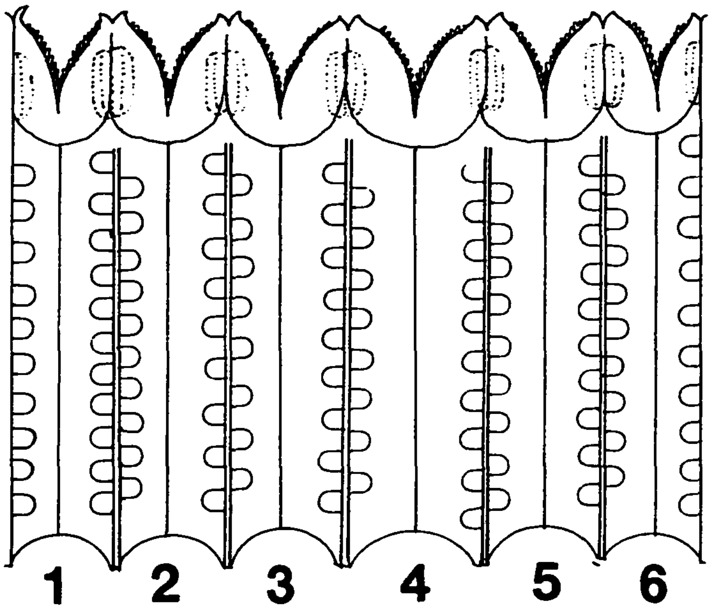

1
2
3
4
5
6

Figure 54. *Saruma henryi* (*Pruski 3748)*. A. Sepal, abaxial surface, showing a trichome (left) and a stoma. Bar = 10 µm. B. Petal, surface. Bar = 10 µm.


A
B

Figure 55. A. *Saruma henryi* (*Pruski 3748*), stigmatic lobe. B-E. *Asarum arifolium* Michx (*González 3619*). B. The inner stamens (st_1) are alternate with the carpels; the outer stamens (st_2) are opposite the stigmas (arrowhead). Bar = 0.5 mm. C. Bifurcated carpel tips, top view. Bar = 0.5 mm.

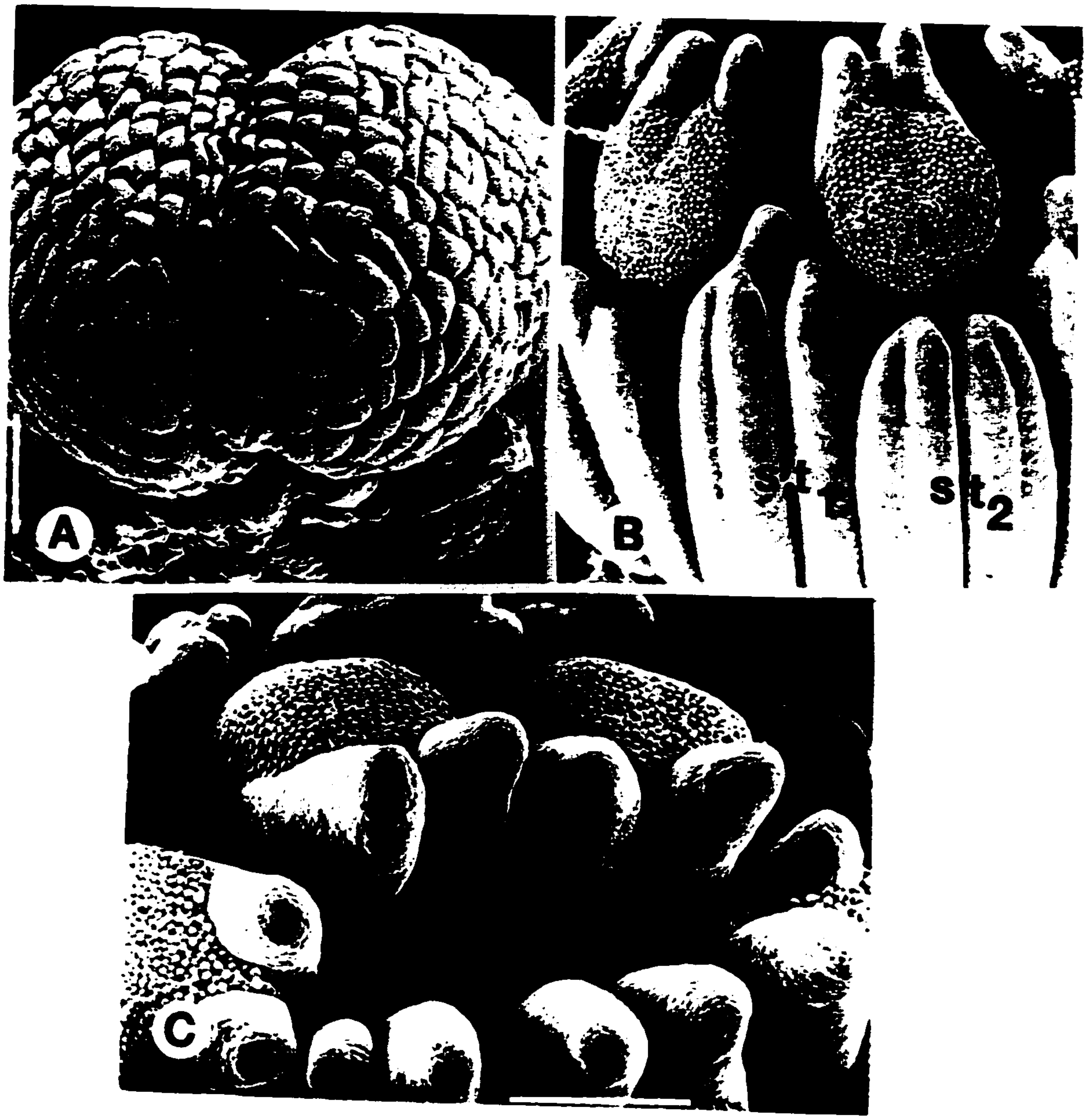
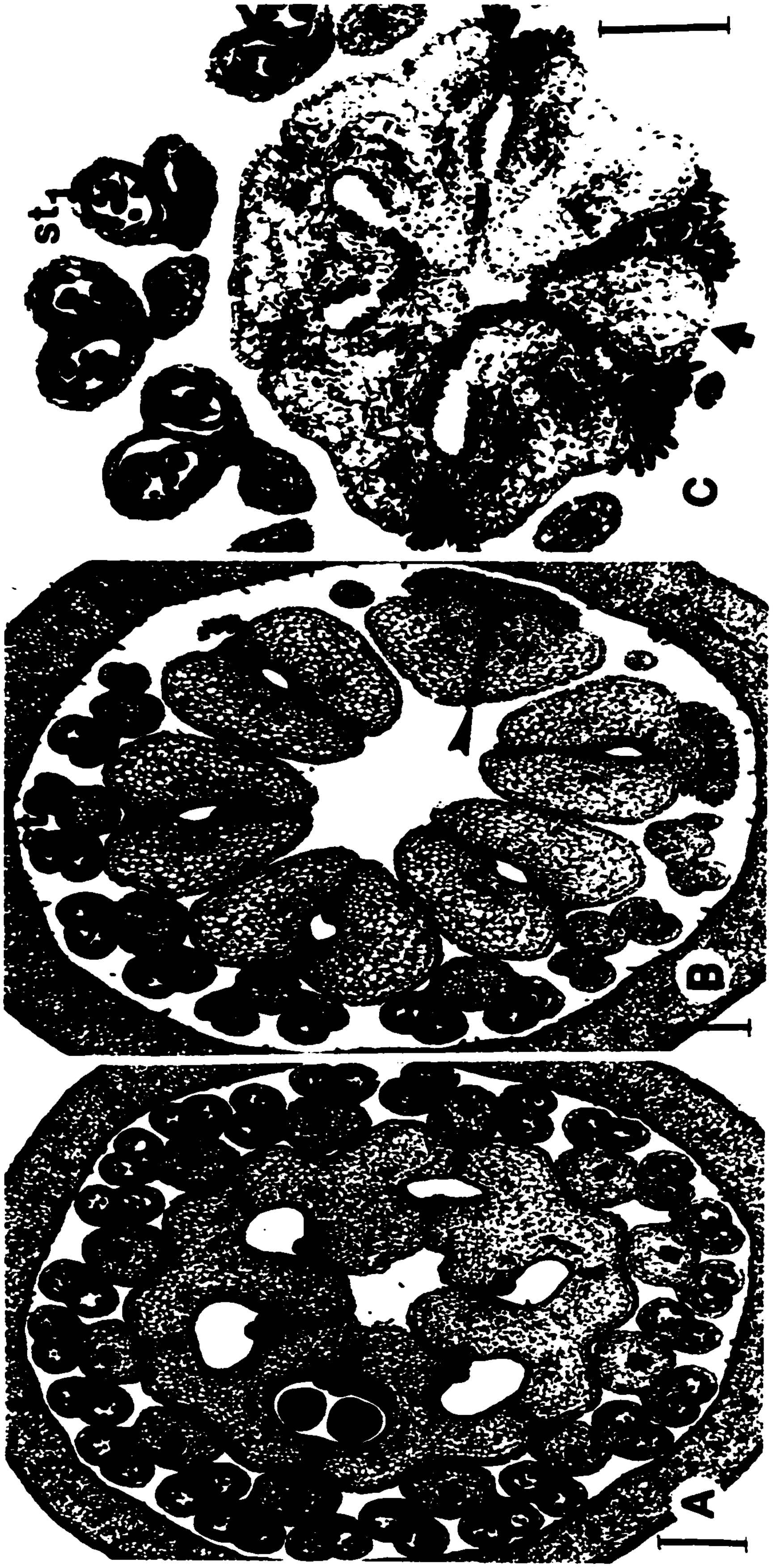

A
B
St1
St2
C

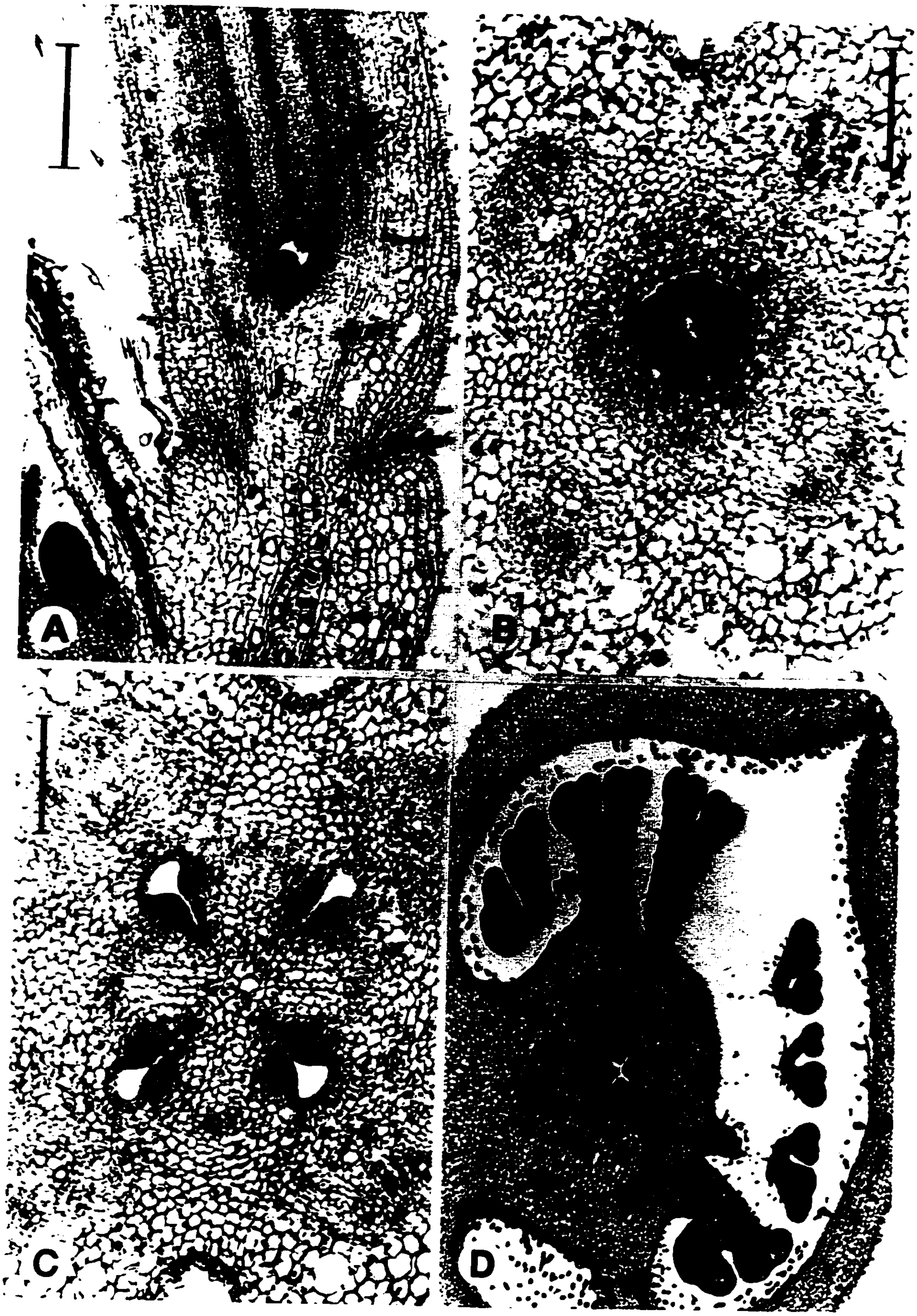
Figure 56. A, B. *Asarum arifolium* Michx (*González 3619)*. A, B. Transverse section of one floral bud through the ovary (D, bar = 0.5 mm) and the stigmatic lobes (E, bar = 0.5 mm); note in B the complete bifurcation of the carpel tips (arrowhead). C. *Asarum canadense* (*González 3577*), transverse section through the stigmas, showing the commissural endings of the carpels; an apparently single lobe (arrow) has been formed by fusion of two branches from the adjacent carpels (arrowheads). Bar = 250 µm. st_1, inner stamen; st_2, outer stamen.


st
C
st
B
A

structures in some *Asarum* and *Thottea* spp. develop on the gaps between the sepals (Fig. 1A-C). Suppression of petals and the outer staminal whorl occurs in *Aristolochia* (Fig. 52). In *Asarum*, the first (i.e. the innermost and longest) paired stamens alternate with the petals (or with petal positions when they are missing), the second whorl with the first and so on. In *Saruma* it is not clear whether the two lateral antesepalous stamens arise before the middle antesepalous stamen or otherwise (cf. Leins & Erbar, 1995 vs. Tucker & Douglas, 1996), but it is clear that the three antepetalous stamens arise last (Fig. 1A). The carpels clearly alternate with the inner whorl (the single whorl in *Aristolochia)* of stamens. The alternate position is, however, not clear in *Thottea*, because there is no strict correspondence in number and position of carpels and the so-called stylar organs or stigmatic lobes (Figs. 2C, 57; see also Leins & al. 1988; Renuka & Swarupanandan 1986). Finally, antesepalous carpels are reported to initiate first and antepetalous carpels last in *Saruma* (Leins & Erbar, 1995).

Monosymmetry in flowers of *Aristolochia, Euglypha* and *Holostylis* is due to two structural transformations, one causing the curvature of the perianth and the formation of utricle and tube (Fig. 4), and the other affecting the symmetry of the limb. The mechanical compression that the floral apex undergoes in many species (Figs. 10B, D, 11D, 20A, 21A, 22A) could be related to the early monosymmetry of the floral bud. Whereas the switch of the flower to a horizontal or pendulous position could be related to the development of the floral curvature. In many species of *Aristolochia*, floral curvature appears late in development, when flowers are pendulous and undergo resupination (Fig. 12a-f). In contrast, the actinomorphic flowers of *Asarum*, and *Saruma* are more or less erect and are not subjected to mechanical constraints, because the

Figure 57. *Thottea siliquosa (Bot. Gard. Univ. Bonn, acc. # 09037)*. A. Longitudinal section showing the abscission zone of the peduncle (arrow) and an aborted carpel at the base of the ovary (arrowhead). Bar = 200 µm. B. Transverse section through the base of the ovary, showing an aborted carpel (arrowhead). Bar = 100 µm. C. Transverse section through the mid-level of the ovary. Bar = 100 µm. D. Transverse section through the top of the ovary showing the free stamens, with a distinct filament and a fan-like vascular supply (arrow). Bar = 500 µm.


A
B
C
D

leaf axils of *Asarum* are usually spread out at a wide angle (Figs. 6A, 7C) and those of *Saruma* have no vegetative structures that can compress the floral meristem (Fig. 6C). Mechanical compression and horizontal position of the (usually lateral) flower have long been proposed as leading to monosymmetry (Delpino, 1886; De Candolle, cited by Robertson, 1888).

Within the family, the genera *Aristolochia, Euglypha* and *Holostylis* exhibit the most elaborate traits in terms of synorganization, a concept redefined by Endress (1990a:155), as the "intimate structural connection of two or several neighbouring structural elements to form a functional system or apparatus... In flowers, it consists of a fusion (congenital or postgenital) or of an otherwise close connection of parts, for example, by sheathing or by hooks". Whereas in *Asarum, Saruma* and, perhaps, *Thottea*, synorganization is restricted to the first whorl, in *Aristolochia, Euglypha* and *Holostylis* it not only reaches the perianth in a more complete manner, but also affects the relation between stamens and carpels by forming a gynostemium, and between the carpels by forming a syncarpous ovary (Figs. 52, 53, 58D). The formation of a gynostemium implies two different processes: congenital connation of the flanks of the carpel tips and postgenital adnation of the stamens with the carpel tips.

Synorganization in flowers of *Aristolochia, Euglypha* and *Holostylis* would allow them to develop some traits that are partially or completely missing in the other members of the family, some of which are crucial in terms of pollination. These are, as follows:

1. Flowers of *Aristolochia, Euglypha* and *Holostylis* resupinate, by

means of torsion of the peduncle and of the narrow, syncarpous, inferior ovary (Fig. 12). The ovary apex can also become variously curved, which affects the position of the rest of the flower (Figs. 23D, 25).

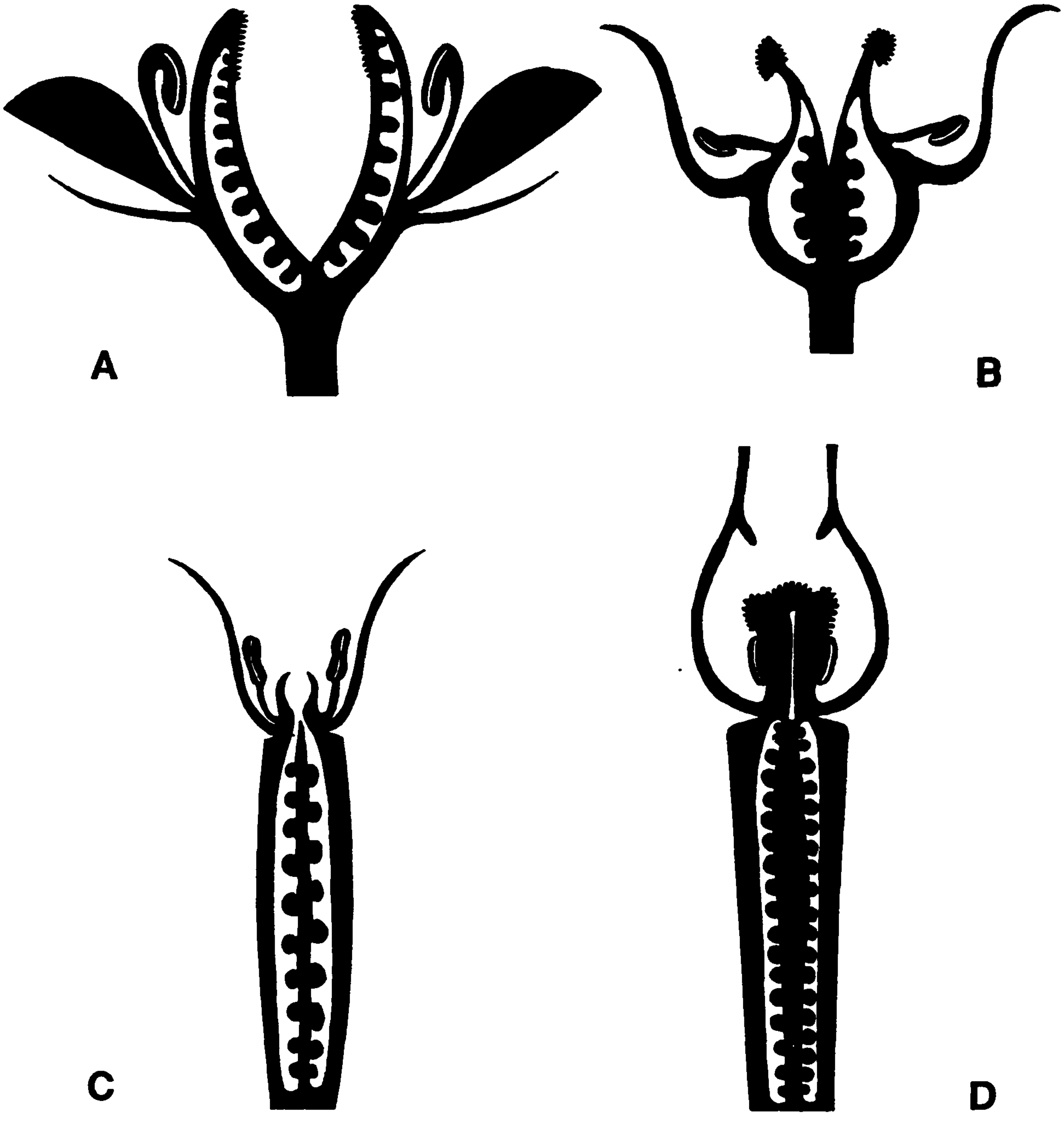
2. Perianth shapes in *Aristolochia* are more elaborated and events of fusion between the perianth members are more diverse (Figs. 24, 52) than in *Asarum*, *Saruma* and *Thottea*. Tube width has been proposed as a factor affecting the type of pollinators that enter the flower (Brantjes, 1980).

3. A common, more or less continuous stigmatic surface is formed on the outside of the gynostemium of *Aristolochia, Euglypha* and *Holostylis*, because the flanks of the gynostemium lobes are fused (Figs. 5, 27D, 37E, F, 39C, 58D). In *Asarum* and *Saruma*, the stigmatic papillae are not continuous (Figs. 55B, C, 56, 58A, B).

4. As a result of syncarpy, a common pollen tube transmitting tract is formed from the upper part of the gynostemium to the inside of the ovary in *Aristolochia*, (Figs. 28D, 30C, E, F, 31B, C, 34E, F, 36G, 38A-C, 39C, 40B, C, 42D-G, 58D), *Euglypha* and *Holostylis*. The tract connects the stigmas to any of the loculae. According to Carr and Carr (1961) and Endress (1982) the formation of a compitum is an important adaptative advantage in terms of equal pollen-ovule ratio and enhanced selection during fertilization.

5. The period of time for pollination in *Aristolochia*, *Euglypha* and *Holostylis* is limited, because the perianth and the gynostemium, which contain the pollen and the receptive stigmatic surface, are caducous;

Figure 58. Diagram of flowers of the Aristolochiaceae. A. *Saruma*. B. *Asarum*. C. *Thottea*. D. *Aristolochia*. Stigmatic papillae and anther dehiscence lines (in white) are indicated.


A
B
C
D

they detach from the ovary through the abscission zone formed above it (Fig. 58D).

6. *Aristolochia* exhibits mechanical signs of protogyny that are different from those reported in *Asarum*. The gynostemium lobes spread as a unit at early anthesis thereby enlarging the receptive surface (Fig. 5C, D; see also Cammerloher, 1922, 1923, Petch, 1924, Razzak et al. 1992; among others). In *Asarum*, stamens bend inward to reach the stigmatic surface (see e.g. Leeman, 1927; Lu, 1982; Mesler & Lu, 1993).

Tucker (1984, 1997) proposed that generalized character states are expressed in early ontogeny of floral development, and that, therefore, this might have some hierarchical implications in the systematics of a particular taxon. For instance, early floral stages such as floral symmetry, and number and position of organs, are mentioned by Tucker (1997) as important for the recognition of suprageneric levels of classification. Early floral symmetry in the Aristolochiaceae support some generic delimitation within the family; the floral apex is actinomorphic in members of *Saruma* and *Asarum*, whereas it is strongly monosymmetric in most of *Aristolochia* (Figs. 20A, 22A). Also, the early abortion of two carpels is a character known to occur only in *Thottea* (Fig. 57). However, other traits that become apparent during early stages, such as the suppression of a stamen and a carpel in *Aristolochia* subsect. *Pentandrae*, or the distinct perianth development in *A. labiata* and *A. ringens*, are characteristic of some derived taxa within *Aristolochia* section *Gymnolobus* (see chapter five).

Subgenera within *Aristolochia* show, to some extent, differences on traits that are determined during the early to mid-development of the flower. These are the degree of fusion of the perianth parts (three distinct parts in subgenera *Siphisia* and *Pararistolochia vs.* one in subgenus *Orthoaristolochia*), the pairwise fusion of gynostemium lobes and the stamens grouped into three groups (in *A.* subgenus *Siphisia*), and the likely "dédoublement" of stamens (in some members of subgenus *Pararistolochia*).

Whereas perianth curvature is U-shaped and develops early in ontogeny in all species of subgenus *Siphisia*, perianth curvature in the other subgenera develop later and show more diversity. Another character that is developed later in ontogeny and is important at lower taxonomic levels is the shape of the tube. Just before anthesis the tube becomes inflated distally as in *A. grandiflora* (Fig. 48D) and the species of subgenus *Pararistolochia* from Australia and New Guinea (Fig. 46F) or inflated almost as much as the utricle as in all species of subgenus *Siphisia* (Fig. 46B, D). The tube is not inflated in the remaining species. Other defining traits appear late in the development of the perianth as synapomorphies of several crown clades, for example the asymmetrical perianth base, found in the clade formed by *A. mishuyacensis, A. trilobata* and the species of *Aristolochia* sect. *Dipharus* (character 24, Fig. 23D); and a perianth tube obliquely oriented in relation to the utricle (character 30, Figs. 23, 25D).

Late events of floral development, such as elaboration of the epidermis of the perianth and the gynostemium, elongation of the ovary, elongation of the stamens, and formation of accessory flanges (syrinx and annulus) are mostly related to differentiation of sections, series, subseries, and species groups. However, conical trichomes on the inner surface of the perianth, a synapomorphy that links subgenera

Orthoaristolochia and *Pararistolochia* (chapter five) is a late event in perianth development.

The systematic value of the gross shape of mature flowers is usually limited, because the final shape of the perianth does not always correspond to the same developmental process. In addition, the mature perianth forms of apparently peltate, unilabiate or bilabiate belie its development because the perianth is not univalent, but rather built up from three primordia. Therefore, the use of these terms (i. e. peltate, unilabiate, bilabiate) to define series and subseries within *Aristolochia,* as prevails in the systems of Duchartre (1854a, 1864), Schmidt (1935), Hoehne (1927, 1942) and Ma (1989) is no longer tenable.

CHAPTER FOUR

Pollen grains

I. INTRODUCTION

Pollen grains of the Aristolochiaceae are more or less spherical, with a diameter ranging from about 20 µm in *Saruma*, to 73 µm in *Aristolochia grandiflora* (Dickison, 1992; Erdtman, 1952). Differences in the type of sculpture and apertures have been reported at the generic level. *Saruma* has semitectate, per-reticulate, monosulcate pollen (Dickison, 1992; Ying & Boufford, 1993). *Asarum* pollen is verrucate or gemmate, and may be either inaperturate, colpate (often 3-4-colpate) or (3-poly-)porate (Bowman, 1973; Mi & Yang, 1991; Nakamura & Nagasawa, 1987; Walker 1974a, b, 1976). Pollen of *Thottea* (varying in diameter from ca. 27 µm in *T. corymbosa* to 41 µm in *T. grandiflora*) is inaperturate and has a sculpture composed of perforate, more or less circular exine subunits (Bowman, 1973; Hou, 1981; Nair, 1965; Tissot & al., 1994; Walker, 1976b; Fig. 59). Pollen of *Aristolochia* shows a greater diversity of size and sculpture types. The sculpture ranges from psilate to coarsely verrucate (Moncada, 1985; Walker, 1976b).

The presence of uniaperturate pollen in *Saruma* has revealed a key character that connects the family with other 'primitive' families

(Agababian, 1969; Erdtman, 1952; Huber, 1977; Thanikaimoni & Roland-Heydacker, 1980; Walker, 1974a, b) and specifically to the 'paleoherbs' (see chapter one).

Use of pollen characters in the systematics of the Aristolochiaceae, and in particular of the Aristolochioideae have been overlooked. Perhaps the only application of pollen for systematic purposes in *Aristolochia* is that by Lobreau-Callen (in Poncy, 1978), who used palynological characters to support the segregate *Pararistolochia*. Moncada (1985) studied pollen of eleven neotropical species of *Aristolochia*, and found some differences in sculpturing. She reported two main types, verrucate and rugulate, but no systematic implications were discussed.

This chapter presents the results of a comparative study of pollen grains in the Aristolochiaceae, with emphasis on the members of the Aristolochioideae (*Aristolochia*, *Euglypha* and *Holostylis*). The results presented here were included as a subset of characters in the cladistic analysis (characters 47-50) presented in chapter five.

II. MATERIALS AND METHODS

Pollen grains of all the genera of the Aristolochiaceae, including the majority of the species sampled in the cladistic analysis (Table VII) were examined with light and scanning electron microscopy. Pollen was treated by conventional acetolysis

(Erdtman, 1960). The slides were mounted using glycerol-jelly and paraffin. The light microscopic studies were made with an apochromatic oil immersion objective (x100, NA 1.32) and periplan eyepieces. Measurements were taken from 10 grains per specimen. Sets of slides are deposited in the Palynological Laboratory of the Natural History Museum, Stockholm; the Harding Laboratory of the New York Botanical Garden; and the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá. For SEM studies, both acetolysed and non-acetolysed pollen samples were mounted on aluminum stubs, coated with gold and photographed with a Jeol (JSM-6300) scanning microscope at 5 KV.

The descriptive terms used follow Punt et al. (1994).

III. RESULTS

Saruma

Pollen of *Saruma* is nearly spherical. The diameter ranges from 23-32 µm. The sculpture is semitectate and coarsely perreticulate; the muri are sometimes discontinuous; the lumina are large, usually more than 2 µm in width, and some free baculae are scattered on them. A poorly differentiated sulcus is present. These observations (based on *Pruski 3748*) confirm the previous reports by Dickison (1992), Erdtman (1952), Ying & Boufford (1993), and Walker (1974b).

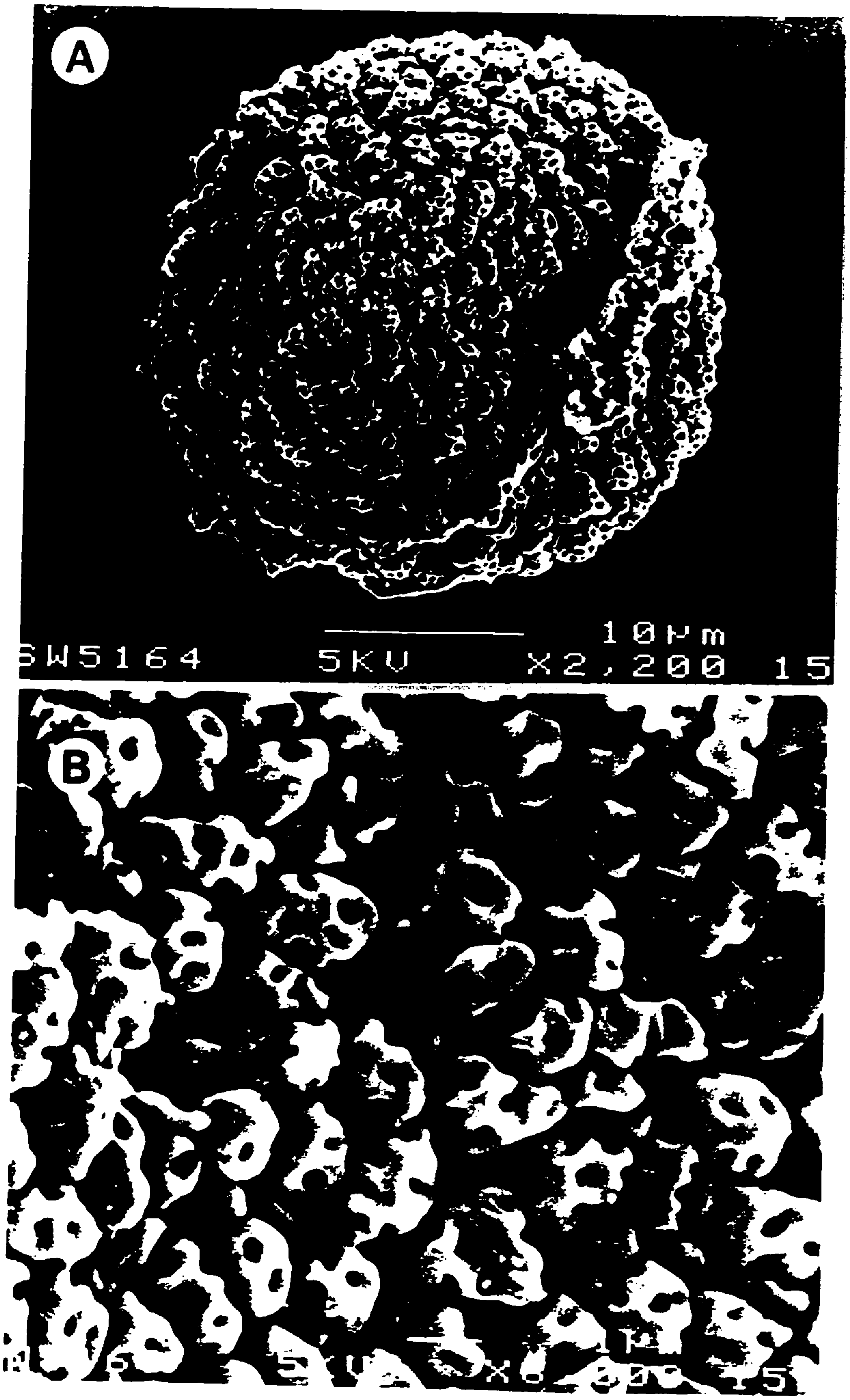
Asarum

Pollen grains of *Asarum caudatum* and *A. virginicum* are spherical. The diameter ranges from 54-60 µm and 40-45 µm, respectively. These species have a microreticulate exine, but unlike *Saruma*, the muri are continuous and the width of the lumina is considerably smaller (less than 1 µm). These species also have large supratectal warts, that usually are larger than 1 µm in diameter. Whereas several poorly differentiated pores can be detected in *A. virginicum*, no aperture differentiation was observed in pollen of *A. caudatum*.

Thottea

Pollen of *Thottea* is spherical (Fig. 59A). The diameter ranges from 25-31 µm in *T. siliquosa* and 25-36 µm in *T. corymbosa*, to 33-38 µm in *T. grandiflora*. The sculpture in these three species is areolate with the exine subunits, deeply dissected between them. The areolae are more or less circular (as in *T. corymbosa*) to more or less irregular (as in *T. grandiflora*, Fig. 59). The exine is punctate (Fig. 59B). No aperture differentiation is visible on the exine. Broken grains of *Thottea grandiflora* show well-developed columellae.

Figure 59. Pollen of *Thottea grandiflora (Henderson 24102)*. A. Pollen grain. B. Detail of the punctate, rounded exine subunits.


A
10µm
W5164
5KV
X2,200
15
B

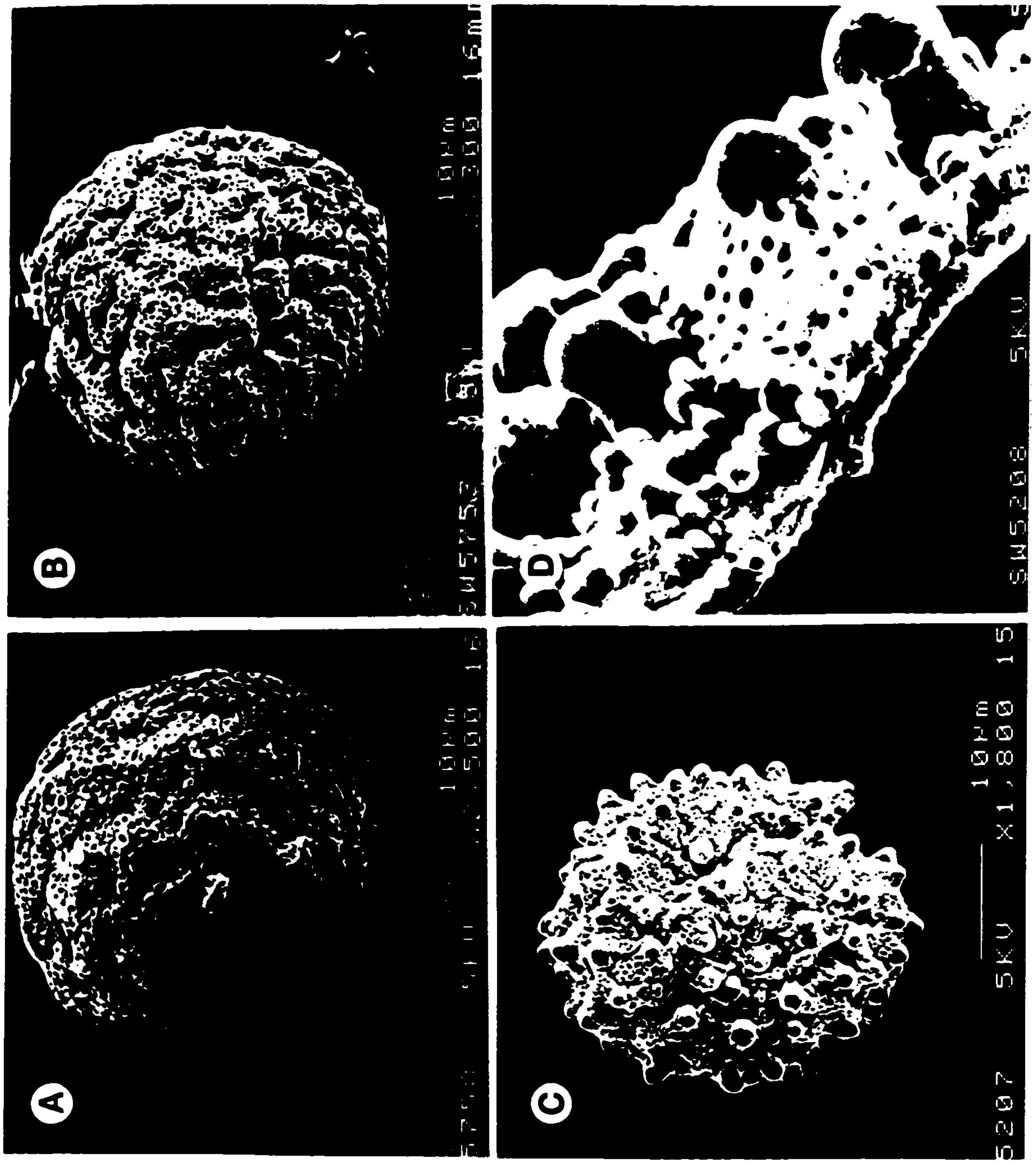
Aristolochia

There are two general types of pollen sculpture in *Aristolochia,* fossulate (Figs. 60, 61, 64, 65) and psilate (Fig. 62, 63B). In the first type, the exine is irregular, thick and dissected in form of exine subunits that give a 'cerebroid' shape to the pollen. In various taxa, other exine patterns are present, either as a long and more or less wide ridge, or as supratectal warts. The tectum in *Aristolochia* pollen may be punctate or imperforate. Psilate pollen occurs when the exine is smooth, thin and relatively homogeneous, and there are no supratectal warts or other additional ornamentation.

Aristolochia* subgenus *Siphisia

Pollen grains of *Aristolochia* subgenus *Siphisia* are fossulate. Diameter ranges between 30 µm in *A. macrophylla* and 46 µm in *A. arborea*. The exine is strongly dissected by means of elongated, irregular grooves, usually up to 5 µm or more in length. Exine subunits are densely punctate and the punctae are homogeneous in diameter (2-3 µm). In *A. macrophylla* a narrow ridge is formed on the exine (Fig. 60A). This ridge is considerably smaller than that found in the species of *A.* subgen. *Pararistolochia* (see below). A ridge on the exine was not observed in the other species of the subgenus *Siphisia*. Irregular warts were found at least in *A. arborea, A. impudica, A. malacophylla,* and *A.*

Figure 60. Pollen of *Aristolochia* subgenus *Siphisia*. A. *Aristolochia macrophylla (González 3421)*. Fossulate pollen grain. B. *A. stevensii (González 3416)*. Fossulate pollen grain. C, D. *A. arborea (Dorantes 2957)*. C. Fossulate, warty pollen grain. D. detail of the thick exine, formed by large supratectal warts and free baculae.


A
B
C
D
5207 5KU 10µm X1,800 15
SW5208 5KU
10µm

tricaudata, but unlike the supratectal elements formed in *Asarum* and in *Aristolochia* subsect. *Pentandrae* (see below) they are much taller and occupy almost the entire width of the sexine. Free clavae are present in the interstices formed between the exine subunites and are particularly numerous and conspicuous in *A. arborea* (Fig. 60D). Exine thickness varies from about 2 µm in *A. tomentosa* to about 5 µm in *A. arborea* (Fig. 60D). The sexine is always thicker than the nexine, in a ratio up to 4:1 in *A. arborea*. Orbicules (i. e. Ubisch bodies) were observed in *A. arborea, A. macrophylla, A. malacophylla, A. serpentaria, A. stevensii,* and *A. tricaudata*.

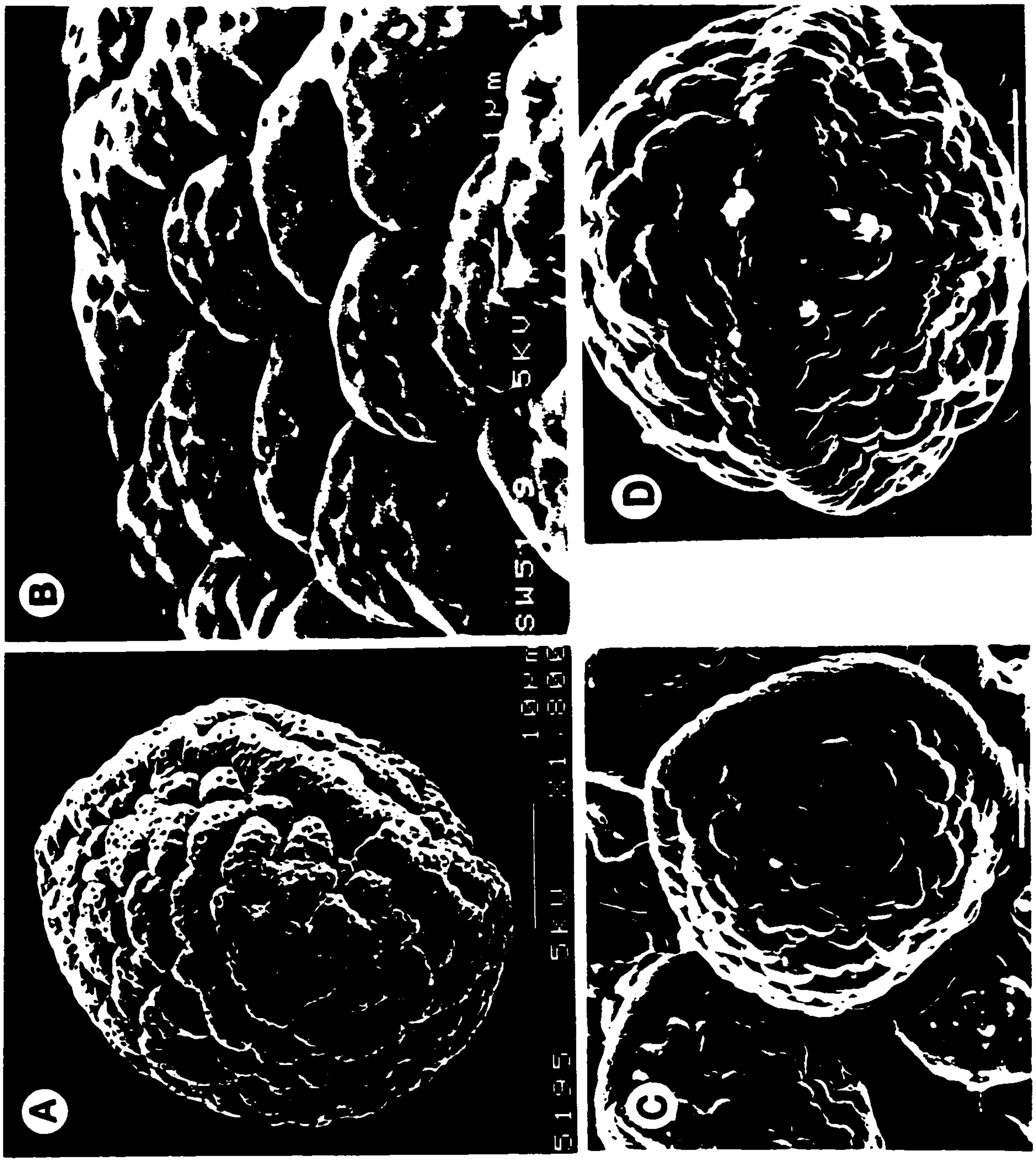
Aristolochia subgenus *Pararistolochia*

Pollen of *Aristolochia* subgen. *Pararistolochia* is fossulate and strongly dissected. Diameter ranges from 27 µm in the New Guinean *A. momandul* and the Australian *A. deltantha*, to 52 µm in the African *A. triactina*.

A long exine ridge, up to 20 µm in length was observed in all the species studied, as has been reported for other species of this subgenus (Lobreau-Callen in Poncy, 1978). The remaining exine subunits are short and form irregular to nearly circular insulae that are usually greater than 5 µm in width (Fig. 61). In some species (e. g., *A. leonensis*, and *A. mannii*) they are loosely spaced. Both the exine ridge and the insulae are punctate (Fig.

Figure 61. Pollen of *Aristolochia* subgenus *Pararistolochia*.

A, B. *A. triactina (Bos 3505)*. A. Pollen grain showing the exine ridge (right) and the large, punctate exine subunits. B. Detail of the punctate exine subunits. C, D. *A. goldieana (Carvalho 4340)*, lateral (C) and frontal (D) view of the exine ridge. Bar in C and D = 10 µm.


A
5195 5KU X1,800 10µm
B
SW51 9 5KU 1µm
C
D

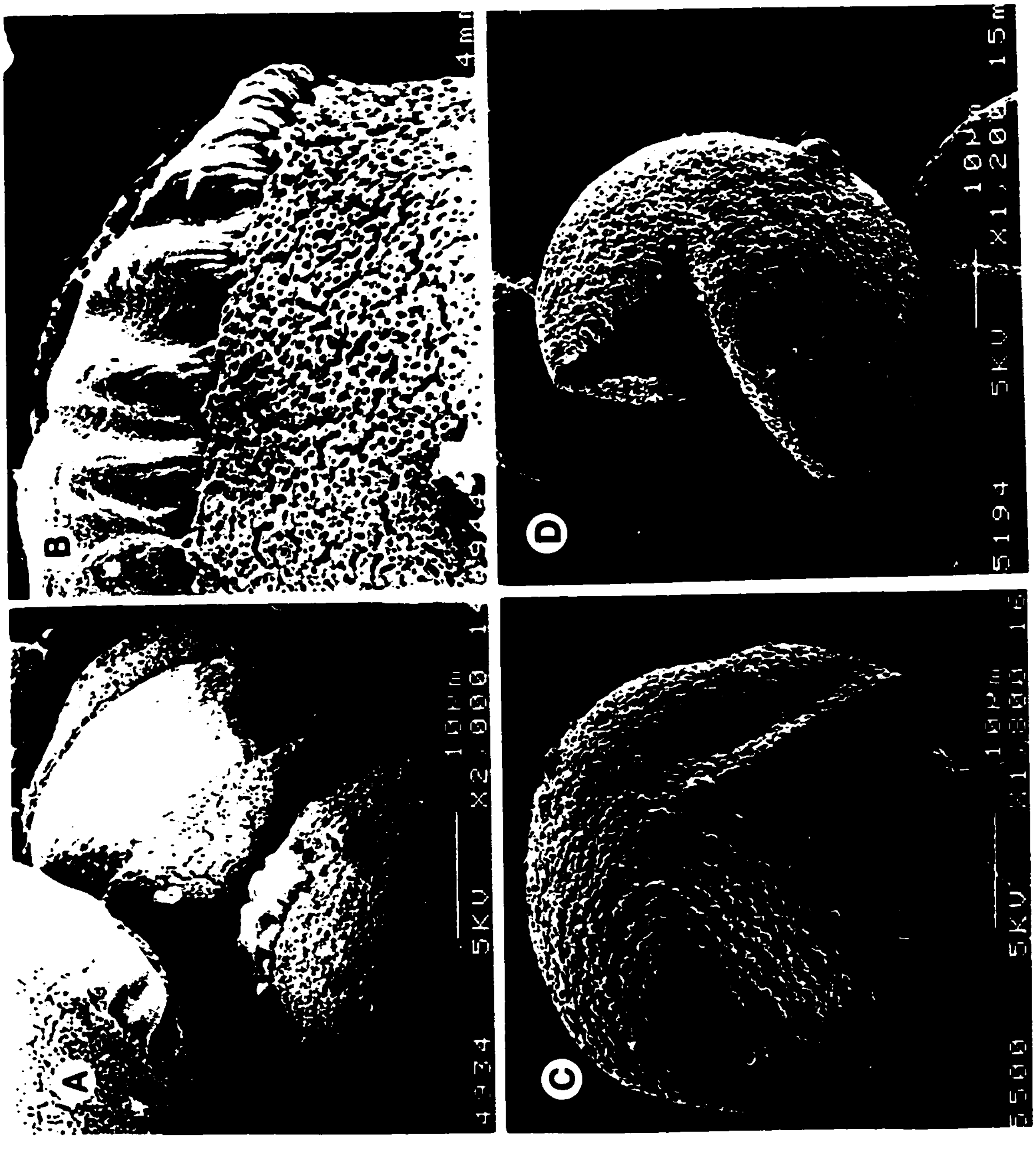
61), and the punctae are quite homogeneous in diameter (0.2-0.4 µm). The infratectum is columellate. Moreover, free clavae are present in some of the interstices formed between the exine insulae (Fig. 61C, D). Sexine is at least twice as thicker than the nexine. Orbicules were observed in *A. macrocarpa*.

Aristolochia* subgenus *Orthoaristolochia

Two different types of sculpture are found in pollen grains of *Aristolochia* subgen. *Orthoaristolochia*, and they are more or less consistent with the two sections described by Duchartre (1854a, 1864), *Diplolobus*, and *Gymnolobus*.

Pollen of *Aristolochia* sect. *Diplolobus* is spherical or nearly spherical. The diameter ranges from 35.5 µm in *A. contorta* to about 67 µm in *A. philippinensis*. The sculpture, rather simple and homogeneous, is psilate or finely fossulate. In the latter, the exine subunits are small, very densely arranged and slightly dissected. The tectum may be complete (as in e.g. *A. clematitis*, Fig. 62A, B) or incomplete (as in *A. acuminata*, Fig. 62C, D). The tectum may be scarcely punctate (as e.g. in *A. acuminata*, Fig. 62C, or *A. bracteolata*, Fig. 62D) or imperforate (as in e.g. *A. philippinensis*). No supractectal elements were detected in the species studied. The infratectum is columellate. The exine is thinner (usually less than 2 µm thick; it reaches up to 3 µm in *A. paucinervis)* than in the remaining species of *Aristolochia*. The sexine : nexine ratio ranges from about 1:1 (in e.g. *A. altissima*,

Figure 62. Pollen of *Aristolochia* section *Diplolobus*. A, B. *A. clematitis (González 3446)*. A. Non-acetolysed pollen grains, germinating *in situ*. B. Detail of the germination zone, showing the even, smooth, thin exine. C. Acetolysed pollen grain of *A. acuminata (Ramos 83484)*. D. Acetolysed pollen grain of *A. bracteolata (Qaiser s.n.)*.


A
B
C
D
5KU X2,000 10µm
5194 5KU X1,200 10µm 15mm
5KU 10µm

and *A. bracteolata*) to ca. 2:1 (in e.g. *A. acuminata, A. indica, A. paucinervis, A. pistolochia*, and *A. tubiflora*); the nexine is thin, always less than 1 µm thick. Orbicules are present at least in *A. clematitis*.

Pollen of the species of *Aristolochia* section *Gymnolobus* is spherical or nearly spherical. The exine is usually strongly dissected. Pollen of a few species is psilate (e.g. *A. grandiflora*, Fig. 63A; *A. lindneri*; *A. pilosa*, Fig. 63B) but it differs from the psilate pollen present in the species of *Aristolochia* sect. *Diplolobus*. For example, the exine of *A. grandiflora* (Fig. 63A) forms large, irregular, flattened flake-shape subunits, a condition not found in the species of section *Diplolobus*. The flake-shaped exine subunits of *A. grandiflora* (Fig. 63A) have irregular borders that superpose each other. This type of sculpture is similar to that found in the species of *Aristolochia* subsect. *Pentandrae* (see below). Pollen of *A. pilosa* is tectate as in some species of section *Diplolobus*, but with small (<0.5 µm in diameter) and large (up to 1.5 µm in diameter; Fig. 63B) puncta, a condition not known in *Aristolochia* sect. *Diplolobus*.

The most frequent type of pollen sculpture in *Aristolochia* sect. *Gymnolobus* is fossulate. The exine units are massive, irregular, "cerebriform", and strongly dissected (Fig. 64). These units usually are smaller than those found in subgenus *Pararistolochia*. The sexine : nexine ratio usually is larger than 2:1. The punctae

Figure 63. Pollen in *Aristolochia* section *Gymnolobus*. A. *A. grandiflora* (*Haught 4717*). B. *A. pilosa (González 3571)*. C, D. *A. maxima (Ruiz 91)*. C. Pollen grain; D. Detail of the fossulate exine.

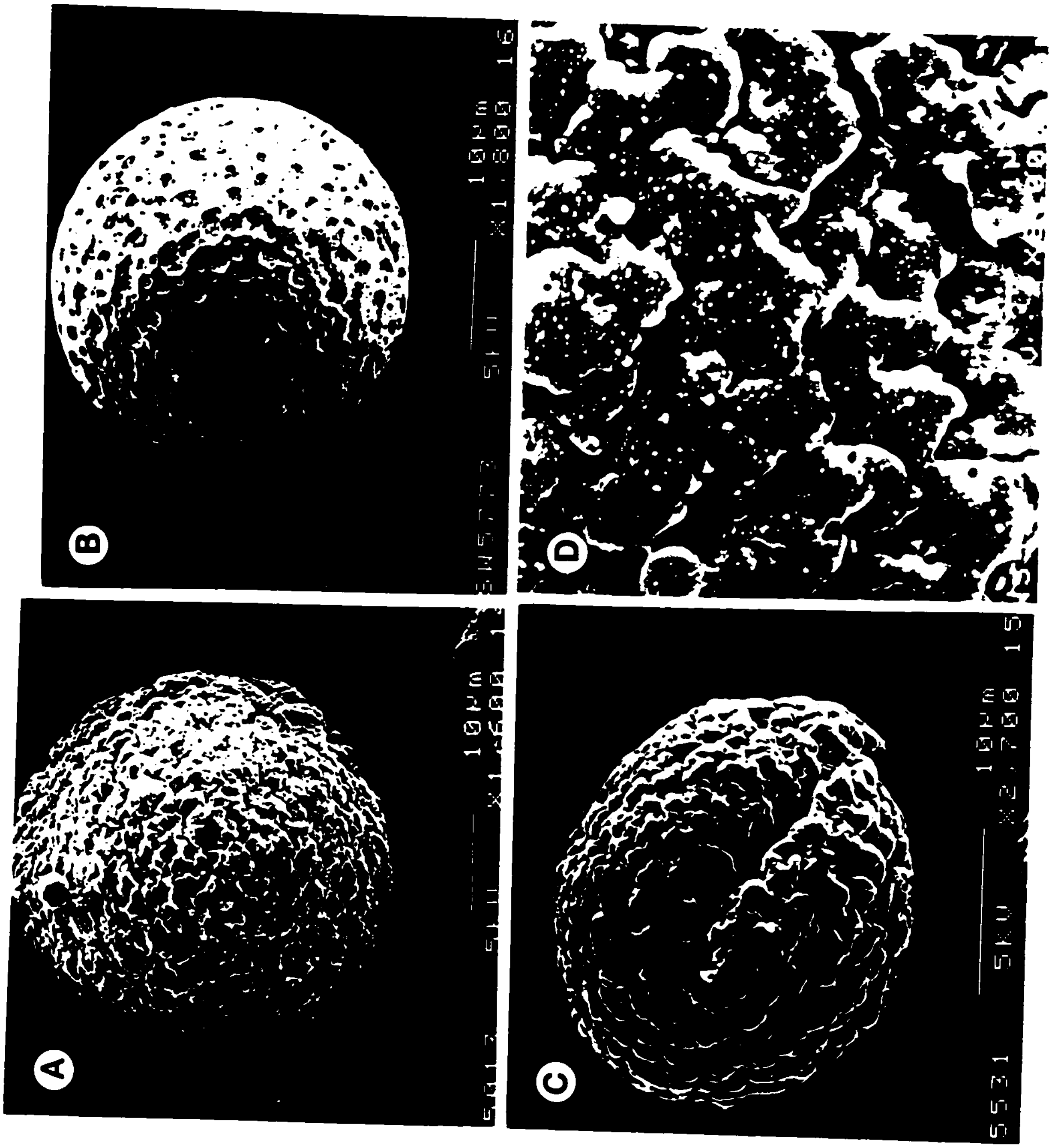
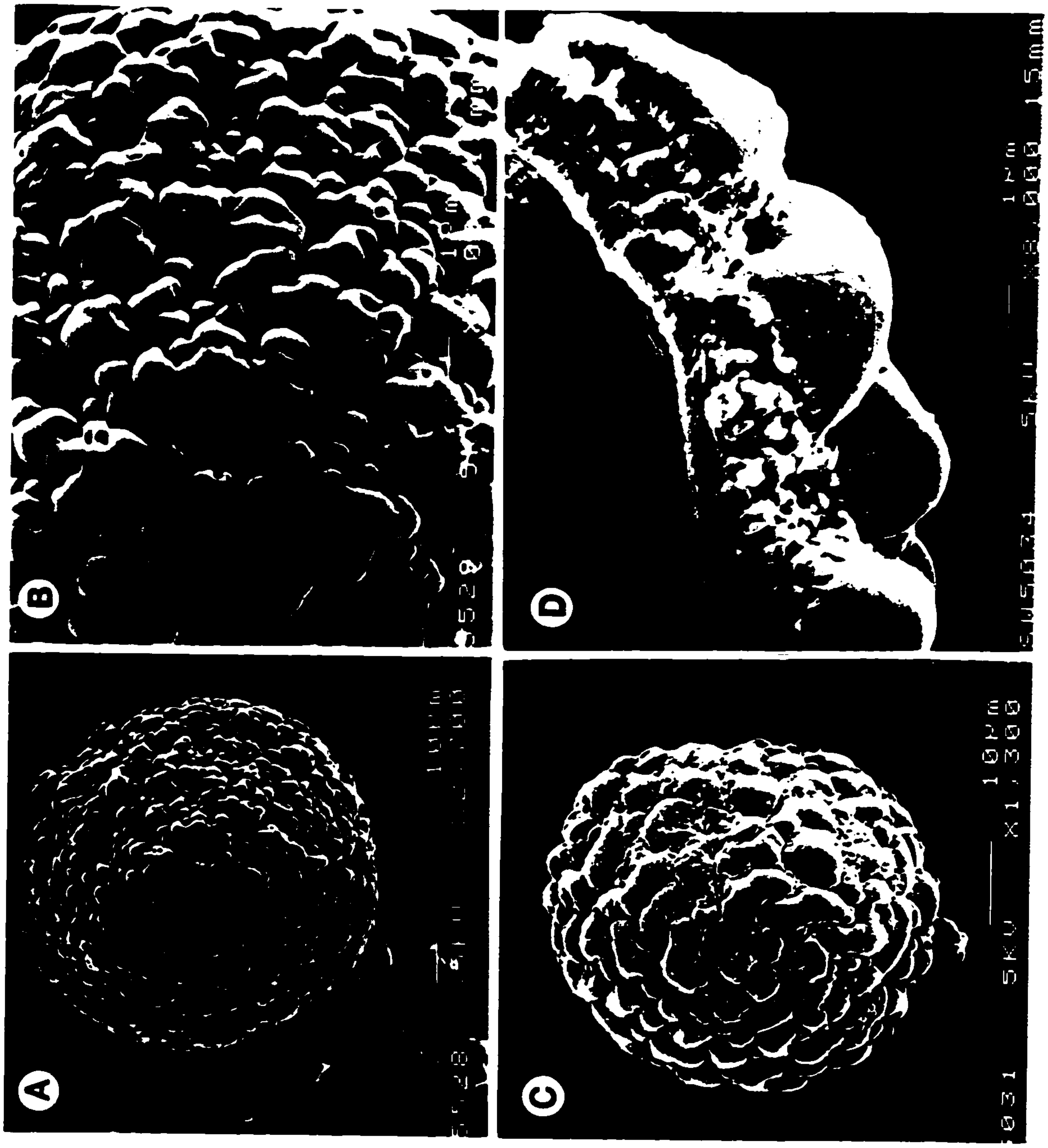

A
B
C
D

Figure 64. Pollen in species of *Aristolochia* subsect. *Hexandrae*. A, B. A. *iquitensis (Vasquez et al. 4476)*. C, D. A. *ridicula (Anderson 9215)*.


A
B
C
D

are missing or very scarce, and the infratectum is columellate (Figs. 63C, D, 64C, D). Orbicules were observed at least in *A. elegans,* and *A. odoratissima*. Previously, orbicules have been reported only in *A. elegans* (Johri & Bhatnagar, 1955).

Diameter of the pollen of *Aristolochia* subsect. *Pentandrae* ranges from ca. 35 µm in *A. mutabilis* to 52 µm in *A. oaxacana*. Exine thickness ranges from 1.8 to 3.7 µm; the sexine is always thicker than the nexine, in an approximate ratio of 2:1 or up to 3:1 (in *A. mutabilis* and *A. oaxacana*, respectively). The exine subunits are numerous, tightly packed, densely punctate, and have a characteristic flake-like shape (Fig. 65) and are not sharply dissected. In all the species studied, there are conspicuous, more or less spherical supractectal warts that are up to 1 µm wide (e.g., *A. wrightii*, Fig. 65).

Euglypha and *Holostylis*

Pollen grains of *Euglypha* (Fig. 66A, B) and *Holostylis* (Fig. 66C, D) do not exhibit significant differences with respect to those of *Aristolochia* sect. *Gymnolobus*. However, pollen of *Euglypha* (47-73 µm in diameter) is considerably larger than that of *Holostylis* (41-49 µm in diameter) and other species of *Aristolochia*. The exine in *Euglypha* (Fig. 66A, B) and *Holostylis* (Fig. 66C, D) is strongly dissected, with irregular subunits that are scarcely punctate (Fig. 66 B). The sexine is considerably wider than the nexine, and the infratectum is columellate (Fig. 66D).

Figure 65. A, B. Pollen of *Aristolochia wrightii* (*Johnson et al. 902*), a species of subsection *Pentandrae*; note in B the rounded supratectal warts (verrucae).

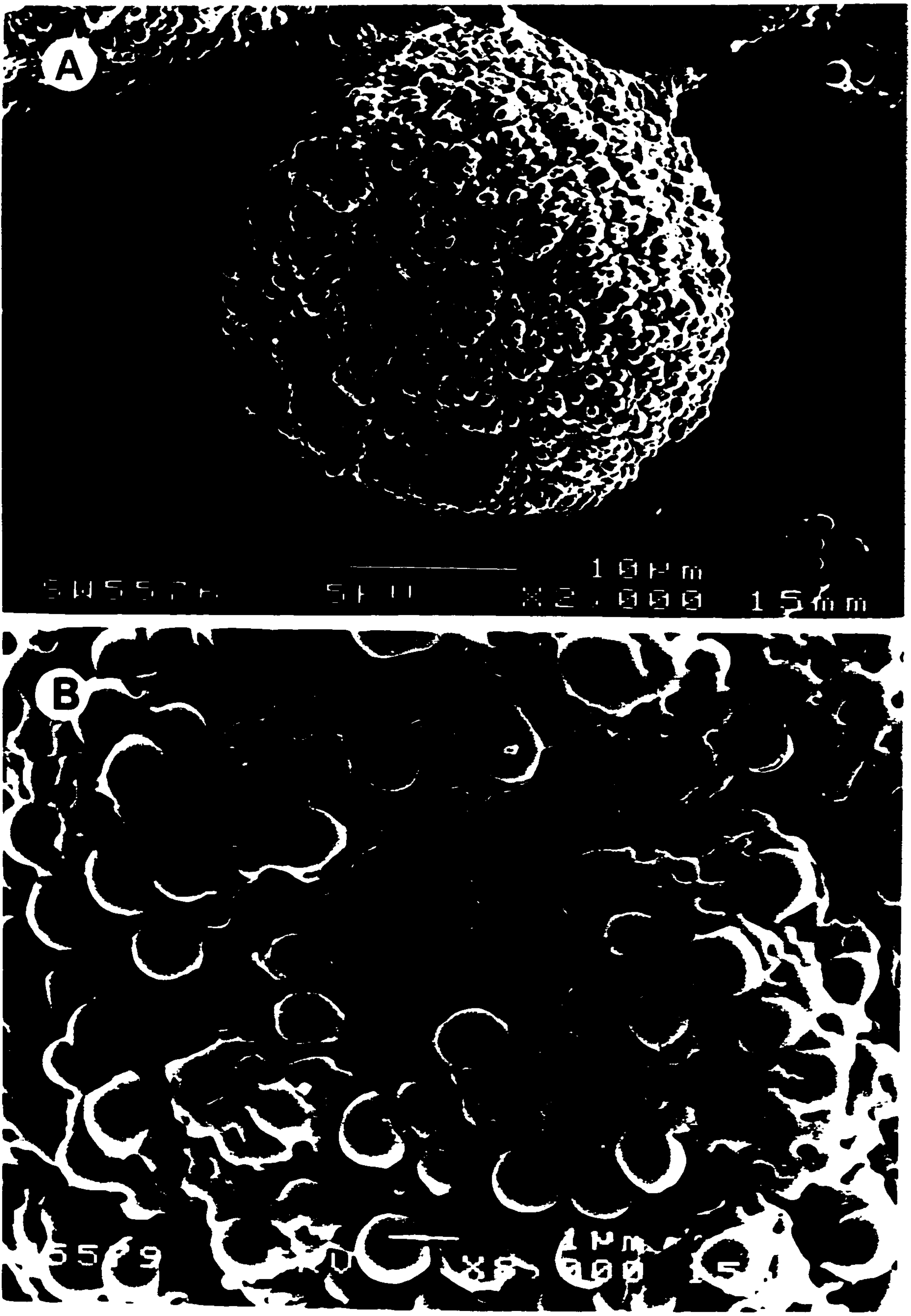
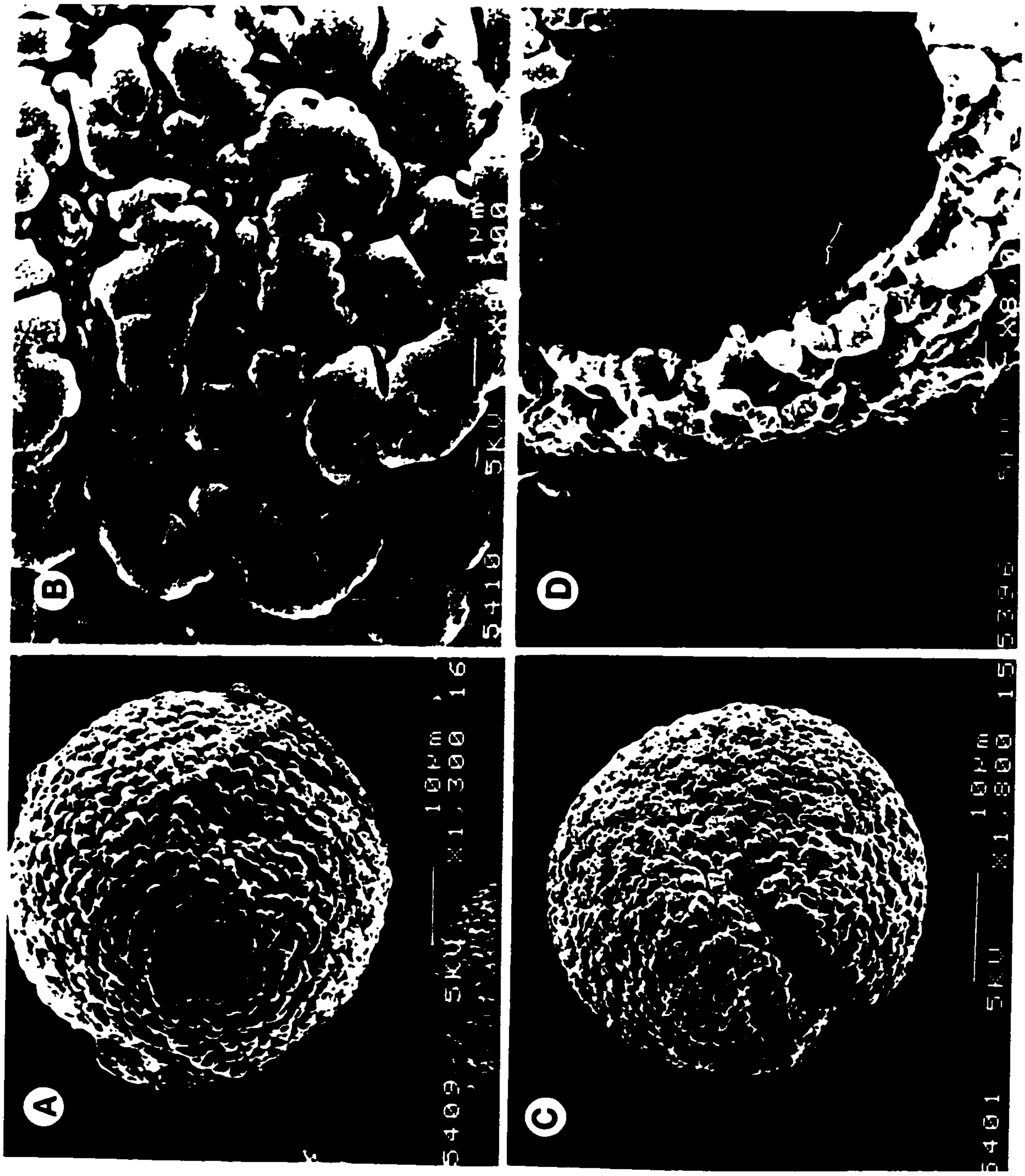

A
10µm
X2,000
15mm
B
1µm

Figure 66. Pollen grains of *Euglypha* and *Holostylis*. A, B. *Euglypha rojasiana (Arenas 337)*. C, D. *Holostylis reniformis (Plowman et al. 9369)*.


A
B
C
D
10µm
X1,300
1µm
10µm
X1,800
5KU

IV. DISCUSSION

The finds of semitectate, monosulcate pollen of *Saruma* and porate pollen at least in *Asarum virginicum* are concordant with previous reports (Bowman, 1973; Dickison, 1992; Erdtman, 1952; Huang et al. 1995; Mi & Yang, 1991; Walker, 1974a, b; and Ying & Boufford, 1993). Whereas the coarsely per-reticulate sculpture of *Saruma* pollen is unique within the Aristolochiaceae, the supratectal warts present in *Asarum* are also found in the species of *Aristolochia* subsect. *Pentandrae.*

Porate pollen was not detected in any of the species of *Aristolochia* studied. According to Walker (1974b), *A. punjabensis* has porate pollen. However, the specimen of *A. punjabensis* examined during the present study (*Stewart 7642*, NY) does not possess porate pollen. Instead, pollen of this specimen resembles that of other members of subgenus *Siphisia*, such as *A. macrophylla* and *A. tomentosa* and none of them have a differentiated aperture.

The main differences of pollen morphology in *Aristolochia* are found in the sculpturing. Three infrageneric taxa show certain homogeneous traits related to pollen sculpture: (1) *Aristolochia* subgenus *Pararistolochia* is characterized by the presence of a large and broad ridge of exine (Fig. 61); (2) *Aristolochia* sect. *Diplolobus* is characterized by the presence of a thin, smooth or nearly smooth exine (Figs. 62, 63B); and (3) *Aristolochia* subsect. *Pentandrae* has pollen with supratectal warts that are more or less spherical (Fig. 65). In the remaining infrageneric taxa (i.e.

subgenus *Siphisia*, and the bulk of hexandrous, Neotropical species of *Aristolochia*; Table III), the pollen sculpture is basically fossulate, and the exine is strongly dissected.

The cladistic analysis (chapter five) suggests that psilate pollen grains (character 47, state 4) evolved independently three times, once in *Aristolochia* section *Diplolobus*, once in the clade formed by *Aristolochia grandiflora and A. lindneri*, and once in *A. pilosa* (Fig. 75). The plesiomorphic condition in *Aristolochia* is the strongly dissected, massive exine that forms a fossulate sculpture.

The results of the cladistic analysis revealed that the presence of a markedly differentiated ridge of exine (character 49; Fig. 74) is one of the synapomorphies for the sister-group relationship between the African and the Australasian species of *Aristolochia* subgen. *Pararistolochia*. This character was previously described in some of the African species by Lobreau-Callen (in Poncy, 1978) to support the recognition of *Pararistolochia* as distinct from *Aristolochia*.

The analysis also revealed that supratectal warts define *Aristolochia* subsection *Pentandrae* (Fig. 77) although they appear independently once in *Asarum* (Fig. 71), once in a crown clade within *A.* subgen. *Siphisia* (which includes *A. arborea* and *A. tricaudata*), and once in *A. burelae*. This suggests that the supratectal warts may have different developmental pathways in these taxa.

No clear-cut differences in pollen morphology were observed between the two subsections described by Duchartre (Table III), *Euaristolochia* (e.g. *A. clematitis*, Fig. 62A; *A. bracteolata*, Fig. 62B), and *Podanthemum* (e.g. *A. acuminata*, Fig. 62C, D). In addition, no palynological evidence was found to support the generic status of *Euglypha* and *Holostylis*. Pollen of these two genera is quite similar to that in most Neotropical species of *Aristolochia*.

Orbicules (or Ubisch bodies) seem to be of common occurrence in the Aristolochiaceae. They are reported here for the first time in *Asarum arifolium*, and in several species of *Aristolochia* (*A. arborea*, *A. clematitis*, *A. macrophylla*, *A. odoratissima*, *A. peruviana*, *A. serpentaria*, *A. stevensii*, and *A. tricaudata*).

Pollen Aperture in the Aristolochiaceae

The absence of aperturate differentiation seems to be general condition in *Aristolochia*, *Euglypha*, *Holostylis* and *Thottea*. Pollen grains in *Aristolochia* and *Thottea* are often described as inaperturate (e.g. Agababian, 1969; Huang, 1972). Some workers, however, describe the pollen in these genera as monocolpate or even trichotomocolpate (Nair, 1965). *In situ* germinating pollen, and non-acetolised pollen often show that germination recurrently occurs through an elongated opening that is, however, undifferentiated in the pollen wall. At least from a functional standpoint, one sulcus-like aperture appears to be the rule in *Aristolochia* (Figs. 59A, 62). Thanikaimoni (1986) mentioned examples of some of the so-called inaperturate pollen grains, which are in fact omniaperturate, since the homogeneous structure of the exine and the intine allows a germination through non-specific sites. This could be the case in *Aristolochia*. Ontogenetic and ultrastructural studies of the pollen wall are necessary to precisely identify any difference that could indicate the presence of a colpus on the nexine/intine.

Several characters of pollen of *Aristolochia* often described in the literature, such as the size and the shape of the pollen, or the type of aperture, are not reliable because they change during pollen germination. The undifferentiated opening of *in situ* germinating pollen (Figs. 59A, 60C, 62, 63, 66) could be interpreted (under LM) as a colpus. Also, pollen shape drastically changes from spherical before germination to ovoid during germination. Similar examples have been previously described by Müller-Stoll (1956) and Thanikaimoni (1986). This would explain why some workers (e.g. Bowman, 1973) have described the aperture length and shape in *Aristolochia* as variable.

V. CONCLUSION

Generic differences are recognized in terms of pollen morphology of the Aristolochiaceae. The semitectate, monosulcate pollen grains of *Saruma* are unique in the Aristolochiaceae. *Asarum* pollen is also different in that it has pores and supratectal warts. In both *Asarum* and *Saruma* the apertures are not strongly differentiated on the exine. Pollen of the remaining genera of the family has been traditionally described as inaperturate. Sculpture differences also exist between *Thottea*, on the one hand, and *Aristolochia, Euglypha* and *Holostylis* on the other hand. *Thottea* pollen has more or less isodiametric exine subunits that are usually densely puntate. Similar sculpture was not found in *Aristolochia*, despite the remarkable diversity of sculpture types in this genus.

The cladistic analysis shows that characters related to pollen morphology support the monophyly of three infrageneric taxa of *Aristolochia* as previously described (Table III): *Aristolochia* subgenus *Pararistolochia,* and two monophyletic groups inside *Aristolochia* subgenus *Orthoaristolochia:* section *Diplolobus* and subsection *Pentandrae*. Pollen characters are more heterogeneous in the remaining groups, i.e. subgenus *Siphisia*, and the bulk of Neotropical species of subsection *Hexandrae*.

CHAPTER FIVE

A phylogenetic analysis of the subfamily Aristolochioideae

I. INTRODUCTION

In this chapter a cladistic analysis based on morphological characters, of the subfamily Aristolochioideae *sensu* Schmidt (1935; Tables I, VII) is presented. The ingroup taxa include *Euglypha rojasiana*, *Holostylis reniformis*, and 106 species of *Aristolochia* (Table VII). Each of the subgenera of *Aristolochia* and most of the sections, subsections, series and subseries that have been previously described are represented in the present analysis.

With about 380 species of primarily tropical distribution, *Aristolochia* is by far the largest genus of the family Aristolochiaceae. The genus is here treated in its broad sense, but most of the segregates (Table II) described by Dumortier (1822), Rafinesque (1828, 1836), Klotzsch (1859), Hutchinson and Dalziel (1927), and Huber (1985, 1993) were sampled. As explained

Table VII . Formal classification of the Aristolochiaceae followed here, based on Duchartre (1854a), Schmidt (1935), Ma (1989) and González (1990, 1991). Species sampled in the cladistic analysis are listed. Numbers in parenthesis indicate number of species sampled/approximate number of species.

- Subfamily **Asaroideae** Schmidt
  - Tribe **Sarumeae** Schmidt
    - *Saruma henryi* Oliv.
  - Tribe **Asareae** Duchartre
    - *Asarum caudatum* Lindl.
    - *A. virginicum* L.
  - Tribe **Bragantieae** Schmidt
    - *Thottea corymbosa* (Griff.) Ding Hou
    - *T. grandiflora* Rottb.
    - *T. siliquosa* (Lamk.) Ding Hou

- Subfamily **Aristolochioideae** Schmidt
  - Tribe **Aristolochieae** Schmidt
    - *Holostylis reniformis* Duchartre
    - *Aristolochia* L.
      - **Subgenus *Siphisia* Schmidt**
        - **Section *Asterolytes* Duchartre (2/2)**
          - *A. reticulata* Nutt.
          - *A. serpentaria* L.
        - **Section *Siphisia* (Raf.) Duchartre (13/40)**
          - *A. californica* Torr.
          - *A. cucurbitifolia* Hayata
          - *A. fulvicoma* Merr. & Chun
          - *A. impudica* Ortega
          - *A. macrophylla* Lamk.
          - *A. malacophylla* Standl.
          - *A. manshuriensis* Komarov
          - *A. panamensis* Standl.
          - *A. paracleta* Pfeifer
          - *A. punjabensis* Craib
          - *A. stevensii* K. Barringer
          - *A. tomentosa* Sims
          - *A. tricaudata* Lem.
        - **Section *Hexodon* Duchartre(1/2)**
          - *A. kaempferi* Willd.
        - **Section *Nepenthesia* Klotzsch (1/3)**
          - *A. hainanensis* Merr.

      - **Subgenus *Orthoaristolochia* Schmidt**
        - **Section Gymnolobus**
          - **Subsection *Pentandrae* Duchartre (33/37)**
            - *A. bracteosa* Duchartre
            - *A. brevipes* Bentham
            - *A. buntingii* Pfeifer
            - *A. cardiantha* Pfeifer
            - *A. conversiae* Pfeifer
            - *A. cordata* Eastwood

Table VII . Continued.

- A. *coryi* Johnst.
- A. *duranguensis* Pfeifer
- A. *erecta* L.
- A. *flexuosa* Duchartre
- A. *foetida* H.B.K.
- A. *islandica* Pfeifer
- A. *karwinskii* Duchartre
- A. *micrantha* Duchartre
- A. *monticola* Brandg.
- A. *mutabilis* Pfeifer
- A. *nana* Watson
- A. *nelsonii* Eastwood
- A. *oaxacana* Eastwood
- A. *palmeri* Watson
- A. *pentandra* Jacq.
- A. *porphyrophylla* Pfeifer
- A. *pringlei* Rose
- A. *secunda* Pfeifer
- A. *sinaloae* Brandg.
- A. *socorroensis* Pfeifer
- A. *tequilana* Watson
- A. *teretiflora* Pfeifer
- A. *tresmariae* Ferris
- A. *variifolia* Duchartre
- A. *versabilifolia* Pfeifer
- A. *watsonii* Wooton & Standl.
- A. *wrightii* Seem.

Subsection *Hexandrae*
- **Series *Thyrsicae* F. González (4/16)**
  - A. *acutifolia* Duchartre
  - A. *maxima* Jacq.
  - A. *melastoma* Manso
  - A. *trianae* Duchartre
- **Series *Hexandrae***
  - **Subseries *Anthocaulicae* F. González (3/14)**
    - A. *cordiflora* Mutis ex H.B.K.
    - A. *iquitensis* Schmidt
    - A. *leuconeura* Linden

  - **Subseries *Hexandrae* (28/ca. 100)**
    - A. *arborea* Lindl.
    - A. *burelae* Herz.
    - A. *cymbifera* Mart. & Zucc.
    - A. *deltoidea* H.B.K.
    - A. *didyma* S. Moore
    - A. *esperanzae* O. Kuntze
    - A. *galeata* Mart. & Zucc.
    - A. *gehrtii* Hoehne
    - A. *gibertii* J.D. Hook.
    - A. *grandiflora* Sw.
    - A. *hians* Willd.
    - A. *inflata* H.B.K.
    - A. *labiata* Willd.

Table VII . Continued.

A. *lindneri* Berg.
A. *lingulata* Ule
A. *loefgrenii* Hoehne
A. *mishuyacensis* Schmidt
A. *nummularifolia* H.B.K.
A. *odoratissima* L.
A. *passifloraefolia* A. Rich.
A. *pilosa* H.B.K.
A. *pohliana* Duchartre
A. *ridicula* Brown
A. *ringens* Vahl
A. *tigrina* A. Rich.
A. *trilobata* L.
A. *warmingii* Mast.
A. *xerophytica* Schultes

Section *Diplolobus* Duchartre (13/115)
  Subsection *Euaristolochia* (Klotzsch) Schmidt
    A. *clematitis* L.
    A. *contorta* Bunge
    A. *pistolochia* L.
    A. *rotunda* L.
    A. *tubiflora* Dunn
  Subsection *Podanthemum* (Klotzsch) Duchartre
    A. *acuminata* Lamk.
    A. *bracteolata* Lamk.
    A. *debilis* Sieb. et Zucc.
    A. *foveolata* Merrill
    A. *indica* L.
    A. *petersiana* Kl.
    A. *philippinensis* Warb.
    A. *thozetii* F. Muller

Subgenus *Pararistolochia* (Hutch. & Dalz.) Schmidt
  Section *Pararistolochioides* Ma (1/1)
    A. *goldiana* Hook. f.
  Section *Pararistolochia* (4/6)
    A. *decandra* Hou
    A. *macrocarpa* Duchartre
    A. *promissa* Mast.
    A. *triactina* Hook. f.
  Section *Aristolochioides* Ma (1/2)
    A. *leonensis* Mast.
  Australasian taxa (2/9-22)
    A. *deltantha* F. Muell.
    A. *momandul* K. Sch.

Tribe Euglypheae Schmidt (1/1)
  Euglypha rojasiana Chod. & Hassl.

in chapter one, most of the segregate genera correspond to infrageneric taxa proposed by authors such as Duchartre (1854a, 1864), Schmidt (1935), and Hoehne (1942). The systems differ mainly in the choice of rank at which the various taxa are recognized. For example, the segregate genera *Einomeia* and *Howardia* described by Klotzsch (1859) and maintained by Huber (1985, 1993) correspond to Duchartre's (1854a) subsections *Pentandrae* and *Hexandrae*, respectively (Table III). Section *Polyanthera* (Bentham & Hooker, 1880) was raised to a subgeneric rank by Schmidt (1935). Unfortunately, in the most recent classifications authors have focussed on the rank at which these taxa should be recognized (see e.g. Huber, 1985, 1993, Parsons, 1996), rather than on the relationships or the monophyly of the groups.

The present analysis was conducted to evaluate the relationships between the genera *Aristolochia*, *Euglypha* and *Holostylis*, and to test the monophyly of the infrageneric taxa of *Aristolochia*, including the previously proposed segregated genera of the latter (Tables I-III). In addition, the analysis will provide a basis for the evaluation of the congruence of floral characters that are traditionally used in the classification of the Aristolochioideae with other characters, and to suggest hypotheses of character evolution, in particular of the traits related to inflorescence, floral morphology, and seed dispersal.

II. METHODS

Sampling

The formal classification followed here for taxon selection essentially corresponds to that of Schmidt (1935), at both subfamilial (Table I) and subgeneric (Table III) ranks, although additional species from Australia and New Guinea have been included in subgenus *Pararistolochia*, following Parsons (1996, who treated the group as a distinct genus). The species sampled in the cladistic analysis are summarized in Table VII. Taxa below the subgeneric level essentially follow Duchartre (1854a, 1864; Tables III, IV), Ma (1989), Hoehne (1942; Table IV), and González (1990, 1991). The sample includes a broad range of morphological diversity and geographical distribution of *Aristolochia*. Some lower rank taxa described by Duchartre (1854a, 1864), Hoehne (1942) and Ma (1989) were not considered because they were delimited primarily by minor differences in floral shape, size or indument. For example, there is no clear-cut difference between subseries *Macranthae* and *Parviflorae,* which were described by Hoehne (1942; Table IV) based on flower size. Such characters are not discrete and are therefore difficult to score.

The ingroup in the present analysis includes 61 species of *Aristolochia* representing all subgenera, sections and subsections, and most of the series and subseries (Table VII). In addition, the analysis includes two groups of species that correspond to subsection *Pentandrae* (Duchartre, 1854a, 1864) of which 33 of 37 species were examined, and section *Dipharus* (Klotzsch, 1859), of which 12 of 18 species were studied (Table VII). Subsection *Pentandrae*, and section *Dipharus* are justifiable as single terminals because the species of each group are very homogeneous. This is reflected in the low number of polymorphic characters scored for each (three and one, respectively). The monophyly of each of these two taxa is very likely, as each has characters that are unique within *Aristolochia*. All species of *A.* subsect. *Pentandrae* have five anthers and five carpels (Figs. 5C, 35, 36, 52F), instead of six stamens and six carpels in the remaining species of *Aristolochia*. Flowers of all the species of *A.* sect. *Dipharus* display an adaxial and an abaxial lip (Figs. 23D, 48F, 52E), instead of the flowers with one or three lobes as in the rest of the genus.

The outgroups for the present analysis are the other three genera of the family Aristolochiaceae, *Asarum*, *Saruma* and *Thottea*. They were chosen on the basis of the cladistic analyses presented by Loconte and Stevenson (1991), and Kelly (1997). Two species of *Asarum* and three of *Thottea* were included in order to cover floral morphological variation within these genera.

Characters

The majority of the morphological characters included in this analysis were taken from my own collections, herbarium specimens, and field observations. Additional preserved specimens were also examined (Appendix II). Literature has been employed only when data were insufficient or unclear. All the multistate characters were treated as unordered.

0. Habit. (0) herbaceous, (1) woody at least in the roots and/or rhizomes.

1. Growth units. (0) sympodial (1) monopodial (i.e. indeterminate; Figs. 8D, 9, 10B, D, 11D, 21A). Whereas growth units of *Saruma* (Fig. 6C) and *Asarum* are sympodial (Figs. 6A, 7A), those of *Aristolochia* (Figs. 8D, 10B, D, 21A), *Euglypha*, *Holostylis*, and *Thottea* are monopodial; some species of subgenus *Pararistolochia* from Australia and New Guinea (as e.g. *A. deltantha*; Fig. 8C) might have sympodial growth units.

2. Elongating shoots. (0) nearly straight, (1) strongly sinuous. The elongating shoots of most of the Aristolochiaceae are nearly straight (Fig. 8A, D, 67B), but in some neotropical members of *Aristolochia*, they are strongly sinuous (Fig. 67A).

3. Number of axillary buds. (0) one, (1) two or more. In *Asarum* and *Saruma* there is one axillary bud per node ((Figs. 6A-C, 7A-C); in *Aristolochia*, *Euglypha*, *Holostylis* and *Thottea* there are at least two axillary buds per node (Figs. 6E, 8A-C, E, F, 9A, 10B).

4. Arrangement of axillary buds. (0) uniseriate, (1) biseriate. When two or more axillary buds occur in the same leaf axil, they are arranged either in one (Figs. 8A, B, 9A, 10D) or in two (Figs. 8F, G, 10B) rows.

Figure 67. Some vegetative characters used in the cladistic analysis. A. *Aristolochia ringens (González 3584)*, strongly sinuous elongating shoot (character 2-1). B. *A. leuconeura (González 3290)*, straight elongating shoot (character 2-0) showing also a non-pseudostipular prophyll (arrow; character 8-0). C. *A. ringens (González 3584)*, apical meristem showing leaves on plastochrones 2 and 3 (normal leaf expansion; character 7-0; bar = 50 µm). D. *A. maxima*, apical meristem showing leaves on plastochrones 2 and 3 (delayed leaf expansion; character 7-1; bar = 50 µm). E. *A. ringens (González 3584)*, pseudostipule (character 8-1).


A
E
B
D
C

5. Mature stems. (0) circular, (1) medially constricted. Stems in some species of *Aristolochia* become medially constricted thus producing a "figure 8" form in transverse section.

6. Hooked trichomes. (0) absent, (1) present. Hooked trichomes are present in both vegetative (Figs. 21A, 22D) and reproductive (Figs. 21C, 25B, 26A, B, F, 32C) organs of *Aristolochia*, *Euglypha*, *Holostylis* (Fig. 51A) and *Thottea*. Although the number of cells on each trichome can vary from 3 to 8 in these taxa, the apical cell is always hook-shaped.

7. Leaf expansion. (0) normal, (1) delayed. In most of the species, the leaf primordium begins differentiation into petiole and blade in plastochrone 3-4 and the blade expands relatively rapidly (Figs. 10D, 67C); in other species the differentiation occurs at a late stage, and blade expansion is delayed (Fig. 67D).

8. Vegetative prophylls. (0) non-pseudostipular (Fig. 67B), (1) pseudostipular (Fig. 67E). In a group of neotropical species, the prophyll of each renewal shoot develops into a sessile, round, clasping leaf called a pseudostipule (Fig. 67E; Duchartre, 1854c; González, 1990).

9. Petiole abscission zone. (0) absent (Fig. 68C), (1) present (Fig. 68D).

10. Petiole base. (0) U-shaped (Fig. 68A), (1) semicircular (Fig. 68B).

11. Position of the partial florescences. (0) along leafy, elongated, main branches (Figs. 6A-C, 8-10), (1) lateral racemes (Fig. 11D), (2) anthoblasts. Anthoblasts (sensu Mora-Osejo 1987) are transformed portions of the main axis, usually with very reduced leaves and internodes, that are specialized in the production of flowers; in the Aristolochiaceae, anthoblasts occur only in *Thottea corymbosa*. It is unclear if partial florescences in *Thottea grandiflora* are cymose. Thus, I have coded this character as unknown in this species.

12. Partial florescence. (0) uniflowered (Figs. 6A-C, 8D, F, 9A, D, 10B, D, 11D, 21A), (1) bi/multiflowered (Figs. 6D, 8A, C, E, 9C, 10A, 11A, C). Inflorescence development of *Thottea corymbosa* and *T. grandiflora* is not known, preventing the coding of this and characters 13-19 in these species.

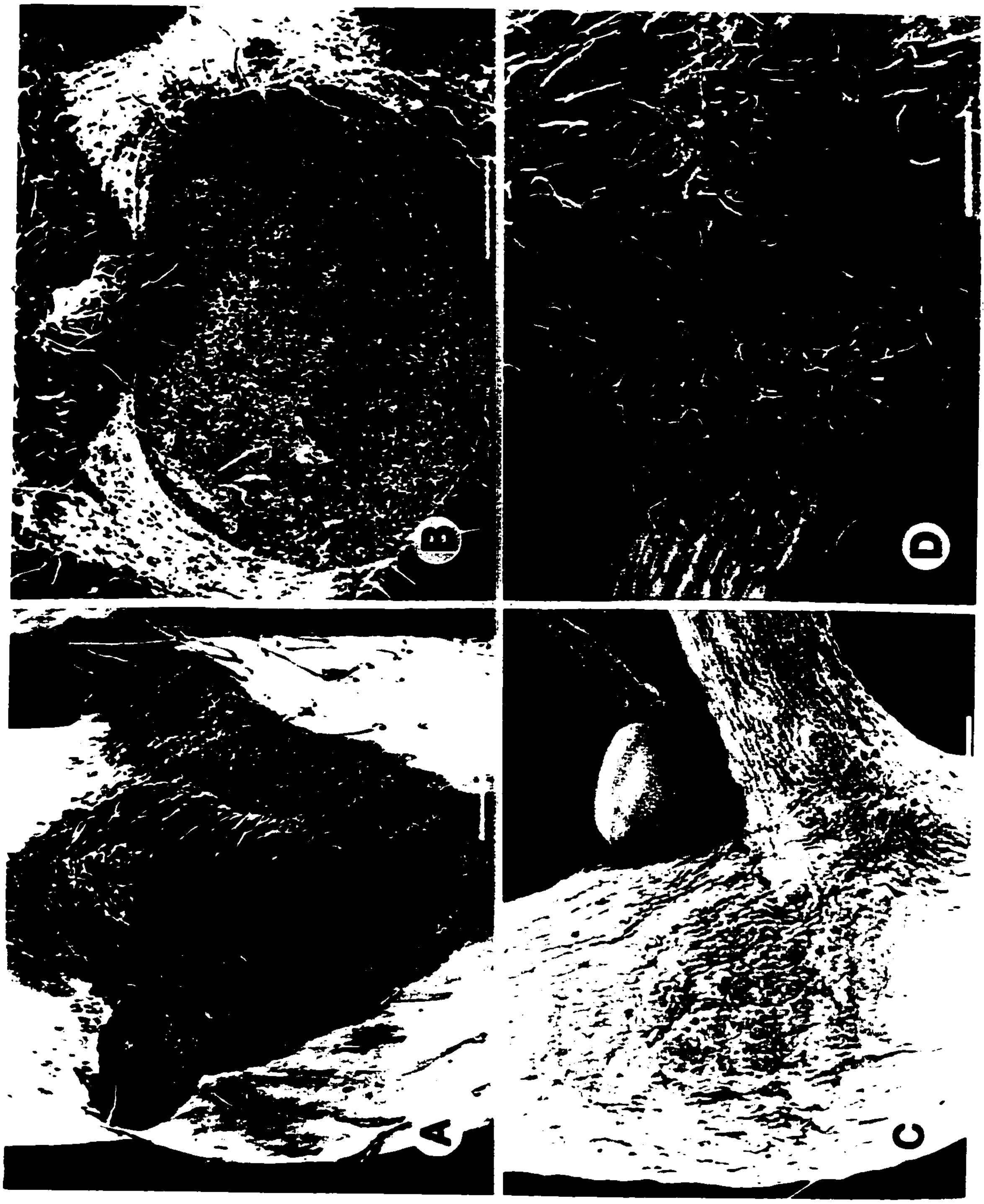
13. Pherophylls (0) leafy (Figs. 6A-D, 8C-F), (1) reduced (Fig. 11D). A pherophyll (sensu Weberling, 1989) is a leaf that subtends on its axil a partial florescence or a solitary flower.

14. Flower. (0) bracteate (Figs. 1, 4, 6-9A, C, D, 10A-C, 11A-C), (1) non-bracteate (Figs. 10D, 11D).

15. Bract expansion. (0) non-clasping (Figs. 8A, C, 9C), (1) clasping (Fig. 9A).

16. Bract base. (0) non-peltate (Figs. 8A, C, 9C, D, 10B, 11A, C), (1) peltate (Figs. 10C, 16A).

Figure 68. A, B. Petiole base. A. *Aristolochia macrophylla (González 3578)*, U-shaped base (character 10-0). Bar = 0.5 mm. B. *A. maxima (González 3248)*, semicircular base (character 10-1). Bar = 0.5 mm. C. *A. nummularifolia (González 1258)*, petiole without basal abscission zone (character 9-0). Bar = 0.1 mm. D. *A. maxima (González 3248)*, petiole with basal abscission zone (arrowhead; character 9-1). Bar = 0.5 mm.


B
D
A
C

17. Bract shape. (0) similar in shape and size to leaves (Fig. 8A), (1) reduced (Figs. 8C-F, 9B, 11B).

18. Inflorescence internodes. (0) elongated, (1) shortened. Internodes along the main axis of the inflorescences are elongated (longer than 2 cm; Fig. 20E); in some species of *Aristolochia*, the internodes are extremely shortened (less than 1 cm in length; Fig. 11D).

19. Inflorescence phyllotaxis. (0) distichous (Figs. 6B, 7A, B, 8B, 9C, 11C, 19D), (1) helicoid (Fig. 10A).

20. Peduncle abscission zone. (0) absent (Fig. 7C), (1) present (Fig. 58A).

21. Perianth series. (0) two (Figs. 1A, 59A), (1) one (Figs. 1D, 52).

22. Perianth shape. (0) rotate (Fig. 59A), (1) campanulate (Figs. 45F, 59B), (2) tubular (Figs. 4, 59D).

23. Perianth. (0) non-stipitate, (1) stipitate. This character is not applicable to *Asarum* and *Saruma*, because the perianth in these genera is continuous with the peduncle. In the other genera, there is a deep constriction between the perianth and the peduncle, above which the perianth may have a stipe (Figs. 18E, 49D, F) or not (Figs. 9-12, 16D, 19D, 23D, 25).

24. Perianth base. (0) symmetrical (Figs. 9A, C, D, 16D, 18E, 19D), (1) strongly asymmetrical (Figs. 23D, 25B, 48F).

25. Perianth. (0) not differentiated, (1) differentiated into utricle, tube and limb. In *Aristolochia*, *Euglypha* and *Holostylis* the perianth has three parts, an inflated portion at its base called utricle, which extends into a more or less narrowed portion, the tube; the distal expanded part of the perianth, above the tube, is called the limb (Fig. 4). The tube in *Holostylis* is shortened, but can be detected as an area between the utricle and the limb that lack indument on the inside. The perianth in the remaining genera is not differentiated into distinct parts (Fig. 59A-C).

26. Perianth concavity. (0) absent (Figs. 45D, F), (1) adaxial, (2) abaxial. In *Aristolochia* subgen. *Siphisia* and subgen. *Pararistolochia*, and in *A. grandiflora* the concave side of the flower is formed on the adaxial side of the flower, i.e. away from the median perianth lobe (Figs. 9A, C, 12 G-J, 16D). In the remaining species, the concavity is formed on the abaxial side of the flower, i.e. towards the median perianth lobe (Figs. 4, 9D, 12A-F, 17D, 19D, 20E, 23D).

27. Perianth abscission zone. (0) absent (Fig. 7), (1) present. In all species of *Aristolochia* and *Thottea*, a constriction is formed above the ovary that functions as an abscission zone by means of which the perianth falls off along with the gynostemium at late anthesis (Figs. 4, 9, 10D, 18C, E, 19D, 23C, D, 25, 28).

28. Second order perianth veins. (0) present (Figs. 45A, C, 46-48, 49E-H), (1) absent (Fig. 49A-D). Flowers of some species of *Aristolochia* lack the second order veins that run longitudinally along the base of the perianth. Thus, the perianth is supplied only by the six veins that enter the perianth from the ovary.

29. Syrinx. (0) absent, (1) incomplete, (1) complete (Fig. 4). The syrinx is an inner flange formed between the utricle and the tube. This character is not applicable to *Asarum*, *Saruma* and *Thottea*, because the flowers in these genera are not differentiated into utricle and tube.

30. Tube position. (0) longitudinal, (1) oblique. At anthesis, the tube extends straight out from the utricle (Figs. 17, 18E, 49) or is oblique to it, thus forming a sharp angle (Figs. 12F, 23D).

31. Tube curvature. (0) strong (U-shaped; Figs. 9A, C, D, 16D), (1) slight (Fig. 17D, 18E, 19E, 23D). Within *Aristolochia* subsect. *Pentandrae*, most of the species have a slightly curved tube; however, *A. acontophylla*, *A. cardiantha*, *A. foetida*, *A. micrantha* (Fig. 9D), *A. monticola*, and *A. tresmariae* have a U-shaped tube. Therefore this character was coded as polymorphic for this subsection.

32. Tube. (0) distally inflated (Figs. 16D, 46F), (1) not inflated (Fig. 17D, 18E), (2) evenly inflated and almost as wide as the utricle (Fig. 9A, C, 46B, D).

33. Conical perianth trichomes. (0) absent, (1) present(Figs. 26D, 31D).

34. Annulus. (0) absent, (1) present. The annulus is a circular flange at the juncture between the tube and the limb. One species of subsection *Pentandrae (A. secunda*) has an annulus, thus I coded this character as polymorphic for this subsection.

35. Limb symmetry. (0) regular (Figs. 1A-C, 7B, D, 14), (1) monosymmetric (Figs. 4, 10B, 15F, 16D, 17D, 18E, 19D, 20, 21, 23D).

36. Limb lobes at anthesis. (0) three (Fig. 15), (1) one (Figs. 16, 17, 20E), (2) two, one upper and one lower (Fig. 23D), (3) two, lateral (Fig. 21D).

37. Tail-like appendages on perianth. (0) absent, (1) present. In some species of *Aristolochia*, the perianth lobe(s) end in a tail, defined here as a slender appendage longer than 4 cm (Fig. 16D). One of the species of subsection *Pentandrae* (*A. nelsonii)* and one of section *Dipharus* (*A. pohliana)* have a tail-like appendage, thus, I have coded this character as polymorphic in both taxa.

38. Limb. (0) non fimbriate, (1) fimbriate. Some species of *Aristolochia* have fimbriae on the margins and/or inner surface of the limb (Fig. 21D).

39. Limb protrusion. (0) absent, (1) present (Fig. 15F). In a few species of *Aristolochia* subgen. *Siphisia*, the limb base has a massive process that projects in front of the tube.

40. Stamen number. (0) 12, (1) 24, (2) 8-10 (Figs. 1C, 2C, 5B, 50), (3) 6, (4) 5, (5) >25. I have coded 8-10 stamens (and 8-10 gynostemium lobes in character 56) because this range corresponds to the infraspecific variation in most of the species of *Aristolochia* subgen. *Pararistolochia* where it occurs (Poncy, 1978).

41. Stamen series. (0) two (Figs. 1A, B, 2A, B,), (1) one (Fig. 1C, D, 52).

42. Stamens. (0) equidistant (Figs. 2D, 5, 31C, 32A, 37D), (1) grouped (Figs. 2C, 41E, 52A, B). In some species of *Thottea* and in *Aristolochia* subgen. *Siphisia*, the stamens are grouped. This character is not simply related to the presence of three gynostemium lobes in subgenus *Siphisia* because in *Thottea* stamens are grouped even though there is no gynostemium. If the stamens are grouped in *Aristolochia* this affects the position of the vascular bundles of the gynostemium, which are arranged in 3 groups of 2.

43. Stamens. (0) free (Figs. 1A-C, 2A-C, 57B-F, 58D, 59A-D), (1) fused forming a gynostemium (Figs. 1D, 2D, 5, 27-44, 50, 51, 52).

44. Stamen dehiscence. (0) functionally introrse, (1) extrorse. Anthers are functionaly introrse in *Saruma* (Figs. 2A, 59A; see also Oliver, 1889; Dickison, 1992; Endress, 1995).

45. Anthers. (0) with filament (Figs. 58D, 59A, C), (1) sessile (Figs. 30D, 32B, 37D, 50).

46. Anther length. (0) short, (1) long. In mature flowers of some species of *Aristolochia*, the length of the anthers is less than half the length of the gynostemium (Fig. 37F). In others, the anthers are considerably longer (Fig. 35D).

47. Pollen sculpturing. (0) reticulate, (1) microreticulate, (2) fossulate (Figs. 64-66), (3) areolate (Fig. 59), (4) psilate (Fig. 62).

48. Pollen aperture. (0) sulcate, (1) porate, (2) inaperturate.

49. Pollen ridge. (0) absent, (1) poorly differentiated, (2) markedly differentiated (Fig. 61). A long, broad ridge of exine is formed in pollen of all members examined of subgenus *Pararistolochia*.

50. Supratectal warts. (0) none, (1) small (Fig. 64), (2) large (Fig. 60C, D). Pollen of *Asarum* and some species of *Aristolochia* develops warts on top of the tectum.

51. Ovary position. (0) semiinferior (Fig. 58A, B), (1) inferior. (Fig. 58C, D).

52. Ovary shape. (0) globose (Fig. 58A, B), (1) elongated and narrow (Fig. 58C, B).

53. Carpels. (0) partially apocarpous (Figs. 57B, C, 58A, B), (1) syncarpous. Carpels are complete syncarpous in *Aristolochia* (e. g. Figs. 42, 52-54), *Euglypha, Holostylis,* and *Thottea* (Figs. 1C, 2C, 58, 59C)

54. Mature carpels. (0) 6, (1) 5, (2) 4. In *Thottea* (Fig. 58) only four of the six carpels develop.

55. Stigmas. (0) free (Fig. 57B, C), (1) connate (Figs. 2B, D). Presence of true stigmas in *Thottea* is controversial (Leins et al. 1988), so I have coded this and the next character as unknown in this genus.

56. Gynostemium lobes. (0) 6, (1) 5, (2) 3, (4) 8-10, (5) 12. I have coded this character as partially polymorphic in *Aristolochia reticulata* and *A. serpentaria,* based on the number of lobes in mature flowers; however, in both species, only three lobes initiate; additional lobes in these species occur by secondary division of the initial three lobes (Fig. 43). *Holostylis,* usually described as having an entire gynostemium, has 6 vestigial lobes (Fig. 51B) and is here coded as state (0). The number of gynostemium lobes is not simply correlated to the number of stamens; for example, all species of *Aristolochia* subgen. *Siphisia* have 6 stamens but only 3 gynostemium lobes; numbers are also different in some species of subgen. *Pararistolochia* (Poncy,

1978), especially in *A. goldieana*, where there are 12 gynostemium lobes and 24 stamens.

57. Stigmatic papillae. (0) present (Figs. 2A, B, 5C, 33, 37F, 39C, D, 40D, 42H, 55, 56), (1) absent (Fig. 2C).

58. Position of the stigmatic papillae. (0) terminal, (1) lateral/basal. By the time of anthesis the stigmatic papillae are either terminal and marginal on the gynostemium lobes (Figs. 5C, 33A) or lateral and more or less basal (Figs. 5D, 32B, 33C, 37F, 39B, C, 42H, 57B, C). In *Aristolochia*, the latter occurs because of a strong outgrowth of the papillate zone, which remains at the base of the gynostemium lobes, giving the impression of a roof-like evagination above the anthers (Figs. 37E, F, 38F, 39B, C). *Aristolochia* subsection *Diplolobus* was described as having the latter condition, but it is also present in the species of subgenera *Siphisia* (Fig. 42H) and *Pararistolochia*.

59. Fruit surface. (0) smooth, (1) verrucate.

60. Pericarp. (0) membranous to chartaceous, (1) strongly lignified.

61. Mesocarp. (0) dry, (1) fleshy.

62. Fruit. (0) ventricidal, (1) septifragal, (2) irregularly dehiscent, (3) indehiscent.

63. Fruit dehiscence. (0) basipetal, (1) acropetal.

64. Fruit septae. (0) entire, (1) lattice-like.

65. Seeds per carpel. (0) >5, (1) 1-2.

66. Seed contour. (0) concave-convex, (1) flattened, (2) trigonous. In transverse section, the contour of the seed proper appear concave-convex (Fig. 69A, B, D), flattened (Fig. 69C, 70A, B, D, E), or extremely curved and with the margins touching each other (Hou, 1981).

67. Shape of the seed proper. (0) ovoid (Figs. 69, 70), (1) ellipsoid.

68. Seed wings. (0) absent or vestigial (Figs. 69, 70A-C), (1) two, rectangular (Fig. 70E), (2) one, triangular-rhomboidal (Fig. 70D). Vestigial wings sometimes exist, as very short, incomplete, spongy projections peripheral to the seed proper; they do not surround the seed margin completely.

69. Funicle. (0) free from the seed, (1) fused to the seed.

70. Funicle. (0) massive, (1) filiform, (2) papyraceous, incomplete(3) papyraceous, complete. When the funicle is papyraceous, it can completely cover the adaxial side of the seed (i.e. complete; Fig. 70A) or it can be narrower (i.e. incomplete; Fig. 70D) than the seed proper.

Figure 69. Seeds (from left to right: abaxial side, adaxial side, lateral view, and transverse section through the middle level). A. *Saruma henryi (Pruski 3748)*. B. *Asarum virginicum*. C. *Aristolochia macrophylla (González 3578)*. D. *A. paracleta (González 3417)*. In all, bar = 1 mm. *f*, funicle.

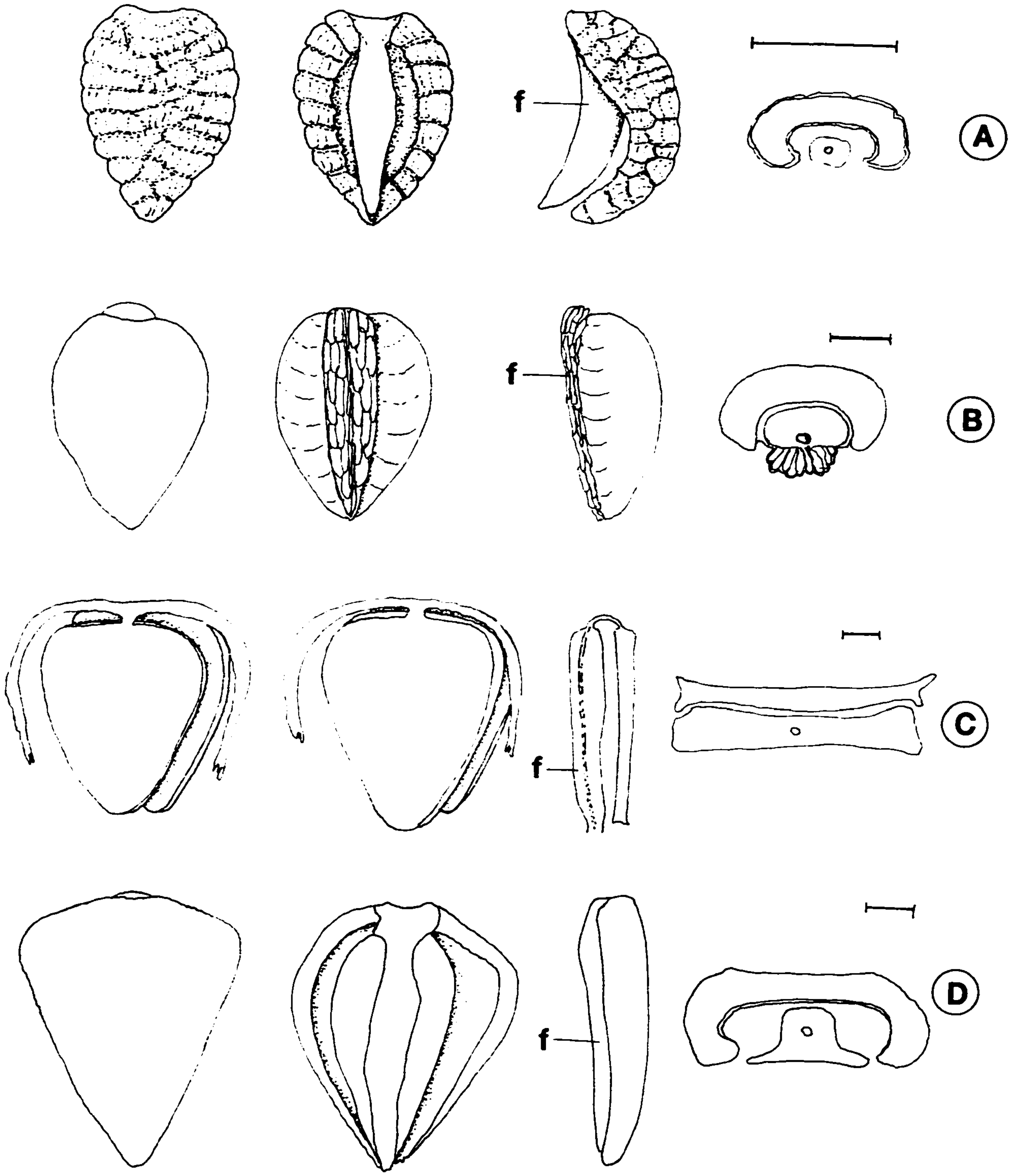
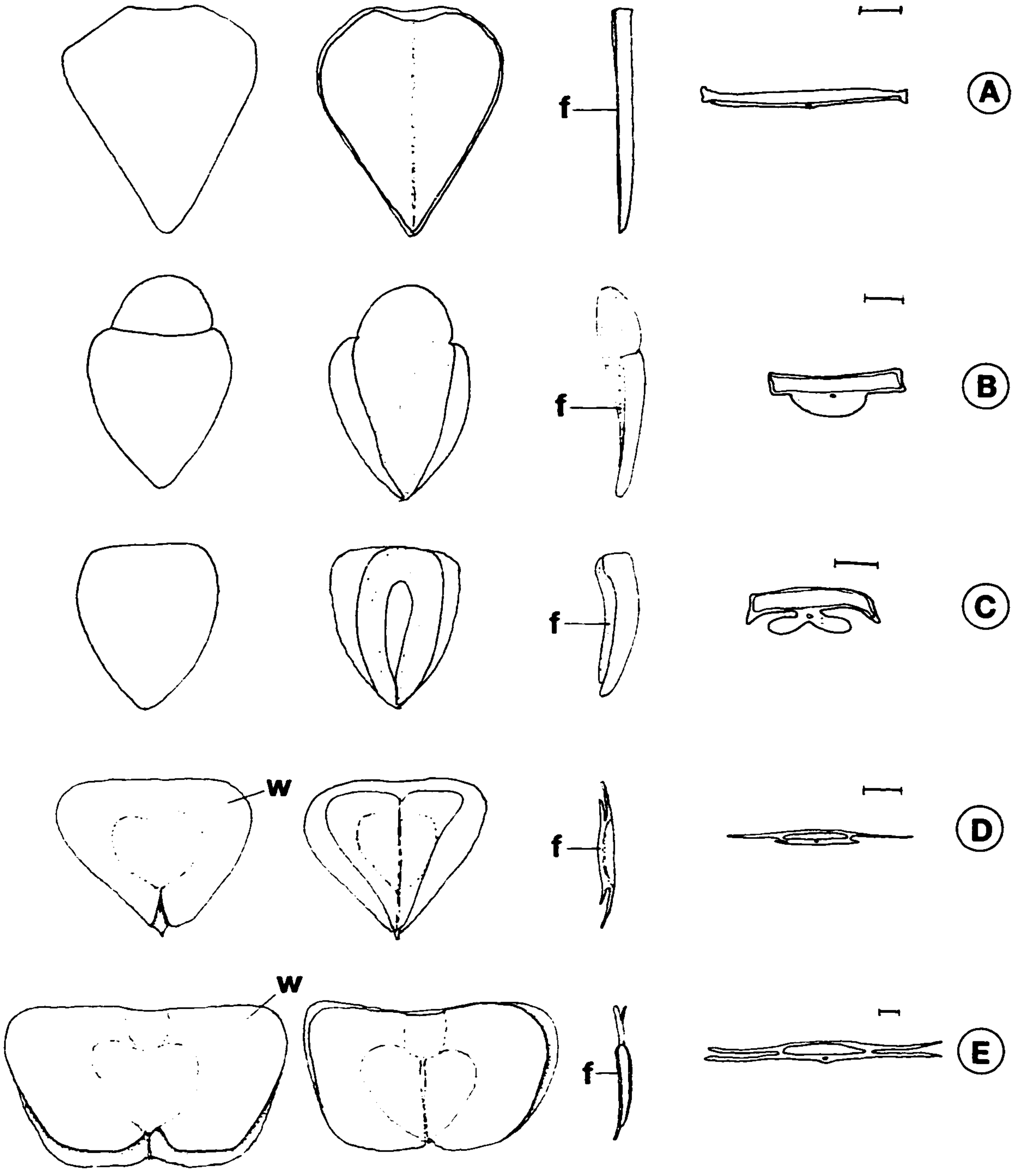

f
A
f
B
f
C
f
D

Figure 70. Seeds of *Aristolochia* (from left to right: abaxial side, adaxial side, lateral view, and transverse section through the middle level). A. *A. burelae (Maruñak et al. 486)*. B. *A. leuconeura (González 3290)*; the sticky aril is shown by the dotted area. C. *A. odoratissima (González 3399)*; the sticky aril is shown by the dotted area. D. *A. contorta* (*Li 10853*). E. *A. maxima (González 3568)*. *f*, funicle; *w*, wing.


f
A
B
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E

71. Sticky aril. (0) absent, (1) chalazal-funicular, *(2) Asarum* type (3) funicular. Whereas in *Asarum* the aril (considered a caruncle by Wyatt, 1955b) is formed by 2-4 layers of large cells, originating from the funicle (Fig. 69A), in *Aristolochia leuconeura* and *A. odoratissima* the aril consists of excretions of epidermal and subepidermal cells of the funicle (in *A. odoratissima;* Fig. 70C) or the funicle and the chalaza (in *A. leuconeura*, Fig. 70B).

Analysis

The data matrix (Appendix I) was compiled using DADA (Nixon 1996a). A parsimony analysis was run using NONA (Goloboff, 1993), with the *hold 1000, mult*50* options. The consensus tree was obtained using the *inters* command. The resulting trees and the character distribution were examined in CLADOS (Nixon, 1996b). Bremer support values (BRS) were calculated on the consensus tree, in order to the number of extra steps to "decay" or collapse a given internode; Bremer, 1988).

III. RESULTS

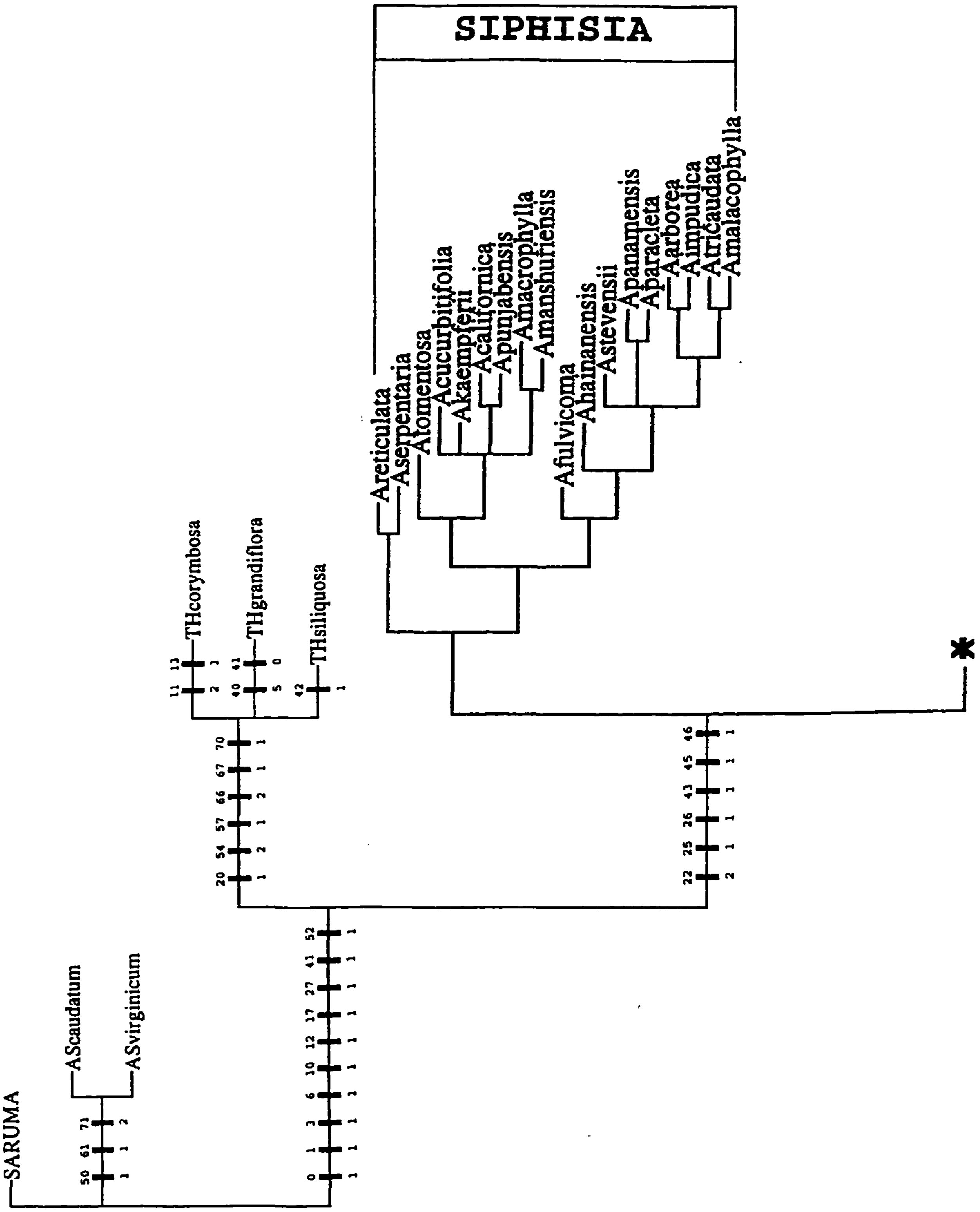
The analysis produced five equally parsimonious trees of 196 steps, CI = 0.49, and RI = 0.85. The results support a sister group relationship between *Thottea* and the subfamily Aristolochioideae sensu Schmidt (= tribe Aristolochieae sensu Huber; compare Table I and Fig. 3E with Fig. 71). The analysis also supports the monophyly of the Aristolochioideae and of two major lineages within this subfamily (Figs. 71, 72). Synapomorphies of the Aristolochioideae include: perianth differentiated into utricle, tube and limb (character 25); perianth adaxially curved (26); and stamens sessile (45) and fused to the stigmas into a gynostemium (43). Other characters that support the subfamily are the flowers having a tubular perianth (character 22), and narrow and long anthers (46). BRS values on the basal node of the ingroup is 9 (Fig. 72).

The first major clade: *Aristolochia* subgenus *Siphisia* (Figs. 71, 73)

The first major clade within the Aristolochioideae conforms to the previously proposed subgenus *Siphisia* (BRS = 3). This clade is defined by the fusion of the carpellary apices into three gynostemium lobes (character 56), a synapomorphy that is unique in the family. Other characters that support this clade are the presence of an annulus (34) and grouped stamens (42); the latter are known outside of the subfamily, in some species of *Thottea*.

Resolution within subgenus *Siphisia* further supports two clades. The first (BRS = 4), containing the sister species *Aristolochia reticulata* and *A. serpentaria*, is defined by being herbaceous plants (character 0) with reduced pherophylls (character 13), clasping bracts (15), and short internodes along the inflorescences (less than 1 cm long, character 18).

Figure 71. Consensus tree of the five most parsimonious trees obtained in the present analysis (length = 196, CI = 0.49, RI = 0.85.). Character and state numbers for the ingroup are mapped on Figures 73, 75-77, on which numbers above and below the hashmarks indicate character number and state number, respectively. Solid black hashmarks represent apomorphies; gray hatchmarks represent homoplasies.


SIPHISIA
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
*
THcorymbosa
THgrandiflora
THsiliquosa
11 13
2 1
40 41
5 0
42
1
20 54 57 66 67 70
1 2 1 2 1 1
22 25 26 43 45 46
2 1 1 1 1 1
SARUMA
AScaudatum
ASvirginicum
50 61 71
1 1 2
0 1 3 6 10 12 17 27 41 52
1 1 1 1 1 1 1 1 1 1

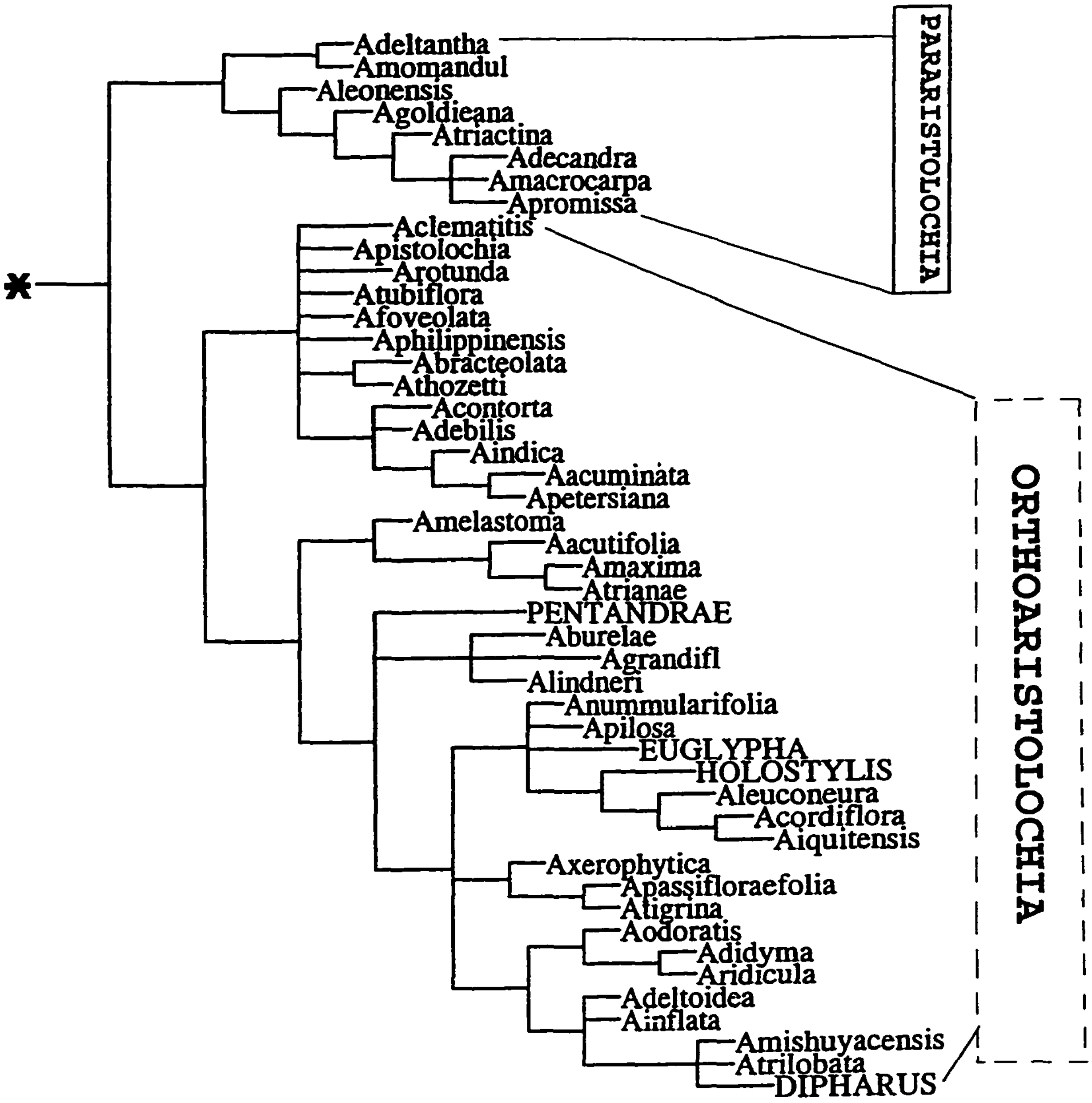
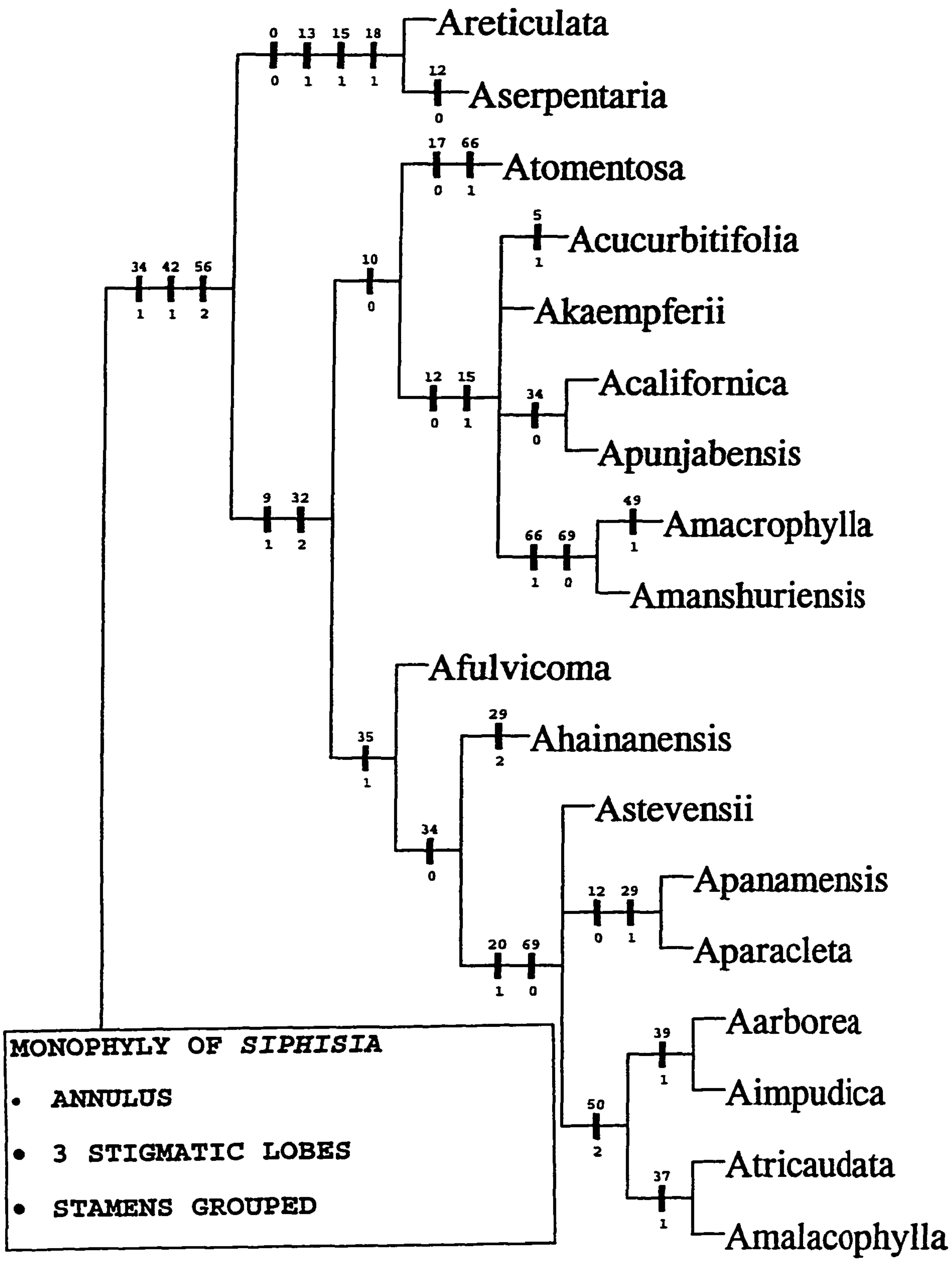

*
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
PARARISTOLOCHIA
ORTHOARISTOLOCHIA

Figura 72. Bremer support values on the nodes of the consensus tree.


SARUMA
AScaudatum
ASvirginicum
THcorymbosa
THgrandiflora
THsiliquosa
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS

BRS

Figure 73. Clade corresponding to *Aristolochia* subgenus *Siphisia*.


Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
MONOPHYLY OF SIPHISIA
• ANNULUS
• 3 STIGMATIC LOBES
• STAMENS GROUPED

The second clade within *Siphisia* (BRS = 2; Fig. 72) contains two subclades. The first, with *A. tomentosa* at the base consists primarily of temperate species, with U-shaped petiole bases (character 10; Fig. 73). The clade is partially resolved, and includes *A. cucurbitifolia*, *A. kaempferi*, plus two groups of Asian-North American disjunct sister species: *A. californica* and *A. punjabensis*, which lack an annulus (character 34), and *A. macrophylla* and *A. manshuriensis*, which have flattened mature seeds (66) that are not attached to the funicle (character 69; Fig. 73). The second subclade, with primarily subtropical and tropical species, is defined by the possession of a monosymmetric perianth limb (character 35; Figs. 9C, 15F, 46D). Within this subclade, the first two branches are Asian species, followed by a crown clade of Central American species.

The Central American clade is defined by the presence of an abscission zone in the base of the peduncle (character 20), and the seed being free from the funicle (69). Three groups are found here, *Aristolochia panamensis* plus *A. paracleta*, both with an incomplete syrinx (character 29) and uniflowered inflorescences (12); *Aristolochia arborea* and *A. impudica*, whose flowers have a lower protrusion at the flower entrance (39); and *Aristolochia malacophylla* and *A. tricaudata*, with tail-like appendages on the flowers (37). The latter four species form a crown clade defined by the possession of large supratectal verrucae on the pollen wall (character 50).

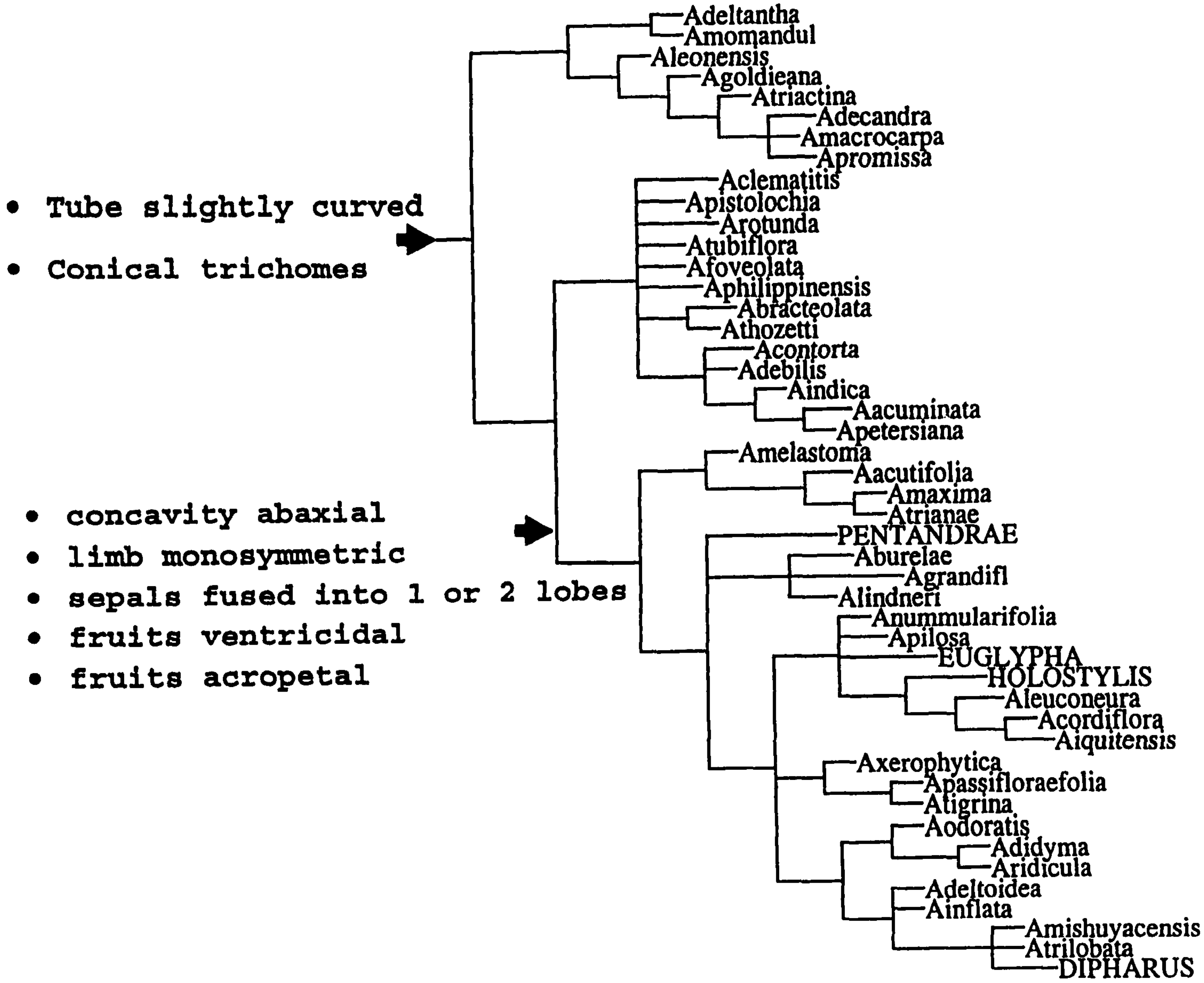
The second major clade: *Aristolochia* plus *Euglypha* plus *Holostylis* (Figs. 71, 72, 74)

The second major clade consists of two subclades, one corresponding to subgenus *Pararistolochia*, and the other equivalent to subgenus *Orthoaristolochia* plus the genera *Euglypha* and *Holostylis*. The characters that emerge as synapomorphies that link the two subgenera are the slightly curved tube (31) and the conical trichomes inside the flower (33). The only member of the clade in which these trichomes are missing is *Holostylis*. *Aristolochia lindneri*, previously reported as lacking trichomes on the inner surface of the flower (Hoehne, 1942), have conical trichomes, which are extremely short.

Subgenus *Pararistolochia* (Figs. 71, 75)

The analysis supports the monophyly of *Pararistolochia* (BRS = 4; Fig. 72). Characters that define this group include a markedly differentiated ridge on the pollen wall (character 49) and indehiscent fruits (62), with a verrucate surface (59), strongly lignified pericarp (60), and fleshy mesocarp (61). Two suclades are found within subgenus *Pararistolochia*; the first consists of *A. deltantha* and *A. momandul*, and is defined by the distally inflated perianth tube (character 32, otherwise present only in the neotropical *A. grandiflora*), and flattened seeds (66), with a filiform funicle (70). The second subclade includes six species

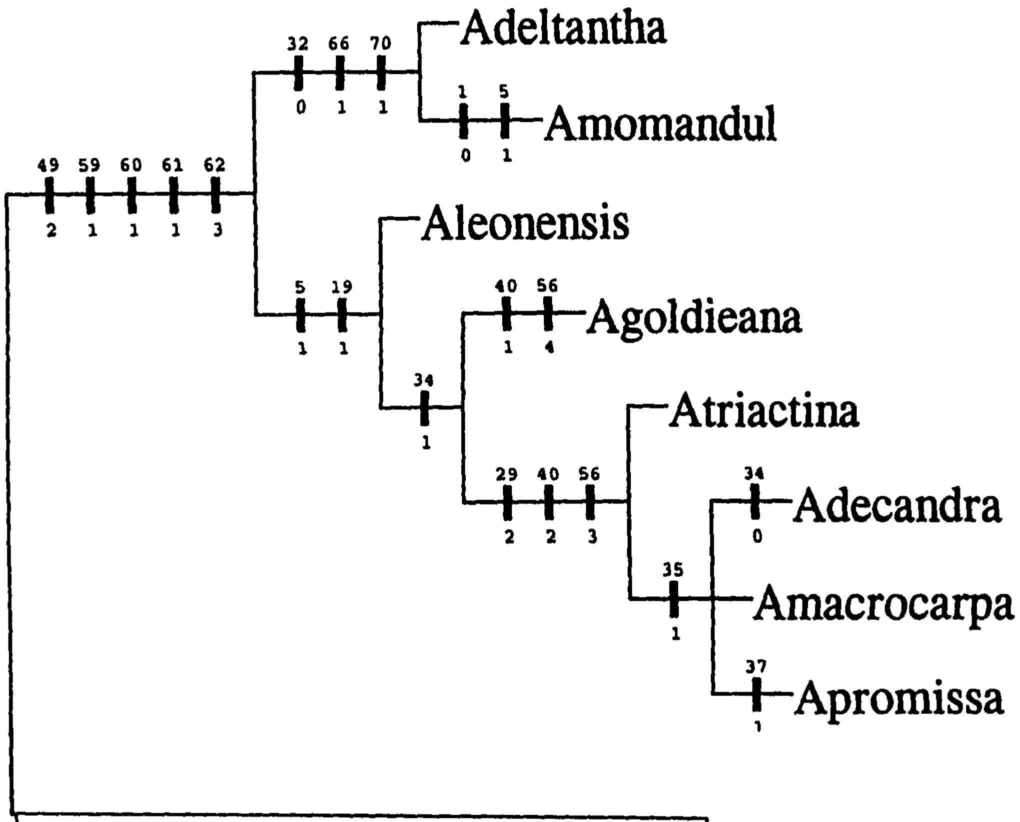
Figure 74. Clade corresponding to the complex *Aristolochia* subgen. *Pararistolochia* + *Aristolochia* subgen. *Orthoaristolochia* + *Euglypha* + *Holostylis*.



- Tube slightly curved
- Conical trichomes

- concavity abaxial
- limb monosymmetric
- sepals fused into 1 or 2 lobes
- fruits ventricidal
- fruits acropetal

Figure 75. Clade corresponding to *Aristolochia* subgen. *Pararistolochia*.



MONOPHYLY OF *PARARISTOLOCHIA*

- ridge on the pollen wall
- fruits indehiscent
- fruit surface verrucate
- pericarp strongly lignified
- mesocarp fleshy

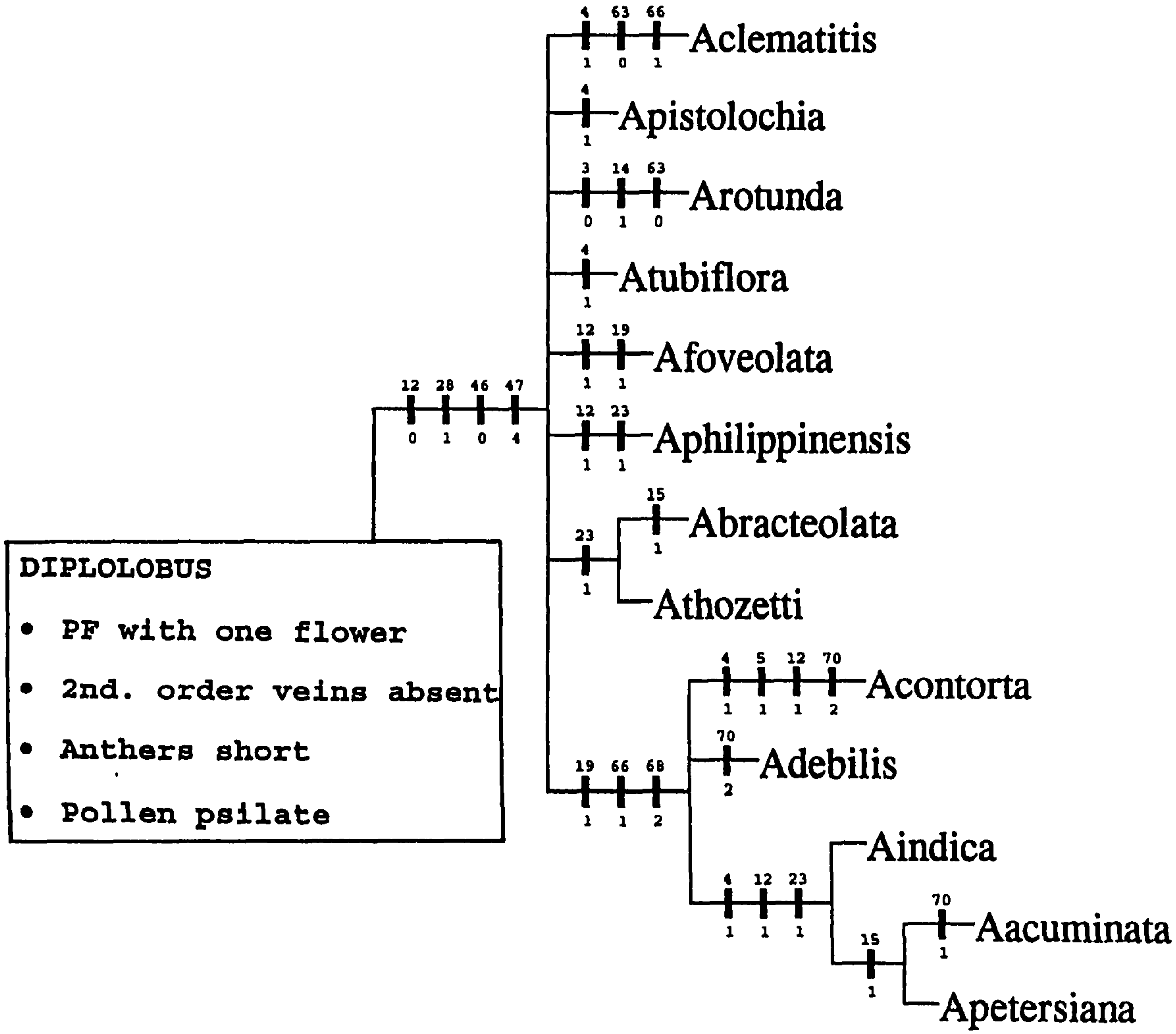
(*A. leonensis, A. goldieana, A. triactina, A. decandra, A. macrocarpa*, and *A. promissa*) that share the stem being constricted and becoming 'figure 8'-shaped in transverse section (character 5), and helicoidal partial florescences (19). The first branch within the latter subclade consists of *A. leonensis*, which is the sister group of the crown clade of five species whose flowers have an annulus (character 34; *A. goldieana, A. triactina, A. decandra, A. macrocarpa, and A. promissa*). The latter four species share the possession of 8-10 stamens (40) and 8-10 gynostemium lobes (56), plus a complete syrinx (29). Three of these (*A. decandra, A. macrocarpa*, and *A. promissa*) all have a monosymmetric perianth limb (character 35) and form an unresolved trichotomy.

Subgenus *Orthoaristolochia* plus *Euglypha* plus *Holostylis* (Figs. 71, 77)

The subgenus *Orthoaristolochia* is paraphyletic because *Euglypha* and *Holostylis* are nested within. Characters that define this third and most complex clade (BRS=3; Fig. 72) are the abaxially concave perianth (26), the monosymmetric limb (35), the fusion of the three perianth parts into one lobe (36), and the ventricidal (62) and acropetal fruits (63).

The data support two subclades within this major clade. The first corresponds to the section *Diplolobus* described by Duchartre (1854a, 1864; Fig. 76). This clade (BRS=3), poorly resolved, contains *A. clematitis* and other European species, plus a number of species from tropical Asian and Australasian species, such as

Figure 76. Clade corresponding to *Aristolochia* sect. *Diplolobus*.

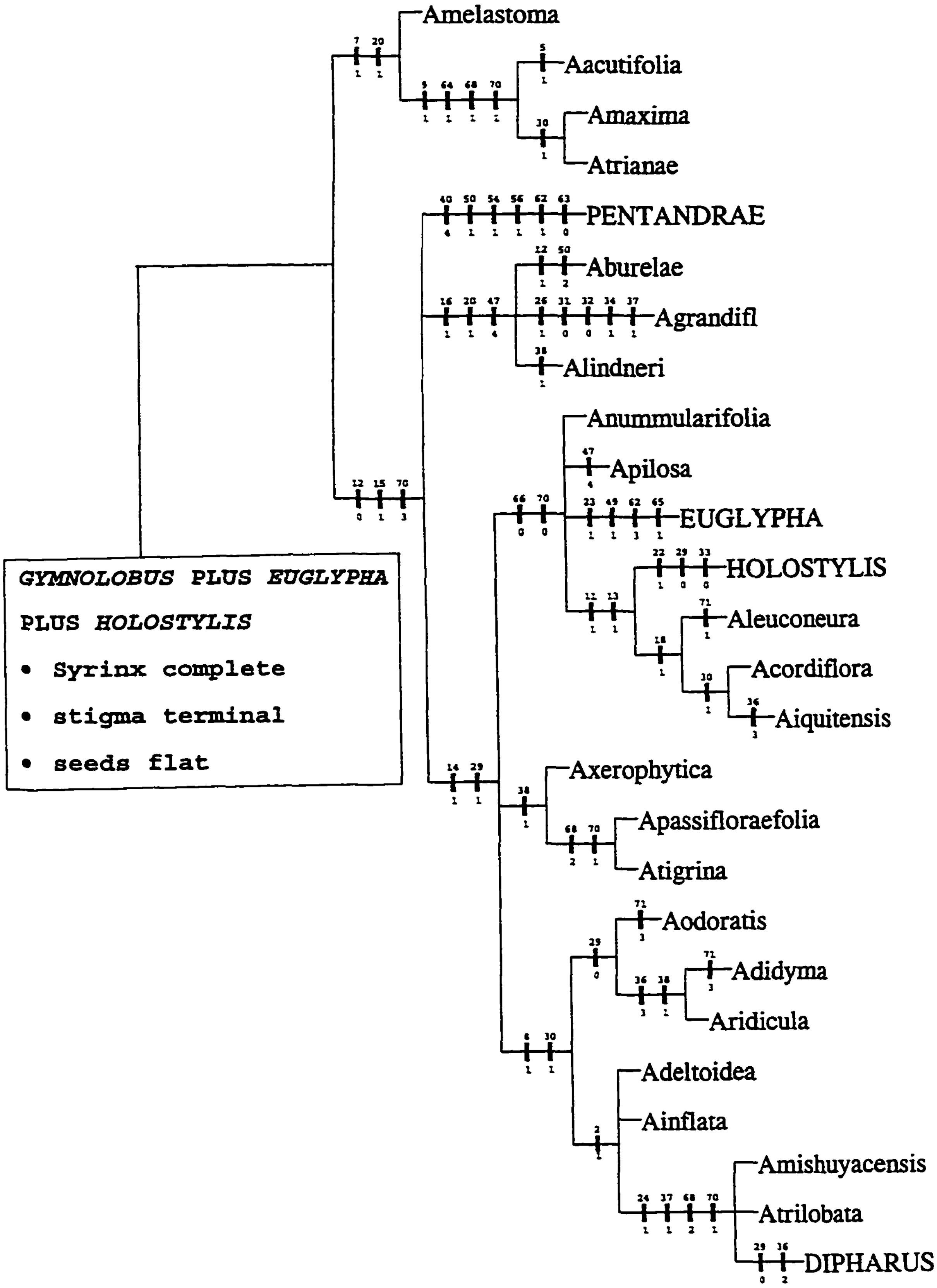

DIPLOLOBUS
• PF with one flower
• 2nd. order veins absent
• Anthers short
• Pollen psilate
12 28 46 47
0 1 0 4
4 63 66
1 0 1
Aclematitis
4
1
Apistolochia
3 14 63
0 1 0
Arotunda
4
1
Atubiflora
12 19
1 1
Afoveolata
12 23
1 1
Aphilippinensis
23
1
15
1
Abracteolata
Athozetti
19 66 68
1 1 2
4 5 12 70
1 1 1 2
Acontorta
70
2
Adebilis
4 12 23
1 1 1
Aindica
15
1
70
1
Aacuminata
Apetersiana

A. acuminata, A. indica, A. philippinensis, and *A. thozetti.*

The second subclade (BRS=2; Fig. 72), exclusively neotropical, includes the bulk of the neotropical species of *Aristolochia* that form *Aristolochia* section *Gymnolobus* (Duchartre 1854a, 1864), plus the monotypic South American genera *Euglypha* and *Holostylis* (Figs. 71, 77). Within this subclade, the first crown clade is formed by *A. melastoma* at the base, followed by *A. acutifolia* and the sister species *A. maxima* and *A. trianae;* all these species correspond to *Aristolochia* ser. *Thyrsicae,* described by González (1990, 1991). The second crown clade is unresolved at its base, with a trichotomy formed by: (1) section *Pentandrae;* (2) the unresolved *A. burelae* + *A. grandiflora* + *A. lindneri,* supported by the presence of peltate bracts (character 16; Fig. 77), an abscission zone in the base of the peduncle (character 20), and psilate pollen (character 47); and (3) and the remaining crown clade containing *Euglypha, Holostylis* and all the Neotropical species of *Aristolochia,* defined by non-bracteate flowers (character 14), which have an incomplete syrinx (character 29). The latter crown clade is also unresolved, with a trichotomy formed by:

(1) A clade containing several species of *Aristolochia* plus *Euglypha* plus *Holostylis,* defined by concave-convex seeds (character 66), with a massive funicle (character 70). Whereas the position of *Euglypha* is not precisely defined, *Holostylis* emerges as the sister taxon of *Aristolochia* subser. *Anthocaulicae* (Fig. 77), the latter a taxon described by González (1990, 1991). This sister group relationship is based on the presence of flowers

Figure 77. Clade corresponding to the complex *Aristolochia* sect. *Gymnolobus* + *Euglypha* + *Holostylis*.



GYMNOLOBUS* PLUS *EUGLYPHA* PLUS *HOLOSTYLIS

- Syrinx complete
- stigma terminal
- seeds flat

in lateral racemes (character 11), and the pherophylls reduced (character 13).

(2) A clade with A. *xerophytica* plus the sister species A. *passifloraefolia* and A. *tigrina*, all with fimbriate flowers (character 38; Fig. 77).

(3) A clade with the species with 'pseudostipules' (character 8) and the tube oblique with respect to the utricle (character 30; Fig. 77).

IV. DISCUSSION

Monophyly of *Aristolochia* and its segregate genera

The analysis shows that the genus *Aristolochia* sensu lato is paraphyletic because the two other genera of the subfamily, *Euglypha* and *Holostylis*, are nested inside one of the crown clades of *Aristolochia* (Fig. 71). Therefore, the recognition of the tribes Aristolochieae and Euglypheae (sensu Schmidt, 1935), and the genera *Euglypha* and *Holostylis* is no longer tenable. In contrast, the two major clades generated on the present analysis coincide with the two subtribes described by Huber (1985, 1993; Fig. 2G, Table I). On the basis of their monophyly these groups merit taxonomic status, regardless of the rank at which they are recognized (see below).

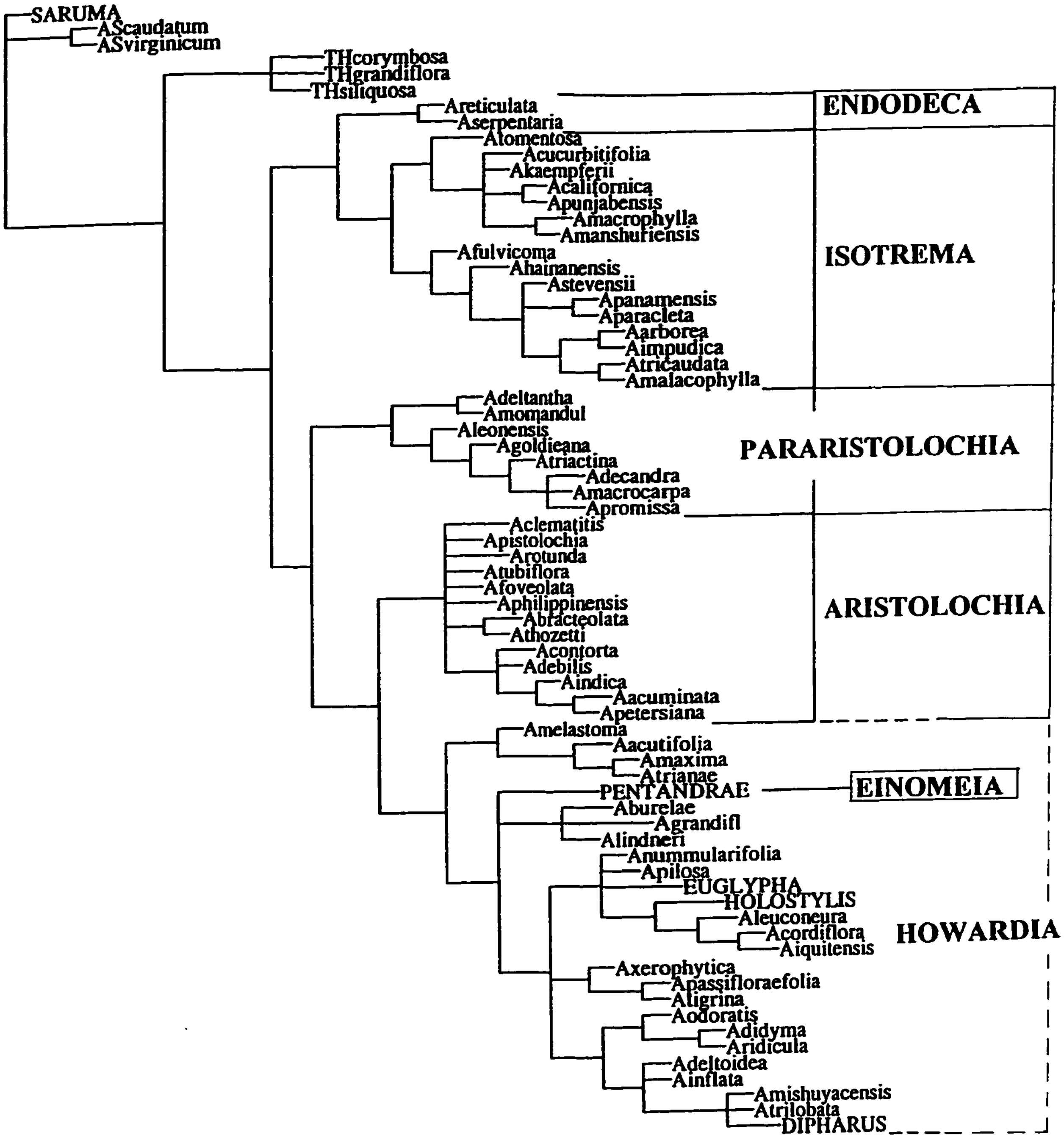
According to this analysis, *Aristolochia* sensu stricto, and its segregate genera *Endodeca, Siphisia* (=*Isotrema;* Rafinesque, 1828, 1836), and *Pararistolochia* (Hutchinson & Dalziel, 1927), further maintained by Klotzsch (1859), Huber (1985, 1993) and Parsons (1996) are each supported as monophyletic units (Fig. 78). The monophyly of each of the other minor Rafinesque segregates (*Ambuya, Diglosselis, Hexaplectris, Pistolochia, Plagistra, Psophiza, Pteriphis*, and *Tropexa;* Table II) is not subject to evaluation because their specific composition was not fully described.

Howardia, originally proposed by Klotzsch (1859; Tables II, III), and subsequently maintained by Huber (1984, 1993) and Mabberley (1997), is the largest segregate from *Aristolochia*, with about 150 species. The conclusion from the data presented here is that *Howardia* (equivalent to section *Gymnolobus* Duchartre, 1854a, 1864) is paraphyletic and thus does not merit recognition as a taxon.

***Aristolochia* subgenus *Siphisia* (=*Isotrema*) (Figs. 71, 73)**

The analysis supports the monophyly of subgenus *Siphisia* Schmidt, which requires the inclusion of *Aristolochia arborea* as a member of the subgenus. *Aristolochia arborea* was misplaced as a member of subgenus *Orthoaristolochia* by Duchartre (1864) and Schmidt (1935). The present analysis shows that this species is a member of subgenus *Siphisia*, and confirms the observations by Wyatt

Figure 78. Clades corresponding to the *Aristolochia* segregates. Dotted line in *Howardia* indicates that this segregate is not monophyletic, because *Einomeia, Euglypha* and *Holostylis* are nested within the clade.


SARUMA
AScaudatum
ASvirginicum
THcorymbosa
THgrandiflora
THsiliquosa
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
ENDODECA
ISOTREMA
PARARISTOLOCHIA
ARISTOLOCHIA
EINOMEIA
HOWARDIA

(1955a), and Pfeifer (1966) that the gynostemium of *A. arborea* has three lobes, as do all the other members of subgenus *Siphisia*. Duchartre (1854a, 1864) divided his group (subgenus) *Siphisia* into three different sections, *Asterolytes*, *Siphisia*, and *Hexodon*, which were subsequently maintained by Wyatt (1955a). The first section consisting of the species *Aristolochia reticulata* and *A. serpentaria* (Figs. 73, 77), which is equivalent to the Rafinesque (1828) segregate *Endodeca* (Table III), is shown to be monophyletic. Klotzsch (1859) described *Endodeca* as having a six-lobed gynostemium. My observations indicate, however, that the gynostemium lobes in both species vary in number from 3 to 5 (no hexamery was observed!). These lobes begin as 3 primordia as in the other species of subgenus *Siphisia* and late in development one or two of them secondarily divide.

With respect to the remaining two sections, two species of section *Siphisia* (*A. macrophylla* and *A. tomentosa*) and one of section *Hexodon* (*A. kaempferi*) were included in the present analysis. *A. kaempferi* is nested inside the clade that contains the other two, which suggests that section *Siphisia* is not monophyletic unless section *Hexodon* is included. These sections were described by Duchartre (1854a, 1864) based primarily on minor differences on the shape of the gynostemium at maturity as detected on herbarium specimens. Gynostemium in *Aristolochia* undergoes significant changes during its development (chapter three), and its reconstruction from herbarium specimens is not accurate.

Karyological evidence supports the hypothesis that subgenus *Siphisia* forms a lineage distinct from at least subgenus

Orthoaristolochia (Fiorini, 1987; Gregory, 1956; Morawetz, 1985; Nardi, 1984; Sharma & Varma, 1959; Sugawara & Murata, 1992). Unfortunately, no karyotype information is known for species of subgenus *Pararistolochia*. All chromosome counts are 2n = 28, or 2n = 32 in species of subgenus *Siphisia*, and 2n=8, 12, 14 in species of subgenus *Orthoaristolochia* (one count of *A. longa*, however, is reported as 2n=28; Gregory 1956).

***Aristolochia* plus *Euglypha* plus *Holostylis* (Figs. 71, 73)**

Within this large clade two major lineages can be defined according to the analysis: *Aristolochia* subgenus *Pararistolochia* and its sister group, the complex *Aristolochia* subgen. *Orthoaristolochia* plus *Euglypha* and *Holostylis*. This relationship is in agreement with the recognition of subtribe Aristolochiineae (Huber 1985, 1993; Fig. 2G, Table I), regardless of the rank at which the former clades are recognized. Based on the regular floral limb and the high number of stamens, Wyatt (1955a) and Ma (1989) proposed that *Pararistolochia* is the most primitive subgenus of *Aristolochia*. This assumption is not confirmed in the present analysis, because subgenus *Pararistolochia* is not a basal clade within the Aristolochioideae (Fig. 71). Whereas the regular floral limb is plesiomorphic, the high number of stamens present in some species of this subgenus emerges as a derived character in *Aristolochia*.

Subgenus *Pararistolochia*

Pararistolochia, described as a genus by Hutchinson & Dalziel (1927) restricted to West and Central African species, was subsequently maintained by Poncy (1978). Parsons (1996) redelimited *Pararistolochia* as consisting of the 8-10 West and Central African species traditionally recognized (Poncy, 1978; Ma, 1992) plus 24 other species from Malesia, New Guinea, and Australia. This close relationship was anticipated by Duchartre (1864:496) who joined the African A. *macrocarpa* and the Australian A. *praevenosa* while at the same time recognizing that these two species did not belong to any of the other groups that he had established. Hou (1984), Huber (1960, 1985, 1993) and Ma (1992) also pointed out the similarity of some species from Malasia, Australia and New Guinea (including A. *decandra*) to the African members of this taxon. The present analysis indicates that *Pararistolochia* is a monophyletic lineage regardless of the rank at which is recognized and that there is a sister group relationship between Australasian and African taxa as anticipated by Duchartre (1864).

The available data do not precisely indicate the position of the Malesian A. *decandra,* which forms an unresolved clade with the African A. *macrocarpa* and A. *promissa*. Perhaps, this trichotomy could be resolved when fruits and seeds of A. *decandra* become available for study.

Subgenus Orthoaristolochia plus *Euglypha* plus *Holostylis* (Figs. 71, 77)

One of the two clades within this major clade corresponds to the monophyletic *Aristolochia* section *Diplolobus* (Fig. 76) described by Duchartre (1854, 1864) and is equivalent to *Aristolochia* sensu stricto (Klotzsch, 1859; Huber, 1985, 1993; Table III; Fig. 77). The lack of resolution within the clade prevents an evaluation of the monophyly of the two subsections traditionally recognized, *Euaristolochia* and *Podanthemum* (Table III). Within section *Diplolobus*, Duchartre (1864) described a third subsection, *Acerostylis*, composed only of the East African *Aristolochia rigida*. This species was not included in the analysis, because it has identical score as other species of subsection *Euaristolochia*. Duchartre (1964) described subsection *Acerostylis* as having a truncate gynostemium, which is a misinterpretion as Franchet (1882) and my own observations (based on the specimen *Thesiger s.n.*, BM) have shown. The gynostemium of this species has essentially the same morphology found in the other members of *Aristolochia* subsection *Euaristolochia*.

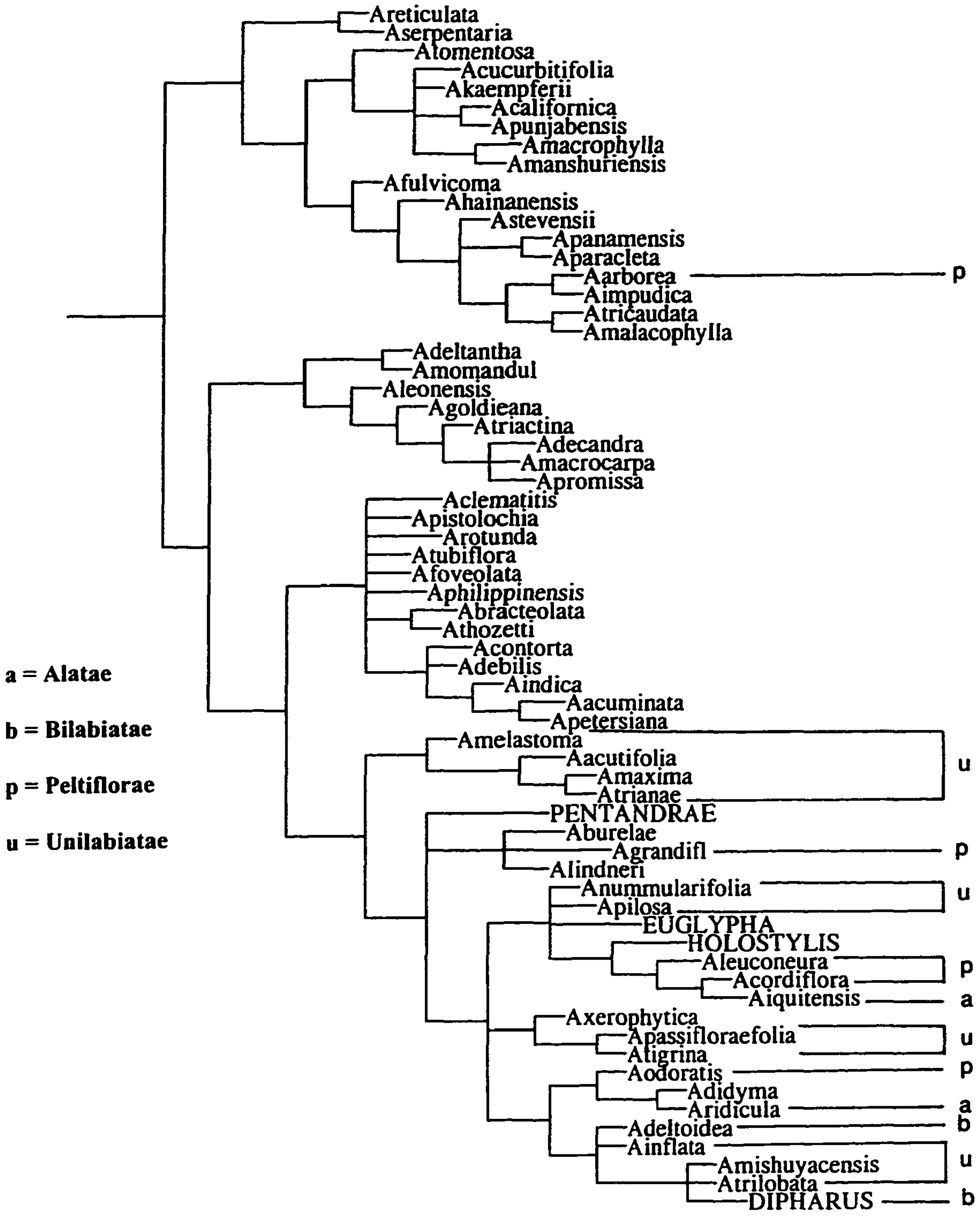
The second clade includes the complex *Aristolochia* section *Gymnolobus* Duchartre (1854a, 1864; equivalent to the segregate *Howardia* Klotzsch, 1859) plus *Euglypha* and *Holostylis*. Thus, section *Gymnolobus* (i.e. *Howardia*) is shown to be paraphyletic (Figs. 77, 78). The first subclade within the aforementioned complex corresponds to *Aristolochia* ser. *Thyrsicae*, proposed by González (1990, 1991) and this series remains as monophyletic (Fig. 77).

The placement of *Aristolochia* subseries *Pentandrae* is unclear (Fig. 77). The limited resolution within the clade that contains subseries *Pentandrae* is due to conflicting characters which prevents the suggestion of a sister group relationship between *Pentandrae* and either *A. grandiflora* + *A. burelae* + *A. lindnerii*, or with the clade that contains *Euglypha*, *Holostylis*, and the species of *Aristolochia* with non-bracteate flowers. The pentandrous species have in common with the first potential sister group the presence of a single, bracteate flower per node (character 14), and the complete syrinx (character 29), whereas they have in common with the second potential sister group the absence of an abscission zone at the base of the peduncle (20) and fossulate pollen (47).

The infrageneric taxa proposed within subsection *Hexandrae* (Duchartre, 1854a, 1864; Hoehne, 1942; Schmidt, 1935), based primarily on habit, and shape and size of the flowers, are not monophyletic (Figs. 79, 80). For example, the group *Bilabiatae*, which contains all the species with 2-lobed flowers, are polyphyletic in either system of classification (Figs. 79, 80). This is consistent with the fact that flowers with two lobes in e.g. *A. ringens* vs. *A. ridicula* develop differently (chapter three).

The present analysis shows that *Aristolochia* ser. *Hexandrae* (as described by González 1990, 1991; Table VII) is paraphyletic. This series was characterized by the absence of an abscission zone at the base of the petiole (character 9) and the floral peduncle

Figure 79. Infrageneric taxa as defined by Duchartre (1854a, 1864) and Schmidt (1935) mapped on the cladogram.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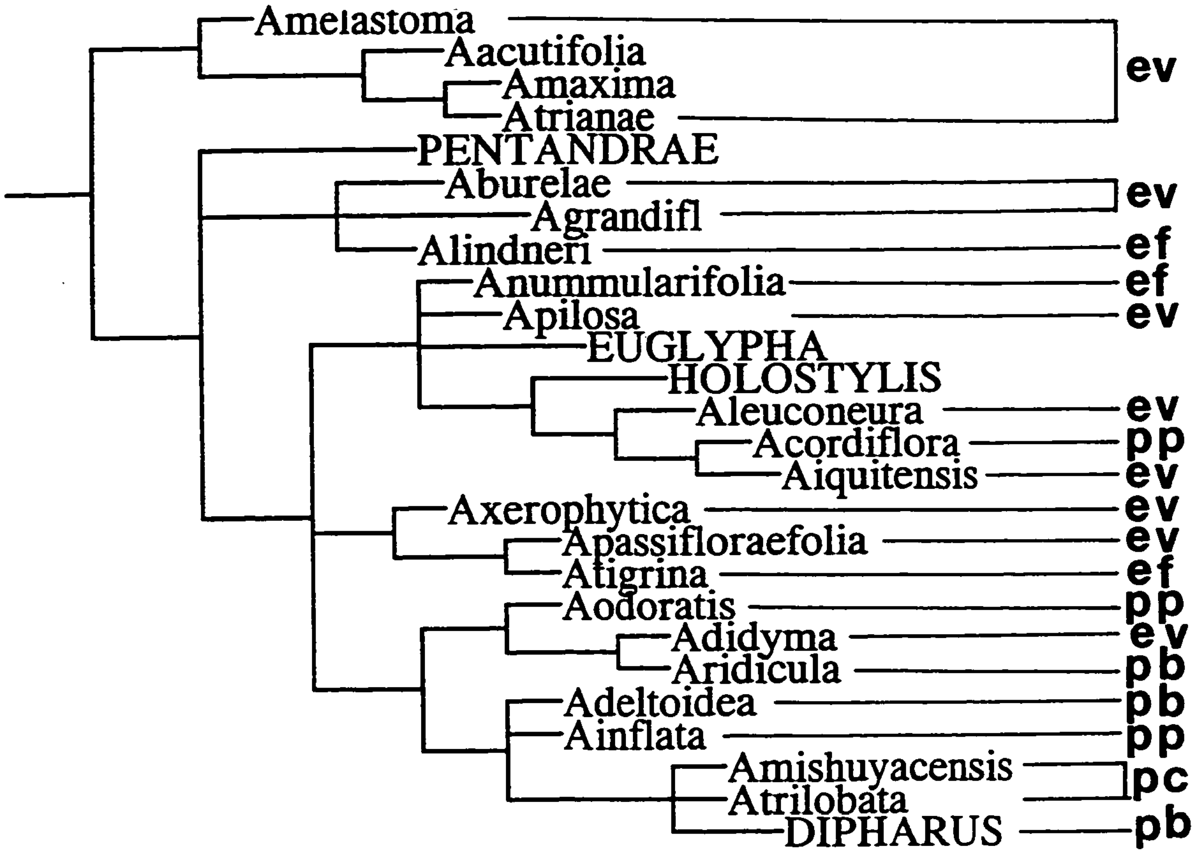
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
p
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
u
PENTANDRAE
Aburelae
Agrandifl
p
Alindneri
Anummularifolia
Apilosa
u
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
p
Aiquitensis
a
Axerophytica
Apassifloraefolia
Atigrina
u
Aodoratis
p
Adidyma
Aridicula
a
Adeltoidea
b
Ainflata
Amishuyacensis
Atrilobata
u
DIPHARUS
b
a = Alatae
b = Bilabiatae
p = Peltiflorae
u = Unilabiatae

Figure 80. Infrageneric taxa as defined by Hoehne (1942) mapped on the cladogram.



EF = "Exstipulosae, Fruticulosae"

EV = "Exstipulosae, Volubilis"

PB = "Pseudostipulosae, Bilabiatae"

PC = "Pseudostipulosae, Caudatae"

PP = "Pseudostipulosae, Peltiflorae"

(20), the absence of bracts (14), the flowers in racemes (11), the fruits with entire septae (64) and the seeds lacking wings or having one wing (68). All these traits are shown to be symplesiomorphies of ser. *Hexandrae*.

The genus *Euglypha* is part of an unresolved clade formed by a group of species with concave-convex seeds (character 66) and a massive funicle (character 70). *Euglypha* was named (Chodat & Hassler 1906) and subsequently maintained by other workers (e.g. Ahumada, 1967; Hauman, 1923; Hoehne, 1927, 1942; Huber, 1993; Schmidt, 1935), because of the presence of a stipe at the base of the perianth (character 23), extremely shortened capsules that fail to dehisce (62) and usually contain only one seed per carpel (65). The latter three characters are autapomorphies of *Euglypha*. The stipe (character 23, Fig. 18E) is also present in a number of species of section *Diplolobus* (Fig. 76), but their vasculature is different. In *Euglypha*, the vascular plexus of the base of the perianth is complete (Fig. 49E; Table VI) and there are additional 2nd-order veins along the stipe (character 28), whereas in the species of section *Diplolobus* (Fig. 49A-D), the plexus is incomplete and the 2nd-order veins are lacking.

Aristolochia subser. *Anthocaulicae* (González, 1990, 1991) survives as a monophyletic group, defined by the cauliflorous inflorescences with extremely shortened internodes (Fig. 11D; character 18). Furthermore, a sister-group relationship is seen between this subseries and the genus *Holostylis* (Fig. 77), based on the presence of lateral racemes (11) and the reduced pherophylls (13). This is consistent with additional anatomical characters that support a close relationship between *Aristolochia* and *Holostylis* (Carlquist, 1993; Solereder, 1889a), especially the presence of idioblasts filled with brown, tanniferous material in *Holostylis* (Solereder, 1889a) and at least in one species of its sister group (*A. leuconeura;* González, 1990).

A brief comment on biogeography

The present cladistic analysis shows additional examples of some well docummented disjunct taxa. The first, found in *Aristolochia* subgenus *Siphisia*, consist of two pairs of sister species that are disjunct between temperate Asia and North America, *Aristolochia californica* + *A. punjabensis;* and A. *macrophylla* + *A. manshuriensis*. The latter two species, Eastern North American-Eastern Asian disjuncts, are remarkable similar in terms of morphological characters.

The second pair of disjunct taxa that form a sister group relationship are the two major clades of subgenus *Pararistolochia,* one formed by the Australian and the New Guinean species, and its sister group formed primarily by the West African species.

The third subgenus, *Orthoaristolochia*, has a much wider geographical distribution, but the two major lineages are primarily Paleotropical (section *Diplolobus*)-Neotropical (section *Gymnolobus* + *Euglypha* + Holostylis) disjuncts.

Two major geographic regions are important in term of sympatric distribution of major clades: Southeast Asia and Central America. Members of all the three subgenera converge only in Malesia, where several species of subgenus *Orthoaristolochia*, a few species of subgenus *Siphisia*, and one species of subgenus *Pararistolochia*, (*A. decandra*) occur (Hou, 1984). On the other hand, in Mexico and Central America, several species of the subgenus *Siphisia* are sympatric with several of subgenus *Orthoaristolochia*. It is also in this area where the approximately 35 pentandrous species of *Aristolochia* have evolved, an important fact in terms of diversity within subgenus *Orthoaristolochia*.

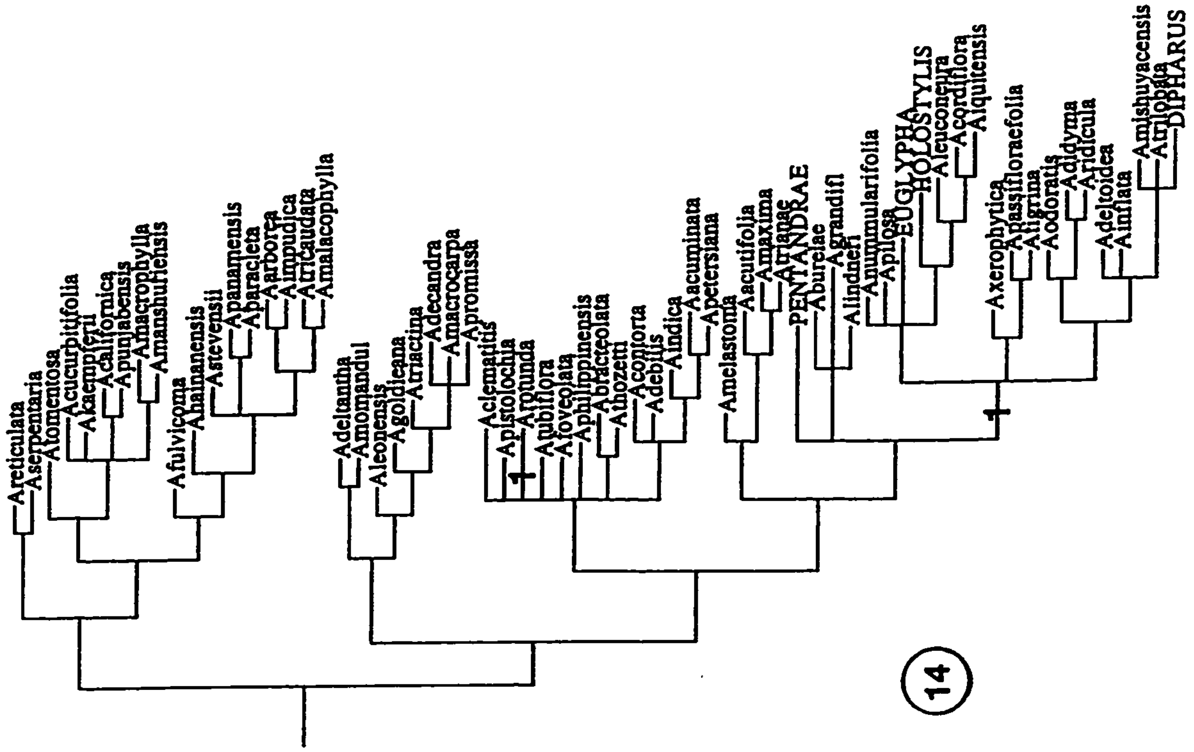
Character Evolution

Inflorescence morphology

The cladistic analysis indicates that monopodial growth (character 1) is a synapomorphy of *Thottea* and the Aristolochioideae (Fig. 71); some exceptions may occur in some species of subgenus *Pararistolochia* from Australia and New Guinea, which may have sympodial growth (Fig. 8C).

Within the Aristolochioideae, a transformation from thyrsic to racemose inflorescences has occurred, *via* a reduction in the number of flowers to one per node and the loss of the bract (characters 12 and 14, respectively; Fig. 81). Whereas partial florescences with one flower have arisen several times in the

Figure 81. Distribution of characters 12 (0, partial florescence uniflowered; 1, partial florescence bi/multiflowered; the latter is a sinapomorphy of *Thottea* plus the ingroup) and 14 (0, flower bracteate; 1, flower non-bracteate).


Areticulata
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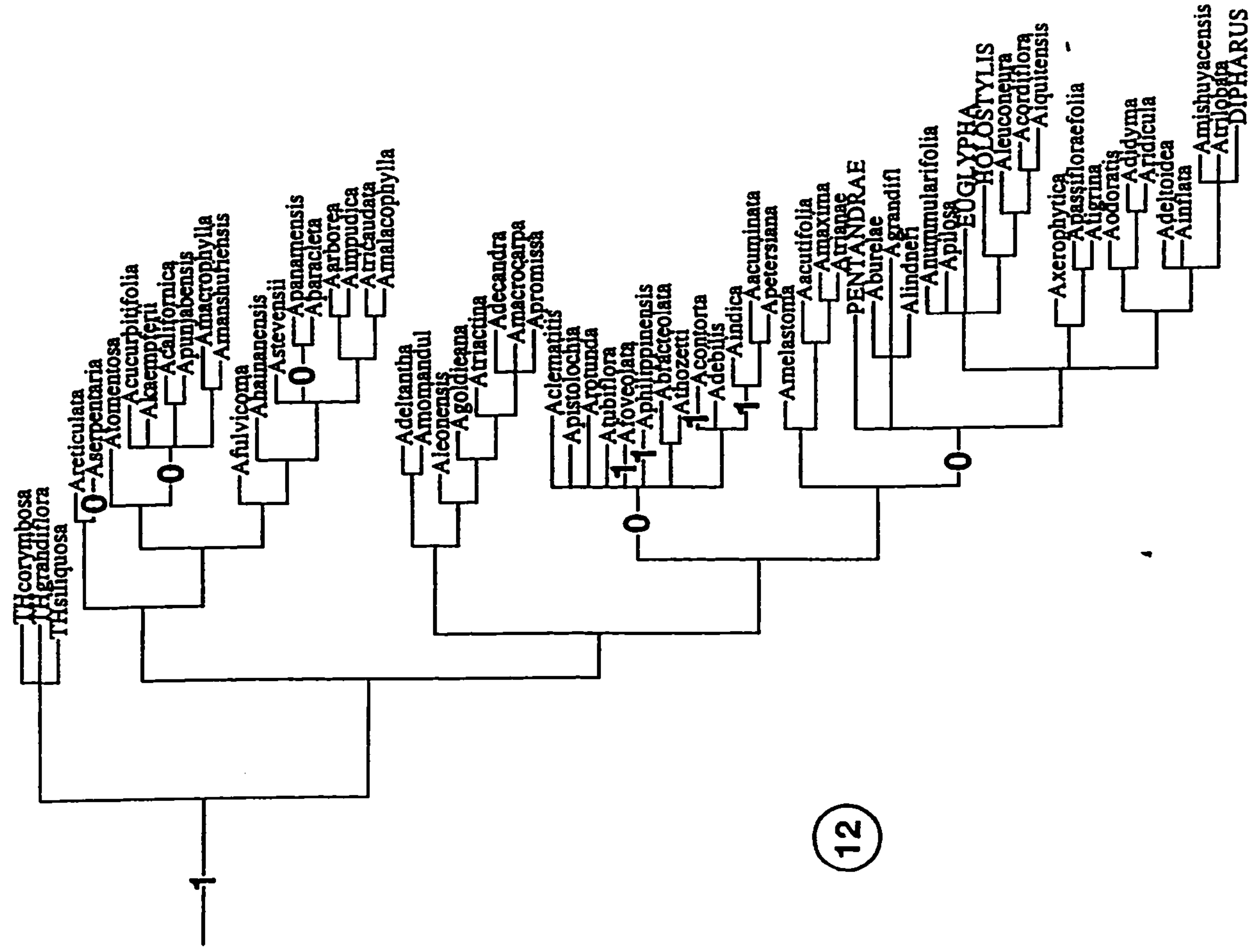
Atomentosa
Acucurbitifolia
Akaempferi
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Abaracleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Alquitensis
Axerophytica
Apassifloraefolia
Aligrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
1
1

⑭


THcorymbosa
THgrandiflora
THsiliquosa
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferi
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Abaracleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Alquitensis
Axerophytica
Apassifloraefolia
Aligrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
0
0
0
0
0
1
1
1
1
1

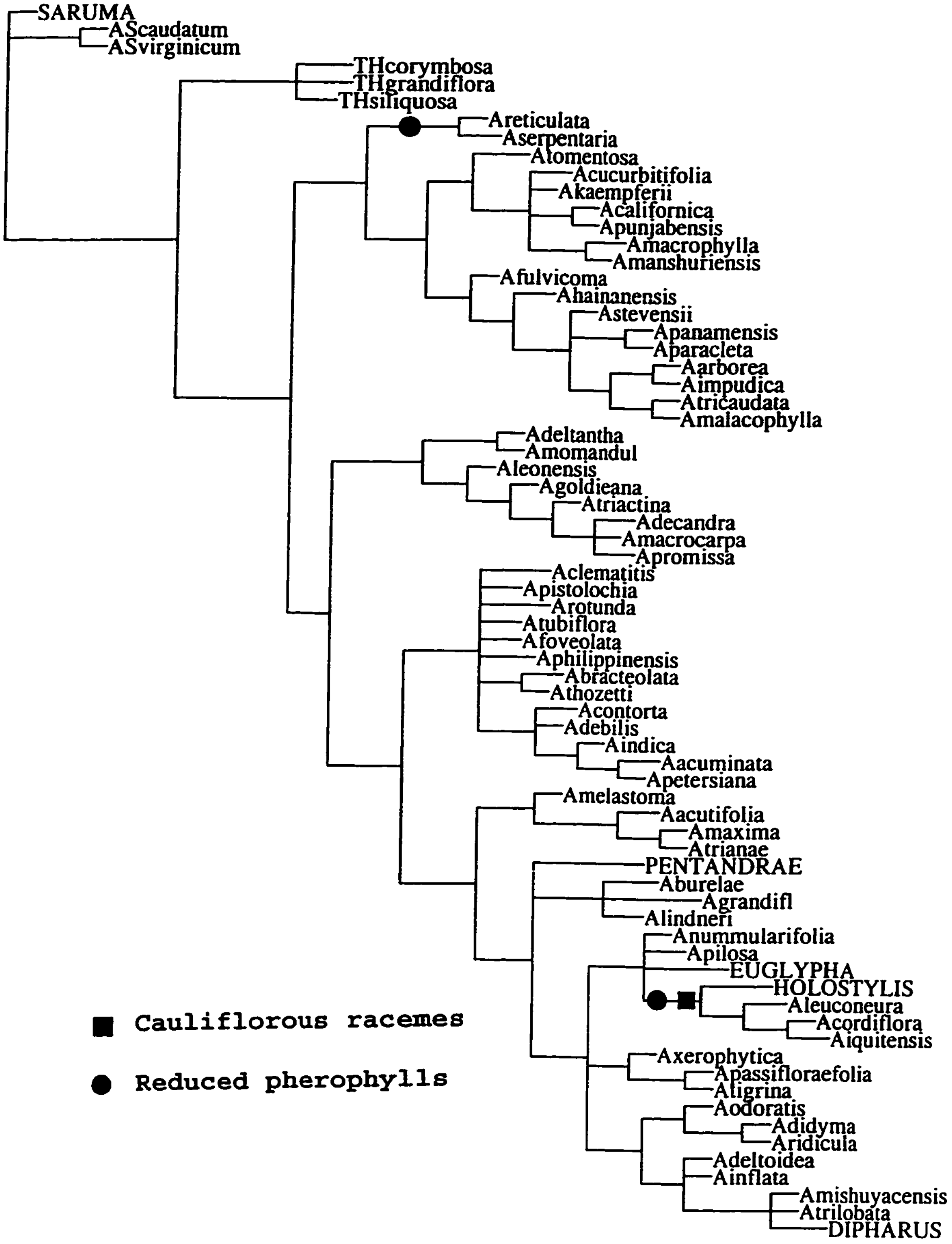
⑫

Aristolochioideae (at least twice within the subgenus *Siphisia*, and twice within the subgenus *Orthoaristolochia*), the loss of the bract (i.e. non-bracteate flowers) has evolved independently only two times, once in the majority of the neotropical species of *Aristolochia* plus *Euglypha* and *Holostylis*, and once in a few species of *Aristolochia* section *Diplolobus* (Fig. 81B; character 14).

In addition, the analysis shows that helicoid cymes (character 19) are a derived feature; helicoid PFs occur at least in two different clades, once in the African species of *Aristolochia* subgenus *Pararistolochia*, and twice within *A.* section *Diplolobus*. The analysis also indicates that buds arranged in two rows occur as a derived character, which is present only in some species of section *Diplolobus*, e. g. *A. acuminata, A. clematitis, A. contorta, A. indica, A. petersiana, A. pistolochia,* and *A. tubiflora*. The low resolution within this clade, however, prevents further interpretation of this character as uniquely derived in these species.

Lateral racemes with shortened internodes (character 11) and reduced pherophylls (character 13) are derived (Fig. 82). Whereas the first supports a sister group relationship between *Holostylis* and *A.* subser. *Anthocaulicae*, the second appear independently in two clades, once within subgenus Siphisia (in the sister species *A. reticulata* and *A. serpentaria*) and once as a synapomorphy for the species of *A.* subser. *Anthocaulicae* plus *Holostylis*.

Figure 82. Distribution of characters 11 (position of the partial inflorescence; 0, along leafy, elongated main branches; 1, lateral racemes) and 13 (pherophylls: 0, leafy; 1, reduced).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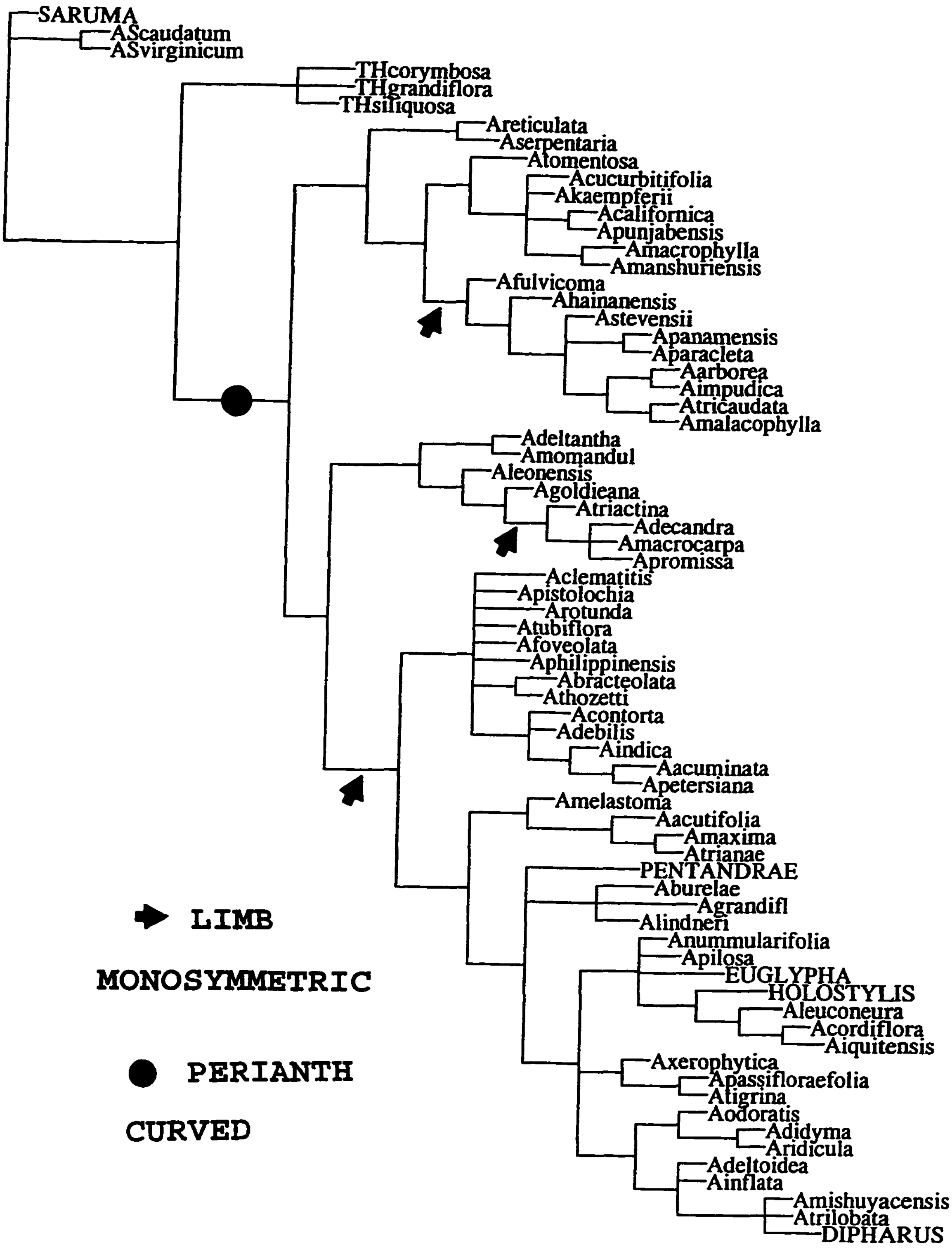
AScaudatum
ASvirginicum
THcorymbosa
THgrandiflora
THsiliquosa
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
■ Cauliflorous racemes
● Reduced pherophylls

Floral morphology

Monosymmetry in flowers of *Aristolochia*, *Euglypha* and *Holostylis* is due to two independent structural transformations, one causing the curvature of the perianth, and the other affecting the symmetry of the limb (Fig. 83). Thus, flowers of some species of subgenera *Siphisia* and *Pararistolochia*, maintain the plesiomorphic condition, i.e. a regular perianth even though the fact that have a curved perianth. According to the present analysis, the curvature (character 26) evolves prior to the monosymmetric limb (35). The latter has evolved three times, once in a clade within *Aristolochia* subgenus *Siphisia*, once in a clade within subgenus *Pararistolochia*, and once as a synapomorphy for the whole subgenus *Orthoaristolochia* plus *Euglypha* plus *Holostylis* (Fig. 83).

The present analysis suggests that a monosymmetric floral limb and/or early fusion of the perianth primordia might play an important role in the morphological diversification of the flowers of the Aristolochiaceae. The actinomorphic limb might limit further elongation and expansion of the apex, where the three meristematic areas are located, and from where most of the morphological variation is derived ("tails," "wings," "antennae," etc.). For example, within *Aristolochia* subgenus *Siphisia*, floral shape in the clade composed of species with an actinomorphic limb is not as morphologically diverse as in its sister clade (Fig. 83) that includes species with flowers having tails (e.g. *A. tricaudata*) or protrusions of the limb (e.g. *A. arborea*, Fig. 15F). Similarly, the most remarkable variation in perianth shape and size occurs in *Aristolochia* subsection *Hexandrae* where an

Figure 83. Distribution of the character states 26-1 and 26-2 (perianth curved) and 35-1 (limb monosymmetric).


SARUMA
AScaudatum
ASvirginicum
THcorymbosa
THgrandiflora
THsiliquosa
Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
LIMB
MONOSYMMETRIC
PERIANTH
CURVED

early fusion of the perianth primordia occurs resulting in the perianth tip growing as a single unit. This is not the case in the species of *Aristolochia* section *Diplolobus*, particularly those of subsection *Podanthemum*, where the tips of the perianth parts remain distinct until maturity (Fig. 18 C, D). In the latter, limb shape is uniform. This is consistent with the low diversification of the shape of actinomorphic flowers of *Asarum* (see e.g. Cheng & Yang, 1983; Kelly, 1997) and *Thottea* (see Hou, 1984).

A perianth limb with two lobes, although restricted to some members of *Aristolochia* section *Hexandrae* (Group *Bilabiatae* in Figs. 79, 80) is not homologous in all cases because there are at least two different developmental processes. The first of these occurs in the species *A. labiata* and *A. ringens* (Figs. 22, 23), in which one lobe (corresponding to the median perianth lobe) is adaxial and the other lobe (formed by the fusion of the two lateral perianth lobes) is abaxial. The other process occurs in *A. ridicula*, in which the two lateral lobes develop as distinct lateral extensions and the median perianth lobe is reduced (Fig. 21).

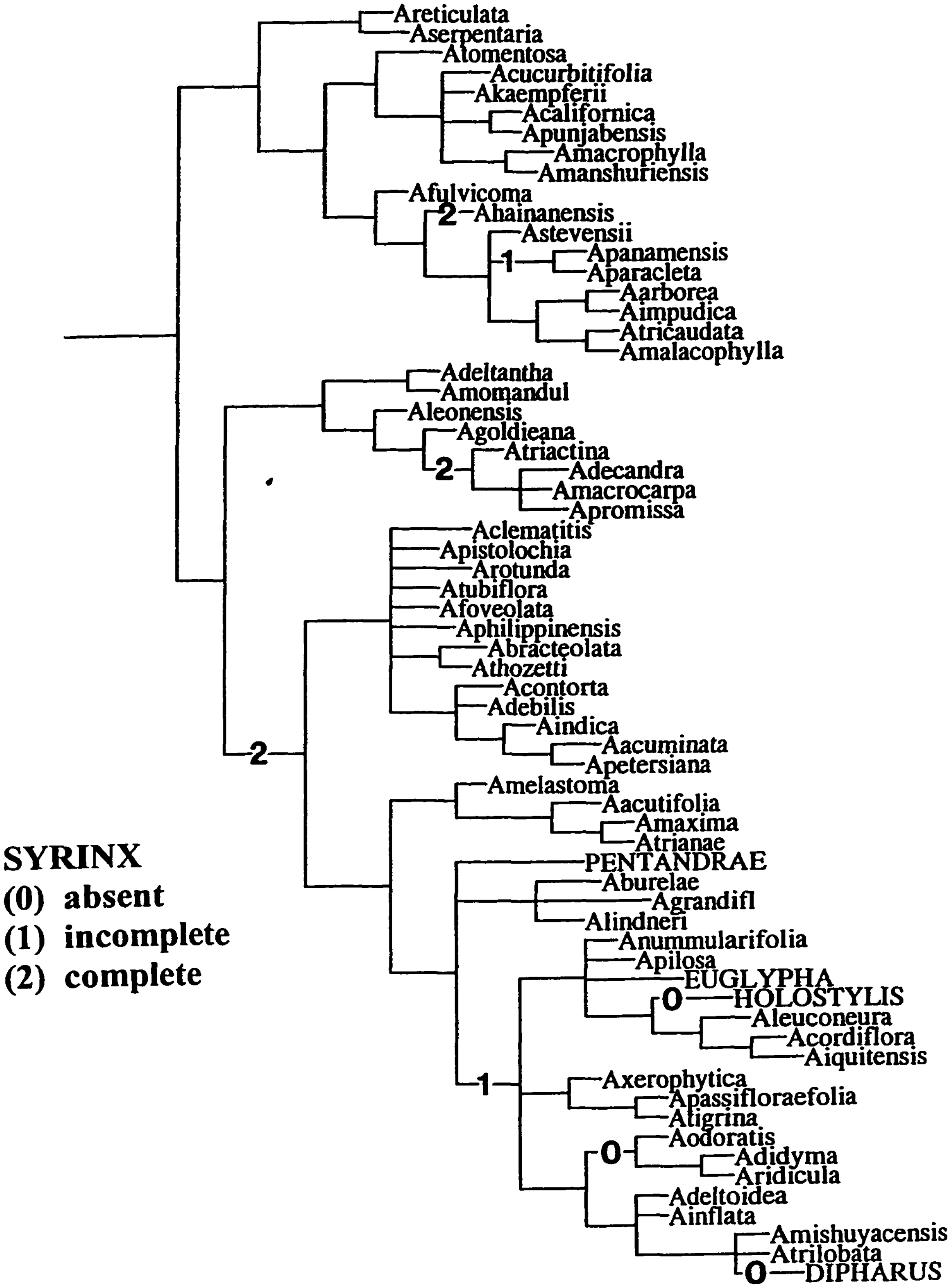
The stipe in the perianth (Fig. 49B, D, F), traditionally used as a diagnostic trait to define the subsection *Podanthemum* (within *Aristolochia* section *Diplolobus*; Table III), and the genus *Euglypha*, has evolved independently in these two taxa (character 23 in Figs. 76 and 77). However, it is not clear if it evolved in parallel several times within section *Diplolobus* (Fig. 76). Another derived characters related to the base of the perianth in

Aristolochia is the strongly asymmetrical perianth base (character 24), which plays a role in positioning the flower during anthesis. This emerges as a synapomorphy of the neotropical crown clade formed by *A. mishuyacensis, A. trilobata* (Fig. 23D) and the species of *A.* sect. *Dipharus* (Fig. 25).

The syrinx (Fig. 4; character 29) and the annulus (character 34) seem to have been acquired independently several times (Fig. 84). A complete syrinx appears twice, once within subgenus *Pararistolochia*, in the clade composed of *A. triactina, A. decandra* and *A. macrocarpa*, and once in subgenus *Orthoaristolochia* subsection *Gymnolobus*. Within the latter, an incomplete syrinx is a synapomorphy of a clade composed of *Aristolochia* subsection *Hexandrae* plus *Euglypha* plus *Holostylis*; then, three reversals (lack of syrinx) occur, once in section *Dipharus*, once in the clade *A. odoratissima, A. didyma* and *A. ridicula*, and once in *Holostylis*. The annulus appears independently four times (Fig. 84), once in subgenus *Siphisia* (with two losses inside), once in some species of subgenus *Pararistolochia* (i.e. the clade composed of *A. goldieana* plus *A. triactina* plus *A. macrocarpa*), once in the pentandrous species *A. secunda*, and once in *A. grandiflora*. The conical trichomes on the inside of the tube evolved, however, as a unique event in the lineage subgenus *Pararistolochia* and subgenus *Orthoaristolochia* (Fig. 84).

According to the present analysis, traits such as tail-shaped appendages (character 37) or fimbriae (character 38) on the limb arise independently in different species (Fig. 85). For example, tail-like appendages develop in one species of subgenus *Siphisia*

Figure 84. Distribution of character 29 (syrinx: 0, absent; 1, incomplete; 2, complete), character state 33-1 (conical perianth trichomes) and character 34 (annulus: 0, absent; 1, present).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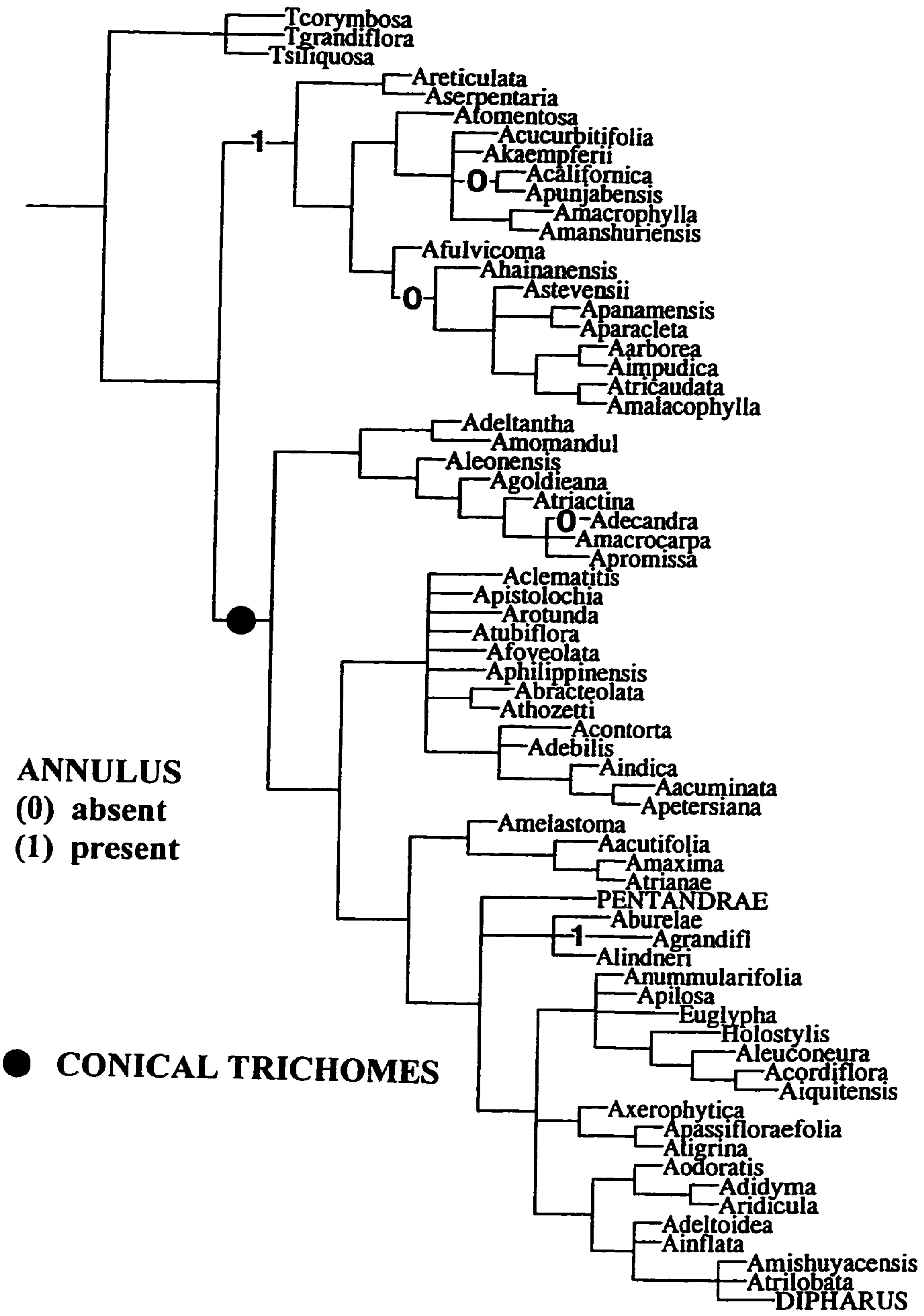
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
2
Ahainanensis
Astevensii
1
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
2
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
2
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
0
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
1
Axerophytica
Apassifloraefolia
Atigrina
0
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
0
DIPHARUS
SYRINX
(0) absent
(1) incomplete
(2) complete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Tgrandiflora
Tsiliquosa
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Aserpentaria
Atomentosa
Acucurbitifolia
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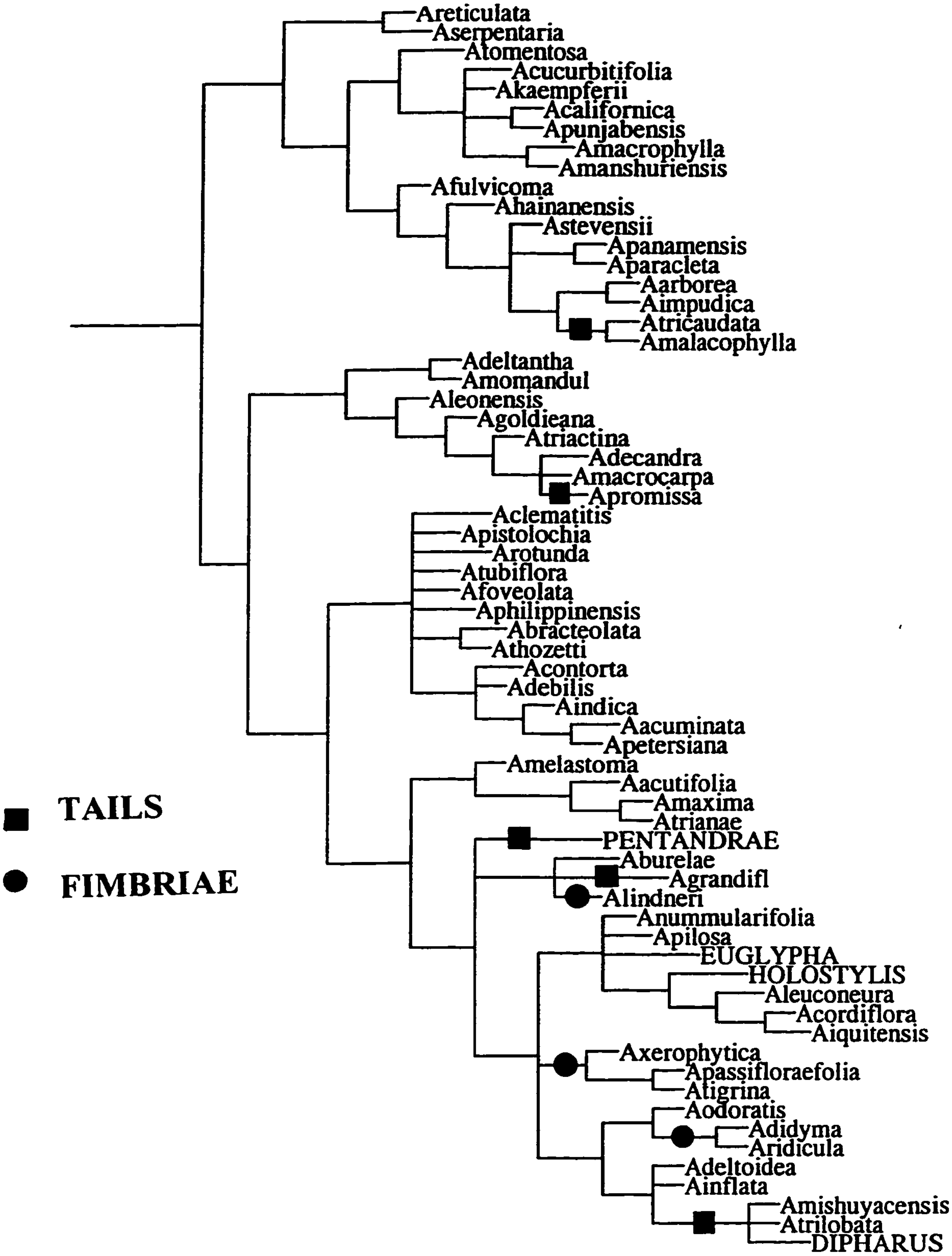
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
0
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
0
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
1
Agrandifl
Alindneri
Anummularifolia
Apilosa
Euglypha
Holostylis
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
ANNULUS
(0) absent
(1) present
● CONICAL TRICHOMES

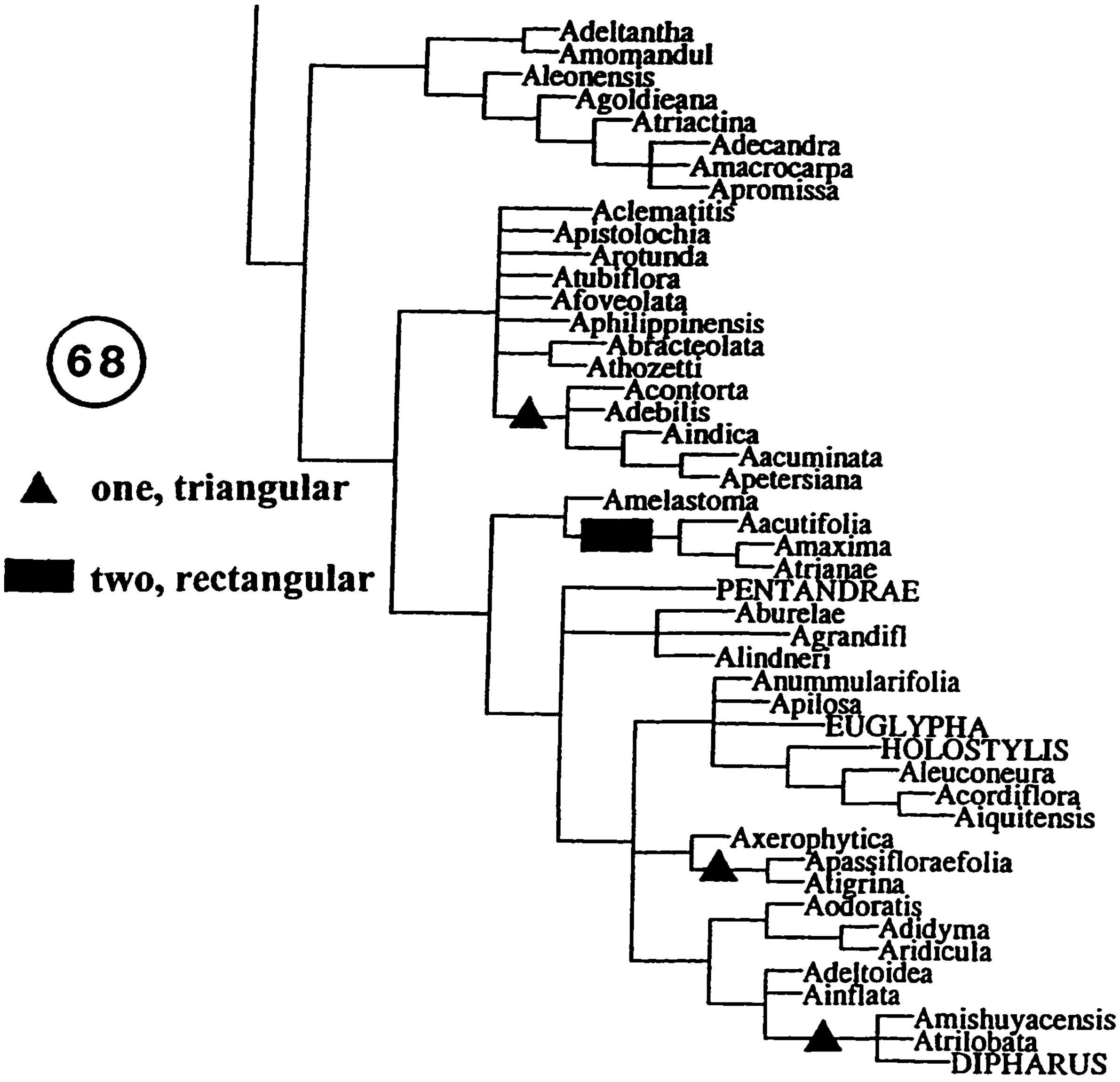
Figure 85. Distribution of character states 37-1 (tail-like appendages on the perianth) and 38-1 (fimbriate limb).

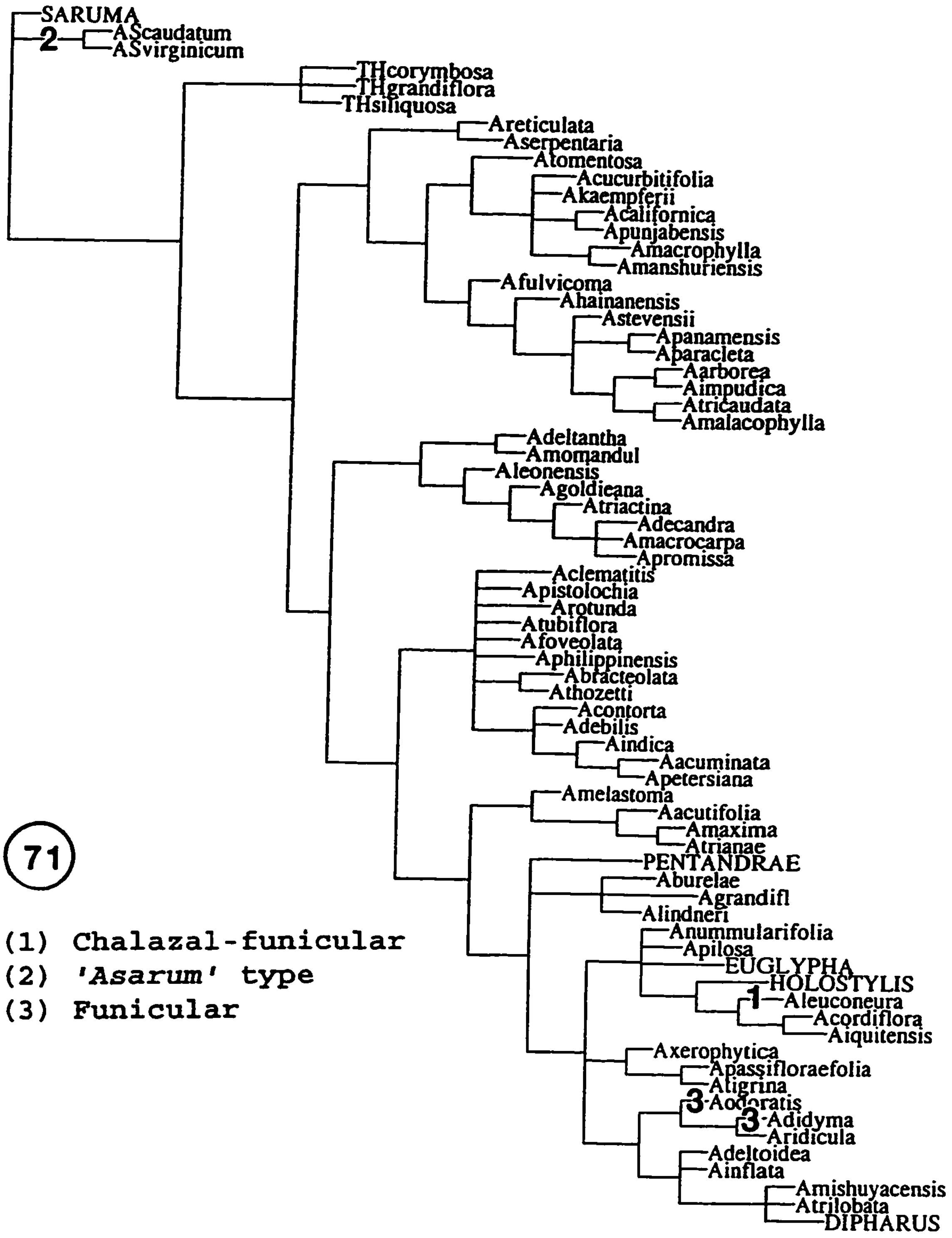

Areticulata
Aserpentaria
Atomentosa
Acucurbitifolia
Akaempferii
Acalifornica
Apunjabensis
Amacrophylla
Amanshuriensis
Afulvicoma
Ahainanensis
Astevensii
Apanamensis
Aparacleta
Aarborea
Aimpudica
Atricaudata
Amalacophylla
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
■ TAILS
● FIMBRIAE

(*A. tricaudata*), one of subgenus *Pararistolochia* (*A. promissa*), one of subsection *Pentandrae (A. nelsonii*), two of subsection Hexandrae (*A. mishuyacensis* and *A. trilobata)*, once in group *Dipharus* (*A. pohliana*), and once in *A. grandiflora*. Fimbriae are restricted only to some species of subsection *Gymnolobus;* however, they have evolved independently at least three times, one in *A. lindnerii*, one in *A. didyma* plus *A. ridicula*, and one in the *A. passifloraefolia* + *A. tigrina* + *A. xerophytica* clade.

Changes in stamen and carpel merosity within *Aristolochia* are all derived traits, with respect to the plesiomorphic hexamerous condition. The presence of more than six stamens in some members of *Aristolochia* subgen. *Pararistolochia* is a derived trait. The presence of five stamens, five stigmatic lobes, and five carpels are also derived traits that appear as unique events in the lineage *Aristolochia* subsect. *Pentandrae*. These characters are not simply correlated with each other, because the number of carpels in other members of the family does not always correspond to the number of stamens; for example, there are twelve stamens and six carpels in *Asarum* and *Saruma*, four carpels and 6-36 stamens in *Thottea*, or six stamens and three gynostemium lobes in *Aristolochia* subgen. *Siphisia*. The correspondence in number between the stamens and the carpels in most species of *Aristolochia*, and in *Euglypha* and *Holostylis*, might be related to the fact that both stamen and carpel primordia develop in close contact with each other (chapter 3).

Figure 86. Distribution of character states 68-1 (seeds with two rectangular wings), 68-2 (seeds with one, triangular seed), 71-1 (sticky aril in chalazal-funicular position), 71-2 ("*Asarum*" type aril), and 71-3 (aril in funicular position).


68
▲ one, triangular
■ two, rectangular
Adeltantha
Amomandul
Aleonensis
Agoldieana
Atriactina
Adecandra
Amacrocarpa
Apromissa
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Amelastoma
Aacutifolia
Amaxima
Atrianae
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Atigrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS



(1) Chalazal-funicular
(2) *'Asarum'* type
(3) Funicular

Seed dispersal

Seeds of many species of *Aristolochia* are adapted to at least two different dispersal mechanisms, anemochory and zoochory. Winged, flattened seeds are found in a number of species. Whereas rectangular seeds with two wings (Fig. 70E) are synapomorphic for the clade *A. acutifolia, A. maxima* and *A. trianae* (Fig. 86), 1-winged, triangular or rhomboidal seeds (Fig. 70D) have evolved three different times, once in a clade within subsection *Diplolobus*, and two times within subsection *Gymnolobus* (Fig. 86).

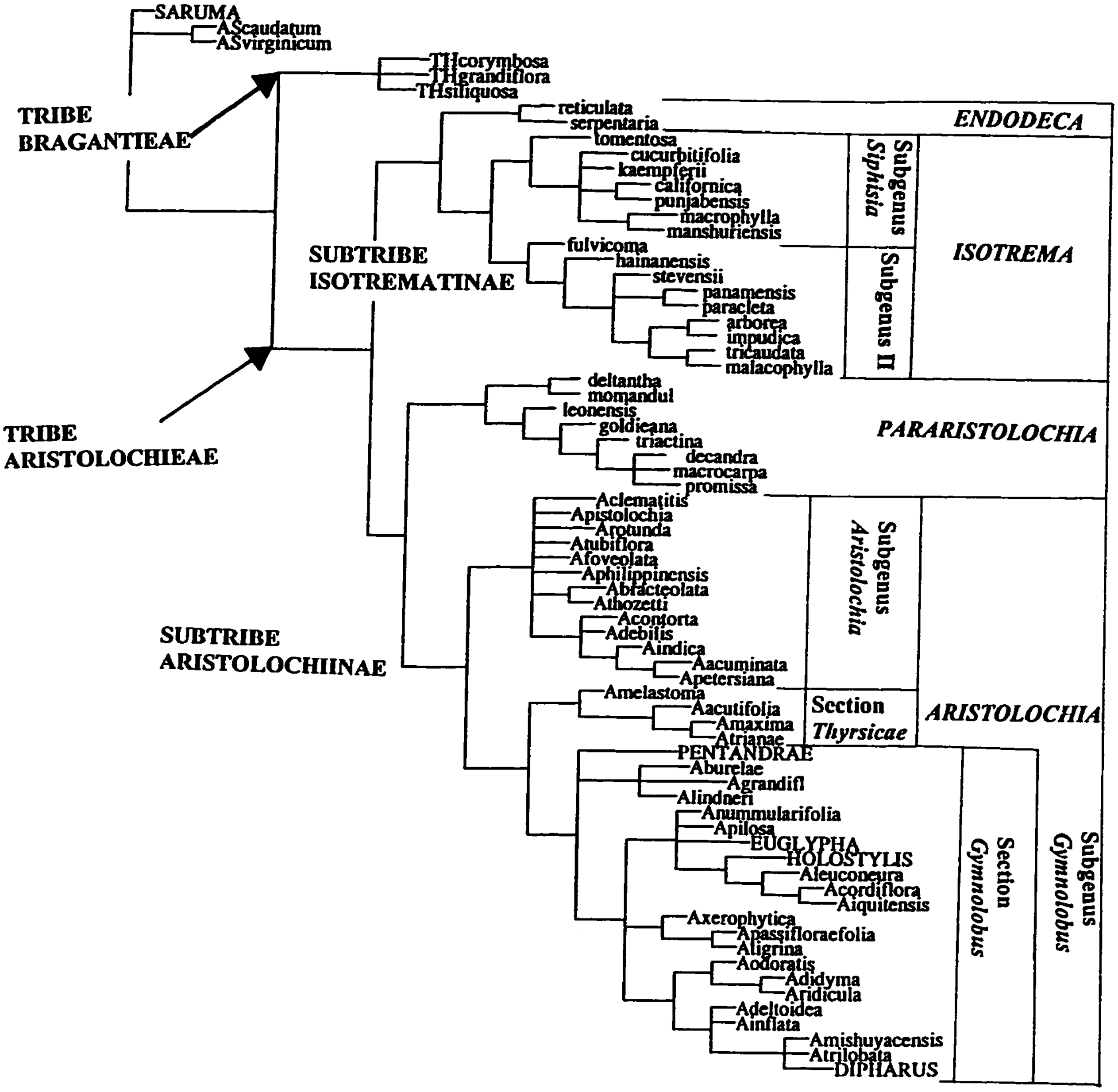
On the other hand, sticky arils that play a role in zoochory (including myrmecochory) evolved four different times in the Aristolochiaceae, once in *Asarum*, once in *Aristolochia odoratissima*, once in *A. leuconeura*, and once in *A. didyma* (Fig. 86). This is reflected in at least three different structural differences of the arils. In *Asarum*, sticky arils are formed by 2-4 layers of large, translucent cells formed from the funicle (Fig. 69B). In *Aristolochia*, it consists of a massive secretion from the epidermal and subepidermal cells of the funicle (in *A. didyma* and *A. odoratissima;* Fig. 70C) or the funicle plus the chalaza (in *A. leuconeura*, Fig. 70B).

V. Conclusion: A revised classification of the subfamily Aristolochioideae

The relatively well supported basal clade *Thottea* + *Aristolochia* (Fig. 72) gives reason to recognize these two genera as forming a single lineage within the Aristolochiaceae, as was implicit in Huber's (1985, 1993) system of classification (Fig. 3G). Based on this and the other resulting monophyletic groups (Fig. 87), a revised classification of the subfamily Aristolochioideae consisting of two tribes, two subtribes, five genera and several infrageneric taxa, is proposed here. For practical reasons, I am in favor of recognizing *Aristolochia* in a wider sense than that given by Huber (1985, 1993), because the generic recognition of *Euglypha*, *Holostylis* and *Einomeia* would require the establishment of as many as 12 distinct genera, and would collapse the nomenclature of the largest groups of species of *Aristolochia*. The formal classification proposed (Fig. 87) is:

- Tribe Bragantieeae
  - *Thottea*
- Tribe Aristolochieae
  - Subtribe Isotrematinae
    - *Endodeca*
    - *Isotrema*
      - Subgenus *Siphisia*
      - Subgenus II (primarily tropical species species with monosymmetric flowers) subsect. nov.
  - Subtribe Aristolochiineae
    - *Pararistolochia*
    - *Aristolochia*
      - Subgenus *Aristolochia* stat. nov.
      - Subgenus *Gymnolobus* stat. nov.
        - Section *Thyrsicae* stat. nov.
        - Section *Gymnolobus* (including *Euglypha* and *Holostylis*).

Figure 87. Revised system of classification of the Aristolochioideae. Names to the right in capital letters are genera. Subgenus *Gymnolobus* includes section *Thyrsicae* and section *Gymnolobus*.


SARUMA
AScaudatum
ASvirginicum
THcorymbosa
THgrandiflora
THsiliquosa
TRIBE
BRAGANTIEAE
reticulata
serpentaria
tomentosa
cucurbitifolia
kaempferii
californica
punjabensis
macrophylla
manshuriensis
fulvicoma
hainanensis
stevensii
panamensis
paracleta
arborea
impudica
tricaudata
malacophylla
SUBTRIBE
ISOTREMATINAE
ENDODECA
Subgenus
Siphisia
Subgenus II
ISOTREMA
TRIBE
ARISTOLOCHIEAE
deltantha
momandul
leonensis
goldieana
triactina
decandra
macrocarpa
promissa
PARARISTOLOCHIA
Aclematitis
Apistolochia
Arotunda
Atubiflora
Afoveolata
Aphilippinensis
Abracteolata
Athozetti
Acontorta
Adebilis
Aindica
Aacuminata
Apetersiana
Subgenus
Aristolochia
SUBTRIBE
ARISTOLOCHIINAE
Amelastoma
Aacutifolia
Amaxima
Atrianae
Section
Thyrsicae
ARISTOLOCHIA
PENTANDRAE
Aburelae
Agrandifl
Alindneri
Anummularifolia
Apilosa
EUGLYPHA
HOLOSTYLIS
Aleuconeura
Acordiflora
Aiquitensis
Axerophytica
Apassifloraefolia
Aligrina
Aodoratis
Adidyma
Aridicula
Adeltoidea
Ainflata
Amishuyacensis
Atrilobata
DIPHARUS
Section
Gymnolobus
Subgenus
Gymnolobus

Conclusion

The present dissertation addresses the morphology and systematics of a primarily tropical group of plants, the Aristolochioideae. The first chapter points out the morphological and systematic questions that are addressed, and shows that the different systems of classification of the Aristolochiodeae are variations of the same theme. In chapter two, positional and developmental criteria are used to infer homology of the inflorescences of the Aristolochiaceae. Two major theses are proposed: (1) there is a clear-cut difference in the growth units between the Asaroideae, with sympodial growth units, and the Aristolochioideae, with monopodial growth units; and (2) there is an evolutionary change within the Aristolochioideae, from thyrsic to racemose inflorescences. Several traits related to the inflorescences are shown to be informative not only as a subset of characters for the phylogenetic analysis presented in chapter five, but also as key characters for species identification. Moreover, the study of the development and morphology of inflorescences in the family demonstrates that the groundplan of the ultimate structural unit, the flower and the corresponding bract, follows a distichous pattern. This implies that the flower is always in the same position with respect to its bract, providing a reliable point of reference for studying floral development.

Chapter three describes the development of the two most crucial structures in the systematics of *Aristolochia* and its allies *Euglypha*, *Holostylis*, and

Thottea. It was demonstrated that the perianth corresponds to a trimerous calyx, and that its development follows at least five different pathways. The results presented in chapter three confirm that the gynostemium is formed by both carpels and stamens (i.e. a true gynostemium!). In addition to having systematic implications, the development of the perianth and the gynostemium of *Aristolochia* is *per se* one of the most specialized and unique processes in the angiosperms. Together, the perianth and gynostemium make possible one of the most fascinating pollination syndromes found in flowering plants. The presence of these sophisticated processes of floral synorganization and the complete differentiation of the four floral whorls in the Aristolochiaceae shows that these processes arose early in evolution because the Aristolochiaceae are one of the basal groups of the angiosperms.

In closing, chapter five presents a cladistic analysis of representative species of the large genus *Aristolochia* sensu lato and its allies, based on 72 morphological characters. The analysis was used to evaluate the different systems of classification of the Aristolochioideae, and to propose an alternative system of classification. Whereas some groups remain monophyletic, two of the traditionally recognized genera, *Euglypha* and *Holostylis* are nested in a large lineage, *Aristolochia*. A number of less diverse taxa are also shown to be paraphyletic or polyphyletic.

Cladistic analysis permits the evaluation of character distribution in a broad framework and facilitates the prediction of evolutionary hypotheses. Searching and scoring characters for each taxon is perhaps one of the most challenging tasks for a systematist. During the process, more questions arise and more gaps in our knowledge are detected. But some answers are also discovered. And this is the best way to integrate the knowledge of taxa that are "old" and "new", small and large, and endemic and widespread. Failure to employ this method of information synthesis results in systems of classification that can not be tested and challenged by others.

Appendix I. Data matrix used in the cladistic analysis. Polymorphisms are indicated in brackets. Innaplicable characters are indicated with "-", and unknown characters with "?".

	1	1 2	2 3	3 4	4 5	5 6	6 7	7
	01234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
SARUMA	0000-000000	0000000000	00-00000--	--00000000	0000000000	0000000000	0000000000	0
AScaudatum	0000-000000	0000000000	11-00000--	--00000000	0001001201	1010100000	1100000010	2
ASvirginicum	0000-000000	0000000000	11-00000--	--00000000	0001001101	0010000100	1100000010	2
THcorymbosa	1?010010001	2?1??????1	11000010--	--00000002	1001003200	1112??1?00	01?0021011	0
THgrandiflora	11010010001	?????????1	11000010--	--00000005	0001003200	1112??1?00	01??021011	0
THsiliquosa	11010010001	0100001001	11000010--	--00000002	1101003200	1112??1?00	01?0021011	0
HOLOSTYLIS	11010010001	1011---0-0	1100121000	--00110003	1011112200	1110100000	0010000010	0
Areticulata	01010010001	0110101100	1200111000	0101000003	1111112200	11101[12]0100	0100000010	0
Aserpentaria	01010010001	00101011-0	1200111000	0101000003	1111112200	11101[12]0100	0100000010	0
Acalifornica	11010010010	00001010-0	1200111000	0200000003	1111112200	1110120100	0100000010	0
Acucurbitifolia	11010110010	00001010-0	1200111000	0201000003	1111112200	1110120100	0100000010	0
Amacrophylla	11010010010	00001010-0	1200111000	0201000003	1111112210	1110120100	0100010000	0
Atricaudata	11010010011	0100001001	1200111000	0200101003	1111112202	1110120100	0100000000	0
Amalacophylla	11010010011	0100001001	1200111000	0200101003	1111112202	1110120100	0100000000	0
Amanshuriensis	11010010010	00001010-0	1200111000	0201000003	1111112200	1110120100	0100010000	0
Apanamensis	11010010011	0000001001	1200111010	0200100003	1111112200	1110120100	0100000000	0
Aparacleta	11010010011	0000001001	1200111010	0200100003	1111112200	1110120100	0100000000	0
Apunjabensis	11010010010	00001010-0	1200111000	0200000003	111111??0?	111012010?	????0?????	?
Astevensii	11010010011	0100001001	1200111000	0200100003	1111112200	1110120100	0100000000	0
Atomentosa	11010010010	0100000000	1200111000	0201000003	1111112200	1110120100	0100010010	0
Afulvicoma	11010010011	0100001000	1200111000	0201100003	1111112200	1110120100	0100000010	0
Akaempferii	11010010010	00001010-0	1200111000	0201000003	1111112200	1110120100	0100000010	0
Ahainanensis	11010010011	0100001000	1200111020	0200100003	1111112200	1110120100	0100000010	0
Aarborea	11010010011	0100001001	1200111000	0200100013	1111112202	1110120100	0100000000	0
Aimpudica	11010010011	0100001001	1200111000	0200100013	1111112202	1110120100	0100000000	0
PENTANDRAE	11010010001	00001010-0	1200121020	[01]11[01]11[01]004	1011112201	1111110000	0100010013	0
Amelastoma	11010011001	0100001001	1200121020	1110110003	1011112200	1110100000	0010010010	0
Aacutifolia	11010111011	0100001001	1200121020	1110110003	1011112200	1110100000	0011010111	0
Amaxima	11010011011	0100001001	1200121021	1110110003	1011112200	1110100000	0011010111	0
Atrianae	11010011011	0100001001	1200121021	1110110003	1011112200	1110100000	0011010111	0
Aburelae	11010010001	0100111001	1200121020	1110110003	1011114202	1110100000	0010010013	0
Adidyma	11010010?01	0001---0-0	1200121001	1110130103	1011112200	1110100000	0010010013	3
Agrandifl	11010010001	00001110-1	1200111020	0011111003	1011114200	1110100000	0010010013	0
Alindneri	11010010001	00001110-1	1200121020	1110110103	1011114200	1110100000	0010010013	0
Anummularifolia	11010010001	0001---0-0	1200121010	1110110003	1011112200	1110100000	0010000010	0
Apassifloraefolia	11010010001	0001---0-0	1200121010	1110110103	1011112200	1110100000	0010010211	0
Atigrina	11010010001	0001---0-0	1200121010	1110110103	1011112200	1110100000	0010010211	0
Apilosa	11010010001	0001---0-0	1200121010	1110110003	1011114200	1110100000	0010000010	0
Aridicula	11010010101	0001---0-0	1200121001	1110130103	1011112200	1110100000	0010010013	0

Appendix I. Data matrix. Continued.

	1	1 2	2 3	3 4	4 5	5 6	6 7	7
	01234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Axerophytica	11010010001	0001---0-0	1200121010	1110110103	1011112200	1110100000	0010010013	0
Adeltoidea	11110010101	0001---0-0	1200121011	1110110003	1011112200	1110100000	0010010013	0
Ainflata	11110010101	0001---0-0	1200121011	1110110003	1011112200	1110100000	0010010013	0
Amishuyacensis	11110010101	0001---0-0	1201121011	1110111003	1011112200	1110100000	0010010211	0
Aodoratis	11010010101	0001---0-0	1200121001	1110110003	1011112200	1110100000	0010010013	3
Atrilobata	11110010101	0001---0-0	1201121011	1110111003	1011112200	1110100000	0010010211	0
DIPHARUS	11110010101	0001---0-0	1201121001	111012[01]003	1011112200	1110100000	0010010211	0
Acordiflora	11010010001	1011---1-0	1200121011	1110110003	1011112200	1110100000	0010000010	0
Aiquitensis	11010010001	1011---1-0	1200121011	1110130003	1011112200	1110100000	0010000010	0
Aleuconeura	11010010001	1011---1-0	1200121010	1110110003	1011112200	1110100000	0010000010	1
Abracteolata	11010010001	00001010-0	1210121100	1110110003	1011104200	1110100100	0010000010	0
Aclematitis	11011010001	00000010-0	1200121100	1110110003	1011104200	1110100100	0000010010	0
Acontorta	11011110001	0100001010	1200121100	1110110003	1011104200	1110100100	0010010212	0
Adebilis	11010010001	00000010-0	1200121100	1110110003	1011104200	1110100100	0010010212	0
Apistolochia	11011010001	00000010-0	1200121100	1110110003	1011104200	1110100100	0010000010	0
Arotunda	11000010001	0001---0-0	1200121100	1110110003	1011104200	1110100100	0000000010	0
Atubiflora	11011010001	00000010-0	1200121100	1110110003	1011104200	1110100100	0010000010	0
Aacuminata	11011010001	0100101010	1210121100	1110110003	1011104200	1110100100	0010010211	0
Afoveolata	11010010001	0100001010	1200121100	1110110003	101110??0?	1110100100	0010000010	0
Aindica	11011010001	0100001010	1210121100	1110110003	1011104200	1110100100	0010010210	0
Apetersiana	11011010001	0100101010	1210121100	1110110003	1011104200	1110100100	0010010210	0
Aphilippinensis	11010010001	0100001000	1210121100	1110110003	1011104200	1110100100	0010000010	0
Athozetti	11010010001	00000010-0	1210121100	1110110003	1011104200	1110100100	0010000010	0
Agoldieana	11010110001	0100001010	1200111000	1111000001	1011112220	1110140111	13-0000010	0
Adecandra	11?1011?001	0100001010	1200111020	1110100002	1011112220	11101301??	??????????	?
Amacrocarpa	11010110001	0100001010	1200111020	1111100002	1011112220	1110130111	13-0000010	0
Apromissa	11010110001	0100001010	1200111020	1111101002	1011112220	1110130111	13-0000010	0
Atriactina	11010110001	0100001010	1200111020	1111000002	1011112220	1110130111	13-0000010	0
Aleonensis	1101011?001	0100001010	1200111000	1110000003	1011112220	1110100111	13-0000010	0
Adeltantha	1?010010001	0100001000	1200111000	1010000003	1011112220	1110100111	13-0010011	0
Amomandul	10010110001	0100001000	1200111000	1010000003	101111?220	1110100111	13-0010011	0
EUGLYPHA	11010010001	0001---0-0	1210121010	1110110003	1011112210	1110100000	03-0100010	0

Appendix II. References and geographical distribution of the species included in the cladistic analysis. References consist primarily of voucher specimens (acronyms after Holmgren et al. 1990). References without acronyms are from the literature. Asterisks indicate collections with fixed specimens.

Species	**Distribution**	**Reference**
Aristolochia acuminata	Tropical Asia	KEW, acc. 1997-5826*; van Steenis 1277 (BO)
A. acutifolia	Amazon basin	González 3573 (NY)*
A. arborea	Mexico, Guatemala Salvador	González 3415 (NY)*
A. bracteolata	Tropical Asia	Deflers 704 (P);
A. burelae	Argentina, Bolivia, Brazil	Maruñak & al. 486 (MO); Specht s.n. (NY)*;
A. californica	California, US	Raz s.n. (NY)*
A. clematitis	Europe	González 3446 (NY)*; Mullins s.n. (NY)*. Correns (1891); Mohana Rao (1989).
A. contorta	China, Korea, Japan	Li 10853 (UC). Nakai (1936)
A. cordiflora	Panama, Colombia, Ecuador	González 909 (COL)*
A. cucurbitifolia	Taiwan	Tsou 1180 (COL)*. Hayata (1915); Hou (1996)
A. debilis	China, Japan	Hance 17612 (BM)
A. decandra	Kalimantar	Winkler 1256 (HBG). Hou (1983, 1984)
A. deltantha	Australia	Foster PIF 9572 (BRI); Moriarty 2025 (BRI). Bailey (1901); Bentham (1873); Harden (1990); Jones & Gray (1977); von Mueller (1867)
A. deltoidea	Peru	Woytkowski 5657 (MO, UC)
A. didyma	Amazon basin	Vogel 44 (US)
A. foveolata	Taiwan, Malesia	Clemens & al. 4405 (BM). Hou (1984)
A. fulvicoma	China	How 71931 (GH)
A. goldiana	W Africa	Carvalho 4450 (P); L. Aké s.n. (G). Hooker f. (1865); Hutchinson & Dalziel (1954); Mutsaers & Lowe (1988); Poncy (1978)
A. grandiflora	West Indies, Central America, Colombia, Ecuador	González 3443 (NY)*
A. hainanensis	China	McClure 9333 (BM)
A. impudica	Mexico	Ortega 512 (MO)
A. indica	India	Koyama & al. 15969 (NY)
A. inflata	Central America, Colombia	Haught 2394 (COL)
A. iquitensis	Amazon basin	González 1772 (COL); Vásquez 2869 (MO)
A. kaempferi	Taiwan, Japan	Kurata & al. 2306 (GH); Tsou 1179 (COL)*. Hou (1996)
A. leonensis	W Africa	Adam 21123 (MO), 21649 (MO). Hutchinson & Dalziel (1954); Poncy (1978)
A. leuconeura	Costa Rica, Colombia	González 3569 (COL)*
A. lindneri	Bolivia	Schinini 14906, 18016 (CTES)
A. macrocarpa	Africa	Jondkind 48 (WAG); de Wilde 617 (WAG). Poncy (1978)
A. macrophylla	SE United States	González 3421 (NY)*
A. malacophylla	Mexico, Guatemala, Honduras	Mexia 2772 (A). Pfeifer (1966)
A. manshuriensis	China, USSR, Korea	s.c. 3953 (GH); Campbell s.n.* (NY);Farges 522(P). Nakai (1936)
A. maxima	Central America, Colombia, Venezuela	González 3289 (NY)*
A. melastoma	Amazon basin	Dusén 16616 (MO)

Appendix II. Continued.

Species	**Distribution**	**Reference**
A. *mishuyacensis*	Amazon basin	Lozano & al. 646 (COL); Fróes 32177 (RB).
A. *momandul*	Malesia	Brass 5229 (NY). Hou (1984); Jebb (1993)
A. *nummularifolia*	Colombia, Venezuela	González 3367 (NY)*
A. *odoratissima*	Neotropics	González 3574 (NY)*
A. *panamensis*	Panama	Carrasquilla 182 (F); Standley 29515 (US)
A. *paracleta*	Guatemala	Castillo 2215 (AGUAT); Contreras 1686 (TEX); González 3417 (NY). Pfeifer (1966).
A. *passifloraefolia*	Cuba, Bahamas	Wright 463 (MA)
A. *petersiana*	E Africa	NYBG acc. 151/97*; J.D. & E.G. Chapman 9106 (MO). Hauman (1948)
A. *philippinensis*	Philippines	Ramos 46432 (S); Hou (1984);
A. *pilosa*	Neotropics	González 3571 (NY)*
A. *pistolochia*	Spain	Vargas 3026 (COL) *
A. *promissa*	W Africa	Bot. Gard. Univ. Bonn, acc. # 13014*; Talbot 2318 (BM).
A. *punjabensis*	India, Pakista, Nepal	Stewart 7642 (NY). Qaiser (1977)
A. *reticulata*	SE United States	González 3594 (NY)*
A. *ridicula*	Brazil	KEW, acc. 1995-246*; Macedo 1755 (UEC)
A. *rotunda*	Europe	Correns (1891); Davis & Khan (1961); Huber (1960); Nardi (1984)
A. *serpentaria*	SE United States	González 3604 (NY)*
A. *stevensii*	Central America	González 3416 (NY)*
A. *tigrina*	Cuba	Britton 7608 (NY); Ekman 16S49 (S);
A. *thozetii*	E Australia	Clarkson & al. 6652 (BRI). Bailey (1901); Bentham (1863); von Mueller (1860)
A. *tomentosa*	SE United States	Allen 7560 (FLAS); Janovec s.n.*(NY)
A. *triactina*	W Africa	Bos 3505 (WAG). Hauman (1948); Hooker f. (1865); Hutchinson & Dalziel (1954); Poncy (1978); Verdcourt (1986)
A. *trianae*	W Colombia, NW Ecuador	Fuchs et al. 21926 (COL); González 525 (COL);
A. *tricaudata*	S Mexico	Zurich Bot. Gard.*
A. *trilobata*	Neotropics	González 3445 (NY)*
A. *tubiflora*	China	Ma s.n. (BNU)
A. *xerophytica*	Ecuador, Peru	Woytkowski 5659 (MO)
Asarum caudatum	United States	Mohana Rao (1989); Whittemore & al. (1997); Wyatt (1955b).
A. *virginicum*	United States	Mohana Rao (1989), Whittemore & Gaddy (1997); Wyatt (1955b).
Euglypha rojasiana	Bolivia, Brazil, Paraguay, Argentina	Vargas 1905 (NY)
Holostylis reniformis	Bolivia, Brazil, Paraguay, Argentina	Hatschbach & al. 65556 (NY); Schatz & al. 880 (NY)
Saruma henryi	C China	Pruski *3748* (NY)*. Dickison (1992); Wagner (1907).
Thottea corymbosa	Sumatra, Malay Peninsula, Borneo	Griffith (1845, as *Asiphonia piperiformis*); Hou (1981, 1984)
T. *grandiflora*	Peninsular Burma, Malay Peninsula	Griffith (1845); Hou (1981, 1984)
T. *siliquosa*	India	BONN*; Kew, acc. No. 1996-1265*. Hou (1981, 1984); Nair & Narayanan (1962); Renuka & Swarupanandan (1986).

Appendix III. References of the studied species of *Aristolochia* sect. *Dipharus*, and *A.* subsect. *Pentandrae*. References consist primarily of voucher specimens (acronyms after Holmgren et al. 1990). References without acronyms are from the literature. Asterisks indicate collections with fixed specimens.

Section Dipharus	**Reference**
A. cymbifera	Hoehne (1942)
A. esperanzae	Eskuche et al. 5233 (GH); West 8419 (MO)
A. galeata	Melo & Franca 623 (FCAB)
A. gerhtii	Hoehne (1942)
A. gibertii	Morel 1065 (MO); Nee 45401 (NY). Hoehne (1942)
A. hians	Hoehne (1942)
A. labiata	González 3441 (NY)*
A. lingulata	Cerón 232 (MO)
A. loefgrenii	Hoehne (1942)
A. pohliana	Pohl 1835 (F); Masters (1875a); Hoehne (1942).
A. ringens	González 3575 (NY)*
A. warmingii	Macedo 98 (NY)
Subsection Pentandrae	**Reference**
A. bracteosa	Pringle 3714 (GH)
A. brevipes	Pringle 8458 (BM)
A. buntingii	Pfeifer (1970)
A. cardiantha	Pfeifer (1970)
A. conversiae	Converse s.n. (UC)
A. cordata	Pfeifer (1970)
A. coryi	González 3612 (NY)*; Chiang & al. 5718 TEX)
A. duranguensis	Pfeifer (1970)
A. erecta	González 3593 (NY)*;
A. flexuosa	McVaugh 24502 (CONN)
A. foetida	Soto & Ramos 1150 (MEXU)
A. islandica	Barkelew 169 (GH)
A. karwinskii	McVaugh 23312 (CONN)
A. micrantha	González 3605 (NY)*; Palmer 226 (GH)
A. monticola	Brandegee s.n. (UC)
A. mutabilis	Pfeifer (1970)
A. nana	Fryxell 3824 (NY)
A. nelsonii	Pfeifer (1970)
A. oaxacana	Conzatti 1838 (F)
A. palmeri	Palmer 180 (GH)
A. pentandra	González 3603 (NY)*; Pringle 13804 (TEX)
A. porphyrophylla	Palmer 174 (GH)
A. pringlei	Pringle 6383 (GH, P)
A. secunda	Mueller 1014 (P)
A. sinaloae	H.S. Gentry 1872 (GH)
A. socorroensis	J.T. Howell 8404 (F)
A. tequilana	Palmer 413 (GH)
A. teretiflora	Conzatti 2223 (F)
A. tresmariae	McVaugh 25459 (CONN)
A. variifolia	Palmer 151 (GH)
A. versabilifolia	Purpus 2717 (GH)
A. watsonii	Palmer 187 (K)
A. wrightii	Pringle 9 (P)

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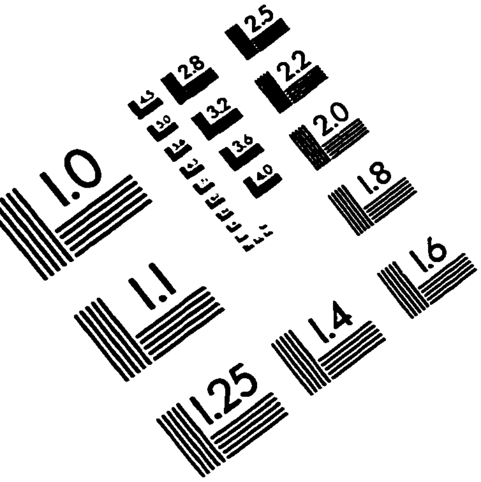

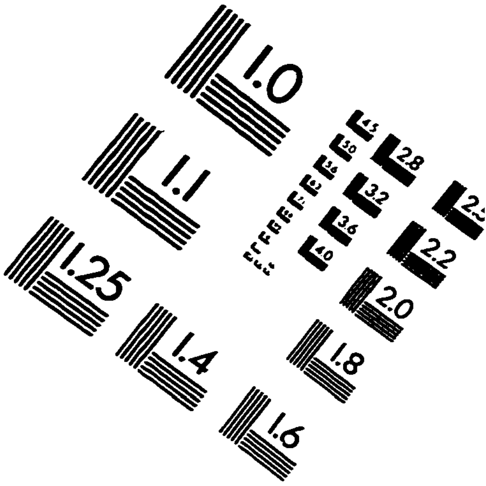

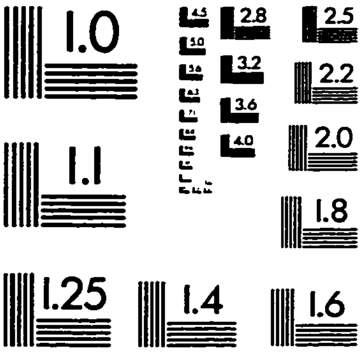

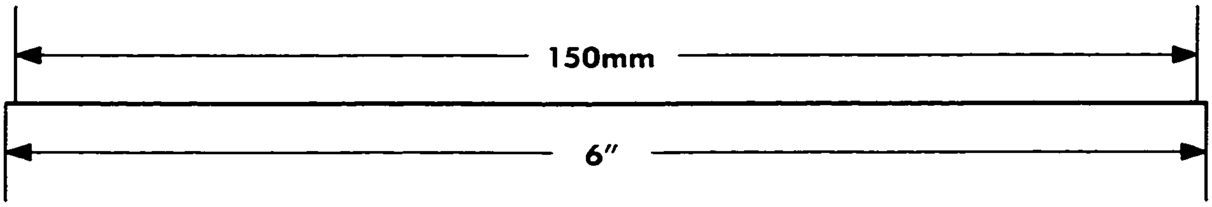

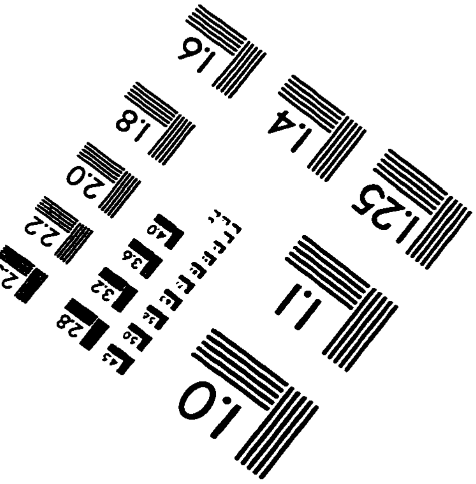

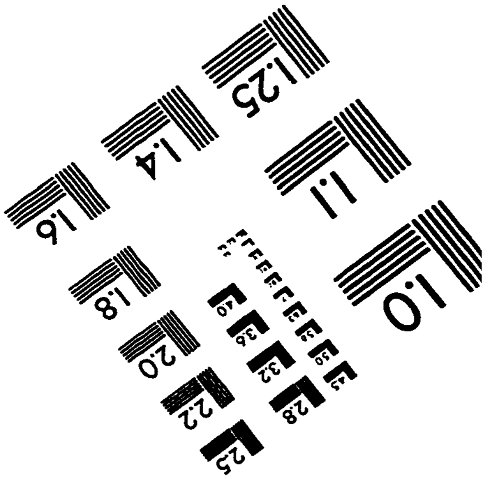

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