

A PHYLOGENETIC ANALYSIS OF THE SUBFAMILY ARISTOLOCHIOIDEAE (ARISTOLOCHIACEAE)

by

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Abstract

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A cladistic analysis of the subfamily Aristolochioideae (Aristolochiaceae) based on morphological characters is presented. The analysis includes 65 taxa within the ingroup, which represent all the tribes, subtribes, genera, and infrageneric taxa formally described within the subfamily Aristolochioideae *sensu* Schmidt. 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 recognized within *Aristolochia* (*Siphisia* and *Pararistolochia*) are shown to be monophyletic. The third subgenus (*Aristolochia*) is paraphyletic. Most taxa at lower rank levels (sections, subsections, series, and subseries) are shown to be either polyphyletic or paraphyletic. The characters traditionally used for the recognition of these taxa are evaluated and new characters are introduced. Finally, a revised system of classification of the Aristolochioideae based on monophyletic groupings and consisting of two tribes, two subtribes, and five genera is proposed here.

Key words: *Aristolochia*; Aristolochiaceae; *Euglypha*; *Holostylis*; *Pararistolochia*; *Siphisia*.

Resumen

Se presenta un análisis cladístico de la subfamilia Aristolochiaceae (Aristolochiaceae), basado en caracteres morfológicos. El grupo de estudio (grupo propio) incluye 65 taxones, los cuales representan todas las tribus, subtribus, géneros y taxones infragenéricos descritos formalmente dentro de la subfamilia Aristolochioideae *sensu* Schmidt. El análisis muestra que *Aristolochia* s.l. es parafilético y que *Euglypha* y *Holostylis* no son linajes diferentes de *Aristolochia*. Dos de los tres subgéneros reconocidos dentro de *Aristolochia* (*Siphisia* y *Pararistolochia*) son monofiléticos. El tercer subgénero (*Aristolochia*) es parafilético. Muchos taxones a nivel de sección, subsección, serie y subserie son poli- o parafiléticos. Los caracteres tradicionalmente usados en la circunscripción de estos taxones son evaluados y nuevos caracteres son empleados. Finalmente y con base en este análisis, se presenta la clasificación revisada de la subfamilia, la cual consta de dos tribus, dos subtribus y cinco géneros.

Palabras clave: *Aristolochia*; Aristolochiaceae; *Euglypha*; *Holostylis*; *Pararistolochia*; *Siphisia*.

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Introduction

The Aristolochiaceae consist of ca. 500 species, most of which inhabit the tropics and subtropics of both hemispheres. The sparse fossil records of the family date back to the early Tertiary and perhaps the late Cretaceous of India (**Kulkarni & Patil**, 1977), Europe (**Kolakovski**, 1957, 1964), and North America (**MacGinitie**, 1953, 1969, 1974). Although generic circumscription within the family is currently in dispute, most authors recognize six genera in two subfamilies. Asaroideae, with an actinomorphic perianth, consists of three genera and about 130 herbaceous species: *Asarum*, with ca. 100 species, distributed in temperate areas of North America, Europe, and Asia; the monotypic *Saruma*, endemic from central China; and *Thottea* with ca. 30 species restricted to tropical Asia. Aristolochioideae, with a monosymmetric perianth, consists of three genera: *Aristolochia*, with ca. 400 species, principally tropical, but with some species found in subtropical and temperate areas of both hemispheres; and the monotypic *Euglypha* and *Holostylis*, both endemic to South America.

The most consistent synapomorphies of the Aristolochiaceae are in the seed coat. The 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 fibers (**Kratzer**, 1918; **Periasamy**, 1966; **Corner**, 1976; **Huber**, 1985, 1993; **Mohana Rao**, 1989). In addition, 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; oil cells; perianth essentially trimerous; androecium and gynoecium essentially hexamerous; and pollen in monosulcate or inaperturate monads.

The taxonomic position of the Aristolochiaceae is controversial. There are three competing hypotheses about their closest relatives: (1) Members of the order Magnoliales (**Cronquist**, 1981; **Dahlgren**, 1983; **Leins & Erbar**, 1995; **Takhtajan**, 1996), based mainly on the presence of P-type sieve-element plastids (**Behnke**, 1988, 1991), ethereal oil cells, aporphine alkaloids, and several carpels that are apocarpous and pluriovulate. Additional embryological (see **Cocucci**, 1983), karyological (**Morawetz**, 1985), and ultrastructural (**Hennig et al.**, 1994) evidence has been presented in support of this concept. (2) The Rafflesiales (**Brown**, 1821; **Bartling**, 1830; **Solereider**, 1889b; **Delpino**, 1893; **Baldacci**, 1894; **Hutchinson**, 1969; **Endress**, 1990,

1994; **Kubitzki**, 1993), based on the similarities in floral structure, particularly the presence of a simple, fleshy, sapromyophilous perianth, with connate portions and a ring-like structure at the entrance, the extrorse anthers, the fusion of stamens and styles into a gynostemium, the ring-like, uninterrupted stigmas, and the inferior, pluriovulate ovary. (3) The so-called paleoherbs (**Donoghue & Doyle**, 1989; **Loconte & Stevenson**, 1991; **Tucker & Douglas**, 1996; **Nandi et al.**, 1998) from which two sister groups have been proposed for the Aristolochiaceae, the piperalean Lactoridaceae and the monocots. The relationship between Aristolochiaceae and Lactoridaceae, anticipated by **Dahlgren & Bremer** (1985), is supported by wood anatomy (**Carlquist**, 1993), and molecular data (**Qiu et al.**, 1999; **Soltis et al.**, 1997), although these families strongly differ in morphological, embryological, karyological, and palynological characters (**Lammers et al.**, 1986; **Loconte & Stevenson**, 1991; **Tobe et al.**, 1993; **Tucker & Douglas**, 1996). On the other hand, the sister-group relationship between Aristolochiaceae and monocots, proposed by **Stevenson & Loconte** (1995), among others, is supported by the presence of adaxial prophylls, trimerous flowers, monosulcate or inaperturate pollen, and sieve-element plastids of the specific type PIIc. The latter relationship is supported by 18S ribosomal DNA sequences (**Bharathan & Zimmer**, 1995). Since Jussieu's (1789) placement of the Aristolochiaceae as the closest member to the monocots, this relationship has been repeatedly emphasized over time (**Blume**, 1827; **Bartling**, 1830; **Lindley**, 1853; **Suessenguth**, 1921; **Huber**, 1977, 1985; **Dahlgren & Clifford**, 1982; **Leins & Erbar**, 1985; **Behnke**, 1988, 1991; **Erbar & Leins**, 1994).

Systematics of the Aristolochiaceae. **Adanson** (1763) proposed the placement of *Aristolochia* close to *Asarum*, for the first time. **Jussieu** (1789) established the Aristolochiaceae with the genera *Aristolochia*, *Asarum* and *Cytinus*. **Brown** (1821) added the genus *Thottea* and questioned the inclusion of *Cytinus* in the family. The latter genus was transferred to the Rafflesiaceae by **Lindley** (1831), who at the same time, assigned *Trichopus* to the Aristolochiaceae, a genus that was later placed into the Dioscoreaceae by **Klotzsch** (1859). By the middle of the 19th century, the core of the family (i. e. *Aristolochia*, *Asarum*, *Thottea*, and some of their segregates) was established. Since then, three more monotypic genera, *Holostylis*, *Saruma*, and *Euglypha* have been added to the family.

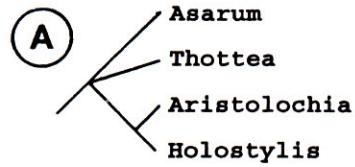
Eight systems of classification, based primarily on floral and fruit morphology, have been proposed at the infrafamilial level: (1) **Klotzsch** (1859) divided the fam-

ily into two groups (Table 1): the Cleistostigmata (*Asarum*, *Thottea* and some of their segregates), with free anthers, a solid style, and discoid or radiate stigmas which are closed at the middle; and the Aristolochieae (*Aristolochia* and

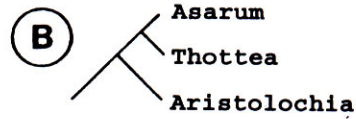
some of its segregates), with anthers fused to the hollow styles and stigmas. (2) **Duchartre** (1864) divided the family into three groups (Fig. 1A; Table 1), the Asareae (*Asarum*), the Bragantieae (*Thottea*), and the Aristo-

Table 1. Comparison of five different classification systems of the Aristolochiaceae

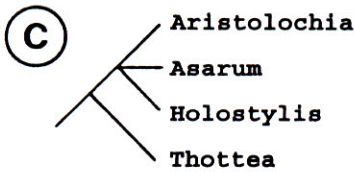
Authority	Subfamily (or equivalent)	Tribe (or equivalent)	Subtribe	Genus	
Klotzsch (1859)	Cleistostigmata	Asarineae		<i>Asarum</i> <i>Heterotropa</i>	
		Bragantieae		<i>Bragantia</i> <i>Thottea</i>	
		Cyclodiscineae		<i>Cyclodiscus</i>	
	Aristolochieae			<i>Aristolochia</i> <i>Endodeca</i> <i>Einomeia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



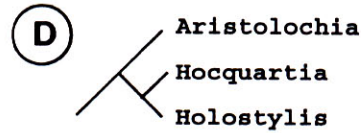
DUCHARTRE (1864)



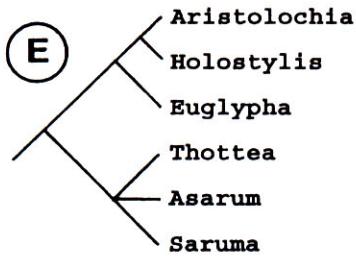
KLOTZSCH (1859)



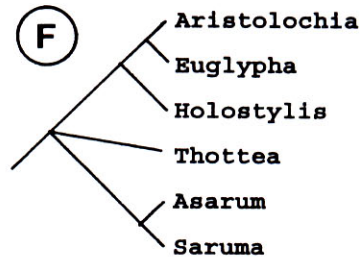
BALDACCI (1894)



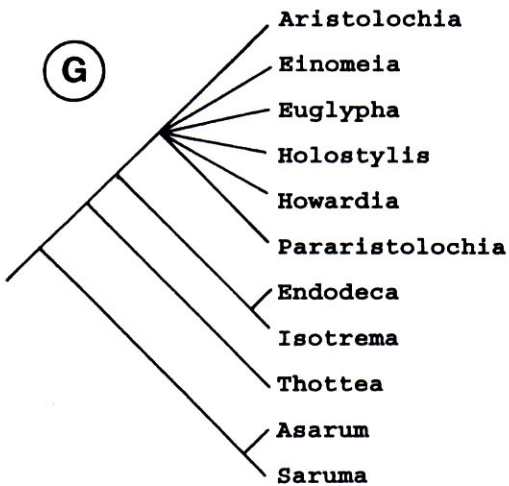
VAN TIEGHEM (1900)



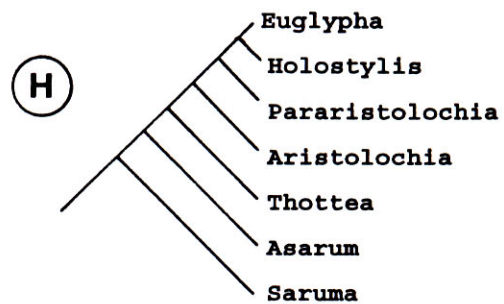
SCHMIDT (1935)



GREGORY (1956)



HUBER (1985, 1993)



WEINTRAUB (1995)

1.

Figure 1. A-G. Implicit generic relationships in seven different systems of classification of the Aristolochiaceae. H. Published cladogram of the Aristolochiaceae by Weintraub (1995), redrawn.

lochieae (*Aristolochia* and *Holostylis*). This system was followed by **Solereider** (1889b), and **Gregory** (1956; Fig. 1F). (3) **Baldacci** (1894) proposed two groups, one consisting of *Thottea* and the other consisting of *Aristolochia*, *Asarum* and *Holostylis* (Fig. 1C; Table 1). The latter group was proposed because the shape of the perianth of *Holostylis* seems to be intermediate between that of *Asarum* and *Aristolochia*. (4) **Van Tieghem** (1900) proposed a close relationship between *Hocquartia* (an *Aristolochia* segregate) and *Holostylis* (Fig. 1D), implicitly placing into question the monophyly of *Aristolochia*. (5) **Schmidt** (1935) formally proposed the subfamilies Asaroideae for the members with actinomorphic flowers (*Asarum*, *Saruma*, and *Thottea*), and Aristolochioideae for the members with a monosymmetric perianth (*Aristolochia*, *Euglypha*, and *Holostylis*). This system (Fig. 1E; Table 1) has been adopted by many authors (e.g., **Hoehne**, 1942; **Cheng & Yang**, 1988; **Hwang**, 1988; **Ma**, 1990). (6) **Nakai** (1936) placed *Aristolochia*, *Thottea*, and their segregates along with *Euglypha* and *Holostylis* in the Aristolochiaceae (Table 1), and raised *Asarum* and *Saruma* to the family level, the Asaraceae and the Sarumataceae. (7) **Huber** (1985, 1993) recognized the two subfamilies proposed by **Schmidt** (1935) but transferred *Thottea* to the Aristolochioideae (Fig. 1G; Table 1), because it shares with *Aristolochia*, *Euglypha*, and *Holostylis* the presence of hooked hairs, epigynous flowers, a constriction between the perianth and the ovary, a perianth shedding after anthesis, stamens frequently 6, and fruits usually dehiscent. (8) **Weintraub** (1995) implicitly called into question the monophyly of *Aristolochia* in proposing

Euglypha and *Holostylis* as sister groups, forming a crown clade that is merged within *Aristolochia* plus *Pararistolochia* (Fig. 1H).

Subfamily Aristolochioideae. This subfamily (equivalent to the tribe Aristolochiineae sensu **Huber**, 1985, 1993), as proposed by **Schmidt** (1935), is supported by the following synapomorphies: monosymmetric, tubular perianth differentiated into utricle, tube and limb; and six uniseriate stamens, which are fused with the styles/stigmas forming a gynostemium (**González**, 1997). Within Aristolochioideae, the large and complex genus *Aristolochia* stands in contrast with the monotypic *Euglypha* and *Holostylis*. The latter two genera have been recognized by many authors (**Masters**, 1875; **Solereider**, 1889b; **Schmidt**, 1935; **Hoehne**, 1942; **Wyatt**, 1955; **Ahumada**, 1967; **Huber**, 1993), but its taxonomic placement is controversial (Fig. 1; Table 1).

The genus *Aristolochia*. Despite the fact that many authors treat *Aristolochia* in its broad sense (**Duchartre**, 1854a, 1864; **Hoehne**, 1942; **Davis & Khan**, 1961; **Pfeifer**, 1966, 1970; **Hou**, 1984; **Nardi**, 1984, 1991; **Phuphathanaphong**, 1987; **Ma**, 1989), several generic segregates have been proposed (Tables 1-3; see also Figs. 1, 11), on the basis of differences in the morphology of the perianth and the gynostemium. Most of the segregate genera correspond to infrageneric taxa proposed by authors such as **Duchartre** (1854a, 1864), and **Schmidt** (1935)(Table 3). Recently, **Huber** (1985, 1993) reestablished some of the segregates made by **Rafinesque** (1836), **Klotzsch** (1859), and **Hutchinson & Dalziel** (1927) by

Table 2. Segregate genera from *Aristolochia* sensu lato

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

Table 3. Systems of classification of *Aristolochia* by *Duchartre* (1854a, 1864), *Bentham & Hooker* (1880), and *Schmidt* (1935), and the corresponding segregates (bold capital letters) by *Klotzsch* (1859)

Duchartre (1854a, 1864)	Klotzsch (1859)	Bentham & Hooker (1880)	Schmidt (1935)
Aristolochia Group I Sect. <i>Asterolytes</i> Sect. <i>Siphisia</i> Sect. <i>Hexodon</i>	ENDODECA SIPHISIA	Aristolochia Sect. <i>Siphisia</i>	Aristolochia Subgen. <i>Siphisia</i> Sect. <i>Asterolytes</i> Sect. <i>Siphisia</i> Sect. <i>Hexodon</i>
Group II Sect. <i>Gymnolobus</i> Subsect. <i>Pentandrae</i> Subsect. <i>Hexandrae</i> Ser. <i>Unilabiatae</i> Ser. <i>Bilabiatae</i> Ser. <i>Peltiflorae</i>	EINOMEIA HOWARDIA	Sect. <i>Gymnolobus</i>	Subgen. <i>Orthoaristolochia</i> Sect. <i>Gymnolobus</i> Subsect. <i>Pentandrae</i> Subsect. <i>Hexandrae</i> Ser. <i>Unilabiatae</i> Ser. <i>Ecaudata</i> Ser. <i>Alatae</i> Ser. <i>Bilabiatae</i> Ser. <i>Peltiflorae</i>
Sect. <i>Diplolobus</i> Subsect. "Calyx sessile" Subsect. "Calyx stipitate"	ARISTOLOCHIA <i>Euaristolochia</i> <i>Podanthemum</i>	Sect. <i>Diplolobus</i>	Sect. <i>Diplolobus</i> Subsect. <i>Euaristolochia</i> Subsect. <i>Podanthemum</i>
Sect. <i>Acerostylis</i>		Sect. <i>Polyanthera</i>	Subgen. <i>Pararistolochia</i>

splitting *Aristolochia* into six genera (Tables 1, 2) based on characters related to the leaf anatomy, gynostemium morphology, inner surface of the flower, fruit and seed morphology, and to some extent, karyology. Huber's scheme recognizes two subtribes (Table 1): 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) neither provides clear evidence for the recognition of relationships within the segregates nor unique features for them. 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 (Fig. 1G).

Schmidt (1935) proposed three subgenera of *Aristolochia* s. l., based on the perianth morphology and the number of gynostemium lobes: Subgenus *Siphisia*, with a 3-lobed perianth and 3-lobed gynostemium, which is essentially **Duchartre's** (1854a, 1864) Group I; subgenus *Pararistolochia*, with a 3-lobed perianth, and 6-12-lobed gynostemium, which is based on the genus *Pararistolochia* proposed by **Hutchinson & Dalziel** (1927); and subgenus *Orthoaristolochia*, with a 1-2-lobed

perianth and 5-6-lobed gynostemium, which equals Group II of **Duchartre** (1854a, 1864).

Most of the infrageneric taxa were first described by **Duchartre** (1854a; Tables 3, 4). **Klotzsch** (1859) independently proposed a classification, which is essentially the same as that proposed by **Duchartre** (1854a), but raised several groups as distinct genera (Table 3). **Duchartre** (1864), rather than use **Klotzsch's** segregates, kept his previous system intact. **Duchartre's** system has been the most widely used system since then, having undergone no substantial changes (e.g. in **Masters**, 1875; **Bentham & Hooker**, 1880; **Schmidt**, 1935; **Hoehne**, 1942; **Wyatt**, 1955; **Ahumada**, 1967; **Ma**, 1989). The characters that define sections, subsections, series and subseries are based on the morphology of the perianth and the gynostemium.

Hoehne (1942) used the presence or absence of the so-called pseudostipules (Fig. 2A, E; see also **Duchartre**, 1854b; **González**, 1990) as the primary criterion of classification (Table 4), and recommended abandoning **Duchartre's** scheme because it "não representa um sistema de afinidades baseado nos órgãos 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 has been over-emphasized in the recognition of infrageneric taxa, resulting in

Table 4. 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
Masters (1875)	Pararistolochia	Diplolobus	Pentandrae	Alatae Bilabiatae Peltiflorae unnamed group	
		Pararistolochioides Pararistolochia Aristolochioides			
		Peltiflorae	'Flores racemose' 'Flores solitarii vel gemini'		
Hoehne (1942)		Unilabiatae	Caudatae Ecaudatae		
		Bilabiatae	'Perianthii labia subequilonga' Perianthii labium superior longissimum'		
			Pseudostipulosae	Peltiflorae	Macranthae Mediocriflorae Parviflorae
				Bilabiatae	Parviflorae Macranthae Caudatae Alatae
				Caudatae	Trilobatae Integrifolia
			Exstipulosae	Volubilis	Subpeltiflorae Euunilabiatae Hiantiflorae Alatilobae Ciliatilobae
				Fruticulosae	

Table 5. 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 (1/1)
<i>Saruma henryi</i> Oliv.
Tribe Asareae Duchartre (2/100)
<i>Asarum caudatum</i> Lindl.; <i>A. virginicum</i> L.
Tribe Bragantieae Schmidt (3/30)
<i>Thottea corymbosa</i> (Griff.) Ding Hou; <i>T. grandiflora</i> Rottb., <i>T. siliquosa</i> (Lamk.) Ding Hou
Subfamily Aristolochioideae Schmidt
Tribe Aristolochieae Schmidt
<i>Holostylis reniformis</i> Duchartre (1/1)
<i>Aristolochia</i> L.
Subgenus Siphisia Schmidt
Section Asterolytes Duchartre (2/2)
<i>A. reticulata</i> Nutt., <i>A. serpentaria</i> L.
Section Siphisia (Raf.) Duchartre (13/40)
<i>A. californica</i> Torr., <i>A. cucurbitifolia</i> Hayata, <i>A. fulvicoma</i> Merr. & Chun, <i>A. impudica</i> Ortega, <i>A. macrophylla</i> Lamk., <i>A. malacophylla</i> Standl., <i>A. manshuriensis</i> Komarov, <i>A. panamensis</i> Standl., <i>A. paraclata</i> Pfeifer, <i>A. punjabensis</i> Craib, <i>A. stevensii</i> K. Barringer, <i>A. tomentosa</i> Sims, <i>A. tricaudata</i> Lem.
Section Hexodon Duchartre (1/2)
<i>A. kaempferi</i> Willd.
Section Nepenthesia Klotzsch (1/3)
<i>A. hainanensis</i> Merr.
Subgenus Orthoaristolochia Schmidt
Section Gymnolobus
Subsection Pentandrae Duchartre (33/37)
<i>A. bracteosa</i> Duchartre, <i>A. brevipes</i> Bentham, <i>A. buntingii</i> Pfeifer, <i>A. cardiantha</i> Pfeifer, <i>A. conversiae</i> Pfeifer, <i>A. cordata</i> Eastwood, <i>A. coryi</i> Johnst., <i>A. duranguensis</i> Pfeifer, <i>A. erecta</i> L., <i>A. flexuosa</i> Duchartre, <i>A. foetida</i> H.B.K., <i>A. islandica</i> Pfeifer, <i>A. karwinski</i> Duchartre, <i>A. micrantha</i> Duchartre, <i>A. monticola</i> Brandg., <i>A. mutabilis</i> Pfeifer, <i>A. nana</i> Watson, <i>A. nelsonii</i> Eastwood, <i>A. oaxacana</i> Eastwood, <i>A. palmeri</i> Watson, <i>A. pentandra</i> Jacq., <i>A. porphyrophylla</i> Pfeifer, <i>A. pringlei</i> Rose, <i>A. secunda</i> Pfeifer, <i>A. sinaloae</i> Brandg., <i>A. socorroensis</i> Pfeifer, <i>A. tequilana</i> Watson, <i>A. teretiflora</i> Pfeifer, <i>A. tresmariae</i> Ferris, <i>A. varitifolia</i> Duchartre, <i>A. versabilifolia</i> Pfeifer, <i>A. watsonii</i> Wooton & Standl., <i>A. wrightii</i> Seem.
Subsection Hexandrae
Series Thysicae F. González (4/16)
<i>A. acutifolia</i> Duchartre, <i>A. maxima</i> Jacq., <i>A. melastoma</i> Manso, <i>A. trianae</i> Duchartre
Series Hexandrae
Subseries Anthocaulicae F. González (3/14)
<i>A. cordiflora</i> Mutis ex H.B.K., <i>A. iquitensis</i> Schmidt, <i>A. leuconeura</i> Linden
Subseries Hexandrae (28/ca. 100)
<i>A. arborea</i> Lindl., <i>A. burelae</i> Herz., <i>A. cymbifera</i> Mart. & Zucc., <i>A. deltoidea</i> H.B.K., <i>A. didyma</i> S. Moore, <i>A. esperanzae</i> O. Kuntze, <i>A. galeata</i> Mart. & Zucc., <i>A. gehrtii</i> Hoehne, <i>A. gibertii</i> J.D. Hook., <i>A. grandiflora</i> Sw., <i>A. hians</i> Willd., <i>A. inflata</i> H.B.K., <i>A. labiata</i> Willd., <i>A. lindneri</i> Berg., <i>A. lingulata</i> Ule, <i>A. loefgrenii</i> Hoehne, <i>A. mishuyacensis</i> Schmidt, <i>A. nummularifolia</i> H.B.K., <i>A. odoratissima</i> L., <i>A. passifloraefolia</i> A. Rich., <i>A. pilosa</i> H.B.K., <i>A. pohliana</i> Duchartre, <i>A. ridicula</i> Brown, <i>A. ringens</i> Vahl, <i>A. tigrina</i> A. Rich., <i>A. trilobata</i> L., <i>A. warmingii</i> Mast., <i>A. xerophytica</i> Schultes
Section Diplolobus Duchartre (13/115)
Subsection Euaristolochia (Klotzsch) Schmidt
<i>A. clematitidis</i> L., <i>A. contorta</i> Bunge, <i>A. pistolochia</i> L., <i>A. rotunda</i> L., <i>A. tubiflora</i> Dunn.
Subsection Podanthemum (Klotzsch) Duchartre
<i>A. acuminata</i> Lamk., <i>A. bracteolata</i> Lamk., <i>A. debilis</i> Sieb. et Zucc., <i>A. foveolata</i> Merrill, <i>A. indica</i> L., <i>A. petersiana</i> Kl., <i>A. philippinensis</i> Warb., <i>A. thozetii</i> F. Muller.
Subgenus Pararistolochia (Hutch. & Dalz.) Schmidt
Section Pararistolochioides Ma (1/1)
<i>A. goldieana</i> Hook. f.
Section Pararistolochia (4/6)
<i>A. decandra</i> Hou, <i>A. macrocarpa</i> Duchartre, <i>A. promissa</i> Mast., <i>A. triactina</i> Hook. f.
Section Aristolochioides Ma (1/2)
<i>A. leonensis</i> Mast.
Unplaced Australasian taxa (2/9-22)
<i>A. deltantha</i> F. Muell., <i>A. momandul</i> K. Sch.
Tribe Euglypheae Schmidt (1/1)
<i>Euglypha rojasiana</i> Chod. & Hassl.

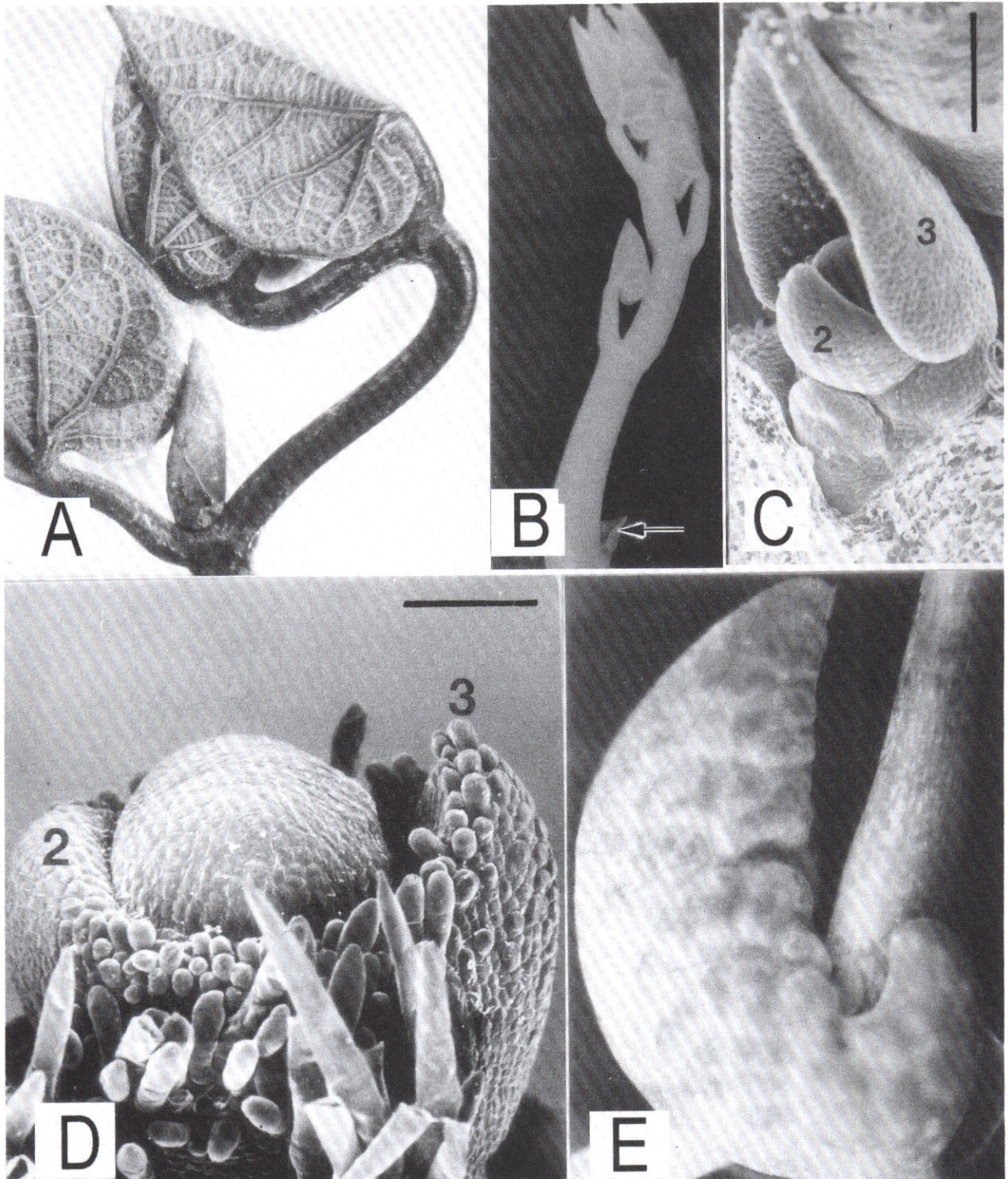


Figure 2. Some vegetative characters used in the cladistic analysis. **A.** *Aristolochia ringens* (González 3584), strongly sinuous elongating shoot (character state 2-1). **B.** *A. leuconeura* (González 3290), straight elongating shoot (2-0) showing also a non-pseudostipular prophyll (arrowed; 8-0).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

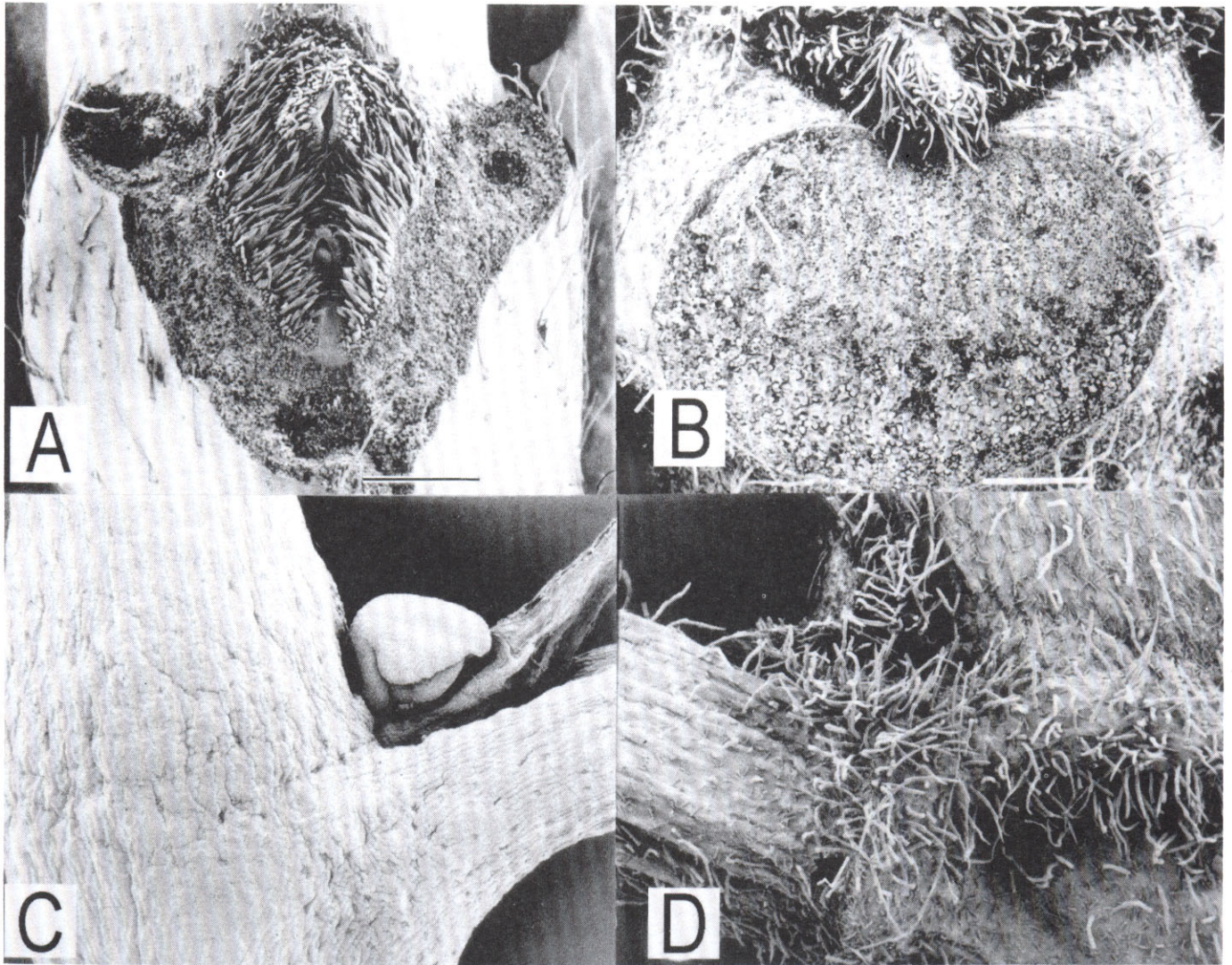


Figure 3. A, B. Petiole base, frontal view. **A.** *Aristolochia macrophylla* (González 3578), U-shaped base (character state 10-0; bar = 0.5 mm). **B.** *A. maxima* (González 3248), semicircular base (10-1; bar = 0.5 mm). C, D. Stem-petiole junction, lateral view. **C.** *A. nummularifolia* (González 1258), petiole without basal abscission zone (9-0; bar = 0.1 mm). **D.** *A. maxima* (González 3248), petiole with basal abscission zone (arrowed; 9-1; bar = 0.5 mm).

a single character taxonomy. Instead, he has found characters such as the presence of an abscission zone on the petiole (Fig. 3B, D) and the peduncle, the architecture of inflorescences, and the morphology of fruits and seeds (Fig. 4), which have been useful to reevaluate the systematics and to propose an alternative classification for the Neotropical species of *Aristolochia*.

Unfortunately, recent authors have focused on the rank at which these taxa should be recognized (see e.g. Huber, 1985, 1993; Parsons, 1996), rather than on the

relationships and/or the monophyly of the groups. This paper presents a cladistic analysis of the Aristolochioideae, based on morphological characters. The analysis was conducted to evaluate the relationships between *Aristolochia*, *Euglypha*, and *Holostylis*; to test the monophyly of the infrageneric taxa of *Aristolochia*, including the segregate genera of the latter (Tables 1-3); and to evaluate the congruence of floral characters that are traditionally used in the classification of the Aristolochioideae with other characters that appear not to have been exploited.

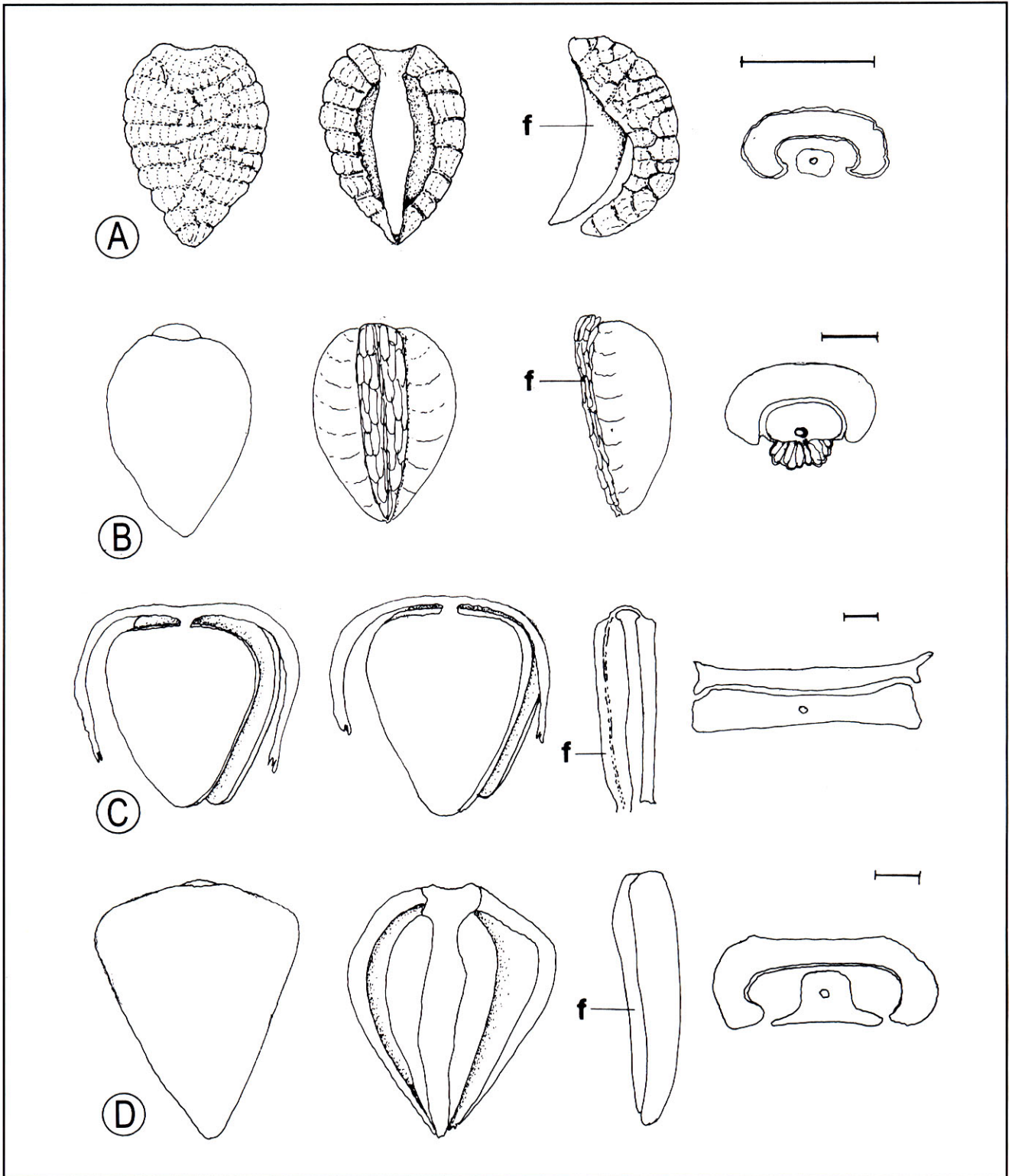


Figure 4a. Seeds in Aristolochiaceae (from left to right: abaxial side, adaxial side, lateral view, and transverse section through the middle level). **A.** *Saruma henryi* (Pruski 3748). **B.** *Asarum virginicum*. **C.** *Aristolochia macrophylla* (González 3578). **D.** *A. paracleta* (González 3417).

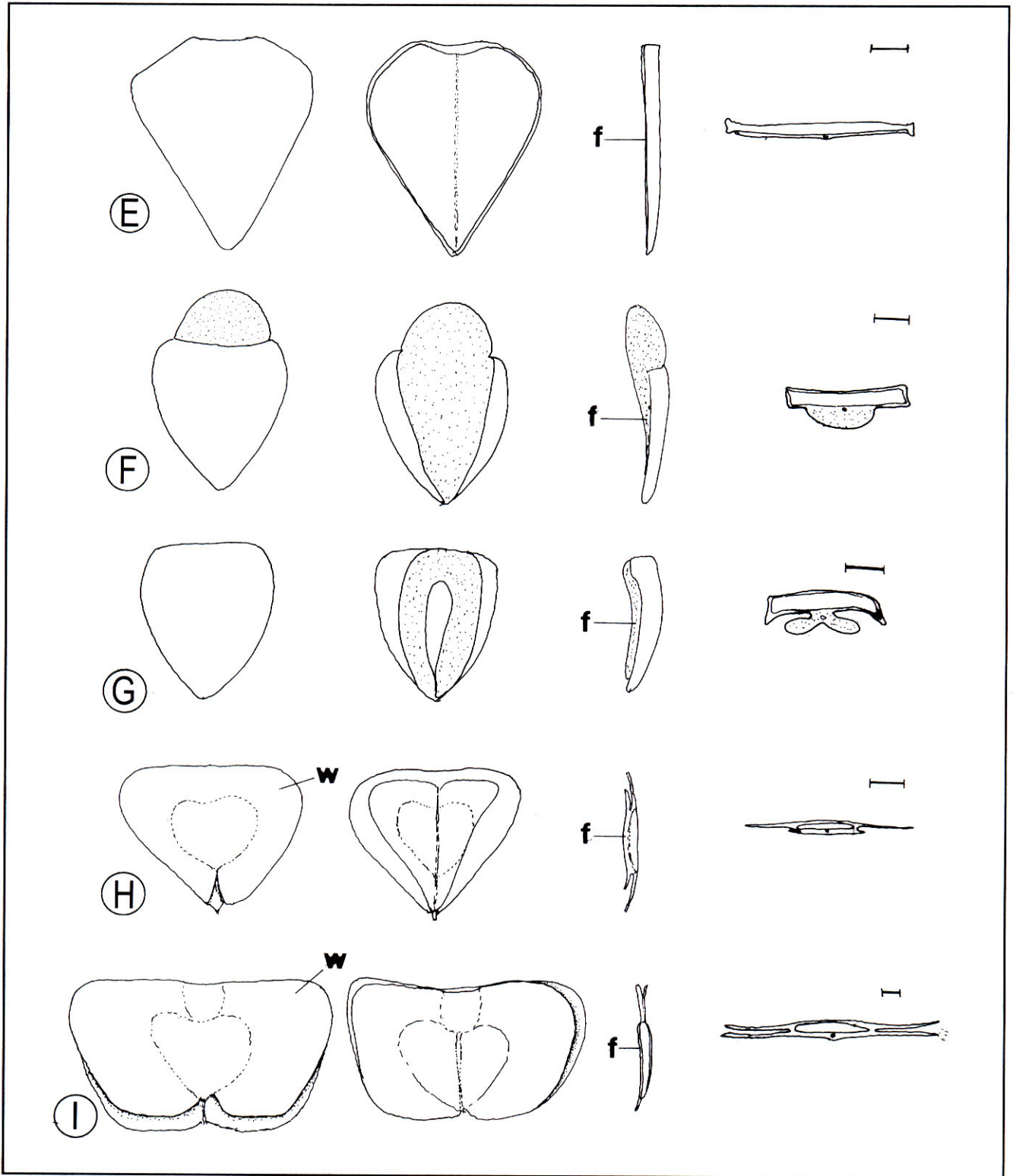


Figura 4b. E. *A. burelae* (Maruñak et al. 486). F. *A. leuconeura* (González 3290); the sticky aril is shown by the dotted area. G. *A. odoratissima* (González 3399); the sticky aril is shown by the dotted area. H. *A. contorta* (Li 10853). I. *A. maxima* (González 3568). In all, bar = 1 mm; f, funicle; w, wing.

Materials and Methods

The classification followed here for sampling essentially corresponds to that of **Schmidt** (1935), at both subfamilial (Table 1) and subgeneric (Table 3) 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 ingroup taxa include *Euglypha*, *Holostylis*, and a large sampling within *Aristolochia* (Table 5), the latter treated in its broad sense. Sampling within *Aristolochia* includes 61 species representing all subgenera, sections and subsections, and most of the series and subseries (Table 5). Most of the segregates (Table 2) described by **Dumortier** (1822), **Rafinesque** (1828, 1836), **Klotzsch** (1859), **Hutchinson & Dalziel** (1927), and **Huber** (1985, 1993) were sampled, thus including a broad range of morphological diversity and geographical distribution within *Aristolochia*. Taxa below subgeneric level essentially follow **Duchartre** (1854a, 1864; Tables 3, 4), **Hoehne** (1942; Table 4), **Ma** (1989), and **González** (1990, 1991). However, 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 which are not discrete and, therefore, are not realistically codable. In addition, the analysis includes two supraspecific taxa, subsection *Pentandrae* (**Duchartre**, 1854a, 1864) with 33 of the 37 species examined and section *Dipharus* (**Klotzsch**, 1859) with 12 of the 18 species examined (Table 5). 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 because each has characters that are unique within *Aristolochia*, as for example, five anthers and five carpels in all species of subsection *Pentandrae* (**Pfeifer**, 1970), and flowers with an adaxial and an abaxial lip in all the species of section *Dipharus* (**Duchartre**, 1854a, 1864; **Hoehne**, 1942).

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 & Stevenson** (1991) and **Kelly** (1997, 1998). Two species of *Asarum* and three of *Thottea* were included in order to cover floral morphological variation within these genera.

The majority of the morphological characters included in this analysis were taken from our own collections, herbarium and fixed specimens, and field observations. Lit-

erature has been employed only when material was unavailable for study. The matrix contained 72 characters with a total of 100 apomorphic states. A complete list of characters, character states, and source of data from the literature are given in Appendix 1. The data matrix (Appendix 2) was compiled using Winclada (**Nixon**, 2001). All multistate characters were treated as nonadditive (un-ordered). A parsimony analysis was run using NONA (**Goloboff**, 1993), with the *hold 1000*, *h/10*, *mult*1000*, *max** options. The consensus tree was obtained using the *inters* command. The resulting trees and the character distribution were examined in CLADOS (**Nixon**, 2001). Bremer support values (**Bremer**, 1988) were calculated on the consensus tree using the *bs* command in NONA.

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 1 and Fig. 1E with Fig. 5). The analysis also supports the monophyly of the Aristolochioideae and of two major lineages within this subfamily (Fig. 5). Synapomorphies of the Aristolochioideae include: perianth differentiated into utricle, tube, and limb (character 25), adaxially curved (26), 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 (22), and long anthers (46).

The First Major Clade: *Aristolochia* subgen. *Siphisia* (Figs. 5, 6): The first major clade within the Aristolochioideae conforms to the previously proposed subgenus *Siphisia*. This clade is defined by the fusion of the carpellary apices into three gynostemium lobes (character 56). Other characters that support this clade are the presence of an annulus (34) and grouped stamens (42) with the latter known outside of the subfamily only in some species of *Thottea*.

Resolution within subgenus *Siphisia* further supports two clades. The first, containing the sister species *Aristolochia reticulata* and *A. serpentaria* is defined by being herbaceous plants (character 0) with reduced subtending leaves (13), clasping bracts (15), and short inflorescence internodes (18). The second clade within *Siphisia* (Fig. 5) contains two subclades. The first subclade, with *A. tomentosa* at the base and consisting primarily of temperate species, has U-shaped petiole base (character 10; Fig. 3A). This first subclade, partially resolved, also includes *A. cucurbitifolia*, *A. kaempferi* plus

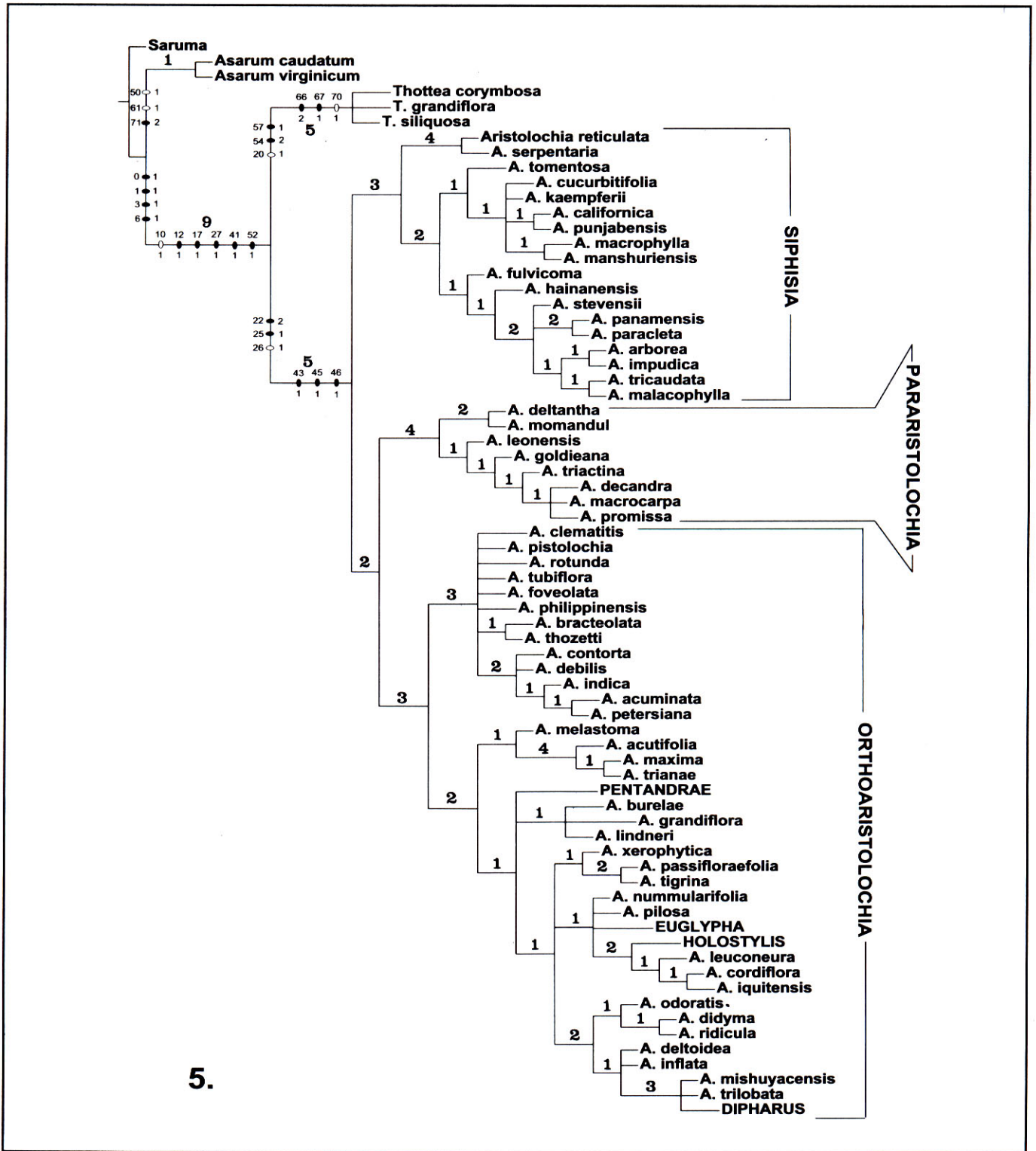


Figure 5. Consensus tree of the five most parsimonious trees obtained in the present analysis (length = 196, CI = 0.49, RI = 0.85). Character and state numbers for the ingroup are mapped on Figs. 6, 8-10, on which numbers above and below the marks indicate character number and state number, respectively. Larger numbers on the nodes correspond to the Bremer support values. For Figs. 5-10 solid black marks represent apomorphies, and white or grey marks represent homoplasies.

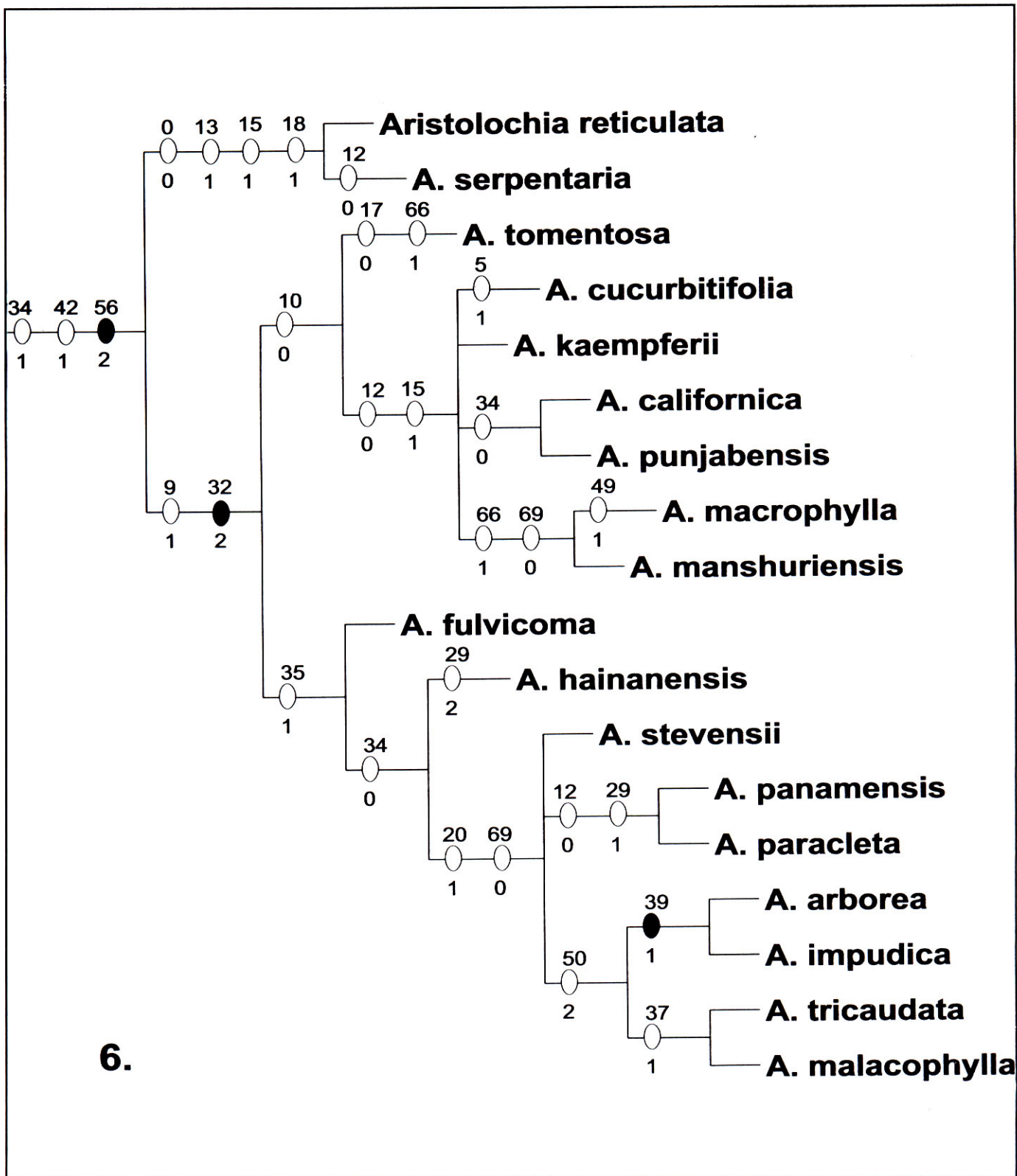


Figure 6. Clade corresponding to *Aristolochia* subgen. *Siphisia* (= *Isotrema*).

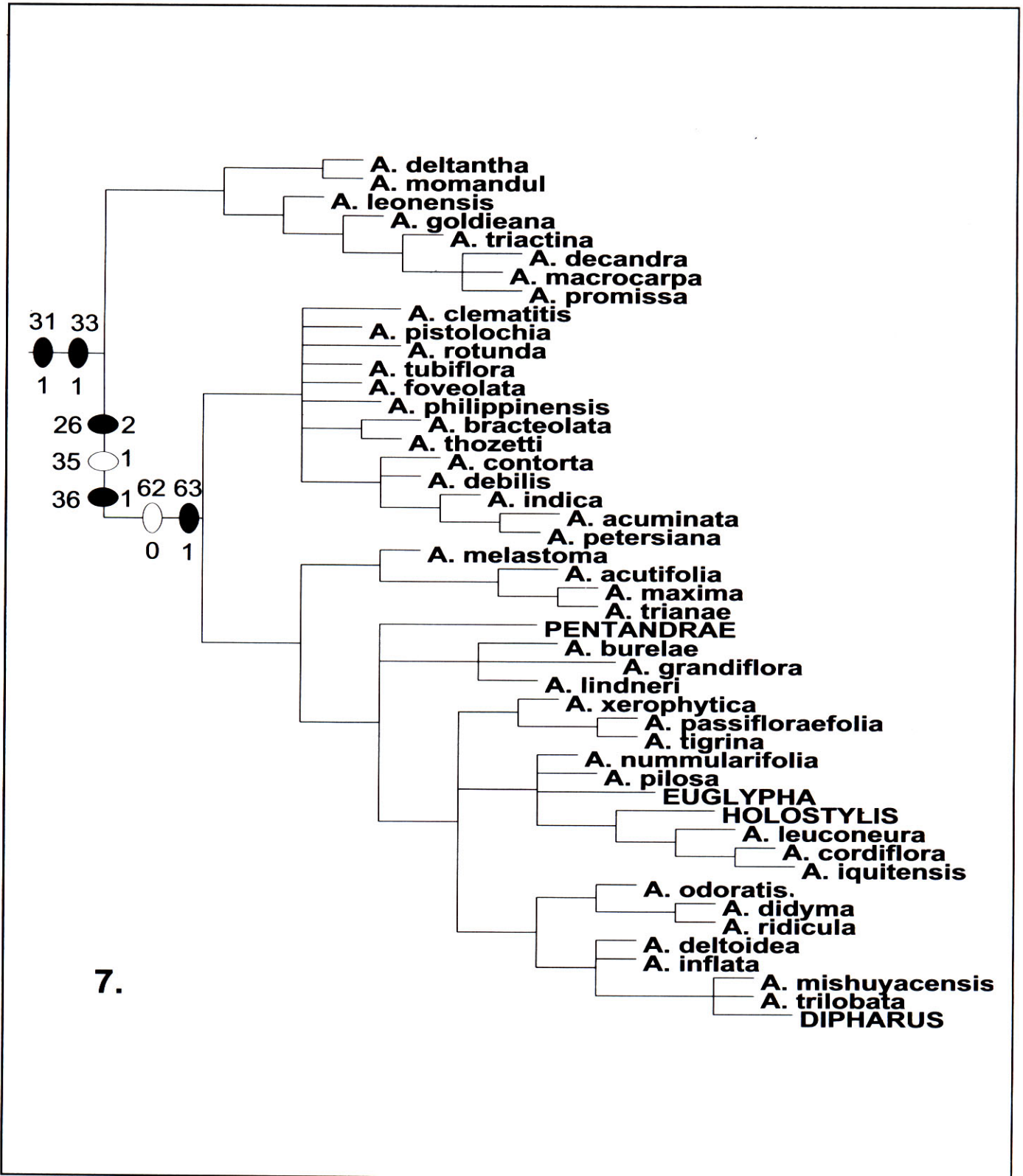


Figure 7. Clade corresponding to *Aristolochia* subgen. *Pararistolochia* + *A.* subgen. *Orthoaristolochia* + *Euglypha* + *Holostylis*.

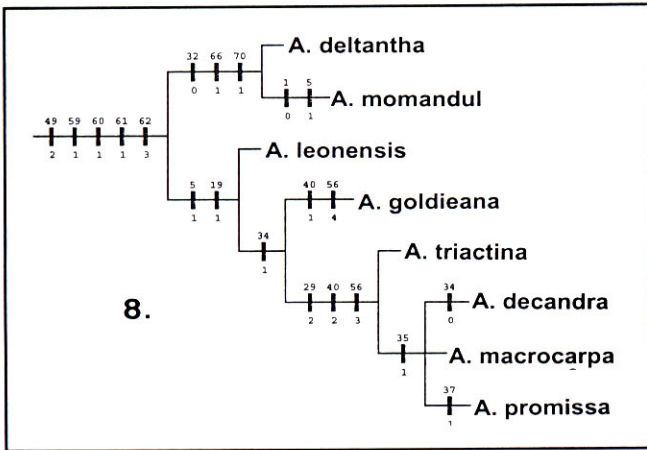


Figure 8. Clade corresponding to *Aristolochia* subgen. *Pararistolochia*.

two pairs of sister species, *A. californica* and *A. punjabensis* which lack an annulus (34) and *A. macrophylla* and *A. manshuriensis* which have flattened seeds (66) that are not attached to the funicle (character 69; Fig. 4C). The second subclade, with primarily subtropical and tropical species, is defined by the possession of a monosymmetric perianth limb (35). Within this second subclade, the first two branches are Asian species followed by a crown group 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. paraclata* both with an incomplete syrxix (29) and unflowered inflorescences (12), *A. arborea* and *A. impudica* whose flowers have a lower protrusion at the flower entrance (39), and *A. 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 supracteal warts on the pollen wall (50).

The Second Major Clade: *Aristolochia* subgen. *Pararistolochia* + *A.* subgen. *Orthoaristolochia* + *Euglypha* + *Holostylis* (Figs. 5, 7): 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 synapomorphies that link these taxa are the slightly curved tube (character 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

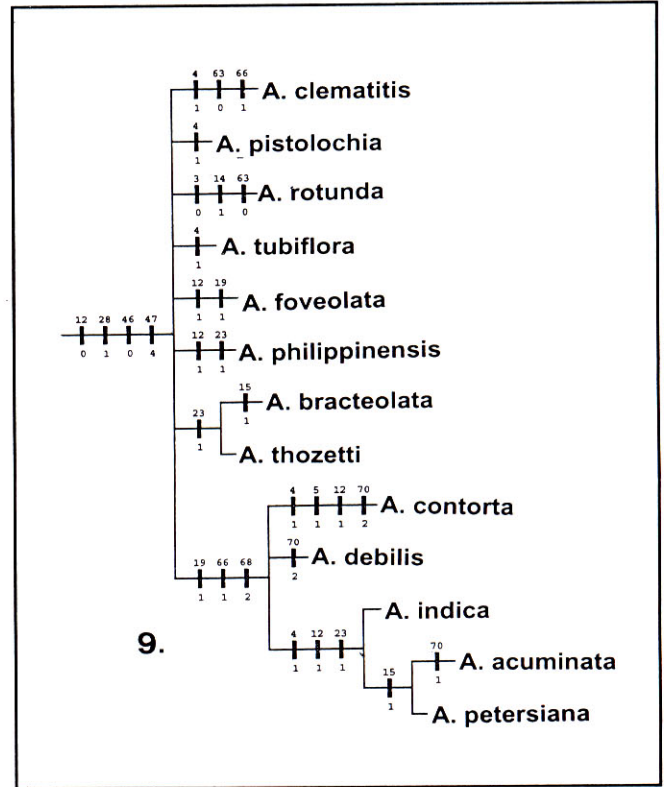


Figure 9. Clade corresponding to *Aristolochia* sect. *Diplobolus*.

(Hoehne, 1942), have conical trichomes that are extremely short.

The analysis supports the monophyly of *Pararistolochia* (Figs. 5, 7, 8). Characters that define this group include a markedly differentiated ridge on the pollen wall (character 49) and indehiscent fruits (62) with a warty surface (59), a strongly lignified pericarp (60), and a fleshy mesocarp (61). Two subclades 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 fili-form funicle (70). The second subclade includes six species (*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 (5) and flowers in partial florescences arranged spirally (19). The first branch within the latter subclade consists of *A. leonensis* which is the sister group of the crown clade of five species (*A. goldieana*, *A. triactina*, *A. decandra*, *A. macrocarpa*, and *A. promissa*) whose flowers have an annulus (34). The latter four spe-

cies share the possession of 8-10 stamens (40), 8-10 gynostemium lobes (56) and a complete syrinx (29). Three of these (*A. decandra*, *A. macrocarpa*, and *A. promissa*) have a monosymmetric perianth limb (35) and form an unresolved crownclade.

Subgenus *Orthoaristolochia* is paraphyletic because *Euglypha* and *Holostylis* are nested within it (Figs. 5, 7, 10). Characters that define this third and most complex clade are the abaxially concave perianth (character 26), the monosymmetric limb (35), the fusion of the three perianth parts into one lobe (36), and the ventricidal (62), acropetal (63) capsule. The data support two subclades within this major clade. The first corresponds to the section *Diplolobus* as described by Duchartre (1854a, 1864; Fig. 9). This clade, poorly resolved, contains *A. clematidis* and other European species plus a number of tropical Asian and Australasian species such as *A. acuminata*, *A. indica*, *A. philippinensis*, and *A. thozetti*. The second subclade, exclusively Neotropical, includes the bulk of the species of *Aristolochia* sect. *Gymnolobus* (= *Howardia*) + *Euglypha* + *Holostylis* (Figs. 5, 10).

Within the Neotropical clade mentioned above (Fig. 10), the first crown clade is formed by *Aristolochia melastoma* at the base, followed by *A. acutifolia* and the sister species *A. maxima* and *A. trianae*. All these species correspond to series *Thysicae* as described by González (1990, 1991). The second crown clade is unresolved at its base, with a trichotomy formed by: section *Pentandrae*; the unresolved *A. burelae* + *A. grandiflora* + *A. lindneri* supported by the presence of peltate bracts (character 16), an abscission zone in the base of the peduncle (20), and psilate pollen (47); and the remaining crown clade defined by non-bracteate flowers (14) which have an incomplete syrinx (29) and containing *Euglypha*, *Holostylis* and all the Neotropical species of *Aristolochia*. The latter crown clade is also unresolved with a trichotomy formed as follows: a clade with *A. xerophytica* plus the sister species *A. passifloraefolia* and *A. tigrina*, all with fimbriate flowers (38); a clade with species having 'pseudostipules' (8) and the tube oblique with respect to the utricle (30; Fig. 10); and a clade containing several species of *Aristolochia* plus *Euglypha* plus *Holostylis* and defined by concave-convex seeds (66) with a massive funicle (70). Whereas the position of *Euglypha* is not precisely defined, *Holostylis* emerges as the sister taxon of *Aristolochia* subser. *Anthocaulicae* as described by González (1990, 1991). This sister group relationship is based on the presence of flowers in lateral racemes (11) and reduced subtending leaves (13).

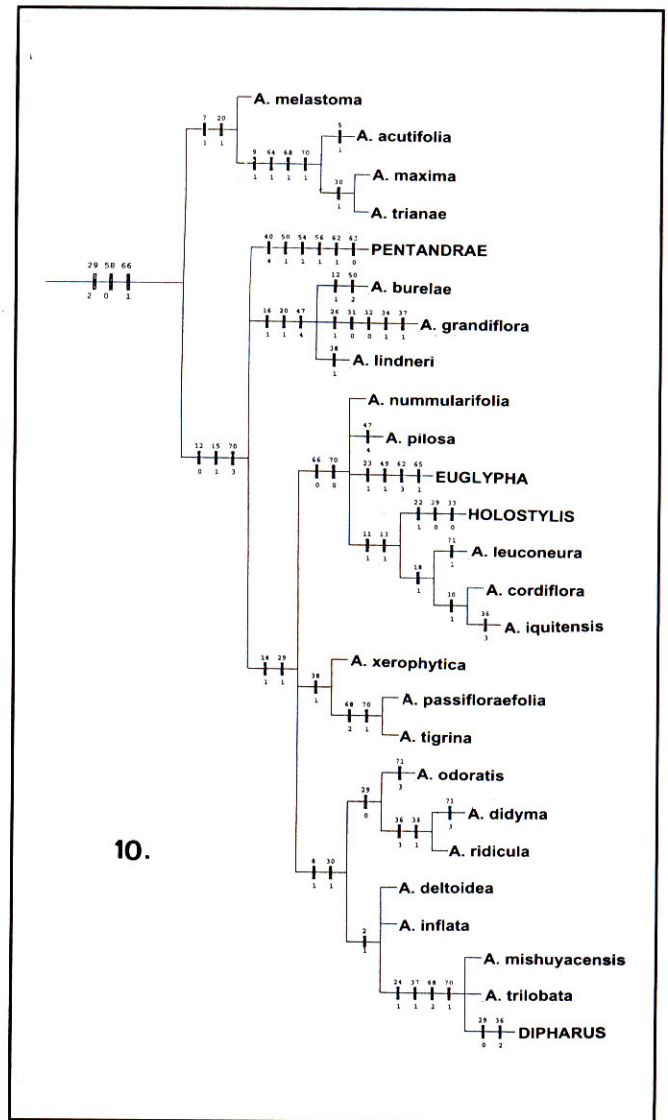


Figure 10. Clade corresponding to *Aristolochia* sect. *Gymnolobus* + *Euglypha* + *Holostylis*.

Discussion

The analysis shows that *Aristolochia* s. l. is paraphyletic because the two other genera, *Euglypha* and *Holostylis*, are nested inside one of the crown clades of *Aristolochia* (Figs. 5, 7, 10). Therefore, the recognition of the tribes Aristolochieae and Euglypheae (*sensu* Schmidt, 1935), and the genera *Euglypha* and *Holostylis* is no longer tenable. Consequently merging of these two genera within *Aristolochia* has recently been proposed (González, 1997, 1999c). Molecular data from trtT-trnF sequences have also shown that *Holostylis* is nested within *Aristolochia* (Nein-

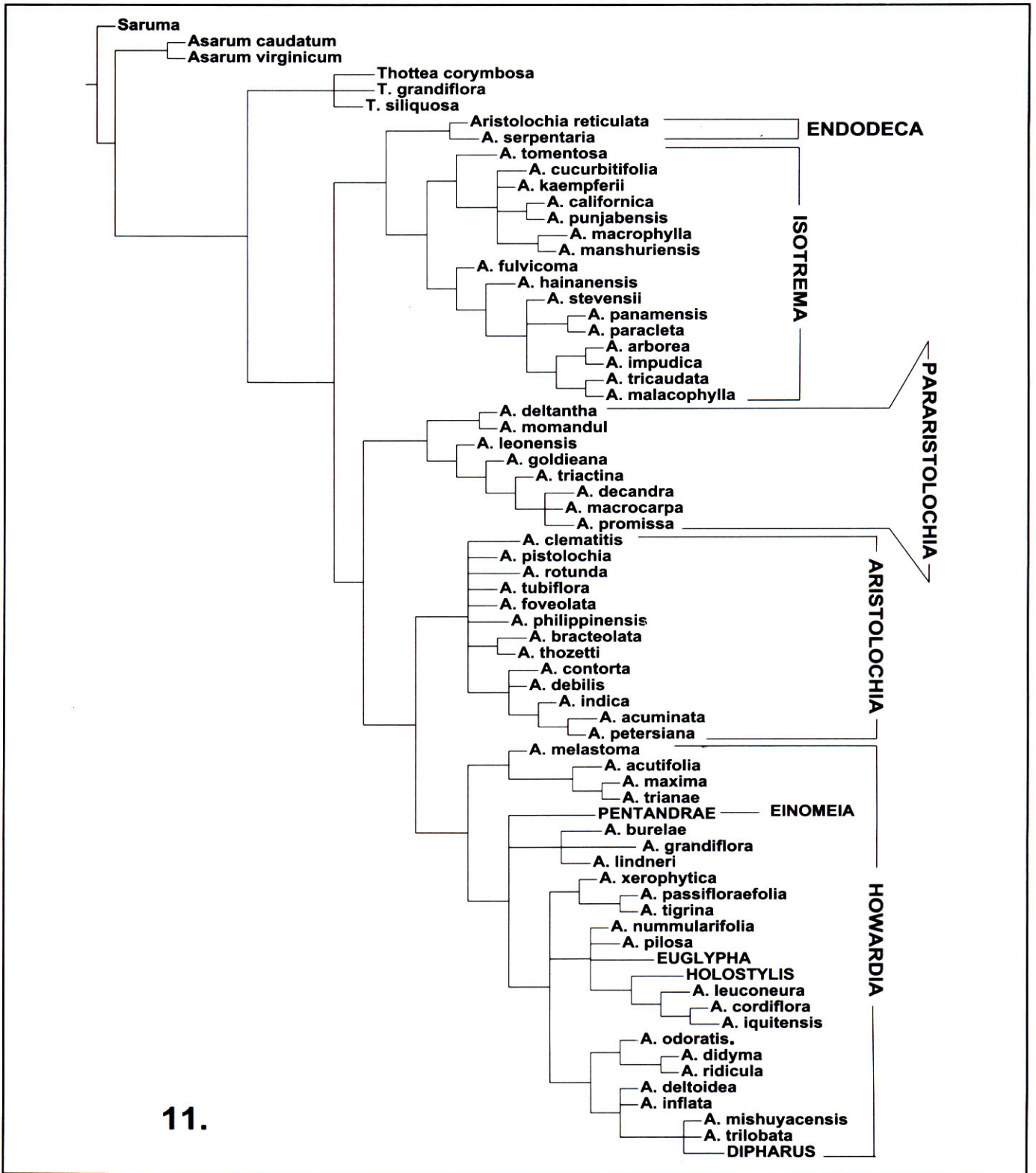


Figure 11. Clades corresponding to the *Aristolochia* segregates. Segregate *Howardia* is not monophyletic as *Einomeia*, *Euglypha* and *Holostylis* are nested within it.

huis *et al.*, 1999). The two major clades generated in the present analysis are congruent with the two subtribes described by **Huber** (1985, 1993; Table 1). 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* s. str. and the segregate genera *Endodeca*, *Siphisia* (= *Isotrema*), and *Pararistolochia* are each supported as monophyletic units (Fig. 11). The monophyly of each of the other minor Rafinesque's segregates (*Ambuya*, *Diglosselis*, *Hexaplectris*, *Pistolochia*, *Plagistra*, *Psophiza*, *Pteriphis*, and *Tropexa*; Table 2) is not subject to evaluation because their specific composition was not fully described by **Rafinesque** (1828, 1836). *Howardia* (= Sect. *Gymnolobus Duchartre*, 1854a, 1864), the largest segregate genus which was originally proposed by **Klotzsch** (1859; Tables 2, 3) and maintained by **Huber** (1984, 1993), is paraphyletic and thus does not merit recognition as a taxon (Fig. 11).

The analysis supports the monophyly of subgenus *Siphisia* (= *Isotrema*) but also requires the inclusion of *Aristolochia arborea* as a member of that subgenus (Figs. 5, 6, 11). *A. 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** (1955) and **Pfeifer** (1966) that the gynostemium of *A. arborea* has three lobes as do all the other members of this subgenus. Molecular evidence also supports the monophyly of subgenus *Siphisia* (**Murata et al.**, 1999; **Neinhuis et al.**, 1999).

Duchartre (1854a, 1864) divided his subgenus *Siphisia* into three different sections, *Asterolytes*, *Siphisia*, and *Hexodon*, that were subsequently maintained by **Wyatt** (1955). The first section consisting of *Aristolochia reticulata* and *A. serpentaria* (Figs. 5, 6), equivalent to the **Rafinesque's** (1828) segregate *Endodeca* (Table 3), is shown to be monophyletic. **Klotzsch** (1859) described *Endodeca* as having a six-lobed gynostemium. Our observations indicate, however, that the gynostemium in both species is primarily trilobed (**González & Stevenson**, 2000b). 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 suggesting that section *Siphisia* is not monophyletic unless section *Hexodon* is included. A phylogenetic analysis based on sequences of the matK gene show similar results

(**Murata et al.**, 1999). These sections were described by **Duchartre** (1854a, 1864) and based primarily on minor differences in the shape of the gynostemium at maturity as detected on herbarium specimens. However, the gynostemium in *Aristolochia* undergoes significant changes during its development (**González & Stevenson**, 2000b) and its reconstruction from herbarium specimens is not accurate.

A phylogenetic analysis based on trnT-trnF sequences is congruent with our results in that it supports a sister group relationship between *Aristolochia reticulata* and *A. serpentaria* on the one hand and the remaining species of subgenus *Siphisia* on the other (**Neinhuis et al.**, 1999). In addition, karyological evidence supports the hypothesis that subgenus *Siphisia* forms a lineage distinct from at least subgenus *Orthoaristolochia* (**Gregory**, 1956; **Sharma & Varma**, 1959; **Nardi**, 1984; **Morawetz**, 1985; **Fiorini**, 1987; **Sugawara & Murata**, 1992). Unfortunately, karyotype information is not known for species of subgenus *Pararistolochia*. All chromosome counts are $2n=28$ or 32 in species of subgenus *Siphisia* and $2n=8$, 12 , or 14 in species of subgenus *Orthoaristolochia* (one count of *A. longa*, however, has been reported as $2n=28$ by **Gregory**, 1956).

The second large clade contains two major lineages *Aristolochia* subgen. *Pararistolochia* and its sister group a complex of *Aristolochia* subgen. *Orthoaristolochia* plus *Euglypha* plus *Holostylis* (Figs. 5, 7). This relationship is in agreement with the recognition of subtribe Aristolochiinae (**Huber**, 1985, 1993; Table 1) regardless of the rank at which the former clades are recognized. However, molecular evidence based on trnT-trnF sequences suggests that subgenus *Pararistolochia* is the sister-group to subgenus *Siphisia* (**Neinhuis et al.**, 1999). Based on the regular floral limb and the high number of stamens, **Wyatt** (1955) and **Ma** (1989) proposed that subgenus *Pararistolochia* is the most primitive subgenus of *Aristolochia*. This assumption is not confirmed here because subgenus *Pararistolochia* is not basal within the Aristolochioideae (Fig. 5) based upon the morphological analysis presented here as well as on molecular evidence (**Neinhuis et al.**, 1999). The position of subgenus *Pararistolochia* is still equivocal given the disparity between the results of morphological and molecular analyses.

Pararistolochia, described as a genus by **Hutchinson & Dalziel** (1927) and subsequently maintained by **Poncy** (1978), was redelimited by **Parsons** (1996) 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) who joined the African *Aristolochia 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** (1985, 1993), and **Ma** (1992) also pointed out the similarity of some species from Malasia, Australia, and New Guinea to the African members of this taxon. The present analysis, as well as others based on molecular evidence (**Murata et al.**, 1999; **Neinhuis et al.**, 1999), indicate that *Pararistolochia* is a monophyletic lineage regardless of the rank at which it is recognized and that there is a sister group relationship between Australasian and African taxa. However, 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.

The clade *Aristolochia* subgen. *Orthoaristolochia* + *Euglypha* + *Holostylis* (Figs. 5, 7) has, in turn, two clades. The first clade corresponds to the monophyletic *Aristolochia* sect. *Diplolobus* (Fig. 9) described by **Duchartre** (1854a, 1864) and is equivalent to *Aristolochia* s. str. (**Klotzsch**, 1859; **Huber**, 1985, 1993; Table 3). The lack of resolution within the clade prevents an evaluation of the monophyly of the two subsections traditionally recognized, *Euaristolochia* and *Podanthemum* (Table 3). 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 coding identical to other species of subsection *Euaristolochia*. **Duchartre** (1864) described subsection *Acerostylis* as having a truncate gynostemium which is a misinterpretation as observations of **Franchet** (1882) as well as our own (based on the specimen *Thesiger s.n.*, BM) have shown. The gynostemium of this species has essentially the same morphology as the other members of subsection *Euaristolochia*.

The second clade includes *Aristolochia* sect. *Gymnolobus* (= *Howardia*) plus *Euglypha* plus *Holostylis* (Figs. 5, 10, 11). The recognition of these latter two genera (see below), as well as the segregate *Einomeia* (= *A.* subser. *Pentandrae*) would make Sect. *Gymnolobus* paraphyletic (Fig. 11). The first subclade within this complex corresponds to *Aristolochia* ser. *Thyrsicae* as proposed by **González** (1990, 1991) and this series is monophyletic (Fig. 10). The placement of *A.* subser. *Pentandrae* is unclear (Figs. 5, 10, 11). The limited resolution within the clade that contains subseries *Pentandrae* is due to conflicting characters

which militates against resolution of a sister group relationship between this subseries and either *A. grandiflora* plus *A. burelae* plus *A. lindnerii* or the clade that contains *Euglypha*, *Holostylis*, and the remaining *Aristolochia* spp. 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 syrxinx (29). 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).

Euglypha is part of an unresolved clade formed by a group of species with concave-convex seeds (character 66) and a massive funicle (70). *Euglypha* has been maintained as a distinct genus (**Schmidt**, 1935; **Hoehne**, 1942; **Ahumada**, 1967; **Huber**, 1993) because of the presence of a stipe at the base of the perianth (23), extremely shortened capsules that fail to dehisce (62), and usually only one seed per carpel (65). The latter three characters are autapomorphies of *Euglypha*. The stipe (23) is also present in a number of species of section *Diplolobus* (Fig. 9) but their vasculature is different suggesting an independent origin. In *Euglypha*, the vascular plexus of the base of the perianth is complete (**González & Stevenson**, 2000a) and there are additional second order veins along the stipe (28), whereas in the species of section *Diplolobus*, the plexus is incomplete and the second order veins are lacking (**González & Stevenson**, 2000a).

The genus *Holostylis* is the sister group of *Aristolochia* subser. *Anthocaulicae* (**González**, 1990, 1991; Fig. 10). The synapomorphies are the presence of lateral racemes (character 11) and dramatically reduced leaves subtending the individual flowers (13). This is consistent with additional anatomical characters that support a close relationship between *Aristolochia* and *Holostylis* (**Solereder**, 1889a; **Carlquist**, 1993) especially the presence of idio-blasts filled with brown, tanniferous material in *Holostylis* (**Solereder**, 1889a) and at least in one species of its sister group such as *A. leuconeura* (**González**, 1990). The subseries *Anthocaulicae* is a monophyletic group defined by cauliflorous inflorescences with extremely shortened internodes (18; Fig. 10).

The infrageneric taxa proposed within *Aristolochia* subsect. *Hexandrae* (**Duchartre**, 1854a, 1864; **Hoehne**, 1942; **Schmidt**, 1935) which are based primarily on habit and shape and size of the flowers are not monophyletic. For example, the group *Bilabiatae* which contains all the species with a 2-lobed perianth is polyphyletic (Figs. 12, 13). This is consistent with the fact that the 2-lobed perianth in p. ej. *A. ringens* and *A. ridicula* develop differ-

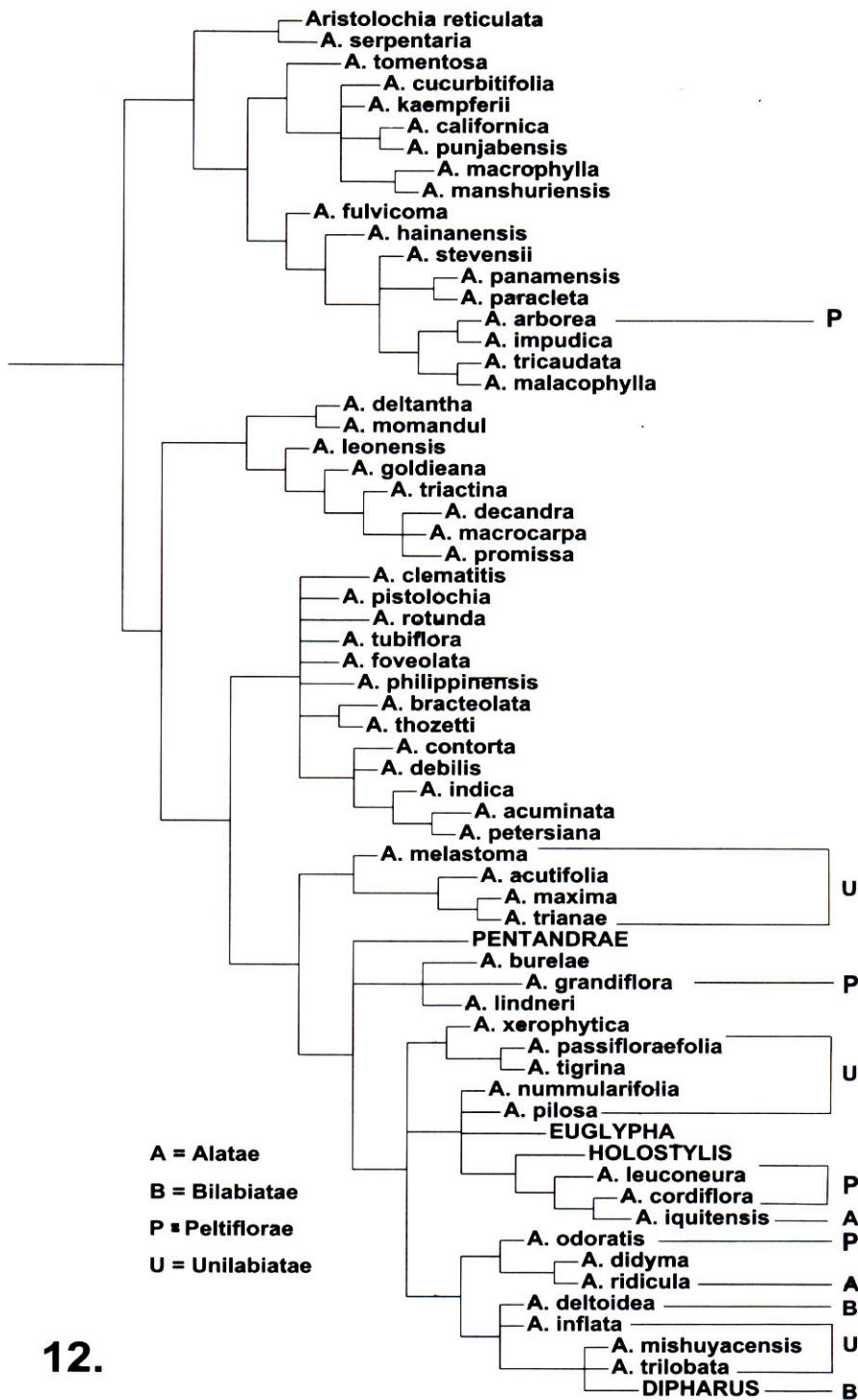


Figure 12. Infrageneric taxa as defined by Duchartre (1854a, 1864) and Schmidt (1935) mapped on the cladogram.

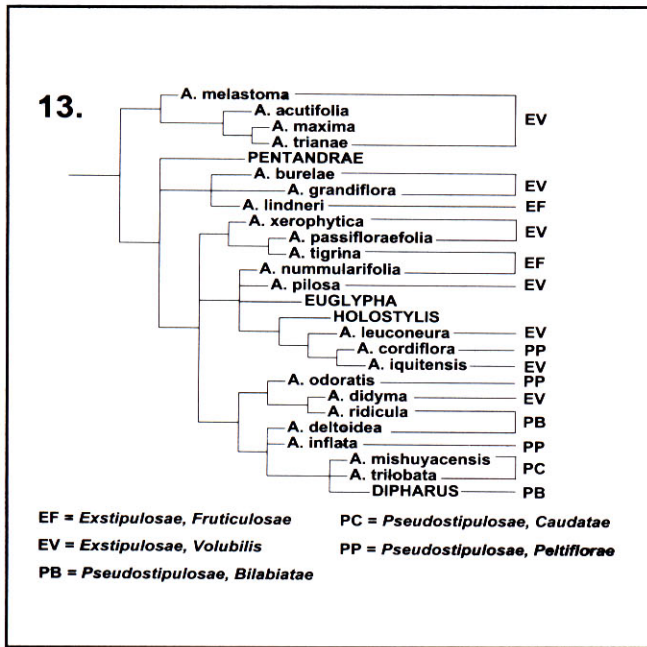


Figure 13. Infrageneric taxa as defined by Hoehne (1942) mapped on the cladogram.

ently (González & Stevenson, 2000a). The analysis also shows that *Aristolochia* ser. *Hexandrae* as described by González (1990, 1991; Table 5) is paraphyletic. This series was originally characterized by the absence of an abscission zone at the base of the petiole (character 9) and the floral peduncle (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 now shown to be symplesiomorphies of series *Hexandrae*.

Character Evolution - Inflorescence Morphology:

The cladistic analysis indicates that monopodial growth (character 1) is a synapomorphy of *Thottea* and the Aristolochioideae (Fig. 5) although some exceptions may occur in some species of subgenus *Pararistolochia* from Australia and New Guinea which may have sympodial growth (González, 1999b). Within the Aristolochioideae, a transformation from thyrscid to racemose inflorescences has occurred *via* a reduction in the number of flowers to one per node and the loss of the bract (12 and 14, respectively). Whereas partial florescences with one flower have arisen several times in the Aristolochioideae (at least twice within subgenus *Siphisia* and twice within 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

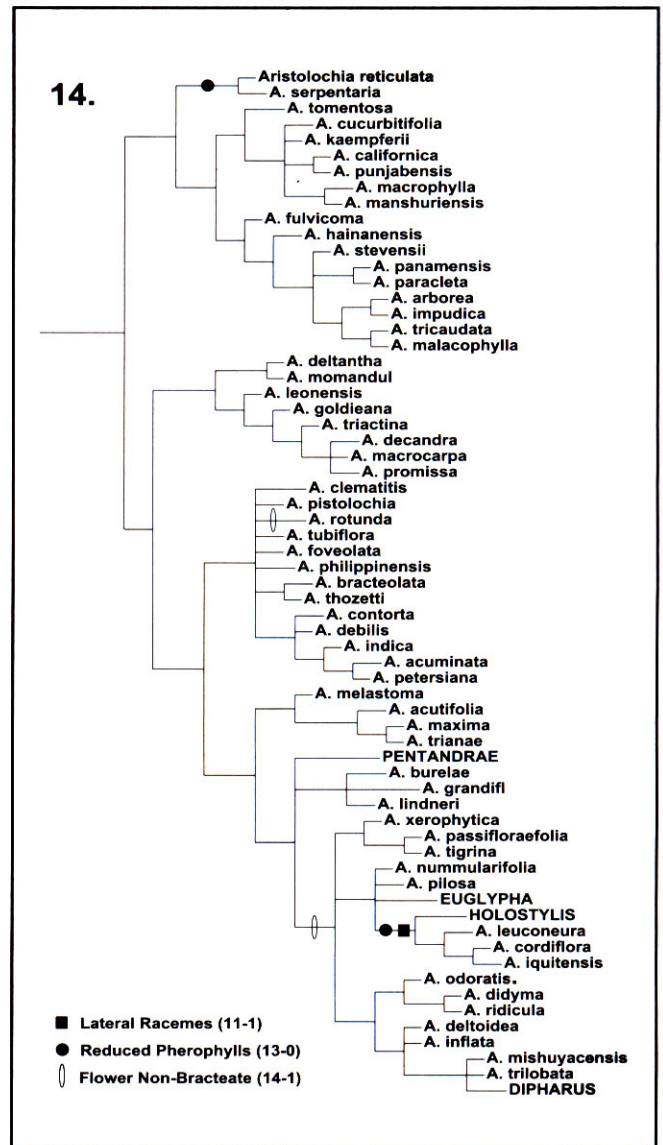


Figure 14. Distribution of character states: lateral racemes, reduced perophylls, and non-bracteate flowers.

Aristolochia plus *Euglypha* and *Holostylis* and once in a few species of *Aristolochia* sect. *Diplolobus* (14; Fig. 14).

In addition, the analysis shows that helicoid cymes (character 19) are a derived feature and flowers arranged in a spiral in partial florescences occur at least in two different clades, once in the African species of *Aristolochia* subgen. *Pararistolochia* and twice within 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.*

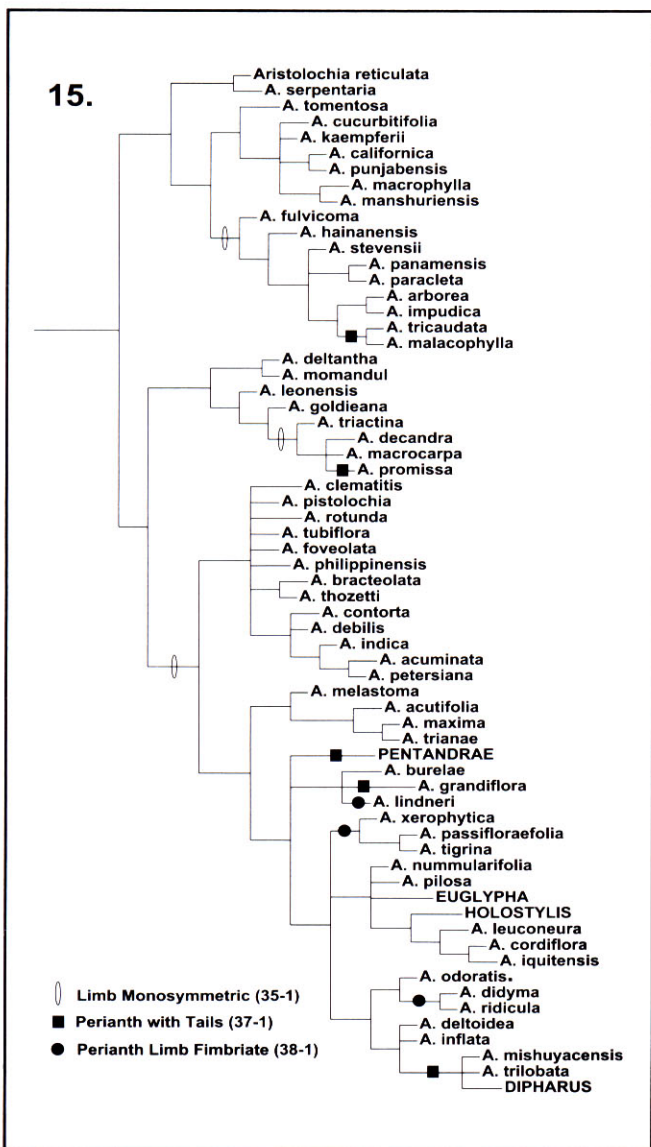


Figure 15. Distribution of character states: monosymmetric, tailed or fimbriate perianth limb.

acuminata, *A. clematitidis*, *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 subtending leaves (13) are both derived (Fig. 14). Whereas the first supports a sister group relationship between *Holostylis* and *A.* subser. *Anthocaulicae*, the second appears independently in two clades, once within subgenus *Siphisia* (in the sister species *A. reticulata* and

A. serpentaria) and once as a synapomorphy for *A.* subser. *Anthocaulicae* plus *Holostylis*.

Character Evolution - 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. Thus, flowers of some species of subgenera *Siphisia* and *Pararistolochia* maintain the plesiomorphic condition, i.e. a regular perianth limb even though they have a curved perianth (Gonzalez & Stevenson, 2000a). According to the present analysis, the curvature (character 26) evolves prior to the monosymmetric limb (35; Fig. 15). The latter has evolved three times, once in a clade within *Aristolochia* subgen. *Siphisia*, once in a clade within subgenus *Pararistolochia*, and once as a synapomorphy for the subgenus *Orthoaristolochia* + *Euglypha* + *Holostylis* (Fig. 15).

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* subgen. *Siphisia* floral shape in the clade composed of species with an actinomorphic limb is not as morphologically diverse as in its sister clade that includes species with flowers having tails (e.g. *A. tricaudata*; Fig. 15) or protrusions of the limb (e.g. *A. arborea*). Similarly, the most remarkable variation in perianth shape and size occurs in *Aristolochia* subsect. *Hexandrae* where an early fusion of the perianth primordia occurs resulting in the perianth tip growing as a single unit (González & Stevenson, 2000a). This is not the case in the species of *Aristolochia* sect. *Diplobus* particularly those of subsection *Podanthemum* where the tips of the perianth parts remain distinct until maturity. In the latter, limb shape is uniform. This is consistent with the low diversification of the shape of actinomorphic flowers of *Asarum* (Cheng & Yang, 1983; Kelly, 1997, 1998) and *Thottea* (Hou, 1984).

A perianth limb with two lobes, although restricted to some members of *Aristolochia* sect. *Hexandrae* (Group *Bilabiatae* in Figs. 12, 13) 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* 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. In contrast, in *A. ridicula* the two lateral lobes develop as distinct lateral extensions that are much larger than the median perianth lobe at maturity (González & Stevenson, 2000a).

The stipe in the perianth, traditionally used as a diagnostic trait to define the subsection *Podanthemum* within *Aristolochia* section *Diplolobus* (Table 3) and the genus *Euglypha*, has evolved independently in these two taxa (character 23 in Figs. 9, 10). However, it is not clear if it evolved in parallel several times within section *Diplolobus* (Fig. 9). Another derived character related to the base of the perianth in *Aristolochia* is the strongly asymmetrical perianth base (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* and the species of section *Dipharus*.

The syrinx (character 29) and the annulus (34) seem to have been acquired independently several times. 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* subsect. *Gymnolobus*. Within the latter, an incomplete syrinx is a synapomorphy of a clade composed of *Aristolochia* subsect. *Hexandrae* plus *Euglypha* plus *Holostylis*. 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, 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 composed of subgenus *Pararistolochia* and subgenus *Orthoaristolochia*.

In the present analysis, traits such as tail-shaped appendages (character 37) or fimbriae (38) on the limb arise independently in different species (Fig. 15). For example, tail-like appendages develop in one species of subgenus *Siphisia* (*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 subgenus *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*, including *Euglypha* and *Holostylis*, might be related to the fact that both stamen and carpel primordia develop in close contact with each other (González & Stevenson, 2000b).

Character Evolution - Seed dispersal: Seeds of many species of *Aristolochia* are adapted to at least two different dispersal mechanisms, anemochory and zoochory (Fig. 4). Winged, flattened seeds are found in a number of species. Whereas rectangular seeds with two wings (Fig. 4I) are a synapomorphy for the clade *A. acutifolia*, *A. maxima* and *A. trianae*, 1-winged, triangular or rhomboidal (Fig. 4H) seeds have evolved three different times, once in a clade within subsection *Diplolobus*, and two times within subsection *Gymnolobus* (Fig. 16).

On the other hand, sticky funicular outgrowths (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. 16). This is reflected in at least three distinct structural differences of these arils. In *Asarum*, sticky arils are formed by 2-4 layers of large, translucent cells formed from the funicle (Fig. 4B). In *Aristolochia*, it consists of a massive secretion from the funicle plus the chalaza (in *A. leuconeura*, Fig. 4F), or from epidermal and subepidermal cells of the funicle (in *A. didyma* and *A. odoratissima*; Fig. 4G).

A Brief Comment on Biogeography. The analysis suggests that the two major clades (subgenus *Siphisia* vs. the remaining Aristolochioideae; Fig. 5) more or less coincide with the Laurasian-Gondwanic vicariant event. Subgenus *Siphisia* is found primarily in North America and W temperate Asia. In addition, late cladogenesis events for the Central American species (i.e. *Aristolochia arborea*, *A.*

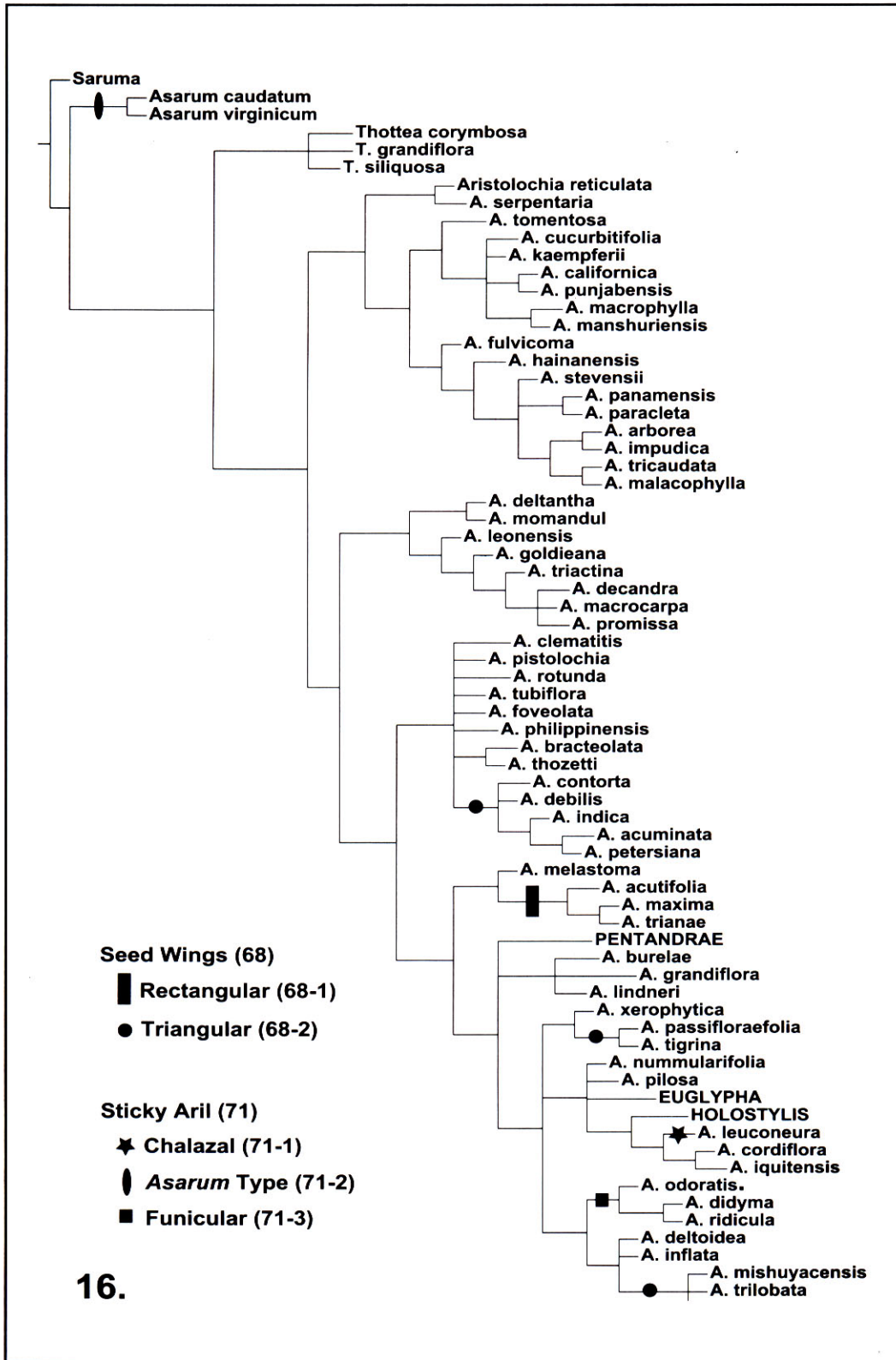


Figure 16. Distribution of characters related to seed appendages.

impudica, *A. malacophylla*, *A. panamensis*, *A. paraclata*, and *A. tricaudata*; Fig. 6) coincide with a later formation of most of Central America with respect to North America (see e.g., Briggs, 1987). Within the temperate species, two pairs of sister species are disjunct between temperate Asia and North America, *A. californica* + *A. punjabensis*; and *A. macrophylla* + *A. manshuriensis* (Fig. 6). The latter are an Eastern North American-Eastern Asian disjunct pair that are remarkably similar in terms of morphological characters. The current analysis, as well as molecular data (Murata *et al.*, 1999), shows them as sister species which argues against the viewpoint of Wen (1999) that such disjuncts may not be sister species. The remaining species of subgenus *Siphisia* in Asia are mainly temperate and subtropical. The tropical species are fewer and do not extend beyond India to the west or the Wallace line to the east.

The two major clades of subgenus *Pararistolochia* are also disjunct, one formed by the Australian and the New Guinean species and its sister group formed primarily by West African species (Fig. 8).

The third subgenus, *Orthoaristolochia*, has a much wider geographical distribution but the two major lineages within the subgenus are primarily Paleotropical (section *Diplolobus*)-Neotropical (section *Gymnolobus* + *Euglypha* + *Holostylis*) vicariants (Fig. 7).

Two major geographic regions are important in terms of sympatric distribution of major clades: Southeast Asia and Central America. Members of all the three subgenera occur together only in Malesia where several species of subgenus *Orthoaristolochia*, a few species of subgenus *Siphisia*, and one species of subgenus *Pararistolochia* (*A. decandra*) are found sympatrically (Hou, 1984). On the other hand, in Mexico and Central America, several species of the subgenus *Siphisia* are sympatric with several species 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*.

Several authors (e.g. Raven & Axelrod, 1974; Simpson & Neff, 1985) have assumed a North-South dispersal route of *Aristolochia* in America. The present analysis argues against that point of view because the Laurasian elements have not been found south of Panama. In addition, *Aristolochia* in America is not a monophyletic group, indicating that sympatry of different clades in Central America is secondary in terms of the presence of the predominantly Laurasian subgenus *Siphisia* and the predominantly Gondwanian sect. *Gymnolobus*.

Conclusions

The present analysis supports the concept of the monophyly of *Thottea* + *Aristolochia* (Fig. 5) and this warrants to the conclusion that these two genera form a single lineage within the Aristolochiaceae as was implicit in Huber's (1985, 1993) system of classification (Fig. 1G). The analysis also shows that *Aristolochia s.l.* is paraphyletic and that most of the infrageneric taxa within *Aristolochia* are either para- or polyphyletic. Most of the traits related to the floral shape of the perianth, upon which these groups have been recognized, are shown to be independently acquired. Based on the resulting monophyletic groups, a revised classification of the subfamily Aristolochioideae consisting of two tribes, two subtribes, and five genera is proposed here. The new combinations and nomenclatural aspects of infrageneric taxa will be published elsewhere. For practical reasons, we are in favor of recognizing *Aristolochia* in a broader sense than that given by Huber (1985, 1993), because the generic recognition of *Euglypha*, *Holostylis* and *Einomeia* (i.e. the pentandrous species; Fig. 11) would require the establishment of as many as 12 distinct genera, and would collapse the nomenclature of the largest groups of species of *Aristolochia*. Thus, the formal classification proposed here is:

Aristolochioideae

Tribe Bragantieae Klotzsch

Thottea Rottbøll

Tribe Aristolochieae

Subtribe Isotrematinae H. Huber

Endodeca Rafinesque

Isotrema Rafinesque

Subtribe Aristolochiineae

Pararistolochia Hutchinson & Dalziel

Aristolochia L. (including *Euglypha* Chodat & Hassler and *Holostylis* Duchartre)

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Appendix 1. Characters and character states used in the cladistic analysis

0. Habit. (0) herbaceous, (1) woody at least in the roots and/or rhizomes. 2 steps. CI = .50 RI = .75
1. Growth units. (0) sympodial, (1) monopodial. 2 steps. CI = .50 RI = .66. Whereas growth units of *Saruma* and *Asarum* are sympodial, those of *Aristolochia*, *Euglypha*, *Holostylis*, and *Thottea* are monopodial; some Australian and New Guinean species of subgenus *Pararistolochia* (e.g. *A. deltantha*) might have sympodial growth units (**González**, 1999a, b).
2. Elongating shoots. (0) nearly straight (Fig. 2B), (1) strongly sinuous (Fig. 2A). 1 step. CI = 1.00 RI = 1.00
3. Number of axillary buds. (0) one, (1) two or more (see **González**, 1999a, b). 2 steps. CI = .50 RI = .66
4. Arrangement of axillary buds. (0) uniseriate, (1) biseriate. 5 steps. CI = .20 RI = .33. When two or more buds occur in the same leaf axil, they are arranged either in one or in two rows (**González**, 1999a, b).
5. Mature stems. (0) circular, (1) medially constricted. 5 steps. CI = .20 RI = .55. 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. 1 steps. CI = 1.00 RI = 1.00
7. Leaf expansion. (0) normal, (1) delayed. 1 step. CI = 1.00 RI = 1.00. In most of the Aristolochiaceae, the leaf primordium begins differentiation into petiole and blade in plastochrone 3-4 and the blade expands relatively rapidly (Fig. 2C); in other species the differentiation occurs at a late stage, and blade expansion is delayed (Fig. 2D).
8. Vegetative prophyll. (0) non-pseudostipular (Fig. 2B), (1) pseudostipular (Fig. 2E). 1 step. CI = 1.00 RI = 1.00. In a group of Neotropical species, the prophyll of each renewal shoot develops into a sessile, round, clasping leaf called a pseudostipule (**Duchartre**, 1854b; **González**, 1990).
9. Petiole abscission zone. (0) absent (Fig. 3C), (1) present (Fig. 3D). 2 steps. CI = .50 RI = .94
10. Petiole base. (0) U-shaped (Fig. 3A), (1) semicircular (Fig. 3B). 2 steps. CI = .50 RI = .88
11. Position of the partial florescence. (0) along leafy, elongated, main branches, (1) in lateral racemes, (2) along bracteate, terminal portions of the main axis, which usually have shortened internodes (see **González**, 1999b). 2 steps. CI = 1.00 RI = 1.00. It is unclear if partial florescences in *Thottea grandiflora* are cymose. Thus, we have coded this character as unknown in this species.
12. Partial florescence. (0) uniflorous, (1) bi/multiflorous (see **González** 1999 b). 11 steps. CI = .09 RI = .64. Inflorescence development of *Thottea corymbosa* and *T. grandiflora* is unknown, preventing the coding of this and characters 13-19 in these species.
13. Subtending leaves (0) expanded, (1) reduced (**González**, 1999b). 3 steps. CI = .33 RI = .66
14. Flower. (0) bracteate, (1) non-bracteate (see **González**, 1999b). 2 steps. CI = .50 RI = .94
15. Bract expansion. (0) non-clasping, (1) clasping. 5 steps. CI = .20 RI = .71
16. Bract base. (0) non-peltate, (1) peltate. 1 step. CI = 1.00 RI = 1.00
17. Bract shape. (0) similar in shape and size to leaves, (1) reduced. 2 step. CI = .50 RI = .66
18. Inflorescence internodes. (0) elongated, (1) shortened (see **González**, 1999b). 2 steps. CI = .50 RI = .75. Internodes along the main axis of the inflorescences are elongated (> 2 cm); in some species of *Aristolochia*, the internodes are extremely shortened (< 1 cm).
19. Inflorescence phyllotaxis. (0) distichous, (1) spiral (helicoïd; see **González**, 1999b). 3 steps. CI = .33 RI = .80
20. Peduncle abscission zone. (0) absent, (1) present (see **González**, 1999b). 4 steps. CI = .25 RI = .81
21. Perianth series. (0) two, (1) one. 1 step. CI = 1.00 RI = 1.00
22. Perianth shape. (0) rotate, (1) campanulate, (2) tubular. 3 steps. CI = .66 RI = .80
23. Perianth. (0) non-stipitate, (1) stipitate. 4 steps. CI = .25 RI = .50. This character is not applicable to *Asarum* and *Saruma*, because the perianth in these genera is continuous with the peduncle. In the other genera, the perianth may have a basal stipe or not (see **González & Stevenson**, 2000a).
24. Perianth base. (0) symmetrical, (1) strongly asymmetrical (see **González & Stevenson**, 2000a). 1 step. CI = 1.00 RI = 1.00
25. Perianth. (0) not differentiated, (1) differentiated into utricle, tube and limb. 1 step. CI = 1.00 RI = 1.00
26. Perianth concavity. (0) absent, (1) adaxial, (2) abaxial. 3 steps. CI = .66 RI = .96. 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. In the remaining species, the concavity is formed on the abaxial side of the flower (see **González & Stevenson**, 2000a).
27. Perianth abscission zone. (0) absent, (1) present. 1 step. CI = 1.00 RI = 1.00. 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 and the gynostemium fall off (see **González & Stevenson**, 2000a).

28. Second order perianth veins. (0) present, (1) absent (see **González & Stevenson**, 2000a). 1 step. CI = 1.00 RI = 1.00
29. Syrix. (0) absent, (1) incomplete, (2) complete. 8 steps. CI = .25 RI = .76. The syrix is an inner flange formed between the utricle and the tube. This and the characters 30-32 are 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. 3 steps. CI = .33 RI = .81. At anthesis, the tube extends straight out from the utricle or is oblique to it, thus forming a sharp angle.
31. Tube curvature. (0) strong (U-shaped), (1) slight (see **González & Stevenson**, 2000a). 2 steps. CI = .50 RI = .94. Within *Aristolochia* subsect. *Pentandrae*, most of the species have a slightly curved tube; however, *A. acontophylla*, *A. cardiantha*, *A. foetida*, *A. micrantha*, *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, (1) not inflated, (2) evenly inflated and almost as wide as the utricle. 3 steps. CI = .66 RI = .94
33. Conical perianth trichomes. (0) absent, (1) present (see **González & Stevenson**, 2000a). 2 steps. CI = .50 RI = .95
34. Annulus. (0) absent, (1) present. 6 steps. CI = .16 RI = .58. The annulus is a circular flange at the flower entrance. One species of subsection *Pentandrae* (*A. secunda*) has an annulus, thus we coded this character as polymorphic for this subsection.
35. Limb symmetry. (0) regular, (1) monosymmetric. 3 steps. CI = .33 RI = .89
36. Limb lobes at anthesis. (0) three, (1) one, (2) two, one upper and one lower, (3) two, lateral (see **González & Stevenson**, 2000a). 4 steps. CI = .75 RI = .96
37. Tail-like appendage(s) on perianth. (0) absent, (1) present. 4 steps. CI = .25 RI = .40. In some species of *Aristolochia*, the perianth ends in a tail(s). One species of subsection *Pentandrae* (*A. nelsonii*) and one of section *Dipharus* (*A. pohliana*) have a tail-like appendage, thus, we have coded this character as polymorphic in both taxa.
38. Perianth limb. (0) non fimbriate, (1) fimbriate. 3 steps. CI = .33 RI = .60. Some species of *Aristolochia* have fimbriae on the limb.
39. Limb protrusion. (0) absent, (1) present (see **González & Stevenson**, 2000a). 1 step. CI = 1.00 RI = 1.00. In a few species of *Aristolochia* subgen. *Siphisia*, the limb base has a massive process that projects in front of the flower entrance.
40. Stamen number. (0) 12, (1) 24, (2) 8-10, (3) 6, (4) 5, (5) >25. 6 steps. CI = .83 RI = .85. We 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, (1) one. 2 steps. CI = .50 RI = .66
42. Stamens. (0) equidistant, (1) grouped. 2 steps. CI = .50 RI = .94. 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 (see **González & Stevenson**, 2000b).
43. Stamens. (0) free, (1) fused forming a gynostemium (see **González & Stevenson**, 2000b). 1 step. CI = 1.00 RI = 1.00
44. Stamen dehiscence. (0) functionally introrse (see **Dickison**, 1992), (1) extrorse. 1 step. CI = 1.00 RI = 1.00
45. Anthers. (0) with filament, (1) sessile. 1 step. CI = 1.00 RI = 1.00
46. Anther length. (0) less than half the length of the gynostemium, (1) > half the length of the gynostemium. 2 steps. CI = .50 RI = .94
47. Pollen sculpturing. (0) reticulate, (1) microreticulate, (2) fossulate, (3) areolate, (4) psilate (see **González** 1999a). 6 steps. CI = .66 RI = .88
48. Pollen aperture. (0) sulcate, (1) porate, (2) inaperturate. 2 steps. CI = 1.00 RI = 1.00
49. Pollen ridge. (0) absent, (1) poorly differentiated, (2) markedly differentiated (see **González**, 1999a). 3 steps. CI = .66 RI = .87. A long, broad ridge of exine is formed in pollen of all members examined of subgenus *Pararistolochia*.
50. Supratectal warts. (0) none, (1) small, (2) large (see **González**, 1999a). 4 steps. CI = .50 RI = .66
51. Ovary position. (0) semiinferior, (1) inferior (see **González & Stevenson**, 2000b). 2 steps. CI = .50 RI = 0
52. Ovary shape. (0) globose, (1) elongated and narrow. 1 step. CI = 1.00 RI = 1.00
53. Carpels. (0) partially apocarpous, (1) syncarpous (see **González & Stevenson**, 2000b). 1 step. CI = 1.00 RI = 1.00
54. Mature carpels. (0) 6, (1) 5, (2) 4. 2 steps. CI = 1.00 RI = 1.00. In *Thottea* only four of the six carpels develop (**González & Stevenson**, 2000b).
55. Stigmas. (0) free, (1) connate (see **González & Stevenson** 2000b). 2 steps. CI = .50 RI = 0. Presence of true stigmas in *Thottea* is controversial (**Leins et al.**, 1988), so we have coded this and the next character as unknown in this genus.

56. Gynostemium lobes. (0) 6, (1) 5, (2) 3, (3) 8-10, (4) 12. 4 steps. CI = 1.00 RI = 1.00. We 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, and additional lobes in these species occur by secondary division of the three lobes. *Holostylis*, usually described as having an entire gynostemium, has 6 vestigial lobes (**González & Stevenson**, 2000b) 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* (**Poncey**, 1978), especially in *A. goldieana*, where there are 12 gynostemium lobes and 24 stamens.
57. Stigmatic papillae. (0) present, (1) absent. 1 step. CI = 1.00 RI = 1.00
58. Position of the stigmatic papillae. (0) terminal, (1) lateral/basal. 3 steps. CI = .33 RI = .92. By the time of anthesis these papillae are either terminal and marginal or lateral/basal with respect to the gynostemium lobes. 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. *Aristolochia* subsection *Diplolobus* has traditionally been described as having the latter condition, but this is also present in the species of subgenera *Siphisia* and *Pararistolochia* (**González & Stevenson**, 2000b).
59. Fruit surface. (0) smooth, (1) warty. 1 step. CI = 1.00 RI = 1.00
60. Pericarp. (0) membranous to chartaceous, (1) strongly lignified. 1 step. CI = 1.00 RI = 1.00
61. Mesocarp. (0) dry, (1) fleshy. 2 steps. CI = .50 RI = .87
62. Fruit. (0) ventricidal, (1) septifragal, (2) irregularly dehiscent, (3) indehiscent. 5 steps. CI = .40 RI = .89
63. Fruit dehiscence. (0) basipetal, (1) acropetal. 4 steps. CI = .25 RI = .86
64. Fruit septae. (0) entire, (1) lattice-like. 1 step. CI = 1.00 RI = 1.00
65. Seeds per carpel. (0) >5, (1) 1-2. 1 step. CI = 1.00 RI = 1.00
66. Seed contour. (0) concave-convex, (1) flattened, (2) trigonous. 8 steps. CI = .25 RI = .80. In transverse section, the contour of the seed proper appears concave-convex (Fig. 4A, B, D), flattened (Fig. 4C, E-I), or extremely curved and with the margins touching each other (**González**, 1999a; **Hou**, 1981; **Huber**, 1985).
67. Shape of the seed proper. (0) ovoid (Fig. 4), (1) ellipsoid. 1 step. CI = 1.00 RI = 1.00
68. Seed wings. (0) absent or vestigial (Figs. 4A-G), (1) two, rectangular (Fig. 4I), (2) one, triangular-rhomboidal (Fig. 4H). 4 steps. CI = .50 RI = .81. 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 (Fig. 4C, D), (1) fused to the seed (Fig. 4A, B, E-I). 3 steps. CI = .33 RI = .77
70. Funicle. (0) massive (Fig. 4A-D, F), (1) filiform (Fig. 4I), (2) papery, incomplete (Fig. 4H), (3) papery, complete (Fig. 4E, G). 10 steps. CI = .30 RI = .69. When the funicle is papery, it can completely cover the adaxial side of the seed (i.e. complete; Fig. 4E) or not (i.e. incomplete; Fig. 4H).
71. Sticky aril. (0) absent, (1) chalazal-funicular, (2) *Asarum* type, (3) funicular. 4 steps. CI = .75 RI = .50. Whereas in *Asarum* the aril is formed by 2-4 layers of large cells originating from the funicle (Fig. 4B), in *Aristolochia leuconeura* and *A. odoratissima*, the aril consists of excretions from the funicle and the chalaza in the former (Fig. 4F) or from epidermal and subepidermal cells of the whole funicle in the latter (Fig. 4G).

