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NOTES ON THE SYSTEMATICS  
OF *ARISTOLOCHIA* SUBSECT.  
*HEXANDRAE*<sup>1</sup>

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ABSTRACT

Using comparative morphology studies from 123 species of *Aristolochia* sect. *Gymnolobus* subsect. *Hexandrae*, this taxon is reevaluated. Two series (*Hexandrae* and *Thyrsicae*, ser. nov.) and two subseries (*Anthocaulicae*, ser. nov., and *Hexandrae*) are recognized. *Aristolochia* (*Thyrsicae*) *maxima* and *Aristolochia* (*Anthocaulicae*) *iquitensis* are designated as types.

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The Aristolochiaceae are represented in America by the genera *Aristolochia*, *Asarum*, *Euglypha*, and *Holostylis*. The noteworthy diversity and wide distribution of *Aristolochia* (250 species ranging from ca. 40°N latitude to ca. 35°S latitude) contrasts with the restricted distributions of *Asarum* (southeastern and northwestern United States) and the monotypic genera *Euglypha* and *Holostylis* (central South America). Most New World species of *Aristolochia* belong to *Aristolochia* sect. *Gymnolobus* Duchartre (1854, 1864).

While working on a revision of *Aristolochia* in Colombia, I (González, 1989) studied the comparative morphology of the 27 species reported from this country, as well as another 96 neotropical species. All species belonged to *Aristolochia* sect. *Gymnolobus* Duchartre subsect. *Hexandrae* Duchartre (1854, 1864; lectotype here designated, *A. ringens* Vahl). Based on this study, it was possible to recognize two new series and two new subseries into that subsection.

The present treatment appears as an alternative to the classical works of the subsection made by Duchartre (1854, 1864), Masters (1875), Schmidt (1935), and Hoehne (1942). These authors considered the characters of the perigonium to be essential for grouping species; such characters are unstable, however, and suggest that convergence or parallelism have occurred (González, 1989).

The new series and subseries are recognized by the correlation of characters related to: abscission

basal zone in the petiole, whose appearance is here reported for the first time in the Aristolochiaceae; typology of inflorescences; and morphology of capsule and seeds. The concepts and terminology used here to describe inflorescences were developed by Mora-Osejo (1987), Troll (1950, 1964, 1969), and Weberling (1981, 1983, 1985). These new concepts made it possible to establish the basic types of inflorescences in *Aristolochia* and to apply these types to the recognition of natural groups.

In order to increase the understanding of the following descriptions, a short explanation of unfamiliar concepts related to the inflorescence morphology is desirable. Holocaulic plants (sensu Mora-Osejo, 1987) have stem systems (holocauls) with high innovation (branching) capacity, with vegetative elements (i.e., bracts, buds, and leaves) included in the floriferous zone (Figs. 1, 2A, 3, 5A) or synflorescence (sensu Troll, 1950, 1964). In *Aristolochia*, the synflorescence is polytelic (lacking a terminal flower on the main axis or the lateral branches of various order); the growth of the shoots is indeterminate. The synflorescence is formed by the florescence (fl, distal floriferous unit of the polytelic main axis; Figs. 1, 3) and the cofillorescences (cfl, florescences of the lateral branches, or paracladia, pc; Figs. 1, 3). The florescence and the cofillorescences become equivalent to the anthotagma (sensu Mora-Osejo, 1987) or floriferous zone, subtended by a vegetative zone called hypotagma (sensu Troll, 1964); the hypotagma (hptg,

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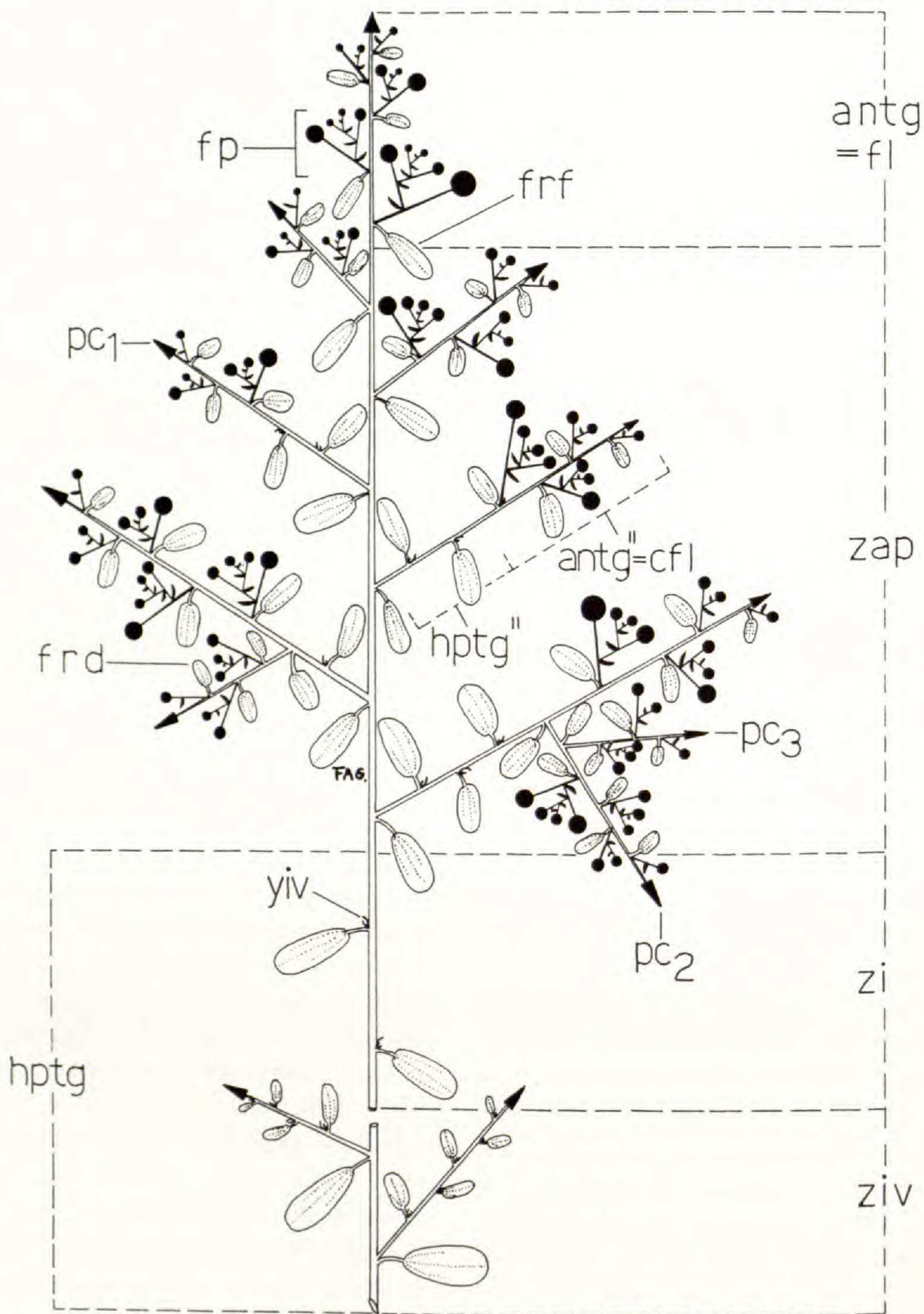


FIGURE 1. Diagram of a frondose, polytelic, thyrsoid holocauste, from *Aristolochia* ser. *Thyrsicae*; antg, anthotagma; cfl, coflorescence; fl, florescence; fp, partial florescence; frd, frondulose pherophyll; frf, frondose pherophyll; hptg, hypotagma; pc, paracladia of first ( $pc_1$ ), second ( $pc_2$ ) and third ( $pc_3$ ) order; yiv, innovation bud; zap, anthoparacladial zone; zi, inhibition zone; ziv, enrichment or innovation zone.

Figs. 1, 3) includes the inhibition zone (zi) and the innovation zone (ziv).

In the species of *Aristolochia* ser. *Thyrsicae*, the partial florescences (ultimate elements of the florescence and the coflorescences) are rhipidia or helicoid cymes (Figs. 1, 2A, B); this implies that the synflorescence is thyrsoid. On the other hand, the synflorescence in the species of *Aristolochia* ser. *Hexandrae* subser. *Hexandrae* is racemose (botrytic) because each partial florescence is reduced to a terminal flower (Figs. 3, 5A, B). In both taxa the pherophylls (vegetative elements that sub-

tend each partial florescence) are leaves, and the synflorescence is therefore frondose (frf, Figs. 1, 3); however, in some higher-order paracladia the pherophylls become frondulose (frd, Figs. 1, 3; sensu Weberling, 1981).

In contrast, the inflorescences in the anthocaulic species of *Aristolochia* subser. *Anthocaulicae* are restricted to lateral shoots called anthocauls (sensu Mora-Osejo, 1987); they tend to be strongly homogeneous and specialized for the reproductive function. Each shoot is a short paracladium; this implies that it is truncate and has indeterminate

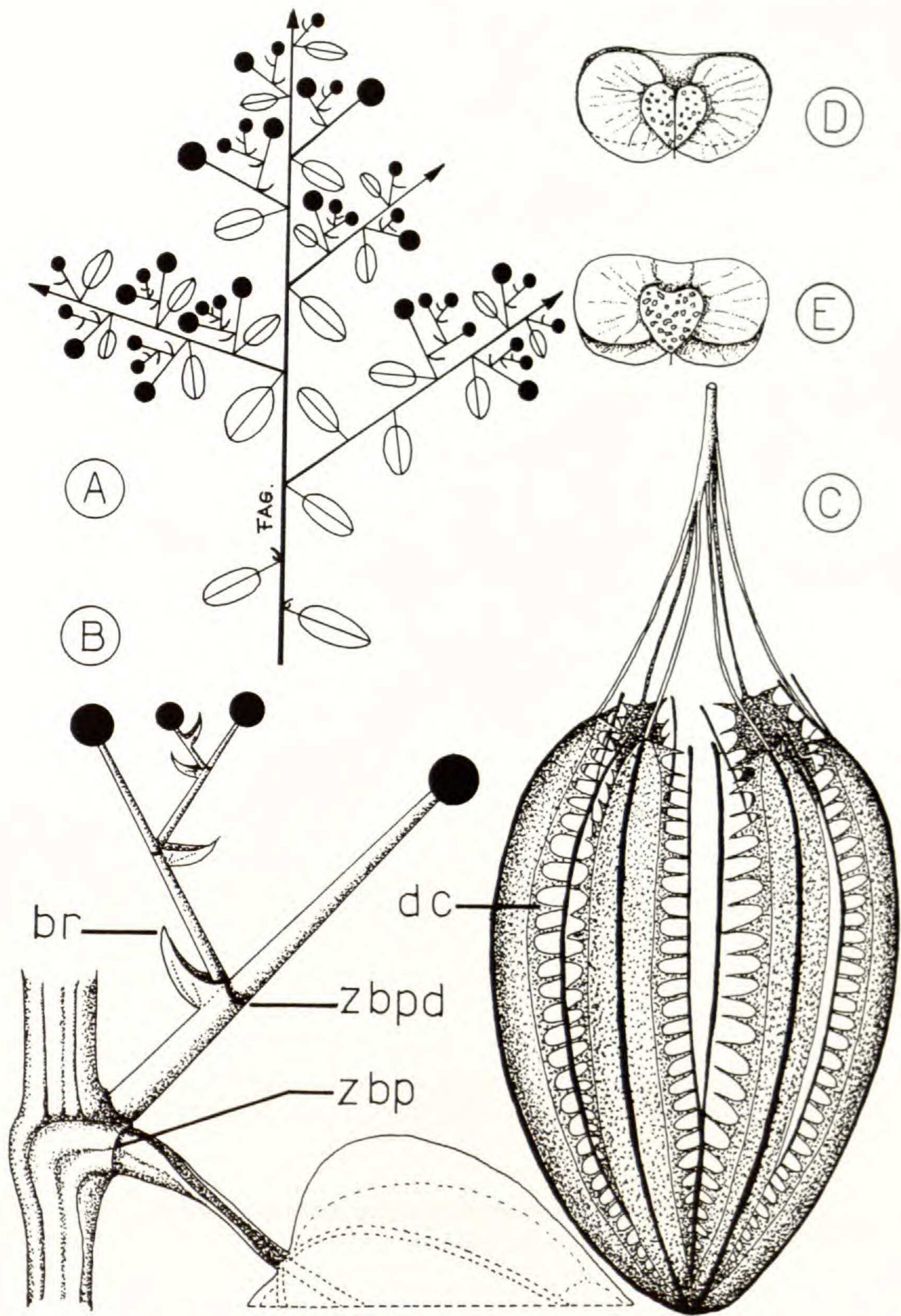


FIGURE 2. *Aristolochia* ser. *Thyrsicae*. Diagram of diagnostic characters.—A. Synflorescence.—B. Partial florescence; br, bracteole; zb, abscission basal zone of the petiole (zbp) and the peduncle (zbpd).—C. Capsule; dc, laticelike dissepiment. D, E. Seeds.—D. Adaxial view.—E. Abaxial view.

growth. Its vegetative impulse is not strong; its vegetative elements (buds, internodia, and leaves) are extremely reduced; the shoot is unbranched and is occupied totally by the cofilorescence (the hypotagma disappears); these shoots correspond to the paracladial anthoblast model (sensu Mora-Osejo, 1987). These paracladia are restricted to a basal zone of the plant, here called the anthoparacladial

zone (zap, Fig. 4). As in the species of *Aristolochia* subser. *Hexandrae*, these floriferous shoots are racemose, but each flower is subtended by a bracteal pherophyll (fb, Figs. 4, 5F, G).

The outline of the new taxonomic treatment here proposed is the following (the order of the taxa belongs with the typological derivation, discussed in González, 1989):

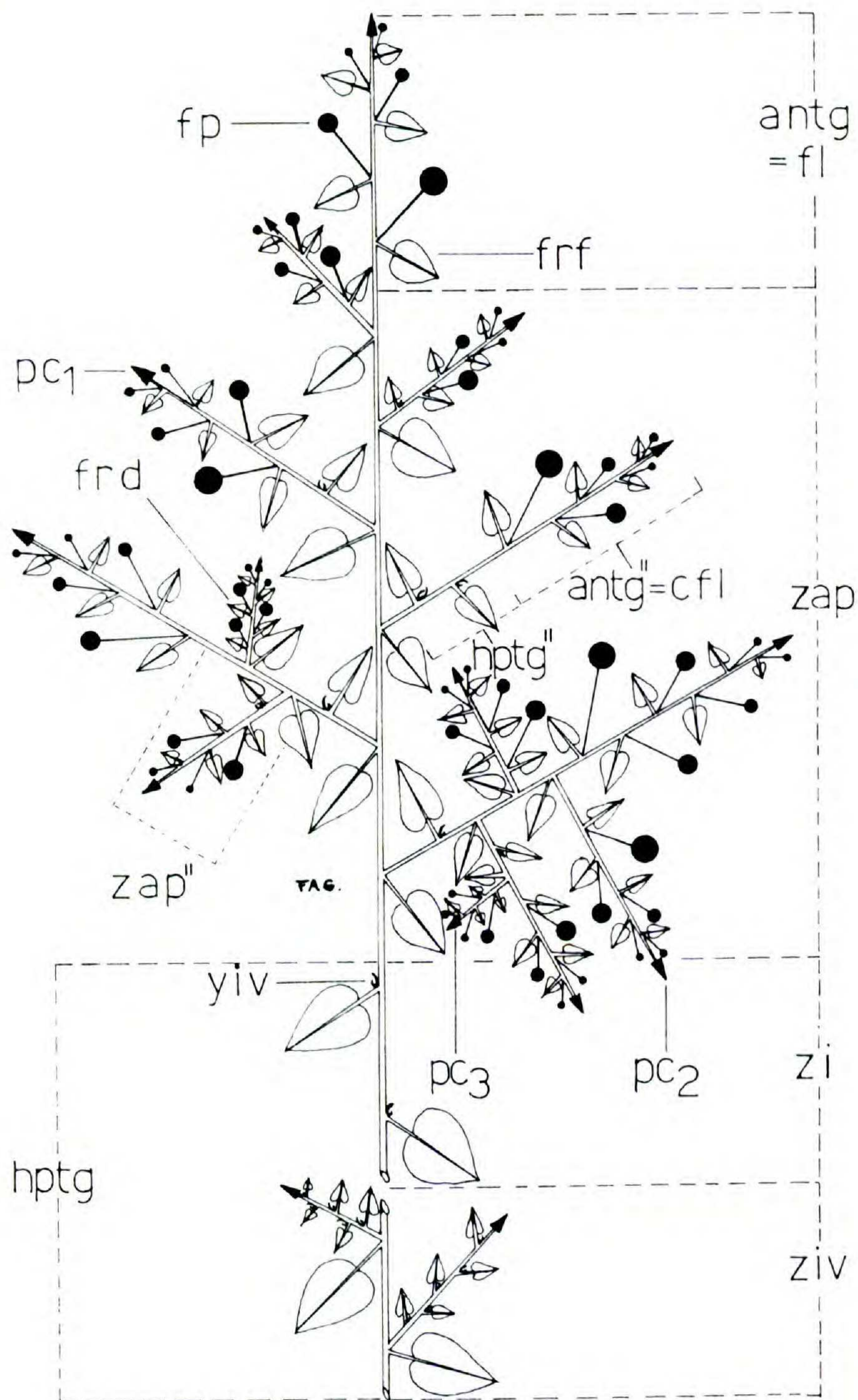


FIGURE 3. Diagram of a frondose, polytelic, racemose holocauste, from *Aristolochia* ser. *Hexandrae* subser. *Hexandrae*. (Abbreviations as in Fig. 1.)

*Aristolochia* subsect. *Hexandrae*  
ser. *Thyrsicae* ser. nov.  
ser. *Hexandrae*  
subser. *Hexandrae*  
subser. *Anthocaulicae* subser. nov.

***Aristolochia*** ser. ***Thyrsicae*** F. González, ser. nov. HOLOTYPE: *Aristolochia maxima* Jacq. Figures 1, 2.

Plantae holocausticae, synflorescentia frondosa, thyrsica; paracladia interdum pseudocauliflora vel cauliflora, ad florescentiam partialem reducta; florescentiae partiales ripidiis vel cymis helicoidalibus conformatae. Flores brac-

teolati. Zona abscissionis basi petioli et pedunculi. Dissepimenta capsulae cancellata. Semina transversim oblonga, plana, bialata, ala abaxialis quam adaxialis brevior.

Holocaustic plants, synflorescence frondose, thyrsoid, paracladia sometimes pseudocauliflorous or cauliflorous and then reduced to a partial florescence; partial florescence a rhipidium or helicoid cyme; flowers bracteolate. Petiole and peduncle with basal abscission zone. Capsule with dissepiments latticelike. Seeds transverse-oblong, two-winged, abaxial wing shorter than adaxial.

*Distribution:* Neotropics (southern Mexico to Argentina).

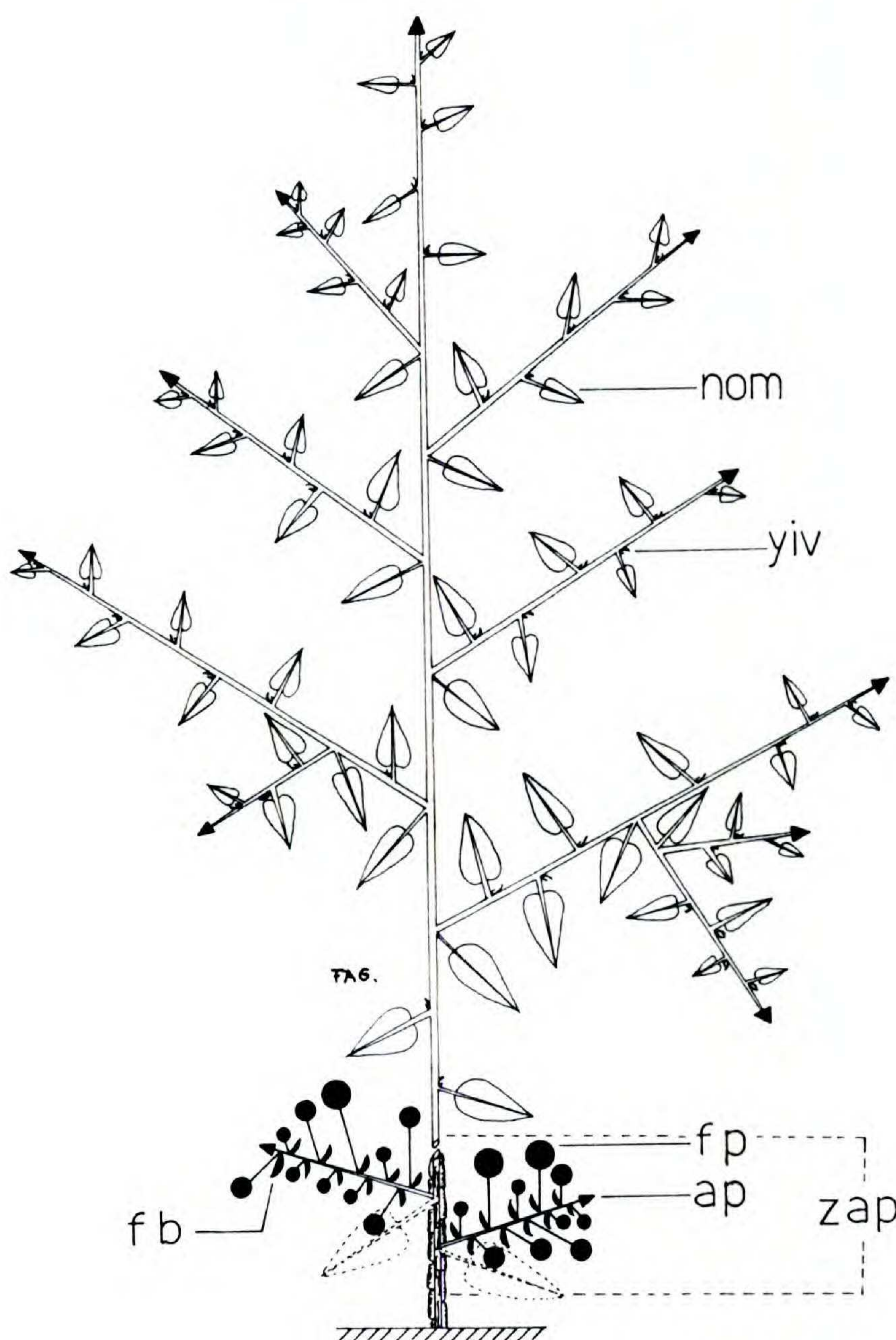


FIGURE 4. Diagram of an anthocaul from *Aristolochia* ser. *Hexandrae* subser. *Anthocaulicae*; ap, paracladial anthoblast; fb, bracteal pherophyll; fp, partial florescence; nom, nomophyll; yiv, vegetative innovation bud; zap, anthoparacladial zone.

The following species belong in *Aristolochia* ser. *Thyrsciae*: *A. acutifolia* Duchartre, *A. colossifolia* Hoehne, *A. mathewsii* Duchartre, *A. maxima* Jacq., *A. melastoma* Manso, *A. ovalifolia* Duchartre, *A. pannosoides* Hoehne, *A. pfeiferi* Barringer, *A. silvatica* Barb. Rodr., *A. sprucei* Mast., *A. tonduzii* Schmidt, *A. translucida* Pfeifer, and *A. trianae* Duchartre.

***Aristolochia* ser. *Hexandrae*. Figures 3–5.**

Holocaustic or anthocaustic plants, synflorescence racemose; partial florescence reduced to the terminal flower. Flowers ebracteolate (except in *A. grandiflora*). Petiole and peduncle without basal abscission zone. Capsule dissepiments entire. Seeds rhomboid, ellipsoid, or from wide- to narrowly ovoid, unwinged or having one wing.

Into this series are recognized two subseries, described below.

***Aristolochia* ser. *Hexandrae* subser. *Hexandrae*. Figures 3, 5A–E.**

Holocaustic plants; synflorescence with distal, frondose florescence and coflorescences; florescence and coflorescences sparsely flowered with elongate internodes, more than 1 cm long; pherophylls frondose, sometimes frondulose, petiolate, 10 mm long and  $\geq 6$  mm wide.

*Distribution*: Neotropics and adjacent subtropical, temperate areas; the highest density of species occurs in the Neotropics.

The species now recognized in *Aristolochia* ser. *Hexandrae* subser. *Hexandrae* are: *A. albertiana*

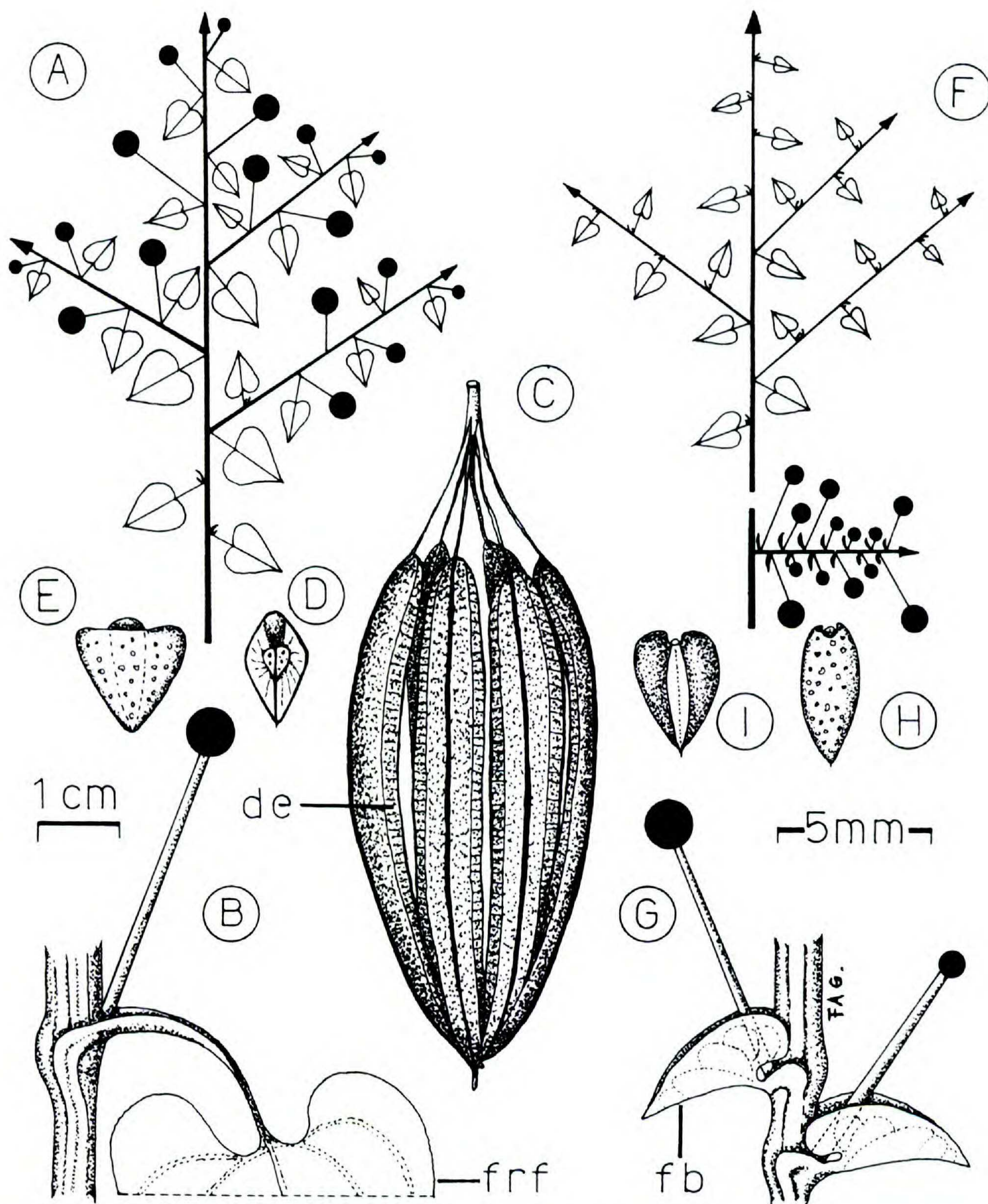


FIGURE 5. *Aristolochia* ser. *Hexandrae*. Diagram of diagnostic characters. A-E. *Aristolochia* ser. *Hexandrae* subser. *Hexandrae*.—A. Synflorescence.—B. Partial florescence at the axil of a frondose pherophyll (frf).—C. Capsule; de, entire dissepiment.—D. E. Seeds. F-I. *Aristolochia* ser. *Hexandrae* subser. *Anthocaulicae*.—F. Synflorescence.—G. Two partial florescences at the axil of one each bracteal pherophylls (fb).—H, I. Seeds (not to scale, except B and G).

Ahumada, *A. andahuaylensis* Ahumada, *A. anguicida* Jacq., *A. angustifolia* Cham., *A. arcuata* Mast., *A. argentina* Griseb., *A. barbouri* Barringer, *A. bilobata* L., *A. brasiliensis* Mart. & Zucc., *A. brevifolia* (Cham.) Haum., *A. burchellii* Mast., *A. burkartii* Ahumada, *A. cabreræ* Ahumada, *A. castellanosi* Ahumada, *A. caudata* Jacq., *A. cerasensis* Kuntze, *A. clausenii* Duchartre, *A. clavi-*

*denia* Griseb., *A. compta* Hoehne, *A. cordigera* Willd. ex Duchartre, *A. curviflora* Malme, *A. cymbifera* Mart. & Zucc., *A. chachapoyensis* Ahumada, *A. chilensis* Miers, *A. deltoidea* HBK, *A. didyma* S. Moore, *A. ehrenbergiana* Cham., *A. ekmanii* Schmidt, *A. elegans* Mast., *A. eriantha* Mart. & Zucc., *A. esperanzae* Kuntze, *A. fimbriata* Cham., *A. fuertesii* Urb., *A. gabrielis* Du-

chartre ex Briq., *A. galeata* Mart. & Zucc., *A. gehrtii* Hoehne, *A. gibertii* J.D. Hook., *A. gigantea* Mart. & Zucc., *A. ginzbergeri* Ahumada, *A. glandulosa* J. Kickz fil., *A. glossa* Pfeifer, *A. grandiflora* Sw., *A. guianensis* Poncy, *A. haitensis* Ekman & Schmidt, *A. hatschbachii* Ahumada, *A. hians* Willd., *A. hutchisonii* Ahumada, *A. hypoglauca* Kuhl., *A. inflata* HBK, *A. killipiana* Schmidt, *A. labiata* Willd., *A. leptosticta* Urb., *A. lindeniana* Duchartre, *A. lingua* Malme, *A. lingulata* Ule, *A. loefgrenii* Hoehne, *A. macrorhyncha* Hoehne, *A. macrota* Duchartre, *A. malmeana* Hoehne, *A. manaosensis* Ahumada, *A. marianensis* Ahumada, *A. melanoglossa* Speg., *A. mishuyacensis* Schmidt, *A. mossii* S. Moore, *A. nummularifolia* HBK, *A. odoratissima* L., *A. orbicularis* Duchartre, *A. papillaris* Mast., *A. passifloraefolia* A. Rich., *A. paulistana* Hoehne, *A. peltata* L., *A. peltato-deltaidea* Hoehne, *A. physodes* Ule, *A. pilosa* HBK, *A. pohliana* Duchartre, *A. prostrata* Duchartre, *A. pubescens* Willd., *A. pucarensis* Ahumada, *A. raja* Mart. & Zucc., *A. ringens* Vahl, *A. rugosa* Lam., *A. rumicifolia* Mart. & Zucc., *A. schreiteri* Ahumada, *A. schultzeana* Schmidt, *A. schulzii* Ahumada, *A. smilacina* (Klotzsch) Duchartre, *A. stomachoides* Hoehne, *A. taliscana* Hook. & Arn., *A. tentaculata* Schmidt, *A. tigrina* A. Rich., *A. triangularis* Cham., *A. trilobata* L., *A. truncata* Fielding & Gardner, *A. urupaensis* Hoehne, *A. xerophytica* R. E. Schultes, *A. warmingii* Mast., and *A. weddellii* Duchartre.

***Aristolochia* ser. *Hexandrae* subser. *Anthocaulicae* F. González, subser. nov. HOLOTYPE: *Aristolochia iquitensis* Schmidt. Figures 4, 5F-I.**

Plantae anthocaulicae; synflorescentia truncata, ad anthoblastos paracladiales, pseudocaulifloros vel caulifloros bracteosos reducta; anthoblasti paracladiales ad coflorescentiam saepe confertifloram reducti; internodia coflorescentiae constricta, ad 1 cm longa. Phorophylla bracteosa sessilia vel subsessilia, usque ad 7 mm longa et 4 mm lata.

Anthocaulic plants; synflorescence reduced to paracladial anthoblasts, pseudocauliflorous or cau-

liferous, bracteate; paracladial anthoblasts reduced to the coflorescence (hypotagma absent), usually densely flowered, the internodes constricted, to 1 cm long; phorophylls bracteal, sessile or subsessile, to 7 mm long and 4 mm wide.

*Distribution:* Primary, wet tropical forests, especially the Amazon basin.

The following species are recognized in this subseries: *Aristolochia bukuti* Poncy, *A. cauliflora* Ule, *A. cordiflora* Mutis ex HBK, *A. cornuta* Mast., *A. cremersii* Poncy, *A. flava* Poncy, *A. goudotii* Duchartre, *A. guentheri* Schmidt, *A. iquitensis* Schmidt, *A. klugii* Schmidt, *A. lagesiana* Ule, *A. leuconeura* Linden, and *A. ruiziana* Duchartre.

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