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Source: *Systematic Botany*, Vol. 18, No. 4 (Oct. - Dec., 1993), pp. 593-613

Published by: [American Society of Plant Taxonomists](#)

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Septal Nectary Anatomy and Phylogeny of the Haemodoraceae

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ABSTRACT. Septal nectary anatomy of members of the Haemodoraceae is described, with emphasis on nectary number and relative position within the ovary. Three types of septal nectaries are defined: infralocular, interlocular, and supralocular. The phylogenetic and possible adaptive significance of these features are assessed by adding the data to a previous cladistic analysis of the Haemodoraceae and considering cladistic patterns in terms of functional floral morphology. I hypothesize that: 1) three interlocular septal nectaries are ancestral for the Haemodoraceae, but were secondarily acquired in the genus *Anigozanthos* (Conostylideae) in response to selective pressure for increased nectar production for bird pollination; 2) three supralocular nectaries constitute a synapomorphy for all or most of the tribe Conostylideae, but evolved independently in the genus *Dilatris* of the Haemodorea; 3) two infralocular nectaries evolved concomitantly with unique "perianth apertures" and arose via the evolution of zygomorphy and basal displacement of nectaries into the receptacular tissue; and 4) septal nectaries were independently lost in the genera *Xiphidium* and *Phlebocarya*, perhaps in response to a shift in pollination mechanism.

The Haemodoraceae are a monophyletic group consisting of 13 currently recognized genera and approximately 100 species (Anderberg and Eldenäs 1991; MacFarlane et al. 1987; Simpson 1990); the monotypic *Macropidia fuliginosa* has recently been reclassified as a member of the genus *Anigozanthos* by Anderberg and Eldenäs (1991), a viewpoint with which I wholly agree. Members of the Haemodoraceae are rhizomatous to stoloniferous herbs, with equitant, unifacial leaves and mostly cymose inflorescences and have distributions spanning Australia, South Africa, South and Central America, and eastern North America. The family exhibits considerable diversity in floral morphology. Flowers range in size from approximately 5 mm long in the bee-pollinated genera *Xiphidium* (South and Central America) and *Phlebocarya* (southeastern Australia) to over 6 cm long in species of the bird-pollinated *Anigozanthos* (southwestern Australia). Flowers may be either actinomorphic or zygomorphic, enantiostylous or symmetrically-styled, glabrous or densely tomentose (ranging in color from white, yellow, green, orange, red, to black); the perianth can be either imbricate or valvate; stamen number is 6, 3, or 1; ovary position is superior, half-inferior, or inferior; locule number and fertile carpel number is either 3 or 1; and ovules and seeds may be 1, 2, 4, 5–7, or indefinite in number, epitropous or hypotropous in position, and considerably variable in shape and size (see Simpson 1990).

I recently analyzed the phylogenetic relationships of genera and species complexes within the Haemodoraceae and proposed some changes in classification (Simpson 1990). In order to understand better the evolution of the diverse floral morphology in the group and to help resolve incompatibilities of certain hypotheses of character evolution, I have initiated studies of floral anatomy, ovary development, and ovule/seed development in the family. This paper describes observations on the anatomy and spatial relationship of septal nectaries in the Haemodoraceae (and near outgroups) and the phylogenetic significance of these new data. More detailed anatomical descriptions of septal nectary epithelial cells, subepithelial cells, and surrounding vasculature and ergastic substances will appear in another publication.

Dahlgren and Clifford (1982) reviewed the occurrence of floral nectaries in monocotyledons, relying primarily on the work by Dautmann (1970). The three major types of nectaries in monocots that they defined are: 1) perigonal—nectaries at the adaxial bases of tepals; 2) androecial—nectaries on filaments of stamens or staminodes; and 3) septal—nectaries found in the septal regions of the gynoecium. Rare types of monocot nectaries include those found at style bases, stigmas, surface of carpels or ovary, and nectariferous disks. Septal nectaries are by far the most common type found in monocotyledons and are entirely lacking in dicots (Schmid 1985). Septal nectaries are nectar-se-

creting cavities that occur in the septal region between adjacent carpels by the incomplete fusion of carpels during the development of the gynoeceium ("lack of intercarpellary postgenital fusion," Schmid 1985). Smets and Cresens (1988) proposed that the name "gynopleural" nectary replace that of "septal" nectary in order to indicate possible homology between nectaries that occur on outer carpellary surfaces and those occurring internally. However, I choose to retain the term "septal" nectary in the present paper because of its widespread use in the literature. The cavities of septal nectaries are generally vertically oriented and are delimited by one or more layers of nectar-secreting epithelial cells and subepithelial cells. The nectaries may be found in either superior- or inferior-ovary taxa and secrete nectar via pores or slits at the base or apex of the ovary (Daumann 1970). Schmid (1985) recognized morphological criteria for distinguishing septal nectary types, among these being: transectional outline (including whether simple, or labyrinthine/convoluted), distinctiveness (whether unfused or confluent), vertical extent, distance from ovarian center, and position of opening in gynoeceium.

In the Haemodoraceae, septal nectaries have been reported in all but one of the 13 genera defined here (Dahlgren and Clifford 1982; Simpson 1990). The closest relatives to the Haemodoraceae have recently been considered to be the Pontederiaceae and Typhales, with the Philydraceae, Bromeliaceae, Velloziaceae, and Zingiberales, respectively, more distantly related (Dahlgren and Rasmussen 1983). [The Velloziaceae have been suggested to be rather distant relatives to the Haemodoraceae based on chloroplast DNA *rbcL* sequence data (Clark et al. 1993).] Simpson (1987, 1990) argued that the Pontederiaceae are the most likely sister group to the Haemodoraceae, based largely on pollen ultrastructural evidence. Recent molecular work by Clark et al. (1993) places the Haemodoraceae, Philydraceae, Pontederiaceae, and (in some analyses) Commelinaceae as near relatives. Among these possible outgroups, septal nectaries are absent in all Typhales (Dahlgren and Clifford 1982) and in all Philydraceae (Hamann 1966). In the Pontederiaceae, septal nectaries are reported to occur in *Pontederia* and *Eichornia* but are absent in *Heteranthera* (Dahlgren and Clifford 1982; Van Heel 1988; Simpson 1990). In the Commelinaceae (as well as in the entire

Commeliniflorae, sensu Dahlgren and Clifford 1982), septal nectaries are absent. Only *Commelina* is reported to have nectaries at all, these being of the androecial type (Dahlgren and Clifford 1982). Among other putative close relatives of the Haemodoraceae, (sensu Clark et al. 1993; Dahlgren and Clifford 1982), septal nectaries are widespread in the Bromeliaceae and Zingiberales. In the Bromeliaceae, septal nectaries have been reported in 35 investigated genera (ca. 90 species) of all three subfamilies (Böhme 1988). Among these taxa, septal nectary anatomy is quite diverse; the position of the nectaries is either below (equivalent to "infralocular" used here), within (equivalent to "interlocular" used here), or above (equivalent to "supralocular" used here) the locular region of the ovary. In the Zingiberales, all members of which have predominantly inferior ovaries, septal nectaries are known to occur in seven of the eight families (lacking only in Lowiaceae). Of those families possessing septal nectaries, nectary position varies. The nectaries occur within the locular region (equivalent to "interlocular" used here) in members of the Cannaceae, Heliconiaceae, Marantaceae, and Strelitziaceae (a portion of the nectaries also occurring below the locules in the Heliconiaceae); nectaries occur above the locules (equivalent to "supralocular" used here) in members of the Costaceae, Musaceae, and Zingiberaceae (Kirchoff, pers. comm.; Newman and Kirchoff 1992). Although the Bromeliaceae and Zingiberales were not designated as outgroups in the present cladistic study, they should be considered in broader phylogenetic analyses of the complex.

MATERIALS AND METHODS

Live, mature buds or recently opened flowers were fixed in formalin-acetic acid-alcohol or in 4% glutaraldehyde, embedded in Paraplast, and serially cross-sectioned at thicknesses ranging from 10–18 μm . Preparations were stained with safranin, fast-green, and haemotoxylin according to standard procedures (Berlyn and Miksche 1976; Johansen 1940; Sass 1958). Investigated taxa are listed in Appendix 1.

In order to visualize the spatial distribution of major floral components more clearly, sections approximately 10–50 μm apart (depending on the structure) were drawn using a camera-lucida device attached to a compound or

dissecting microscope. Pencil outlines of the boundaries of tepals, locules, placentae, ovules, septal nectaries, and ovary/style were prepared. For more detailed study of floral vasculature, crystal distribution, and ovule morphology, color slide photographs using partial polarization optics were prepared and projected onto the digitizing pad for outlining. These floral outlines were computer-digitized using a Summagraphics digitizing pad on an IBM-compatible, AT&T 386 computer using the IBM PC-Based Three-Dimensional Reconstruction System (HVEM-3D, version 1.2: Laboratory for High Voltage Electron Microscopy, Department of Molecular, Cellular and Developmental Biology, Boulder, Colorado 80309). This system implements computer-image stacking of serial sections to portray a more three-dimensional view. Programming is allowed for changes in line thickness, coloring and shading, outline (contour) fill-in, and section or object overlap, and the final image may be inclined at any angle and rotated freely around the X, Y, and Z axes. Spatial distributions of the receptacular region, locules, septal nectaries, and inferior/superior ovary regions were graphically drawn to illustrate comparisons between taxa (summary diagram of Fig. 1).

Cladistic analyses of the Haemodoraceae were implemented using PAUP, Version 3.0s (Swofford 1991). The defined septal nectary characters (see "Phylogenetic and Evolutionary Implications," below) were added to the original character-taxon data set of Simpson (1990), the only additional modification being that a species of *Conostylis*, *C. preisii*, was added and that the genus *Xiphidium* was treated as two taxa: *X. coeruleum* and *X. xanthorrhizon*. This change of taxa resulted in no additional change in cladogram topology whether the original character set or the original plus septal nectary character set was used. Septal nectary characters were mapped on the most parsimonious cladogram using MacClade, version 2.1 (Maddison and Maddison 1987).

In the results below, "ovary" is equivalent to the non-stylar gynoecium, which is composed of three syncarpous carpels in all taxa. Ovaries are either superior, predominantly inferior, or partially inferior; thus, all ovaries have at least a portion that is superior (above the point of attachment of the perianth/androecium). For

purposes of comparison, the bottom (base) of the ovary is defined to be either its lowest point of detachment from the perianth/androecium or (in the case of ovaries that are at least partially inferior) the lowest extent of the locules. The superior portion of an ovary generally has a lowermost level (lowest point of detachment) and an uppermost level, the highest level at which some portion of the ovary remains fused to the perianth/androecium. The top (apex) of the ovary is designated as the point of abrupt transition to a style. The receptacle is defined as the tissue occurring above the terete, unexpanded pedicel but below the ovary (as defined above). "Posterior" is equivalent to adaxial (the side toward the inflorescence axis) and corresponds to the top side in those flowers that are horizontally oriented. "Anterior" is equivalent to abaxial (the side away from the inflorescence axis) and corresponds to the bottom side in those flowers that are horizontally oriented.

RESULTS AND DISCUSSION

Haemodoraceae. Of the 13 genera in the family, 11 show some evidence of septal nectaries, the exceptions being both species of *Xiphidium*, which lack any trace of septal nectaries, and the one investigated species of *Phlebocarya*. The absence of septal nectaries in *Xiphidium* is an evolutionary reversal according to previous cladistic analyses and may be correlated with its pollination mechanism (Simpson 1990; see "Phylogenetic and Evolutionary Implications," below). *Phlebocarya* was previously listed as having septal nectaries (Simpson 1990); however, this paper offers a reinterpretation as determined by more detailed anatomical evidence (see "Supralocular Septal Nectaries," below). Of the 11 genera with septal nectaries, I have recognized three basic patterns that are based on nectary number and the vertical extent and position of the nectaries relative to other floral components. These are termed infralocular, interocular, and supralocular.

Infralocular Septal Nectaries. Infralocular septal nectaries are found in four genera: *Barberetta*, *Pyrrorrhiza*, *Schiekia*, and *Wachendorfia*. Along with *Xiphidium*, these taxa are the only members of the Haemodoraceae with a superior ovary position (that of *Pyrrorrhiza* being slightly inferior). In the above four genera, the nectaries are positioned proximal to and/or at the ex-

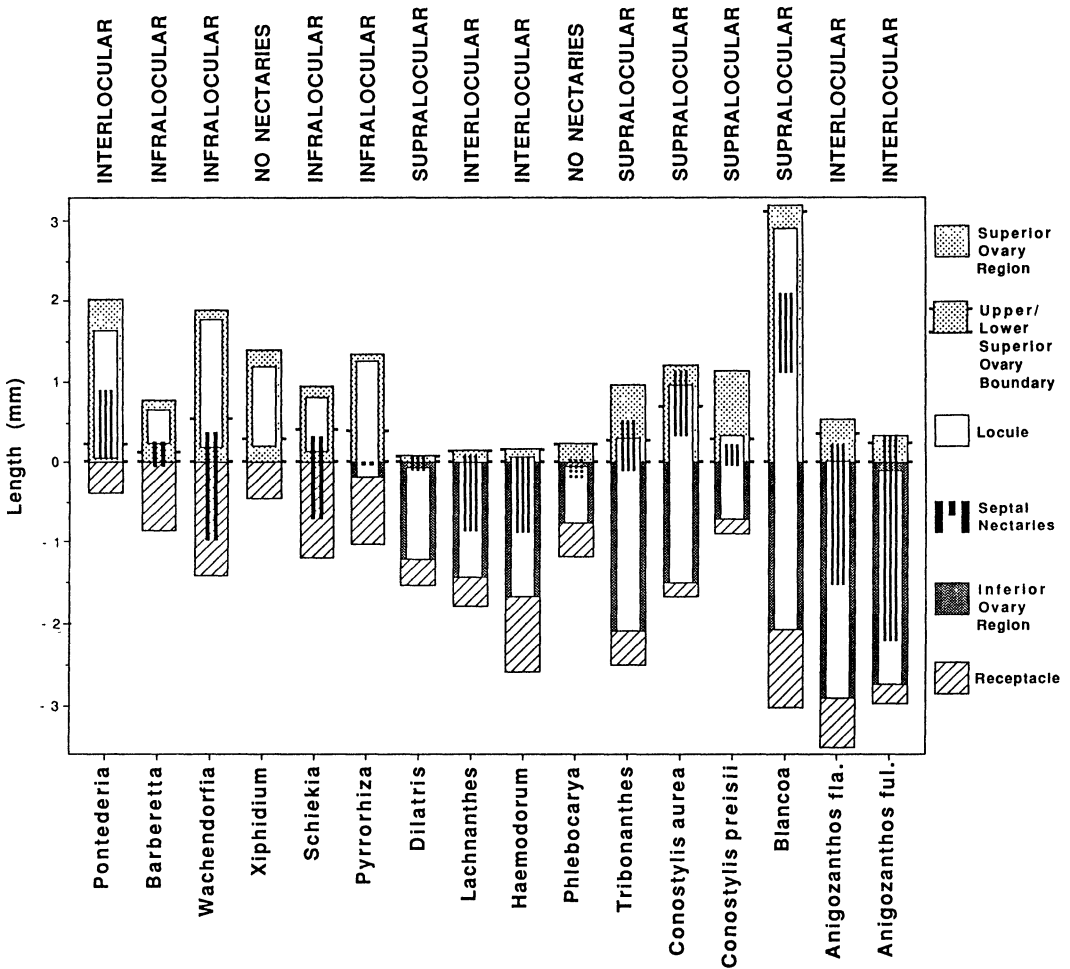
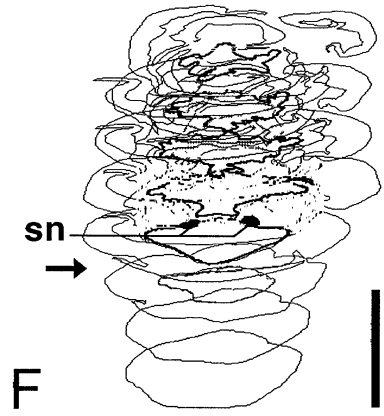
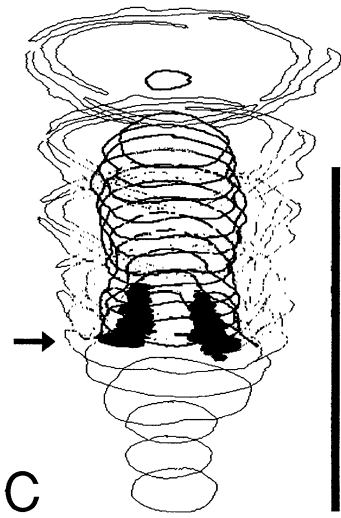
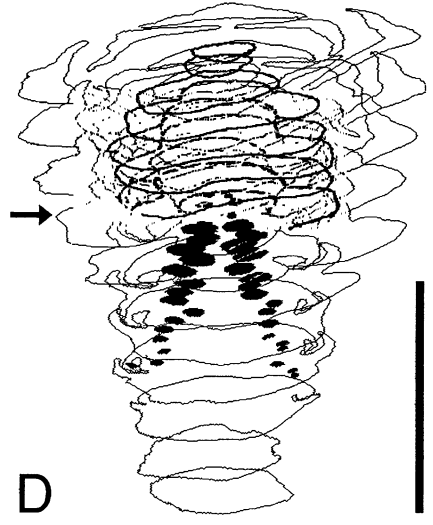
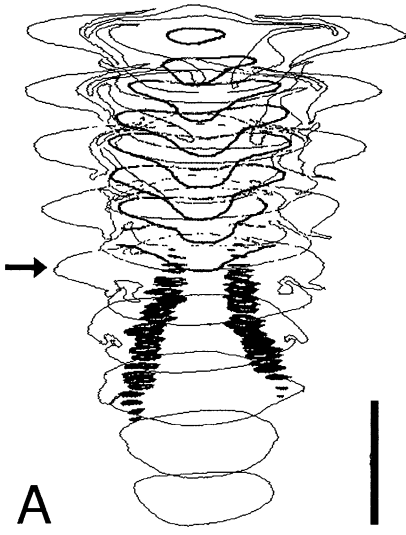


FIG. 1. Graph comparing vertical dimensions of six floral structures or regions for all investigated taxa of the Haemodoraceae plus *Pontederia* of the outgroup Pontederiaceae. Diagrams are centered at the lowermost level of the superior portion of the ovary (see "Materials and Methods" for definitions of floral components). Within the Haemodoraceae, note: 1) four genera with two infralocular septal nectaries (*Barberetta*, *Wachendorfia*, *Schiekia*, and *Pyrrothiza*); 2) four genera (five species) with three supralocular septal nectaries (*Dilatris*, *Tribonanthes*, *Conostylis* spp., and *Blancoa*); 3) three genera (four species) with three interloocular septal nectaries (*Lachnanthes*, *Haemodorum*, and *Anigozanthos* spp.); and 4) absence of septal nectaries in *Xiphidium* and *Phlebocarya*. The genus *Phlebocarya* possesses three septal cavities (dashed vertical lines), interpreted as being non-homologous with septal nectaries of other family members (see text). The outgroup *Pontederia* also has interloocular nectaries, but these are located in the basal region of a superior ovary (rather than in the apical region of an inferior ovary; see text).

FIG. 2. Three-dimensional reconstructions of mature flowers. A-B. *Wachendorfia thrysiflora*. C. *Barberetta aurea*. D-E. *Schiekia orinocensis*. F. *Pyrrothiza neblinae*; note two minute septal nectaries (sn). Posterior side of flower is facing in A and F; anterior side of flower is facing in C and D and is below in B and E. Shading and symbols: ovary surface (superior portion) = dark lines; locules = grey; septal nectaries = solid black; ovary base (superior portion) = arrow. Scale bars = 1 mm.



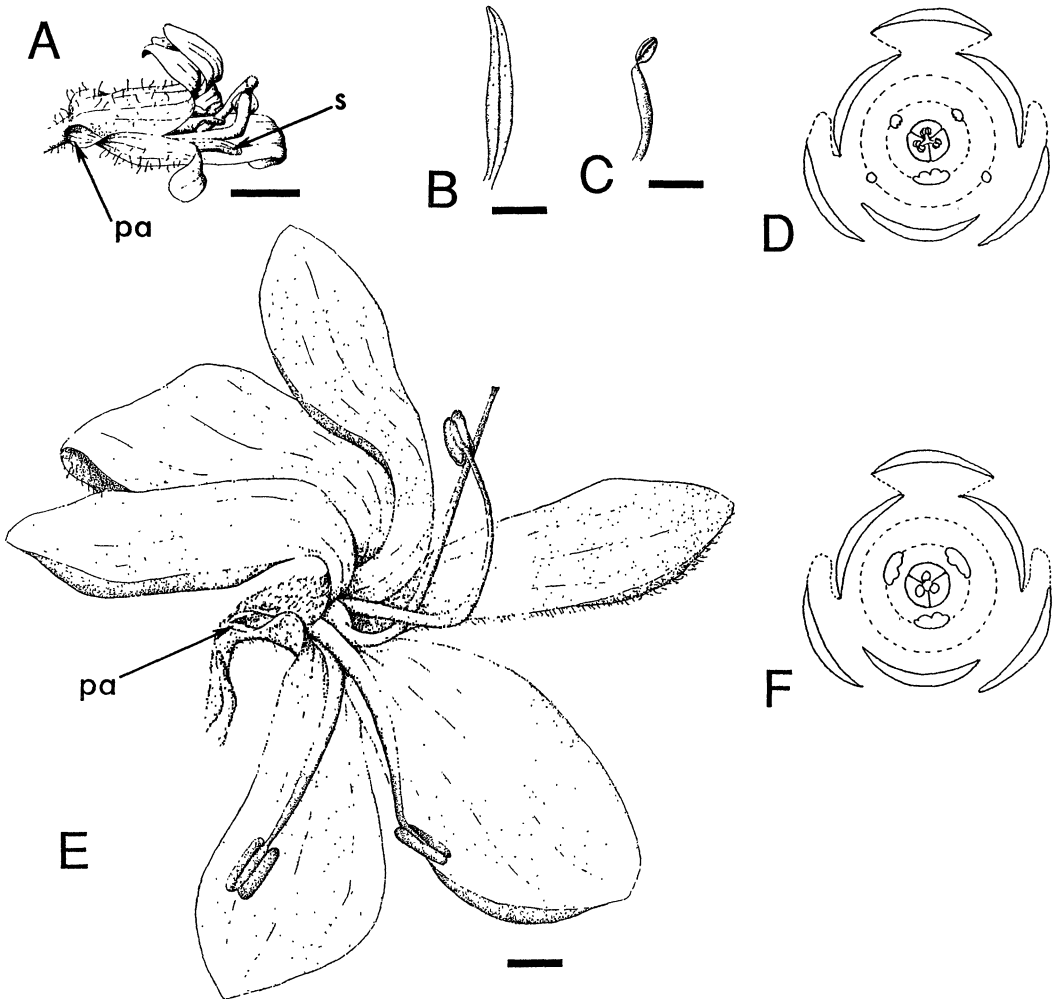


FIG. 3. Floral morphology of *Schiekia* and *Wachendorfia*, after Simpson (1990). A-D. *Schiekia orinocensis*. A. Whole flower, showing staminode (s) and perianth aperture (pa), posterior (adaxial) side above. Scale bar = 2 mm. B. Staminate close-up. Scale bar = 1 mm. C. Posterior reduced stamen. Scale bar = 1 mm. D. Floral diagram, posterior (adaxial) side above. Note basal fusion of upper five tepals. E-F. *Wachendorfia thrysi-flora*. E. Whole flower, showing perianth aperture (pa), posterior (adaxial) side above. Scale bar = 2 mm. F. Floral diagram, posterior (adaxial) side above. Note basal fusion of upper five tepals.

treme base of the locules (Figs. 1, 2A-F). In all cases only the two latero-posterior septal nectaries are present; the median anterior nectary is absent (see, e.g., Fig. 2B, E).

Among these four genera, *Wachendorfia* and *Schiekia* are unique in the Haemodoraceae (and perhaps among flowering plants) in possessing "perianth apertures" (Ornduff and Dulberger 1978; Simpson 1990). These two taxa have an extensive receptacular region, and, in both, the five upper tepals (all except the median anterior

inner tepal) are basally fused (Fig. 3). However, the upper margins of the two latero-anterior outer tepals and the lower margins of the two latero-posterior inner tepals are decurrent along the length of the receptacle and may overlap with one another. These decurrent tepal margins form flaps that surround a cup-shaped cavity at the base of the receptacle, the "perianth aperture" (see Figs. 3A, D-F, 4A). In these two genera the two septal nectaries run adjacent to the perianth apertures and extend distally only

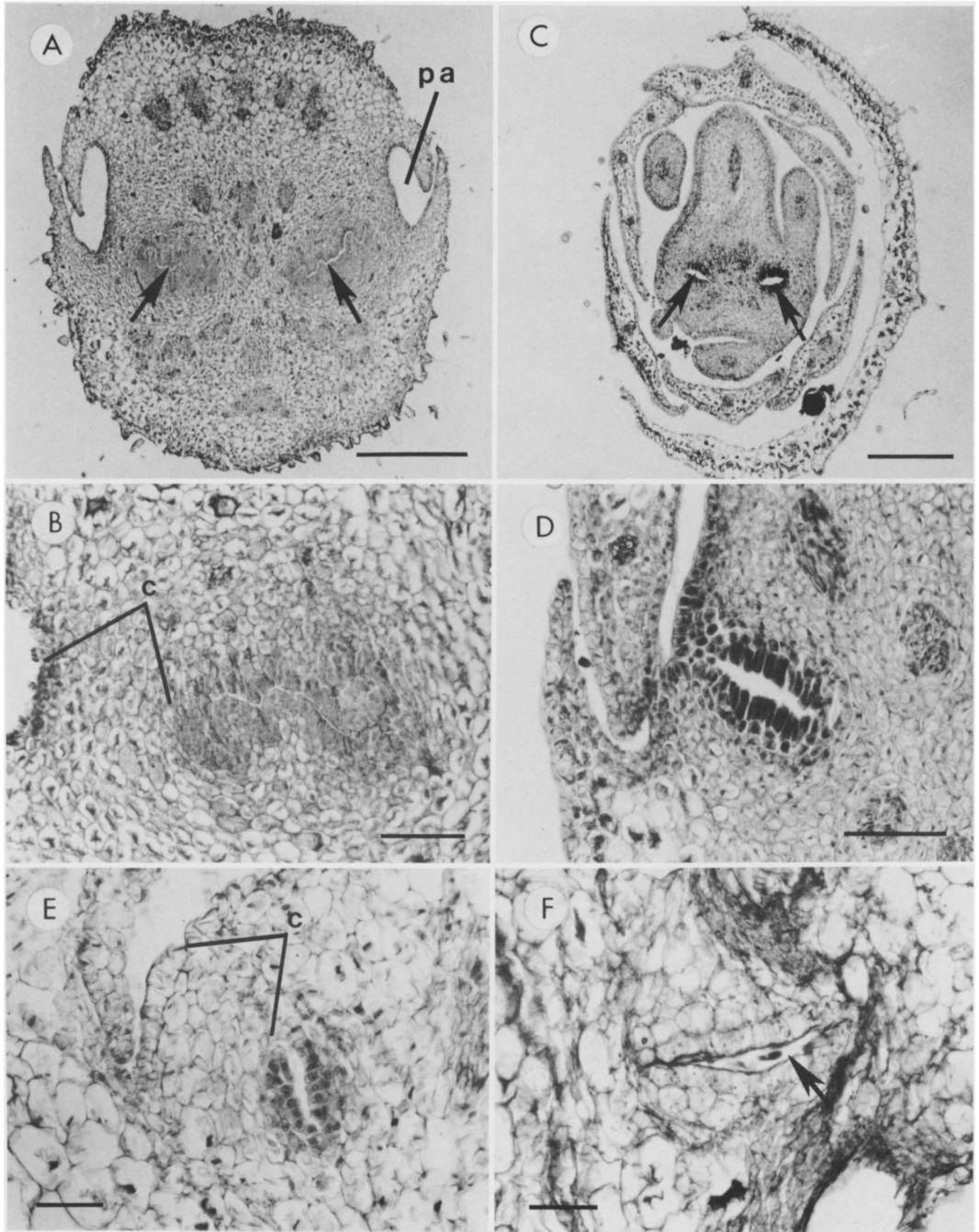
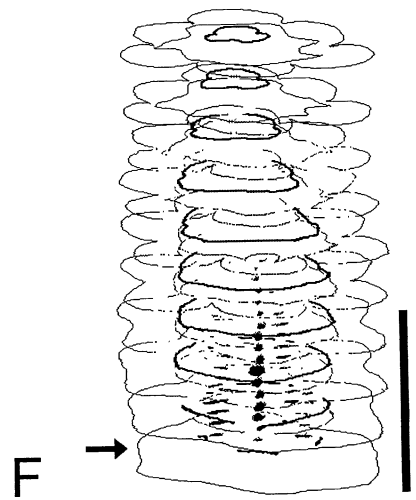
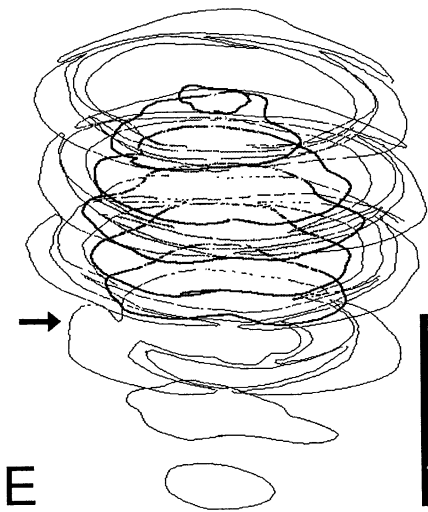
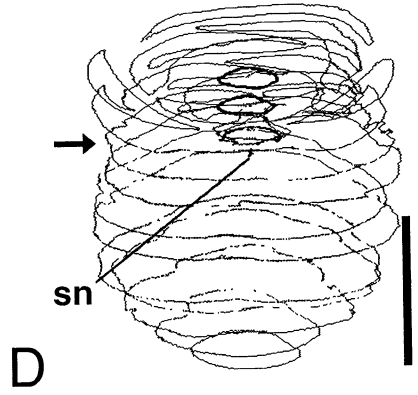
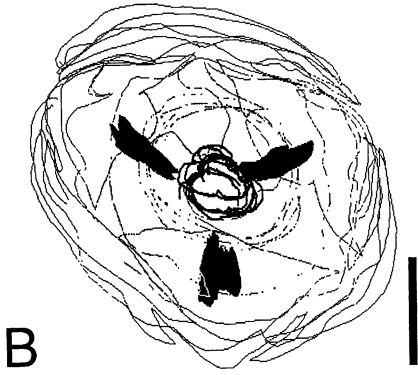
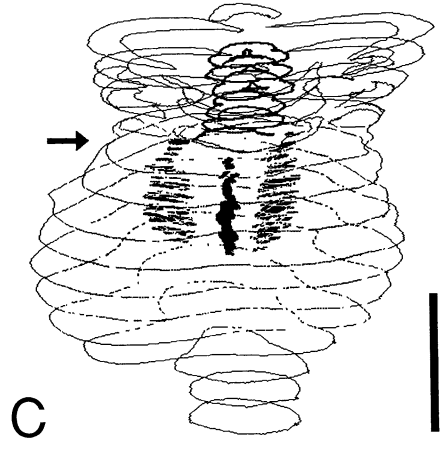
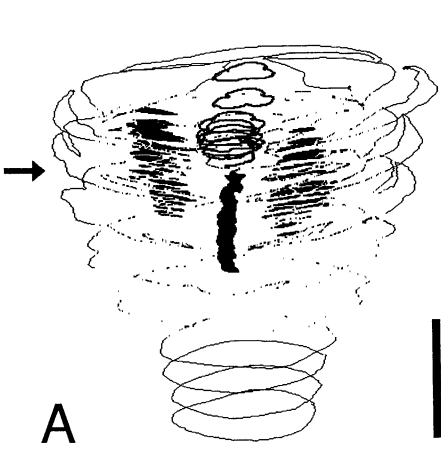


FIG. 4. Flower cross-sections from histological preparations. A-B. *Wachendorfia paniculata*. A. Receptacular region, posterior side above. Note two septal nectaries (arrows) and two perianth apertures (pa) defined by overlapping of latero-anterior outer tepals upon latero-posterior inner tepals. Scale bar = 500 μ m. B. Close-up of septal nectary, showing convoluted canal. Note commissure (c) between nectary (right) and perianth aperture cavity (left). Scale bar = 100 μ m. C-D. *Barberetta aurea*. C. Receptacular region, posterior side above. Note two septal nectaries (arrows). Scale bar = 200 μ m. D. Close-up of septal nectary, showing single layer of densely staining epithelial cells. Scale bar = 100 μ m. E. *Schiekia orinocensis*. Close-up of septal nectary. Note commissure (c) between nectary canal (lower right) and perianth aperture cavity (upper left). Scale bar = 50 μ m. F. *Pyrrorhiza neblinae*. Close-up of septal nectary (arrow). Note absence of densely staining epithelial cells. Scale bar = 50 μ m.



to the base of the ovary locules (at the level of perianth attachment), where they become attenuated before terminating (Fig. 2A, B, D, E). The septal nectaries open directly to the outside via a short slit at the basal region of the perianth aperture, which is the most proximal extent of the septal nectaries (where the nectaries themselves are relatively small in cross-sectional area). However, a slit-like commissure occurs between the septal nectaries and the outer tissue surface throughout its length (Fig. 4B, E). This commissure represents a vestige of the ontogenetic origin of the nectaries by accelerated differential growth and appression of flanking receptacular and gynoeical tissue (Simpson and McMillan, in manuscript). The commissure may serve as an additional conduit for nectar secretion, as it occurs essentially throughout the extension of the perianth aperture.

In both *Wachendorfia* and *Schiekia*, the septal nectaries in the proximal receptacular region are composed of single-celled epithelial layers (Fig. 4E). In *Schiekia*, this structure continues throughout the length of the septal nectaries. In *Wachendorfia*, the nectaries distally become quite large and convoluted in outline, surrounded by several layers of smaller, differentiated, subepithelial cells (Fig. 4A, B).

The monotypic genera *Pyrrothiza* and *Barberetta* show no external evidence of perianth apertures. However, these taxa are very similar to *Wachendorfia* and *Schiekia* in having only two septal nectaries at similar infralocular positions (Figs. 1, 2C, F). Those of *Barberetta* extend from the extreme base of the locules through the proximal ovarian tissue to the distal receptacular region (Figs. 2C, 4C); the basal marginal regions of the outer latero-anterior tepals overlap those of the inner latero-posterior tepals, exhibiting some similarity to perianth apertures (Fig. 4D). The septal nectaries of *Pyrrothiza* are very short, occurring only at the base of the locules near the junction of the superior and inferior portions of the ovary (Fig. 2F). In both

Pyrrothiza and *Barberetta* the septal nectaries consist of a single layer of epithelial cells and are considerably smaller than those of *Wachendorfia* and *Schiekia*. The nectaries of *Pyrrothiza*, in fact, appear non-functional because of their extremely limited vertical extent, the absence of specialized, densely staining epithelial cells, and the apparent absence of an opening or commissure for nectar secretion (Fig. 4F).

Interocular Septal Nectaries. Interocular septal nectaries are found in three genera, all of which have an inferior ovary: *Haemodorum* (Fig. 5A, B), *Lachnanthes* (Fig. 5C), and *Anigozanthos* (including *Macropidia*; Fig. 7E, F). In these taxa three nectaries are positioned in the distal half to three-quarters of the locular region, almost entirely within the inferior portion of the ovary (see Fig. 1).

In all three genera, the septal nectaries are prominent in the central septal tissue (Fig. 6A, C, E); they extend from a level just below the insertion of the placentae to the ovary apex (Figs. 5A-C, 7E, F; see Fig. 1). The septal nectaries are lined with papillate epithelial cells (Fig. 6B). In all taxa the nectaries open at the extreme apex of the ovary (e.g., Fig. 6D) near the junction of ovary and style. In *Haemodorum*, *Lachnanthes*, and *Anigozanthos flavidus*, septal nectaries consist of a single layer of epithelial cells and 3-5 layers of surrounding differentiated cells that have densely staining cytoplasmic contents (Fig. 6B). *Anigozanthos fuliginosus* Hook. D. Don in Sweet differs in having very massive septal nectaries, each with numerous layers of surrounding differentiated cells defining a cavity that is convoluted in outline (Fig. 6E, F).

Supralocular Septal Nectaries. Four genera have what are termed supralocular septal nectaries: *Blancoa*, *Conostylis*, *Dilatris*, and *Tribonanthes*. (*Phlebocarya* is interpreted as lacking septal nectaries; see below.) All four genera have a predominantly inferior or half-inferior ovary position; thus, in all taxa, part of the ovary is inferior and part is superior. Septal nectaries in

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FIG. 5. Three-dimensional reconstructions of mature flowers. A-B. *Haemodorum spicatum*. C. *Lachnanthes caroliniana*. D. *Dilatris pilansii*; note minute septal nectaries (sn) at ovary apex. (These are difficult to see in this 3-D reconstruction; see Fig. 9C-E.) E. *Xiphidium caeruleum*; note absence of septal nectaries. F. *Pontederia cordata*. Anterior side of flower is facing in A and C-F and below in B. Shading and symbols: ovary surface (superior portion) = dark lines; locules = grey; septal nectaries = solid black; ovary base (superior portion) = arrow. Scale bars = 1 mm.

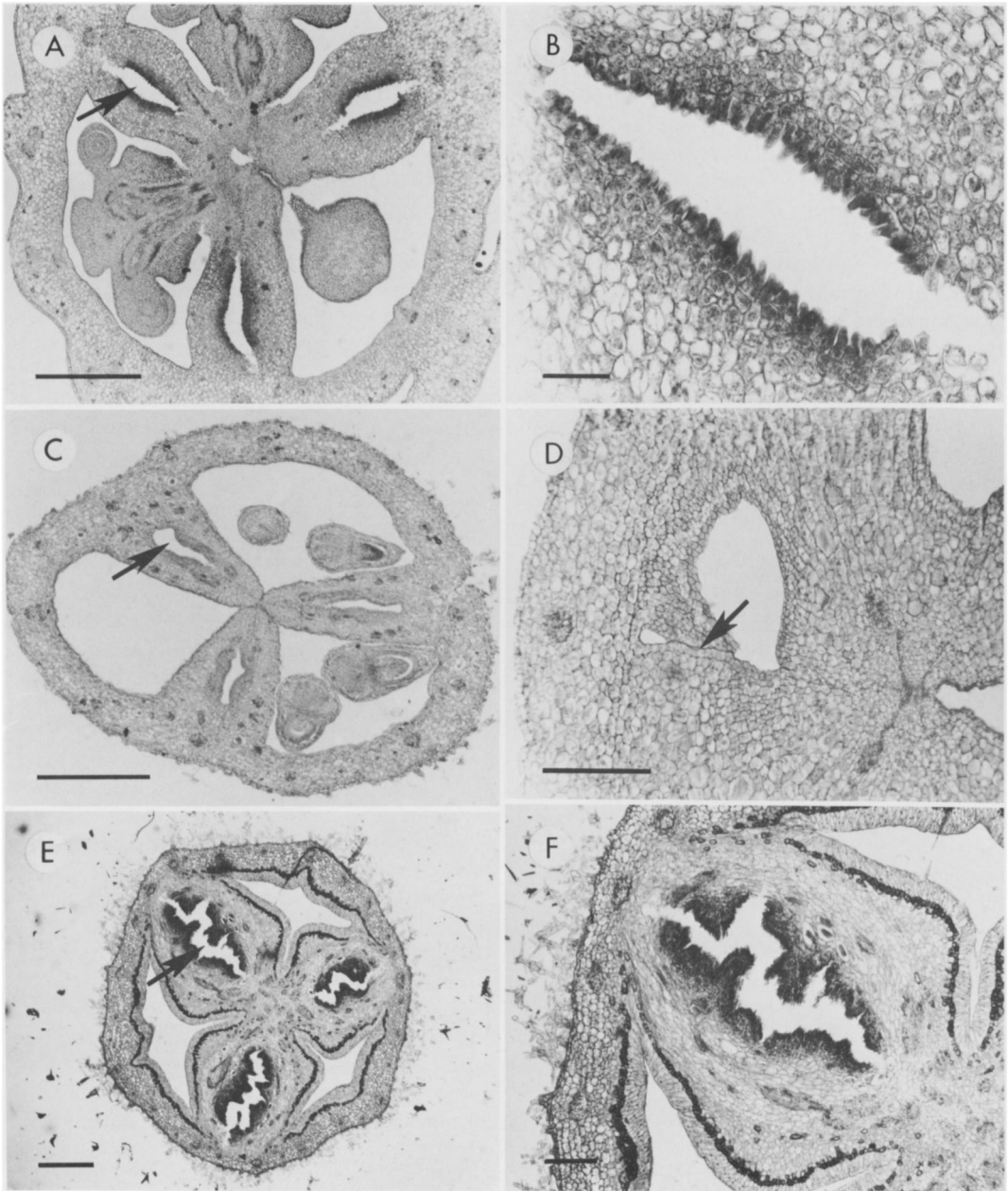


FIG. 6. Flower cross-sections from histological preparations. **A–B.** *Haemodorum spicatum*. **A.** Cross-section of inferior ovary, showing three septal nectaries (arrow at one of these). Scale bar = 500 μm . **B.** Close-up of septal nectary. Note densely staining, papillate epithelial cells. Scale bar = 50 μm . **C–D.** *Anigozanthos flavidus*. **C.** Cross-section of inferior ovary, showing three septal nectaries (arrow at one of these). Scale bar = 500 μm . **D.** Apex of ovary, showing commissure (arrow) between septal nectary (left of arrow) and cavity at style base (upper right of arrow). Scale bar = 200 μm . **E–F.** *Anigozanthos fuliginosus*. **E.** Cross-section of inferior ovary, showing three septal nectaries (arrow at one of these). Scale bar = 500 μm . **F.** Close-up of septal nectary, showing several layers of densely staining cells and convoluted canal. Scale bar = 200 μm .

these taxa are positioned in the most distal region of the ovary; these nectaries are also entirely or almost entirely in the superior part of the ovary (see Fig. 1).

Septal nectaries of the genera *Blancoa* and *Conostylis* are well developed (Figs. 7C, D, 8A, C, E; see Fig. 1), consisting of a single layer of radially elongate epithelial cells (Fig. 8D, F). These taxa are unique in the family in that cavities occur opposite the septa; these apparently develop by the incomplete separation of the superior portion of the ovary and the perianth tube in the regions opposite the carpels (Fig. 8A–C, E). In the *Conostylis* species investigated (*C. preisii* and *C. aurea*) the nectaries clearly empty into these cavities over a considerable region (Fig. 8B). The monotypic *Blancoa* differs in that no evident opening from the septal nectaries is present; only a thin commissural line occurs in the tissue opposite the nectaries (Fig. 8F), which apparently serves as the outlet for nectar secretion to the outside into the cavities.

Tribonanthes variabilis resembles the above two genera in that the septal nectaries are well developed and primarily traverse the superior portion of the ovary (Figs. 1, 7B, 9A). However, the nectaries open to the outside only at the extreme distal end of their extent, near the style base (Fig. 9B) and not directly into cavities as in *Blancoa* and *Conostylis*. These septal nectaries are also composed of a single layer of radially elongate epithelial cells (Fig. 9B).

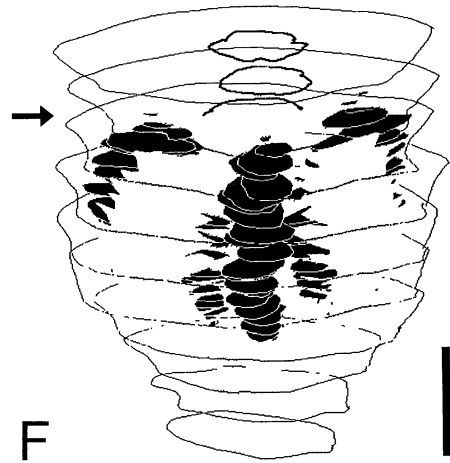
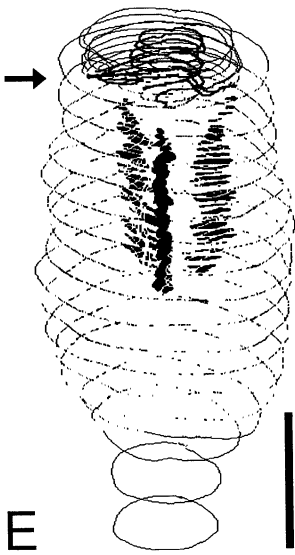
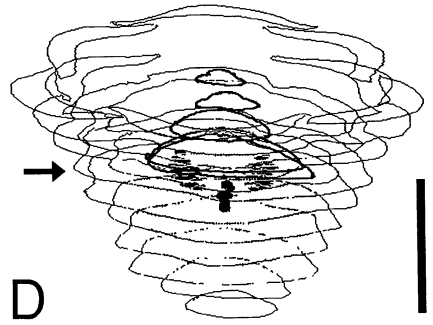
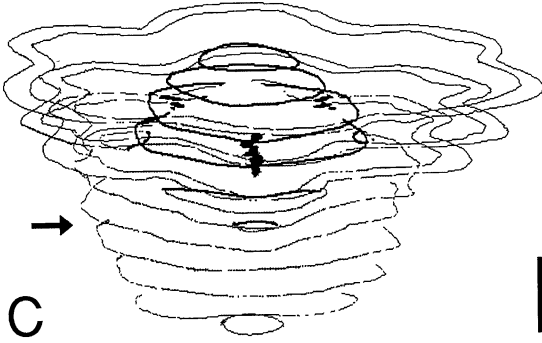
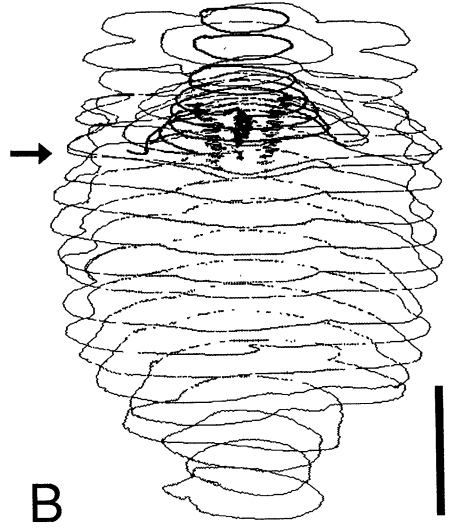
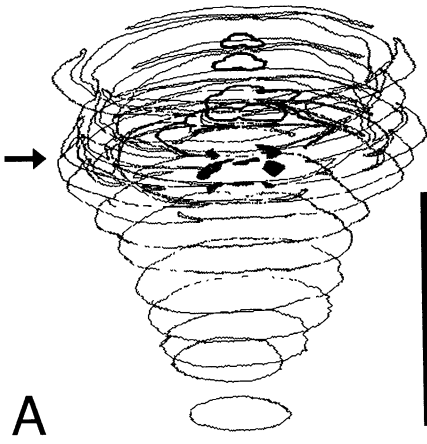
Septal nectaries in *Dilatris pilansii* (and *D. corymbosa*, not illustrated) consist of small cavities (radially-oriented in outline) that are contiguous with a slit-like commissure between the nectaries and the stylar canal (Fig. 9C, D). These septal nectaries are quite small and extend a very short distance at the ovary apex (Fig. 5D). The septal nectaries open to the outside at the extreme apex of the ovary; at this level they are lined with at least a semblance of an epithelial layer (Fig. 9E). Although the septal nectaries of *Dilatris* are quite small, they share the basic anatomy of septal nectaries of other genera in the family.

Phlebocarya ciliata possesses three cavities at the extreme apex of the ovary (Figs. 7A, 9F). Although these cavities are similar in position to septal nectaries previously described, they are structurally, and apparently developmentally, quite different from all other investigated

taxa. Unlike all other investigated taxa with septal nectaries, the cavities of *Phlebocarya*: 1) are tangentially-oriented (not radially-oriented); 2) lack any specialized epithelial layer at any position; 3) appear to have originated ly-sigenously (unlike the development of all other septal nectaries in the complex, which appear to have developed by incomplete carpellary fusion; see Schmid 1985); and 4) do not open to the outer surface, either directly or via a commissural slit. Thus, the cavities in *Phlebocarya* are very doubtfully homologous to septal nectaries in the rest of the complex.

Outgroups. In the present cladistic analyses the Pontederiaceae are treated as the closest outgroup to the Haemodoraceae and the Philydraceae as the next closest. As previously mentioned, septal nectaries are absent in all species of the family Philydraceae (Dahlgren and Clifford 1982; Hamann 1966; Simpson 1990, present study). Within the Pontederiaceae, septal nectaries are known to occur in species of *Pontederia* and *Eichhornia*; they are known to be absent in species of *Heteranthera* (Dahlgren and Clifford 1982; Simpson 1990; Van Heel 1988). Flowers of *Pontederia cordata*, investigated here, have three septal nectaries located in the lower half of the superior ovary (Fig. 9G). The nectaries open at the ovary base within the perianth tube (Fig. 5F). Septal nectaries in *Eichhornia paniculata* Solms in DC. are similar to those of *Pontederia* in having pores at the ovary base and nectaries extending up into the septal regions (Van Heel 1988). Van Heel described septal nectary development in *Eichhornia* as occurring "by the lack of meristematic fusion on the periphery of the gynoecium and by the concomitant upwards growth of the carpel primordia and the convex apex."

Despite the absence of septal nectaries in *Heteranthera*, the Pontederiaceae are coded in this analysis as possessing septal nectaries. The rationale for this judgement is that possession of three septal nectaries is likely the ancestral condition for many monocotyledons; the *de novo* evolution of septal nectaries in the family seems unlikely. (See "Phylogenetic and Evolutionary Implications," below, for an alternative possibility.) Because the septal nectaries of *Pontederia* traverse the bulk of the locular region (Figs. 1, 5F), the family is coded as "interlocular" in this analysis. (The vertical extent of septal nectaries



in *Eichhornia* is unknown.) However, *Pontederia* has a septal nectary morphology rather different from any member of the Haemodoraceae and its homology with respect to position is questionable (see "Phylogenetic and Evolutionary Implications," below).

Phylogenetic and Evolutionary Implications. Data from septal nectary morphology were coded for phylogenetic analysis as the following two unordered characters and character states: 1) septal nectary number: three, two, zero, and 2) septal nectary position: infralocular, interocular, supralocular ("?" if nectaries absent). The addition of these septal nectary characters to the original data set of Simpson (1990) resulted in two equally most parsimonious cladograms that are equivalent to the two equally parsimonious topologies reported in that study. Figure 10 portrays the strict consensus tree of these two cladograms, which differ only in the relative placement of *Dilatris*.

Evolutionary patterns in septal nectary morphology in the Haemodoraceae show some interesting trends (Fig. 10). With regard to septal nectary number (character #1), the ancestral condition for the Haemodoraceae is three septal nectaries (Fig. 10A), which is found in most genera. A major novelty within the family was the evolution of two septal nectaries in the clade containing *Barberetta*, *Wachendorfia*, *Xiphidium*, *Schiekia*, and *Pyrrothiza* (Fig. 10A). The occurrence of only two septal nectaries has not been reported in any other tricarpetate monocot taxa with the exception of some members of the family Costaceae (Newman and Kirchoff 1992). Note that the most parsimonious cladogram portrays *Xiphidium* as the sister taxon to the *Barberetta*-*Wachendorfia* clade; the placement of *Xiphidium* among the other genera is unaffected by this character and is dependent on other characters. The absence of septal nectaries in *Xiphidium* is interpreted as an autapomorphy for that lineage as well as for the lineage containing *Phlebocarya* (Fig. 10A).

With regard to septal nectary position (char-

acter #2), the ancestral condition for the family is most parsimoniously explained as interocular (Fig. 10B). This is somewhat uncertain, however. Although the Pontederiaceae are coded as having an interocular nectary position, their homology with the Haemodoraceae is unclear. If the Pontederiaceae are coded having a unique or inapplicable state, then the ancestral condition of nectary position in the Haemodoraceae would be equivocal because of the absence of septal nectaries in the Philydraceae, the second outgroup. Note from Figure 10B that the clade united by the acquisition of two septal nectaries (*Barberetta*, *Wachendorfia*, *Xiphidium*, *Schiekia*, and *Pyrrothiza*) is also united by the presence of infralocular nectaries. Again, the two species of *Xiphidium*, because they lack nectaries, are nested within this clade based on other data. The supralocular septal nectary position in *Dilatris* is interpreted as an autapomorphy. With the exception of *Phlebocarya*, which is equivocal in septal nectary position because of the doubtful homology of its septal "cavities," the bulk of the tribe Conostylideae (the right-hand clade) has a supralocular nectary position, interpreted as a synapomorphy for this portion of the tribe (Fig. 10B); in this clade only the investigated species of *Anigozanthos* have an interocular type.

Information on the phylogenetic pattern of septal nectaries in the Haemodoraceae permits speculation on the adaptive significance of these structures. The hypothesized ancestral condition of three interocular nectaries is rather typical among monocotyledons (Daumann 1970; Schmid 1985). *Haemodorum* and *Lachnanthes*, the two genera that inherited this feature from the common ancestor (Fig. 10), both have relatively small (ca. 1 cm long), erect, actinomorphic flowers that are visited by bees and other small insects (Simpson, pers. obs.); prolific visitation by monarch butterflies has been recorded for *Lachnanthes* (see Robertson 1976). Nectar is secreted via pores near the apex of the (inferior) ovary, presumably as a pollination reward. The interocular extension of septal nectaries, in this case

FIG. 7. Three-dimensional reconstructions of mature flowers. A. *Phlebocarya ciliata*. (NOTE: solid black regions in *Phlebocarya* correspond to septal cavities, not septal nectaries; see text.) B. *Tribonanthes variabilis*. C. *Conostylis aurea*. D. *Conostylis preisii*. E. *Anigozanthos flavidus*. F. *Anigozanthos fuliginosus*. Anterior side of flower is facing in all diagrams. Shading and symbols: ovary surface (superior portion) = dark lines; locules = grey; septal nectaries = solid black; ovary base (superior portion) = arrow. Scale bars = 1 mm.

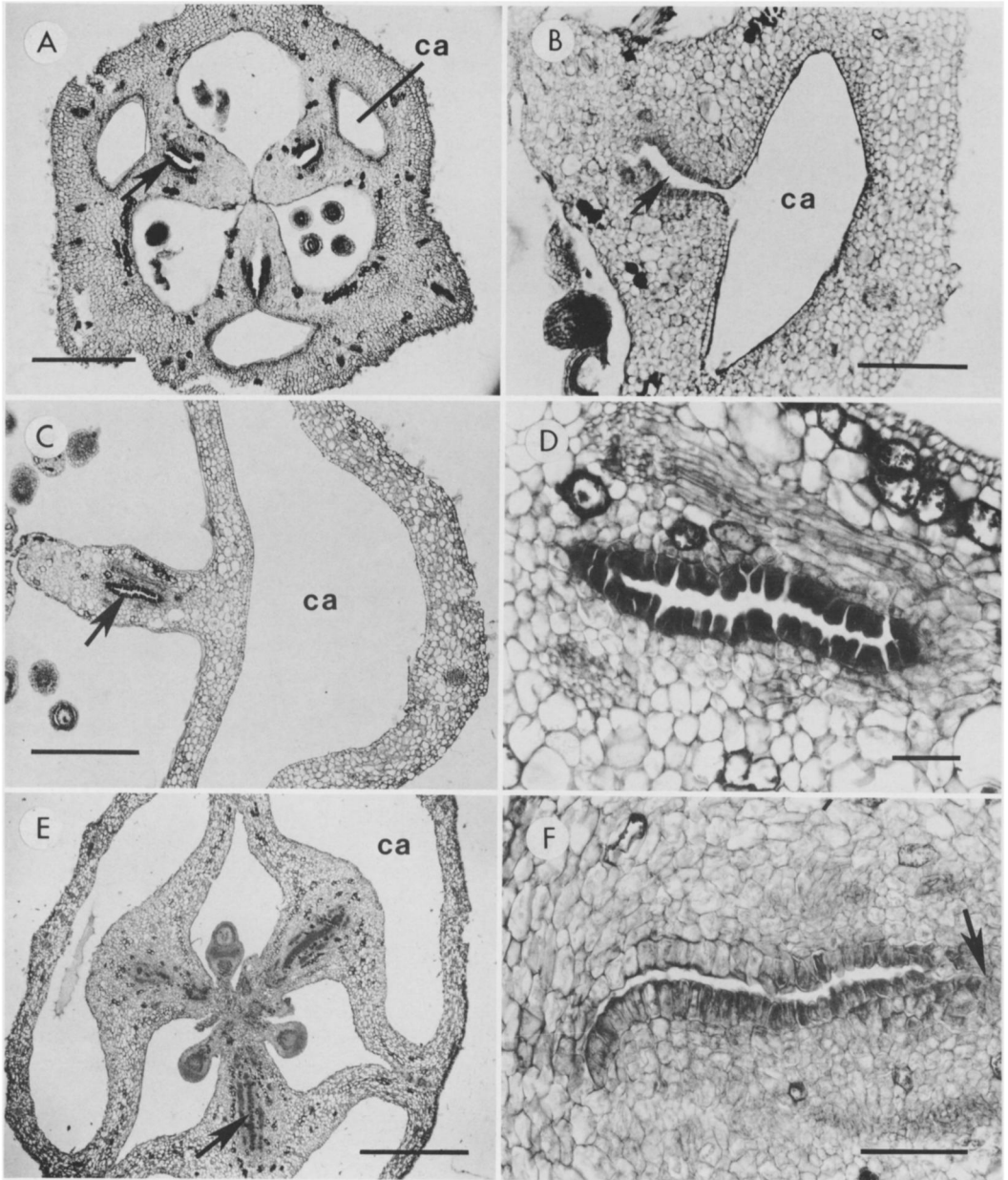


FIG. 8. Flower cross-sections from histological preparations. A-B. *Conostylis preisii*. A. Cross-section of inferior ovary, near ovary apex. Note three septal nectaries (arrow at one of these) and perianth tube cavities (ca). Scale bar = 500 μ m. B. Septal nectary (arrow) confluent with perianth tube cavity (ca). Scale bar = 200 μ m. C-D. *Conostylis aurea*. C. Cross-section of inferior ovary, near ovary apex. Note one of three septal nectaries (arrow) and perianth tube cavity (ca). Scale bar = 500 μ m. D. Close-up of septal nectary, showing single layer of densely staining, papillate epithelial cells. Scale bar = 50 μ m. E-F. *Blancoa canescens*. E. Cross-section of inferior ovary, near ovary apex, showing three septal nectaries (arrow at one of these) and three perianth tube cavities (ca). Scale bar = 100 μ m. F. Close-up of septal nectary, showing single layer of densely staining epithelial cells and part of commissure (arrow). Scale bar = 100 μ m.

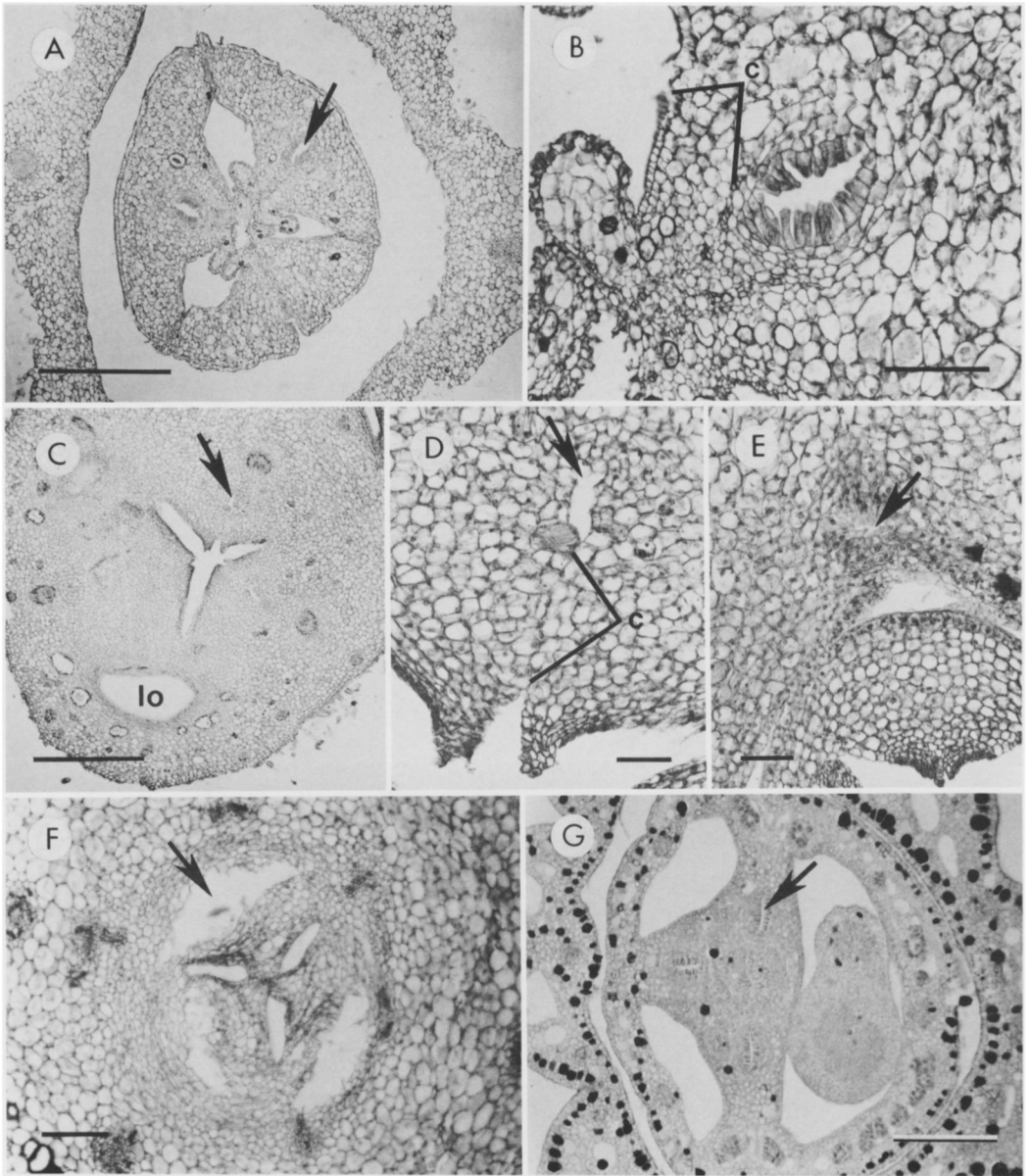
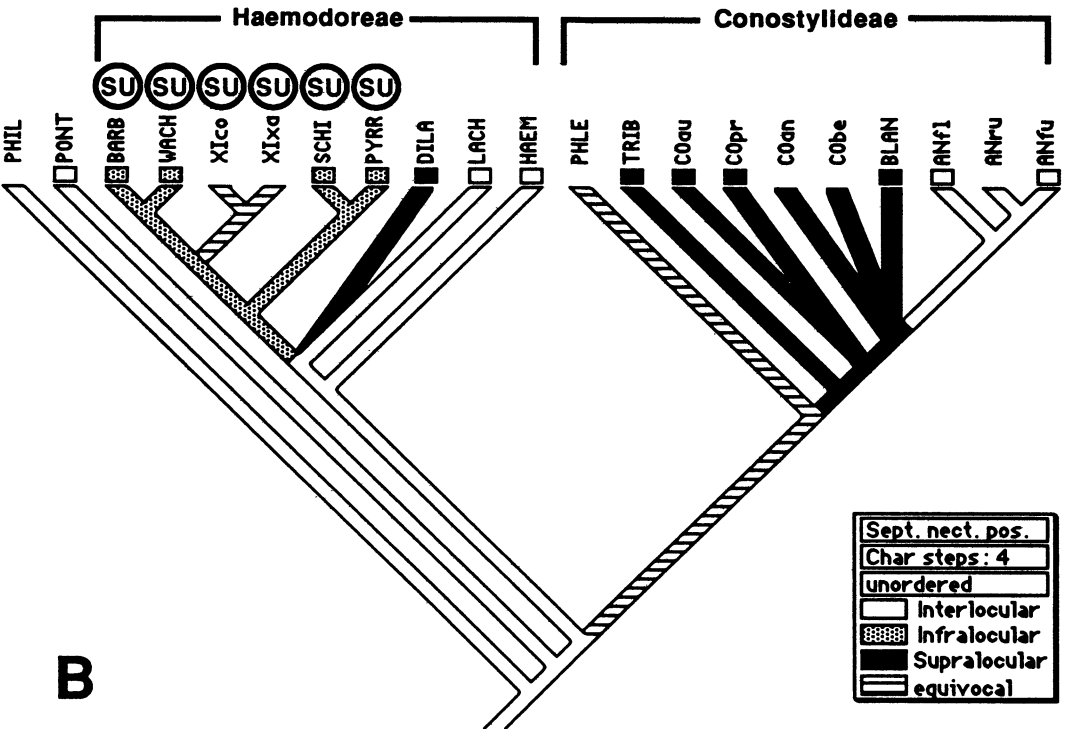
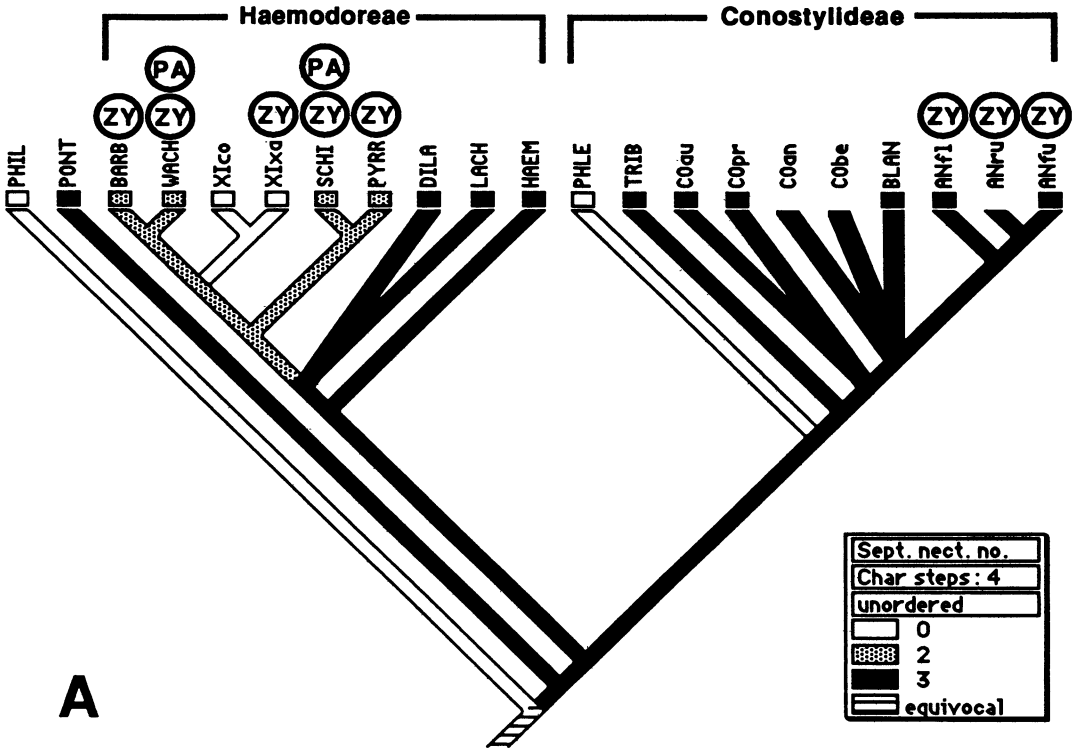


FIG. 9. Flower cross-sections from histological preparations. A-B. *Tribonanthes variabilis*. A. Apical, superior region of ovary and surrounding perianth tube. Note three septal nectaries (arrow at one of these). Scale bar = 500 μ m. B. Close-up of septal nectary, showing commissure (c). Scale bar = 100 μ m. C-E. *Dilatris pilansii*. C. Apical region of inferior ovary, showing small minute septal nectaries (arrow at one of these) between lobes of styler canal. Note locule (lo). Scale bar = 500 μ m. D. Close-up of septal nectary (arrow), showing commissure (c). Scale bar = 50 μ m. E. Septal nectary (arrow) opening at style base (below). Note surrounding epithelial cells. Scale bar = 50 μ m. F. *Phlebocarya ciliata*, at apex of inferior ovary. Note three, apparently lysigenous cavities (arrow at one of these) between lobes of styler canal. Scale bar = 100 μ m. G. *Pontederia cordata*, showing ovary cross-section and surrounding perianth tube. Note three septal nectaries (arrow at one of these). Scale bar = 200 μ m.



along most of the ovary length, can be viewed as a plesiomorphic retention of an evolutionary mechanism resulting in increased nectar production (Schmid 1985). *Dilatris*, the sister-group of *Lachnanthes*, has vestigial (essentially non-functional) supralocular septal nectaries, an autapomorphy for the genus. The adaptive significance of the vestigial septal nectaries in *Dilatris* is unknown. A shift in the selective pressure for pollination reward may have resulted in the functional loss of septal nectaries in *Dilatris*; however, its pollination system has not been studied to date.

Of special interest is the evolution of two infralocular septal nectaries in the Haemodoraceae, possessed by four genera and a synapomorphy for five genera (the genus *Xiphidium* hypothesized as losing nectaries altogether; Fig. 10). One key to understanding this distinctive nectary type may reside in the mechanism of nectar secretion in *Schiekia* and *Wachendorfia*. As discussed earlier, *Wachendorfia* and *Schiekia* are unique in possessing "perianth apertures," which develop by basal connation of five tepals and the formation of cavities bordered by the decurrent margins of two pairs of adjacent tepals (Fig. 3). However, the adaptive significance of these perianth apertures is unclear. In the South African genus *Wachendorfia*, the two perianth apertures may function to align an insect in order to effect pollination between left- and right-handed enantromorphs (Ornduff and Dulberger 1978). Helme and Linder (1992) observed copious nectar dripping from the flow-

ers of certain species of *Wachendorfia*, noting that the perianth apertures function as "semi-extrafloral" nectaries and serve as the outlet for "significant quantities of nectar . . . , which may persist even after the flower itself has withered." However, these authors further state that a function for the extrafloral nectar is unknown. Because nectar is produced to the outside, nectar "stealing" would be relatively easy, appearing to be maladaptive. Alternatively, the nectar doesn't appear to function in feeding "ant guards" (Faegri and Van der Pijl 1979), because "ants are seldom seen on the plants due to the glandular hairs on the stem" (Helme and Linder 1992). Unfortunately, pollinators of *Wachendorfia* are unknown. Helme and Linder (1992) suggest a number of possible pollinators, including carpenter bees, tabanid flies, and small beetles, but stress the need for further detailed study to determine pollination mechanism and evolutionary significance of the perianth apertures. Perianth apertures of the South American genus *Schiekia* are identical to those of *Wachendorfia*. Maas and Maas-van de Kamer (1993) report only that "in *Schiekia* pollinators are probing for nectar collected in the two lateral pouches [=perianth apertures] at the base of the flower."

Despite the lack of specific data on the current function of perianth apertures, it seems reasonable to suggest that strong selective pressures were involved in their evolution. It also seems certain that the acquisition of these unique perianth apertures occurred concomitantly with both a reduction in nectary number (by loss of

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FIG. 10. Cladogram of the Haemodoraceae (tribes Haemodoreae and Conostylideae) and outgroups Phylodraceae and Pontederiaceae, modified from Simpson 1990. A. Distribution of septal nectary number. Note that *Barberetta*, *Wachendorfia*, *Schiekia*, *Pyrrothiza*, and *Xiphidium* spp. share the synapomorphy of two septal nectaries (derived from the widespread and ancestral condition of three septal nectaries); the two *Xiphidium* spp. share the synapomorphy of loss of septal nectaries. Note also (within the Haemodoraceae only) the distribution of zygomorphic perianths (ZY), a synapomorphy for all five of the above genera (with a reversal in *Xiphidium caeruleum*) and independently derived in the genus *Anigozanthos*. Perianth apertures (PA) occur only in the genera *Schiekia* and *Wachendorfia*, most parsimoniously explained as independent acquisitions (however, see "Phylogenetic and Evolutionary Implications" of text). B. Distribution of septal nectary position. Note that *Barberetta*, *Wachendorfia*, *Schiekia*, *Pyrrothiza* and *Xiphidium* share the synapomorphy of infralocular septal nectaries (derived from the ancestral condition of interocular septal nectaries); the absence of septal nectaries in the two *Xiphidium* spp. results in an equivocal designation for this character. Note also the distribution of supralocular septal nectaries, having evolved independently in *Dilatris* and in the clade containing *Tribonanthes*, *Conostylis* spp., and *Blancoa*. Species of *Anigozanthos* share the synapomorphy of an interocular position, interpreted here as a secondary acquisition. The distribution of a superior ovary position (SU) is shown for the Haemodoraceae only, representing a synapomorphy for the infralocular taxa plus *Xiphidium*.

the anterior nectary) and with displacement of the nectaries (from an interocular to an infralocular position). I hypothesize that perianth apertures and their associated two infralocular septal nectaries evolved only *once* in the Haemodoraceae. This suggests that perianth apertures were retained in the lineages to *Schiekia* and *Wachendorfia* but independently lost in the lineages to *Barberetta*, *Pyrrothiza*, and probably *Xiphidium*. If true, the two infralocular septal nectaries of *Barberetta* and *Pyrrothiza* are vestiges of an ancestral association with perianth apertures that were later lost, presumably by depletion of the original selective pressure leading to their origin. The reduced, apparently non-functional pair of septal nectaries in *Pyrrothiza* may represent a further reduction, resulting in the loss of both perianth apertures and functional nectaries. The total absence of perianth apertures and septal nectaries in *Xiphidium* may represent a more nearly complete loss (see below). This hypothesis of a unique origin of perianth apertures is not the most parsimonious explanation, based on the presented cladistic analyses (Simpson 1990, present study). It is most parsimonious to infer that perianth apertures were acquired independently in *Schiekia* and *Wachendorfia* (requiring only two steps as opposed to four steps for a single acquisition followed by multiple losses; Fig. 10A). However, I feel it very unlikely that such a complex structure could have evolved more than once (Simpson 1990). In addition, the presence of two, infralocular nectaries in *Barberetta* and *Pyrrothiza* makes no evolutionary sense except as the vestigial association with two ancestral perianth apertures.

The question remains as to the significance of the nectaries in the above clade being reduced in number from three to two and displaced in position from interocular to infralocular. The evolution of only two septal nectaries (and only two perianth apertures in the two genera possessing them) may be correlated with floral orientation. The clade containing these five genera is (with the exception of *Xiphidium caeruleum*) further united by the derived feature of a zygomorphic perianth, illustrated in Figure 10A. (Zygomorphy in the genus *Anigozanthos* arose independently, by longitudinal splitting along the anterior tube; Simpson 1990.) Thus, the loss of the abaxial (anterior) septal nectary may be evolutionary correlated with the shift

to a zygomorphic perianth. One possible adaptive explanation is that zygomorphy (and a somewhat divergent orientation) evolved first, the selective pressure being a more efficient pollination mechanism. If this occurred, the evolution of two (not three) perianth apertures and the loss of the median anterior septal nectary might have been developmentally correlated somehow with the evolution of a bilaterally symmetric flower (an analog to this being the common reduction or loss of the median stamen in taxa that have evolved zygomorphy, e.g., many Scrophulariaceae).

With regard to the infralocular septal nectary position, it is apparent that the receptacular region was co-opted for the evolution of perianth apertures and the associated change in septal nectary position from an interocular to an infralocular position. In *Schiekia* and *Wachendorfia*, which have perianth apertures, the two septal nectaries extend deeply into the receptacular tissue (Figs. 1, 2A, D). Developmental studies of *Wachendorfia* (Simpson and McMillan, in manuscript) indicate that the septal nectaries initially are positioned as in other taxa, but become displaced by: 1) a shift of locule formation to the apical region of the central floral column; 2) early elongation in the receptacular region (accompanied by decurrent growth of tepals); and 3) late elongation of the locular region of the ovary. It is significant that only those taxa sharing two infralocular septal nectaries as a synapomorphy (including *Xiphidium*, which subsequently lost nectaries) have a predominantly superior ovary position. Based on cladistic analyses using a suite of characters (Simpson 1990), the superior ovary in these five genera is inferred to have evolved from an ancestral inferior-ovary condition (Fig. 10B). If correct, the extensive receptacular region in *Schiekia* and *Wachendorfia* containing the septal nectaries may be positionally homologous to the ancestral inferior ovary. By this notion, initial ovary development in *Wachendorfia* is inferior (below the ultimate attachment of the perianth/androecium). However, locule development is suppressed basally, the locule-containing part of the ovary elongating only apically and relatively late relative to the receptacular region. Thus, an ancestral inferior ovary in the ancestor to this clade of five genera was co-opted for the development of infralocular septal nectaries and perianth apertures by

basal suppression and apical expansion of carpellary tissue (Simpson and McMillan, in manuscript).

The apparent complete loss of nectaries in *Xiphidium* may be correlated with its pollination mechanism. *Xiphidium caeruleum* is pollinated by pollen-feeding bees via a "buzz" pollen collecting process, in which high frequency vibrations from the insect dislodge the pollen grains (Buchmann 1980). In fact, the nearly poricidal dehiscence in *Xiphidium caeruleum* is indicative of this type of pollination (see Simpson 1990). The implication is that septal nectaries were lost when the pollination reward shifted from nectar to pollen (Simpson 1990). One problem with this idea is that *Xiphidium xanthorrhizon*, the sister-species to *X. caeruleum*, has longitudinal anther dehiscence (pers. obs.; Maas and Maas-van de Kamer 1993). Given that *Xiphidium* is monophyletic (supported by the synapomorphy of absence of septal nectaries), then longitudinal anther dehiscence would most parsimoniously represent the primitive condition in the genus, implying that septal nectaries were lost before any selective pressure for poricidal dehiscence.

Within the Conostylidae, the adaptive significance for apparent loss of nectaries in *Phlebocarya*, the most basal lineage, is unclear. The fact that this genus has relatively small, unshowy flowers may be correlated with a change in the pollination reward system via a loss of nectar secretion. The adaptive significance of the shift in septal nectary position to a supralocular position in *Tribonanthes*, *Conostylis*, and *Blancoa* (Fig. 10B) is uncertain and may simply be correlated with increased growth of the ovary apex in these taxa, resulting in an approximately half-inferior ovary position (see Fig. 1). The evolution of unique cavities in the base of the perianth of *Conostylis* spp. and *Blancoa* may also be correlated with supralocular septal nectaries; selective pressure for greater output of nectar (to fill the perianth cavities) may have directed the vertical evolutionary extension of these nectaries via growth of the superior portion of the ovary. In species of *Anigozanthos*, the evolution of an interocular nectary position is most parsimoniously explained as a secondary event, being derived from an ancestrally supralocular condition (Fig. 10B). The secondarily interocular nectaries of *Anigozanthos* may have been an evolutionary response to a shift in pol-

lination mechanism. Among the Haemodora-ceae only *Anigozanthos* and *Blancoa* are bird-pollinated (Hopper and Burbidge 1978; Hopper and Campbell 1977; Keighery 1981). Septal nectaries of *Anigozanthos* are significantly longer (Fig. 1) and greater in cross-sectional area than those of *Tribonanthes*, *Conostylis*, and *Blancoa*. Increase in vertical extent and transectional area are two evolutionary mechanisms cited by Schmid (1985) resulting in increased nectar production. Thus, the overall larger amount of nectariferous tissue in *Anigozanthos* probably represents an adaptation for bird pollination, the greater quantity of nectar being needed to maintain a sufficient pollination reward. *Blancoa*, which is also bird-pollinated but does not have as specialized a floral morphology (Simpson 1990; see also Keighery 1981), has only slightly longer nectaries than the insect-pollinated *Tribonanthes* and *Conostylis*, but it is somewhat intermediate between these genera and *Anigozanthos* in nectary position (Fig. 1). In addition, convoluted nectaries with a greater quantity of surrounding, differentiated subepithelial cells are found in both *Anigozanthos fuliginosus* (Fig. 6F) and *Wachendorfia* (Fig. 4B), having independently evolved in these two taxa. In both taxa this convoluted nectary anatomy, resulting in significant increase in epithelial surface area (Schmid 1985), may have been the result of selective pressure for increased nectar production, that of *Anigozanthos fuliginosus* functioning in bird pollination (above) and that of *Wachendorfia* related to the great quantities of nectar secreted from the perianth apertures, this of unknown function (Helme and Linder 1992; see previous discussion).

In conclusion, this study illustrates the value of considering structural evolution in terms of function. Evaluation of floral anatomical data in a phylogenetic context has provided insight into the adaptive significance of evolutionary events in the Haemodoraceae. The historical patterns of septal nectary anatomy and ovary position in the family can be explained at least partially in terms of known pollination mechanisms. However, additional data on pollination mechanisms in the complex are needed. A more nearly complete knowledge of pollination biology of *Wachendorfia* (South Africa) and *Schiekia* (South America) might aid in better understanding the function of the perianth apertures, and observations on the pollination

mechanism of *Dilatris* (South Africa) might help elucidate the effective loss of nectaries in that genus.

ACKNOWLEDGMENTS. I thank Scott McMillan, Kim Marsden, and Marci Benzel for their help in histological preparations, three-dimensional reconstruction, and photographic work. I also thank Arne A. Anderberg, Peter K. Endress, and Bruce K. Kirchoff for reviewing the paper and offering a number of useful suggestions. This project was supported in part by NSF grant BSR-8822606.

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APPENDIX 1. Voucher information for investigated taxa. Synonyms are listed in brackets. Herbarium abbreviations are after Holmgren et al. (1990).

Haemodoraceae

- Anigozanthos flavidus* DC.—Simpson 24IX81J (DUKE)
A. fuliginosus Hook. (*Macropidia fuliginosa* (Hook.) Druce)—Simpson 18IX81DD (DUKE)
Barberetta aurea Harv.—Ornduff 7661 (UC)
Blancoa canescens Lindl.—Simpson 18IX81AA (DUKE)
Conostylis aurea Lindl.—Simpson 13IX81S (SDSU)
C. preisii Endl. (*C. aculeata* R. Br. ssp. *preisii* (Endl.) J. Green)—Simpson 9IX81N (SDSU)
Dilatris corymbosa Berg.—Goldblatt 3242 (MO)
D. pilansii Barker—Meriwe 30X81-2 (STEU)
Haemodorum spicatum R. Br.—Simpson 16IX81C (DUKE)
Lachnanthes caroliniana (Lam.) Dandy (*L. caroliniana* (Lam.) Dandy)—Simpson 14VI80A (DUKE)
Phlebocarya ciliata R. Br.—Simpson 16IX81A (DUKE)
Pyrrothiza neblinae Maguire & Wurdack—Boom and Weitzman 5741 (NY)
Schiekia orinocensis (Kunth) Meisn.—Maguire 41569 (NY)
Tribonanthes variabilis Lindl.—Simpson 8IX81A (DUKE)
Wachendorfia paniculata L.—Meriwe 30X81-1 (STEU)
Wachendorfia thyrsiflora L.—Ornduff 7691 (UC)
Xiphidium caeruleum Aubl. [*X. caeruleum* Aubl.]—MacDougal 1043 (DUKE)
X. xanthorrhizon Wright ex Grisebach—Maas 30-6-90 (U)

Philydraceae

- Helmholtzia acorifolia* F. V. Mueller—Simpson 81-16A (DUKE)
Philydrella pygmaea (R. Br.) Caruel—Simpson 28IX81A (DUKE)

Pontederiaceae

- Heteranthera reniformis* R. & P.—Simpson 4VIII82A (DUKE)
Pontederia cordata L.—Simpson 4VIII82B (DUKE)
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