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Annals of the Missouri Botanical Garden, Vol. 77, No. 4. (1990), pp. 722-784.

Stable URL:
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Annals of the Missouri Botanical Garden is currently published by Missouri Botanical Garden Press.

PHYLOGENY AND CLASSIFICATION OF THE HAEMODORACEAE[1]

Michael G. Simpson[2]

ABSTRACT

A phylogenetic analysis of the monocot family Haemodoraceae is presented to assess the classification and interrelationships of tribes, genera, and species complexes and to determine patterns of evolutionary and biogeographic change. Evidence is reviewed for the monophylesis of the family (as here delimited) and of some family genera. In order to assign character polarities, two families, Philydraceae and Pontederiaceae, were hypothesized as closest outgroups based on presumed synapomorphies shared with the Haemodoraceae, including: (1) unifacial leaves (Philydraceae) and (2) verrucate pollen wall sculpturing and non-tectate-columellate exine structure (Pontederiaceae). A detailed analysis of the selection, definition, and coding of characters and character states is presented. Computer parsimony algorithms were used to construct most parsimonious trees. Utilizing all characters, including several for which polarity could not be determined, two equally most parsimonious cladograms were derived, differing only in the relative placement of the genera *Dilatris* and *Lachnanthes*. A cladistic analysis restricted to only those characters for which polarity could be determined yielded the same two equally parsimonious topologies; one in which correlated characters were scaled yielded one of the two topologies. Cladistic analyses support the monophylesis of the (herein defined) tribes Haemodoreae and Conostylideae. However, of the fourteen genera in the family, *Wachendorfia, Haemodorum,* and *Xiphidium* could not be a priori established as monophyletic, and the genera *Anigozanthos* and *Conostylis* are paraphyletic. Evolutionary events, as portrayed in the cladograms, are reviewed with emphasis on evolution of trichome anatomy, ovary position, ovule morphology, seed morphology, and chromosome number. Possible biogeographic scenarios support a Gondwanan origin for the Haemodoraceae with one major vicariance event occurring by the continental separation of present Antarctica from South America-Africa. With regard to interfamilial relationships, the Haemodoraceae are hypothesized as the sister group of the family Pontederiaceae, with both families more distantly related to the Philydraceae. Relationships to the Typhales, Bromeliaceae, and Zingiberales are still ambiguous, but the possibility of a close relationship of the Haemodoraceae-Pontederiaceae to the Zingiberales is considered.

The Haemodoraceae R. Br. are a monocot family of 14 genera and approximately 80 species with distributions in southern Africa, northern South America, Central America, Mexico, eastern North America, Australia, and New Guinea (Fig. 1). Members of the family are characterized as perennial, rhizomatous and stoloniferous or (more rarely) cormose to bulbous herbs with mostly basal to subbasal, equitant leaves and a terminal, generally cymose inflorescence (Geerinck, 1968, 1969a; Hutchinson, 1973; Robertson, 1976; present study). The leaves are "ensiform" (unifacial), resembling those of *Iris*. The flowers, typical of monocotyledons, are bisexual, with 6 tepals, 1–3–6 stamens, and a tricarpellate gynoecium developing into a capsular fruit. Flower symmetry is actinomorphic or zygomorphic; ovary position, ovule type, ovule number, and placentation are variable. Trichomes characteristically cover pedicels, hypanthia (if present), and outer perianth surfaces, often forming a dense tomentum. Several genera of the family possess a red sap in the roots and rhizome, accounting for the common name Bloodwort Family.

The Haemodoraceae have had some interesting economic uses. Several Australian species were used as a "nutritious food" by the aborigines, who roasted and consumed the "roots" (undoubtedly the rhizomes; Millspaugh, 1887). Narcotic effects have been attributed to the eastern North American *Lachnanthes caroliniana* (Lam.) Dandy (red root), the "roots" (again, likely rootstocks) of which were "esteemed as an invigorating tonic by the aborigines, especially the Seminoles, in whom it is said to cause brilliancy and fearless expression of the eye and countenance, a boldness and fluency of speech, and other symptoms of heroic bearing, with, of course, the natural opposite after-effects" (Millspaugh, 1887). Millspaugh also described a recipe for a red root tonic, with numerous medicinal

[1] Support from National Science Foundation grants DEB-8109909 and BSR-8400157 is acknowledged. This study is an expansion and modification of a Ph.D. dissertation presented to the Department of Botany at Duke University, Durham, North Carolina. I thank, in particular, Patricia G. Gensel, Donald E. Stone, and Richard A. White for help and encouragement on the initial stages of this study. Robert Ornduff provided the plates for Figures 2 and 3.

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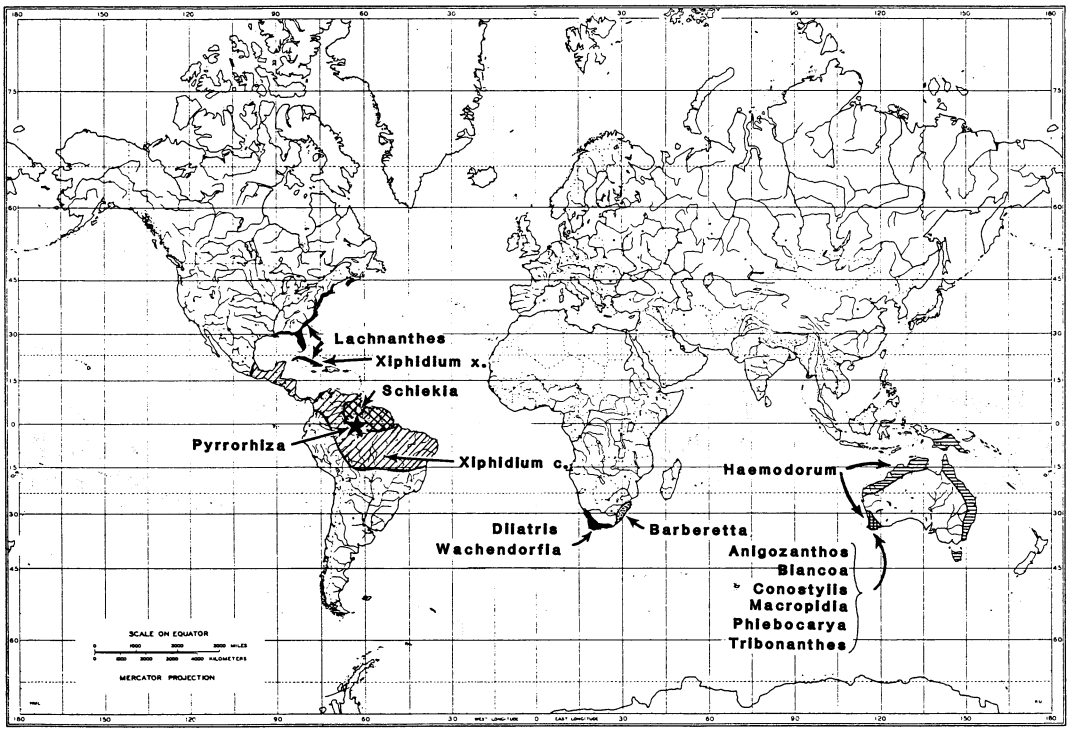


FIGURE 1. Geographic distribution of the genera of the Haemodoraceae. *Xiphidium x.* = *Xiphidium xanthorhiza*; *Xiphidium c.* = *Xiphidium coeruleum.*

benefits, including remedies for "rheumatic stiffness of the neck and shoulders," "typhus and thyroid fevers, pneumonia, various severe forms of brain disease, rheumatic wry-neck, and laryngeal cough." Charles Darwin (1872) in *The Origin of Species* (citing an example of selection) described the consumption of *Lachnanthes* by feral pigs in the southern United States; Virginia farmers had recorded that pigs with light-colored hair were poisoned by eating red root whereas dark-haired pigs were unaffected. Cooke & Edwards (1981) stated that this correlation between hair color and selective poisoning is presumed to be a photodynamic phenomenon, evidence being the induction of phototoxicity in microorganisms by extracts of *Lachnanthes* (Kornfeld & Edwards, 1972). The Australian *Haemodorum corymbosum* Vahl produces a red pigment (termed haemocorin), which has antitumor activity (Schwenk, 1962) and antibacterial activity (Narasimhachari et al., 1968). Several Australian members of the Haemodoraceae, including *Blancoa canescens* Lindl. (red bugles), *Haemodorum corymbosum* (blood root lily), *Macropidia fuliginosa* (Hook.) Druce (black kangaroo paw), *Tribonanthes* Endl. spp., and numerous species and forms of *Anigozanthos* Labill. (kangaroo paws, cats paws) and *Conostylis* R. Br., are horticulturally grown for their showy flowers (Dixon & Hopper, 1979). *Lachnanthes caroliniana* is listed as an agricultural pest, being a "rather aggressive weed in commercial cranberry (*Vaccinium macrocarpon*) bogs" (Robertson, 1976).

History of Classification

As Geerinck (1968) and Robertson (1976) noted, the classification of the Haemodoraceae has been variable and uncertain, authors having proposed several different combinations of tribes and genera. Robert Brown (1810) first recognized the Haemodoraceae as a formal taxonomic unit composed of three southern African genera, *Dilatris*, *Lanaria*, and *Wachendorfia*, and four Australian genera, *Anigozanthos*, *Conostylis*, *Haemodorum*, and *Phlebocarya*. Diagnostic characteristics of the family were the six-parted, generally superior perianth (and thus an inferior ovary), capsular fruit, equitant leaves, and three or six stamens, if three then opposite the inner perianth lobes. Brown specifically distinguished the Haemodoraceae from the Iridaceae, members of which possess flowers with three stamens opposite the outer whorl of tepals.

TABLE 1. Classification of the Haemodoraceae sensu Bentham & Hooker (1883).

Tribe [Eu]Haemodoreae: perianth persistent; biseriate, the inner +/− enclosed by the outer; tube above the ovary absent or shortly developed. Stamens 3 or rarely 6.

1. *Haemodorum*
2. *Wachendorfia*
3. *Schiekia*
4. *Hagenbachia*
5. *Dilatris*
6. *Lachnanthes*
7. *Barberetta*
8. *Xiphidium*
9. *Lanaria*
10. *Phlebocarya*

Tribe Conostyleae: perianth persistent; lobes subequal, those of uniseriate species subvalvate. Stamens 6. Ovary locules with numerous ovules.

11. *Tribonanthes*
12. *Conostylis*
13. *Blancoa*
14. *Anigozanthos*
15. *Macropidia*
16. *Lophiola*
17. *Aletris*

Tribe Ophiopogoneae: perianth marcescent, persistent beneath the fruit; segments subequal, similar, flat. Ovary locules 2-ovulate. Pericarp after anthesis ruptured, not enlarged. Seeds berry-shaped, subglobose, extruded. Raceme unbranched. Flowers small.

18. *Peliosanthes*
19. *Ophiopogon*
20. *Liriope*
21. *Sansevieria*

Tribe Conanthereae: perianth at length around and above the ovary circumscissilly deciduous, segments subequal, similar or the exterior small and dissimilar, flat. Stamens or staminodes 6, equal or 1 or 3 of the other dissimilar; locules of anthers frequently terminally pored or rarely short dehiscent. Ovary locules (except *Odontostomum*) with numerous ovules. Capsules superior, loculicidally dehiscent. Flowers in loose panicles or rarely racemose or solitary.

22. *Conanthera*
23. *Cyanella*
24. *Zephyra*
25. *Tecophilaea*
26. *Odontostomum*

Subsequent to Brown's treatment, additional genera were included in the Haemodoraceae. Lindley (1830) placed the American genera *Lachnanthes*, *Lophiola*, and *Xiphidium* in the family. Endlicher (1836–1840) added the genera that Lindley contributed plus *Aletris*, *Androstemma*, *Blancoa*, *Hagenbachia*, *Tribonanthes*, *Vellozia*, and *Barbacenia* (the latter two genera of the tribe Vellozieae sensu Brown, 1810).

Bentham & Hooker (1883) provided the first critical treatment of the Haemodoraceae, considering the family to be intermediate between the Bromeliaceae and Iridaceae. Four tribes were designated: "Euhaemodoreae" (= Haemodoreae), "Conostyleae" (= Conostylideae), Ophiopogoneae, and Conanthereae (Table 1). Bentham & Hooker distinguished the tribes based on stamen number (3 vs. 6), perianth duration (persistent or deciduous), anther dehiscence (poricidal in the Conanthereae), ovary position (inferior vs. superior), and inflorescence type (Table 1). *Vellozia* and *Barbacenia* were excluded from the family as constituted by Endlicher, and placed in the Amaryllidaceae by Bentham & Hooker. The genus *Androstemma* was considered a generic section of *Conostylis*. Although subsequent treatments of the Haemodoraceae have varied considerably in the position and/or rank of certain genera and tribes, the four tribes proposed by Bentham & Hooker have remained essentially intact.

Pax (1888) in *Die natürlichen Pflanzenfamilien*, limited the Haemodoraceae to Bentham's tribe (Eu)Haemodoreae with the deletion of *Lanaria* and *Phlebocarya* and the addition of *Pauridia* (Table 2). According to this treatment, the Conostylideae (= Bentham's Conostyleae minus *Aletris* and plus *Lanaria* and *Phlebocarya*) and Conanthereae (minus *Odontostomum* of Bentham's classification) were transferred to the Amaryllidaceae, subfamily Hypoxidoideae, with the tribes Alstroemerieae and Hypoxideae. The tribe Ophiopogoneae was placed in the Liliaceae. Thus, of the original four tribes of Bentham, Pax considered only two, Conanthereae and Conostylideae, to be closely related. Ballion (1894) transferred the genera of the Haemodoraceae, sensu Pax, to the Amaryllidaceae. He argued that the Haemodoraceae are an artificial taxon essentially indistinguishable from members of the Liliaceae and Amaryllidaceae. Pax (1930) and Pax & Hoffmann (1930) did not support Ballion's view and made no changes in the group's classification relative to the previous edition.

Hutchinson (1934, 1959) advanced an original classification of the family. He united the Haemodoreae and "Conostyleae" (= Conostylideae) as two tribes of the Haemodoraceae, considering the family (as defined) to be a natural assemblage; and he treated the tribe Conanthereae of Bentham & Hooker (1883) as a distinct family, the Tecophilaeaceae (Table 3). Hutchinson classified the Haemodoraceae with five other families in the order Haemodorales, considering the group to be intermediate to the Amaryllidaceae and Orchidaceae. The Tecophilaeaceae, however, were placed in the Liliales and thought to be rather distantly related to the Haemodoraceae. In his third edition, Hutchinson (1973) added the newly discovered South American *Pyrrorhiza* (Maguire & Wurdack, 1957) to the tribe Haemodoreae.

Subsequent treatments of the Haemodoraceae have continued to vary with regard to tribal interrelationships and generic placement. Melchior

TABLE 2. Classification of the Haemodoraceae and Amaryllidaceae, subfamily Hypoxidoideae sensu Pax (1888).

Haemodoraceae	
1. *Haemodorum* Sm.	6. *Wachendorfia* L.
2. *Barberetta* Harv.	7. *Schiekia* Meissn.
3. *Hagenbachia* Nees	8. *Xiphidium* Aubl.
4. *Dilatris* Berg.	9. *Pauridia* Harv.
5. *Lachnanthes* Elliott	
Amaryllidaceae subfamily Hypoxidoideae	
Tribe Alstroemerieae	
1. *Alstroemeria* Blh.	3. *Leontochir* Philippi
2. *Bomarea* Mirb.	
Tribe Hypoxideae	
1. *Curculigo* Gartn.	2. *Hypoxis* L.
Tribe Conanthereae	
1. *Conanthera* Ruiz & Pav.	3. *Zephyra* D. Don
2. *Cyanella* L.	4. *Tecophilaea* Bert.
Tribe Conostylideae	
1. *Lanaria* Ait.	5. *Lophiola* Ker
2. *Phlebocarya* R. Br.	6. *Blancoa* Lindl.
3. *Macropidia* Drummond	7. *Conostylis* R. Br.
4. *Tribonanthes* Endl.	8. *Anigozanthos* Labill.

(1964) grouped the tribes Haemodoreae, Conostylideae, and Conanthereae as the Haemodoraceae, thus mirroring (with the exception of tribe Ophiopogoneae) Bentham's classification. In the most recent classification of the family, Geerinck (1969a) essentially concurred with Hutchinson in recognizing two tribes: Haemodoreae (10 genera) and Conostylideae (3 genera) (Table 4). Geerinck's system differs from that of Hutchinson in removing *Lanaria* and *Hagenbachia* from the family (to status "incertae sedis"), transferring *Lophiola* from the Conostylideae to the Haemodoreae, treating *Blancoa* as a section of the genus *Conostylis* and treating *Macropidia* as section of *Anigozanthos*. As a result of a multivariate morphometric analysis of *Macropidia fuliginosa* and 12 species of *Anigozanthos*, however, Hopper & Campbell (1977) argued for the reinstatement of *Macropidia* as a distinct genus.

The interfamilial classification of the Haemodoraceae has also been variable. Hutchinson (1973) classified the Haemodoraceae with the Apostasiaceae, Hypoxidaceae, Philydraceae, Taccaceae, and Velloziaceae in his order Haemodorales. Cronquist (1981) placed the Haemodoraceae in the order Liliales of the subclass Liliidae, "near" the families Pontederiaceae, Cyanastraceae, Philydraceae, and Liliaceae. In contrast, Takhtajan (1980) grouped the Haemodoraceae, Hypoxidaceae, and Velloziaceae in the suborder Haemodorineae of the Liliales. The Haemodoraceae were grouped with the Philydraceae and Pontederiaceae by Dahlgren (1980) and by Dahlgren & Clifford (1982). More recently, Dahlgren & Rasmussen (1983) grouped the Haemodoraceae, Pontederiaceae, and Typhales (Typhaceae and Sparganiaceae) as a tritomy (sharing a presumably derived amoeboid tapetum) in their superorder Bromeliiflorae. The Philydraceae were treated as a more basal clade, united with the above in having distichous leaves. Dahlgren & Rasmussen also included the Bromeliaceae and Velloziaceae as basal clades of the Bromeliiflorae (see Interfamilial Classification).

OBJECTIVES

The primary objective of the present study is to assess the phylogenetic relationships of the Haemodoraceae. A detailed analysis of the characters possessed by taxa is included and the rationale for character coding is discussed. A phylogenetic analysis, using these data, is presented in an attempt to answer the following: (1) Are the Haemodoraceae monophyletic? (2) Are the genera in the family monophyletic? (3) What is the basis for the traditionally recognized tribes Conostylideae and Haemodoreae? (4) What monophyletic subgroups of genera are evident and what are the character changes evident from the cladistic analysis? (5) Can inferences be made as to biogeographic history

TABLE 3. Classification of the Haemodoraceae and Tecophilaeaceae sensu Hutchinson, 1934, 1959, 1973. *Pyrrhorhiza* added in 1973.

Haemodoraceae

Tribe Haemodoreae: "perianth-segments 2-seriate; tube very short or absent; stamens 3 or rarely 6"

1. *Barberetta*
2. *Dilatris*
3. *Haemodorum*
4. *Hagenbachia*
5. *Lachnanthes*
6. *Lanaria*
7. *Phlebocarya*
8. *Pyrrorhiza*
9. *Schiekia*
10. *Wachendorfia*
11. *Xiphidium*

Tribe Conostyleae: "perianth-segments 1-seriate, subvalvate; tube often fairly long and curved; stamens 6; flowers always tomentose or woolly"

1. *Anigozanthos*
2. *Blanca* (sic)
3. *Conostylis*
4. *Lophiola*
5. *Macropidia*
6. *Tribonanthes*

Tecophilaeaceae

1. *Conanthera*
2. *Cyanastrum*
3. *Cyanella*
4. *Odontostomum*
5. *Tecophilaea*
6. *Walleria*
7. *Zephyra*

TABLE 4. Classification of the Haemodoraceae sensu Geerinck (1969a).

Haemodoraceae

Tribe Haemodoreae: "flowers glabrous or with simple or glandular trichomes; tepals distinct or rarely basally connate; functional stamens 6 (in 2 whorls of 3) or 3 (the outer whorl absent or replaced by 2 staminodes); anthers nonappendicular at apex; ovary superior, half-inferior, or inferior"

1. *Barberetta*
2. *Dilatris*
3. *Haemodorum*
4. *Lachnanthes*
5. *Lophiola*
6. *Phlebocarya*
7. *Pyrrorhiza*
8. *Schiekia*
9. *Wachendorfia*
10. *Xiphidium*

Tribe Conostylideae: "flowers covered with simple or branched trichomes (rarely both); perianth tube present; stamens 6, in 2 whorls of 3; anthers sometimes appendiculate apically; ovary half-inferior or inferior"

1. *Anigozanthos* (including *Macropidia*)
2. *Conostylis* (including *Blancoa*)
3. *Tribonanthes*

Genera of uncertain affinities: *Hagenbachia* & *Lanaria*

of the Haemodoraceae? (6) What families are most closely related to the Haemodoraceae and what is the evidence for this relationship? (7) What is the position of the Haemodoraceae within the Bromeliiflorae (sensu Dahlgren & Rasmussen, 1983)?

MONOPHYLESIS OF THE HAEMODORACEAE

It is essential in a phylogenetic study to demonstrate that the group to be analyzed is monophyletic (in the sense of Hennig, 1966; equivalent to "holophyletic" of other authors), i.e., that it includes all and only all descendants of a common ancestor as evidenced by one or more synapomorphies. Despite past discrepancies in classification, the Haemodoraceae are recognized in the present study to comprise a natural, monophyletic group made up of 14 genera: *Anigozanthos*, *Barberetta*, *Blancoa*, *Conostylis*, *Dilatris*, *Haemodorum*, *Lachnanthes*, *Macropidia*, *Phlebocarya*, *Pyrrorhiza*, *Schiekia*, *Tribonanthes*, *Wachendorfia*, and *Xiphidium*. The primary evidence for the monophylesis of the family is chemical composition. The Haemodoraceae are chemically unique in being the only family of vascular plants to possess phenalenones (specifically "arylphenalenones," derivatives of 9-phenyl-1H-phenalen-1-one; Cooke & Edwards, 1981). These compounds are responsible for the floral pigmentation and/or red coloration prominent in the roots and rootstocks of family members. The occurrence of phenalenones was first reported in *Haemodorum corymbosum* Vahl by Cooke & Segal (1955), who named the isolated phenalenone glycoside "haemocorin." Subsequently, the following ten species in eight genera of the family have been found to possess phenalenones or derivatives thereof: *Haemodorum corymbosum*, *H. distichophyllum*, *Lachnanthes caroliniana*, *Phlebocarya ciliata*, *Wachendorfia paniculata*, *W. thyrsiflora*, *Xiphidium coeruleum*, *Anigozanthos rufus*, *Conostylis setosa*, *Macropidia fuliginosa* (Cooke & Edwards, 1981, and references therein). The eight genera not investigated to date for the presence of phenalenones are, in the author's view, very closely related to those that have been, as determined by morphological and palynological similarity; it is hypothesized that, when chemically analyzed, they will be found to have arylphenalenones as well. It should be emphasized that among all investigated flowering plants, arylphenalenones have been found only in the cited members of the Haemodoraceae. Phenalenones are otherwise biologically known only in four genera of the Hyphomycetes (Fungi Imperfecti) and in one genus of the Discomycetes (Ascomycotina); these, however, are synthesized by a different biochemical pathway (Cooke & Edwards, 1981) and are obviously not homologous with those of the

TABLE 5. Embryological characters of the Haemodoraceae and relatives.

Taxon	Tapetal type	Microspore division	Nucellus type	Documentation
Haemodoraceae				
Anigozanthos	Amoeboid	Successive	Crassinucellate	Stenar (1927)
Dilatris	Amoeboid	Successive	Crassinucellate	De Vos (1956)
Lachnanthes	Amoeboid	Successive	Crassinucellate	Simpson (1981, 1988)
Wachendorfia	Amoeboid	Successive	Crassinucellate	Dellert (1933); De Vos (1956)
Xiphidium	Amoeboid	Successive	Crassinucellate	Stenar (1938)
Bromeliaceae				
	Glandular	Successive	Crassinucellate	Dahlgren et al. (1985)
Cyanastraceae				
Cyanastrum	Glandular	Simultaneous	Crassinucellate	Fries (1919); Nietsch (1941)
Hypoxidaceae				
Hypoxis	Glandular	Successive	Tenuinucellate	De Vos (1948)
Pauridia	Glandular	Successive	Tenuinucellate	De Vos (1949)
Philydraceae				
Helmholtzia	Glandular	Successive	Crassinucellate	Hamann (1966)
Orthothylax	Glandular	Successive	Crassinucellate	Hamann (1966)
Philydrella	Glandular	Successive	Crassinucellate	Hamann (1966)
Philydrum	Glandular	Successive	Crassinucellate	Hamann (1966)
Pontederiaceae				
Eichhornia	Amoeboid	Successive	Crassinucellate	Banerji & Gangulee (1937); Schurhoff (1922)
Monochoria	Amoeboid	Successive	Crassinucellate	Banerji & Haldar (1942)
Sparganiaceae				
Sparganium	Amoeboid	Successive	Crassinucellate	Dahlgren & Clifford (1982)
Taccaceae				
Schizocapsa	Glandular	Simultaneous	Crassinucellate	Hakansson (1921)
Tecophilaeaceae				
Cyanella	Glandular	Simultaneous	Crassinucellate	De Vos (1950)
Odontostomum	Glandular	Simultaneous	Crassinucellate	Cave (1952)
Typhaceae				
Typha	Amoeboid	Successive	Crassinucellate	Dahlgren & Clifford (1982)
Velloziaceae				
Vellozia	Glandular	Successive	Tenuinucellate (Pseudocrassinucellate)	Schnarf (1931); Stenar (1925)

Haemodoraceae. Because of the uniqueness of these compounds and their restriction to the Haemodoraceae, their presence is hypothesized as a synapomorphy, uniting the family as a monophyletic group. Other major similarities that the 14 genera have in common are: (1) occurrence of a fibrous layer ("mechanischen Cylinder") in the stem (Schulze, 1893); (2) presence of unifacial leaves with paracytic stomata (Schulze, 1893; Stenar, 1927, 1938; Green, 1959; Simpson & Dickison, 1981; Simpson, unpublished); (3) common embryological development, including occurrence of an amoeboid tapetum, successive microsporogenesis, and crassinucellate ovules (Table 5, and references therein); and (4) a similar and intergrading non-tectate-columellate pollen exine wall structure (Simpson, 1983; see Character Analysis). However, there is no evidence that any of these features are synapomorphic for the Haemodoraceae; they may, however, be synapomorphic for two or more families within the complex (see Interfamilial Relationships).

The family Tecophilaeaceae have often been classified as the tribe Conanthereae of the Haemodoraceae, but they definitely do not belong in

the latter. All investigated members of the Tecophilaeaceae (delimited as the genera *Conanthera*, *Cyanella*, *Odontostomum*, *Tecophilaea*, *Walleria*, and *Zephyra*; Simpson, in press) differ from the Haemodoraceae in having: (1) bifacial leaves and anomocytic stomata (Schulze, 1893; Simpson, unpublished); (2) a glandular tapetum and simultaneous microsporogenesis (Table 5); (3) phytomelaniferous seeds (except *Walleria*; Huber, 1969); and (4) pollen grains with a foveolate to reticulate sculpturing, an apertural operculum (except *Cyanella orchidiformis*), and a tectate-columellate exine architecture with an inner endexinous layer (Simpson, 1985b). In addition, members of the Tecophilaeaceae lack fluorescent cell wall-bound compounds found in the Haemodoraceae (Harris & Hartley, 1980; see Outgroup Taxa). All the evidence suggests that the Tecophilaeaceae are comparatively distantly related to the Haemodoraceae.

The taxonomic placements of *Hagenbachia*, *Lanaria*, *Lophiola*, and *Pauridia* have been variable in past treatments. Each has been included in the Haemodoraceae by various authors (e.g., Pax, 1930; Hutchinson, 1973; Melchior, 1964; Geerinck, 1969a; see History of Classification). However, a major conclusion reached from the present study is that no synapomorphies are known that unite any of these genera with the Haemodoraceae. The South American *Hagenbachia brasiliensis* (monotypic in its genus) is undoubtedly a case of taxonomic misplacement. It clearly belongs as a species of the genus *Chlorophytum* of the Liliaceae, as Ravenna (1977) determined. Corroborating this is the fact that "*Hagenbachia*" differs from all Haemodoraceae in having a tectate-columellate exine wall (Simpson, unpublished) and lacks UV-fluorescent cell-wall-bound compounds (Simpson, unpublished).

The monotypic, eastern North American *Lophiola* (which resembles some Haemodoraceae in having unifacial leaves, a corymb of helicoid cymes, and tomentose flowers and inflorescence) differs from the Haemodoraceae in many respects, including: (1) absence of a stem fibrous layer ("mechanischen Cylinder"), absence of subsidiary cells, and differing trichome anatomy (Schulze, 1893; Simpson & Dickison, 1981); (2) reticulate pollen with a tectate-columellate architecture (Simpson, 1983; Zavada, 1983a); (3) glandular tapetal development (Simpson, 1981); (4) absence of the diagnostic arylphenalenones (Edwards et al., 1970); and (5) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). Ambrose (1980, 1985) presented convincing evidence for the classification of *Lophiola* in the Liliaceae, Melanthioideae (= Melanthiaceae of Dahlgren & Clifford, 1982); there is no doubt that it belongs with at least some members of that group.

The monotypic South African genus *Lanaria* resembles members of the Haemodoraceae in having a corymb of helicoid cymes and in having multiseriate, dendritic trichomes remarkably similar to those of some Haemodoraceae (see Character Analysis). However, *Lanaria* shows many differences from the Haemodoraceae, including: (1) bifacial leaves without stomatal subsidiary cells (Schulze, 1893; Simpson, unpublished); (2) glandular tapetal development and simultaneous microsporogenesis (Table 5); (3) reticulate pollen grains with a tectate-columellate exine wall structure (Simpson, 1983); (4) phytomelaniferous seedcoat (Huber, 1969); and (5) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). (*Lanaria* has not been investigated chemically for the presence of arylphenalenones.) Similarities between *Lanaria* and the Tecophilaeaceae have prompted some (e.g., De Vos, 1961, 1963; Dahlgren & Clifford, 1982) to include the genus in that family. However, Dahlgren (pers. comm.) argued for the recognition of a segregate family, Lanariaceae, with close affinities to the Tecophilaeaceae.

Finally, the monotypic southern African genus *Pauridia* (usually placed in the Hypoxidaceae but sometimes classified in the Haemodoraceae) differs from the Haemodoraceae in having: (1) bifacial leaves; (2) tenuinucellate ovules and a glandular tapetum (Table 5); (3) disulculate pollen grains with a tectate-columellate exine having an endexinous basal layer (Simpson, 1983); and (4) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). *Pauridia* has not been investigated for the presence of arylphenalenones. No characters evidently unite *Pauridia* to the Haemodoraceae; the genus is here retained in the Hypoxidaceae.

Monophylesis of Family Genera

In a cladistic analysis all defined operational taxonomic units (OTUs) should either be monophyletic taxa, be split up into monophyletic groups, or have exemplar species assigned for them. Otherwise, it is possible that one or more species of previously circumscribed genus "A" may be more closely related to species of genus "B" than to other species of genus "A." In the Haemodoraceae, the monophyly of six genera—*Barberetta*, *Blan-*

coa, *Lachnanthes*, *Macropidia*, *Pyrrorhiza*, and *Schiekia*—is accepted by virtue of their being monotypic. (See Platnick, 1976, for an alternate view.) A review of the monophyly of the remaining eight genera is essential before a valid cladistic analysis can be undertaken.

The genus *Dilatris* (five species) is commonly distinguished from other family members by having an inferior ovary and one ovule per carpel. Each of these features are possessed by other members of the family and thus cannot be recognized as synapomorphies (being unique only in combination). *Dilatris* has a trichome type not found in other genera of the family (see Character Analysis), yet if the proposed evolutionary gradation of trichome types (Fig. 28) is valid, then it is possible that the trichomes of *Dilatris* may not be uniquely derived for the genus as a whole. A feature that may show synapomorphy for the genus is the presence of dotted glands in the distal region of tepals (see Fig. 73). These glands were observed in *D. pilansii* and *D. corymbosa* but were not found in species of any other genus in the family. It is hypothesized that these tepal glands are likely synapomorphic for the genus as a whole.

Haemodorum (20 species) has a semibulbous underground rootstock, which is almost certainly derived from a primitive rhizomatous rootstock, present in almost all other family members (of both tribes) and in outgroups. This type of rootstock may not be unique to *Haemodorum*, as three other genera have a cormose rootstock (see Character Analysis, *Stem type*). Most species of *Haemodorum* are glabrous, which itself may be synapomorphic for the genus. The trichomes observed in *H. spicatum* (see Character Analysis, *Trichome anatomy*; Fig. 13) may be homologous with the pilate trichomes found in several genera of the tribe; thus, vestiture may not be a reliable indicator of synapomorphy (and therefore monophylesis) for the species of *Haemodorum*. In view of these difficulties and because relatively few of the 20 species of *Haemodorum* were observed in this study, monophylesis cannot be established for the genus.

No evident synapomorphies occur for investigated species of the genus *Wachendorfia* (five species). Possible derived characters in *Wachendorfia*, relative to the family as a whole, include zygomorphy and one ovule per carpel. However, these features also occur in other genera of the family and cannot be recognized as synapomorphies for this genus. The distinctive perianth apertures in *Wachendorfia* are also found in the genus *Schiekia* (see Character Analysis, *Perianth apertures*; Fig. 51). Monophylesis of *Wachendorfia*, therefore, cannot be affirmed in the present study.

Xiphidium consists of *X. coeruleum* and *X. xanthorhiza*, which differ only in minor morphological features and are likely more closely related to one another than to any other genus. However, because no definitive synapomorphy is evident for *Xiphidium*, its monophyly cannot be affirmed.

Tribonanthes has a unique, "stem tuberous" rootstock present in all five species (Pate & Dixon, 1981). This rootstock type may be derived for the genus; however, a cormose stem type is present in other genera and could be indicative of a common evolutionary origin for them (see Character Analysis, *Stem structural type*). Species of *Tribonanthes* do, however, have one feature that is very likely unique for the genus: the presence of distinctive appendages arising from the connective of the anther (see Character Analysis, *Stamen connective appendages*; Fig. 59). This feature is accepted as an autapomorphy, and *Tribonanthes* is hypothesized to be monophyletic.

The three species of *Phlebocarya* are quite similar to one another, differing primarily in leaf shape and vestiture. The similarities among *Phlebocarya* species in inflorescence and floral morphology provide good evidence of their very close relationship. In addition, flowers of *Phlebocarya* have a unilocular ovary and epitropous ovules; these are unique within the Haemodoraceae and may be synapomorphies for the genus. Therefore, *Phlebocarya* is accepted as being monophyletic.

Conostylis is the largest genus in the family, with ca. 25 species. No feature appears to be synapomorphic for the genus. The species of *Conostylis* show considerable variability in vegetative and floral morphology. In fact, *C. androstemma* and *C. bealiana* have an elongate perianth tube very similar to and possibly homologous with that of the monotypic *Blancoa* (see Character Analysis, *Perianth tube*). Although much more detailed studies of this genus are needed to resolve its intergeneric relationships, it is very likely paraphyletic; there is no evidence that one or more species of *Conostylis* might not be more closely related to *Blancoa* or even to species of *Anigozanthos*.

Anigozanthos is the second largest genus in the family, with ca. 10 species. Species of *Anigozanthos*, together with the monotypic *Macropidia*, almost certainly constitute a monophyletic group. Both have zygomorphic perianth tubes derived via a unique mechanism (see Character Analysis, *Perianth splitting*; Figs. 53, 54). *Anigozanthos* differs from *Macropidia* in trichome color and in having either two or numerous ovules per carpel (as op-

posed to one per carpel in *Macropidia*). However, trichome color is quite variable among species of *Anigozanthos*, and ovule number is likely not a shared derived feature for the genus. Because the characters distinguishing *Anigozanthos* from *Macropidia* are variable or likely to be plesiomorphic, it is uncertain that *Anigozanthos* is monotypic; one or more species of *Anigozanthos* may be more closely related to *Macropidia* than to other species of *Anigozanthos*.

Thus, five of the eight nonmonotypic genera of the Haemodoraceae cannot be reasonably shown, by evidence of synapomorphy, to be monophyletic. In this cladistic analysis of the Haemodoraceae, the following exemplar species are designated for these five genera: *Haemodorum spicatum*, *Wachendorfia thyrsiflora*, *Xiphidium coeruleum*, *Conostylis androstemma*, *Conostylis aurea*, *Conostylis bealiana*, *Anigozanthos flavidus*, and *Anigozanthos rufus*. Wherever *Haemodorum*, *Wachendorfia*, and *Xiphidium* are used in the analysis, it should be assumed that only the species indicated above applies. For *Conostylis* and *Anigozanthos*, it should be kept in mind that very few of the species in the genera will be considered and that these are exemplars. Future studies considering all species of these genera will be needed to assess fully their phylogenetic relationships.

Outgroup Taxa

In the following cladistic analysis character state polarity of ingroup taxa was determined using outgroup comparison. This basically entails performing a cladistic analysis on the ingroup plus one or more closely related taxa (outgroups), which serve to root the cladogram. The plesiomorphic state for the ingroup (at the outgroup node; see Maddison et al., 1984) is that which yields maximum parsimony among ingroups and outgroups. The major difficulty in applying outgroup comparison, however, is in determining which taxa indeed share most recent common ancestry with the Haemodoraceae. As previously discussed (see History of Classification) the interfamilial classification of the Haemodoraceae has been quite variable, a number of families having been proposed as close relatives. Therefore, in the present study, every monocot family that has ever been classified with or considered closely related to the Haemodoraceae was assessed as a possible outgroup. These families are: Apostasiaceae, Bromeliaceae, Cyanastraceae, Hypoxidaceae, Philydraceae, Pontederiaceae, Sparganiaceae, Taccaceae, Tecophilaeaceae, Typhaceae, and Velloziaceae. A comprehensive analysis of the phylogenetic relationships of these families to one another is beyond the scope of the present investigation and will be pursued in the future. Selective features from the literature and from ongoing studies by the author were assessed in order to determine the most likely closest outgroups. It was hoped that at least the two closest outgroups could be identified, as a minimum of two outgroups is required for unequivocally assessing character state polarity (see Maddison et al., 1984).

Evidence for the sister group relationship of the Haemodoraceae comes mainly from studies of pollen wall ultrastructure (Simpson, 1983, 1987). All investigated members of the Haemodoraceae have a 1–3-layered, non-tectate-columellate exine structure, which is almost certainly derived among the monocotyledons as a whole (Simpson, 1983; see Character Analysis). In contrast, all investigated members of the Apostasiaceae, Bromeliaceae, Cyanastraceae, Hypoxidaceae, Philydraceae, Sparganiaceae, Taccaceae, Tecophilaeaceae, Typhaceae, and Velloziaceae have a typical tectate-columellate exine structure (Ayensu & Skvarla, 1974; Nilsson et al., 1977; Brighigna et al., 1981; Simpson, 1983, 1985a, b; Zavada, 1983b). A tectate-columellate exine structure is presumed to be a plesiomorphic condition among the monocots (Zavada, 1983b) and cannot be utilized to define monophyletic groups. Among the taxa previously proposed to be closely related to the Haemodoraceae, only the Pontederiaceae are similar in pollen ultrastructure. Several members of the Pontederiaceae possess an exine sculpturing and structure identical to that of members of the Haemodoraceae (Simpson, 1987; see Character Analysis, *Pollen sculpturing*, *Exine wall structure*). The palynological similarities between the Haemodoraceae and Pontederiaceae constitute excellent evidence for the close relationship of the two families and are hypothesized here as synapomorphies linking the Haemodoraceae and Pontederiaceae as sister taxa (Simpson, 1987).

Identification of the next most closely related outgroup of the Haemodoraceae-Pontederiaceae complex is rather uncertain, however. Dahlgren & Rasmussen (1983) proposed that the presence of an amoeboid tapetum in the Haemodoraceae, Pontederiaceae, Typhaceae, and Sparganiaceae constitutes a synapomorphy for these four families, uniting them as a monophyletic group within their Bromeliiflorae. However, because an amoeboid tapetum occurs in numerous other monocot taxa, its use as a synapomorphy for these families seems less than certain, particularly with respect to differing opinions as to the classification of the Ty-

phales (Typhaceae and Sparganiaceae). Details of leaf morphology may provide less ambiguous evidence. Of the possible outgroups considered, the Haemodoraceae are similar only to the Philydraceae, Pontederiaceae, Sparganiaceae, and Typhaceae in possessing distichous leaves, a feature that Dahlgren & Rasmussen (1983) considered synapomorphic for these families. Of these families, only the Haemodoraceae and Philydraceae have unifacial (= ensiform) leaves. The presence of unifacial leaves is generally considered to be apomorphic among the monocotyledons. Occurrence of such leaves in the Philydraceae and Haemodoraceae is tentatively hypothesized as synapomorphic for the two families and evidence for their recent common ancestry, especially in light of numerous other similarities of the two families (see below). The evolutionary directionality of this feature may need further consideration, as Walker (1989) considers unifacial leaves to be plesiomorphic for the monocots as a whole.

Several other features link the Haemodoraceae to the Philydraceae and/or Pontederiaceae (and in many cases to other families), but the relative ancestry of these characters is uncertain or nonconclusive in outgroup selection. For example, among all outgroup candidates, the Bromeliaceae, Philydraceae, Pontederiaceae, Sparganiaceae, and Typhaceae are similar to the Haemodoraceae in having fluorescent, lignin-precursor acids (ferulic, diferulic, and p-hydroxybenzoic) bound to unlignified cell walls (Harris & Hartley, 1980). In contrast, these bound acids are absent in investigated members of all other considered outgroup families (i.e., Hypoxidaceae, Taccaceae, Tecophilaeaceae, and Velloziaceae). The data base for this character is quite small. Only one to a few genera or species have been investigated for many monocot families, and numerous families have yet to be investigated at all. Dahlgren & Rasmussen (1983) hypothesized that the presence of these fluorescent cell-wall-bound acids is a derived feature within the monocots, since these compounds are lacking in presumably closely related dicotyledons. Although many more taxa need investigation with regard to this feature, and although its biochemical significance needs elucidation, the presence of these fluorescent cell-wall-bound acids seems to constitute good evidence for the close relationship of the above families (see Interfamilial Relationships).

In addition, among the possible outgroups, only investigated members of the Haemodoraceae, Philydraceae, Pontederiaceae, and Sparganiaceae possess a common anatomical feature: presence of distinctive placental sclereid idioblasts (work in progress; see Character Analysis, *Placental sclereids*). These compounds are present in members of the Zingiberaceae as well (see Interfamilial Relationships). Although few taxa in families other than the Haemodoraceae have been investigated for this feature, it appears to provide yet another piece of evidence linking the Haemodoraceae, Philydraceae, Pontederiaceae, and Typhales.

In summary, the Pontederiaceae are chosen as the hypothesized sister taxon to the Haemodoraceae because of a similar and hypothetically derived pollen wall structure. The identification of the next most closely related outgroup is less certain. The Philydraceae are tentatively selected as this next most closely related outgroup because of the occurrence of similar, presumably derived, unifacial leaves in the Philydraceae and Haemodoraceae. Both outgroup families show similarity to the Haemodoraceae in anatomy (placental sclereids) and chemistry (fluorescent cell-wall-bound compounds), further supporting a close relationship. Certainly, additional studies are needed to assess interfamilial relationships in the complex (see Interfamilial Classification). However, rather than treat these outgroup families as unresolved or polytomous (Maddison et al., 1984), the evidence seems strong enough to utilize the Philydraceae and Pontederiaceae as most closely related outgroups to the Haemodoraceae in ascertaining the directionality of character state transformations.

Character Analysis

The following is a list and discussion of those characters and character states thought by the author to be important in resolving intrafamilial relationships. It should be stressed that the initial character selection makes this study "subjective," as it does all taxonomic studies, whether phylogenetic or not. Only characters that show clear discontinuities between the states are included in the analysis. Included in the character analysis are: (1) selection of characters; (2) selection and definition of character states; (3) assessment of homology of characters and character states; and (4) assessment of polarity of character states based on comparison with the designated outgroups (Philydraceae and Pontederiaceae) or other criteria.

Both outgroups were treated as operational taxonomic units (OTUs) in the data matrix. Characters with common states in all members of the Haemodoraceae (characters 52–55) are included in the analysis only to establish relationships of the two outgroups to the ingroup. A given character was coded as missing data ("?" in the data matrix)

if the taxon is polymorphic for the character, if data are unknown (e.g., chromosome numbers of *Schiekia* and *Pyrrorhiza*), or if X-coding is used (see below). Multistate characters were initially coded as two or more binary characters for ease of discussion. Where a multistate morphocline is illustrated in the character analysis, a character number in brackets portrays a coding such that taxa possessing the character to the left of the arrow are coded as state "0" and those to the right are coded as state "1."

For certain characters, the "X character" method (Doyle & Donoghue, 1986) was utilized, which codes the character state for certain taxa as "X" (equivalent to missing data, "?," in the computer algorithm), allowing for either of two alternative state changes. This technique is valuable in that the number of characters assigned to a given transformation series (morphocline) may often be reduced, thus minimizing unintentional weighting and unintentional bias, e.g., with regard to uncertain patterns of evolutionary direction.

MATERIALS AND METHODS

For studies of floral trichome anatomy and perianth cell types, small pieces of tepals and pedicels were removed and mounted in 50% glycerin. Preparations were left unstained or were occasionally stained with 0.01% aqueous Toluidine blue. For studies of perianth aestivation, immature buds were embedded in paraffin, and serial cross sections were prepared according to standard anatomical technique (Johansen, 1940). For observations of placental cell types, ovaries of mature flowers were paraffin-embedded and longitudinal sections were prepared as above. All sections were stained with safranin, iron hematoxylin, and fast green. Line drawings were made using a Wild Heerbrugg brightfield microscope with camera lucida attachment. Photographs were taken with a Leitz Wetzlar or Nikon Microphot-FX photomicroscope using Panatomic X film (ASA 32).

Plant material was fixed in either formalin/acetic acid/alcohol (noted "FAA" below) or 4% gluteraldehyde ("GLUT" below). Some material ("DRIED" below) was obtained from herbarium sheets and reexpanded in Aerosol OT for 2–5 days, followed by several water rinses and then fixation in FAA. Materials and methods for the ultrastructural observations of pollen grains are discussed in Simpson (1983, 1985a, b, 1987). Documentation for the taxa studied in the present work is as follows (parentheses indicate herbaria that house vouchers):

HAEMORDORACEAE

Anigozanthos flavidus DC. "FAA"—*M. G. Simpson 24IX81J* (DUKE)

Anigozanthos rufus Labill. "FAA"—*M. G. Simpson 27IX81F* (SDSU)

Barberetta aurea Harv. "FAA"—*R. Ornduff 7661* (UC)

Blancoa canescens Lindl. "GLUT"—*M. G. Simpson 18IX81AA* (DUKE)

Conostylis androstemma F. Muell. "DRIED"—*S. R. Preif 1409* (K)

C. aurea Lindl. "FAA"—*M. G. Simpson 13IX81S* (SDSU)

C. bealiana F. Muell. "FAA"—*Arboretum, U.C. Santa Cruz, 3XI80*

Dilatris corymbosa Berg. "FAA"—*P. Goldblatt 3242* (MO)

D. pilansii Barker "FAA"—*P. V. D. Meriwe 30X81-2* (STEU)

Haemodorum simplex Lindl. "GLUT"—*M. G. Simpson 20IX81A* (DUKE)

H. spicatum R. Br. "FAA"—*M. G. Simpson 16IX81C* (DUKE)

Lachnanthes caroliniana (Lam.) Dandy "FAA"—*M. G. Simpson 14VI80A* (DUKE)

Lanaria lanata (L.) Dur. & Schinz "DRIED"—*R. D. A. Bayliss 4369* (US)

Lophiola aurea Ker-Gawler "FAA"—*M. G. Simpson 14VI80B* (DUKE)

Macropidia fuliginosa (Hook.) Druce "FAA"—*M. G. Simpson 18IX81DD* (DUKE)

Pauridia minuta (L.f.) Dur. & Schinz "DRIED"—*P. MacOwan & H. Bolus 291* (US)

Phlebocarya ciliata R. Br. "GLUT"—*M. G. Simpson 16IX81A* (DUKE)

P. pilosissima F. Muell. "FAA"—*M. G. Simpson 16IX81K* (DUKE)

Pyrrorhiza neblinae Maguire & Wurdack "DRIED"—*B. Maguire, J. J. Wurdack & G. S. Bunting 37222* (US)

Schiekia orinocensis (Kunth) Meisn. "FAA"—*B. Maguire 41569* (NY)

Tribonanthes australis Endl. "DRIED"—*A. J. Eames & A. T. Hotchkiss, 23VIII1953* (US)

T. variabilis Lindl. "FAA"—*M. G. Simpson 8IX81A* (DUKE)

Wachendorfia paniculata L. "FAA"—*P. V. D. Merwe 30X81-1* (STEU)

W. thyrsiflora L. "FAA"—*R. Ornduff 7691* (UC)

Xiphidium coeruleum Aubl. "FAA"—*J. M. MacDougal 1043* (DUKE)

HYPOXIDACEAE

Curculigo capitulata (Lour.) Kuntze "FAA"—*M. G. Simpson 29VI80* (FTG)
Hypoxis micrantha Pollard "FAA"—*M. G. Simpson 5V82A* (DUKE)

LILIACEAE TRIBE OPHIOPOGONEAE

Liriope muscari (Decne.) L. H. Bailey "FAA"—*M. G. Simpson 7VII81A* (DUKE)

PHILYDRACEAE

Helmholtzia acorifolia F. V. Mueller "FAA"—*M. G. Simpson 81-16A* (DUKE)
H. novo-guineensis (Krause) Skottsberg "DRIED"—*L. J. Brass 12859* (A)
Orthorthylax glaberrimus (Hooker fil.) Skottsberg "FAA"—*U. Hamann 1183* (Herb., U. Hamann, Berlin)
Philydrum lanuginosum Gaertner "FAA"—E. F. Constable; *U. Hamann 959* (NSW)
Philydrella pygmaea (R. Brown) Caruel "FAA"—*M. G. Simpson 28IX81A* (DUKE)

PONTEDERIACEAE

Heteranthera reniformis R. & P. "GLUT"—*M. G. Simpson 4VIII82A* (DUKE)
Pontederia cordata L. "GLUT"—*M. G. Simpson 4VIII82B* (DUKE)
Reussia rotundifolia (L.f.) Castell "DRIED"—*G. T. Prance 23284 & J. F. Ramos* (US)

SPARGANIACEAE

Sparganium eurycarpum Engelm. "FAA/GLUT"—*M. G. Simpson 21VI86A* (SDSU)

STRELITZIACEAE

Strelitzia reginae Ait. "FAA"—*M. G. Simpson 11XI86A* (SDSU)

TACCACEAE

Tacca integrifolia Ker.-Gawl. "FAA"—*M. G. Simpson 23V82* (Duke Univ. greenhouses 81-0379)

TECOPHILAEACEAE

Conanthera bifolia R. & P. "DRIED"—*E. P. Killip & E. Pisano 39690* (US)
C. trimaculata Don. "DRIED"—*C. Grandjot* (MO 1126476)
Cyanastrum cordifolium Oliv. "DRIED"—*B. O. Daramola 41029* (MO)
Cyanella alba L.f. "FAA"—*R. Ornduff 7463* (UC)
C. hyacinthoides L. "FAA"—*R. Ornduff 7501* (UC)
C. lutea L.f. var. *lutea* "FAA"—*R. Ornduff 7565* (UC)
Odontostomum hartwegii Torr. "FAA"—UCBG 53.845
Tecophilaea violiflora Bert. ex Colla. "DRIED"—*O. Buchtien 10VIII1895* (US)
Walleria mackenzii Kirk. "DRIED"—*J. Buchanan 1891* (US)
W. muricata N. E. B. "DRIED"—*N. C. Chase 5182* (MO)
Zephyra elegans D. Don. "DRIED"—*E. Werdermann 776* (US)

VELLOZIACEAE

Barbecenia seubertiana Goeth. & Henr. "FAA"—*Hatschbach 30095* (Duke Univ. greenhouses)

CHARACTER CODING

Character #1. Root and stem coloration. Dilatris, Haemodorum, Lachnanthes, Pyrrorhiza, Wachendorfia, and *Xiphidium* have a red, red-orange, or maroon coloration of the roots and underground stems (Thiselton-Dyer, 1896–1897; Adamson & Salter, 1950; Maguire & Wurdack, 1957; Geerinck, 1969a; Simpson, pers. obs.), accounting for the family name Haemodoraceae (Gr. *haima*, blood), the Bloodwort Family. This reddish coloration results from the presence of one or more forms of the distinctive class of chemical compounds, phenalenones. Although all investigated family members contain phenalenones (Cooke & Segal, 1955; Cooke et al., 1958; Cooke & Edwards, 1981; see Introduction), only the above six genera show red pigmentation in the roots and rootstocks. The possible adaptive significance of this coloration is unknown; it may simply be correlated with a high concentration of one or more forms of this class of compounds. The fact that these pigments are toxic to certain livestock, at least in *Lachnanthes* (see Characterization and Economic Importance), may be significant in this regard.

Character #2. Stem structural type. Most members of the Haemodoraceae have an elongate to congested, sympodially branched rhizome, commonly bearing proliferative stolons, although four genera deviate from the rhizomatous habit. *Pyrrorhiza, Tribonanthes,* and *Wachendorfia* possess

an underground corm (illustrated for *Wachendorfia* in Fig. 2). In *Tribonanthes* the corm (termed a "root tuber," sensu Pate & Dixon, 1981) develops from a downward-directed axillary bud which penetrates the outer scale leaves of the old corm (initially resembling a root); further growth results in the formation of a globose mass of tissue. *Pyrrorhiza* and *Wachendorfia* (Fig. 2) have a basal cluster of globose corms; it is not known whether they develop similarly to those of *Tribonanthes*. *Haemodorum* has a somewhat bulbous corm, not like a typical bulb, but consisting of an aggregate of the swollen, fleshy bases of primarily nonphotosynthetic leaves (Thiselton-Dyer, 1896–1897; Pate & Dixon, 1981; Simpson, pers. obs.). The bulbous corm of *Haemodorum* is tentatively coded as homologous to that of the above three genera. (*Barberetta* is somewhat intermediate between the rhizomatous and the cormose taxa, having short, horizontal, rather fleshy proliferative shoots; however, these are probably a slight specialization of the rhizomatous/stoloniferous habit and are not coded as evolutionarily intermediate to the cormose stem type.)

The hypothesized morphocline for stem structural types in the family is: [#2] RHIZOMATOUS ↔ CORM OR BULBOUS CORM. However, such a hypothesis seems to be very tentative. Deviations from a strictly rhizomatous stem habit likely have occurred secondarily more than once (e.g., via strong selective pressure for dormancy) and thus may not indicate homology.

Of the outgroups, a rhizomatous/stoloniferous stem is present in all members of the Pontederiaceae. In the Philydraceae three of the five species have a rhizomatous stem type, but *Philydrum lanuginosum* has a basal caudex (Dahlgren et al., 1985), and *Philydrella pygmaea* has corms similar to those of the cormose Haemodoraceae (Pate & Dixon, 1981; pers. obs.). Thus, the Philydraceae are coded as polymorphic for stem structural type. Interestingly, *Philydrella* is found with *Tribonanthes* (in southwest Australia); they occur together in similar habitats (low, winter-wet flats). It is probable, however, that the common stem habit of these two taxa is not by homology, but is the result of separate, secondary adaptations to a winter-wet, summer-drought environmental regime.

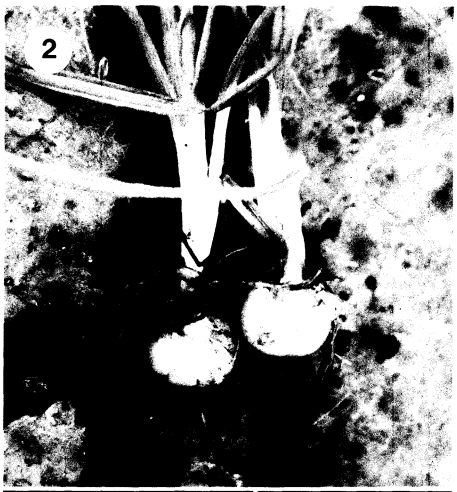
Character #3. Plicate leaves. *Barberetta* and *Wachendorfia* have longitudinally plicate leaves (Figs. 3–5), a condition found in no other member of the Haemodoraceae nor in any of the outgroups. (*Helmholtzia* of the Philydraceae has unifacial leaves with a pseudo-costa but no evidence of plication.) Plication in these two genera arises by the occurrence of longitudinal folding and development of tissue ridges opposite the major vascular bundles (Fig. 5). The presence of similar plicate leaves in *Barberetta* and *Wachendorfia* constitutes strong evidence for their common evolutionary origin within the Haemodoraceae and is coded as derived (from an ancestral leaf with smooth posture).

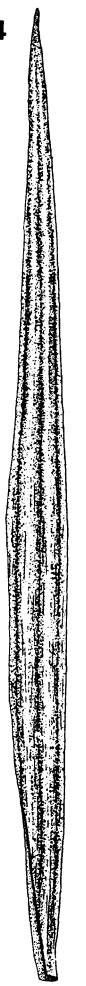
Characters #4–6. Inflorescence type. Inflorescences in the Haemodoraceae are quite variable, but most have a common theme, consisting of a network of helicoid cymes (e.g., Fig. 6) arranged as a panicle, raceme, corymb, or capitulum. The inflorescence of *Haemodorum* differs in being a raceme, panicle, or corymb of either flower pairs or cymules containing paired flowers. In addition, corymblike aggregates of bifurcate or trifurcate helicoid cymes occur in *Dilatris* and *Lachnanthes*, and bifurcate helicoid cyme aggregates (in the form of a raceme, panicle, corymb, or capitulum) occur in *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, *Phlebocarya*, and *Tribonanthes*. *Barberetta* is unique in the family in having a simple raceme.

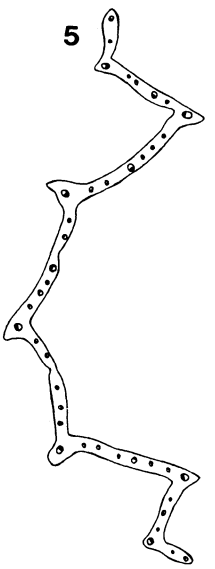
The possible evolutionary intergradation between these varied inflorescence types is uncertain. A coding of inflorescence types that may likely represent homologies in the family is related to the cyme unit itself rather than to the type of aggregation of these cyme units. The morphocline used in the present study is: CYME ABSENT ←[#4]→ CYME SIMPLE ←[#5]→ CYME BIFURCATE ←[#6]→ CYME BIFURCATE OR TRIFURCATE. In this morphocline only the simple raceme of *Barberetta* would be coded as lacking a cyme unit. The flower pairs or cymules in *Haemodorum* are interpreted as being a modification of the bifurcate cyme. A tendency for trifurcate cyme units is found only in *Dilatris* and *Lachnanthes*.

Among the outgroups all members of the Philydraceae lack cyme units; the inflorescence is either a simple spike or a spike of spikes. The inflorescence type in the Pontederiaceae is generally a spike or raceme of simple cyme units. A priori, it seems most probable that the simple cyme inflorescence unit, which is common in the monocotyledons as a whole, may be most ancestral for the Haemodoraceae; this hypothesis will be tested by the cladistic analysis.

Characters #7–13. Trichome anatomy. Trichomes are present on the inflorescence axes, bracts, outer perianths, and/or ovary surfaces of all genera of the Haemodoraceae and on the leaves

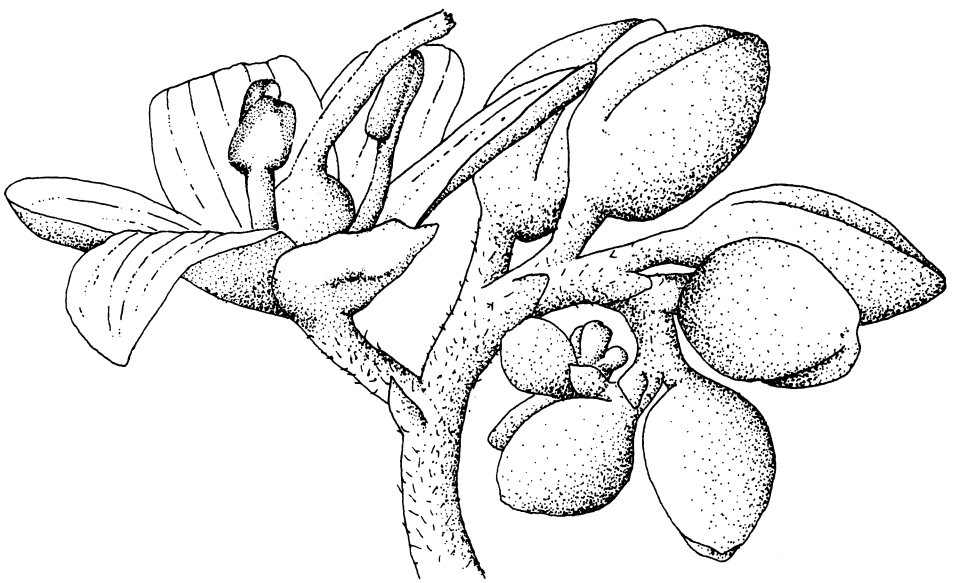


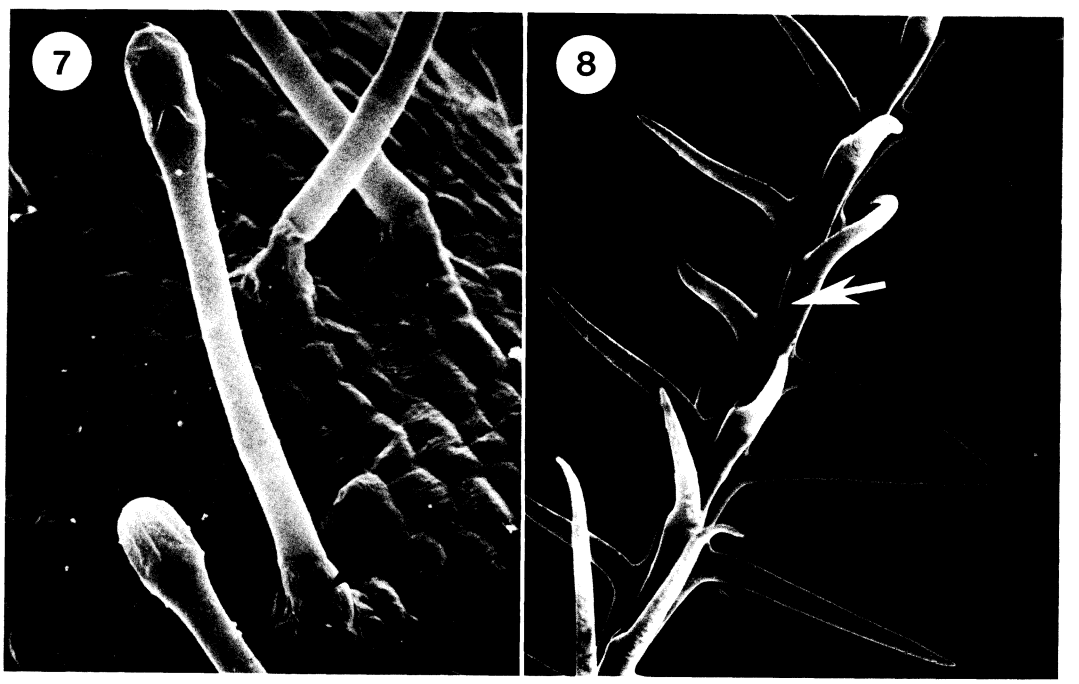




FIGURES 2–5. Vegetative characters of *Wachendorfia*.—2. Cormose rootstock of *W. paniculata*; ×0.35.—3. *Wachendorfia paniculata* plant, showing plicate leaves; ×0.35.—4. Leaf of *W. thyrsiflora*. Note plication of blade; ×0.35.—5. Leaf cross section of *W. thyrsiflora*. Note plication and ridges of tissue at major vascular bundles; ×7.4.

of some family members. Distinctive pilate trichomes (Figs. 7, 9), consisting of a basal rosette of generally 3–5 cells (having characteristic transverse ridges; see Fig. 11), a uniseriate column of (1–)2–5(–7) cells, and a terminal, ovoid glandlike cell, are found in *Barberetta*, *Dilatris*, *Lachnanthes*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia*, and *Xiphidium*. As their anatomical similarity reveals, the trichomes in these taxa are undoubtedly homologous. Within these seven genera various combinations with other trichome types may occur. *Barberetta* (Fig. 9) and *Xiphidium* (Fig. 20) possess only the pilate trichome type. *Pyrrorhiza* (Fig. 17), *Schiekia* (Fig. 18), and *Wachendorfia* (Fig. 19) have both pilate trichomes and sharply tapering, unicellular trichomes, both trichome types with a basal rosette of cells. *Dilatris* possesses the typical pilate trichome type (Figs. 10, 11) plus long,





FIGURES 6–8. Inflorescence and trichome morphology in the Haemodoraceae.—6. *Xiphidium coeruleum*, helicoid cyme inflorescence unit; ×7.0.—7. Pilate trichomes of *Barberetta aurea*; ×310.—8. Multiseriate, dendritic trichome of *Anigozanthos flavidus*. Note decurrent lateral trichome branches (arrow); ×470.

many-celled, uniseriate, tapering trichomes with a basal rosette of cells (Fig. 12). *Lachnanthes* has mostly long, uniseriate, tapering trichomes (Fig. 14) with *no* distinctive basal rosette (Fig. 15). However, unicellular trichomes with a glandlike terminal cell and a basal rosette of epidermal cells (resembling those of the pilate trichome type) occasionally occur on the leaf margins in *Lachnanthes* (Fig. 16).

Species of *Haemodorum* are usually glabrous throughout. However, at least *H. spicatum* (Fig. 13) has uniseriate, generally three-celled trichomes without specialized basal epidermal cells. These trichomes have a rounded, somewhat elongate terminal cell with densely brown-colored cytoplasmic contents, resembling (and possibly homologous with; see below) the terminal cell of the pilate trichome type.

Anigozanthos, *Blancoa*, *Conostylis*, and *Macropidia* have identical short to very elongate, multiseriate, highly branched, "dendritic" trichomes (Figs. 8, 21, 22). The bases of these dendritic trichomes consist of a few small, thick-walled cuboidal cells (as in Fig. 22); cells that form the branches are decurrent along the trichome axis (see Fig. 8). *Tribonanthes* has long, many-celled, generally uniseriate trichomes (Fig. 27) that are characteristically branched at the base and have 2–4 rounded to short-cylindrical basal cells (Fig. 26). One species of *Phlebocarya*, *P. pilosissima*, has branched dendritic (Fig. 24) to stellate (Fig. 25) trichomes; these are similar to but less highly branched than the dendritic trichomes of the above four genera. A second species of *Phlebocarya*, *P. ciliata*, is, like *Haemodorum*, usually glabrous but has occasional, slightly elongate, unicellular trichomes (Fig. 23) resembling those of *Haemodorum spicatum*. Thus the trichomes of *Phlebocarya* might be interpreted as a morphological and evolutionary intermediate to those of *Haemodorum* and the taxa with dendritic trichomes.

A hypothesized intergradation series for trichome anatomy in the Haemodoraceae is seen in Figure 28. Note that the homology of the trichomes of *Haemodorum* with the pilate trichome type of *Barberetta* and *Xiphidium* and with the unicellular type of *Phlebocarya* is questionable. The seven genera with pilate trichomes (having a basal rosette of epidermal cells) are arranged in a linear series depending on the presence and length of an additional trichome type, whether: (1) absent (*Barberetta*, *Xiphidium*); (2) unicellular (*Pyrrorhiza*, *Schiekia*, and *Wachendorfia*); (3) long-uniseriate (*Dilatris*); or (4) long-uniseriate lacking a basal rosette (*Lachnanthes*). The basally branched, uniseriate trichomes of *Tribonanthes* and the highly branched, dendritic trichomes of *Anigozanthos*, *Blancoa*, *Conostylis*, and *Macropidia* are depicted as intergrading with the sparsely branched dendritic trichomes of *Phlebocarya*. The long-uniseriate trichomes of *Lachnanthes* and the long-uniseriate, basally branched trichomes of *Tribonanthes* are possibly homologous; both trichome types lack a basal rosette of epidermal cells.

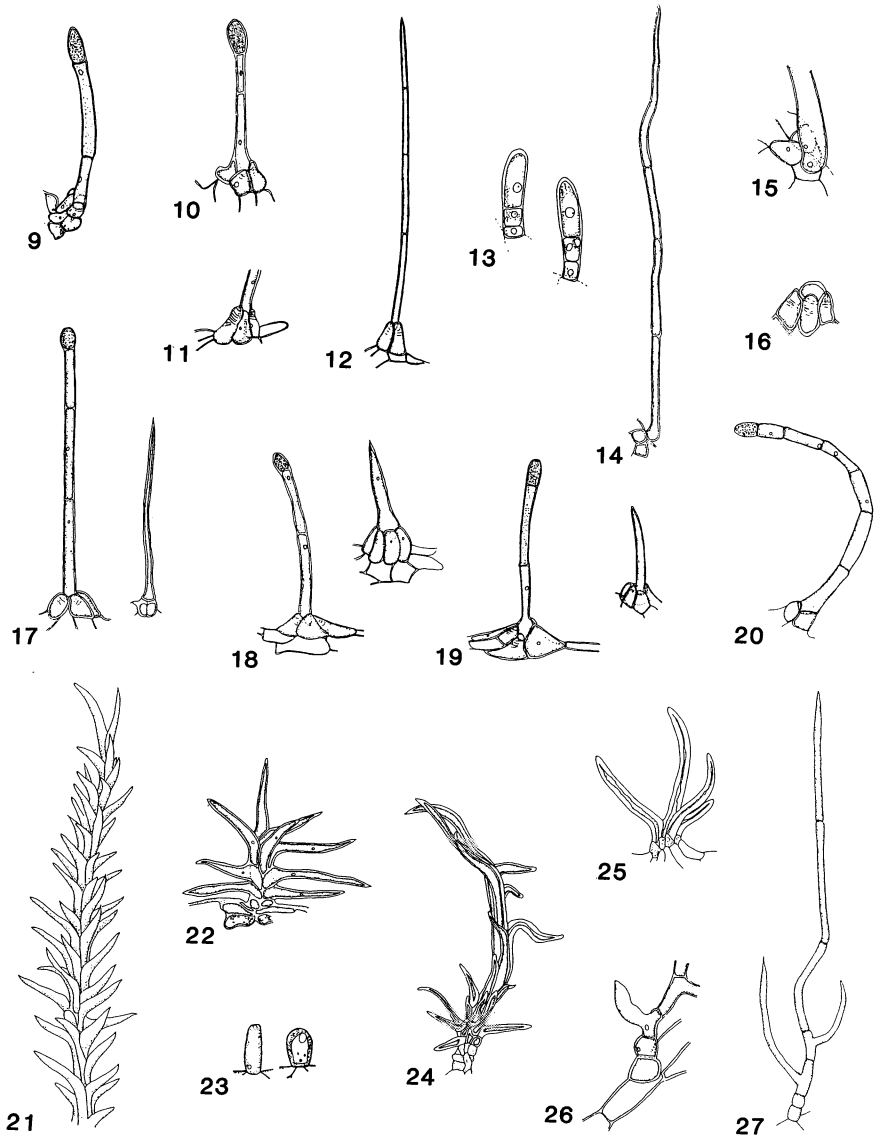
Because of the uncertainty of some of the intergrading states of Figure 28, and because the groupings of this morphocline would tend to bias the cladistic analysis if (as often happens) any conflicts in character evolution are evident, the character "trichome anatomy" was subdivided into the following discrete two-state characters (see Table 7 and Fig. 165A):

Character #7: Presence/absence of pilate trichomes. *Haemodorum*, whose trichomes are quite different than those of other taxa, is coded as possessing pilate trichomes. *Lachnanthes*, which has unicellular trichomes with a basal rosette of cells (similar to that of other taxa), is coded as "X" because of the uncertainty of homology with the pilate type. The genus *Phlebocarya*, which has unicellular trichomes in one species (*P. ciliata*), is also coded as "X" for this character so as not to bias the possibility of homology between its trichome type and that of *Haemodorum* (see Figs. 28, 165A).

Character #8: Presence/absence of trichomes which, if pilate, have a basal rosette of epidermal cells. The trichomes of *Haemodorum*, although pilate, lack this distinctive basal rosette. The unicellular trichomes of *Lachnanthes*, while coded as questionably pilate, do possess a basal rosette; thus, character #8 is coded as "present" for this species. Taxa lacking pilate trichomes are coded as "X" (including *Phlebocarya*).

Character #9: Presence/absence of trichomes with a sharply tapering apex. The basally branched trichomes of *Tribonanthes* are interpreted as being sharply tapering, as are the uniseriate trichomes of *Dilatris* and *Lachnanthes* and the unicellular trichomes of *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. Taxa with multiseriate, dendritic trichomes were also coded as possessing tapering trichomes because of the presumed homology of the sharply tapering trichome branches with the sharply tapering apices of the uniseriate trichomes.

Character #10: Trichomes which, if tapering, are either unicellular (*Pyrrorhiza*, *Schiekia*, and *Wachendorfia*) or multicellular. Taxa lacking tri-



FIGURES 9–27. Trichome anatomy in the Haemodoraceae.—9. *Barberetta aurea*, pilate trichome. Note terminal granular cell and basal rosette of cells; ×120. 10–12. *Dilatris pilansii*.—10. Pilate trichome; ×120.—11. Basal rosette cells with apical transverse ridges; ×73.—12. Long, uniseriate tapering trichome with basal rosette cells; ×54.—13. *Haemodorum spicatum*, short, uniseriate (generally 3-celled) trichome. Note oblong, granular terminal cell; ×133. 14–16. *Lachnanthes caroliniana*.—14. Long, uniseriate tapering trichome; ×55.—15. Close-up of trichome base. Note absence of rosette cells; ×120.—16. Unicellular trichome of leaf margins. Note basal rosette cells with transverse ridges; ×146.—17. *Pyrrorhiza neblinae*, pilate (left) and unicellular, sharply tapering (right) trichomes, both with basal rosette cells; ×51 (left), ×40 (right).—18. *Schiekia orinocensis*, pilate (left) and unicellular, sharply tapering (right) trichomes; ×73.—19. *Wachendorfia thyrsiflora*, pilate (left) and unicellular, sharply tapering (right) trichomes; ×73.—20. *Xiphidium coeruleum*, pilate trichome with basal rosette cells; ×120. 21, 22. *Anigozanthos flavidus*.—21. Long, dendritic trichome with decurrent lateral branches; ×40.—22. Short, dendritic trichome with small cuboidal basal cells; ×69.—23. *Phlebocarya ciliata*, unicellular trichomes with granular contents; ×67. 24, 25. *Phlebocarya pilosissima*.—24. Dendritic trichome, with decurrent lateral branches and cuboidal basal cells; ×73.—25. Stellate trichome; ×91. 26, 27. *Tribonanthes variabilis*.—26. Trichome base, showing cuboidal basal cells and basal, lateral branches; ×120.—27. Uniseriate, tapering, basally brached trichome; ×50.

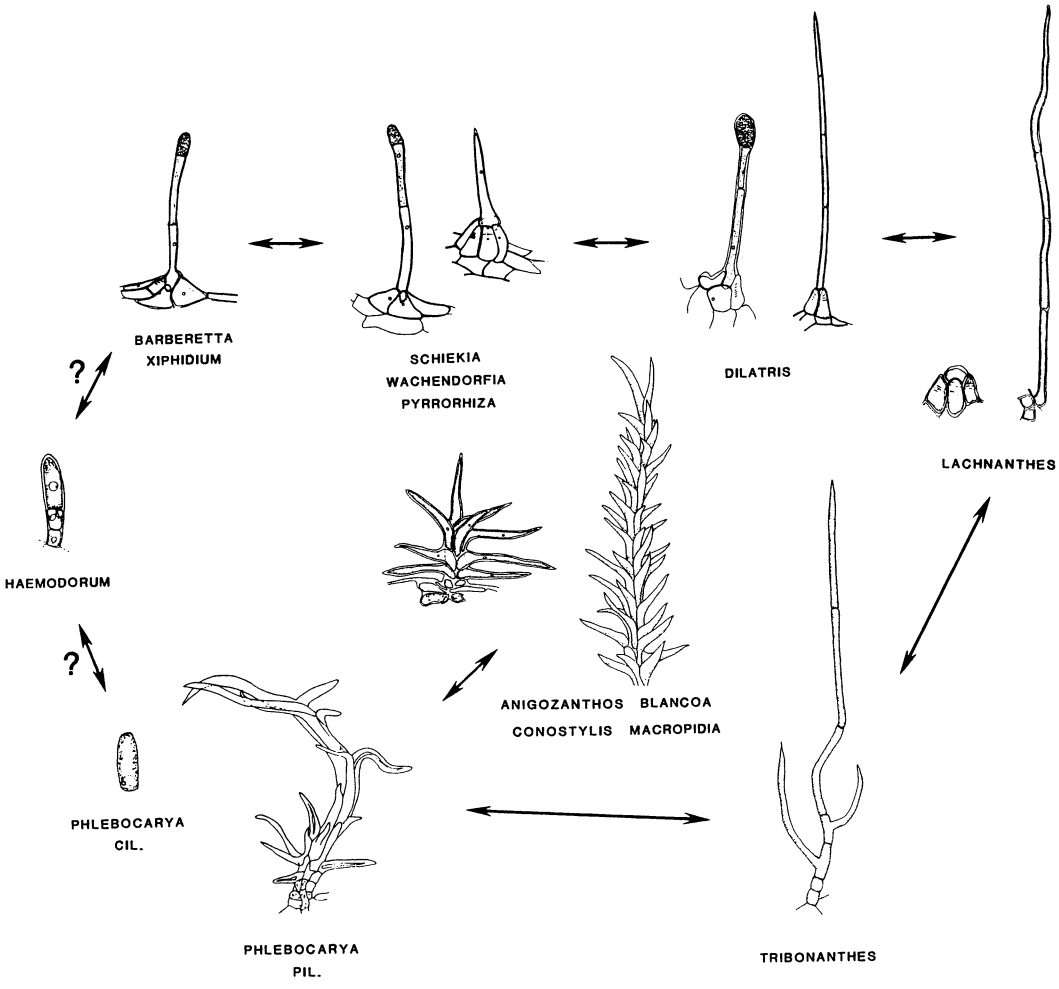


FIGURE 28. Hypothesized intergradation series of trichome types in the Haemodoraceae. Note the uncertainty (indicated by "?") of homology of the trichomes of *Haemodorum*. (See text for character state coding.)

chomes with sharply tapering apices are coded as "X."

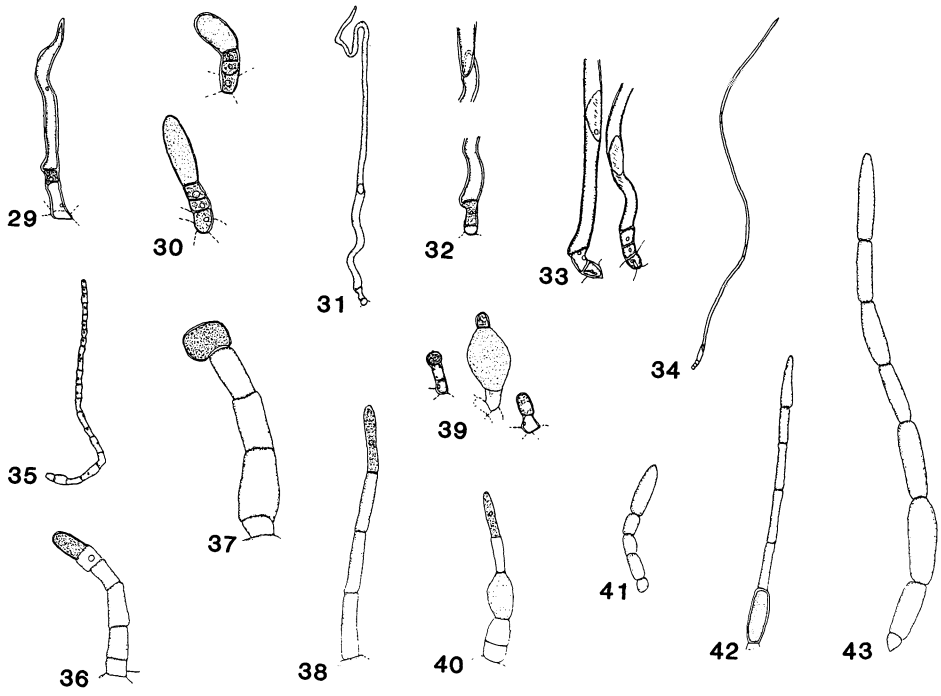
Character #11: Trichomes which, if tapering, are either uniseriate or multiseriate, the latter also being dendritic with decurrent branches and with multiseriate cuboidal basal cells. Taxa lacking tapering trichomes are coded as "X."

Character #12: Trichomes which, if tapering, are unbranched vs. branched. Branched trichomes include both the multiseriate, dendritic trichomes and the basally branched trichomes of *Tribonanthes*. Taxa lacking tapering trichomes are coded as "X."

Character #13: Presence/absence of trichomes which, if tapering, possess a basal rosette of epidermal cells. *Lachnanthes*, *Tribonanthes*, and the multiseriate taxa are coded as lacking the basal rosette (in the tapering trichomes) possessed by *Dilatris*, *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. Taxa lacking tapering trichomes are coded as "X."

For character #9 it might be argued that taxa with dendritic trichomes should not be coded as "tapering"; i.e., the sharply tapering branches of these multiseriate trichomes may not be homologous with the sharply tapering apices of the uniseriate trichomes. However, if taxa with multiseriate trichomes (*Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Phlebocarya*) are coded as either "0" or as "X" for this character, the topology of the most parsimonious cladogram(s) is unaffected (see Cladistic Analysis).

Trichomes of the outgroup families show some resemblances to those of the Haemodoraceae. For



FIGURES 29–43. Trichome anatomy in the Philydraceae and Pontederiaceae. 29–32. *Helmholtzia acorifolia*. — 29. Three-celled, uniseriate trichome, middle cell cuboidal with granular contents; ×117.—30. Four-celled, pilate trichomes, the terminal cell with orange-brown contents; ×146.—31. Long, uniseriate, tapering trichome; note short basal cells; ×52.—32. Close-up of trichome illustrated in Figure 31, showing oblique cross-walls at junction of cells (above) and trichome base with short, basal cells (below); ×117. 33–34. *Philydrum lanuginosum*.—33. Trichome bases. Note oblique cross-walls and cuboidal basal cells; ×117.—34. Long, uniseriate, tapering trichome; ×40. 35–37. *Heteranthera reniformis*.—35. Uniseriate, many-celled trichome of stamen filament; ×40.—36. Short, uniseriate pilate trichome of style; note granular contents of terminal cell; ×146.—37. Pilate trichome of outer tepal surface. Note granular contents of terminal cell; ×106. 38–40. *Pontederia cordata*.—38. Four-celled uniseriate trichome. Note granular contents of terminal cell; ×51.—39. Two- or three-celled trichomes. Note small terminal cell with granular contents and (in middle trichome) enlarged subapical cell containing orange-brown ergastic substance; ×73.—40. Five-celled uniseriate trichome, having granular contents in terminal cell and orange-brown ergastic substance in middle cell; ×51. 41–43. *Reussia rotundifolia*.—41. Five-celled, uniseriate trichome; ×39.—42. Six-celled, uniseriate trichome, with granular contents in supra-basal cell; ×39.—43. Eight-celled, uniseriate trichome; ×39.

example, *Helmholtzia* (Figs. 29, 31, 32) and *Philydrum* (Figs. 33, 34) of the Philydraceae have elongate, uniseriate, tapering trichomes with two or three isodiametric basal cells and, in the more distal regions, steeply inclined, overlapping end walls (see Figs. 32, 33). These trichomes most resemble *Tribonanthes*, which, however, are basally branched and have transverse, not inclined, end walls. *Helmholtzia* possesses, in addition to the above trichome type, occasional three- to four-celled, pilate trichomes (Fig. 30) with an ovoid to slightly elongate terminal cell containing a clear orange-brown ergastic substance similar to that found in perianth idioblasts in this and other genera (see *Perianth tannin cells/idioblasts*). These trichomes show some resemblance to the pilate trichomes of the Haemodoraceae, differing primarily in the contents and appearance of the terminal cell and in lacking the distinctive basal rosette of epidermal cells. Within the investigated members of the Pontederiaceae, the genus *Heteranthera* is largely glabrous but has some floral trichomes; these include: (1) multicellular, uniseriate staminal filament trichomes (Fig. 35); (2) short, pilate stylar trichomes with a terminal cell containing granular contents (Fig. 36); and (3) larger pilate trichomes, located on the outer tepal surfaces, with a globose terminal cell containing granular contents (Fig. 37). The so-called pilate trichomes of *Heteranthera* resemble somewhat the pilate trichomes in the Haemodoraceae, but (as in *Helmholtzia*) they lack the distinctive basal rosette cells. The one investigated species of *Pontederia* has several different, intergrading trichome types, ranging from: (1) linear,

uniseriate, 3–6-celled, with a densely granular terminal cell (Fig. 38); (2) short, 2–3-celled and capitate with a spherical to ellipsoid terminal cell (Fig. 39); and (3) uniseriate, of variable length, with one or more cells enlarged and containing a clear, orange ergastic substance similar to that in *Helmholtzia* (Fig. 40). The pilate trichomes of *Pontederia* are like those in *Helmholtzia* of the Philydraceae and show some resemblance to the pilate trichomes in the Haemodoraceae. *Reussia* of the Pontederiaceae has several types of uniseriate perianth trichomes (Figs. 41–43), some of which have a terminal cell containing densely granular contents.

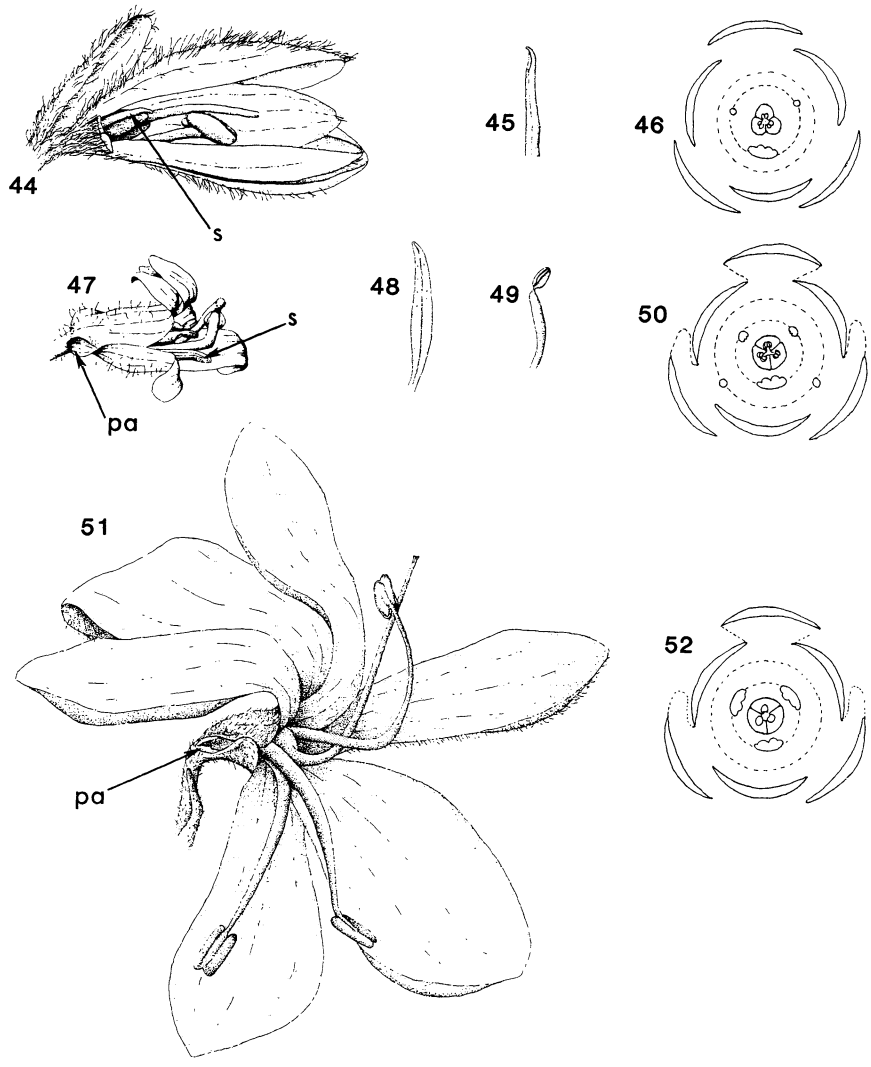
Many similarities are seen between the Haemodoraceae and the outgroups with respect to trichome anatomy. In the present analysis if one or more outgroup(s) possessed a trichome type similar to that designated in the character analysis, then that feature was coded as being homologous with the condition found in the Haemodoraceae. It is thus hypothesized that the similarity of the pilate trichomes of *Heteranthera* (Pontederiaceae) or the uniseriate trichomes of *Helmholtzia* (Philydraceae), as examples, with members of the Haemodoraceae reflects common ancestry. A possible difficulty with this, however, is that both outgroups are polymorphic with regard to trichome type. However, when the two were coded as polymorphic ("?") for all trichome characters (characters #7–13) in a separate cladistic analysis, the topology of the resultant most parsimonious cladograms remains unchanged (see Cladistic Analysis).

Character #14. Perianth apertures. *Schiekia* (Fig. 47) and *Wachendorfia* (Fig. 51) are similar in that the outer posterior tepal is basally fused to the two outer latero-anterior tepals and to the two inner latero-posterior tepals (Figs. 50, 52). At the basal junctions between the two outer latero-anterior tepals and the outer posterior tepal are distinctive slitlike pouches (termed "apertures" for *Wachendorfia* by Ornduff & Dulberger, 1978). Ornduff & Dulberger reported that in *Wachendorfia paniculata* nectar is produced from these perianth apertures. However, in view of the presence of septal nectaries in *Wachendorfia* species (see *Septal nectaries*), it is probable that these apertures function solely as a collection site for nectar secreted from the ovary. The significance of these sites is unknown, as no insect or other visitors have been described for *Wachendorfia*. The perianth apertures in *Schiekia* probably function similarly to those in *Wachendorfia*, although no observations have been published. All other genera of the Haemodoraceae with basically distinct tepals have no basal fusion of the tepals and no perianth apertures. Many genera of the Haemodoraceae have a syntepalous perianth, but fusion in these taxa is in the form of a complete basal perianth tube (see *Perianth tube*) and is treated as nonhomologous with the rather unique tepallary fusion in *Schiekia* and *Wachendorfia*.

Among the outgroup taxa, all members of the Philydraceae have a four-parted perianth, the upper component consisting of the fusion product of the inner posterior and outer latero-posterior tepals (Hamann, 1966). Members of the Pontederiaceae possess six imbricate tepals variously fused into a basal tube; in some taxa (e.g., *Pontederia*) lateral and anterior open slits are present at the base of the perianth tube. However, neither outgroup has the distinctive perianth apertures seen in *Schiekia* and *Wachendorfia* and are coded as lacking this feature.

Characters #15, 16. Perianth tube. A basal perianth tube is possessed by five genera in the Haemodoraceae: *Anigozanthos* (Figs. 53, 54), *Blancoa* (Fig. 55), *Conostylis* (Fig. 56), *Macropidia* (Fig. 57), and *Tribonanthes* (Fig. 58). (*Conostylis breviscapa* lacks a perianth tube and has distinct tepals. In view of the numerous (ca. 24) species of *Conostylis* that possess a perianth tube, the distinct tepals of *C. breviscapa* are tentatively hypothesized to have evolved secondarily from an ancestral perianth tube; this matter needs further investigation.) All other members of the family, including *Phlebocarya* (Fig. 60), lack a complete perianth tube. As discussed under *Perianth apertures*, the unique tepallary fusion in *Schiekia* and *Wachendorfia* is coded as nonhomologous with the tubular perianth of the above genera and is treated as a separate character. Of the taxa with perianth tubes, *Anigozanthos*, *Blancoa*, *Conostylis androstemma*, *C. bealiana*, and *Macropidia* have a very elongate perianth tube (Figs. 53–55, 57). The evolution of an elongate perianth tube in at least *Anigozanthos*, *Blancoa*, and *Macropidia* is almost certainly correlated with selective pressure for bird pollination (Hopper, 1977; Hopper & Burbidge, 1978; Keighery, 1981). Therefore, presence of an elongate perianth tube is designated as derived from an ancestor with a short perianth tube: PERIANTH TUBE ABSENT ←[#15]→ SHORT PERIANTH TUBE ←[#16]→ LONG PERIANTH TUBE.

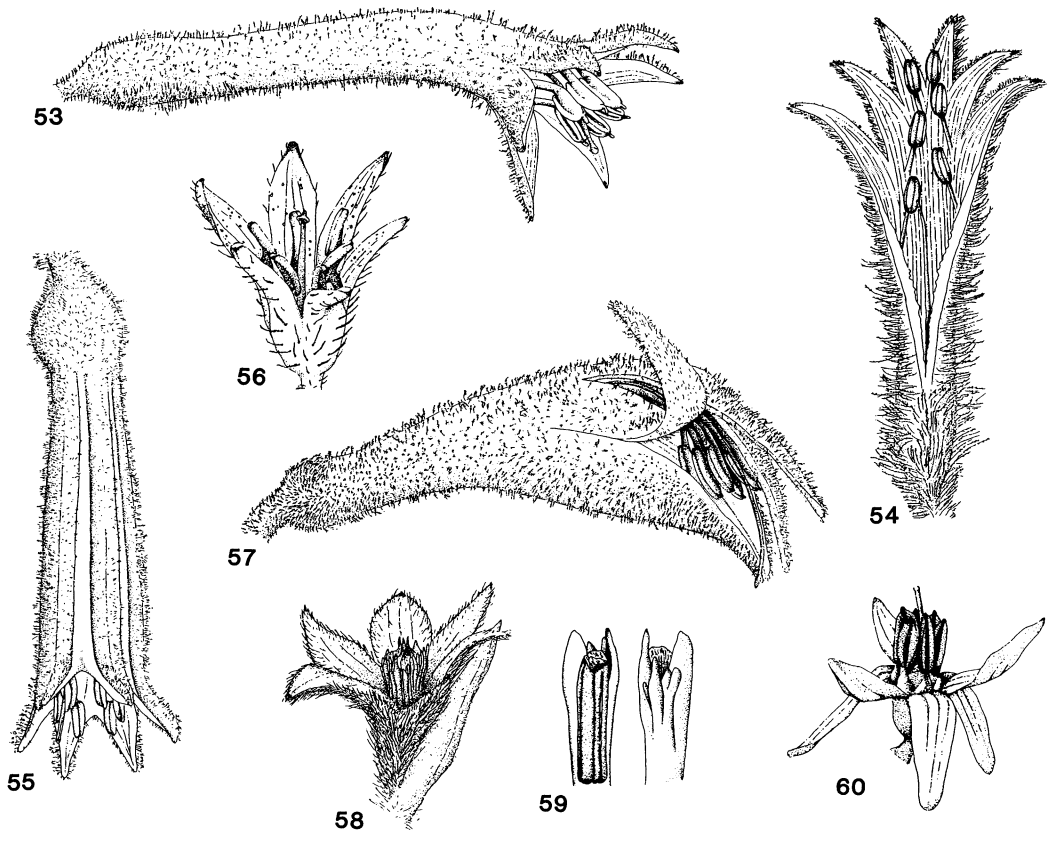
As discussed above (see *Perianth apertures*), the outgroup taxa have some variation of perianth fusion. All members of the Philydraceae have a



FIGURES 44–52. Floral morphology in the Haemodoraceae. 44–46. *Pyrrorhiza neblinae*.—44. Whole flower, two tepals removed, showing one of two staminodes (s) and single stamen; ×2.8.—45. Adaxial view of staminode; ×5.7.—46. Floral diagram. 47–50. *Schiekia orinocensis*.—47. Whole flower. Note perianth aperture (pa) and one of two staminodes (s); ×3.6.—48. Staminode, adaxial view; ×5.7.—49. One of two latero-posterior stamens. Note small (caducous) anther with basal constriction.—50. Floral diagram. 51, 52. *Wachendorfia paniculata*.—51. Whole flower. Note perianth aperture (pa); ×2.8.—52. Floral diagram.

rather specialized four-parted perianth, the upper component consisting of the fusion product of the inner posterior and outer latero-posterior tepals. Because tepallary fusion in the Philydraceae is incomplete and rather specialized, it is coded nonhomologous with the short or long perianth tube of the Haemodoraceae, which results from fusion of all six tepals. Members of the Pontederiaceae possess six imbricate tepals which vary from essentially distinct to being connate and forming a short or long perianth tube; thus, the Pontederiaceae are coded as polymorphic for both characters.

Character #17. Perianth symmetry. *Pyrrorhiza* (Fig. 44), *Schiekia* (Fig. 47), and *Wachendorfia* (Fig. 51) have zygomorphic perianths. All other family members have basically actinomorphic perianths, with the exception of *Anigozanthos* and *Macropidia*, in which zygomorphy is thought to have been derived independently (see *Perianth splitting*).



FIGURES 53–60. Floral morphology in the Haemodoraceae. 53, 54. *Anigozanthos*.—53. *A. flavidus*; ×1.4.—54. *A. humilis*; ×1.35.—55. *Blancoa canescens*; ×3.0.—56. *Conostylis aurea*; ×3.5.—57. *Macropidia fuliginosa*; ×2.4. 58–59. *Tribonanthes variabilis*.—58. Whole flower; ×2.4.—59. Stamen, adaxial (left) and abaxial (right) views. Note connective appendages; ×2.0.—60. *Phlebocarya ciliata*; ×3.75.

Among the outgroups, all species of the Philydraceae have zygomorphic perianths. However, because this family possesses a rather specialized perianth consisting of fusion of the posterior tepals and reduction of the latero-anterior tepals, perianth symmetry in the Philydraceae is coded as having uncertain homology ("?") with that in the Haemodoraceae. In the Pontederiaceae perianth symmetry is either actinomorphic or more rarely zygomorphic and is coded as polymorphic ("?").

Among angiosperms as a whole, zygomorphy is generally considered to be a derived feature, usually correlated with specialized pollination systems (Faegri & van der Pijl, 1966; Sporne, 1975). The relative ancestry of this feature and its significance in pollination mechanisms in the Haemodoraceae will be discussed with reference to the cladistic analysis.

Character #18. Perianth splitting. Two other family genera, *Anigozanthos* (Figs. 53, 54) and *Macropidia* (Fig. 57), also have zygomorphic perianths. However, the perianths of these taxa are syntepalous and tubular, not basically apotepalous as in the zygomorphic *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. More importantly, zygomorphy in *Anigozanthos* and *Macropidia* arises primarily by the longitudinal "splitting" of the tube along an anterior line (Fig. 54). Zygomorphy in these two genera almost certainly has evolved independently from (and is not homologous to) that in *Pyrrorhiza*, *Schiekia*, and *Wachendorfia* and is treated as a separate character.

Among the outgroups and monocots as a whole, such perianth splitting is absent. It is extremely likely that zygomorphy in *Anigozanthos* and *Macropidia* was derived from an ancestral tubular, actinomorphic condition, as occurs in *Blancoa*. This hypothesis is supported by the fact that all three of these genera have identical valvate perianths during the early bud stage (see below). Zygomorphy in *Anigozanthos* and *Macropidia* prob-

ably evolved due to strong selective pressure for specialized bird pollination (Hopper & Campbell, 1977; Hopper & Burbidge, 1978).

Character #19. Perianth aestivation. *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Tribonanthes* possess a valvate perianth at anthesis, in which the perianth lobes of the mature flower show no evidence of overlap (Figs. 53–58, 62). In *Anigozanthos*, *Blancoa*, and *Macropidia* the perianth lobes are valvate even during the earliest bud developmental stage (Fig. 61). However, *Conostylis* species (Fig. 63) and *Tribonanthes* (Fig. 64) clearly have an imbricate perianth aestivation in the bud stage; only when the flowers open are the tepals valvate. In all other genera of the Haemodoraceae, tepals are imbricate throughout floral development.

An imbricate perianth, or evidence of such in cases of fusion, occurs in all species among the outgroups. It seems very likely then that the valvate perianth of the above five genera is a derived feature. The apparent developmentally valvate perianth of *Anigozanthos*, *Blancoa*, and *Macropidia* may represent a further specialization, one probably correlated with the long perianth tube in these taxa (see *Perianth tube*). Because other species of *Conostylis* having elongate perianth tubes have not been studied for this feature, possession of a valvate perianth throughout floral development is not coded separately from a valvate perianth present only at flower anthesis.

Character #20. Perianth tannin cells. Distinctive perianth idioblast cells are present in *Haemodorum*, *Phlebocarya*, and *Tribonanthes* (Figs. 65–67). These perianth idioblasts vary in length (1.5–6 times longer than broad), are oriented parallel to the tepal axis in the subepidermal layer, and are completely filled (presumably the vacuoles) with an orange to red-brown ergastic substance. The cells are scattered in the tepal among the more predominant clear parenchymatous cells. The ergastic substance looks like oil; yet staining reaction for fats and oils with Sudan IV (Johansen, 1940) was negative. Safranin red positively stains these contents, indicating the possible presence of tannins. The idioblasts are located throughout the perianth and occasionally in the ovary wall and placentae. Among all investigated members of the Haemodoraceae, perianth idioblasts are not present in the following genera: *Anigozanthos*, *Barberetta*, *Blancoa*, *Conostylis*, *Dilatris* (two species), *Lachnanthes*, *Macropidia*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia* (two species), and *Xiphidium*. All of the former taxa possess only clear, generally rectangular parenchyma cells comprising the nonvascularized tissue of the perianth (illustrated for *Wachendorfia* in Fig. 70). (Incidentally, raphide sacs are present in the tepals of all investigated members of the Haemodoraceae and both outgroups.)

Among the outgroup families, perianth tannin cells virtually identical to those in *Haemodorum*, *Phlebocarya*, and *Tribonanthes* are present in all genera of the Philydraceae (Fig. 68) and in all investigated genera of the Pontederiaceae (Fig. 69), except for *Heteranthera*. Because of the great anatomical similarity between the perianth idioblasts of the outgroups and those found in the Haemodoraceae, it seems highly probable that they are homologous structures and are so coded. The absence of these perianth idioblasts in *Heteranthera* is tentatively hypothesized to be a secondary derivation within the Pontederiaceae.

Characters #21, 22. Stamen number. The number of fertile stamens per flower in taxa of the Haemodoraceae is either six, three, or one. *Schiekia* has three fertile stamens, the anterior one of which is considerably larger than the other two, plus two staminodes (Fig. 48) positioned latero-anteriorly in a whorl outer to the fertile stamens (Fig. 50). Because the two staminodes of *Schiekia* may represent vestiges (or evolutionary precursors) of an outer stamen whorl, the androecium of *Schiekia* is coded as evolutionarily intermediate between six stamens per flower and three or one stamen(s) per flower. *Pyrrorhiza* has only one fertile stamen, plus two staminodes (Fig. 45) morphologically similar to those in *Schiekia* but differing by being in the same whorl as the single

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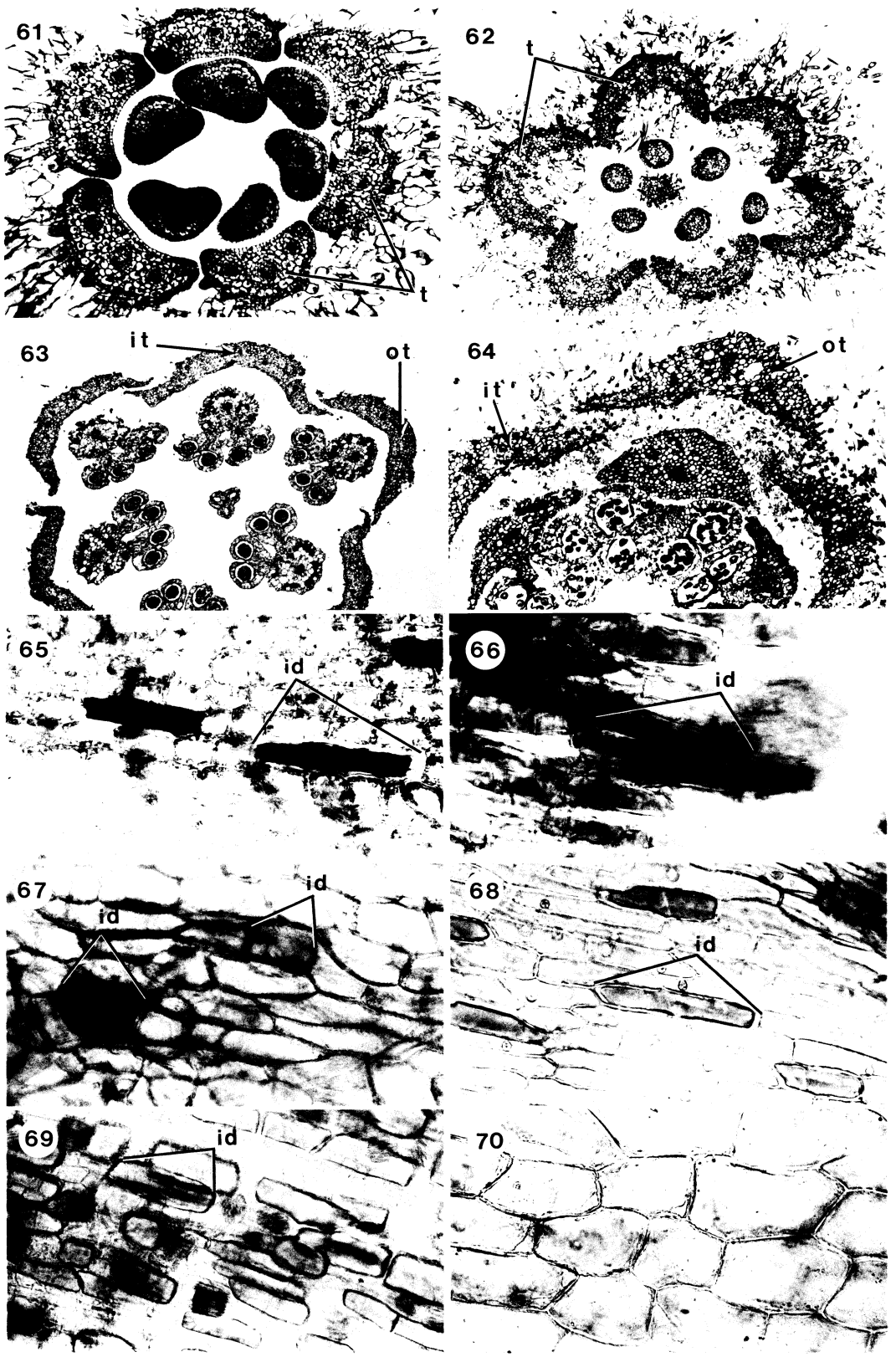
FIGURES 61–70. 61–64. Perianth aestivation. 61, 62. *Anigozanthos flavidus*.—61. Immature bud cross section. Note valvate arrangement of tepals (t); ×86.—62. Mature bud cross section. Tepals (t) remain valvately arranged; ×30.—63. *Conostylis priesii*. Mature bud cross section. Note imbricate aestivation, with outer tepal whorl (ot) overlapping inner tepal whorl (it); ×14.—64. *Tribonanthes variabilis*. Bud cross section, intermediate stage. Note outer tepal (ot) overlapping inner tepals (it); ×26. 65–69. Perianth tannin idioblast cells (id).—65. *Haemodorum spicatum*; ×200.—66. *Phlebocarya pilosissima*; ×194.—67. *Tribonanthes variabilis*; ×200.—68. *Helmholtzia acorifolia*; ×194.—69. *Pontederia cordata*; ×164.—70. Perianth cells of *Wachendorfia thyrsiflora*, which lack tanniniferous idioblasts; ×164.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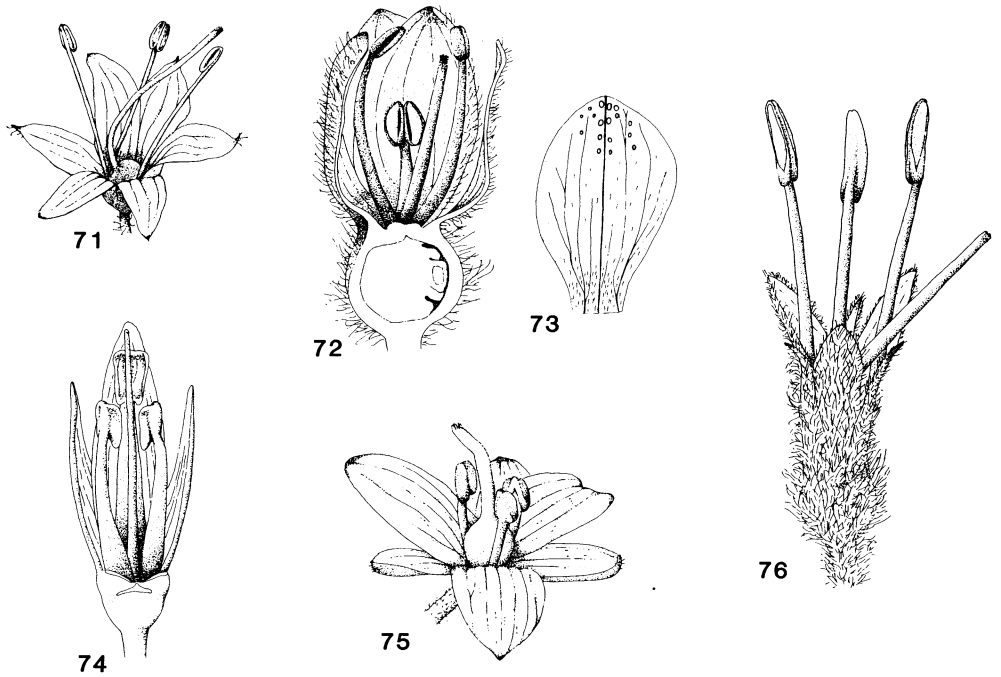


FIGURES 71–76. Floral morphology in the Haemodoraceae.—71. *Barberetta aurea*; ×3.4. 72–73. *Dilatris corymbosa*.—72. Whole flower longitudinal section. Note inferior ovary; ×3.0.—73. Outer tepal. Note apical glands; ×3.4.—74. *Haemodorum spicatum*; ×3.4.—75. *Xiphidium coeruleum*; ×3.4.—76. *Lachnanthes caroliniana*; ×3.1.

fertile stamen, i.e., opposite the inner whorl of tepals, not the outer as in *Schiekia* (Fig. 50). The staminodia in *Pyrrorhiza* are thus hypothesized to be homologous with stamens of an inner whorl. Based on this interpretation, the assigned morphocline for stamen number in the Haemodoraceae is: 6 STAMENS ←[#21]→ 3 STAMENS + 2 LATERO-ANTERIOR STAMINODES ←[#22]→ 3 OR 1 STAMEN(S).

One difficulty with the above morphocline concerns *Schiekia* and *Pyrrorhiza*. Although *Schiekia* may be intermediate between a six-staminate and three-staminate condition (because of the presence of two latero-posterior staminodia), it is more likely intermediate between a three-staminate condition and the one-staminate morphology of *Pyrrorhiza*. This latter interpretation is based on the presence in *Schiekia* of two reduced latero-posterior stamens with caducous anthers that greatly resemble and are likely homologous with the two staminodia of *Pyrrorhiza*. However, so as not to bias the present study, the latter hypothesis is treated as an independent character (see *Stamen dimorphism*).

In general, fewer than six stamens in monocotyledons is a condition thought to have arisen by reduction from the ancestral condition of six stamens in two whorls (Dahlgren & Clifford, 1982); however, such generalized trends must be viewed with caution. With regard to outgroup comparison, all members of the Philydraceae have one stamen per flower, which interestingly is median anterior in position (similar to that in, e.g., *Pyrrorhiza*). The Pontederiaceae can have either six, three, or one stamen(s) per flower and are coded as polymorphic ("?").

Characters #23–25. Stamen dimorphism. In the members of the Haemodoraceae with six stamens, all six anthers are of equal size. However, of the taxa with three anther-bearing stamens, in *Dilatris* (Fig. 72), *Haemodorum* (Fig. 74), *Schiekia* (Figs. 47–50), and *Xiphidium* (Fig. 75), the anther of the adaxial stamen (relative to cyme axis) is significantly larger than those of the abaxial stamens. (*Schiekia* also has two staminodia; see characters #21, 22, *Stamen number.*) All three stamens and anthers are equal in the other genera with three stamens: *Barberetta* (Fig. 71), *Lachnanthes* (Fig. 76), and *Wachendorfia* (Figs. 51, 52). The filament of the odd stamen may be either longer (*Haemodorum*, *Schiekia*, and *Xiphidium*) or shorter (*Dilatris*) than the filaments of the two

equal stamens. Because of the positional similarity of the odd anther, however, these are all viewed as homologous features. In *Schiekia* the median anterior stamen is considerably enlarged relative to the two latero-posterior stamens (Fig. 47). The anthers of the two latero-posterior stamens of *Schiekia* are somewhat caducous (Figs. 47, 49), and the filaments of these stamens greatly resemble the staminodia of *Pyrrorhiza* (Figs. 44, 45). Therefore, it is hypothesized here that the two latero-posterior stamens of *Schiekia* are homologous (and evolutionarily intermediate) to the two latero-posterior staminodia of *Pyrrorhiza*. Furthermore, the occurrence of two latero-posterior staminodia in *Pyrrorhiza* may be interpreted as an extreme endpoint in anther dimorphism. Thus, a hypothesized morphocline for anther dimorphism in the family is: ANTHERS OF EQUAL SIZE ←[#23]→ 1 LARGE ANTERIOR + 2 SMALL POSTERIOR ANTHERS ←[#24]→ 1 LARGE ANTERIOR + 2 CADUCOUS LATERO-POSTERIOR ANTHERS ←[#25]→ 1 ANTERIOR ANTHER + 2 LATERO-POSTERIOR STAMINODIA.

Among the outgroup families stamen dimorphism (or apparent stamen reduction) is common. All species of the Philydraceae have a single stamen in posterior position, as is the odd stamen in the dimorphic members of the Haemodoraceae. However, because the homology of stamen dimorphism in the Philydraceae is uncertain, and because the presence of a single stamen in this family was taken into account previously (characters #21, 22, *Stamen number*), the Philydraceae were coded as uncertain ("?") for characters #23–25. Anther dimorphism varies considerably in the Pontederiaceae. Some species exhibit no anther dimorphism. Dimorphic stamens are present in *Heteranthera, Monochoria, Pontederia,* and *Scholleropsis*; in *Heteranthera* there is usually one large anterior stamen and two smaller latero-anterior stamens. (Note the positional difference to that in the Haemodoraceae.) In some *Heteranthera* species and in *Hydrothrix* of the Pontederiaceae, only one stamen is present. The Pontederiaceae are coded as polymorphic ("?") for characters #23–25.

Character #26. Stamen connective appendages. Distinctive lobed appendages are present on the upper abaxial stamen connective in all species of *Tribonanthes* (Fig. 59). Such stamen appendages are not found in the family or outgroups, although *Anigozanthos* may have mucronate anthers.

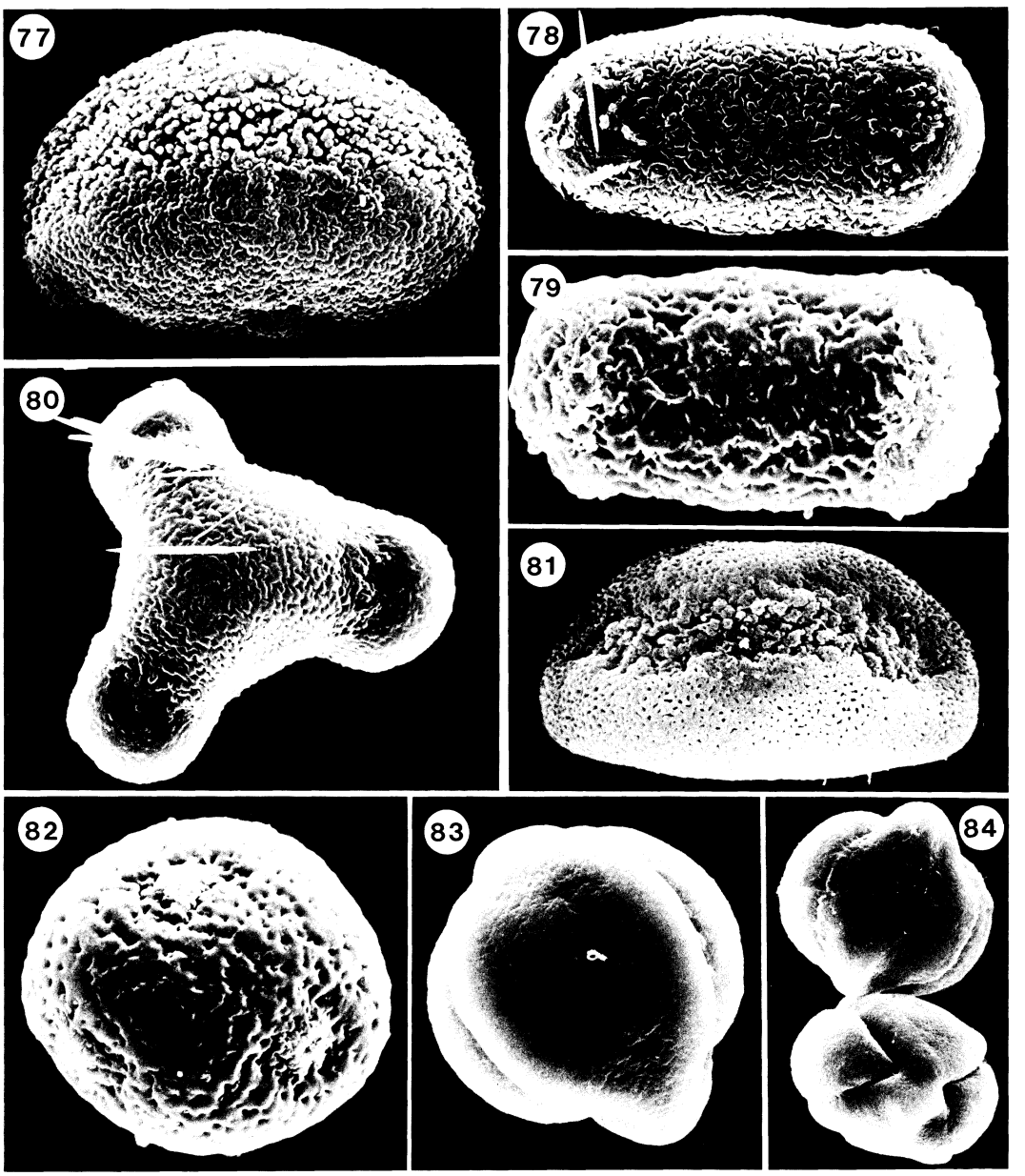
Characters #27, 28. Pollen aperture. Eight genera of the Haemodoraceae have a monosulcate pollen aperture type, as in *Haemodorum* (Fig. 77), whereas six genera have porate apertures (Figs. 78–80, 82; see Simpson, 1983). Of the latter, five genera have 2–3 apertures (Figs. 78–80). *Tribonanthes* differs in having 5–7 porate apertures (i.e., oligoforaminate; Fig. 82). Thus, this character is coded as: MONOSULCATE ←[#27]→ 2–3-PORATE ←[#28]→ OLIGOFORAMINATE.

Of the six genera with porate pollen apertures, four (*Anigozanthos, Blancoa, Conostylis,* and *Macropidia*) are similar in having protruding, hemispheric aperture walls essentially devoid of exine (Figs. 78, 80); the other two genera, *Phlebocarya* (Fig. 79) and *Tribonanthes* (Fig. 82), have rather flattened aperture walls with scattered exinous elements (Simpson, 1983). Although this additional feature is not taken into account in the character coding, it will be discussed after the cladistic analysis.

A monosulcate aperture type is considered to be ancestral for both the monocotyledons and the angiosperms (Zavada, 1983b; Walker & Doyle, 1975) and is likely ancestral for the Haemodoraceae. Among the outgroup taxa, all members of the Philydraceae have a monosulcate aperture (illustrated by *Helmholtzia* in Fig. 81; see Simpson, 1985a). All members of the Pontederiaceae have disulculate apertures (illustrated by *Pontederia* in Figs. 83, 84; see Simpson, 1987). Because the disulculate aperture type in the Pontederiaceae is probably derived from a monosulcate condition, and is almost certainly not homologous with the diporate aperture type in the Haemodoraceae, the Pontederiaceae are coded as having the equivalent of a monosulcate aperture type.

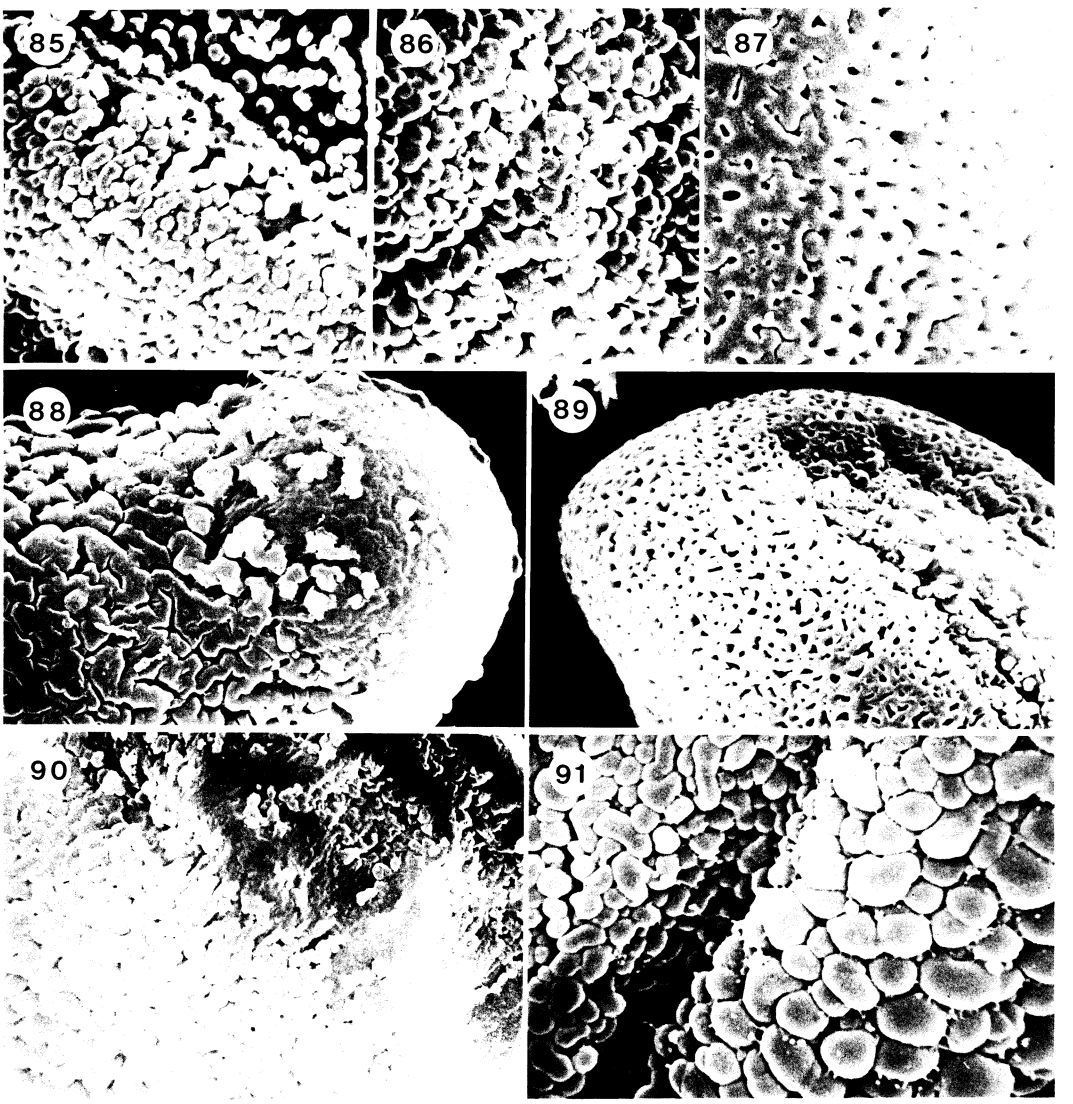
Characters #29, 30. Pollen sculpturing. Seven genera of the Haemodoraceae (all with monosulcate apertures) possess verrucate exine wall sculpturing, consisting of appressed wart-like projections of exine (illustrated by *Haemodorum* in Fig. 85 and by *Dilatris* in Fig. 86). *Schiekia,* also monosulcate, differs from the above in having foveolate sculpturing with minute outer pores (Fig. 87). Six genera of the family, all of which have porate apertures, have distinctive rugulate (brainlike) exine sculpturing (Fig. 88; see Simpson, 1983).

All three types of pollen wall sculpturing seen in the Haemodoraceae are found in the outgroups. Within the Philydraceae three of four genera have foveolate (to reticulate) sculpturing (Fig. 89), which somewhat resembles *Schiekia*; *Philydrella* of the Philydraceae possesses what is described as a rugulate sculpturing, but which does not greatly re-



FIGURES 77–84. Pollen shape and aperture morphology in the Haemodoraceae and outgroups.—77. *Haemodorum spicatum* (monosulcate); ×3,320.—78. *Anigozanthos flavidus* (diporate with hemispheric apertures); ×1,110.—79. *Phlebocarya ciliata* (diporate); ×2,160.—80. *Conostylis beliana* (triporate with hemispheric apertures); ×1,390.—81. *Helmholtzia acorifolia* (monosulcate); ×2,570.—82. *Tribonanthes variabilis* (oligoforaminate); ×1,760. 83–84. *Pontederia cordata* (disulculate);—83; ×1,630.—84. ×970.

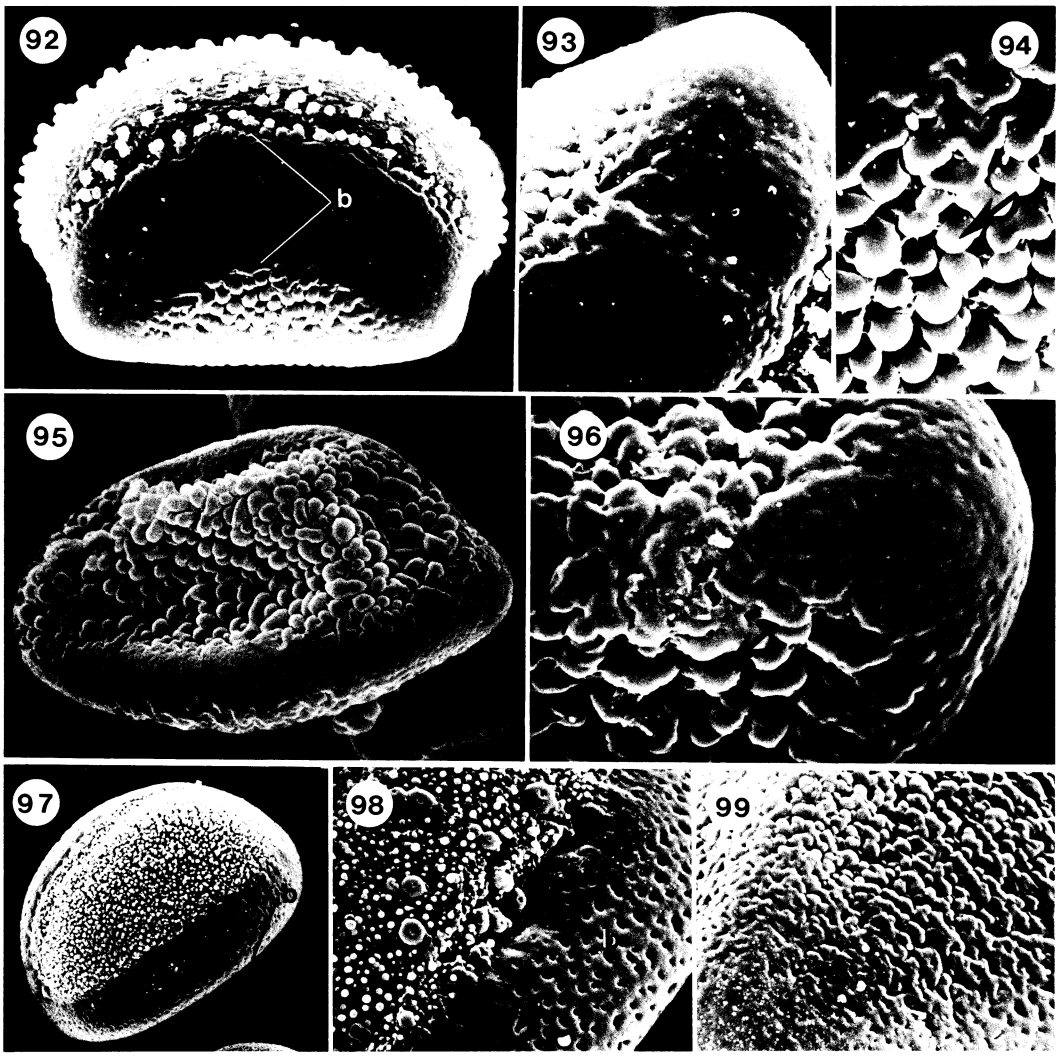
semble the rugulate sculpturing found in six genera of the Haemodoraceae (see Simpson, 1985a). Because the Philydraceae have two of the sculpturing types of the Haemodoraceae, they are coded as polymorphic ("?") for both characters. In fact, it seems quite likely that the resemblance in sculpturing between the Philydraceae and the Haemodoraceae is homoplasious anyway, as all Philydraceae have a quite different exine structure (see below, *Exine wall structure*). In the Pontederiaceae all investigated genera except *Pontederia* have verrucate sculpturing (illustrated for *Heteranthera*



FIGURES 85–91. Pollen wall sculpturing in the Haemodoraceae and outgroups.—85. *Haemodorum spicatum* (verrucate); ×6,610.—86. *Dilatris pilansii* (verrucate); ×4,400.—87. *Schiekia orinocensis* (foveolate); ×8,090.—88. *Anigozanthos flavidus* (rugulate); ×2,420.—89. *Helmholtzia acorifolia* (foveolate-reticulate); ×4,740.—90. *Heteranthera reniformis* (verrucate); ×2,480.—91. *Zosterella dubia* (verrucate); ×5,970.

in Fig. 90 and *Zosterella* in Fig. 91), which is virtually identical to that found in seven genera of the Haemodoraceae. In view of the similarity of exine structure between the Pontederiaceae and the verrucate Haemodoraceae (see *Exine wall structure*), it is very probable (and is coded as such) that the two families are homologous in terms of exine sculpturing as well.

The most likely morphocline for pollen sculpturing in the Haemodoraceae seems to be the following: FOVEOLATE ←[#29]→ VERRUCATE ←[#30]→ RUGULATE. Although the intergradation between the sculpturing types is not clear in itself, it is quite probable that the verrucate sculpturing type is ancestral for the Haemodoraceae as a whole, evidence for this being the identical sculpturing type (and exine structure; see below) in the Pontederiaceae. Thus, the rugulate and foveolate sculpturing types in the Haemodoraceae are hypothesized to have evolved independently from an ancestral verrucate type (to be tested by the cladistic analysis).



FIGURES 92–99. Palynological features in the Haemodoraceae. 92–94. *Wachendorfia thyrsiflora*.—92. Whole pollen grain, aperture above. Note psilate, micropore-pitted aperture border (b) and enlarged proximal verrucae (below); ×1,460.—93. Close-up of aperture border (b) and proximal verrucae (upper left); ×2,710.—94. Close-up of enlarged proximal verrucae (arrow); ×5,070. 95–96. *Barberetta aurea*.—95. Whole pollen grain, aperture facing. Note psilate, micropore-pitted aperture border (b); ×2,430.—96. Proximal surface, showing aperture border (b) and enlarged proximal verrucae (arrow); ×5,090. 97–99. *Dilatris corymbosa*.—97. Whole pollen grain, aperture facing, showing aperture border (b); ×925.—98. Close-up of psilate, foveolate aperture border (b); ×2,460.—99. Close-up of proximal surface. Note absence of enlarged verrucae; ×2,570.

Character #31. Pollen apertural border. Smooth pollen grain apertural borders, consisting of a band of psilate material with minute perforations, are present in *Wachendorfia* (Figs. 92, 93), *Barberetta* (Figs. 95, 96), and *Dilatris* (Figs. 97, 98). The pollen apertural borders in *Dilatris* differ slightly from those in the other two genera in having larger perforations (being "foveolate") in contrast to the micropores present in *Barberetta* and *Wachendorfia*. Because of their overall similarity, all three genera are coded as possessing this feature. Similar pollen grain apertural borders are absent in other investigated members of the Haemodoraceae, although a tendency for such a border may be seen in *Xiphidium* (Simpson, 1983). An apertural border is absent also in all investigated members of the Philydraceae (Simpson, 1985a) and Pontederiaceae (Simpson, 1987).

Character #32. Pollen with large proximal verrucae. Large verrucate exine elements are present on the proximal pollen grain surface of *Barberetta* (Fig. 96) and *Wachendorfia* (Figs. 92–94). Similar elements do not occur elsewhere in the family or among any investigated outgroups. In particular, *Dilatris*, which resembles *Barberetta* and *Wachendorfia* in having a pollen apertural border, lacks any indication of enlarged verrucate elements on the proximal pollen grain surface (see Fig. 99).

Characters #33–37. Exine wall structure. Five basic types of pollen grain exine wall structure can be identified in the Haemodoraceae (see Simpson, 1983). *Lachnanthes* (Figs. 100, 101) and *Haemodorum* (Fig. 102) have a "one-layered" exine structure, consisting of baculate (rod-shaped) elements that are closely appressed and generally basally fused. Ten other genera of the family have a two-layered exine wall, with inner and outer layers delimited by a distinctive "commissural line" (Figs. 103, 104); these inner and outer exine layers are ektexinous based on cytochemical tests and have similar TEM staining properties (Simpson, 1983). Of these ten genera, six differ in having an inner exine layer composed of papillate exinous elements (Fig. 104), while those of *Phlebocarya* are restricted to the apertural region. *Pyrrorhiza* (Fig. 105) and *Schiekia* (Fig. 106) possess, respectively, two- and three-layered exine walls. These two genera resemble one another (and differ from other family members) in that the subexterior exine wall is granular and discontinuous in composition.

In *Haemodorum* and *Lachnanthes*, the single-layered exine wall resembles and is probably homologous with the outer exine layer of those taxa that have a two-layered structure. In fact, the pollen exine wall of *Haemodorum* has an occasional scanty inner exine layer, perhaps indicative of an ancestral inner layer (Simpson, 1983). (Developmental studies to test this hypothesis are in progress by the author.) Similarly, in *Pyrrorhiza* and *Schiekia* the outermost layer of exine is probably structurally homologous to the single exine layer of *Haemodorum* and *Lachnanthes*. This can be seen near the apertural region, where all but the outermost exine layer disappears (Simpson, 1983).

As seen in Figure 112 (after Simpson, 1983), a gradation among observed exine wall structural types of genera in the Haemodoraceae can be identified. However, because of the uncertainty of some of the intergrading states of this morphocline, and because its length could possibly bias the study, the character "exine wall structure" was divided into the following two-state (absence or presence) characters:

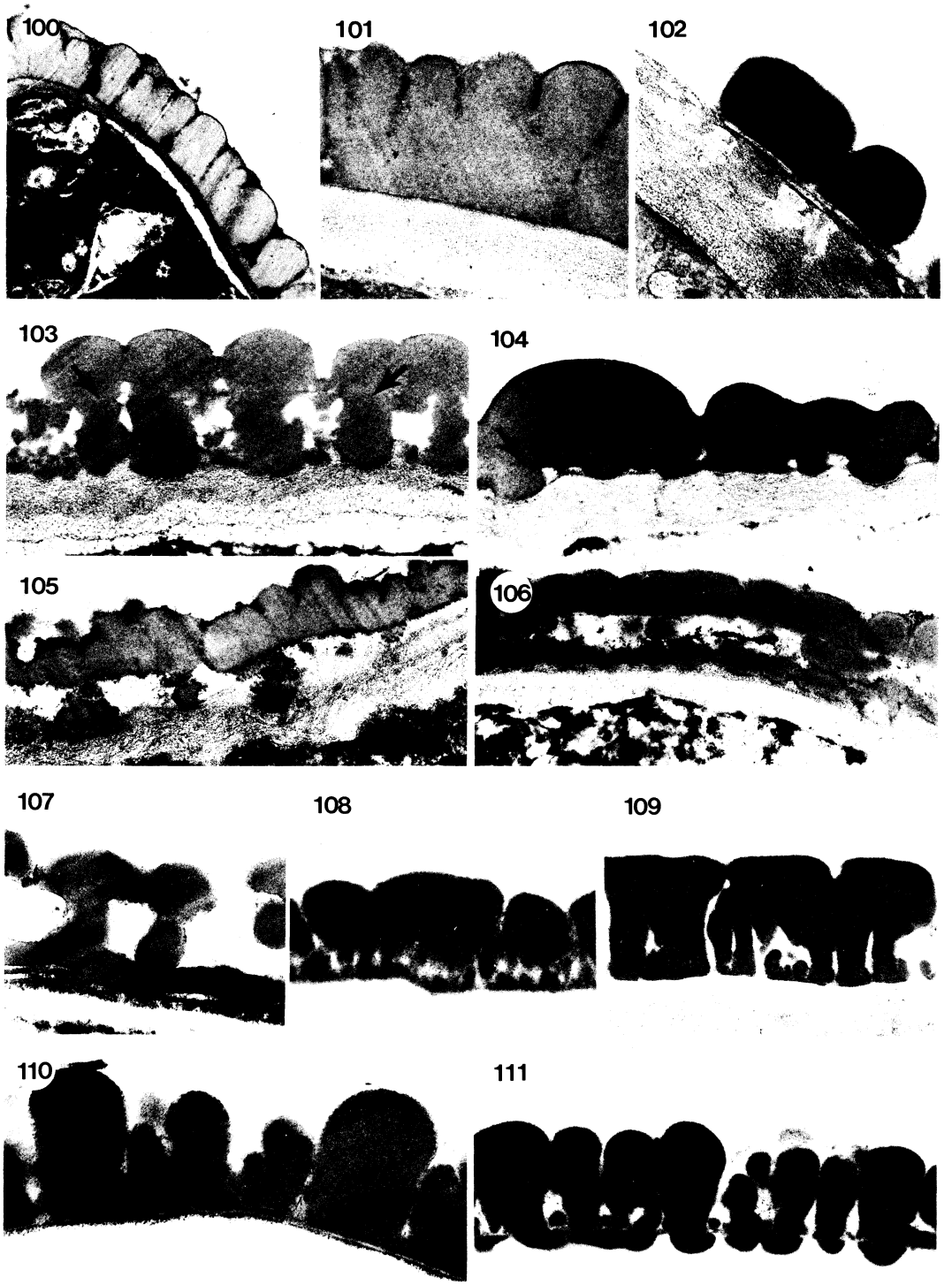
Characters #33, 34: Number of exine wall layers, coded as the following linear morphocline: 1-LAYERED ←[#33]→ 2-LAYERED ←[#34]→ 3-LAYERED.

Character #35: Exine wall, if two-layered, with papillate inner exine elements. This includes *Phlebocarya*, which possesses papillate inner exine elements only near the apertural region. Taxa without a two-layered exine (*Haemodorum*, *Lachnanthes*, and *Schiekia*) are coded as "X."

Character #36: Exine wall, if two-layered, with only papillate elements making up the inner wall. This condition is present in *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Tribonanthes*. Again, the three taxa which lack a two-layered exine are coded as "X."

Character #37: Subexterior exine wall discontinuous. This feature links the common exine morphology of *Pyrrorhiza* and *Schiekia*. Figure 165B illustrates the character coding for exine wall structure (characters #33–37).

Among the outgroups, all Philydraceae have a typical homogeneous tectate-columellate exine structure (Fig. 107) with characteristic lamellar deposits inner to the foot-layer (see Simpson, 1985a). The directionality of the tectate-columellate exine structure with reference to the specific types occurring in the Haemodoraceae is uncertain; thus, the Philydraceae are coded as having uncertain homology ("?") for characters #33–37. In contrast, several members of the Pontederiaceae have an exine structure very similar to that in the Haemodoraceae (see Simpson, 1987). A "one-layered" exine structure, identical to that of *Haemodorum* and *Lachnanthes* of the Haemodoraceae, is seen in two genera of the Pontederiaceae: *Eichhornia* and *Hydrothrix* (Fig. 110). *Heteranthera*, *Reussia*, and *Zosterella* (Fig. 111) of the Pontederiaceae have a two-layered exine with a "commissural line" delimiting inner and outer layers, resembling that found in ten genera of the Haemodoraceae. Four genera of the Pontederiaceae, *Heteranthera*, *Monochoria* (Fig. 108), *Pontederia* (Fig. 109), and *Scholleropsis*, have what is described as a tectate-columellate exine structure. However, in these taxa the foot-layer is thin or discontinuous, the columellae are short and ill-defined, and the tectum is thick and composed of rod-shaped elements (resembling the rod-shaped elements of the verrucate members of the Hae-



FIGURES 100–111. Exine wall ultrastructure in the Haemodoraceae and outgroups.—100, 101. *Lachnanthes caroliniana* (one-layered exine composed of laterally appressed and basally fused rod-shaped elements); ×11,400 (100), ×26,200 (101).—102. *Haemodorum simplex* (one-layered, composed of laterally appressed rod-shaped elements); ×29,900.—103. *Xiphidium coeruleum* (two-layered exine, inner layer papillate; note commissural line at arrows); ×20,700.—104. *Tribonanthes variabilis.* (two-layered exine, inner layer papillate; note commissural

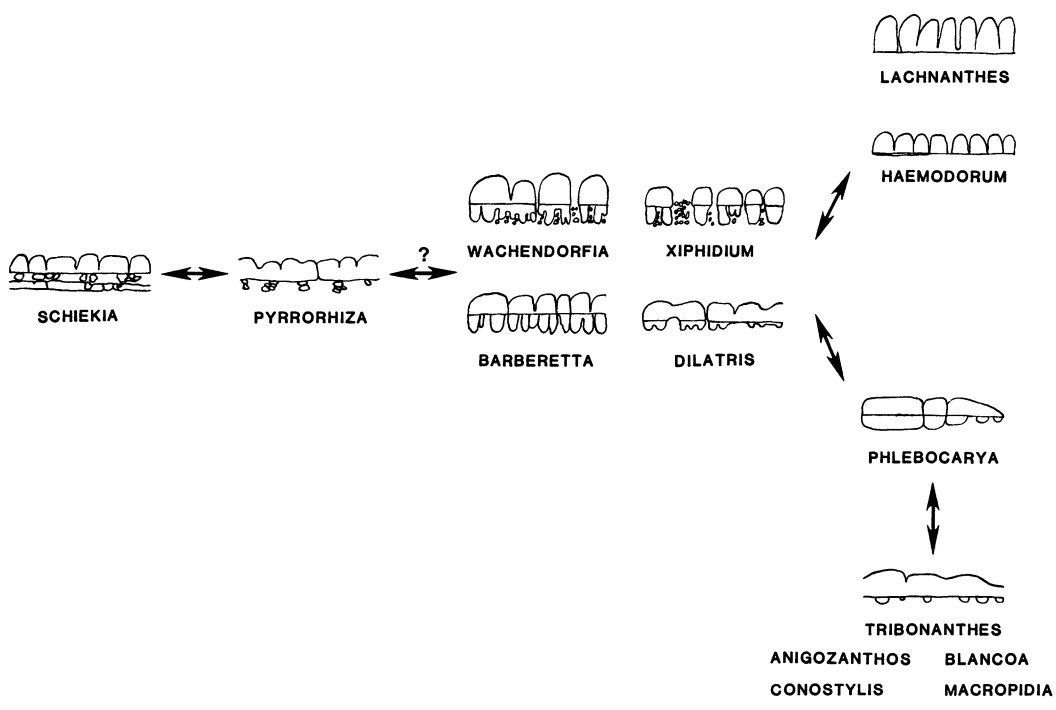


FIGURE 112. Hypothesized intergradation series of exine ultrastructure morphology in the Haemodoraceae. Note uncertainty as to homology of two-layered exine of *Pyrrorhiza*.

modoraceae). Thus, Simpson (1987) proposed that this "modified" tectate-columellate exine structure in the Pontederiaceae may not be homologous with the more typical tectate-columellate structure (e.g., in the Philydraceae and in many other monocots) and may have been secondarily derived from an exine structure comprised of rod-shaped elements. (Developmental studies are underway by the author to test this hypothesis.) Because both a one-layered exine and a two-layered exine (with a delimiting "commissural line") occur in the Pontederiaceae, this outgroup is coded as polymorphic ("?") for characters #33 and #35, 36. Character #34 is coded as lacking (state 0) a three-layered exine, and character #37 is coded as lacking (state 0) a discontinuous subexterior exine wall.

Character #38. Enantiostyly. Enantiostyly is the curvature of the style to either the right or left, thus defining so-called "right-handed" and "left-handed" flowers. Displacement of one or more stamens usually accompanies enantiostyly, which results in an asymmetric flower. In the Haemodoraceae several genera exhibit enantiostyly. All five species of the zygomorphic *Wachendorfia* have enantiostylous flowers, in which the arcuate style is deflected to one side of the flower and the median anterior stamen is deflected to the other side (Fig. 51). Ornduff & Dulberger (1978) have hypothesized that such stylar enantiomorphy functions to promote pollination between flowers of different morphs, in effect promoting outcrossing. Flowers of *Schiekia* have a similar enantiostyly in which the style and median anterior stamen are oppositely displaced (Fig. 47); the two latero-posterior stamens (unlike those of *Wachendorfia*) are considerably smaller. Both *Schiekia* and *Wachendorfia* have what are presumed to be nectar guides near

←

line at arrows); ×17,700.—105. *Pyrrorhiza neblinae* (two-layered exine; note amorphous, discontinuous inner exine layer); ×19,400.—106. *Schiekia orinocensis* (three-layered exine; note amorphous and discontinuous middle layer); ×21,200.—107. *Orthothylax glaberrimus* (tectate-columellate exine with lamellae inner to foot-layer); ×38,600.—108. *Monochoria vaginalis* (tectate-columellate exine with ill-defined interstitial layer); ×24,300.—109. *Pontederia cordata* (tectate-columellate exine with discontinuous foot-layer); ×18,500.—110. *Hydrothrix gardneri* (one-layered exine composed of laterally appressed and basally fused rod-shaped elements); ×39,000.—111. *Zosterella dubia* (two-layered exine, inner layer papillate; note commissural line at arrows); ×13,900.

the base of the posterior tepals. Thus, it is probable that in both of these genera (which have zygomorphic, horizontal flowers) an insect visitor would alight in a consistent orientation, forwardly directed toward the ovary base where nectar would collect. Pollen initially transferred to one side of the insect's body would, in subsequent visitations, more likely contact the stigma of a flower of opposite handedness (see Ornduff & Dulberger, 1978, re. *Wachendorfia*). *Pyrrorhiza*, the only other genus of the family with zygomorphic flowers (not caused by longitudinal splitting of the perianth; see *Perianth splitting*), does not possess enantiostyly. The style of *Pyrrorhiza* is relatively straight and is positioned directly above the single anterior stamen (Fig. 44).

Styles of four other family genera, *Barberetta* (Fig. 71), *Dilatris* (Fig. 72), *Lachnanthes* (Fig. 76), and *Xiphidium* (Fig. 75), also are strongly curved to one side of the flower. In *Haemodorum* the styles of adjacent flowers in a flower pair are each slightly incurved, forming mirror image pairs. These styles are only slightly curved and are not strongly displaced to one side (Fig. 74); however, they are probably homologous with the strongly displaced stylar curvature in the other six genera and are so coded. In contrast to *Schiekia* and *Wachendorfia*, however, the above genera have *actinomorphic* and *erect* (not zygomorphic and horizontal) flowers without any type of bilaterally symmetric nectar guides. It is, therefore, likely that an insect visitor to flowers of any of these four genera would be positioned inconsistently with regard to the deflected style. Enantiostyly in these taxa may be adaptive in simply decreasing the chance of self-pollination by physically displacing the stigma from anthers.

Among the outgroup taxa, enantiostyly occurs in all species of the Philydraceae. In fact, the style is displaced to one side of the (sole) anterior stamen, similar to enantiostyly in the Haemodoraceae. In the Pontederiaceae only *Heteranthera* and *Monochoria* have "weakly enantiostylous flowers" (Eckenwalder & Barrett, 1986); all other Pontederiaceae lack enantiostyly. The Pontederiaceae are thus coded as polymorphic ("?") for this character.

Character #39. Ovary position. Nine genera of the Haemodoraceae have an inferior ovary. Certain species of *Conostylis* have a *mostly* inferior ovary; these are coded as having inferior ovaries. The other five family genera clearly have superior ovaries.

Within the angiosperms as a whole, an inferior ovary is generally considered to be a derived feature (Bessey, 1915; Sporne, 1975), evolving possibly because of selective pressure by floral herbivores or pollinators (Grant, 1950) or in response to an adaptive advantage caused by increased protection of seeds or increased energy allocation to developing ovules (Stebbins, 1974). (See, however, Eyde & Tseng, 1969, regarding a possible case of derivation of a superior ovary from an ancestral inferior ovary.) All members of the two designated outgroups in this study have superior ovaries and are so coded.

Character #40. Septal nectaries. Within the Haemodoraceae all genera possess septal nectaries, with the exception of *Xiphidium*. In genera with inferior ovaries, the septal nectaries consist of slit-like channels, lined with a single epithelial layer, which traverse the septa at the upper part of the ovary and release nectar at the ovary apex near the base of the style. Among family members with inferior ovaries, *Dilatris* and *Phlebocarya* are exceptional in having extremely minute septal nectaries, consisting of a very short chamber located at the extreme ovary apex. Of the genera with superior ovaries, *Barberetta*, *Pyrrorhiza*, *Schiekia*, and *Wachendorfia* have very small septal nectaries, arising and opening up at the ovary base. In the case of *Schiekia* and *Wachendorfia*, nectar secretions presumably arise from these septal nectaries and collect in the two lateral "apertures" characteristic of these two genera. The complete absence of septal nectaries in *Xiphidium* (which has a superior ovary) may be correlated with the fact that it is visited by pollen-feeding, not nectar-feeding, bees via an anther vibrational ("buzz") mechanism (Buchmann, 1980). Thus *Xiphidium* may represent a specialization in which the selective pressure for nectar secretion was eliminated, establishing pollen as the primary visitor attractant. In view of the reduced septal nectaries in most superior-ovary taxa, it is not unreasonable to envision a loss of these structures in *Xiphidium*, particularly in light of its pollination mechanism.

Among the outgroup taxa, septal nectaries are absent from all four genera of the Philydraceae. Septal nectaries are present in at least *Eichhornia* and *Pontederia* of the Pontederiaceae but are absent in *Heteranthera* of that family (present study). The septal nectaries of the Haemodoraceae are very likely homologous with those in the Pontederiaceae and probably with those of numerous other monocots. However, because of their variability, the Pontederiaceae are coded as polymorphic ("?") for this character.

Character #41. Fertile carpels. All species of the Haemodoraceae have three connate carpels.

In the monotypic genus *Barberetta*, however, the seeds of two carpels abort during development; only the posterior carpel is fertile at maturity. Regularly aborting carpels are not found in any other members of the Haemodoraceae. (*Barberetta* is also unique in the family in having the style displaced laterally relative to the ovary apex; this displacement is certainly correlated with the development of only one carpel containing one ovule.)

Among the outgroup taxa, abortive carpels are absent in the Philydraceae. Abortive carpels are found only in *Pontederia* and *Reussia* of the Pontederiaceae, being absent in all other genera of the family. Thus, the Pontederiaceae are coded as polymorphic ("?") for this character.

Character #42. Locule number. All members of the Haemodoraceae have three locules, with the sole exception of *Phlebocarya*. Ovaries of *Phlebocarya* possess three basal, epitropous ovules with rudimentary or only partially protruding lateral septa and no apical septa. Thus, the ovary of *Phlebocarya* is technically uniloculate.

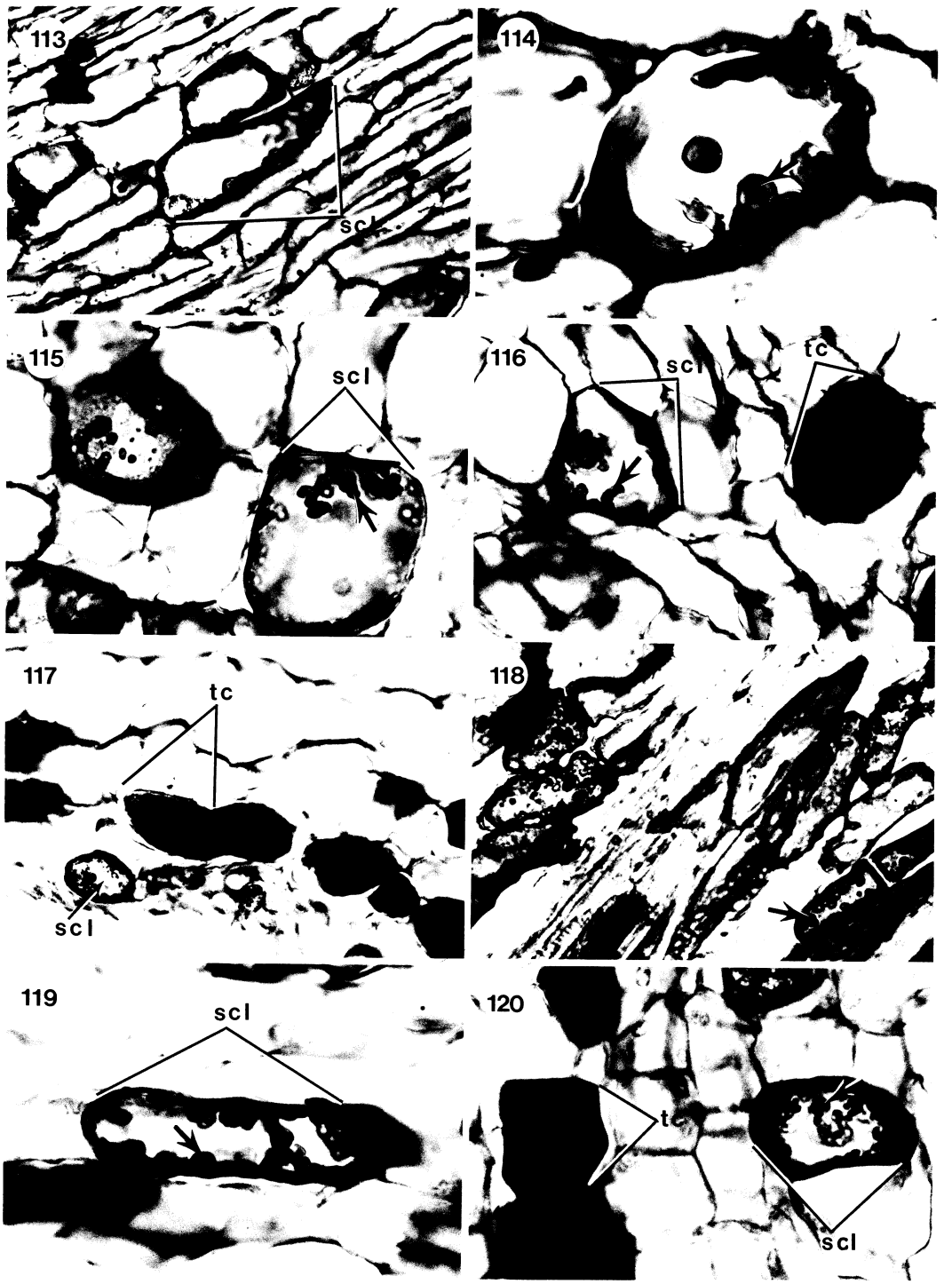
A three-loculate ovary is found in all members of the Pontederiaceae, and in all Philydraceae with the exception of *Philydrum*. Here most of the apical volume of the ovary is unilocular, with protruding, bibrachiate parietal placentae bearing numerous ovules. Thus the Philydraceae are coded as polymorphic ("?") for this character.

Character #43. Placental sclereids. Distinctive sclereids occur in the ovary placental tissues in six family genera: *Anigozanthos* (Figs. 113, 114), *Blancoa*, *Conostylis*, *Macropidia*, *Tribonanthes* (Fig. 115), and *Phlebocarya* (Fig. 116). These placental sclereids consist of isodiametric to slightly elongate (generally 3–4 times longer than broad) cells with moderately thick secondary cell walls. Characteristic of these sclereids are the presence of numerous spherical, nodulelike structures attached to the inner surface of the secondary cell wall (Figs. 114–116, 119, 120); both walls and nodules stain densely with safranin and are apparently lignified. The placental sclereids are distributed somewhat randomly, either singly or in small clusters, throughout the nonvascular tissue of placentae and styles and occasionally the ovary wall. Placental sclereids were not observed in any organ of the other eight family genera: *Barberetta*, *Dilatris*, *Haemodorum*, *Lachnanthes*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia*, and *Xiphidium*.

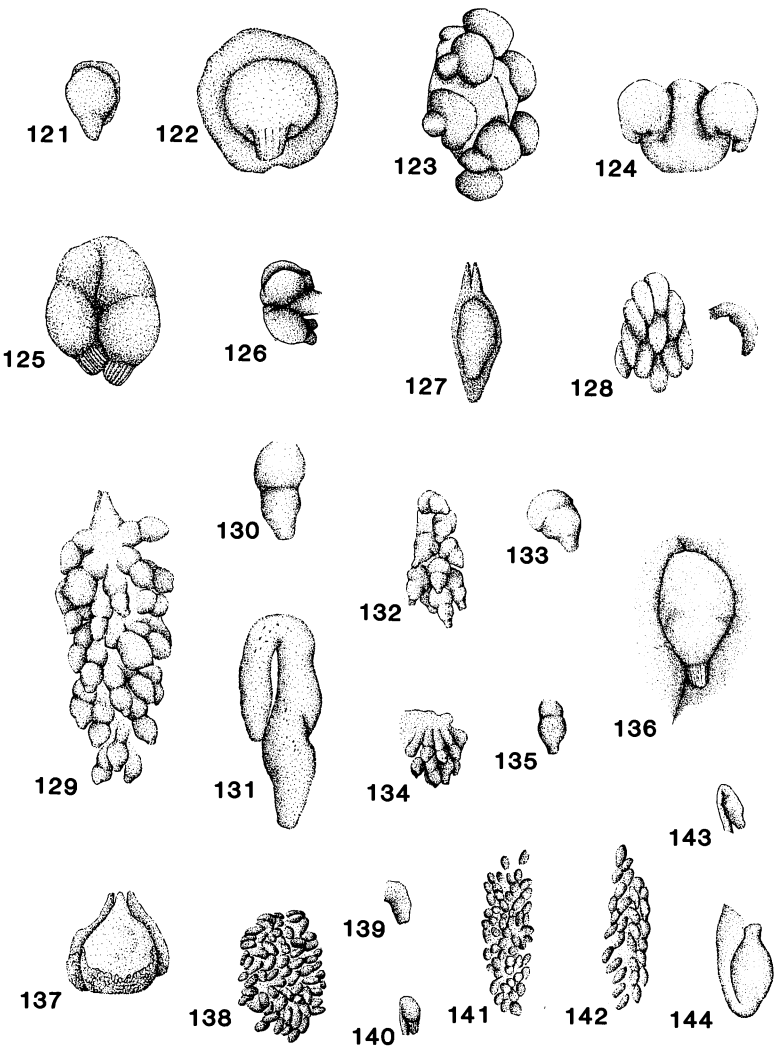
These characteristic placental sclereids are present in all four genera of the Philydraceae (illustrated by *Philydrum* in Figs. 117–119). These sclereids also occur in at least *Pontederia* of the Pontederiaceae (Fig. 120) but are absent in *Heteranthera reniformis* of that family. Despite the observed polymorphism, it seems very likely that the sclereids of the Pontederiaceae are homologous to those of the Haemodoraceae in view of their anatomical and positional similarity. Because the independent evolution of sclereids in the Pontederiaceae seems quite unlikely, this family is coded as having placental sclereids present.

Of the above genera having placental sclereids, four also possess tannin cells in the ground tissue of ovary placentae: *Helmholtzia*, *Philydrum* (Fig. 117), *Phlebocarya* (Fig. 116), and *Pontederia* (Fig. 120); the remaining five genera possess *only* placental sclereids. These placental tannin cells are usually found in small clusters in the ground tissue of ovary placentae. They consist of generally isodiametric (occasionally slightly elongate) cells with thin, unlignified cell walls. The entire cell lumen of these cells is filled with an ergastic substance that stains very densely with safranin; this is characteristic of tanniniferous compounds (Johansen, 1940), though no specific chemical tests were made. These placental tannin cells are very similar to and very likely homologous with the perianth tannin cells discussed above (see *Perianth tannin cells*).

Characters #44–47. Ovule morphology and number. The morphology and number (per carpel) of ovules in the Haemodoraceae are quite variable (see Figs. 121–139). Virtually all ovules in the family have a narrow micropylar "neck" arising from the ovule body. The shape of the ovule body itself, however, can be somewhat globose, as in *Dilatris* (Fig. 122), *Haemodorum* (Fig. 124), and *Lachnanthes* (Fig. 123), or variably elongate and often flask-shaped. Placenta morphology, ovule position, and ovule number also vary. In most taxa the ovules are hypotropous in position, with the micropyle directed downward (proximally). *Phlebocarya* is the only genus of the family with epitropous ovules; these are arranged, one per carpel, in a ring, arising from the base of the ovary (Fig. 137). *Lachnanthes* (Fig. 123) and *Schiekia* (Fig. 126) are similar in having 5–7 and (3)4 ovules, respectively. These ovules are pleurotropously positioned (i.e., with the micropyle directed sidewise, towards the central flower axis) on a placenta that protrudes into the locule. This placenta is quite enlarged and peltiform in *Lachnanthes*, having marginally disposed ovules (Fig. 123). Curiously, however, *Pyrrorhiza* (Fig. 125) and *Haemodorum* (Fig. 124), which possess two hypotropous ovules per carpel, have an enlarged placenta similar to that of *Lachnanthes* and *Schiekia*. In addition, an



FIGURES 113–120. Placental tissue anatomy in the Haemodoraceae and outgroups. 113, 114. *Anigozanthos flavidus.*—113. Elongate sclereid (scl) with lignified cell wall; ×347.—114. Close-up of sclereid, showing nodulelike structures (arrow) appressed to inner cell wall; ×910.—115. *Tribonanthes variabilis.* Note lignified sclereid (scl) with nodulelike structures (arrow); ×856.—116. *Phlebocarya ciliata.* Note sclereid (scl) with nodules (arrow) and tannin cell (tc); ×856. 117–119. *Philydrum lanuginosum.*—117. Sclereid (scl) and tannin cell (tc); ×443.—118. Elongate sclereids with nodulelike structures (arrow); ×437.—119. Close-up of sclereid (scl), showing nodules (arrow); ×949.—120. *Pontederia cordata.* Note tannin cells (tc) and sclereid (scl) with nodules (arrow); ×887.



FIGURES 121–144. Ovule morphology in the Haemodoraceae and outgroups.—121. *Barberetta aurea*; ×19.—122. *Dilatris corymbosa*; ×19.—123. *Lachnanthes caroliniana*; ×19.—124. *Haemodorum spicatum*; ×19.—125. *Pyrrorhiza neblinae*; ×19.—126. *Schiekia orinocensis*; ×19.—127. *Wachendorfia thyrsiflora*; ×19.—128. *Xiphidium coeruleum*; ×19.—129, 130. *Anigozanthos flavidus*; ×9.5 (129), ×19 (130).—131. *Anigozanthos rubra*; ×19.—132, 133. *Blancoa canescens*; ×9.5 (132), ×19 (133).—134, 135. *Conostylis aurea*; ×9.5 (134), ×19 (135).—136. *Macropidia fuliginosa*; ×19.—137. *Phlebocarya ciliata*; ×19.—138, 139. *Tribonanthes variabilis*; ×9.5 (138), ×19 (139).—140, 141. *Helmholtzia acorifolia*; ×19 (140), ×9.5 (141).—142, 143. *Heteranthera reniformis*; ×9.5 (142), ×19 (143).—144. *Pontederia cordata*; ×19.

enlarged placenta consisting of a ringlike mass of tissue surrounding the base of the ovule is present in *Barberetta* (Fig. 121), *Dilatris* (Fig. 122), and *Wachendorfia* (Fig. 127). (In *Dilatris* this ring of tissue expands during seed development, forming a false aril; see De Vos, 1956.) It seems likely that the enlarged placentae of all seven of these genera are homologous; however, it is not immediately evident which morphology (i.e., the ringlike placenta surrounding a single ovule or the peltiform placenta bearing several marginal ovules) is most ancestral.

Among other OTUs, *Anigozanthos rubra* (Fig. 131) has two hypotropous ovules per carpel, and *Macropidia* (Fig. 136) has a single ovule per carpel. In both of these taxa, a distinct ringlike or enlarged placenta like that found in other Haemodoraceae is lacking; however, the inner ovary wall surrounding the ovule(s) is somewhat swollen and may be homologous to the enlarged placenta

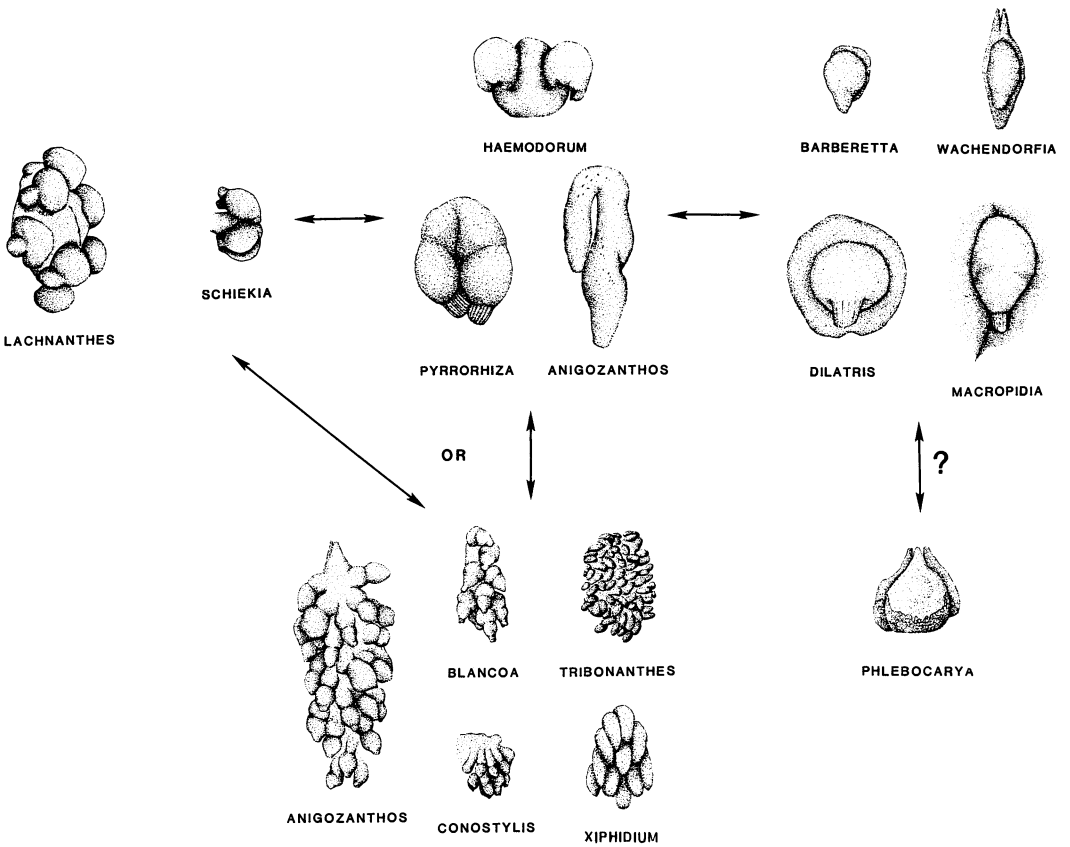


FIGURE 145. Hypothesized intergradation series of ovule types in the Haemodoraceae. Note uncertainty of evolutionary direction of single, epitropous ovule in *Phlebocarya*.

discussed above. Finally, numerous (up to 40) ovules per carpel are found in *Anigozanthos flavidus* (Figs. 129, 130), *Blancoa* (Figs. 132, 133), *Conostylis* (Figs. 134, 135), *Tribonanthes* (Figs. 138, 139), and *Xiphidium* (Fig. 128). Although the placentae in these taxa may be somewhat expanded (e.g., certain species of *Conostylis*), it appears unlikely that the greater ovule number in these taxa is directly related evolutionarily to that in *Schiekia* and *Lachnanthes*.

The possible evolutionary changes in ovule number, ovule morphology, and placenta morphology in the Haemodoraceae are rather complex. An unambiguous intergradation series is not evident. However, the morphocline presented in Figure 145 is presented as the most likely a priori hypothesis. Note that *Lachnanthes* and *Schiekia*, having 4–7 pleurotropous ovules/carpel, are coded either as derived from two-ovulate taxa *or* as intermediate between two-ovulate taxa and numerous-ovulate taxa. *Phlebocarya*, with one epitropous ovule/carpel, is questionably linked to taxa with one hypotropous ovule/carpel.

In order to code the character "ovule morphology and number" numerically without biasing the input, this feature was divided into the following four characters.

Characters #44, 45: Ovule position: PLEUROTROPOUS ←[#44]→ HYPOTROPOUS ←[#45]→ EPITROPOUS. Note that the epitropously positioned ovules of *Phlebocarya* are evolutionarily linked to the hypotropous condition (Fig. 145). Correspondingly, it seems quite unlikely that the specialized pleurotropous ovules arising from a peltiform placenta are evolutionarily intermediate to a hypotropous and epitropous condition (Fig. 145).

Character #46: Ovule number one per carpel vs. two–numerous per carpel. This character allows for a single evolutionary step between those taxa

with one ovule and those with two or more (see Figs. 145, 165C).

Character #47: Ovule number one or two per carpel vs. numerous per carpel. *Lachnanthes* and *Schiekia*, having (respectively) 4 and 5–7 ovules per carpel are coded as "X" so as to avoid bias for evolutionary linkage either directly with two-ovulate taxa or intermediate between two- and numerous-ovulate taxa (Fig. 165C). Figure 165C illustrates the character coding for ovule position and number (characters #44–47). Note that the number of steps between adjacent ovule groupings is one.

Among the outgroup families, all members of the Philydraceae have numerous ovules per carpel with a hypotropous to pleurotropous position (illustrated for *Helmholtzia* in Figs. 140, 141). However, in view of the distinctive placental morphology of those Haemodoraceae with pleurotropous ovules (i.e., positioned along the margin of a protruding placenta), the pleurotropous ovule position in the Philydraceae is not coded as being homologous with that in the Haemodoraceae. In the Pontederiaceae all genera have numerous, generally hypotropous ovules (illustrated for *Heteranthera* in Figs. 142, 143), with the exception of *Pontederia* (Fig. 144) and *Reussia*, which have one epitropous ovule per ovary (contained in the single fertile carpel). Thus, the Pontederiaceae are coded as polymorphic ("?") with respect to characters #45–47 (but not, of course, with respect to character #44).

Characters #48–50. Seed morphology. Seed morphology in the Haemodoraceae is quite variable. *Dilatris*, *Haemodorum*, and *Lachnanthes* have glabrous, discoid seeds (generally concave proximally and convex distally) which are peltately attached (i.e., the funiculus is positioned centrally on the proximal face). Various degrees of a marginal wing occur on the seeds of these taxa. Seeds of *Dilatris* (Fig. 146) are comparatively large (certainly correlated with having only one ovule per carpel) and have a narrow encircling wing. *Haemodorum* seeds (two per carpel) are slightly smaller and have a prominent marginal wing (Fig. 147). Seeds of *Lachnanthes* (5–7 per carpel) have only a slight marginal wing (Fig. 148), which develops from the growth and "buckling" of the outer integument (Simpson, 1988). Seeds of *Pyrrorhiza* (Figs. 149, 150) resemble those of the above three genera in being rather discoid and peltately attached but differ in having a dense tomentum of mostly marginal trichomes. *Wachendorfia* seeds range from globose (Fig. 154) to ovoid (Fig. 155) but are consistently pubescent to tomentose throughout. The individual trichomes of the seeds of *Wachendorfia* are quite similar to those of *Pyrrorhiza*; thus the seed morphology of *Pyrrorhiza* seems intermediate between that of *Wachendorfia* and the three genera with discoid glabrous seeds. Seeds of *Xiphidium* (Fig. 151) and *Schiekia* (Fig. 152) are globose and tuberculate. *Barberetta* (Fig. 153) has ovoid, glabrous seeds, which are very similar in size and shape to some species of *Wachendorfia*. *Phlebocarya* (Fig. 156) and *Tribonanthes* (Fig. 157) have glabrous and somewhat globose seeds. Seeds of *Anigozanthos* (Fig. 158), *Blancoa*, and *Conostylis* (Fig. 159) are quite similar to one another, being ellipsoid and ridged longitudinally. *Macropidia* (Fig. 160) has similar seeds to these three genera, but the ridges are much shallower and the seeds are significantly larger.

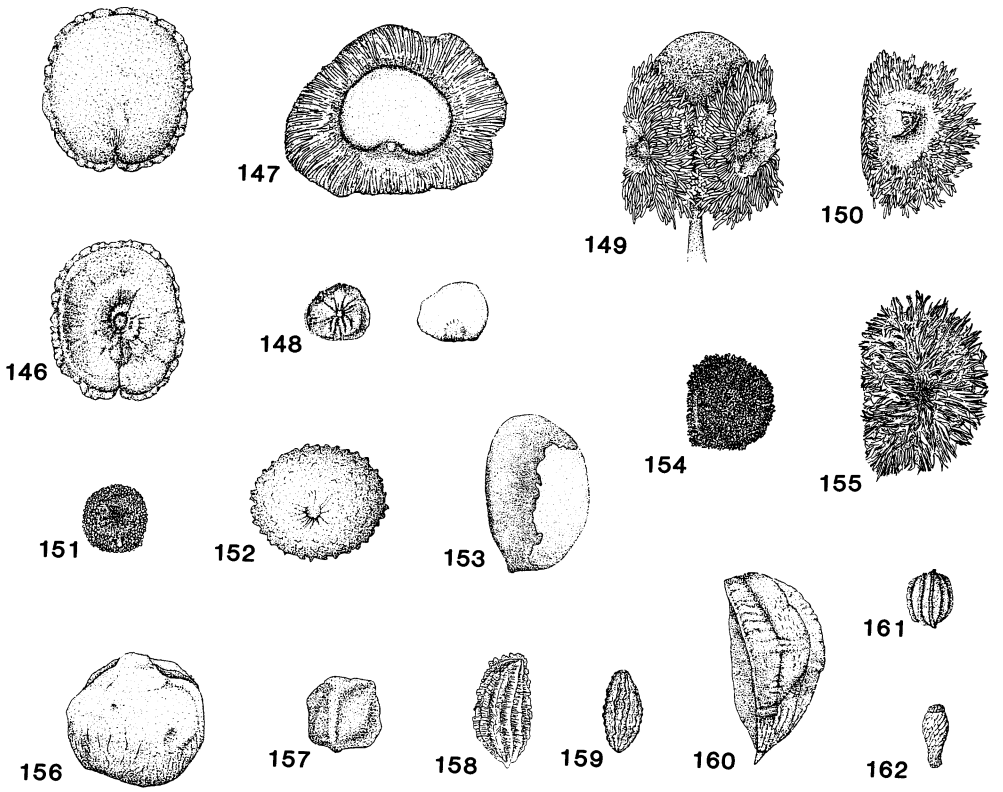
The hypothesized intergradation series for seed morphology in the Haemodoraceae is seen in Figure 163. Note that the direct evolutionary linkage between taxa with discoid, marginally winged seeds and the somewhat discoid, marginally tomentose seeds of *Pyrrorhiza* is questionable; developmental and anatomical studies are needed for confirmation. Because of the length of the morphocline of Figure 163 and the possibility of biasing the data if the groupings are coded sequentially, the character "seed morphology" was subdivided into the following discrete characters:

Character #48: Seed shape ovoid-globose or ellipsoid (and longitudinally ridged) vs. discoid. This allows for a single evolutionary step between taxa having the distinctive discoid seed morphology and all other taxa. *Pyrrorhiza* is coded as "X" for this character because of the uncertainty of homology between its somewhat flattened seeds and the discoid seeds of *Dilatris*, *Haemodorum*, and *Lachnanthes*.

Character #49: Seed shape ellipsoid vs. discoid, flattened, or ovoid-globose. This allows for a single evolutionary step between taxa having ellipsoid (and longitudinally ridged) seeds and all other seed types.

Character #50: Seed vestiture glabrous vs. pubescent or marginally winged. Taxa having discoid seeds with marginal wings are coded with those having tomentose seeds because of the presumed homology between the marginal wing and the trichomes. Figure 165D illustrates the character coding for seed morphology (characters #48–50).

Among the outgroups, seeds of all members of



FIGURES 146–162. Seed morphology in the Haemodoraceae and outgroups.—146. *Dilatris viscosa*, proximal (below) and distal (above) sides; ×3.8.—147. *Haemodorum spicatum*, distal side; ×3.8.—148. *Lachnanthes caroliniana*, proximal (left) and distal (right) sides; ×3.8. 149–150. *Pyrrorhiza neblinae*.—149. Face view of placenta with two attached seeds; ×3.8.—150. Proximal side of seed; ×3.8.—151. *Xiphidium coeruleum*, distal side; ×7.9.—152. *Schiekia orinocensis*, distal side; ×7.9.—153. *Barberetta aurea*, side view; ×7.9. 154–155. *Wachendorfia* seeds (side view).—154. *W. paniculata*; ×3.8.—155. *W. thyrsiflora*; ×3.8.—156. *Phlebocarya ciliata*; ×7.9.—157. *Tribonanthes variabilis*; ×7.9.—158. *Anigozanthos flavidus*; ×7.9.—159. *Conostylis* sp.; ×7.9.—160. *Macropidia fuliginosa*; ×7.9.—161. *Eichhornia* sp.; ×7.9.—162. *Philydrum lanuginosum*; ×7.9.

the Pontederiaceae (see Fig. 161) are consistently small and ovoid with longitudinal ridges. Species of the Philydraceae (see Fig. 162) have twisted, pyriform-terete seeds with longitudinal rows of epidermal cells. Thus the seeds of both outgroups, particularly the Pontederiaceae, resemble *Anigozanthos*, *Blancoa*, *Conostylis*, and *Macropidia* in having longitudinal ridges but differ somewhat in shape. Because of the similarity, seed morphology in the Philydraceae and Pontederiaceae are coded as homologous with the ellipsoid, longitudinally ridged seeds in the Haemodoraceae.

Character #51. Haploid chromosome number. Haploid chromosome numbers for the Haemodoraceae and outgroups are listed in Table 6. The chromosome number of *Xiphidium coeruleum* is here described for the first time as $n = 19$ (Fig. 164; this number confirmed by P. Goldblatt of the Missouri Botanical Garden, pers. comm.). Note that chromosome numbers of *Pyrrorhiza* and *Schiekia* are unknown. Of the genera in the Haemodoraceae, only *Conostylis* has a variable number. However, most species of that genus have a count of $n = 8$, and the exemplar OTUs are either $n = 5$ or $n = 8$.

One possible coding for chromosome number is the arrangement of taxa in classes via a linear morphocline, such as: $n = 5–8 \leftrightarrow n = 15 \leftrightarrow n = 19–21 \leftrightarrow n = 24$. (Chromosome numbers ranging from 5 to 8 in the OTUs are lumped into one class because of the difficulty of assessing evolutionary direction in presumed minor aneuploidy events.) Since nothing in the Haemodoraceae is known regarding karyological details, it is not unlikely that the evolution of chromosome number may have occurred differently from the simple numerical sequence listed above. For example, the fact that *Lachnanthes* ($n = 24$) has a chromosome number

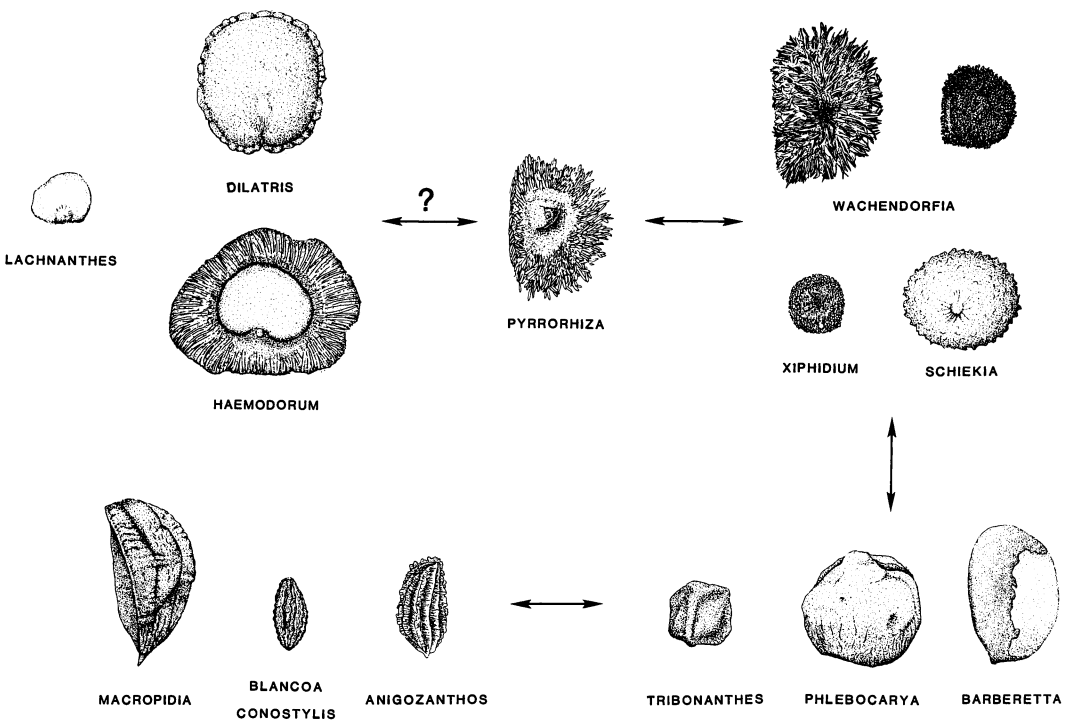


FIGURE 163. Hypothesized intergradation series of seed types in the Haemodoraceae.

exactly 3 times that of the most common number ($n = 8$) may be evidence of a hexaploid derivation from an ancestral $n = 8$; alternatively, a count of $n = 24$ may have arisen from an allopolyploidy event. The $n = 15$ count of some taxa may have been derived via a tetraploidy event, e.g., from an ancestral $n = 7$ or $n = 8$, followed by aneuploidy. A count of $n = 19$ could have arisen directly from a number of $n = 5$–8 or from an immediate ancestor having either $n = 15$ or $n = 24$.

After considerable experimentation with this character, it was concluded that the best coding is simply: $n = 5$–$8 \leftrightarrow n = 15$, 19–21, or 24. The transformation series between the higher haploid numbers is ambiguous, and more elaborate and complex coding schemes result in the same topology in the cladistic analysis.

Chromosome counts in the outgroups vary considerably (Table 6) and are consequently coded as polymorphic ("?"). The only haploid chromosome number found in both outgroups and in the Haemodoraceae is a count of $n = 8$. It seems most likely that the ancestral haploid chromosome number for the Haemodoraceae is near $n = 8$, a hypothesis to be tested with the cladistic analysis.

Character #52. Phenalenones absent vs. present. This character is included to establish the monophyly of the Haemodoraceae relative to the two outgroups (see Monophylesis of the Haemodoraceae). It is very likely that all species of the Haemodoraceae, if investigated, would be found to have these compounds. As a reasonable compromise, however, *genera* of the Haemodoraceae not yet chemically investigated are coded as unknown ("?"). If any species of a genus has been found to have the compounds, *all* species of that genus are coded as possessing them. Both outgroup families are coded as lacking phenalenones.

Character #53. Tapetum glandular vs. amoeboid. This character is included to consider the presence of an amoeboid tapetum in the Haemodoraceae and Pontederiaceae as a possible synapomorphy (see Outgroup Taxa, Table 5). As above, genera of the Haemodoraceae not yet investigated for this feature are coded as unknown ("?"). If any species of a genus has been found to have an amoeboid tapetum, *all* species of that genus are coded as having it.

Character #54. Pollen exine wall structure tetacte-columellate vs. non-tectate-columellate. This feature is included to denote the evidence discussed earlier that the Pontederiaceae are the sister group to the Haemodoraceae (see Out-

TABLE 6. Chromosome numbers in the Haemodoraceae and related families.

Taxon	2n =	n =	Citation
Tribe Haemodoreae			
Barberetta aurea Harv.		15	Hilliard & Burtt (1971); Ratter & Milne (1973); Ornduff (1979a)
Dilatris pilansii Barker		ca. 19–21	Ornduff (1979a)
Haemodorum sp.		8	G. Keighery (pers. comm.)
Lachnanthes caroliniana (Lam.) Dandy		24	Ornduff (1979a)
Lanaria lanata (L.) Dur. & Schinz		36	Ornduff (1979a)
Lophiola aurea Ker-Gawler		21	Ornduff (1979a)
Phlebocarya			
ciliata R. Br.		7	*G. Keighery 691* (PERTH)
filifolia F. Muell.		7	*S. Hopper 840* (PERTH)
Wachendorfia			
paniculata L.		15	Ornduff (1979a)
thyrsiflora L.		ca. 15	Ornduff (1979a)
Xiphidium coeruleum Aubl.		19	Simpson (present paper); P. Goldblatt (pers. comm.)
Tribe Conostylideae			
Anigozanthos			
bicolor Endl.		6	Green (1961)
flavidus DC.		6	Stenar (1927); Green (1961)
humilis Lindl.		6	Green (1961)
manglesii D. Don		6	Green (1961)
viridis Endl.		6	Green (1961)
Blancoa canescens Lindl.		8	Green (1961)
Conostylis			
aculeata R. Br. (7 subspecies)		8	Green (1961); Hopper (1978)
androstemma F. Muell.		5	Green (1961)
aurea Lindl.		5	Green (1961)
bealiana F. Muell.		8	Green (1961)
breviscapa R. Br.		4	Green (1961)
candicans Endl.		8	Green (1961)
caricina Lindl.		7	Green (1961)
filifolia F. Muell.		8	Green (1961)
juncea Endl.		8	Green (1961)
phathyrantha Diels		8	Green (1961)
seorsiflora F. Muell.		8	Green (1961)
serrulata R. Br.		8	Green (1961)
setigera R. Br.		14	Green (1961)
setosa Lindl.		7	Green (1961)
stylidioides F. Muell.		8	Green (1961)
stylidioides F. Muell.		16	Hopper (1978)
vaginata Endl.		8	Green (1961)
Macropidia fuliginosa (Hook.) Druce		6	Green (1961)
Tribonanthes sp.		7	G. Keighery (pers. comm.)
Apostasiaceae (no counts reported)			
Hypoxidaceae			
Curculigo			
orchioides Gaertn.	36		Sharma & Ghosh (1954); Sharma & Chaudhuri (1964); Mitra (1966)
orchioides Gaertn.	18		Raghavan (1957); Sharma & Bhattacharyya (1960)

TABLE 6. Continued.

Taxon	2n =	n =	Citation
recurvata Dryand.	18		Sharma & Ghosh (1954); Sharma & Chaudhuri (1964)
Hypoxis			
acuminata		18, 20	Wilsenach & Papenfus (1967)
aurea Lour.	54		Mehra & Sachdeva (1971, 1976)
decumbens L.	42		Naranjo (1975)
filiformis		7	Wilsenach & Papenfus (1967)
longifolia Baker	72		Wilsenach (1967)
multiceps Buchinge	36		Wilsenach (1967)
nitida		ca. 40–42	Wilsenach (1967)
pusilla Hook.f.	28		Beuzenberg & Hair (1963)
rooperi	96	ca. 43–58	Wilsenach & Papenfus (1967); Wilsenach (1967)
rooperi Moore	76, 114	18	Fernandez & Neves (1962)
stellipilis (Ker.)	16		Fernandez & Neves (1962)
zeyheri Baker (?)	32		Fernandez & Neves (1962)
Rhodohypoxis			
baueri Nel. (9 cultivars)	18, 12		Saito (1975)
Philydraceae			
Helmholtzia			
acorifolia F. Muell.	34		Briggs (1966)
glaberrima (Hook.f.) Caruel	34		Briggs (1966)
Orthothylax			
glaberrimus		16	Hamann (1966)
Philydrum			
langinosum Banks & Soland.	16	8	Hamann (1966) Briggs (1966)
Pontederiaceae			
Eichhornia			
crassipes (Mart.) Solms	36		Briggs (1966)
crassipes Solms	32		Krishnappa (1971)
crassipes Solms	30, 32, 58	16	Banerjee (1974)
speciosa Kunth		8	Sarkar et al. (1975)
Monochoria			
hastifolia Presl.	28, 34–84	14, 40, 42	Banerjee (1974)
korsakowii Rgl.	52		Sokolovskaya (1966)
vaginalis	28		Hsu (1967)
vaginalis	26, 52, 72, 74, 80	30, 40	Sharma (1970)
vaginalis Presl ex Kunth	52		Krishnappa (1971)
vaginalis Presl	80	40	Sharma & Sarkar (1967–1968)
vaginalis Pax. var. *plumbaginia* Solms-Laubch.	52		Sharma & Sarkar (1967–1968)
vaginalis Presl var. *plumbaginea* Solms-Laubch.	52		Banerjee (1974)
var. *plumbaginea* Solms-Laubch.	52		Sharma (1970)
vaginalis (L.) Presl	80	40	Sharma (1970)
vaginalis (L.) Presl	52		Mehra & Pandita (1978)
Pontederia			
cordata L.		8	Ornduff (1969); Lowden (1973)
parviflora Alex.		8	Lowden (1973)
rotundifolia L.f.		16	Lowden (1973)
sagitta Presl		8	Lowden (1973)
Tecophilaeaceae			
Cyanastrum			
cordifolium L.	22		Sato (1942)

TABLE 6. Continued.

Taxon	$2n =$	$n =$	Citation
cordifolium L.		12	Nietsch (1941)
Cyanella			
abla L.f.		12	Ornduff (1979b)
hyacinthoides L.		12, 14, 24	Ornduff (1979b)
lutea L.f. var. *lutea*		8, 12, 24	Ornduff (1979b)
lutea L.f. var. *rosea* Bak.		12	Ornduff (1979b)
orchidiformis Jacq.		12	Ornduff (1979b)
Odontostomum			
hartwegii Torr.		10, 10 + f	Cave (1970)
Tecophilaea			
cyano-crocus		12	LaCour (1956)
Velloziaceae (no counts reported)			
Walleriaceae (*Walleria* spp.)	24		Goldblatt (1989)

group Taxa; Simpson, 1987). Thus, all Pontederiaceae are coded similarly to all Haemodoraceae as having a non-tectate-columellate architecture. Note that this feature was not taken into account with respect to the early characters (#33–37) "exine wall structure," as the Philydraceae were coded as ("?") for number of exine layers (characters #33, 34).

Character #55. Leaves unifacial vs. bifacial. All Haemodoraceae and all Philydraceae have unifacial leaves, whereas all Pontederiaceae have bifacial leaves. This character is included to take into account what may represent a shared derived feature between the Haemodoraceae and Philydraceae.

CLADISTIC ANALYSIS

METHODS

Cladistic analyses were implemented using PAUP (Phylogenetic Analysis Using Parsimony), version 2.4 (Swofford, 1983), on an IBM-AT compatible microcomputer. The most parsimonious trees were constructed using the "branch and bound" algorithm from the data matrix of Table 8. Wagner parsimony was used throughout. Coding is summarized in Table 7. (See Conclusions for results of recent analyses using unordered character coding.)

In the initial analysis all characters were assigned equal weight. In a subsequent analysis characters that could originally have been treated as states of a single character (e.g., characters #4–6, all dealing with inflorescence type) were "scaled," weighted as a proportional fraction of their original weight of "1" (characters #4, 5, and 6 were each given a weight of ⅓). This takes into account (often unintentional) a priori weighting of a feature because it can be subdivided into two or more correlated binary characters. The following characters were fractionally weighted in this second analysis: #4–6, 7–13, 15, 16, 21, 22, 23–25, 27, 28, 29, 30, 33–37, 44–47, 48–50, and 51–53.

In a third cladistic analysis, only those characters for which the polarity could be determined at the outgroup node, using the method of Maddison et al. (1984), were included. Thus, the following eleven characters, for which polarity could not be determined at the outgroup node, were omitted from this analysis: characters #4, 17, 23, 24, 25, 33, 35, 36, 53, 54, and 55.

RESULTS AND DISCUSSION

For the complete data set of Table 8, there are two equally most parsimonious cladograms (Figs. 166, 167). The consistency index of the global analysis, including both outgroups, is 55/88 = 0.625. (If the 10 characters which are nonhomoplasious and autapomorphic for OTUs of the Haemodoraceae are deleted, the consistency index is 45/78 = 0.577.) When "fractional weighting" was performed (see Methods), a single most parsimonious cladogram was computed, equivalent to that of Figure 166. Thus, it could be argued that coding several characters in a multistate transformation series results in little change in cladistic relationships. When the characters for which polarity could not be determined were omitted from the data set, the same two cladograms of Figures 166 and 167 were obtained. This confirmation of results is important because, with some data sets, inclusion versus omission of nonpolarized characters may yield significantly different cladistic re-

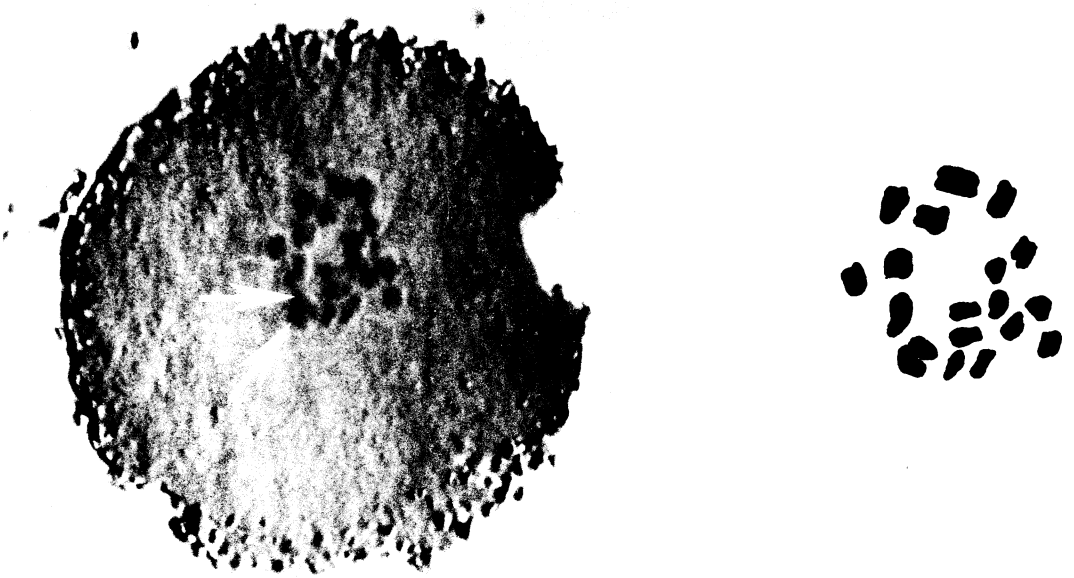


FIGURE 164. Anther microsporocyte squash of *Xiphidium coeruleum* at metaphase I. Note 19 bivalents. Arrows point to overlapping, but different, bivalents. ×1,750 (left), ×2,770 (right).

lationships. (Further comparison of alternative cladograms to Figures 166 and 167 will be discussed below.)

As discussed earlier, the two outgroups were treated as OTUs equivalent in treatment to the intrafamilial OTUs of the Haemodoraceae. Because the outgroup relationships were not coded as resolved, this cladistic analysis confirms the Haemodoraceae as monophyletic; i.e., all OTUs of the ingroup are more closely related to one another than to either outgroup. The overall tree was rooted at the Philydraceae clade, based on assumptions of polarity of characters #52–55 (Table 8; see Fig. 176). The alternative methodology of assigning a hypothetical ancestor and determining the states of that ancestor via the "2-step" algorithm of Maddison et al. (1984) would have yielded identical results within the Haemodoraceae. However, one possible advantage of this "1-step" analysis (sensu Maddison et al.), performed *without* specifying outgroup relationships, is that it provides a test both for the monophyly of the ingroup and for the relationship of the ingroup to the outgroup (see Interfamilial Relationships).

Synapomorphies for the Haemodoraceae (Fig. 166) are: bifurcate cymes (character #5); inferior ovary position (character #39); discoid, flattened, or ovoid-globose, i.e., *not* ellipsoid and ridged, seeds (character #49); and presence of phenalenone compounds (character #52). Of these, only the presence of phenalenone compounds was hypothesized a priori as synapomorphic for the family (see Monophylesis of the Haemodoraceae). Corroboration here confirms its valid use as a synapomorphy for the family. (The indicated occurrence of bifurcate cymes, inferior ovary position, and nonellipsoid, ridged seeds as synapomorphies for the Haemodoraceae is discussed below.)

The two equally parsimonious topologies differ only in the relationship of *Dilatris*, portrayed either as the sister taxon of *Lachnanthes* alone (Fig. 166) or as the sister taxon of the monophyletic group containing SC-PY-XI-BA-WA (Fig. 167). In either topology it is interesting that the initial bifurcation defines two monophyletic groups: designated here tribe Haemodoreae and Conostylideae. These roughly correspond to the traditionally defined tribes Haemodoreae and Conostylideae (e.g., Bentham & Hooker, 1883; Hutchinson, 1973; Melchior, 1964; Geerinck, 1969a) or the subfamilies Haemodoroideae and Conostyloideae (Cronquist, 1981; Dahlgren & Clifford, 1982). Thus, the present analysis confirms the taxonomic "integrity" of tribes Conostylideae and Haemodoreae and provides evidence for their being monophyletic taxa. (Despite the many differences in significant patristic distance between these two major clades of the Haemodoraceae, I conform with historical priority and recent consensus of use in retaining the tribal rather than the subfamilial rank. I see no valid reason for

TABLE 7. Character listing and coding. Originally multistate characters were recoded as two or more binary characters.

1. Reddish root and stem coloration
   0 = absent
   1 = present
2. Stem structural type
   0 = rhizome
   1 = corm
3. Plicate leaves
   0 = absent
   1 = present
4. Inflorescence type
   0 = cyme absent
   1 = cyme simple, bifurcate, or trifurcate
5. Inflorescence type
   0 = cyme absent or simple
   1 = cyme bifurcate or bifurcate and trifurcate
6. Inflorescence type
   0 = cyme absent, simple, or bifurcate
   1 = cyme bifurcate and trifurcate
7. Trichomes pilate
   0 = absent
   1 = present
   ? = homology uncertain
8. Trichomes, if pilate, with basal rosette
   0 = absent
   1 = present
   ? = not pilate
9. Trichomes tapering
   0 = absent
   1 = present
10. Trichomes, if tapering, unicellular or multicellular
   0 = unicellular
   1 = multicellular
   ? = nontapering
11. Trichomes, if tapering, uniseriate or multiseriate
   0 = uniseriate
   1 = multiseriate
   ? = nontapering
12. Trichomes, if tapering, branched
   0 = absent (unbranched)
   1 = present (branched)
   ? = nontapering
13. Trichomes, if tapering, with basal rosette
   0 = absent
   1 = present
   ? = nontapering
14. Perianth apertures
   0 = absent
   1 = present
15. Perianth tube
   0 = absent
   1 = present (short or long)
16. Perianth tube
   0 = absent or short
   1 = long
17. Perianth symmetry
   0 = actinomorphic
   1 = zygomorphic (without perianth splitting)
18. Perianth splitting
   0 = absent
   1 = present
19. Perianth aestivation
   0 = imbricate
   1 = valvate
20. Perianth tannin cells
   0 = absent
   1 = present
21. Stamen (fertile) number
   0 = six
   1 = three or one
22. Stamen (fertile) number
   0 = six or three stamens + two latero-anterior staminodes
   1 = three (without staminodes) or one
23. Anther dimorphism
   0 = anthers equal
   1 = anthers dimorphic
24. Anther dimorphism
   0 = anthers equal *or* one large + two small anthers
   1 = one large + two caducous anthers *or* one anther + two staminodes
25. Anther dimorphism
   0 = anthers equal *or* one large + two small or caducous anthers
   1 = one anther + two staminodes
26. Stamen connective appendages
   0 = absent
   1 = present
27. Pollen aperture
   0 = monosulcate
   1 = porate
28. Pollen aperture
   0 = monosulcate or 2–3-porate
   1 = oligoforaminate
29. Pollen sculpturing
   0 = foveolate
   1 = verrucate or rugulate
30. Pollen sculpturing
   0 = foveolate or verrucate
   1 = rugulate
31. Pollen apertural border
   0 = absent
   1 = present
32. Pollen large proximal verrucae
   0 = absent
   1 = present
33. Number of exine wall layers
   0 = one-layered
   1 = two- or three-layered
34. Number of exine wall layers
   0 = one- or two-layered
   1 = three-layered
35. Exine wall, if two-layered, with papillate inner elements
   0 = absent

TABLE 7. Continued.

1 = present
? = exine one- or three-layered
36. Exine wall, if two-layered, with only papillate inner elements
0 = absent
1 = present
? = exine one- or three-layered
37. Subexterior exine wall discontinuous
0 = absent
1 = present
38. Enantiostyly
0 = absent
1 = present
39. Ovary position
0 = superior
1 = inferior
40. Septal nectaries
0 = absent
1 = present
41. Fertile carpels
0 = three
1 = one
42. Locule number
0 = three
1 = one
43. Placental sclereids
0 = absent
1 = present
44. Ovule position
0 = pleurotropous
1 = hypotropous or epitropous
45. Ovule position
0 = pleurotropous or hypotropous
1 = epitropous
46. Ovule number
0 = one per carpel
1 = two–numerous per carpel
47. Ovule number
0 = one or two per carpel
1 = numerous per carpel
? = four–seven per carpel
48. Seed shape
0 = ovoid-globose *or* ellipsoid (& longitudinally ridged)
1 = discoid
? = flattened (*Pyrrorhiza*)
49. Seed shape
0 = ellipsoid (& longitudinally ridged)
1 = discoid, flattened, or ovoid-globose
50. Seed vestiture
0 = glabrous
1 = pubescent or marginally winged
51. Haploid chromosome number
0 = 5–8
1 = 15, 19–21, or 24
? = unknown or polymorphic
52. Presence of phenalenone compounds
0 = absent
1 = present
? = unknown
53. Tapetum type
0 = secretory
1 = amoeboid
? = unknown
54. Exine structure
0 = tecate-columellate
1 = non-tectate-columellate
55. Leaf type
0 = bifacial
1 = unifacial

promoting a change in rank that conveys no change in cladistic relationships.)

The present circumscription of the tribes differs from past treatments primarily in the removal of *Hagenbachia*, *Lanaria*, *Lophiola*, and *Pauridia* from the family and in the transfer of *Phlebocarya* from its usual placement in the tribe Haemodoreae to the Conostylideae. *Phlebocarya* has traditionally been placed in the tribe Haemodoreae because of its imbricate as opposed to valvate tepals. However, an imbricate perianth is clearly plesiomorphic for members of the family; its occurrence cannot be used to unite taxa in a phylogenetic classification. *Phlebocarya* is united with the other Conostylideae by the common occurrence of derived features (see below).

Synapomorphies shared by the six genera of the Conostyloideae are: loss of pilate trichomes (character #7, although this may be synapomorphic only for members of the tribe other than *Phlebocarya*; see Fig. 166), possession of multiseriate trichomes (character #11, which has an alternative state change possibility; see below), branched trichomes (character #12), six fertile stamens (character #21), six or three stamens + two latero-anterior staminodes (character #22), porate apertures (character #27), rugulate pollen wall sculpturing (character #30), and absence of enantiostyly (character #38). Character #11 exhibits a reversal in the clade to *Tribonanthes* (Fig. 166); an equally parsimonious alternative (but highly unlikely in the author's view) is the independent evolution of multiseriate trichomes in the clades to *Phlebocarya* and to the COau–MA monophyletic group. Of the other indicated synapomorphies, it seems extremely likely that the palynological fea-

TABLE 8. Character × Taxon matrix for the Haemodoraceae. A "?" indicates uncertain ancestry, absent data or "X" coding. (See Table 7 and text for discussion of taxa and character coding.) PHIL = Philydraceae, PONT = Pontederiaceae. Other taxa abbreviations are listed in Figure 166.

	Characters:										
Taxa:	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890	55555 12345
PHIL	0?000	01011	00000	0?001	11???	000??	00???	??100	1?110	11000	?0001
PONT	00010	01011	0000?	??001	?????	00010	00?0?	?0?0?	?011?	??000	?0110
ANfl	00011	00?11	11001	10110	00000	01011	00101	10011	00110	11000	01111
ANru	00011	00?11	11001	10110	00000	01011	00101	10011	00110	10000	01111
BA	00100	0110?	???00	00000	11000	00010	11100	00101	10010	00010	1??11
BL	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	01?11
COan	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	0??11
COau	00011	00?11	11001	00010	00000	01011	00101	10011	00110	11000	0??11
CObe	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	0??11
DI	10011	11111	00100	00000	11100	00010	10100	00111	00010	00111	1?111
HA	11011	0100?	???00	00001	11100	00010	0000?	?0111	00010	10111	01?11
LA	10011	1?111	00000	00000	11000	00010	0000?	?0111	00000	1?111	11111
MA	00011	00?11	11001	10110	00000	01011	00101	10011	00110	00000	0??11
PH	00011	0??11	11000	00001	00000	01011	00101	00011	01111	00010	0??11
PY	11011	01110	00100	01000	11111	00010	00100	01001	00010	10?11	???11
SC	00011	01110	00110	01000	10110	00000	0011?	?1101	00000	1?011	???11
TR	01011	00?11	01001	00011	00000	11111	00101	10011	00110	11010	0??11
WA	11110	01110	00110	01000	11000	00010	11100	00101	00010	00011	11111
XI	10010	0110?	???00	00000	11100	00010	00100	00100	00010	11011	11111

tures are indeed synapomorphic, as supported by pollen investigations of all taxa considered closely related to the Haemodoraceae.

Within the tribe Conostylideae, *Phlebocarya* is the most basal taxon (Fig. 166). Characters shared by *Tribonanthes* and the remaining four genera (CO, BL, AN, & MA) are a short perianth tube (character #15), valvate perianth aestivation (character #19), inner exine layer composed solely of papillate elements (character #36), and numerous ovules per carpel (character #47). The last-mentioned feature (#47) requires a convergence (clade to XI) and a reversal (clade to ANru & MA). The placements of *Phlebocarya* and *Tribonanthes* are questionable. They are similar to one another in chromosome number ($n = 7$; see below), but no coded features argue for their being sister taxa. *Phlebocarya* shares two similarities with CO, BL, AN, & MA that *Tribonanthes* does not: presence of 2–3-porate pollen grains (character #27) and of multiseriate, dendritic trichomes (character #10). The occurrence of 2–3-porate pollen grains, however, is undoubtedly plesiomorphic for the tribe (Fig. 166), and *Tribonanthes* is presumed to have evolved this feature in common with other members of the tribe.

Conostylis, *Blancoa*, *Anigozanthos*, and *Macropidia* are members of a monophyletic group that is defined by two homoplasious synapomorphies: absence of perianth tannin cells (character #20 C) and presence of ellipsoid, longitudinally ridged seeds (character #49 R). All four of these genera have protruding hemispheric aperture walls (not found in *Phlebocarya* or *Tribonanthes*), which may represent a unique evolutionary change and thus constitute further evidence for the monophyly of these four genera. *Conostylis* and *Anigozanthos* are paraphyletic in the present analysis (Fig. 166). In *Conostylis* two exemplar species, COan & CObe, share more recent common ancestry with BL, AN, and MA than with COau as shown by the common presence of an elongate perianth tube (character #16), a derived feature. *Anigozanthos* and *Macropidia* clearly form a monophyletic group, as supported by their common possession of a unique longitudinal perianth splitting (character #18). However, *Anigozanthos* is portrayed as paraphyletic because MA and ANru share a derived feature: reduction of ovule number from numerous to one or two per carpel (character #47 R), a feature not shared with ANfl, which has numerous ovules per carpel.

The present study tends to support Geerinck's (1969a, b, 1970), treatment of *Macropidia* as a species of *Anigozanthos* (*A. fuliginosus*) and *Blancoa* as a species of *Conostylis* (*C. canescens*).

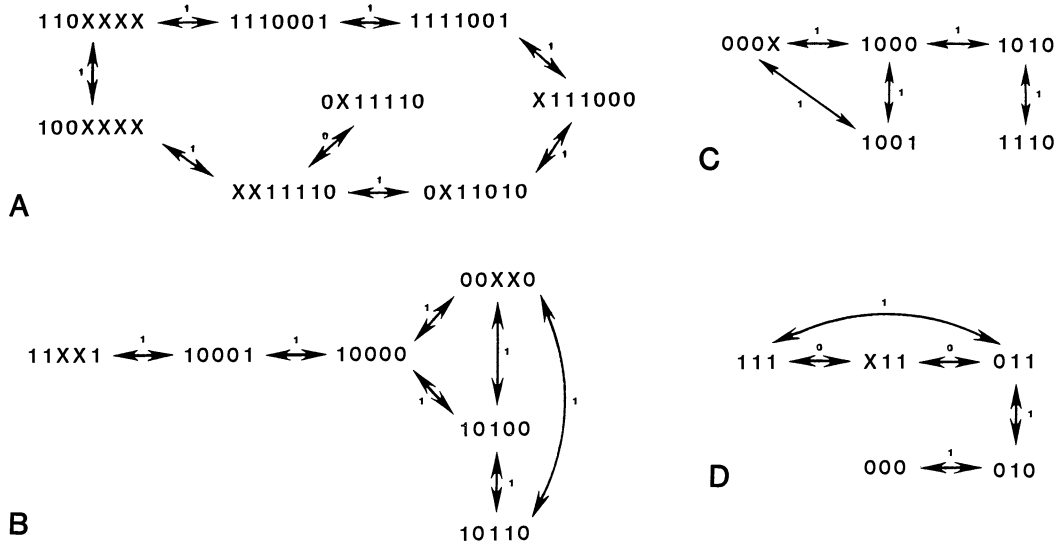


FIGURE 165. "X"-character state coding of OTUs of Haemodoraceae. Sequence of numbers and Xs represent character states of related characters for a given taxon. The "X" symbol represents an equivocal character state coding (coded as a "?" in Tables 7 and 8). Arrows represent evolutionary transitions in the morphocline. Numbers of character state changes are indicated beside arrows.—A. Trichome anatomy (characters #7–13), reflecting morphocline of Figure 28.—B. Pollen exine wall structure (characters #33–37), reflecting morphocline of Figure 112.—C. Ovule morphology (characters #44–47), reflecting morphocline of Figure 145.—D. Seed morphology (characters #48–50), reflecting morphocline of Figure 163.

Following Geerinck's treatment and accepting the results here, *Anigozanthos* s. ampl. would then be monophyletic. On the other hand, *Conostylis*, as currently defined, is still likely paraphyletic, even when merged with *Blancoa*. Much more detailed phylogenetic studies are needed to resolve the phylogenetic relationships of *Anigozanthos* and *Conostylis*, particularly in the recognition of genera segregated from *Conostylis*: *Blancoa*, *Greenia*, and *Androstemma* (see Keighery, 1981). Hopper & Campbell (1977), in study of seed morphology of *Anigozanthos* and *Macropidia*, attained results markedly different from those portrayed in Figure 166. Their phylogenetic tree suggests that *Anigozanthos* is a monophyletic group, and that the lineages to both *Anigozanthos* and *Macropidia* were derived separately from an ancestral taxon most closely related to the extant *Conostylis breviscapa*, the only species of *Conostylis* with distinct tepals. It is my view that *Anigozanthos* and *Macropidia* are likely most closely related to the long-tubular species of *Conostylis*, namely *C. bealiana*, *C. androstemma*, and/or *C.* (*Blancoa*) *canescens*. Clearly, however, a thorough character analysis and phylogenetic study of all species of this complex of taxa is needed.

Characters that unite the genera of the Haemodoreae are: reddish coloration in roots and rootstock (character #1), absence of placental sclereids (character #43), discoid seed shape (character #48, which has an alternative state change possibility; see below), and pubescent or marginally winged seed (character #50). Of these, only character #43 is nonhomoplasious and exhibits no reversals. Character #48 has an equally parsimonious alternative of two convergent events (in the clades to HA and to DI-LA). Additionally, note that characters #23 & #35 may be synapomorphic for *either* of the tribes Haemodoreae or Conostylideae, the uncertainty resulting from the fact that the polarity of these characters at the ingroup node (i.e., the common ancestor of the Haemodoraceae) could not be determined.

Within the tribe Haemodoreae, *Haemodorum* is the most basal (earliest diverging) lineage. The seven other genera of the tribe are united by four synapomorphies (see Fig. 166). Two of these, presence of pilate trichomes with a basal rosette of epidermal cells (character #8) and an increase in chromosome number from $n = 5–8$ to $n = 15–24$ (character #51), are nonhomoplasious in both equally parsimonious topologies and seem good evidence for the recognition of this subgroup. Absence (loss) of perianth tannin cells (character #20 C) occurs independently as a derived feature in the lineage to CO, BL, AN, and MA of the tribe Cono-

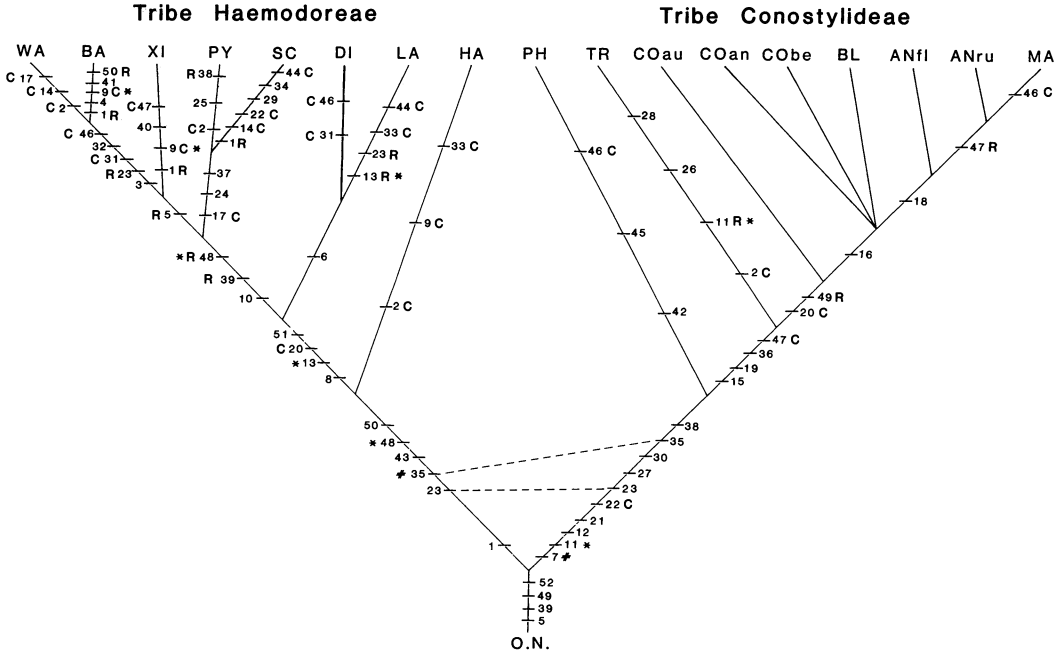


FIGURE 166. One of two equally most parsimonious cladograms of the Haemodoraceae derived from the data matrix of Table 8. Each numbered hash mark along a clade represents an apomorphic character state change of the designated character (Tables 7, 8). Dashed lines between character changes at base of cladogram represent equally parsimonious alternatives of evolutionary change along the lineages to either the tribe Haemodoreae or Conostylideae. Character state changes indicated with a "*" (characters 9, 11, 13, and 48) have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram. State changes indicated with a "#" (characters 7 and 35) may occur with equal probability at the *internode* immediately above the displayed position.

Taxa abbreviations: O.N. = outgroup node; ANfl = *Anigozanthos flavidus*, ANru = *Anigozanthos rufus*, BA = *Barberetta aurea*, BL = *Blancoa canescens*, COau = *Conostylis aurea*, COan = *Conostylis androstemma*, CObe = *Conostylis bealiana*, DI = *Dilatris* spp., HA = *Haemodorum spicatum*, LA = *Lachnanthes caroliniana*, MA = *Macropidia fuliginosa*, PH = *Phlebocarya* spp., PY = *Pyrrorhiza neblinae*, SC = *Schiekia orinocensis*, TR = *Tribonanthes* spp., WA = *Wachendorfia thyrsiflora*, XI = *Xiphidium coeruleum*. C = Convergence; R = Reversal.

stylideae. The occurrence of tapering trichomes having a basal rosette of epidermal cells (character #13) either exhibits a reversal in the clade to LA (Fig. 166) or is synapomorphic only for DI, PY-SC, XI, BA, and WA (Fig. 167).

As mentioned above, the phylogenetic relationships of *Dilatris* and *Lachnanthes* are portrayed in two equally parsimonious topologies. In Figure 166 DI and LA are sister taxa, united by a single synapomorphy: the occurrence of bifurcate *and* trifurcate helicoid cyme units (character #6). Note that the presence of tapering trichomes with a basal rosette (character #13) is seen as an evolutionary event in the lineage preceding the DI-LA clade, and that a reversal of this feature (#13 R in Fig. 166) occurs along the clade to LA alone. The alternative and equally parsimonious possibility of independent evolution of such trichomes in the lineages to both DI and to WA, BA, XI, PY, & SC seems highly improbable. In Figure 167 the lineage terminating in *Dilatris* is depicted as arising after the lineage giving rise to *Lachnanthes*. Note that *Dilatris* is here united with WA, BA, XI, PY, and SC by character #13 (derivation of tapering trichomes with a basal rosette, requiring a single character state change and not two as in Fig. 166). In this scheme, changes in characters #6 (cyme bifurcate and trifurcate) and #33 (exine wall one-layered) may occur equally parsimoniously either as a pair of convergences (illustrated in Fig. 167) or as one unique event and a reversal (not illustrated).

Wachendorfia, *Barberetta*, *Xiphidium*, *Pyrrorhiza*, and *Schiekia* are members of the next monophyletic unit of the tribe. Three derived features support this grouping as seen in Figure 166: derivation of unicellular, tapering trichomes (character #10), a *reversal* to a superior ovary (char-

acter #39 R), and a reversal to an ovoid-globose seed shape (character #48 R*). *Pyrrorhiza* and *Schiekia* compose a monophyletic group by virtue of three synapomorphies. One of these, presence of a zygomorphic perianth (character #17 C), occurs independently in the lineage to *Wachendorfia*; however, this may be questionable, as will be discussed. The other two synapomorphies, anther dimorphism with one large and two caducous anthers (character #24) and a discontinuous inner subexterior exine layer (character #37), furnish excellent evidence for the close phylogenetic relationship of these taxa. *Wachendorfia* and *Barberetta* are a monophyletic assemblage as evidenced by five evolutionary steps (Fig. 166). Only two of these—presence of plicate leaves (character #3) and presence of large proximal verrucae on the pollen grains (character #32)—are nonhomoplasious, but these alone seem sufficient to warrant the monophyly of this group. *Xiphidium* is united with *Wachendorfia* and *Barberetta* by a single (rather weak) synapomorphy: occurrence of a simple cyme unit (character #5 R), a reversal from the occurrence of bifurcate cyme units, indicated as synapomorphic for the Haemodoraceae as a whole.

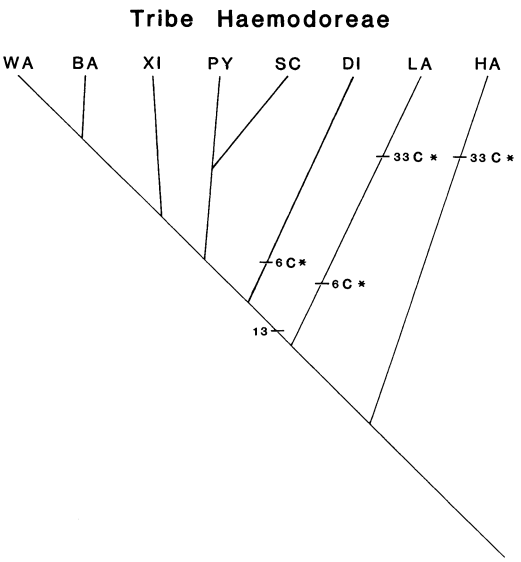


FIGURE 167. Second of two most parsimonious cladograms of the Haemodoraceae (only tribe Haemodoreae shown; tribe Conostylideae identical to that of Fig. 166). Only those character changes that differ from the cladogram of Figure 166 are listed. Character state changes indicated with a "*" (characters 6 and 33) have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only the two convergent events (most likely in the author's view) are displayed in the cladogram. Abbreviations as in Figure 166.

Character convergences and reversals. Certain characters exhibiting reversals or convergences in the cladogram of Figures 166 and 167 are worth discussing. The change in ovary position from superior to inferior (character #39) occurs before the initial bifurcation into two tribes. Thus, the inferior ovary found in DI, LA, HA, and all Conostylideae is interpreted as synapomorphic for the family as a whole (i.e., present in the common ancestor of the family but not in either immediate outgroup). A reversal of ovary position (character #39 R) occurs along the lineage to WA, BA, XI, PY, and SC. This is problematic in that the evolution of an inferior ovary is generally viewed as being irreversible and is often well correlated with other characters in general taxonomic studies. Such an assumption of irreversibility would require an additional three or four evolutionary steps in the most parsimonious cladograms of Figures 166 & 167. (See Alternative Cladograms and Figure 174 for consideration of the unique, irreversible evolution of an inferior ovary and of the independent evolution of an inferior ovary in two independent clades.)

Convergence in exine structural pattern is seen for *Lachnanthes* and *Haemodorum*. Even though both of these taxa have one-layered exine walls, the cladogram of Figure 166 supports the hypothesis that evolution of this exine wall type occurred independently in the lineages leading to the two taxa (character #33 C); as discussed above, the cladogram of Figure 167 permits an equally parsimonious alternative. The occurrence in *Haemodorum* of an occasional inner exine layer (see Simpson, 1983) may lend support to the lack of homology between *Lachnanthes* and *Haemodorum* in this feature and thus the convergent evolution of a one-layered exine.

Convergence in perianth symmetry (character #17 C) is seen in the lineages leading to WA and to PY-SC, arguing that a zygomorphic perianth evolved independently in these lineages. Similarly, the distinctive perianth apertures present in *Wachendorfia* and in *Schiekia* are portrayed as having been derived independently. But in view of the complexity of these perianth apertures, this possibility seems extremely unlikely. Because the monophyletic groupings of WA-BA and PY-SC are well supported by other characters (discussed above), it seems more likely that a reversal of perianth symmetry (zygomorphic to actinomorphic) occurred in the lineages to XI and to BA,

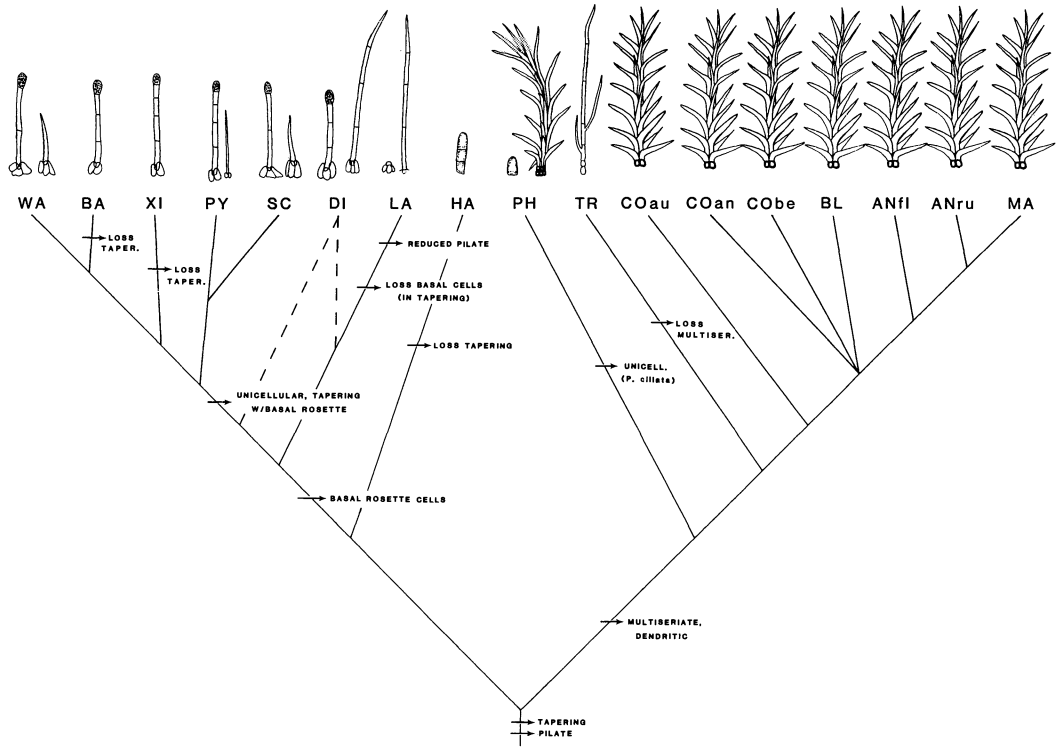


FIGURE 168. Superposition of illustrations of trichome anatomy on cladogram of Figures 166 and 167. Possible evolutionary changes in trichome anatomy are indicated.

and that a loss of perianth apertures occurred in the lineages to XI, BA, and PY. (See Alternative Cladograms, below, for a consideration of this possibility.)

A convergence in stamen number (character #22 C) occurs in the lineage to *Schiekia*. This convergence supports the idea that the staminodia in the outer whorl in *Schiekia* are not direct vestiges of ancestral stamens but rather are de novo floral modifications.

The loss of perianth tannin cells (character #20) occurs independently within each family tribe. The significance of this cell type is not known. Further anatomical studies or a chemical investigation of the precise contents of these tannin cells might be valuable.

Trichome evolution. The hypothesized homologies of trichome types in the Haemodoraceae can be assessed by a comparison of trichome anatomy with the branching patterns of the two most parsimonious cladograms (Fig. 168). First, it is most parsimonious to hypothesize that the common ancestor of the family (at the ingroup node) had pilate trichomes and uniseriate, tapering trichomes (which occur in members of both outgroup families). Second, the cladistic analysis supports the hypothesis of homology between the pilate trichomes of *Haemodorum* and those of the remaining Haemodoreae. The evolution of vestiture in *Haemodorum* involved the loss of ancestral tapering trichomes. Third, the distinctive trichome basal rosette evolved de novo in a separate lineage to that terminating in *Haemodorum*; the basal rosette cells may be correlated with further modification of the pilate trichome to one with a glandular terminal cell. The occurrence in *Lachnanthes* of long, uniseriate, tapering trichomes *lacking* a basal rosette is explained by the *loss* of that basal rosette; further evolutionary modifications in *Lachnanthes* involved the reduction of pilate trichomes to unicellular trichomes (having the basal rosette, however). The unicellular tapering trichomes (in PY, SC, and WA) evolved by reduction from a multicellular tapering trichome, and the presence of *only* pilate trichomes (in XI and BA) evolved by the independent loss of the unicellular type. In the tribe Conostylideae the most parsimonious explanation for the uniseriate, basally branched trichomes in *Tribonanthes* is reduction from the highly branched, dendritic type; the unicellular trichomes of *Phlebocarya ciliata* are portrayed as having arisen de

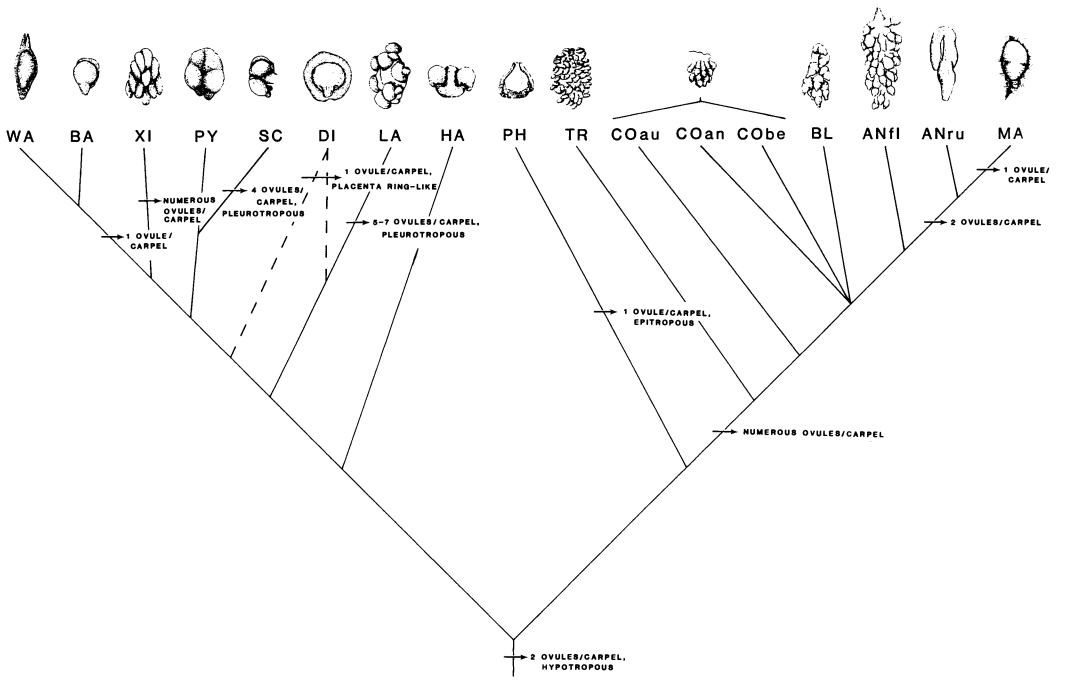


FIGURE 169. Superposition of illustrations of ovule morphology on cladogram of Figures 166 and 167. Possible evolutionary changes in ovule number, shape, and position are indicated.

novo (although it is possible they could be reductions from an ancestral pilate trichome).

Further studies of trichome anatomy in members of the Haemodoraceae may prove useful in confirming or refuting the above hypothesized homologies. Of particular value would be ultrastructural studies (e.g., details of cell wall structure or cytoplasmic contents) or developmental studies (e.g., cell division patterns in trichome ontogeny).

Ovule evolution. The evolution of ovule number and morphology in the Haemodoraceae is somewhat complicated, as seen in Figure 169. The most parsimonious explanation, following the morphocline of Figure 145, is that the ancestral condition for the family is two hypotropous ovules per carpel. An evolutionary step (to numerous ovules per carpel) occurs in the lineages to XI and to the TR-CO-BL-AN-MA clade. A reversal in ovule number from numerous to two per carpel occurs in the lineage to ANru. Reductions to one ovule/carpel occur independently in the clades to WA-BA, DI, PH, and MA. The epitropous ovule position in *Phlebocarya* occurs nowhere else in the family and is portrayed as an autapomorphy for the genus. The pleurotropous ovule position and increase in ovule number in *Lachnanthes* and *Schiekia* are most parsimoniously explained as being derived independently by convergence, which may seem doubtful in view of the distinctiveness of this morphology. The cladogram shows that a hypothesis of common ancestry for this feature in the two genera would necessitate two extra state changes. In fact, the rather thickened placental tissue of *Pyrrorhiza* and the ring of placental tissue in *Dilatris* may both be homologous with the thickened, peltiform placenta of, e.g., *Lachnanthes*. Developmental studies would be extremely informative in assessing the significance of placental morphology and of ovule number, shape, and position.

Seed evolution. As seen in Figure 170, the coded ancestral condition of seed morphology (elliptic, longitudinally ridged seeds) is not supported, as changes from this morphology are indicated in each tribal clade. A discoid, marginally winged seed morphology is portrayed as synapomorphic for the tribe Haemodoreae; presence of seed coat pubescence is synapomorphic for WA, BA, XI, PY, and SC (although this was not coded separately from the marginally winged condition in the analysis). A globose or globose-ovoid seed shape is portrayed as having evolved independently in the lineages to the SC-PY-XI-BA-WA clade and that of the Conostylideae. The flattened, marginally tomentose seeds of *Pyrrorhiza* are portrayed as having arisen de

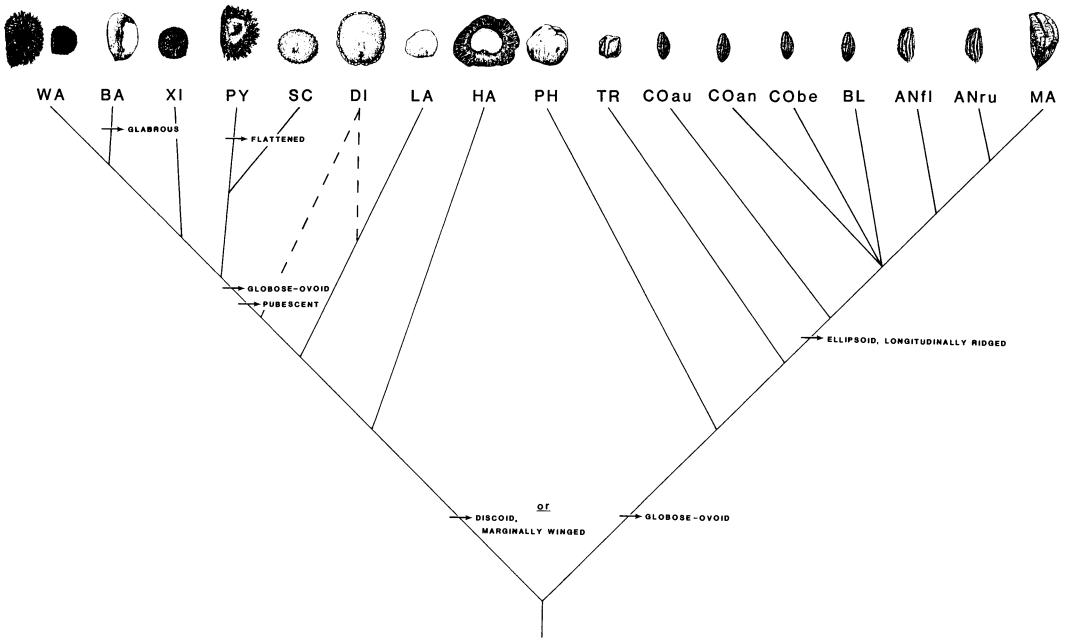


FIGURE 170. Superposition of illustrations of seed morphology on cladogram of Figures 166 and 167. Possible evolutionary changes in seed shape and vestiture are indicated. Note that other equally parsimonious evolutionary events may be possible.

novo, but an equally parsimonious explanation (not illustrated in Fig. 170) is that these flattened seeds are evolutionarily intermediate between the discoid, marginally winged seed and the globose-ovoid, pubescent seed type. In the tribe Conostylideae the ellipsoid, longitudinally ridged seed morphology is synapomorphic for CO, BL, AN, and MA. There is, therefore, no evidence that this seed type is plesiomorphic for either the family or the tribe Conostylideae, even though the seed morphology of both outgroups resemble it (see Character Analysis). It is the globose, glabrous seed type of *Phlebocarya* and *Tribonanthes* that is either synapomorphic for the tribe Conostylideae or possibly ancestral for the whole family. Future studies of seed anatomy and development may prove useful in assessing the homologies of seed evolution in the family.

Chromosome evolution. The cladogram of Figure 171 can be used to assess evolutionary changes in chromosome number in the Haemodoraceae. The two most basal taxa of each tribe have very similar chromosome numbers. Perhaps the most likely possibility is that the chromosome number for the common ancestor of the family was $n = 8$, which agrees with $n = 8$ as one of the more common chromosome counts among the outgroups; however, a base number of $n = 7$ is equally parsimonious. The common chromosome number of $n = 7$ for PH and TR is compatible with their close proximity on the cladogram (although not aiding in resolving their interrelationship) and can be explained possibly as an aneuploidy event from an ancestral $n = 8$ condition. Species of *Conostylis* have a variety of chromosome numbers, $n = 8$ being the most common. Figure 171 shows that the COan clade might be resolved from those of CObe and BL based on a common chromosome number ($n = 5$) with COau. However, the present study is much too incomplete to resolve interrelationships among *Conostylis* species; detailed studies of all species of this genus are needed to assess its karyological history better. A common chromosome number of $n = 6$ in AN and MA supports the very close relationship of these two genera.

Figure 171 portrays an evolutionary step from $n = 8$ to either $n = 15$ or $n = 24$ in the lineage that includes LA, DI, SC, PY, XI, BA, and WA. This event (a synapomorphy for this lineage in the cladistic analysis) could have arisen via tetraploidy or hexaploidy from an $n = 8$ ancestor. However, it is apparent that chromosome number evolution

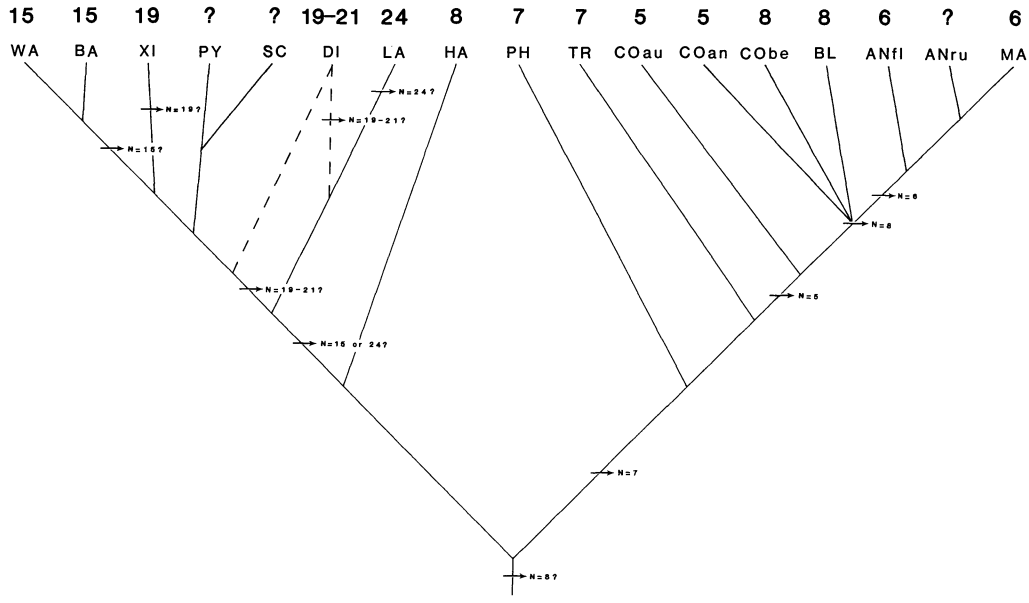


FIGURE 171. Superposition of haploid chromosome number on cladogram of Figures 166 and 167. Possible evolutionary changes in chromosome number are indicated. Note that other equally parsimonious evolutionary events may be possible.

in the tribe Haemodoreae is still virtually unresolved; numerous scenarios of evolutionary change are possible (Fig. 171). Although chromosome number is a valuable taxonomic character, there are problems due to ambiguity of character coding (see Character Analysis) and lack of data. Future karyotypic studies and determination of chromosome numbers for *Pyrrorhiza* and *Schiekia* should aid greatly in testing the hypotheses of Figure 171 and in refining phylogenetic relationships, particularly in the tribe Haemodoreae.

Biogeography. The cladograms of Figures 166 & 167 can be used to assess the biogeographic history of the Haemodoraceae. It should be stressed that biogeographic data, being extrinsic data, were not included in the original data set. As seen in Figure 172, all members of the tribe Conostylideae are restricted to southwestern Australia. *Haemodorum*, the most basal genus of the tribe Haemodoreae, is the only other Australasian member of the family, being distributed in western, northern, and eastern Australia, Tasmania, and parts of New Guinea. This distributional pattern can be explained most simply by a single vicariance event: the splitting of a continuous ancestral population via the separation of (or establishment of an effective reproductive barrier between) Australia–Antarctica from the remainder of Gondwanaland. That portion remaining on Australia–Antarctica eventually gave rise to *Haemodorum*; the ancestral stock remaining on South America–Africa eventually diverged to give rise to the seven other genera of the tribe (Fig. 172). The present distributions of *Pyrrorhiza*, *Schiekia*, *Xiphidium*, *Wachendorfia*, and *Barberetta* could be explained by a single vicariance event: the continental separation of South America and Africa at the point of divergence of the lineages to XI and to WA-BA. As is evident from Figure 172, the phylogenetic relationship of *Dilatris* is problematic with respect to vicariance biogeography. If *Dilatris* is accepted as the sister taxon of *Lachnanthes* (as in Fig. 166), then it could be hypothesized that the splitting of the lineages to *Dilatris* and *Lachnanthes* was via vicariance: the separation of an ancestral population (with subsequent divergence) by the splitting of South America from Africa. *Lachnanthes* could then have attained its present distribution via dispersal or vicariance from South America to North America. This possibility would necessitate an independent (but contemporaneous) vicariance event at the point of divergence of the lineages to XI and to WA-BA. If *Dilatris* is accepted as being the sister taxon to WA, BA, XI, PY, and SC (as in Fig. 167), then its present distribution is most simply explained as long-distance dispersal (Fig. 172). The fact that *Dilatris* and *Wachendorfia* are sympatric over much of their range may be evidence that they attained a common range by

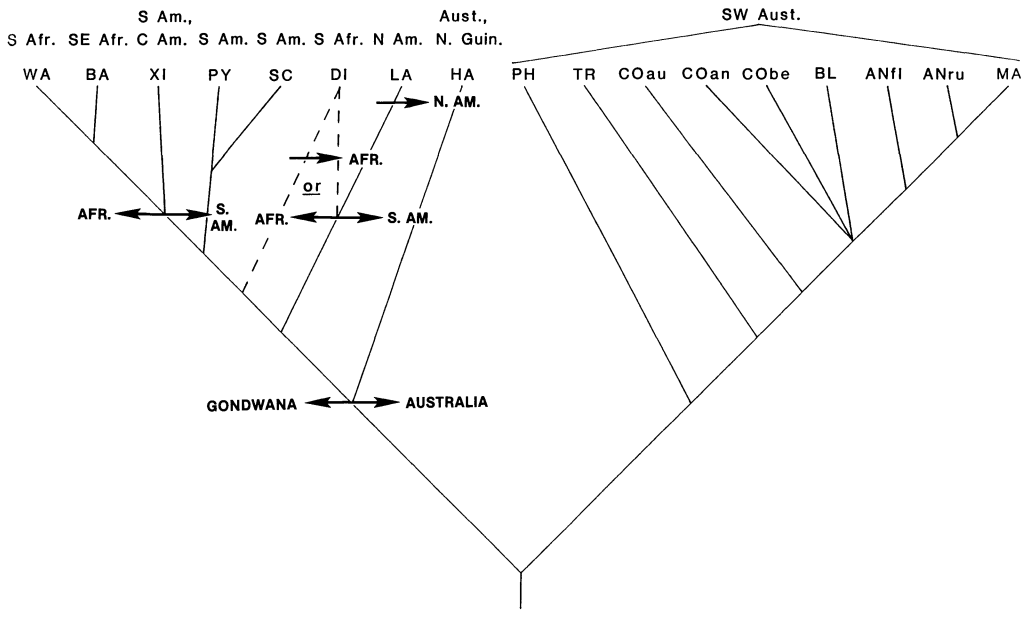


FIGURE 172. Superposition of geographic ranges on cladogram of Figures 166 and 167. Arrows represent major biogeographic changes, including possible vicariance events (double arrows) and dispersals (single arrows).

separate biogeographic processes (Croizat et al., 1974).

Alternative cladograms. In view of the incompatibility of certain character changes in the cladograms of Figures 166 & 167, a few alternative cladistic relationships are worth consideration. One major possibility is that an inferior ovary evolved uniquely and irreversibly in the Haemodoraceae; the resultant cladogram is seen in Figure 173. This topology requires 92 total character state changes (C.I. = 0.598), a length of four state changes greater than the most parsimonious solution of Figures 166 & 167. Note that in Figure 173 the traditionally defined tribe Haemodoreae is now paraphyletic, with *Dilatris*, *Haemodorum*, and *Lachnanthes* more closely related to the six genera of the Conostylideae (the sole synapomorphy being an inferior ovary, character #39) than to other traditionally classified Haemodoreae. This alternative cladogram contains additional problems of conflicting character state changes. These include introduced homoplasy in presence/absence of pilate trichomes with basal rosette cells (character #8), placental sclereids (character #43), seed vestiture (character #50), and chromosome number (character #51). It seems particularly unlikely, for example, that there would have been a secondary decrease in chromosome number (to $n = 8$ in the lineage to *Haemodorum*) as well as the loss (for the Haemodoraceae as a whole) and reacquisition (in the lineage to the Conostylideae) of placental sclereid cells. However, in view of the generally accepted irreversibility of ovary position, the cladogram of Figure 173 is a possible alternative to the more parsimonious cladograms of Figures 166 & 167. Detailed investigation of ovary development and floral vasculature might prove extremely valuable in assessing the uniqueness and irreversibility of the evolution of ovary position in the Haemodoraceae.

Another alternative portrays the independent evolution of an inferior ovary in the Conostylideae and in one clade of the Haemodoreae (Fig. 174A; length = 90; C.I. = 0.611). Such a topology would link DI, LA, and HA as members of a monophyletic group (as in Fig. 173) within the tribe Haemodoreae; synapomorphies for these three genera are: exine one-layered (character #33, necessitating a reversal in lineage to DI, although two convergent events is equally parsimonious), inferior ovary (character #39, convergent in lineage to all members of tribe Conostylideae, although a unique event plus a reversal is equally parsimonious), and discoid seed shape (character #48). Of these, the convergent evolution of an inferior ovary and discoid seeds seem most likely to be synapomorphies for the three genera. The cladogram of Figure 174A is, of course, less parsimonious (two steps greater) than that of Figure 166 or 167 and necessitates

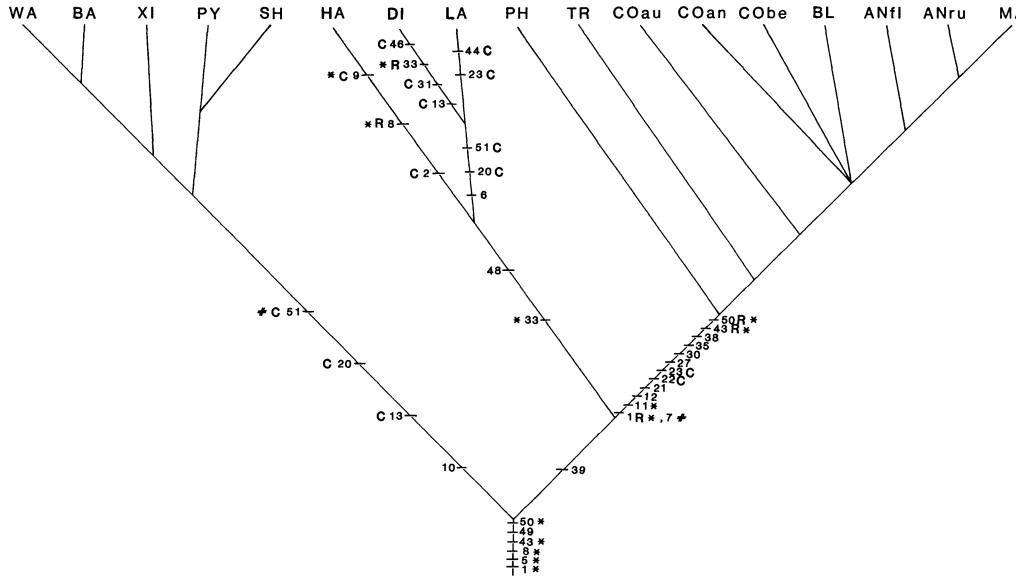


FIGURE 173. Alternative cladogram (to Figs. 166, 167): most parsimonious cladogram in which an inferior ovary position evolves uniquely and irreversibly. Only those characters below the divergence of PY-SC and of PH are listed; all other state changes are identical to Figures 166 and 167. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.

additional homoplasy for some characters, including: trichome anatomy (characters #8 R and #13 C), perianth tannin cells (character #20 C, an additional convergence portrayed), and chromosome number (character #51C).

A third alternative cladogram is presented in Fig. 174B. This possibility differs from the most parsimonious topology of Figures 166 & 167 in placing the lineage to XI basal to that of PY-SC (i.e., in portraying WA-BA and PY-SC as sister groups). Figure 174B requires only a single extra step (length = 89; C.I. = 0.618) compared with the cladograms of Figures 166 & 167. In fact, the phylogenetic relationship of *Xiphidium* as portrayed by Figures 166 & 167 could be viewed as questionable. This most parsimonious explanation, that *Xiphidium* is most closely related to the WA-BA subgroup, is supported by only one synapomorphy: presence of simple cyme units (character #5). The rationale for perhaps preferring the cladogram of Figure 174B is that it is more parsimonious than the cladogram of Figures 166 & 167 *if* it is assumed that zygomorphic perianth symmetry (character #17) and perianth apertures (character #13) are homologous when present (i.e., that they arose by common evolutionary origin, not by convergence). If, for example, the common possession of a zygomorphic perianth is synapomorphic for WA, PY, and SC (as seen in Fig. 174B), then one fewer reversal for this character occurs in the cladogram of Figure 174B (vs. those of Figures 166 & 167). In addition, if perianth apertures arose in WA and SC by a single evolutionary event (at "+" sign in Fig. 174B), then one fewer reversal (i.e., loss of perianth apertures) is required in Figure 174B than is required in Figures 166, 167. It is the author's view that each of these are very likely possibilities, particularly with regard to the distinctive perianth apertures of *Wachendorfia* and *Schiekia*. Thus, the cladogram of Figure 174B is to be preferred over that of Figures 166 & 167 (at least with respect to these five genera of the Haemodoreae) even though it is overall less parsimonious by one step. This reasoning is, in effect, a type of a posteriori weighting of characters. It is similar to utilizing "Dollo" character parsimony, which allows no convergences and minimizes any subsequent character state reversals.

A fourth possible alternative cladogram (length = 90; C.I. = 0.611) is that of Figure 175A, which portrays DI as the sister group of WA-BA, the three taxa united by two synapomorphies: a pollen apertural border (character #31) and a single ovule/carpel (character #46 C). However, this topology is difficult to explain in view of a host of

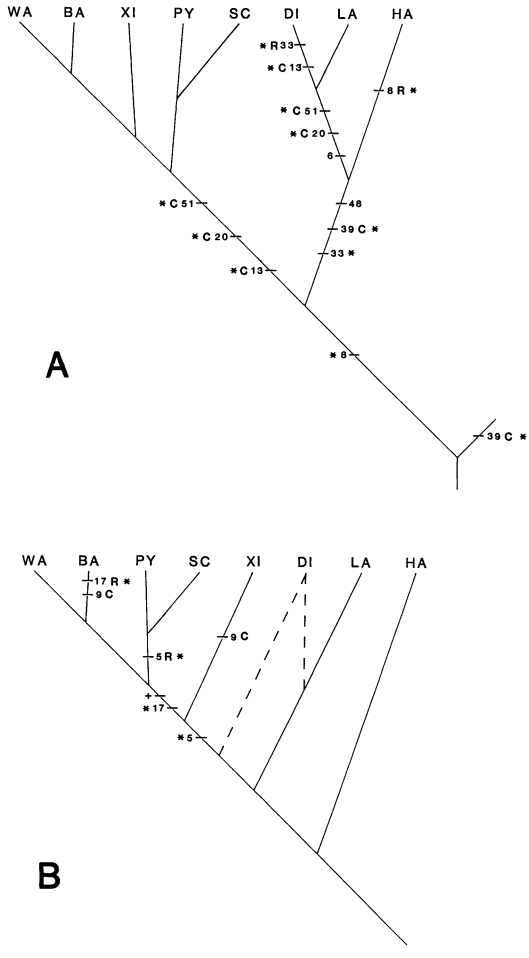


FIGURE 174. Alternative cladograms (to Figs. 166, 167). Only those characters that differ in distribution from Figure 166 are listed. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.—A. Alternative cladogram (only tribe Haemodoreae shown) portraying *Dilatris*, *Lachnanthes*, and *Haemodorum* as members of a monophyletic assemblage.—B. Alternative cladogram (only tribe Haemodoreae shown) portraying *Wachendofia–Barberetta* and *Pyrrorhiza–Schiekia* as sister groups.

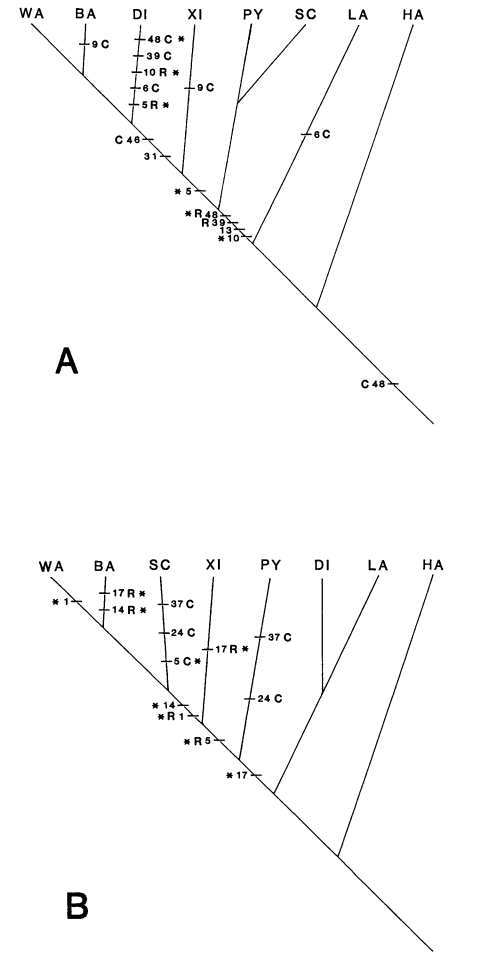


FIGURE 175. Alternative cladograms (to Figs. 166, 167). Only those characters that differ in distribution from Figure 166 are listed. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.—A. Alternative cladogram (only tribe Haemodoreae shown) portraying *Dilatris* as the sister group to *Wachendorfia–Barberetta*.—B. Most parsimonious cladogram (only tribe Haemodoreae shown) portraying *Schiekia* as the sister group of *Wachendorfia–Barberetta*.

other characters and necessitates additional homoplasy in, e.g., inflorescence type (characters #5, #6), trichome anatomy (character #10), ovary position (character #39), and seed shape (character #48 C). Homoplasy in ovary position, trichome anatomy, and seed morphology is particularly difficult to reconcile in view of similarities of *Dilatris* with LA and HA. Thus, the cladogram of Fig. 175A cannot, in the author's opinion, be readily supported over that of Figures 166 and 167.

A final alternative cladogram (length = 92; C.I. = 0.598) is portrayed in Figure 175B. This alternative differs from that of Figures 166 & 167 in removing *Schiekia* as the sister group of *Pyrrorhiza* and placing it as the sister group of WA-BA. Figure 175B has the advantage of treating the distinctive perianth apertures of *Wachendorfia* and *Schiekia* as nonparallel features, necessitating a loss only in the clade to *Barberetta*. However, the evidence for uniting *Schiekia* and *Pyrrorhiza*,

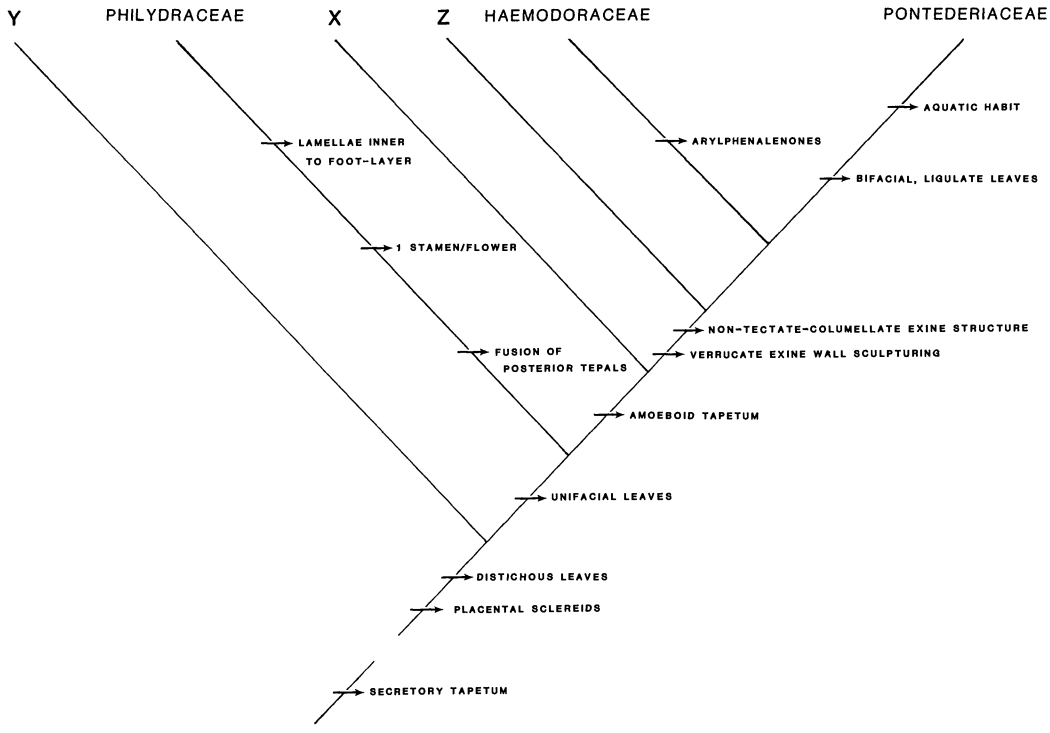


FIGURE 176. Cladogram portraying hypothesized relationships among the Haemodoraceae, Pontederiaceae, and Philydraceae. Major evolutionary events are portrayed. Note possible clades to "X," "Y," and "Z." (See text for discussion.)

based on exine ultrastructure (character #37) and on stamen/staminode morphology (character #24) seems, to the author, more convincing. The cladogram of Figure 174B is accepted as more likely than that of Figure 175B.

Of the above alternative, but less parsimonious, cladograms, that of Figure 175A is most compatible with a vicariance explanation of present distributional ranges. This cladogram would require only two separate vicariance events correlated with the splitting of Gondwanaland into Australia, Africa, and South America. The distribution of *Lachnanthes* could, as above, be explained via dispersal or a vicariance event between South and North America. However, as discussed, acceptance of this cladogram would necessitate several unlikely homoplasious events. Thus, it must be concluded that, despite the better biogeographic "fit" of the alternative cladogram of Figure 175A, the data support those of Figures 166 & 167 (or, perhaps, of Figure 174B) better.

Interfamilial relationships. Although a strict cladistic analysis of the Haemodoraceae and all possible outgroup families in the complex is beyond the scope of this paper, a major premise of the present analysis is that the families most closely related to the Haemodoraceae are the Philydraceae and Pontederiaceae (see Outgroup Taxa). The cladogram of Figure 176 illustrates major hypothesized evolutionary changes among lineages leading to the Philydraceae, Pontederiaceae, and Haemodoraceae, including those treated as characters (#53–55) in the cladistic analysis of the Haemodoraceae. One or more autapomorphies are shown for each terminal clade, evidence that the three families are monophyletic. The cladogram was rooted at the Philydraceae under the assumption that the unique exine structure of the Haemodoraceae and Pontederiaceae (found in no other considered outgroup family) constitutes a very reliable synapomorphy and unites the latter two families as sister taxa. In addition to the evolution of unifacial leaves (character #55 in the cladistic analysis), a possible synapomorphy linking the three families is the presence of placental sclereids and perianth tannin cells. An amoeboid tapetum (character #53) and a non-tectate-columellate, verrucate exinous pollen wall (character #54) constitute synapomorphies for the Haemodoraceae and Pontederiaceae. It is hypothesized that evolution of the Pontederiaceae involved a major adaptive shift and

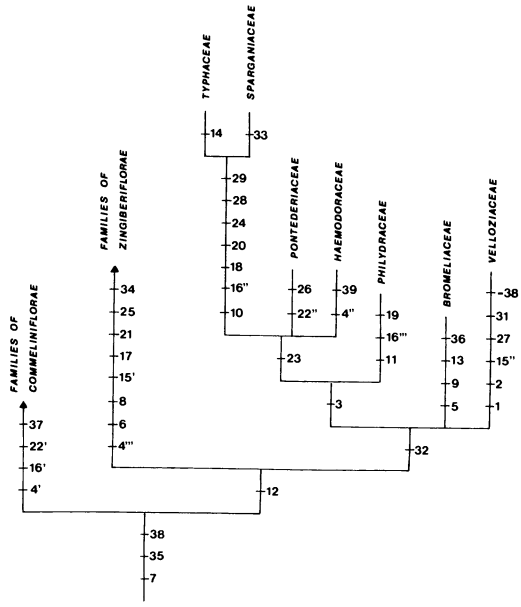


FIGURE 177. Cladogram of the Bromeliiflorae, reprinted from Dahlgren & Rasmussen (1983).

radiation to an aquatic environment with subsequent changes in anatomy, such as the development of spongy aerenchyma in some taxa. This shift to a free-floating or emergent growth form may be correlated with an evolutionary change from unifacial to bifacial leaf morphology. This hypothesis is supported by the fact that the Pontederiaceae typically have inverted vascular bundles analogous to a "radial" (unifacial) origin (Arber, 1925, and references therein).

The grouping of the Philydraceae, Pontederiaceae, and Haemodoraceae as a monophyletic group (Fig. 176) agrees well with the delimitation of the Pontederiinae, sensu Walker (1986). Figure 176 shows many similarities as well with the eclectic cladistic portrayal of the Bromeliiflorae, sensu Dahlgren & Rasmussen (1983; see Fig. 177). Dahlgren & Rasmussen portrayed the Typhales (Sparganiaceae and Typhaceae) in a tritomy with the Haemodoraceae and Pontederiaceae; the Philydraceae are basal to this clade (Fig. 177). I propose the existence of synapomorphies, derived primarily from palynological data, linking the Haemodoraceae and Pontederiaceae as sister taxa. Dahlgren & Rasmussen linked the Typhales to the Pontederiaceae and Haemodoraceae via a single synapomorphy: presence of an amoeboid tapetum. Because investigated members of *Typha* and *Sparganium* have a typical tectate-columellate architecture, it is possible that the lineage to the Typhales could be placed in Figure 176 at "X," i.e., before the evolution of the palynological specializations. In addition, at least one species of the Typhales, *Sparganium eurycarpum*, possesses placental sclereids similar to those found in the Haemodoraceae, Philydraceae, and Pontederiaceae. However, in view of the lack of additional supporting evidence, the linkage of the Typhales to the Haemodoraceae–Pontederiaceae seems quite speculative. Based on these few characters, it is equally parsimonious to hypothesize the cladistic position of the Typhales at "Y" in Figure 176 (assuming the Typhales to belong within the Bromeliiflorae to begin with). This possibility requires the independent origin of an amoeboid tapetum but no reversal to a bifacial leaf. It is apparent that the numerous specializations possessed by the Typhales have obscured their affinities. The relationship of the Typhales to other monocotyledons continues to be an intriguing systematic problem (see Dahlgren & Clifford, 1982).

In contrast to Dahlgren & Rasmussen (1983), Walker (1986) placed the Zingiberiflorae (Zingiberales) as the sister taxon of his Pontederiiflorae (= Pontederiidae; including the Haemodoraceae, Philydraceae, and Pontederiaceae), equivalent to position "Y" in Figure 176. This would fit the distribution of characters in Figure 176 fairly well, as the Zingiberales have mostly distichous leaves (possibly an ancestral character) and at least one species, *Strelitzia reginae*, has placental sclereids similar to those in the Haemodoraceae, Philydraceae, and Pontederiaceae (Simpson, unpublished). However, the Zingiberales possess an amoeboid (not secretory) tapetum, requiring either an independent evolutionary event in the Zingiberales or the separate evolution of a secretory tapetum in the lineage to the Philydraceae. One other possibility is worthy of consideration: that the Zingiberales are the sister group of the Haemodoraceae–Pontederiaceae (position "Z" in Fig. 176). This cladistic hypothesis would necessitate the independent evolution of a bifacial leaf morphology. However, it is intriguing that all members of the Zingiberales have a thin, modified exine wall, often consisting of scattered deposits atop a thick, cellulosic/pectic intine (Kress et al., 1978). In addition, ultrastructural developmental studies by the author (Simpson, 1989) indicate that early exine deposition in *Xiphidium* (Haemodoraceae) is strikingly similar to that occurring in *Heliconia* of the Zingiberales (see Stone et al., 1979). In both taxa sporopollenin is deposited on one to several extruded "white lines," defining an inner and outer exine layer. Thus, the two-layered nature of the exine in most Haemodoraceae may be structurally

homologous with that found in at least one member of the Zingiberiflorae. This developmental evidence would argue for the placement of the Zingiberales at "Z" in Figure 176. Further studies of pollen wall development, especially in other families of the Bromeliiflorae, sensu Dahlgren & Rasmussen (1983) may prove extremely useful in confirming the distinctiveness of this developmental pattern in these taxa.

Conclusions

It is hoped that the detailed description of the characteristics of the Haemodoraceae and of the rationale for character coding will serve as a basis for future criticism and refinement of the phylogenetic relationships presented. The occurrence of incompatibilities between several characters makes difficult any reasonable certainty of phylogenetic relationships among some genera. The interrelationships among the tribe Haemodoreae pose a particular problem. Aside from certain groupings (such as the sister-group relationships of *Pyrrorhiza* and *Schiekia* and of *Wachendorfia* and *Barberetta*), several other possibilities having a minimum of additional evolutionary steps are evident. Recent analyses using alternative coding schemes (emphasizing unordered coding) and new data obtained since this paper went to press have yielded three additional most parsimonious trees for the tribe Haemodoreae; each of these topologies includes *Dilatris*, *Haemodorum*, and *Lachnanthes* as a monophyletic clade most closely related to *Pyrrorhiza–Schiekia*. These possibilities will be considered in light of future research (see below). The major phylogenetic relationships of the Conostylideae appear at this time to be rather firm, with the possible exception of the interrelationships of *Phlebocarya* and *Tribonanthes*. As was emphasized, critical analysis of many more species of *Conostylis* and *Anigozanthos* is needed before their interrelationships can be understood. The included studies suggest, however, that *Conostylis* and *Anigozanthos*, as usually circumscribed, are very likely not monophyletic groups. Merging of *Blancoa* with *Conostylis* and *Macropidia* with *Anigozanthos* may be warranted in a strict phylogenetic classification.

Consideration of the Haemodoraceae and immediate allies are pivotal in analyzing the validity of the Bromeliiflorae sensu Dahlgren & Rasmussen. In fact, a major discordance in the classification of monocots proposed by Walker (1986) versus that of Dahlgren and coworkers centers on the recognition of the Bromeliiflorae and their relationships to the Zingiberales and Commelinidae. Future investigations of the interfamilial relationships of the Haemodoraceae should prove quite intriguing in this regard.

The present study underscores the need for additional research, particularly in karyology, ultrastructure, and development. My current project on morphometric analysis of ovule and seed development in the complex might prove particularly intriguing in tracing discrete evolutionary events. A better understanding of biogeographic history and ecology could provide insight into the possible adaptive significance of these events. Finally, the relatively new techniques of DNA restriction site analysis and sequencing could provide very important data in validating or refuting proposed relationships. This study serves well to exemplify that the problems and uncertainties typically evident in phylogenetic analyses may lead to future research that will further clarify relationships and present new insights into plant evolution.

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