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Pollen ultrastructure of the Pontederiaceae

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Evidence for exine homology with the Haemodoraceae

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Pollen of eight genera and species of the Pontederiaceae was investigated using SEM and TEM in order to elucidate interrelationships to other monocot families. All examined Pontederiaceae are diaperturate with furrow-shaped apertures and have a distinctly verrucate non-apertural exine sculpturing (except *Pontederia*, which is psilate to scabrate in sculpturing). Among investigated taxa the exine wall architecture exhibits a gradation between: (1) a l-layered exine composed of laterally appressed, basally fused baculate elements, (2) a 2-layered exine, the outer layer composed of laterally appressed baculate elements and the inner forming a thin layer or composed of discrete papillate elements, and (3) a tectate-columellate exine, differing, however, from a typical tectate-columellate architecture by having short, narrow columellae and generally baculate tectal elements. Of the palynologically investigated families presumed closely related to the Pontederiaceae, only members of the tribe Haemodoreae of the Haemodoraceae have a verrucate sculpturing similar to that of most Pontederiaceae. In addition, the exine architecture of the non-tectate-columellate genera of the Pontederiaceae is strikingly similar (and presumably homologous) to members of the family Haemodoraceae. It is proposed that the similarities in pollen exine sculpturing and architecture between the Pontederiaceae and Haemodoraceae are so by homology (common evolutionary origin) and constitute evidence for the close relationship and possible sister-group status of these families.

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The Pontederiaceae (Pickerel Weed family) are a small family of monocotyledons, consisting of 7–9 genera and approximately 30 species. Diagnostic morphological features of the family are an aquatic habitat; rhizomatous stems; alternate, distichous, petiolate (and often ligulate) leaves; actinomorphic to zygomorphic flowers with trimerous, sympetalous, hypogynous flowers; and a capsular fruit with l-numerous endospermous seeds per locule.

Concepts as to the affinities of the Pontederiaceae have (like most taxonomic groups) varied. Hutchinson (1934, 1959, 1973) placed the Pontederiaceae in his order Liliales (which also included the Liliaceae, Tecophilaeaceae, Trilliaceae, Smilacaceae, and Ruscaceae), based primarily on the general possession in the order of an actinomorphic and membranous perianth, 6 stamens, and a superi-

or ovary. A similar classification of the Pontederiaceae within the Liliales was proposed by Schwartz (1930), Hamann (1964), Cronquist (1981), and Takhtajan (1980), with Hamann (1966) concluding that the familiy is most closely related to the family Philydaceae. Dahlgren & Clifford (1982) treated the Pontederiaceae as the monofamilial order Pontederiales of their Liliiflorae, "with closest relatives among the Philydrales and Haemodorales". Dahlgren & Rasmussen (1983), in a phylogenetic analysis of the monocotyledons, argued that the Pontederiaceae, Haemodoraceae, and Philydraceae should be transferred from the Liliiflorae to the Commeliniflorae, based on the occurrence in these taxa of hypothesized apomorphic features, including UV-fluorescent cell wall-bound compounds (Harris & Hartley 1980) and seeds with a starchy

endosperm. The authors suggested that the Ponte-
deriaceae, Haemodoraceae, and Typhaceae/Spar-
ganiaceae together comprise a monophyletic group,
the whole assemblage being the sister-group of the
Philydraceae.

Palynological studies of the Pontederiaceae pub-
lished to date are scanty. Rao & Rao (1961) de-
scribed the pollen of *Monochoria vaginalis* and
Eichhornia crassipes as "slightly semilumar and ...
two sulculate or one sulculate, reticulate." Erdtman
(1966), in a review of the then current literature and
original observations of one species, *Pontederia
cordata* L., described the pollen of the family as
"2(-3)-sulculate, longest axis (38-)51-71 μm. Sexine
as thick as nexine or thicker, sometimes +/- areo-
loidate. S-pattern: LO."

The purpose of the following study is to charac-
terize, using SEM and TEM, the basic pollen mor-
phology and wall ultrastructure of members of the
Pontederiaceae and to note similarities and differ-
ences with other monocot families in assessing phy-
logenetic relationships. Of particular interest are
possible indications of a close relationship of the
Pontederiaceae to the Philydraceae, as proposed by
Hamann (1966), or to the Haemodoraceae, as pro-
posed by Dahlgren & Rasmussen (1983).

MATERIALS AND METHODS

Pollen samples were largely obtained from herbarium
sheets. Anthers from dried herbarium specimens
("DRIED") were re-expanded in 10% Aerosol OT for
one week, followed by several H_2O rinses. Flowers from
field collections were fixed in either formalin/acetic acid/
alcohol ("FAA") or in a solution of 4% glutaraldehyde
and 4% formalin in 0.1 M Sörensen's phosphate buffer
("GLUT"). The following 8 taxa were examined: *Eich-
hornia crassipes* (Mart.) Solms "DRIED" — D. B. Zobel
20020 (DUKE); *Heteranthera reniformis* R. & P.
"GLUT" — M. G. Simpson 4VIII82A (SDSU); *Hydro-
thrix gardneri* Hooker f. "DRIED" — O. Fontenele (US);
Monochoria vaginalis (Burm. f.)Presl. ex Kunth "DRIED"
— C. J. Saldanha 16106 (US); *Pontederia cordata* L.
"FAA" — M. G. Simpson 20VII82A (SDSU); *Reussia
rotundifolia* (L. f.) Castell "DRIED" — G. T. Prance 23284
& J. F. Ramos (US); *Scholleropsis lutea* H. Perr.
"DRIED" — P. Morat 2958 bis (TAN); *Zosterella dubia*
(Jacq.) Small "DRIED" — H. F. Loomis 5537 (US).

For SEM studies, whole dehisced anthers containing
mature pollen were placed in a modified capsule between
two 2 μm Millipore filters, which were then dehydrated to
100% ethanol, followed by infiltration in a graduated se-
ries to 100% Freon 113 (the intermediate fluid). The mate-
rial was critical-point dried in a BOMAR SPC 900/EX
drier with CO_2 (transition fluid). Pollen grains were
tapped onto a stub covered with double-stick Scotch tape,

sputter coated (ca. 200 A thickness) with gold/palladium
(60/40), and viewed with a JEOL JSM-S1 SEM.

For TEM analysis, whole anthers were fixed in 4%
glutaraldehyde for 2 hours, rinsed several times in 0.1 M
Sörensen's phosphate buffer, and post-fixed in 2% OsO_4
for 1 hour. After two rapid dH_2O rinses and dehydration
to 100% ethanol, the material was infiltrated in a series of
increasing concentrations of Spurr's resin (Spurr 1969),
placed in a BEEM capsule, and polymerized 8–12 hours at
70°C. Sections ca. 85 nm thick were prepared using a
diamond knife on a Cambridge-Huxley or Reichert ultra-
microtome, and mounted on uncoated 200 mesh grids.
Preparations were post-stained with filtered 4% uranyl
acetate in 50% ethanol (15 minutes) and 2% lead citrate (7
min) and viewed with a Siemens Elmiskop 101 or a Zeiss
EM9S-2 TEM.

Light microscope studies (not illustrated) were made to
determine pollen size and to confirm aperture number.
Pollen samples were acetolyzed in standard 9:1 acetic
anhydride: sulfuric acid solution at 55°C for 8–12 hours.
After rinsing in H_2O and 50% glycerin, the samples were
mounted in glycerin jelly. Mean maximum dimension of
pollen grains (determined from measurements of 50
grains) is indicated in parentheses below.

RESULTS

Eichhornia crassipes (Mart.) Solms. — Pollen
grains (47 μm) diaperturate, apertures furrow-
shaped (Fig. 1 A, C). Sculpturing of non-apertural
region verrucate, that of apertural region psilate
(Fig. 1 B). Non-apertural exine composed of short
baculate elements which are laterally appressed
and basally fused (Fig. 1 D). Exine of apertural
region absent (Fig. 1 C, E). Intine not clearly ob-
served in material examined.

Heteranthera reniformis R. & P. — Pollen grains
(45 μm) diaperturate, apertures furrow-shaped (Fig.
2 A, H). Sculpturing of non-apertural region verru-
cate, that of apertural region psilate with numerous
scattered, minutely verrucate elements (Fig. 2 A,
B). Non-apertural exine usually composed of an
irregular foot-layer and short columellae, each
bearing a short baculate tectal element (Fig. 2 C); in
some areas of the non-apertural region, however,
the exine lacks columellae, being composed of ba-
sally to laterally fused baculate elements with a 2-
layered structure as evidenced by a proximal
"commissural line" in electron micrographs (Fig.
2 D, G). Exine of apertural region composed of
scattered gibbous to short-baculate elements (Fig.
2 E). Intine 2-layered (Fig. 2 E, F), the exintine
thickened in the apertural region and having radial-
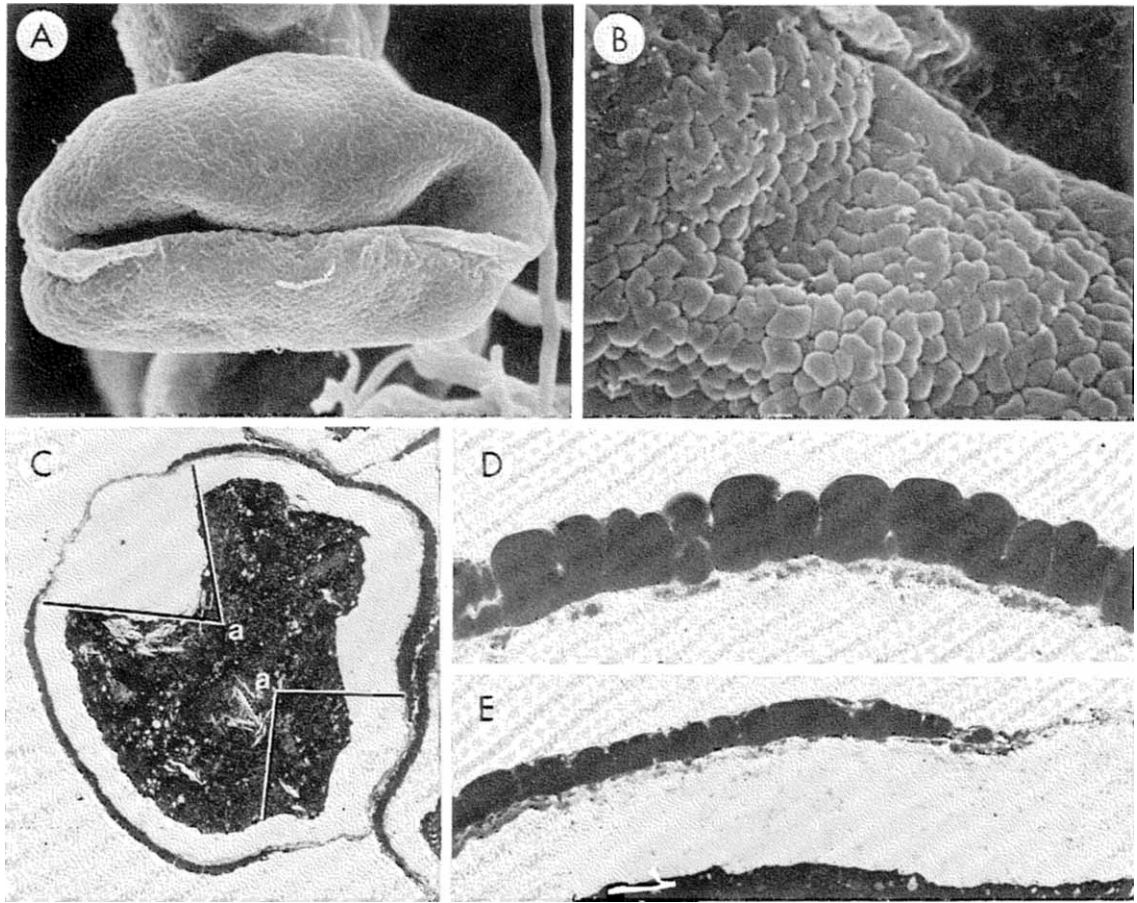ly-oriented channel-like structures (Fig. 2 E).

Fig. 1. Eichhornia crassipes (Mart.) Solms. (A) Whole grain, one of two apertures facing. SEM ×1500. (B) Close-up, exine surface, showing verrucate, non-apertural sculpturing. SEM ×5600. (C) Cross-section of whole grain, showing two apertures (*a*). TEM ×1700. (D) Non- apertural exine wall; note closely appressed, baculate structural elements. TEM ×15000. (E) Interface between non-apertural (left) and apertural (right) region; note absence of exine in apertural region. TEM ×9100.

Hydrothrix gardneri Hooker f. — Pollen grains (22 µm) diaperturate, apertures furrow-shaped (Fig. 3 A, E). Non-apertural exine with a verrucate wall sculpturing (Fig. 3 B), composed of basally-fused, laterally-appressed baculate and clavate elements, with rounded distal ends (Fig. 3 C, D). Exine of apertural region reduced to absent (Fig. 3 E). Intine not clearly observed in material examined.

Monochoria vaginalis (Burm. f.) Presl. ex Kunth. — Pollen grains (34 µm) diaperturate, apertures furrow-shaped (Fig. 4 A, C). Non-apertural exine sculpturing verrucate (Fig. 4 B). Exine of non-apertural region with an irregular foot-layer, a short-columellate interstitium, and a tectum comprised of distinct baculate to oval-shaped elements with rounded to truncate distal ends (Fig. 4 D). Wall of apertural region composed of minute exinous elements atop a thick, 2-layered intine (Fig. 4 E). Exintine of apertural region thickened, with numerous vesicular elements present (Fig. 4 E).

Reussia rotundifolia (L. f.) Castell. — Pollen grains (33 µm) diaperturate, apertures furrow-shaped (Fig. 4 F, H). Non-apertural exine minutely verrucate (Fig. 4 G), composed of laterally-appressed and basally-fused baculate to clavate elements with rounded to truncate distal ends (Fig. 4 I, J, K). Non-apertural exine 2-layered, the inner layer very
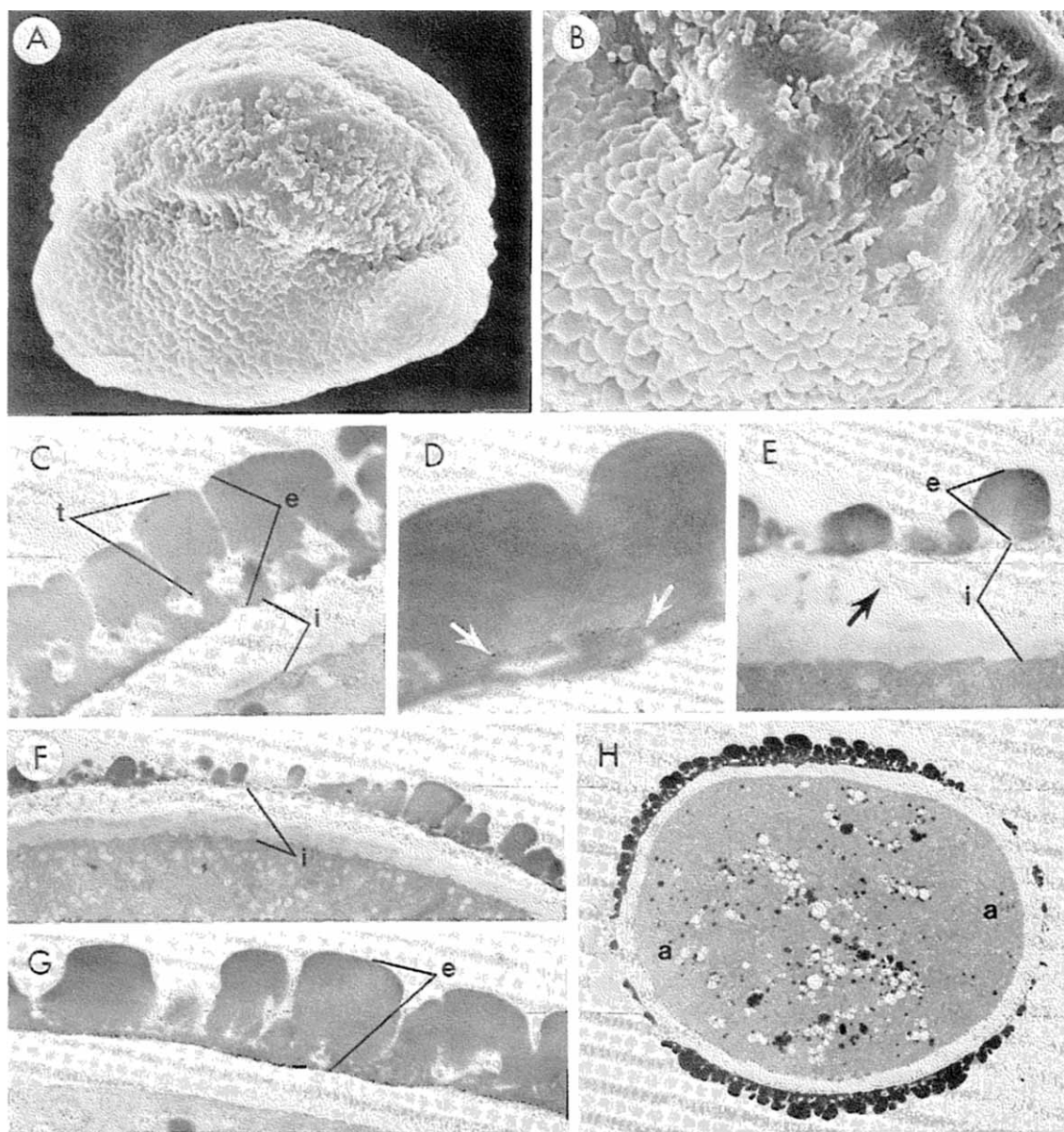
Fig. 2. Heteranthera reniformis R. & P. (A) Whole grain; note one of two apertures, SEM ×1400. (B) Close-up, showing verrucate, non-apertural region (lower left) and apertural region (upper right), the latter with scattered exine elements. SEM ×2700. (C) Non-apertural region. Note intine (*i*) and exine (*e*), the latter with distinct baculate elements composing the tectum (*t*). TEM ×11000. (D) Non-apertural, 2-layered exine. Note commissural line (*arrows*) defining separation between irregular basal layer and outer baculate elements. TEM ×15000. (E) Apertural region. Note exine elements (*e*), 2-layered intine (*i*), and channel-like vesicles (*arrow*) in outer intine layer. TEM ×17000. (F) Interface between apertural (left) and non-apertural (right) regions. Note thick, 2-layered intine (*i*). TEM ×6100. (G) Non-apertural wall. Note absence of columellae in 2-layered exine (*e*). TEM ×8500. (H) Whole grain cross-section, showing two apertures (*a*). TEM ×2000.
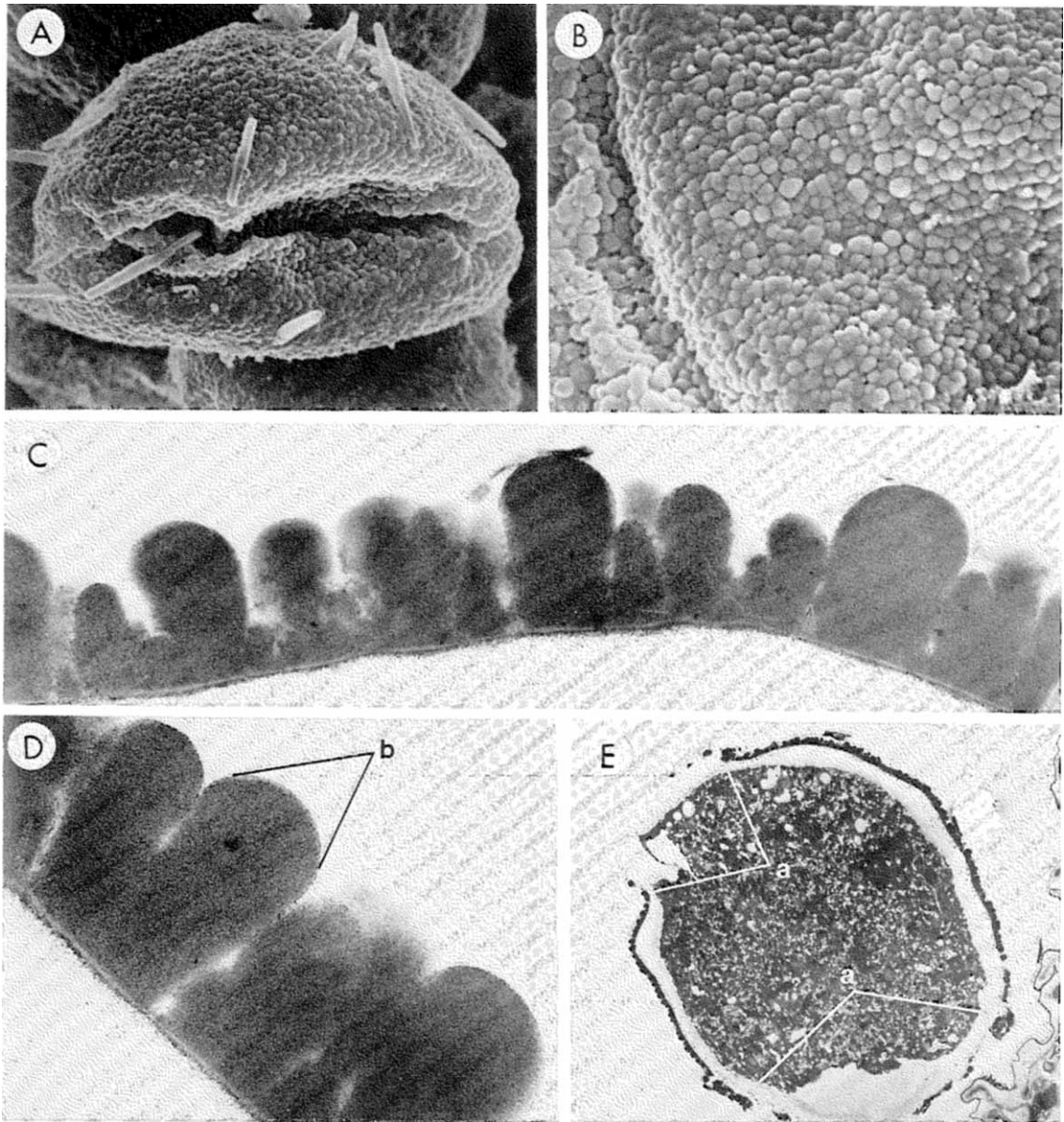
Fig. 3. Hydrothrix gardneri Hooker f. (A) Whole pollen grain, with one of two (invaginated) apertures facing. Note raphide crystals. SEM × 3 200. (B) Close-up, showing verrucate exine. SEM ×6 400. (C) Cross-section of exine wall. Note laterally appressed baculate and clavate elements which are fused basally. TEM ×43 000. (D) Exine wall cross-section. Note baculate to clavate elements (*b*) TEM ×61 000. (E) Whole grain cross-section, showing two apertures (*a*), devoid of exine. TEM ×3 100.

thin and somewhat discontinuous (Fig. 4 K). Intine not observed in material examined.

Pontederia cordata L. — Pollen grains (31 μm) diaperturate, apertures furrow-shaped (Fig. 5 A, B,

D). Grains with two conspicuous extensions at both ends of one side (Fig. 5 B). Non-apertural and apertural exine psilate to somewhat scabrate (Fig. 5 C). Exine of non-apertural region composed of an irregular foot-layer, short proximal columellae, and a
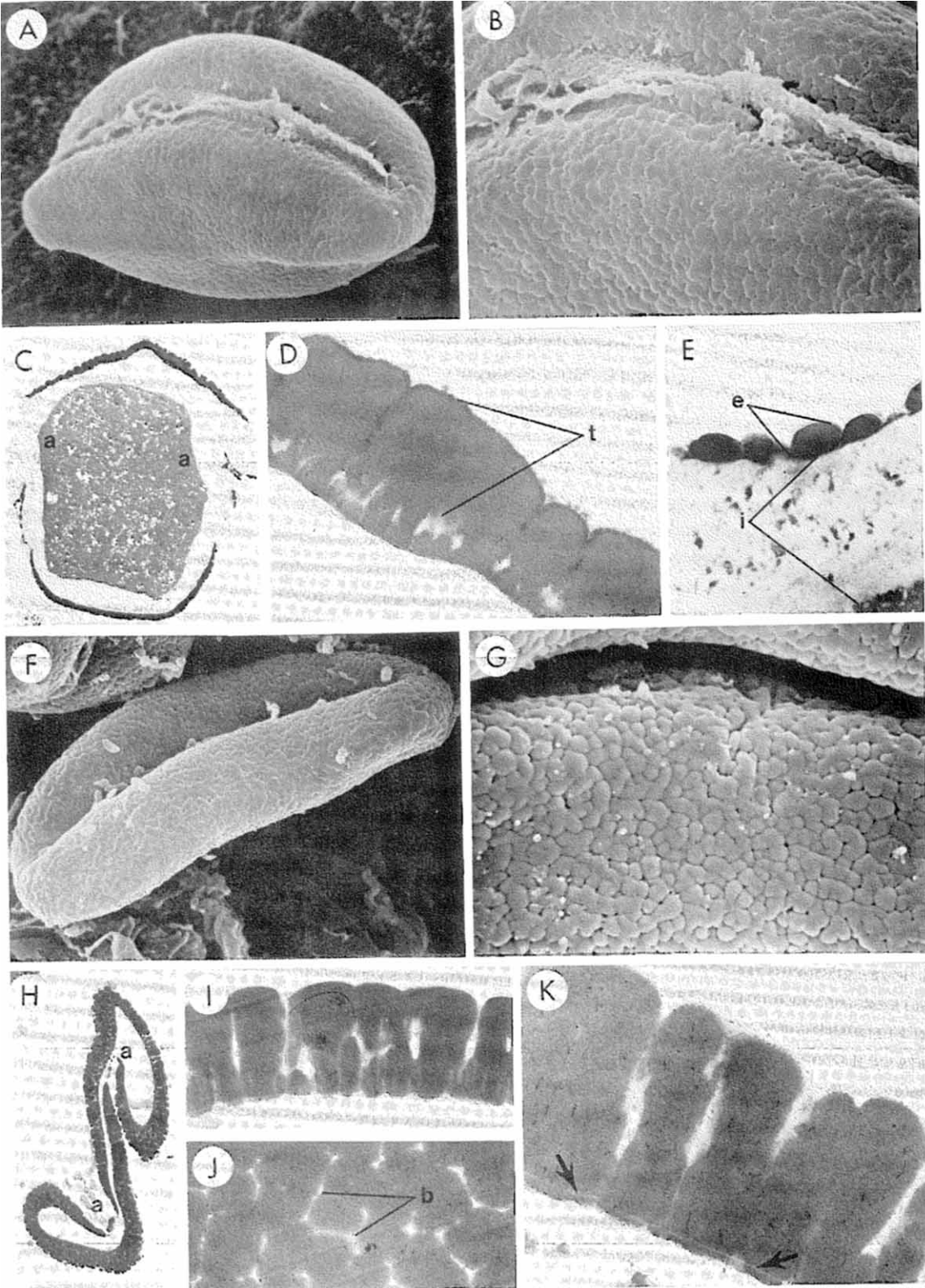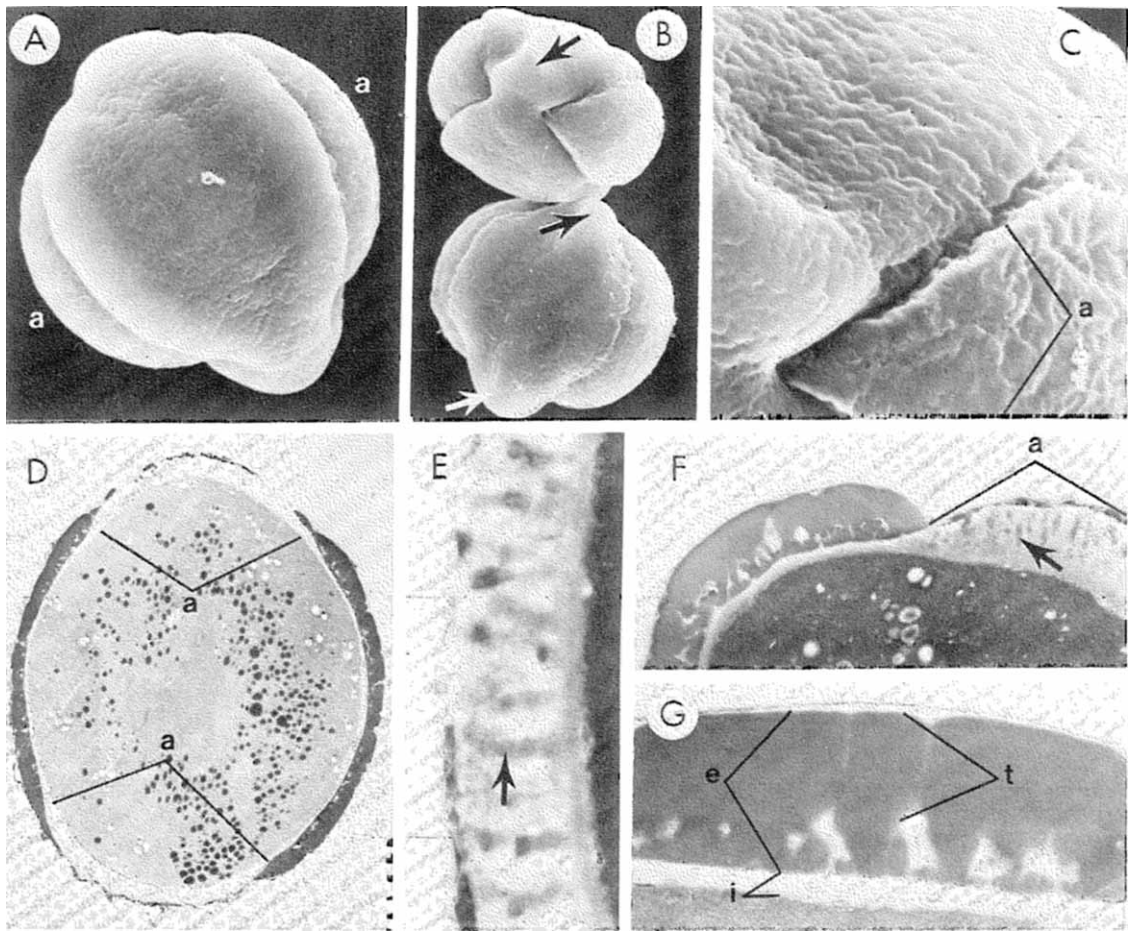
Fig. 5. Pontederia cordata L. (A) Whole grain. Note two apertures (*a*). SEM ×1700. (B) Two pollen grains, viewed from side and end. Note projections (*arrows*) at grain ends on one side of non-apertural wall. SEM ×1000. (C) Close-up, showing psilate apertural region (*a*) and psilate to somewhat scabrate non-apertural region. SEM ×5300. (D) Whole grain cross-section. Note two apertures (*a*), essentially devoid of exine. TEM ×2500. (E) Aperture region, showing thick, 2-layered intine with prominent channel-like structures (*arrow*) of outer exintine layer. TEM ×18000. (F) Interface between non-apertural (left) and apertural (*a*) walls. Note channel-like vesicles (*arrow*) of outer aperture intine. TEM ×5800. (G) Non-apertural wall. Note thin intine (*i*) and exine (*e*) with a discontinuous foot-layer, short columellae, and a thick, baculate to homogeneous tectum (*t*). TEM ×22000.

Fig. 4. A–E. Monochoria vaginalis (Burm. f.) Presl. ex Kunth. (A) Whole pollen grain, one of two apertures above. SEM ×2000. (B) Close-up, showing verrucate, non-apertural wall and invaginated aperture. SEM ×3600. (C) Whole grain cross-section, showing two aperture regions (*a*). TEM ×1700. (D) Exine wall cross-section. Note tectum (*t*) of baculate to oval-shaped elements, granular to short-columellate interstitium, and irregular foot-layer. TEM ×29000. (E) Aperture wall cross-section, showing exinous elements (*e*) atop thick, 2-layered intine (*i*). Note vesicular structures in outer exintine layer. TEM ×21000. F–K: *Reussia rotundifolia* (L. f.) Castell. (F) Whole grain, one of two apertures above. SEM ×2400. (G) Close-up of verrucate non-apertural wall; invaginated aperture above. SEM ×5800. (H) Whole grain cross-section of collapsed pollen grain. Note two apertures (*a*). TEM ×2200. (I) Cross-section of exine. TEM ×17000. (J) Tangential section of exine, showing baculate structural elements (*b*). TEM ×22000. (K) Close-up of exine cross-section. Note 2-layered structure, as defined by commissural line (*arrows*). TEM ×38000.
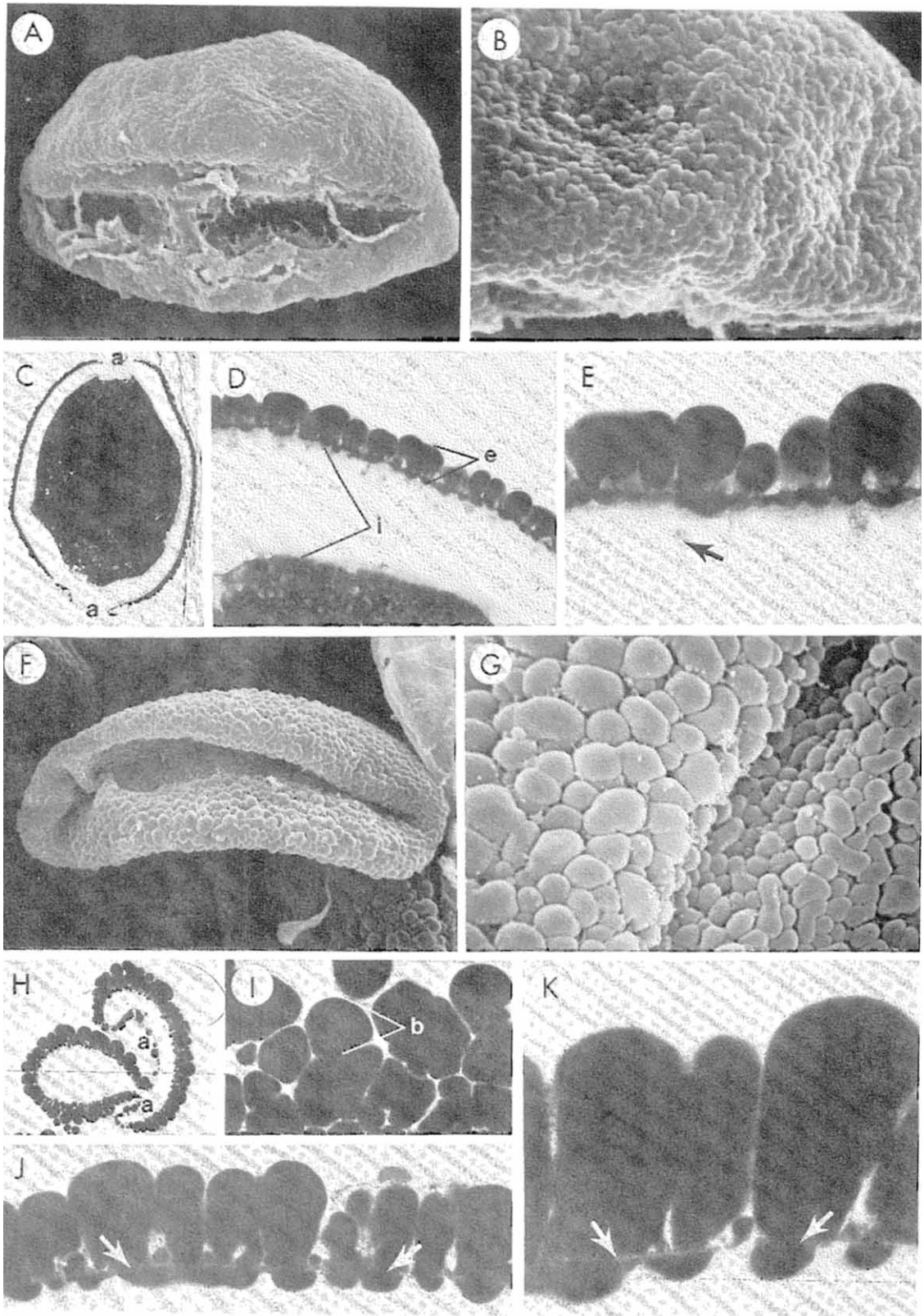
thick tectum which is either homogeneous or comprised of baculate elements (Fig. 5G). Apertural exine absent (Fig. 5D, E, F). Intine of non-apertural region thin (Fig. 5G), that of aperture thick and 2-layered with radially-oriented vesicular structures in the exintine (Fig. 5E, F).

Scholleropsis lutea H. Perr. — Pollen grains (31 μm) diaperturate, apertures furrow-shaped (Fig. 6A, C). Non-apertural region with a verrucate sculpturing (Fig. 6B). Non-apertural exine composed of an irregular foot-layer, an interstitium of very short columellar structures, and a tectum of baculate to gemmate, distally rounded elements (Fig. 6D, E). Intine thick, 2-layered, with radially-oriented channel-like structures in the distal part of the outer layer (Fig. 6D, E).

Zosterella dubia (Jacq.) Small. — Pollen grains (48 μm) diaperturate, apertures furrow-shaped (Fig. 6F, H). Non-apertural sculpturing verrucate (Fig. 6G). Non-apertural exine 2-layered, the outer layer composed of baculate elements (Fig. 6I, J) having rounded distal ends, the inner layer composed of somewhat papillate elements (Fig. 6J). Commissural line evident between inner and outer exine layers (Fig. 6J, K).

DISCUSSION

The pollen of the Pontederiaceae can be characterized as having diaperturate, furrow-shaped aper-

Fig. 6A–E. Scholleropsis lutea H. Perr. (A) Whole grain, one of two apertures facing. SEM ×2300. (B) Close-up, showing verrucate sculpturing of non-apertural wall. SEM ×5200. (C) Whole grain cross-section; note two apertures (*a*). TEM ×1800. (D) Cross-section of non-apertural wall, showing thick intine (*i*) and tectate-columellate exine (*e*). TEM ×14000. (E) Close-up of wall section, showing exine composed of an irregular foot-layer, short columellae, and a tectum of distinct baculate to gemmate elements. Note channel-like structures of outer intine (*arrow*). TEM ×40000. F–K. *Zosterella dubia* (Jacq.) Small. (F) Whole grain, one of two collapsed apertures facing. SEM ×1400. (G) Close-up of non-apertural (left) and apertural (right) region, showing verrucate sculpturing. SEM ×6400. (H) Cross-section of whole (collapsed) pollen grain. Note two apertures (*a*). TEM ×1800. (I) Tangential section of exine wall. Note discrete baculate elements. TEM ×14000. (J) Cross-section of 2-layered exine, composed of outer baculate elements and inner papillate elements, separated by a commissural line (*arrows*). TEM ×15000. (K) Close-up of exine cross-section, showing commissural line (*arrows*). TEM ×32000.

tures with a finely verrucate exine sculpturing (psilate to scabrate in *Pontederia*). The diaperturate condition in the family was difficult to observe in some material; however, careful observations of several grain cross-sections clearly indicated the presence of two oppositely oriented apertures in all taxa. (The two apertures in *Pontederia cordata* are, with reference to the tetrad, parallel to the equatorial plane (Huynh 1976), warranting the term "disulculate" for at least this species.) Aperture condition reported here for 8 family genera concurs with the observations of Erdtman (1966) for *Pontederia* and Rao & Rao (1961) for *Monochoria* and *Pontederia* (although Rao & Rao reported disulcate *and* monosulcate grains in the same species). Among the angiosperms as a whole and the monocotyledons, a monosulcate aperture type is overwhelmingly accepted as the ancestral condition. Because a diaperturate condition is found in no taxa presumed to be closely related to the Pontederiaceae in major taxonomic treatments (see Erdtman 1966), it is likely that this feature constitutes a unique, shared derived character for the family.

Exine architecture of members of the Pontederiaceae shows some variability. In two genera, *Eichhornia* and *Hydrothrix*, the exine is composed of laterally appressed baculate elements which are apparently fused proximally as a very thin basal layer. Two other genera, *Reussia* and *Zosterella*, have a distinctly 2-layered exine, with the outer layer made up of baculate to somewhat clavate elements (resembling the entire exine of *Eichhornia* and *Hydrothrix*) and the inner layer comprised of (in *Reussia*) a thin, discontinuous layer or (in *Zosterella*) of discrete papillate elements; a commissural "line", as apparent in electron micrographs, separates the two layers. Three genera, *Monochoria*, *Pontederia*, and *Scholleropsis*, have what is designated as a tectate-columellate architecture. However, in these taxa the foot-layer is thin and composed of rather discontinuous elements; the interstitium is composed of short, ill-defined columellae; the tectum is often comprised of thick, isodiametric to baculate elements. Finally, *Heteranthera reniformis* has an exine architecture somewhat intermediate to the latter two groups. In this species, the exine is mostly tectate-columellate, with a thin, rather discontinuous foot-layer, short columellae, and a tectum comprised of baculate elements (resembling, e.g., *Pontederia*). However, in a major portion of the non-apertural region, the exine is 2-layered, com-

MONOCHORIA

PONTEDERIA   **HETERANTHERA**

SCHOLLEROPSIS

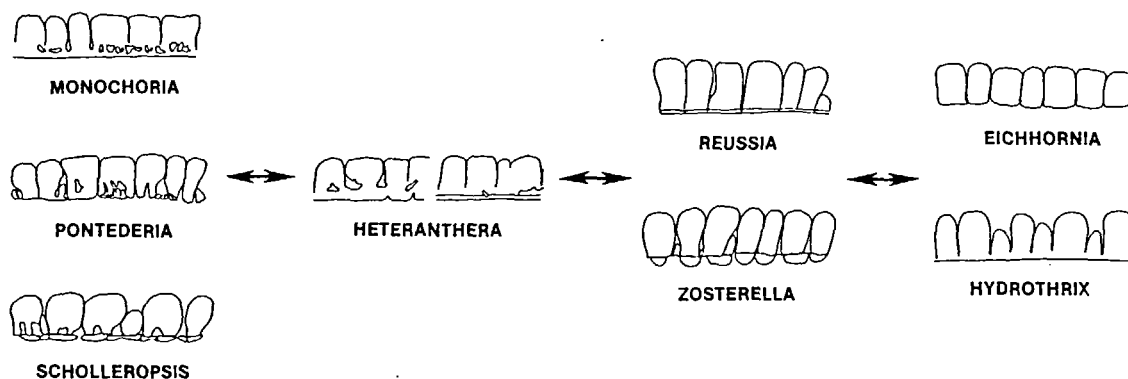**REUSSIA**   **EICHHORNIA**

ZOSTERELLA   **HYDROTHRIX**

Fig. 7. Hypothesized morphocline between genera of the Pontederiaceae. Note intergradation between modified tectate-columellate architecture (*Monochoria, Pontederia,* and *Scholleropsis*), 2-layered exine (*Reussia* and *Zosterella*), and 1-layered exine composed of baculate elements (*Eichhornia* and *Hydrothrix*). *Heteranthera* shows features of both a modified tectate-columellate and a 2-layered exine architecture, evidence for the structural homology of these two types in other family genera.

posed of laterally appressed (to fused) baculate elements having an inner layer and commissural line (similar, e.g., to *Reussia*). Thus, a gradation of exine architectural types can be noted among the members of the Pontederiaceae (Fig. 7). The occurrence of each of two architectural types in *Heteranthera* argues strongly that the similarity between the modified tectate-columellate and 2-layered exine types is by homology.

The intine of members of the Pontederiaceae (where it could be resolved) is 2-layered, the outermost layer becoming thickened in the apertural region and traversed with radially-oriented channel-like or vesicular structures. Although no cytochemical testing was done, it is probable that this structure follows the general pattern or pectic-rich exintine and cellulosic-rich endintine as evidenced in the monocots as a whole (Kress & Stone 1982).

The pollen exine ultrastructure of most of the examined members of the Pontederiaceae is strikingly similar to that of the family Haemodoraceae (see Simpson 1983a). With the exception of *Pontederia,* all examined taxa of the Pontederiaceae have a distinctly verrucate sculpturing, almost identical to the sculpturing found in members of the tribe Haemodoreae of the Haemodoraceae (e.g., *Haemodorum,* Fig. 8A, B). Of perhaps greater significance is that the exine architecture of the Haemodoraceae shows parallel resemblances to that of the Pontederiaceae. Two genera of the tribe Haemodoreae, *Lachnanthes* and *Haemodorum,* have a 1-layered exine of laterally appressed, baculate ele-

ments (Fig. 8C, D), identical to that of *Eichhornia* and *Hydrothrix*. Four genera of the tribe Haemodoreae (e.g., Fig. 8E, F) and all six genera of the tribe Conostylideae of the Haemodoraceae (Fig. 8G) have an exine which is 2-layered, with a commissural line separating the outer and inner layers, resembling *Reussia* and *Zosterella* of the Pontederiaceae.

No other monocotyledon families studied to date have a 1-2-layered, non-tectate-columellate exine architecture resembling that of the Pontederiaceae and Haemodoraceae (see Simpson 1983a, b; 1985a, b). Therefore, it is proposed here that the resemblances in pollen exine sculpturing and architecture between members of the Pontederiaceae and Haemodoraceae are homologous, shared derived features and support the close, probable sister-group relationship of the two families. Thus, the present study supports the recent taxonomic treatment of Dahlgren & Rasmussen (1983), who place the Pontederiaceae and Haemodoraceae together, but actually evidence that the two families are together a monophyletic assemblage. The hypothesis of Simpson (1983a) that the non-tectate-columellate exine architecture found in all Haemodoraceae constitutes a unique, shared derived feature must, therefore, be extended to include the Pontederiaceae. In contrast, the Philydraceae, often proposed as a close relative to the Pontederiaceae, have monosulcate, generally reticulate pollen grains with a typical tectate-columellate architecture having lamellate exine deposits proximal to the
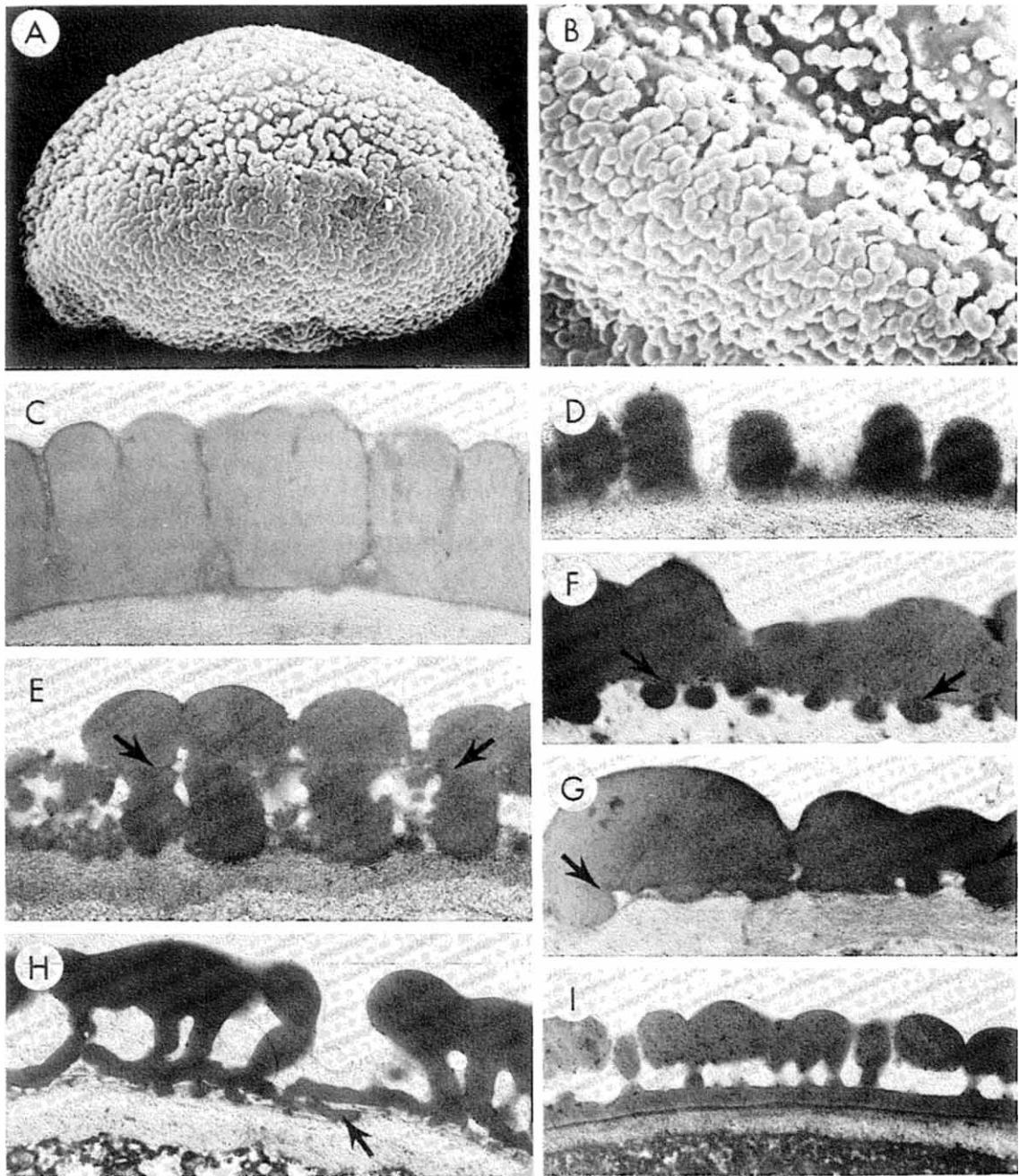
Fig. 8 A–B. Haemodorum spicatum R. Br. (A) Monosulcate pollen grain. SEM ×3 500. (B) Close-up, showing verrucate sculpturing. SEM ×8 100. C. *Lachnanthes caroliniana* (Lam.) Dandy. Exine wall cross-section. Note 1-layered exine composed of laterally appressed baculate elements. TEM ×27 000. D. *Haemodorum spicatum* R. Br. Exine wall cross-section. Note 1-layered, baculate exine elements. TEM ×43 000. E. *Xiphidium coeruleum* Aubl. Exine wall cross-section. Note pilate to baculate exinous elements and 2-layered structure as defined by commissural line (*arrows*). TEM ×27 000. F. *Dilatris pi-*
lansii Bark. Exine wall cross-section. Note 2-layered exine (*arrows*). TEM ×20 000. G. *Tribonanthes australis* Endl. Exine wall cross-section. Note 2-layered exine, defined by commissure (*arrows*). TEM ×21 000. H. *Philydrum lanuginosum* Banks & Solander ex Gaertner. Exine wall cross-section. Note tectate-columellate architecture with lamellate deposits inner to foot-layer (*arrow*). TEM ×12 000. I. *Cyanella lutea* L. f. Exine wall cross-section. Note tectate-columellate architecture. TEM ×14 000. (A–G: From Simpson 1983 *a* H: From Simpson 1985 *a*, I: From Simpson 1985 *b*).
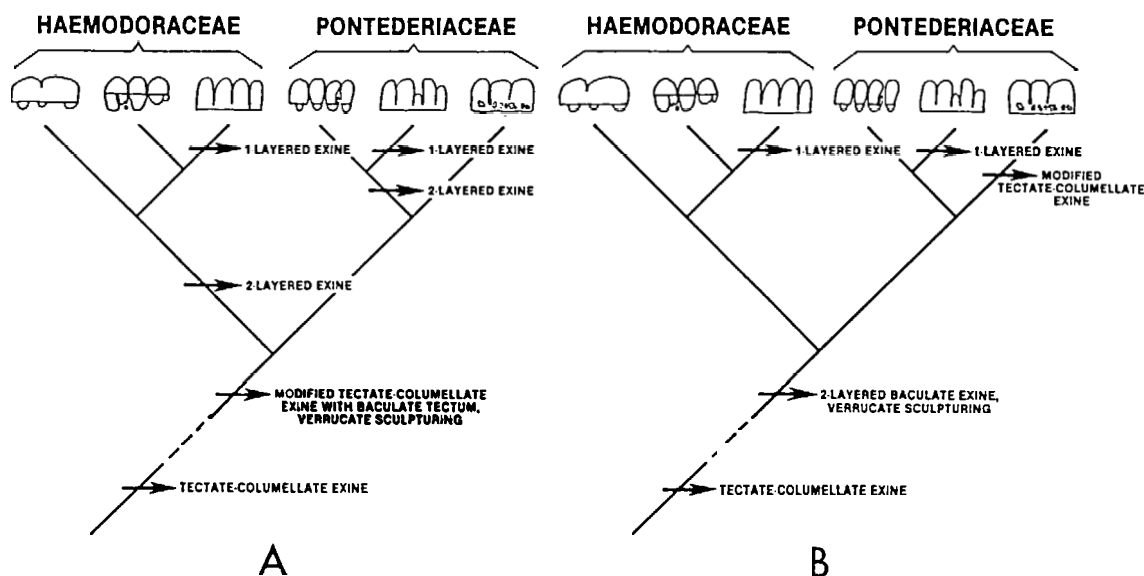
Fig. 9. Hypothesized abbreviated cladograms of the Haemodoraceae and Pontederiaceae, illustrating possible evolutionary changes in pollen structure. Note that each family is presumed to be monophyletic and that the two families are portrayed as sister taxa. In both cladograms a diaperturate pollen grain is hypothesized to have been uniquely derived in the lineage to the Pontederiaceae. A tectate-columellate architecture is assumed to be ancestral for the monocotyledons as a whole. (A) Hypothesis in which the common ancestor of the two families possesses a modified tectate-columellate exine architecture with baculate tectal elements and a verrucate sculpturing. Note that both a 2-layered and a 1-layered exine architecture evolved independently in each family. (B) Hypothesis in which the common ancestor of the two families possesses a 2-layered exine with baculate elements and a verrucate sculpturing. Note that one less evolutionary step (and one less occurrence of convergence) is required. The modified tectate-columellate architecture of members of the Pontederiaceae is hypothesized as being derived independently from the ancestral tectate-columellate type.

foot-layer (e.g., Fig. 8H; see Simpson 1985 a). Thus, palynological evidence does not support the close relationship of these two families as proposed by Hamann (1966).

The hypothesis that the Haemodoraceae and Pontederiaceae are sister groups is problematical, as both families are variable (and somewhat parallel) with respect to palynological features of exine architecture. It seems likely that each family is, by itself, monophyletic: the Haemodoraceae by evidence of a distinctive chemistry (Cooke & Edwards 1981) found nowhere else among vascular plants; the Pontederiaceae by evidence of a diaperturate pollen grain and a (presumed) derived aquatic habitat, leaf morphology, and floral structure. If each family *is* monophyletic, then some of the resemblances between genera in the two groups are examples of convergence. For example, because only a 2-layered exine architecture is found in both (presumably monophyletic) tribes of the Haemodoraceae, it is likely that this is the ancestral condition for the family as a whole (Simpson 1983 b). Therefore, the 1-layered exine structure of *Haemodorum* and *Lachnanthes* of the Haemodoraceae and of *Eichhornia* and *Hydrothrix* of the Pontederiaceae most likely evolved independently within each family, apparently by the loss of the inner exine layer (Fig. 9A, B). There is also the question of the tectate-columellate exine architecture in *Heteranthera, Monochoria, Pontederia*, and *Scholleropsis* of the Pontederiaceae. A tectate-columellate architecture is widespread among angiosperms and is probably primitive for the monocotyledons as a whole (Zavada 1983). However, the typical tectate-columellate condition is one having more prominent columellae and a roof-like tectum (e.g., *Cyanella*, Fig. 8 I). The tectate-columellate members of the Pontederiaceae, in contrast, have a consistently discontinuous foot-layer, short columellae, and a tectum comprised of discrete bacula (which resemble the outer exinous elements of the non-tectate-collumellate members of that family). Two pos-

sibilities are evident with respect to the evolution of this modified tectate-columellate architecture in the Pontederiaceae. First, the modified tectate-columellate structure may represent an intermediate stage toward the more derived non-tectate-columellate (e.g., 2-layered) condition. In this case the common ancestor of the Haemodoraceae and Pontederiaceae possessed this modified tectate-columellate structure having baculate tectal elements with a verrucate sculpturing (Fig. 9 A). Such a hypothesis would necessitate, however, the independent evolution of a 2-layered, commissural exine in both the Pontederiaceae and Haemodoraceae (Fig. 9 A). A second possibility is that the resemblance to a tectate-columellate architecture in the Pontederiaceae is derived secondarily within that family lineage and that a non-tectate-columellate, baculate, 2-layered exine architecture with a verrucate sculpturing was present in the common ancestor of both families (Fig. 9 B). This latter hypothesis would require one less evolutionary step (and one less convergence; Fig. 9 B) and is to be preferred by the principle of parsimony. Rigorous phylogenetic analyses of intrafamilial taxa will be needed to test these competing hypotheses.

In conclusion, recent taxonomic treatments placing the Pontederiaceae "close" to the Haemodoraceae are supported by the included studies of pollen grain ultrastructure. Although more detailed studies of other monocotyledonous taxa are clearly needed, the distinctive pollen exine sculpturing and architecture found only in the Haemodoraceae and Pontederiaceae are proposed to represent a shared derived evolutionary event, supporting the hypothesis that members of the Pontederiaceae and Haemodoraceae uniquely share a common ancestor. In light of the systematic significance of these palynological features, the author is currently studying exine wall development in the Philydraceae, Pontederiaceae, and Haemodoraceae. Determination of the developmental basis for the 1- and 2-layered, non-tectate-columellate exine architecture, as well as for the "modified" tectate-columellate structure in the Pontederiaceae, should be enlightening with regard to their proposed homologies.

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