

Morphology and anatomy of the malagasy genus *Physena* (*Physenaceae*), with a discussion of the relationships of the genus

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Summary : The vegetative and reproductive morphology and anatomy of the puzzling Malagasy dicotyledonous genus *Physena* was studied in an attempt to determine its affinities. The first detailed descriptions of leaf, axis, nodal, wood, floral, pollen, and fruit morphology and anatomy are provided. A summation of available evidence supports recognition of the family *Physenaceae*. The taxon possesses a combination of primitive and advanced character states that suggests different patterns of relationships depending upon emphasis. The tricolpate, spinulose pollen with tectal microperforations, basifixed anthers with an endothecial-like connective hypodermis and linear dehiscence, and specializations related to presumed anemophily are reminiscent of various taxa assigned to the hamamelid complex and support the view that the family represents an isolated Southern Hemisphere member of the *Hamamelididae*. The brochidodromous leaf venation, unilacunar nodal structure, and wood anatomy with solitary vessel elements having simple perforation plates and small alternate intervacular pits most closely resembles certain elements of the thealean complex. With no single recognizable category of close surviving relatives, the most satisfactory placement of the family in the general system of classification remains uncertain.

Résumé : La morphologie et l'anatomie d'organes végétatifs et reproducteurs de l'énigmatique genre malgache *Physena* (Dicotylédones) ont été étudiées pour déterminer ses affinités. Les descriptions détaillées de la morphologie et de l'anatomie des feuilles, axes, nœuds, bois, fleurs, pollen et fruits sont données pour la première fois. L'ensemble des informations recensées confirme la reconnaissance de la famille des *Physenaceae*. Le taxon possède une combinaison de caractères primitifs et évolués qui suggère des relations différentes selon l'importance relative donnée à chaque caractère. Le pollen tricolpé, échinulé, à tectum microperforé, les anthères basifixes à déhiscence longitudinale dont l'hypoderme du connectif a la structure d'une assise mécanique, et des spécialisations liées à une probable anémophilie, évoquent plusieurs taxa assignés au complexe hamamélididéen et appuient l'idée que la famille représente un membre des *Hamamelididae* isolé dans l'hémisphère Sud. La nervation brochidodrome de la feuille, la structure nodale unilacunaire, et l'anatomie du bois à éléments vasculaires isolés avec des perforations simples et des petites ponctuations intervaculars alternes, font penser à certains éléments du complexe théaléen. Puisqu'il n'existe aucune parenté étroite entre *Physena* et d'autres plantes vivantes, le placement de la famille dans le système général de classification demeure incertain.

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INTRODUCTION

The woody, dicotyledonous genus *Physena* Noronh. ex Thouars is currently represented by two species endemic to Madagascar : *P. madagascariensis* Tul. and *P. sessiliflora* Tul. (CAPURON, 1968). The plant is a shrub or small tree, with simple, alternate, exstipulate leaves. Plants are dioecious, with unisexual and apetalous flowers. Since its original description, the relationships of the genus have remained enigmatic. The taxonomic history of *Physena* are summarized by CAPURON (1968) and TAKHTAJAN (1987). Various diverse affinities have been suggested, generally without explanation. BENTHAM & HOOKER (1862) treated the genus as an anomalous taxon within the *Passifloraceae*. HUTCHINSON (1967) also regarded *Physena* to be a component of *Passifloraceae*. The interpretation that *Physena* possesses parietal placentation led to its inclusion in the *Capparaceae* (PAX & HOFFMANN, 1936; WILLIS, 1973) and *Flacourtiaceae* (PERRIER, 1946).

ERDTMAN (1952) briefly described *Physena* pollen and concluded that the genus deviated considerably from the *Capparaceae* but showed some resemblances to certain *Theaceae* (e.g., *Asteropeia*). TAKHTAJAN (1987) subsequently recognized the independent family *Physenaceae* that was positioned in the Sapindales. THORNE (1976, 1983, 1992) listed *Physena* as a taxon *incertae sedis*. CRONQUIST (1988) tentatively proposed aligning the *Physenaceae* with his concept of *Hamamelidae* (Urticales), emphasizing their reduced, unisexual flowers, long, latrorse anthers, and other features.

The recent availability of excellent liquid-preserved materials of *Physena madagascariensis* provided an opportunity to describe thoroughly the vegetative and reproductive morphology and anatomy of the genus for the first time, and assess the role of these evidences in the search for its nearest surviving relatives.

MATERIALS AND METHODS

This study is based upon examination of dried and fluid-preserved leaves, stems, wood, flowers, and fruits (Table 1). Standard microtechnical methods were utilized. Flowers, fruits, leaves, young stems, and nodes were paraffin-embedded, serially sectioned transversely and longitudinally at 5-10 μm , and stained with safranin-fast green (JOHANSEN, 1940). Floral parts were also critical-point dried, sputtercoated with gold-palladium, and viewed with the scanning electron microscope (SEM).

Pollen was prepared by the acetolysis method outlined by ERDTMAN (1960). Acetolyzed pollen was vacuum coated with gold-palladium and observed directly with the SEM. For transmission electron microscopy (TEM), acetolyzed grains were washed, transferred to 1 % osmium tetroxide for 1-2 hours, dehydrated in a graded alcohol series to acetone, embedded in epon-aralidite, and sectioned. Thin sections were stained with uranylacetate and lead citrate. Measurements were obtained by measuring 25 grains mounted in glycerin jelly under oil immersion (ca. $\times 1000$).

Wood samples were boiled in water and cut on a sledge microtome at a thickness of 20 μm . Resulting sections were stained with safranin. Data relating to wood cell length were obtained by making 50 measurements from macerations prepared using Jeffrey's fluid. Cell diameters were measured from transverse sections and included walls. Stomatal patterns were observed in prepared paradermal sections.

Leaf venation was examined using leaves cleared in 5 % NaOH at 60° C (ARNOTT, 1959). All drawings were made from prepared and stained sections with a Wild Heerbrugg camera lucida. In the following descriptions, the extreme and mean values for statistical data are given.

TABLE 1 : Specimens of *Physena* examined.

SPECIES	COLLECTOR AND HERBARIUM	TYPE OF MATERIAL ¹
<i>P. madagascariensis</i> Tul.	<i>Service Eaux et Forêts</i>	P
	<i>de Madagascar 8011 SF (P)</i>	
	<i>F. Badré 2085 (MO, P)</i>	W (MADw 46631) ²
	<i>L. Dorr et al. 3525 (MO, P)</i>	W (MADw 44404)
	<i>G. Schatz et al. 2708 (MO, P)</i>	Fl, Fr, L, Lp, P, S
	<i>G. Schatz et al. 2350 (MO, P)</i>	Fl, Fr, L, Lp, S
<i>P. sessiliflora</i> Tul.	<i>R. Capuron 8464 (P)</i>	P

1. Fl, flower; Fr, fruit and seed; L, leaf; Lp, liquid-preserved; P, pollen; S, stem; W, wood.

2. Abbreviation of xylarium follows STERN (1988).

VEGETATIVE MORPHOLOGY AND ANATOMY

LEAF

Leaves simple, petiolate, exstipulate, and alternate. Petioles short and articulated. Blades of *P. madagascariensis* more or less oblong, with an acuminate apex, obtuse base, and entire margins. Venation of the lamina pinnate. Secondary venation brochidodromous with secondary veins rather fine (Fig. 1, *I*). Tertiary venation reticulate. High order venation forms an incomplete to imperfect areolation of irregular shape and size. Veinlets simple or variously branched. The continuous fibrous sheath system along the venation extends to the ultimate veinlets. Specialized terminal cells thick-walled, irregularly shaped, often dilated, pitted, tracheoid or sclerotic, and occur as single elements or in clusters (Fig. 2, *10*).

PETIOLE

A thick cuticle (8.0 µm) covers the surface. Epidermal cells have dome-shaped outer walls and ground tissue is compact, composed of parenchymatous cells with walls having numerous pits or pit fields. Many cortical cells contain red-staining or golden brown deposits. Vascular tissue throughout the petiole in the form of an arc-shaped bundle that becomes surrounded by a multiseriate fibrous sheath in more distal regions (Fig. 1, *2*). Druses and irregular-shaped crystal deposits are scattered throughout the ground tissues.

LAMINA : IN SURFACE VIEW

Trichomes absent. Adaxial epidermal cells 4-7-sided with straight to slightly curved anticlinal walls; cells not elongated over the veins. Abaxial epidermal cells 4-7(8)-sided with straight to curved anticlinal walls; cells not elongated over the veins. Stomata confined to the abaxial surface, anomocytic; guard cell pairs average $23.0\text{ }\mu\text{m}$ in length and $20.5\text{ }\mu\text{m}$ in width based upon 20 measurements (Fig. 1, 4).

LAMINA : IN TRANSVERSE VIEW

The lamina bifacial (Fig. 2, 9). Adaxial cuticle $4.0\text{ }\mu\text{m}$ thick, smooth; abaxial cuticle $3.5\text{ }\mu\text{m}$ thick, up to $10\text{ }\mu\text{m}$ thick over the midrib, smooth. Adaxial epidermal cells procumbent or commonly square, and only slightly larger than the procumbent or square abaxial cells. Epidermal cells over the midrib have dome-shaped outer walls. Epidermal cells are thin-walled and stomata are level with unspecialized epidermal cells. Guard cells possess small outer cuticular ledges. The mesophyll composed of one or less commonly two layers of palisade cells and a spongy region with moderate intercellular space. Cells of the spongy zone commonly filled with golden brown contents. The lowermost layer of palisade not clearly differentiated from the spongy zone. The midrib contains an arc-shaped vascular strand surrounded by a multiseriate (5-6 layers) sheath of sclerenchymatous fibers (Fig. 1, 3). Ground tissue of midrib parenchymatous. Both major and minor veins completely jacketed by thick-walled, lignified fibrous elements (Fig. 2, 10). The vein sheath is multiseriate around larger vascular bundles and does not extend to the surface. Druses are scattered throughout the mesophyll and ground tissue of the midrib.

YOUNG STEM AND NODE

A cuticle up to $10\text{ }\mu\text{m}$ thick covers the surface. Epidermal cells erect, with dome-shaped or bottle-shaped outer walls in young twigs, rectangular in older stems. Periderm arises in subepidermal layers. The cortex about 8-10 cells thick, parenchymatous, with some cells having golden brown deposits. Vascular tissue forms a complete cylinder, with a well-developed ring (2-3 cells thick) of perivascular sclerenchyma fibers. Secondary phloem is without mechanical tissue. The secondary xylem is traversed by narrow rays and contains solitary vessels that are angular to circular in outline. The pith region composed of parenchyma, with some cells becoming lignified and pitted. Druse and prismatic crystals occur in the cortex and pith.

Nodal anatomy unilacunar, one-trace, with an arc-shaped leaf trace as viewed in transection (Fig. 1, 5).

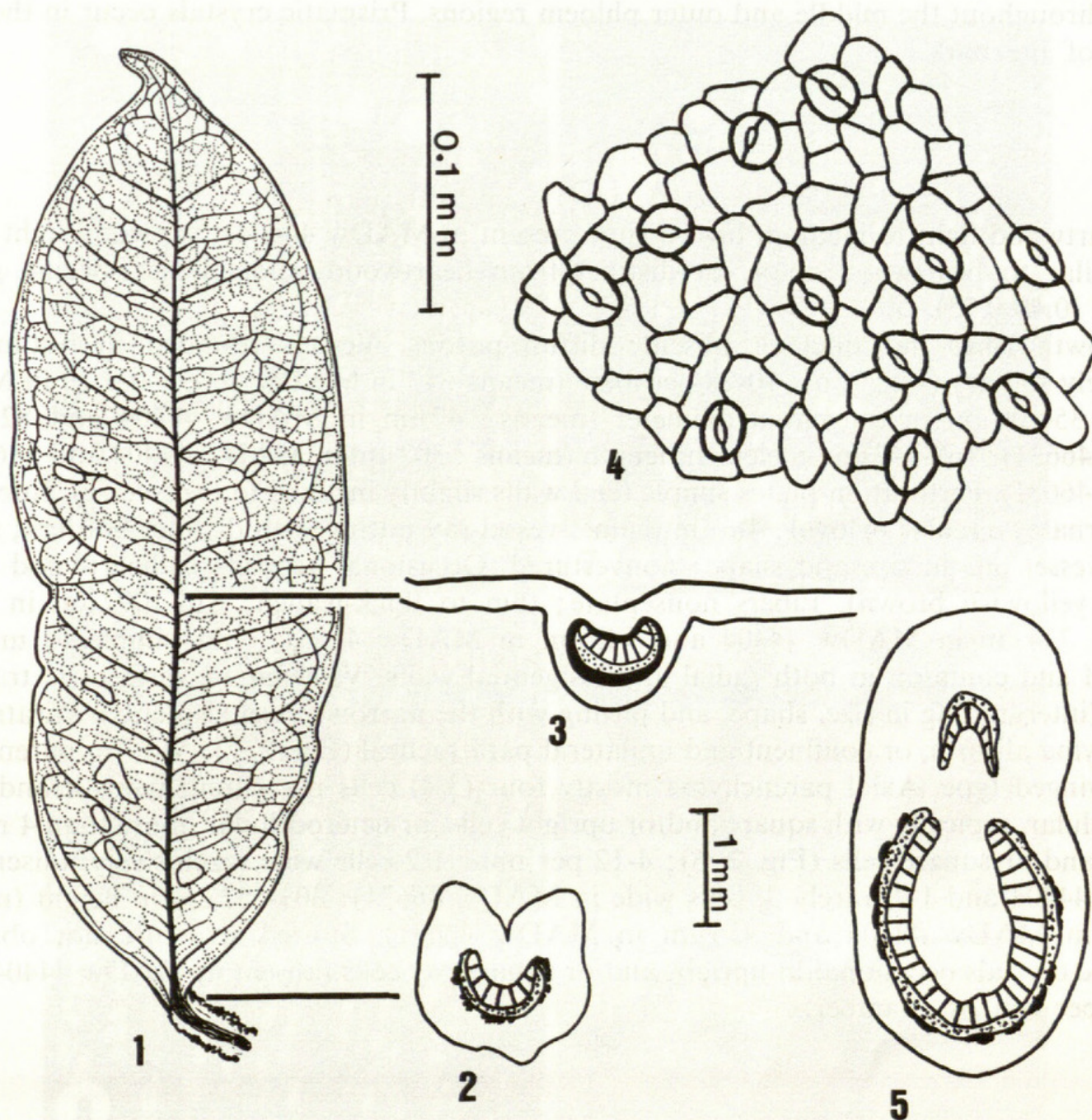


Fig. 1. — Vegetative anatomy of *Physena madagascariensis* : 1, cleared leaf illustrating major venation ; 2, transverse section through the distal region of petiole showing pattern of vascularization ; 3, transverse section through midrib at midlength ; 4, abaxial foliar epidermis showing anomocytic mature stomatal pattern ; 5, transverse section through the node illustrating unilacunar, one-trace condition. Blackened area = sclerenchyma, stippled region = phloem, hatched = xylem.

BARK (OF MATURE STEM)

External periderm cracked and composed of thin-walled compressed phellem cells filled with dark deposits. Secondary phloem abundant, highly sclerified, and composed of sieve-tube elements, companion cells, phloem parenchyma, abundant sclereids, and is traversed by narrow rays that become dilated toward the outside. Numerous, large, and extremely thick-walled brachysclereids ("stone cells") irregularly occur as scattered, solitary sclereids or in

groups throughout the middle and outer phloem regions. Prismatic crystals occur in the older regions of the bark.

WOOD

Heartwood light to medium brown (not present in MADw 44404); sapwood light cream and similar to heartwood color, or distinct from heartwood color. Basic specific gravity medium (0.40-0.75).

Growth rings indistinct or absent; diffuse-porous. Vessels rounded in outline and exclusively solitary (Fig. 2, 6); 10-28 per mm² (means : 13 in MADw 46631 and 20 in MADw 44404); 35-100 μ m in tangential diameter (means : 47 μ m in MADw 44404 and 82 μ m in MADw 46631); 160-547 μ m in element length (means : 302 μ m in MADw 44404 and 316 μ m in MADw 46631). Perforation plates simple (end walls slightly inclined to transverse). Intervessel pits alternate; circular or oval; 4-6 μ m diam.; vessel-ray pitting with distinct borders; similar to intervessel pits in size and shape; nonvestured. Occasional deposits in heartwood vessels (mostly yellowish brown). Fibers nonseptate; thin to thick-walled; 614-1097 μ m in length (means : 734 μ m in MADw 44404 and 948 μ m in MADw 46631); pits simple to minutely bordered and common in both radial and tangential walls. Vascular or vasicentric tracheids present (intergrading in size, shape, and pitting with the narrow vessel elements). Paratracheal parenchyma aliform, or confluent and unilateral paratracheal (Fig. 2, 7). Aliform parenchyma of the winged type. Axial parenchyma mostly four (3-4) cells per parenchyma strand. Rays homocellular, typically with square and/or upright cells, or heterocellular, more than 4 rows of upright and/or square cells (Fig. 2, 8); 4-12 per mm; 1-2 cells wide (exclusively uniseriate in MADw 44404 and 1-2, rarely 3, cells wide in MADw 46631); 303-552 μ m in height (means : 425 μ m in MADw 44404 and 435 μ m in MADw 46631). Storied structure not observed. Prismatic crystals occasional in upright and/or square ray cells (absent in MADw 44404); one crystal per cell or chamber.

REPRODUCTIVE MORPHOLOGY AND ANATOMY

GENERAL FLORAL ORGANOGRAPHY AND ANATOMY

Flowers are borne in axillary racemes. Flowers are pedicellate, actinomorphic, apetalous, and unisexual (Fig. 4, 16, 17, 30). Staminate flowers possess a rudimentary gynoeceium devoid of ovules and have a pair of short styles (Fig. 4, 31). Calyces of both male and female flowers consist of 5-9 weakly imbricate sepals, some of which are slightly united at lower levels. Sepals covered internally with numerous multicellular, uniseriate, unbranched trichomes (Fig. 4, 19). Sepals have stomata that are particularly abundant proximally on the abaxial surface. Stomata often protrude above the surface of the epidermis, with the guard cells surrounded by, and supported on, columns of epidermal cells a single cell high (Fig. 3, 15). Guard cells possess thickened and highly lignified inner and outer walls as viewed in transection. The sepal

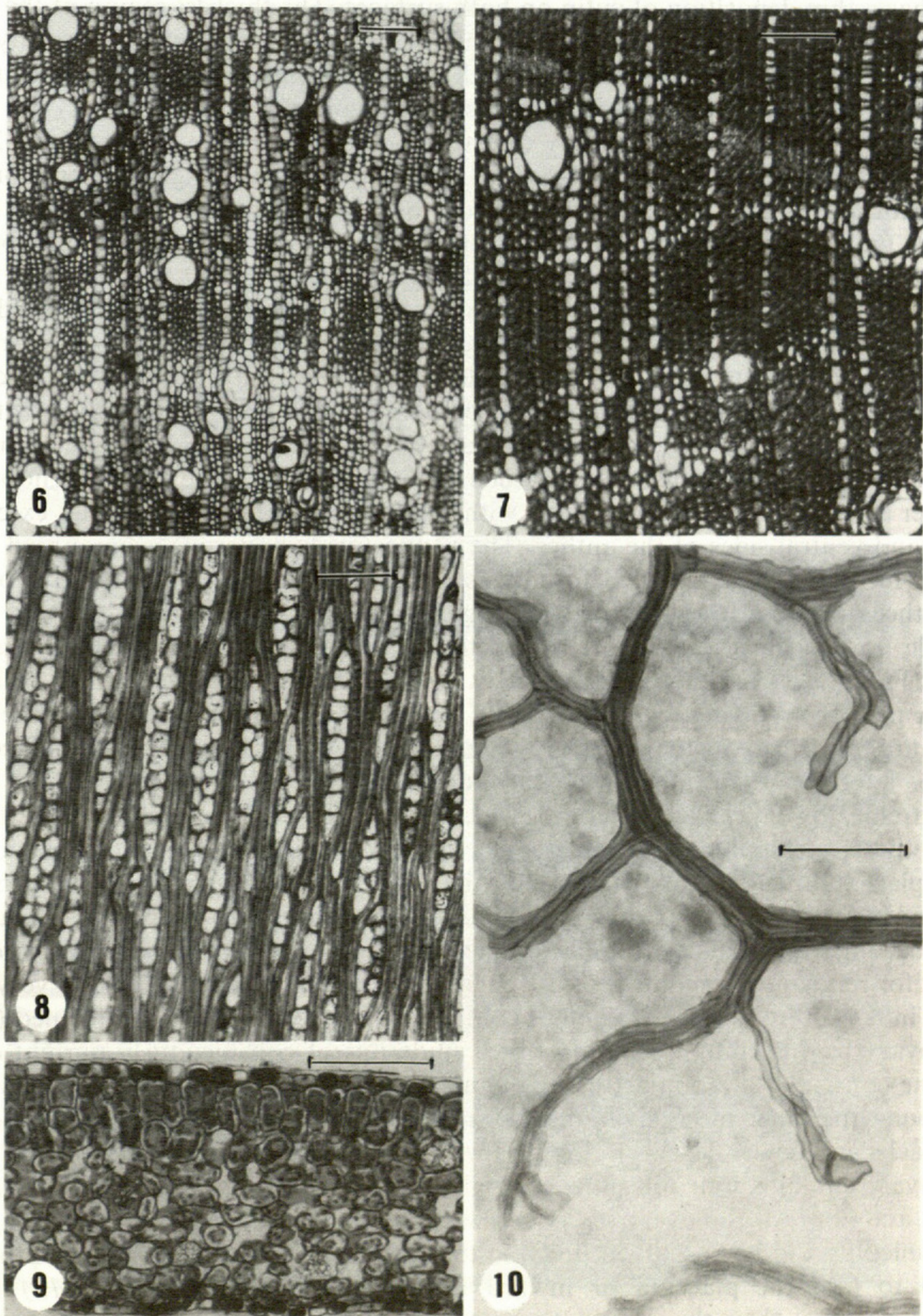


Fig. 2. — Vegetative anatomy of *Physena madagascariensis* : 6, transverse section of wood showing solitary pore distribution ; 7, transverse section of wood showing abundant paratracheal axial parenchyma ; 8, tangential section of wood illustrating uniseriate, and biseriate rays ; 9, transverse section of leaf ; 10, cleared leaf illustrating sclerenchyma ensheathed veinlets and specialized terminal elements. Bar : 0.1 μ m.

epidermis has a thin deposition of cutin on both surfaces. The thickest region of the mesophyll comprises 6-8 layers of undifferentiated, compactly arranged ground parenchyma. Both epidermal and mesophyll cells frequently filled with golden brown contents. Irregular crystal deposits occur infrequently throughout the sepal mesophyll.

Male flowers possess an essentially apostemonous androecium containing 8-25 (mostly 10-14) stamens (Fig. 4, 30). Stamens arise in a single whorl, although one or more stamens may be positioned outside the cycle. At the very base, the filaments of a variable number of stamens are united over a short distance. Each stamen is differentiated into a short filament and an elongated, basifixed anther (Fig. 4, 32, 33). Anthers extend well beyond the sepals. Filaments circular to somewhat rectangular in outline and composed of an epidermis and parenchymatous ground tissue. Each anther contains two pairs of marginal sporangia that dehisce laterally. The thecal lobes protrude below their proximal juncture with the connective. The anther wall differentiates into an outer epidermis, a fibrous endothecium with lignified thickenings in the form of bands, and a single layer of tapetum. Epidermal cells are covered with a striate cuticle and often have golden brown contents. The fibrous endothecium is located over each theca and is continuous with the connective hypodermis that extends across the dorsal and ventral sides of the anther. The connective hypodermis is composed of fibrous, endothelial-like cells (Fig. 4, 40). Before dehiscence, the partition between the two locules of the same theca breaks down to form a single chamber (Fig. 4, 40).

Female flowers have a superior, bicarpellate, glabrous gynoecium that is sessile on the receptacle (Fig. 3, 11). Carpels are completely fused along the length of their abaxial ovarian surfaces. A pair of very long (ca. 3 mm), solid styles arise from a depression at the top of the ovary and are free except at the very base (Fig. 4, 16, 17, 29). Elongate epidermal cells project as delicate, lateral fibrillar appendages around the length of the style (Fig. 3, 12).

At extreme lower levels, the compound, ovoid ovary is two-loculed, and the septum separating the two chambers is complete. The central portion of the septum is enlarged and forms the placental region near the center of the ovary. Slightly higher, although still near the base of the ovary, the enlarged central placental region divides into four distinct placentae and the ovary becomes unilocular. At midlevel, the partition dividing the ovary into two locules is lost except for remnants intruding into the chamber from the ovary wall. At the very top of the ovary, the internal septum again becomes complete and two chambers are formed (Fig. 4, 24-28). The ovary wall is composed of an outer epidermis of conspicuously upright cells and a middle zone consisting of compact parenchyma. Patches of cells with golden brown contents extend around the inner mesophyll zone. Druses are scattered throughout the inner areas of the receptacle and lower levels of the ovary.

The ovary contains four bitegmic, campylotropous ovules (two per locule) attached near the center, and floor, of the ovary on axile placentae. Each ovule is borne on a long, upward-directed funiculus and has a curved body so that at maturity the micropyle is either directed downward to face the placenta or inward toward the funiculus (Fig. 3, 13). The inner integument is longer than the outer integument and forms the micropyle. The megagametophyte is situated below the epidermis at the micropylar end and is separated from the epidermis by one or two layers of subepidermal tissue. The subepidermal layer appears to be derived from the epidermis, suggesting that the ovule is crassinucellate.

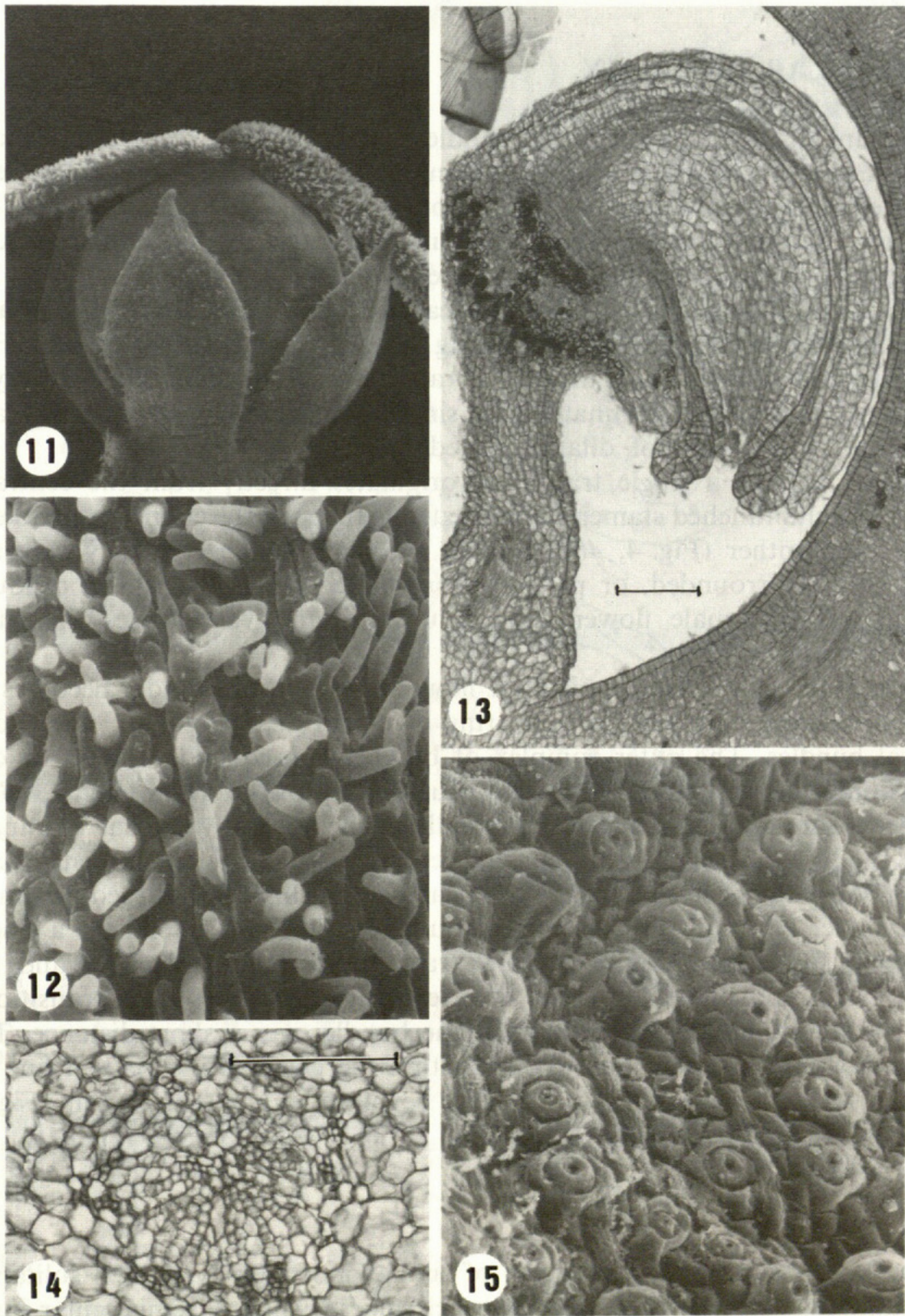


Fig. 3. — Floral anatomy of *Physena madagascariensis* : 11, side view of female flower, SEM $\times 15$; 12, detail of style surface showing lateral appendages, SEM $\times 150$; 13, longitudinal section of campylotropous ovule. Note bitegmic condition. Bar : $0.1\ \mu\text{m}$; 14, transverse section of amphicribral sepallary trace. Bar : $0.1\ \mu\text{m}$; 15, detail of abaxial sepal surface showing numerous raised stomata, SEM $\times 300$.

FLORAL VASCULAR ANATOMY

A ring of many discrete, closely spaced bundles is present in the receptacle. Sepals of both male and female flowers receive a single conspicuous trace that arises at a low level in the receptacle and extends upward and outward through the cortex (Fig. 4, 20-22, 34-36). Each sepal trace is typically associated with a single interfascicular region, although occasionally two sepallary traces confront one gap. Sepal traces are initially amphicribal (Fig. 3, 14), but become collateral and flattened in outline at the calyx base. Median sepal bundles are splayed and appear to be composed of several spreading strands of tracheary elements (Fig. 4, 18). Minor secondary and tertiary veins arise in a random manner and follow a very irregular course. Sepallary veins often terminate in a single irregular-shaped, enlarged and pitted tracheary element or a cluster of dilated, pitted cells.

Each stamen receives a single trace that originates directly from the central cylinder (Fig. 4, 37-39). The unbranched stamen bundle extends through the connective and ends at the upper limits of the anther (Fig. 4, 40). Stamen vascular bundles typically consist of 3 or 4 tracheary elements surrounded, or partially surrounded, by phloem. The residual central vascular cylinder of the male flower extends upward and vascularizes the rudimentary gynoecium.

At the base of the gynoecium in pistillate flowers, the central cylinder becomes organized into an internal vascular core and an outer ring of numerous (ca. 20-30), small to medium-sized, collateral bundles. The outer complex of bundles subsequently enters the ovary as a system of anastomosing wall strands that end near the top of the ovary (Fig. 4, 23-24). Each carpel possesses a somewhat distinct dorsal bundle in the adaxial wall that terminates at the stigma. Below the level of locule formation, the central vascular system consists of a dissected ring of phloem with four or five internal xylem patches. Within the enlarged placental region, the vascular cylinder begins to subdivide into four arcs. Each arc extends as a single bundle into the adjacent funiculus. As the ovulary trace traverses the placenta and enters the funiculus, the xylem and phloem become inverted (Fig. 4, 25, 26). This transition may be accompanied by an amphicribal condition of the bundle over a short distance. The ovular trace extends through the funicle and divides within the chalaza into several fine veins that reach the outer integument but do not extend beyond the chalazal region (Fig. 4, 27).

POLLEN

Both species of *Physena* possess pollen of similar morphology. Pollen solitary, radially symmetrical, small to medium-sized, tricolpate, circular to slightly semiangular in outline in polar view, and spherical to prolate-spheroidal in shape, (20.7-)23.5(-27.6) μm in polar view \times (20.5-)22.6(-25.3) μm in equatorial view (Fig. 5, 41). Colpae comparatively short, wide (ca. 9.2 μm), meridionally elongated, with nontapering ends, and covered with polymorphic granules and prominent spinules (Fig. 5, 42). Exine about 0.8-1.0 μm thick in the center of the mesocolpium, becoming thinner near the colpi. Exine differentiated into a tectum, columellae, footlayer, and endexine. The tectum comprising about one-third of total exine thickness,

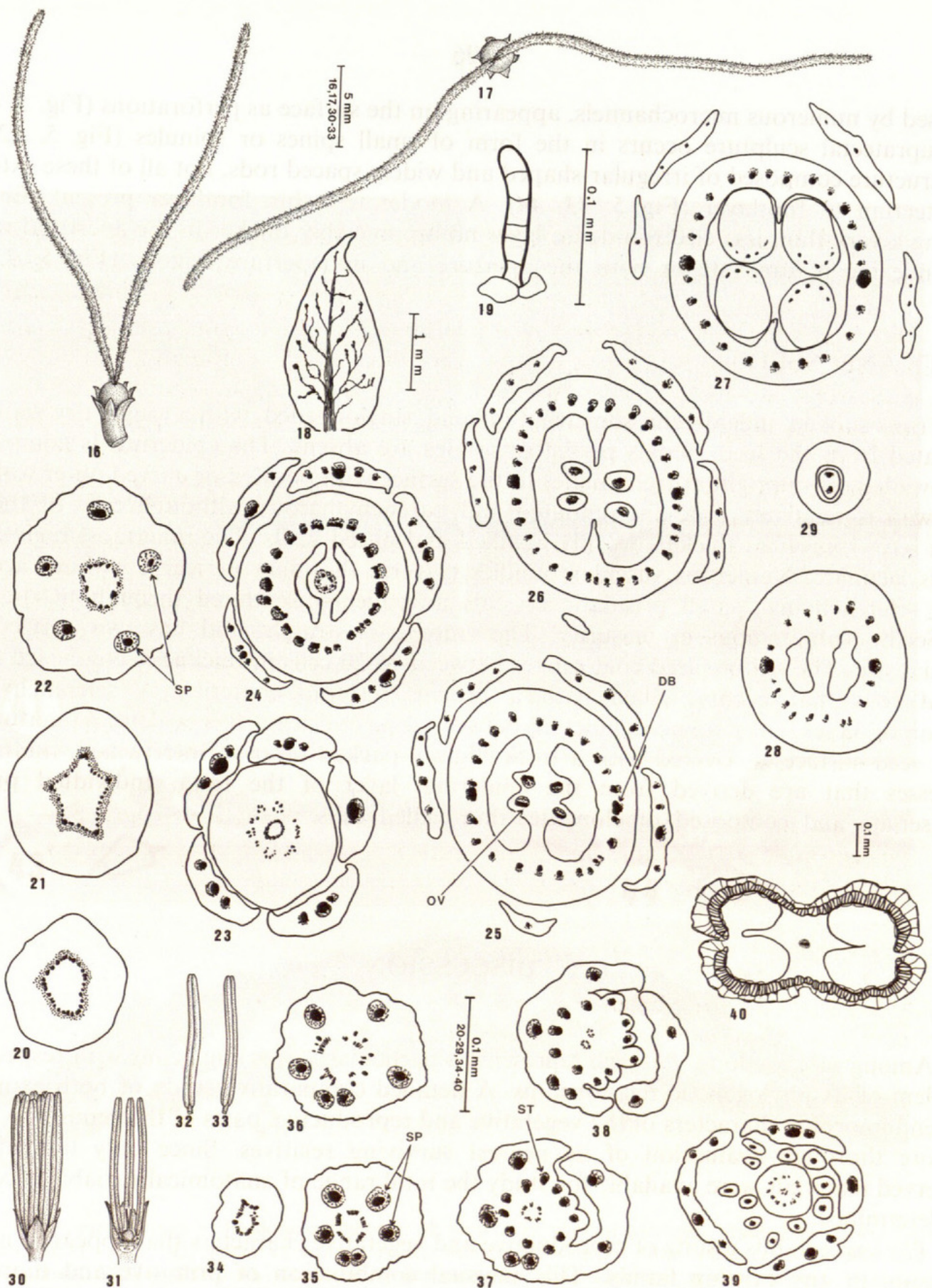


Fig. 4. — Floral morphology and anatomy of *Physena madagascariensis*: 16, female flower from side; 17, female flower from above; 18, sepal showing venation; 19, sepalary trichome; 20-29, camera lucida drawings of serial cross sections of the female flower from pedicel (20) to the top of the ovary (29), showing major vascular patterns (blackened and stippled areas); 30, male flower from side; 31, male flower from side with some stamens and a sepal removed showing rudimentary gynoecium; 32, stamen from side; 33, stamen from side; 34-39, camera lucida drawing of serial cross sections of the male flower from pedicel (34) to just below the level of the anthers (39), showing major vascular patterns (blackened and stippled areas); 40, transverse section of anther showing fibrous endothecium and endothecial-like hypodermal cells in the connective. DB, dorsal carpellary bundle; OV, ovular trace; SP, sepalary trace.

traversed by numerous microchannels, appearing on the surface as perforations (Fig. 5, 42, 43, 45). Supratectal sculpture occurs in the form of small spines or spinules (Fig. 5, 42). The infrastructure composed of irregular-shaped and widely spaced rods, not all of these extending from tectum to footlayer (Fig. 5, 43, 44). A moderately thin footlayer present. Endexine forming a very thin, less electron-dense layer not appreciably thicker in the apertural regions. The endexine is lamellate in both the aperture and nonaperture regions (Fig. 5, 43-45).

FRUIT AND SEED

Fruits stalked, indehiscent, somewhat inflated, single-seeded, with a tough, dry wall that is separated from the seed. Sepals persistent; styles are absent. The epidermis is composed of thick-walled cells upright at right angles to the surface with pointed or curved outer walls. The fruit wall is relatively little-differentiated and parenchymatous, although cells of the outer layers have somewhat thicker, weakly lignified and pitted walls. The innermost region of the wall is lacunate. Numerous vascular bundles traverse the inner pericarp, without accompanying sclerenchyma; small prismatic crystals infrequently scattered throughout the wall.

Seeds exalbuminous at maturity. The embryo is straight and has two cotyledons of unequal size. The mature seed coat ranges between 16-20 cells in thickness, composed of thin-walled cells that become filled with a brown, resinous material. A sclerenchymatous mechanical layer is absent, no distinction between testa and tegmen is evident. At maturity, the outer seed surface is covered with a thick, tightly packed layer of intertwined, multicellular processes that are derived from the epidermal layer of the testa. Individual processes multiseriate and composed of elongate, thin-walled cells.

DISCUSSION

Among dicotyledons, *Physena* represents a particularly puzzling genus with respect to the problem of its phylogenetic relationships. A detailed comparative study of both exomorphic and endomorphic characters of the vegetative and reproductive parts of the genus now permits a more thorough evaluation of its nearest surviving relatives. Since only limited liquid-preserved materials were available for study the total range of anatomical variability could not be determined.

Physena exhibits a suite of reproductive and vegetative characters that appear to negate its inclusion in any existing family. This unusual combination of primitive and more highly evolved features includes exstipulate leaves; unilacunar nodes; arc-shaped petiole bundle; anomocytic stomata; unisexual, apetalous flowers; a bicarpellate, synovarious gynoecium that is partly bilocular and partly monolocular; two long, essentially separate styles; two bitegmic, campylotropous ovules on each axile placenta; variable number of stamens in a single cycle; stamens composed of a long, basifixed anther and short filament; tricolpate, spinulose pollen; and indehiscent fruit, each with a single, essentially exalbuminous seed.

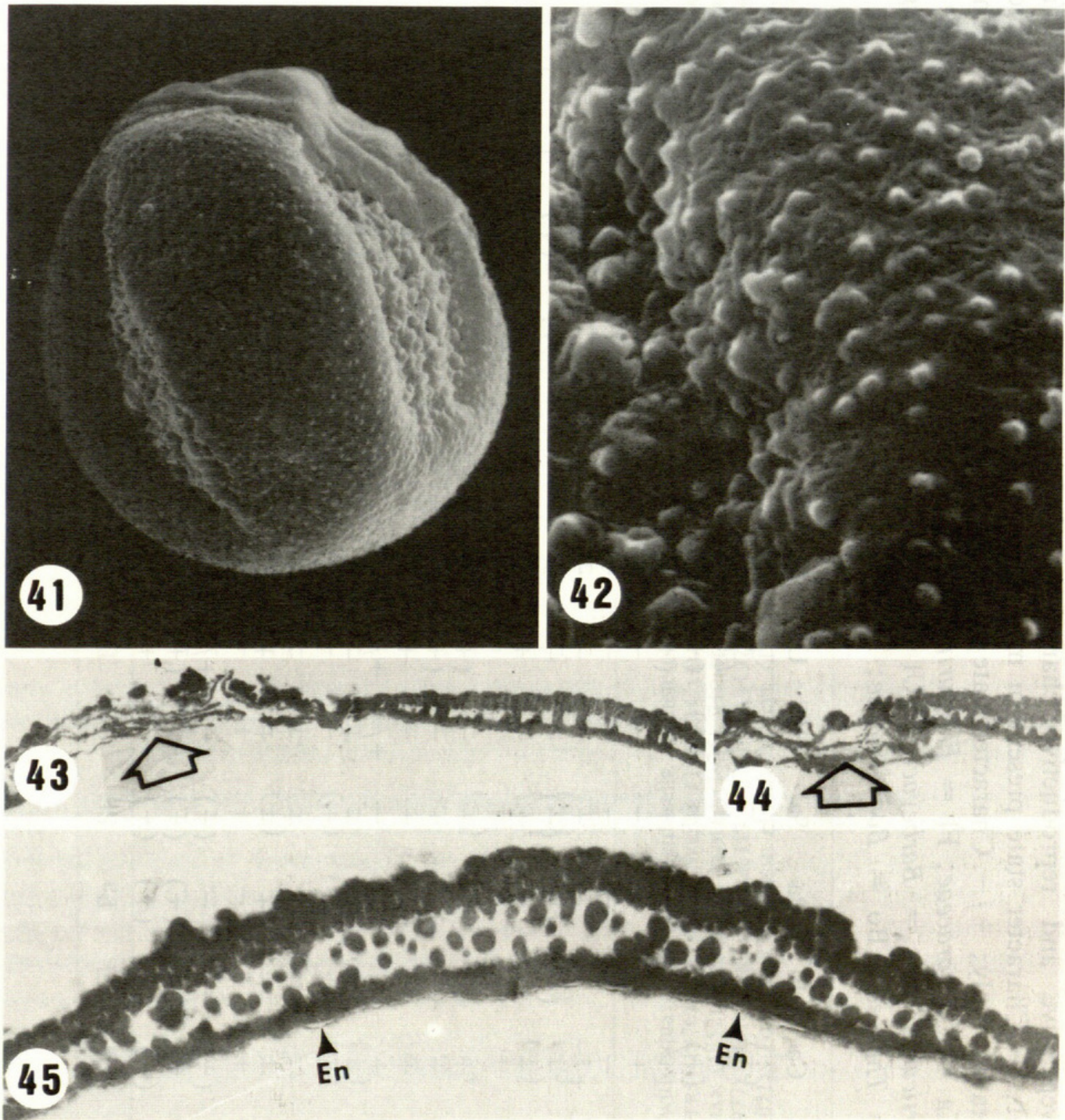


Fig. 5. — Pollen morphology of *Physena sessiliflora* : **41**, equatorial view of tricolpate grain showing wide, granular furrows, SEM $\times 720$; **42**, detail of tectum in the vicinity of colpus. Note suprategal spinules and tectal microchannels, SEM $\times 4700$; **43**, section of pollen wall including apertural region (arrow). Note tectum is traversed by microchannels, TEM $\times 3600$; **44**, section of pollen wall including apertural region (arrow). Note granules on colpus membrane, TEM $\times 3600$; **45**, oblique section of pollen wall showing tectal microperforations, columellate infrastructure, footlayer, and very thin endexine (En) that appears lamellate, TEM $\times 13500$.

TABLE 2 : Comparison of vegetative and reproductive characters of **Physena** and putatively related families.
 - Character state absent; + Character state present in most representatives of the family; (+) Character state present in a few representatives only; +/- Character state variable, present or absent in several taxa; ? Character state unknown. Taxa : Ca = *Capparaceae*; Fl = *Flacourtiaceae*; Pa = *Passifloraceae*; Sa = *Sapindaceae*; St = *Staphyleaceae*; Ur = *Urticaceae*; Ba = *Barbeyaceae*; Ul = *Ulmaceae*; Eu = *Eucommiaceae*; Fa = *Fagaceae*; Gu = *Guttiferae*; Th = *Theaceae*; Bo = *Bonnetiaceae*; As = *Asteropeia*.

Physena	Ca	Fl	Pa	Sa	St	Ur	Ba	Ul	Eu	Fa	Gu	Th	Bo	As
Leaves simple	(+)	+	+	-	-	+	+	+	+	+	+	+	+	+
Leaves alternate	+	+	+	+	(+)	(+)	-	+	+	+	-	+	+	+
Stipules absent	(+)	-	-	+	(+)	(+)	+	-	+	-	+	+	+	+
Anomocytic stomata	+	-	+	+	-	(+)	-	+	+	+	-	(+)	(+)	+
Unilacunar nodes	+	-	-	-	-	-	+	-	+	-	+	+	+	+
Venation brochidodromous	-	-	-	-	-	-	+	(+)	+	(+)	+	+	+	+
Bark nonfibrous	+/-	-	-	+	-	-	-	-	?	-	+/-	-	-	-
Vessels solitary	-	(+)	(+)	(+)	+	-	-	-	+	+/-	(+)	+	+	+
Perforation plate simple	+	+	+	+	-	+	+	+	+	+	+	-	+	+
Intervessel pits small (< 7m), alternate	+	+/-	+/-	+	-	(+)	+	-	+	-	-	-	+	+
Vessel-ray pits similar to above	+	+/-	+/-	+	-	(+)	-	+/-	+	-	-	+/-	-	+
Libriform fibers	+	+	+/-	+	-	+	+	+	-	+	+/-	-	-	+
Fibers nonseptate	+	-	+	-	+/-	+/-	+	+	+	+	+	+	+	+
Tracheids present	-	-	-	-	+	-	-	-	-	+	+/-	(+)	(+)	-
Rays mostly uniseriate (some biseriate)	-	-	-	+	-	-	-	-	-	+/-	-	-	-	+
Rays primitive ¹	-	+	+	-	+	+	-	+/-	-	-	+	+	+	-
Axial parenchyma abundant, aliform or confluent	(+)	-	-	(+)	-	+/-	-	(+)	-	-	-	-	+	+
Inflorescence racemose	+	(+)	(+)	(+)	(+)	(+)	-	-	+	-	-	-	+/-	+
Flowers apetalous	(+)	-	(+)	(+)	-	+	+	+	+	+	-	-	-	-

TABLE 2 (continued)

Physena	Ca	Fl	Pa	Sa	St	Ur	Ba	Ul	Eu	Fa	Gu	Th	Bo	As
Gynoecium bicarpellate, synovarious	+	(+)	-	-	(+)	-	-	+	+	-	-	(+)	-	-
Styles long, separate	-	(+)	-	-	-	-	-	+	+	+	(+)	(+)	+/-	+/-
Ovules bitegmic	+	+	+	+	+	+	-	+	-	+	+	+	+	+
Ovules campylotropous	+	-	-	(+)	-	-	-	-	-	-	-	(+)	-	-
Placentation axile	-	-	-	+	+	-	-	-	-	+	+	+	+	+
Stamens numerous, free	(+)	(+)	(+)	(+)	-	-	+	(+)	+	+	+	+	+	+
Anther long, basifixed	(+)	+/-	-	-	-	-	+	-	+	-	(+)	+/-	-	-
Endothecial-like connective hypodermis	-	-	-	-	-	-	?	-	+	+	-	-	-	-
Pollen tricolpate	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pollen spinulose	+/-	-	-	(+)	-	+	+	+/-	+	(+)	?	(+)	-	+
Pollen columellate	+	+	+	+	+	?	+	+/-	-	+	+	+	?	+
Tectum microperforate	(+)	-	?	(+)	-	?	+/-	+	-	+	?	-	?	-
Fruit indehiscent	(+)	(+)	(+)	(+)	(+)	+	+	+	+	+	+/-	+/-	-	+
Seed exalbuminous	+	-	-	+	-	-	+	+	-	+	+	+	+	+

1. Rays homocellular, typically with square and/or upright cells, or heterocellular, more than 4 rows of upright and/or square cells.

Sources of data : BARETTA-KUIPERS (1976), BONSEN & WELLE (1984), CARLQUIST & HOEKMAN (1985), CRONQUIST (1981), DICKISON (1986, 1987), DICKISON & SWEITZER (1970), ERDTMAN (1952), HICKEY & WOLFE (1975), HUFFORD & ENDRESS (1989), LIANG & BAAS (1990, 1991), MAGUIRE (1972), MENNEGA & LANZING-VINKENBORG (1977), METCALFE & CHALK (1950), MILLER (1975), ROWLEY, SKVARLA & PETTITT (1992), SCHMID et al. (1984), SCHOFIELD (1968), SINNOTT (1914), SWEITZER (1971), TOBE & TAKAHASHI (1990), WOLFE (1974, 1989), ZAVADA & DILCHER (1986).

The wood of *Physena* also shows both primitive and advanced character states. It has exclusively solitary vessels and typically upright or square ray cells suggesting relationships with relatively primitive families, but many more character states point to relationships with more highly evolved families. These more advanced features include simple perforation plates with slightly inclined end walls, small alternate intervacular pits that are the same size and shape as the vessel-ray pits, short tracheary elements, fibers with simple to minutely bordered pits, vascular or vasicentric tracheids, and aliform, confluent and unilateral paratracheal parenchyma.

The following discussion is devoted to the difficult problem of clarifying the relationships of *Physena*. Morphological comparisons are made between *Physena* and putative allies. A family was considered for comparison if it had been previously suggested as a possible close ally by other workers, or if morphological characteristics indicated that the group warranted attention. A summation of available morphological information is presented in Table 2. It must be kept in mind, however, that some possible closely related families may have been overlooked and thus excluded for comparison. An additional problem in comparisons of the type presented is that large families often contain variation in a particular character and some genera in a family may be similar to *Physena* while others are not. Comparative data were obtained from the literature and from original observations.

CAPPARACEAE

In the Englerian system, *Physena* is associated with the genera *Forchhammeria* and *Stixis* to form the tribe *Stixeeae* of *Capparaceae* (PAX & HOFFMANN, 1936). In addition to general features, the following noteworthy resemblances are found between *Physena* and species of *Capparaceae* : racemes, stamens free in one cycle; a mostly bicarpellate, synovarious gynoecium; campylotropous ovules; seeds with endosperm scanty or absent (endosperm abundant in a few *Capparaceae*); unilacunar nodes; multicellular, nonglandular trichomes; anomocytic stomata; and development of numerous sclereids (stone cells) in the nonfunctional secondary phloem. In addition, it is of significance that *Physena* possesses the capparaceous (and cruciferous) feature of inverted collateral placental bundles.

However, suggestions of a close affinity between *Physena* and *Capparaceae* cannot be supported. *Physena* lacks the characteristic gynophore or androgynophore and occasionally jointed fruit stalks of the *Capparaceae*, and importantly, there is no evidence of myrosin cells. Other important differences between these taxa are sepals mostly 5-9 in *Physena*, perianth only occasionally other than 4-merous in *Capparaceae*; sepals one-trace structures in *Physena*, sepals 3-trace in *Capparaceae*; short stamen filaments in *Physena*, generally long filaments in *Capparaceae*; anthers basifixed in *Physena*, anthers most often dorsifixed in *Capparaceae*; pollen tricolpate in *Physena*, pollen tricolporate in *Capparaceae*; axile placentation in *Physena*, mostly parietal placentation in *Capparaceae*; ovules few in *Physena*, ovules mostly numerous in *Capparaceae*; styles long and mostly separate in *Physena*, styles united or short, sessile or lacking in *Capparaceae*; and floral nectary absent in *Physena*, nectary present in *Capparaceae*. Also, few *Capparaceae* are apetalous and unisexual. Although the partly bilocular and partly unilocular condition of the *Physena* gynoecium also occurs in a few capparaceous genera (*Oceanopapaver*, *Crateva*), in the latter, the gynoecium is initially unilocular, becoming

bilocular by fusion of placental protrusions. In contrast, the ovary of *Physena* has presumably more primitive axile placentation and is bilocular at the base and apex, becoming unilocular at midlevel. Furthermore, evidence from wood anatomy does not support a close alliance between *Capparaceae* and *Physena*. Capparaceous woods differ noticeably from *Physena* in vessel distribution, ray histology, and distribution of axial parenchyma.

FLACOURTIACEAE AND PASSIFLORACEAE

Available evidences exclude *Physena* from a position in, or in close proximity to, either *Flacourtiaceae* or *Passifloraceae*. *Physena* lacks the mostly parietal placentation, non-campylotropous ovules, trilacunar nodes, stipulate leaves, tricolporate pollen, and albuminous seeds of these families. Mature stomata of *Flacourtiaceae* are paracytic or anisocytic. The wood of *Flacourtiaceae* is relatively heterogeneous, but the combination of septate fibers, lack of axial parenchyma, and heterocellular rays with many rows of upright cells delimits the family. These characters are not present in *Physena*. HUTCHINSON (1967) cited a personal communication from C. R. METCALFE that read "on balance the (anatomical) characters indicate that *Physena* should be in *Passifloraceae*". We do not concur with this opinion. *Passifloraceae* typically do not have exclusively solitary vessels, short tracheary elements, and paratracheal parenchyma. The one passifloraceous genus with exclusively solitary vessels, *Soyauxia*, also has scalariform perforation plates and opposite intervacular pitting.

SAPINDALES

CAPURON (1968) pointed out apparent similarities in seed morphology between *Physena* and certain *Sapindaceae*. According to TAKHTAJAN (1987), Sapindales are composed of 12 families including *Physenaceae*. Comparative morphology and anatomy is not in harmony with this view.

Sapindaceae, the largest family of the order, are structurally homogeneous, typically having small vessels with radial multiples in a diffuse pattern; simple perforation plates; small alternate intervacular pits the same size as the vessel-ray pits; scanty to vasicentric paratracheal parenchyma; uniseriate homocellular rays; and septate fibers with simple pits. This combination of characters does not relate it to *Physena*. Other families in Sapindales also differ wood anatomically from *Physena*.

Furthermore, sapindalean families have a predominantly trilacunar nodal anatomy in contrast to the unilacunar structure of *Physena*. Pollen of the Sapindales is fundamentally of the reticulate, tricolporate (or derived) type. In our opinion, the few similarities in reproductive morphology are mostly superficial.

HAMAMELIDIDAE

CRONQUIST (1988) concluded that *Physena* fully merits familial status and, emphasizing its reduced flowers and long, latrorse anthers, tentatively assigned it a position in his concept of

Hamamelidaceae (Urticales), which includes *Moraceae* (sensu lato), *Ulmaceae*, *Urticaceae*, *Cannabaceae*, and *Barbeyaceae*. As noted by CRONQUIST, however, *Physena* differs from this assemblage in their exstipulate leaves, axillary racemes, and ovary structure with two ovules. The occurrences of cystoliths and pseudomonomerous gynoecia among urticalean families are not matched in *Physena*. The brochidodromous leaf venation of *Physena* also differs from the actinodromous venation or straight craspedodromous secondary veins typical of various hamamelidid grade taxa.

With the exception of the problematic *Barbeyaceae*, the wood of Urticales generally has large vessels that are often solitary, but never exclusively solitary; simple perforation plates; large alternate intervacular pits that are generally larger than the vessel-ray pits; wide hetero- to homocellular rays; various types of paratracheal parenchyma; and fibers with simple pits that are often septate. These characters do not support a particularly close relationship with *Physena*. Also, nodes of hamamelidid taxa are mostly tri- or multilacunar.

Barbeyaceae, a monotypic family of uncertain affinities, resembles *Physena* anatomically in a number of aspects of xylem structure and the possession of unilacunar nodal anatomy. However, the gynoecium of *Barbeyaceae* is uni-(tri-) carpellate, sepals are enlarged in the fruiting stage, and the pollen wall possesses a granular layer and sculpturing is rugulate (TOBE & TAKAHASHI, 1990). These are features absent from *Physena*.

As a result of a general overall resemblance in aspects of gross floral morphology between *Physena* and *Eucommiaceae*, such as unisexual flowers that are devoid of perianth and staminate flowers having 5-12 stamens with very short filaments and long anthers, direct comparisons were made of all organs and tissues of these two families. *Eucommia*, the only genus in *Eucommiaceae*, and *Physena* have similar vessels (exclusively solitary vessels with similar lengths and diameters, simple perforation plates, and small alternate intervacular pits the same size as the vessel-ray pits). The only difference is the presence of helical thickenings in *Eucommia* that is a reflection of its temperate habitat. The other tissue types are not similar. Unlike *Physena*, the fibers of *Eucommia* have conspicuous bordered pits, ray are homocellular, 2-3 cells wide, with distinctly procumbent cells, and axial parenchyma is apotracheal diffuse and marginal.

Although nodal anatomy of *Eucommia* is unilacunar, its unilocular ovary, pendulous, anatropous, unitegmic ovules, and embryo embedded in copious endosperm document that the affinities between *Physenaceae* and *Eucommiaceae* are very distant. It has been pointed out recently that *Eucommia* has spinulose, tricolporate pollen, making the genus highly anomalous in the *Hamamelididae*. However, note that the brochidodromous leaf venation of *Eucommia*, and *Physena*, is more like members of Theales (WOLFE, 1989).

Despite the previously discussed comparisons, stamen and pollen characteristics lend evidence to corroborate the view that *Physena* has putative hamamelidid connections. HUFFORD & ENDRESS (1989) concluded that the presence of an endothelial-like connective hypodermis in the stamens is an important unifying feature of potential phylogenetic importance among "lower Hamamelididae". This condition, that also occurs in *Physena* and presumably facilitates the opening of the anther, is present in all members of the "lower Hamamelididae" except *Disanthus* (*Hamamelidaceae*). Both *Eucommia* and *Daphniphyllum* also possess an endothelial-like connective hypodermis, suggesting that they, like *Physena*, have retained what is probably a plesiomorphic feature of *Hamamelididae* ancestry (HUFFORD & ENDRESS, 1989). This feature is absent among Urticales.

Lower hamamelid grade taxa have stamens with basifixed anthers and branched stomia which lead to valvate dehiscence (HUFFORD & ENDRESS, 1989); whereas the “higher hamamelids” tend to share the derived stamen attributes of sub-basifixed or dorsifixed anthers with unbranched stomia that lead to “linear” dehiscence. The pollen of lower hamamelids is basically tricolpate, whereas the derived tricolporate condition characterizes the higher families. The presence of a tricolpate pollen aperture condition in combination with the presumably derived features of sculpturing composed of spinules, a tectum traversed by microperforations, and a columellate or columellate-granular infrastructure, represents a suite of characteristics that are unique to the *Hamamelididae* (ZAVADA & DILCHER, 1986). The occurrence of these stamen and pollen features in *Physena* are of considerable taxonomic importance and serve to link the genus with the *Hamamelididae*, although they do not convincingly relate it to any particular family or group of families. The transitional aspect of *Physena* is evidenced by the possession of basifixed anthers with an endothelial-like connective hypodermis and linear dehiscence coupled with a primitive tricolpate, prolate-spheroidal pollen condition that is associated with an advanced tectum traversed by small microchannels and covered with spinulose sculpturing.

THEALES

Because ERDTMAN (1952) pointed out similarities between the spinuliferous pollen of *Physena* and the thealean genus *Asteropeia*, attention has been directed to the Theales as putative surviving relatives. *Physena* approaches many members of the thealean alliance in the imbricate, aposepalous calyx; retention of many free, or essentially free, stamens; syncarpous ovary with few ovules on each of the axile placentae; essentially distinct styles; exstipulate leaves; secondary leaf venation brochidodromous; and unilacunar nodes. In Theales, endosperm varies from abundant to scanty or none and, like *Physena*, seeds are often arillate. In *Theaceae*, each sepal is vascularized by a single trace as in *Physena*. *Physena* deviates markedly from the typical theoid condition in the absence of petals, the presence of tricolpate, spinulose pollen as opposed to tricolporate, reticulate or derived types of pollen, and in the partly monolocate and partly bilocate ovary. Stamen fascicle bundles, tenuinucellate ovules, and diffuse foliar sclereids, characteristics of many thealean plants are absent from *Physena*.

The secondary xylem of many theoid grade taxa is at a conspicuously more primitive level of structural specialization as compared with *Physena*, seemingly negating any close relationships between the two groups. The more advanced xylems of other theoid families, such as *Pellicieraceae* and *Clusiaceae* (*Guttiferae*), are in some instances more comparable to *Physena*, although no close affinity is apparent.

In contrast, the thealean family *Bonnetiaceae*, considered by most phylogenists to be related to *Clusiaceae* (MAGUIRE, 1972; TAKHTAJAN, 1987) shows strong wood anatomical similarities with *Physena*. Following an examination of wood anatomy, BARETTA-KUIPERS (1976) found that *Bonnetiaceae* (excluding *Kielmeyera*) is intermediate between *Theaceae* and *Clusiaceae* (*Guttiferae*). The wood of *Physena* and *Bonnetiaceae* is closely comparable. The vessels are mostly exclusively solitary with small intervacular pits, and the perforation plates are simple and transverse in both. The difference in vessel morphology is the vessel element

length and vessel-ray pits. In *Physena*, the vessel elements are short and the vessel-ray pits are horizontal to vertical. In *Bonnetiaceae*, the rays are exclusively uniseriate or mostly 2-5 cells wide and heterocellular with several rows of upright/square cells that compare closely with the rays of *Physena*. The axial parenchyma in both are similar, that is, paratracheal (generally scanty in *Bonnetiaceae* and aliform to confluent in *Physena*) and unilateral paratracheal. The fibrous elements in *Bonnetiaceae* are septate or nonseptate, long to medium length, with simple or conspicuous bordered pits, and with or without vasicentric tracheids. *Physena* has short nonseptate fibers with simple to minutely bordered pits. These similarities in wood structure suggest that *Physena* may be somewhat related to *Bonnetiaceae*. The same general combination of wood features also occurs in the monotypic theaceous family *Medusagynaceae* (DICKISON, 1990).

The wood anatomy of the small genus *Asteropeia* (*Theaceae* or *Asteropeiaceae*) and *Physena* (both Madagascan endemics) also provides useful comparisons. Both have similar vessels, rays, fibers, and axial parenchyma types and distributions. Both have small alternate intervacular pits with vessel-ray pits similar in size and shape. A notable difference is the uniseriate homocellular rays composed entirely of procumbent cells in *Asteropeia* versus the uniseriate homocellular to heterocellular rays composed mostly of upright or square cells in *Physena*.

CONCLUSIONS

The anatomical and morphological results presented here fully justify the exclusion of *Physena* from existing families and the establishment of the monogeneric *Physenaceae* as initially suggested by TAKHTAJAN. This conclusion has been reached with the understanding that the multiplication of small families should be recommended only after careful consideration. Our results show that *Physena* is characterized by a unique combination of primitive and advanced character states that appear to occur in no other family. In general, certain aspects of *Physena* reproductive morphology, such as pollen morphology, stamen structure including the presence of an endothelial-like connective hypodermis, and specializations correlated with presumed wind pollination, are reminiscent of various taxa often assigned to the *Hamamelididae*. These features support the view that the *Physenaceae* are an isolated Southern Hemisphere family within the *Hamamelididae* that have no obvious single category of close surviving relatives. On the other hand, vegetative anatomy is comparable with certain structurally advanced elements of the thealean complex. The fact that *Physena* shows ambiguous connections to families assigned to both hamamelid and theoid lines emphasizes the complex patterns of relationships that appear to exist and the difficulties of treating such apparently isolated relics.

The present study points out the limitations of morphological and anatomical data when dealing with unusually difficult systematic problems. However, it is equally clear that a broad base of reliable structural evidence cannot be ignored in the search for the relatives of *Physena* and in the reconstruction of phylogeny. Anatomical evidence adds to the summation of evidences that will eventually fully clarify the phylogenetic affinities of *Physena* by the

identification of a convincing outgroup and subsequent cladistic analysis. Clearly, the observations presented here need to be supplemented by additional evidence in order to ultimately resolve this challenging taxonomic problem.

ACKNOWLEDGEMENTS : We thank PH. MORAT and A. LE THOMAS, Laboratoire de Phanérogamie, Muséum National D'Histoire Naturelle (Paris), and George E. SCHATZ, Missouri Botanical Garden (St. Louis) for providing material of *Physena*. The assistance of Barbara F. PALSER (New Brunswick) is also acknowledged with appreciation. This research was partially supported by a grant from the University Research Council, The University of North Carolina at Chapel Hill. This article was written and prepared by U.S. Government employees on official time, and it is therefore in the public domain and not subject to copyright.

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Dickison, W C and Miller, R B. 1993. "Morphology and anatomy of the Malagasy genus *Physena* (Physenaceae), with a discussion of the relationships of the genus." *Bulletin du Muse*

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