THE MORPHOLOGY AND RELATIONSHIPS OF PARACRYPHIA (PARACRYPHIACEAE)

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CONTENTS

SUMMARY

A comprehensive study of floral and vegetative anatomy of the monotypic New Caledonian genus *Paracryphia* Baker was initiated in an attempt to help clarify the evolutionary relationships of the genus. Detailed descriptions of leaf, axis, nodal, wood, floral, pollen, and fruit morphology and anatomy are presented. In general, most vegetative characters are distinctly primitive whereas those of the reproductive organs are regarded as advanced or specialized. The present study confirms the opinion that *Paracryphia* merits familial status. All previously suggested relationships of the genus are rejected in favor of a view that envisions *Paracryphia* as an independent and early divergence from the Thealean, Ericalean, and/or Celastralean lines of evolution. This view is based on similarities of *Paracryphia* with *Sphenostemonaceae*, *Actinidiaceae* and *Theaceae* in a number of characters.

INTRODUCTION

Paracryphia is a monotypic, arborescent, dicotyledonous genus endemic to New Caledonia. The plant ranges in habit from a shrub to a tree 18 meters in height, and available data indicate that it grows in humid forests between 750 and 1500 meters altitude. Although the systematic relationships of the genus are obscure, it has received little attention and

as a result is more often than not excluded from general systems of classification. The genus was initially described by Baker (1921) with the name *P. suaveolens* Baker *f.*; however, the plant had been previously described by Schlechter (1907) as *Ascarina alticola* Schltr, a member of the *Chloranthaceae*. In 1950 Van Steenis combined the two as *P. alticola* (Schltr) Steen.

Baker (*loc. cit.*) originally included *Paracryphia* in the *Eucryphiaceae*, noting, however, that it differed from *Eucryphia* in a number of characteristics. Both Gilg (1925) and Bausch (1938) were of the opinion that its affinities were probably near the primitively vesselless families *Winteraceae* or *Trochodendraceae*. This point of view was also expressed by Guillaumin (1948). Swamy (1953), following a survey of the vegetative and floral characters of the genus, excluded it from the *Chloranthaceae* and emphatically denied that it was related to *Winteraceae*, *Trochodendraceae*, or *Illiciaceae*. *Paracryphia* was elevated to familial status by Airy Shaw (1965) who believed that it was closely related to the *Trochodendraceae* and perhaps should even be included in that family. Airy Shaw also pointed out the superficial similarity between the gynoecium of *Paracryphia* with that of another isolated genus, *Medusagyne*. Agababyan and Zavaryan (1971) have supported the recognition of an independent family, *Paracryphiaceae*, on the basis of pollen morphology. Takhtajan (1973), in an uncertain manner, recognized the family *Paracryphiaceae* and while noting that its affinities were very obscure, placed it near *Eucryphiaceae*.

This study was undertaken to provide a more thorough morphological and anatomical description of the genus with the objective of clarifying its natural affinities.

MATERIALS AND METHODS

Both liquid preserved (FAA) material and dried herbarium specimens were examined. Wood samples were boiled in water and cut on a sledge microtome at a thickness of 20—30 μm. Resulting sections were stained with Heidenhain's haematoxylin and safranin. Data relating to wood cell length were obtained by making at least 25 measurements from macerations prepared using Franklin's method. Cell diameters were measured from transverse sections. Preserved leaves, stems, and flowers were embedded in paraffin and cut on a rotary microtome. Sections were obtained throughout the length of petioles. Flowers and nodes were cut serially. Sections were subsequently stained with a safranin fast-green combination. Details of leaf and floral venation were observed using cleared tissues prepared in 5% hot NaOH followed by safranin staining. Epidermal leaf features were examined using free hand sections. Dried specimens were initially re-expanded in 5% NaOH, placed in FAA, and then treated like preserved materials. Fruits were embedded in celloidin and sectioned on a sledge microtome. Slides are deposited in the Rijksherbarium, and the Department of Botany, University of North Carolina at Chapel Hill.

Pollen was acetolysized and mounted in glycerine jelly. Acetolysized pollen as well as wood and seed samples were gold coated and observed with the Cambridge AII Scanning Electron Microscope at the Geological Institute, University of Leiden. For transmission electron microscopy, nonacetolysized pollen grains from a herbarium specimen were soaked for one week in 0.1% glutaraldehyde in 0.1 M cacodylate buffer to which was added 2% glucose, and subsequently fixed in 1% uranylacetate. The material was embedded in epon and sectioned at 800 Å with a diamond knife. The sections were counterstained according to Reynolds with lead. Observations were made with a Philips EM 300 at the Zoological Laboratory of Leiden University.
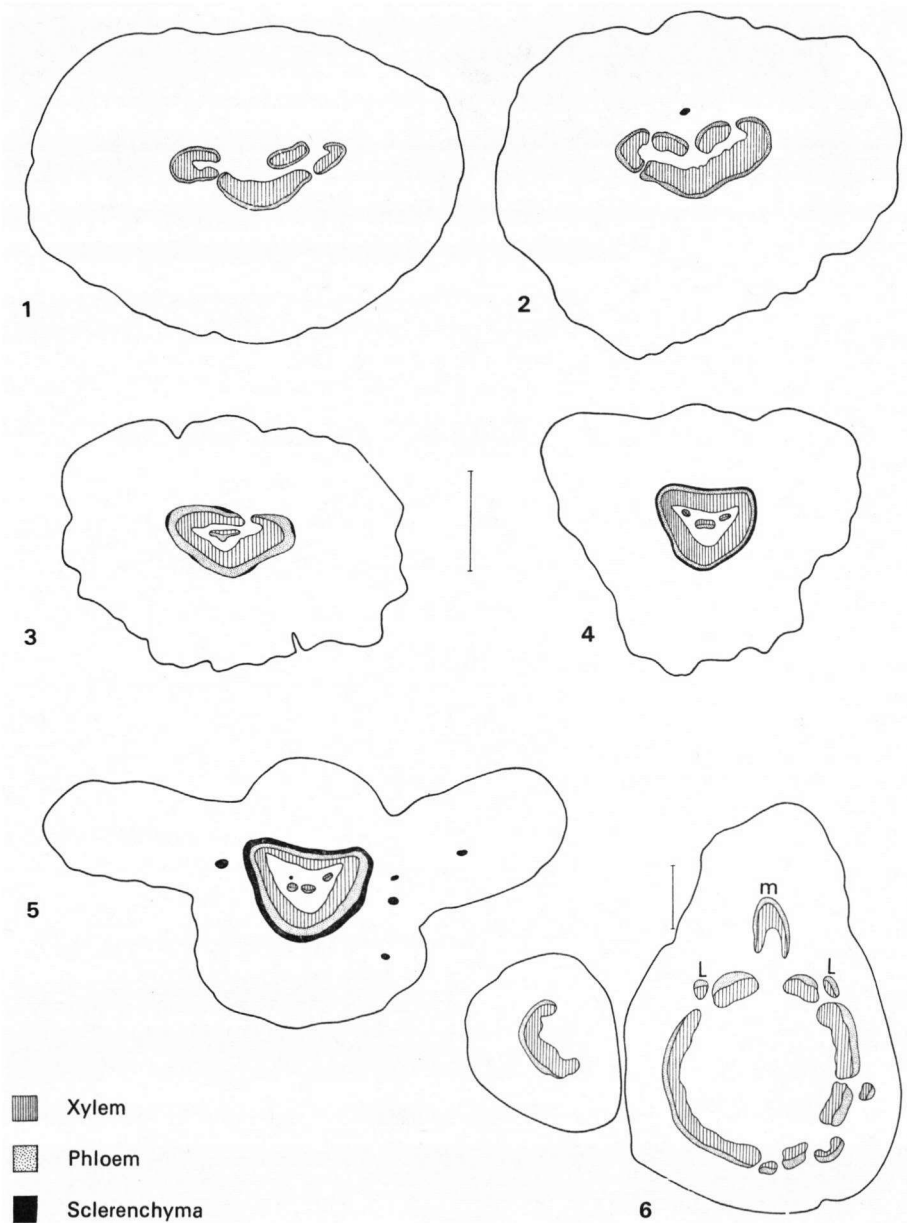
Fig. 1—6. Camera lucida drawings of nodal and petiole anatomy. Line equals 1 mm. — 1—5. Transverse sections from the base (1) to the distal region (5) of the petiole showing changes in the vascular system (*Schlechter 15326*). — 6. Transverse section of the node showing trilacunar, three-trace condition; M = median leaf trace, L = lateral leaf trace (*McKee 31070*).

Wood terminology corresponds to the Multilingual Glossary of Terms used in Wood Anatomy (Committee on Nomenclature, International Association of Wood Anatomists, 1964). Terminology relating to leaf venation and bark anatomy follow suggestions of Hickey (1973) and Zahur (1959) respectively.

The following specimens obtained from the Muséum National d'Histoire Naturelle, Paris (P) and the Rijksherbarium, Leiden (L) were studied: *Paracryphia alticola* (Schltr) Steen., New Caledonia: *H. S. McKee 26820* (P), pickled flowers, dried leaves; *H. S. McKee 31070* (P), pickled leaves, stems, fruits, mature wood, and bark; *H. S. McKee 27400* (P), dried leaves; *H. S. McKee 31490* (P), dried leaves and young fruits; *H. S. McKee 4993* (P), dried leaves, immature wood; *H. S. McKee 5380* (P), dried leaves; *M. Schmid 1575* (P) dried leaves; *L. Bernardi* 10362 (P), dried leaves; *R. Schlechter 15316* (L), dried leaves and twig.

<div align="center">DESCRIPTIVE PART</div>

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Vegetative morphology and anatomy
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Leaf (Figs 1—5, 7—9; Plate I, 1 & 2)

Leaves simple, petiolate, exstipulate, in verticillate to subverticillate arrangement. Blades coriaceous with an acute to acuminate apex, an attenuate base, and finely serrate margins. Leaf primordia protected by well developed bud scales. Young leaves densely pubescent with unicellular, unbranched hairs. Indumentum progressively lost in more mature foliage. Venation pinnate with a straight primary vein. Secondary veins brochidodromous with a series of 2 or 3 orders of ascending marginal loops (fig. 7). Secondary veins fairly thick, diverging at an occasionally variable moderate angle from the midvein, and abruptly curved. Composite intersecondary veins frequently originating from the midvein. Tertiary veins in a predominantly orthogonally reticulate pattern. High order veins forming a reticulum in which the veins arise in an orthogonal manner and in which areolation is well developed, orientated and quadrangular (fig. 8). Veinlets present or absent, mostly linear or curved, occasionally branched. Marginal ultimate venation looped. Teeth vascularized by a single medial vein extending to the tooth apex (fig. 9). Vein endings expanded. Teeth often capped by opaque cells. Low and high order veins sheathed by lignified parenchyma of irregularly shaped cells. Specialized terminal cells absent.

L a m i n a   i n   s u r f a c e   v i e w: *Trichomes* very sparse, unicellular, unbranched. Adaxial *epidermal cells* 4—7 sided with straight to slightly curved anticlinal walls, strongly elongate over veins. Abaxial epidermal cells 5—6 sided with straight to curved anticlinal walls, elongate over veins. *Stomata* confined to the abaxial surface, anomocytic; guard cell pairs 23—33—39 μm long, 21—25—30 μm wide (Plate I, 1).

I n   t r a n s v e r s e   s e c t i o n: *Lamina* bifacial. Adaxial *cuticle* 9—12 μm thick; abaxial cuticle 3—4 μm, up to 13 μm thick over midrib. Adaxial *epidermal cells* upright to procumbent (mainly square), larger than abaxial cells. Epidermal cells over midrib with dome-shaped outer periclinal walls. *Stomata* in level with the unspecialized epidermal cells, with well developed outer and small inner cuticular ledges. *Mesophyll* composed of 2(—3) layers of elongate palisade cells with dark-staining contents and spongy region of which central portion has thick-walled, lignified cells (Plate I, 2). *Midrib* with a raised abaxial and adaxial surface, supplied with a simple to complex (fig. 5) vascular system, sheathed by sclerenchyma fibres. Ground tissue of midrib collenchymatous at periphery,

parenchymatous near vascular system, interspersed with very thin-walled brachysclereids. Major *veins* surrounded by thick-walled, lignified parenchyma with extensions to adaxial surface, usually not reaching abaxial surface; minor veins also with lignified parenchymatous bundle sheaths but embedded in mesophyll. *Styloid crystals*, up to 250 μm long, scattered throughout mesophyll. *Petiole* provided with a thick cuticle (10—15 μm), supplied at the base with three distinct vascular bundles which give rise to a dissected crescent-shaped strand that subsequently invaginates at the distal ends to produce a closed, or nearly closed vascular system in the form of a ventral arc and a flattened dorsal region with a large centrally positioned collateral medullary bundle (figs 1—4). Whole system sheathed by sclerenchyma in distal end. Ground tissue compact at periphery, lacunate around vascular system, interspersed with thick-walled brachysclereids and cells containing styloid crystals.

Node (Fig. 6)

Trilacunar, three-trace in both young and older stems. Collateral traces diverging from cauline system at the same level and close to each other. Median trace C-shaped and larger than laterals.

Axis (young twigs, 3—5 mm in diameter; Plate I, 4)

Unicellular unbranched *hairs* abundant on young stems, absent on older material. *Cuticle* up to 18 μm thick. *Epidermal cells* erect, with dome-shaped outer walls in young twig, flattened rectangular in older material. *Periderm* arising in subepidermal layer. *Cortex* of c. 14 cell layers parenchymatous, compact at periphery, with large intercellular spaces in inner portion, rarely interspersed with brachysclereids. *Vascular tissue* in a complete cylinder, with a well developed ring of *perivascular sclerenchyma* fibres. *Secondary phloem* composed of sieve tubes, companion cells, and parenchyma, without mechanical tissue. Secondary *xylem* traversed by narrow rays and with angular vessels; similar in qualitative characters to mature wood. *Pith* c. 2 mm in diameter, composed of parenchyma, which becomes lignified from periphery inwards in older material, occasionally interspersed with thick-walled brachysclereids. *Styloid crystals* in cortex, pith, and phloem parenchyma (Plate I, 4); those of secondary phloem with a smaller diameter than the others.

Bark (of mature stem; Plate I, 3 & 5)

Bark well developed, 4 mm thick. *Periderm* of thin-walled cells, rectangular in transverse section, up to 20 layers thick, occasionally interspersed with sclerified cells. Secondary *phloem* composed of sieve-tube elements, companion cells, phloem parenchyma, and abundant thick-walled fibres, traversed by heterogeneous rays which are slightly dilated and partly sclerified in the older phloem. *Fibres* in interrupted, 1—5 cells thick tangential bands or clusters, differentiated close to the cambial zone. *Parenchyma* sclerified in older phloem. *Sieve tube elements* scattered or in groups, with compound sieve plates in highly oblique end walls (Zahur's type I—II; Plate I, 5). *Styloid crystals* abundant throughout the bark; prismatic crystals observed in periderm of *McKee 4993* only.

Wood (Plate II)

When two mean figures are given, the first relates to a mature wood sample (*McKee 31070*) and the second to an immature sample (*McKee 4993*).

Growth rings extremely faint to absent. *Vessels* diffuse, (27—)39(—51)/mm², solitary (57%) or in radial multiples of 2—6, angular to rounded in transverse section (Plate II, 1), tangential diameter (35—)47 & 64(—84) μm, vessel element length (1050—)1760 & 2000(—2620)μm. Perforations scalariform in almost vertical end walls, with (58-) 111 (—203) bars (Plate II, 3 & 4). Bars very narrow and closely spaced, occasionally reticulate. Intervessel pits scalariform or transitional (Plate II, 5). Vessel-parenchyma and vessel-ray pits opposite to scalariform, half bordered. Tyloses, vessel contents, or helical thickenings absent. Ground tissue composed of *fiber-tracheids*, 24—32 μm in tangential diameter, (890—)2060 & 2300(—3490) μm long; walls *c.* 7 μm thick with numerous bordered pits radially and tangentially. Pits *c.* 4 μm in diameter with extended slit-like apertures. Helical thickenings absent. *Parenchyma* diffuse and diffuse-in-aggregates, apotracheal as well as scanty paratracheal, strands 4—6 cells long. *Rays* heterogeneous I (Kribs, 1968), of two distinct sizes; uniseriates of erect cells 10/mm; bi- and triseriates with long uniseriate marginal portions of erect cells and central portion of procumbent to square cells 1—2/mm (Plate II, 2). *Styloid crystals* sparsely present in axial parenchyma. *Silica bodies* absent.

Reproductive anatomy

Inflorescence
The multiflowered, branched, terminal inflorescence is paniculate although the flowers are sessile (*i.e.*, a compound spike). Inflorescence axes are covered with unicellular, unbranched trichomes.

Flowers (Figs 10—13; Plate III, 1)
G e n e r a l   o r g a n o g r a p h y   a n d   a n a t o m y: The flowers of *Paracryphia* are either bisexual, or occasionally exclusively staminate. These staminate flowers have no abortive gynoecium and are borne at lower levels on the inflorescence axes. The undifferentiated perianth consists of four caducous, decussate, concave, free segments. Aestivation of the perianth parts is cochleate, *i.e.*, having one large helmet-shaped segment that encloses or covers the others (fig. 10). Perianth parts are covered externally with unicellular (rarely bicellular), unbranched trichomes of the same type as occur on vegetative parts of the plant. Lignified, highly pitted macrosclereids are scattered throughout the perianth tissue. The apostemonous androecium is usually composed of 8 stamens borne in a single cycle. Each stamen consists of a filament and a basifixed anther (fig. 13). Each anther is composed of a connective and four locules, *i.e.*, shows the tetrasporangiate condition. Before longitudinal dehiscence the partition between the two locules of the same theca breaks down, thus forming a single chamber. Each microsporangium has a well developed endothecium with lignified thickenings in the form of bands. The endothecium is interrupted in the region of the connective and locular partition. Filaments do not have a central lacuna associated with the vasculation. Stamens of male flowers develop

Fig. 7—13. Camera lucida drawings of leaf and floral morphology of *Paracryphia*. Line equals 1 mm. — 7. Leaf showing pattern of low order venation (*McKee 26820*). — 8. Details of high order leaf venation (*McKee 26820*). — 9. Details of marginal leaf venation including teeth vasculation (*Bernardi 10362*). — 10. Transverse section of flower showing pattern of vasculation; DB=dorsal carpellary bundle, VB=ventral carpellary bundle (*McKee 26820*). — 11a, b, 12. Cleared stamens from male flowers showing expanded filament and branched venation system, 11b filament in transection (all *McKee 26820*). — 13. Stamen from bisexual flower (*McKee 26820*).
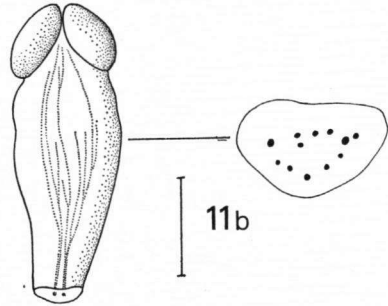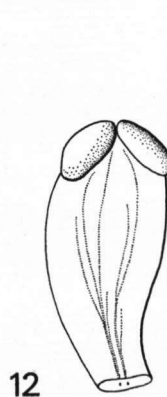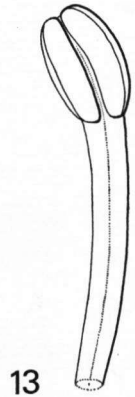
7

8

9

11a

11b

DB
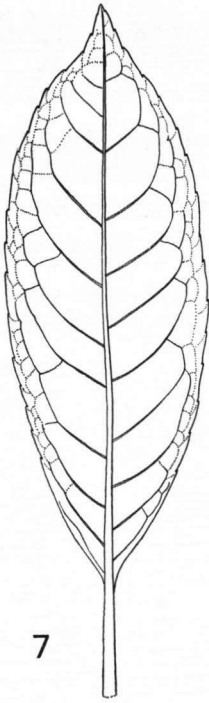
VB

10

12

13

conspicuously swollen filaments while flowers are still in the bud stage (figs 11 & 12). The superior, slightly oblique, gynoecium contains 8—15 laterally concrescent, conduplicate carpels that are also adnate with the solid core of central tissue (fig. 10). Unicellular unbranched trichomes sparsely cover the gynoecium surface. Although ventral sutures may open, the carpels remain closed by the adnation of their ventral margins with the solid central core. Carpels never open ventrally into a central space as illustrated by Swamy (1953). The region of lateral connation is histologically evident as a zone of narrow, compressed cells; however, carpels remain fused along their antire length at all stages of development. Stigmas are equal in number to carpels, sessile, and conduplicately folded. Each locule contains four rather small, anatropous, unitegmic ovules that are borne in a single row on axile placentas, again contradicting Swamy's interpretation. The ovular integument is composed of 3—4 layers, the outer of which is composed of thicker walled cells that are more densely staining (Plate III, 1). The megaspore mother cell is embedded in 2—3 layers of nucellus. The position of the ovules within the locule varies from epitropous dorsal to hypotropous dorsal (sensu Björnstad, 1970). The ovules completely fill the width of the rather narrow locule chamber.

Vascular anatomy: A ring of many discrete bundles is present at the floral base. Each perianth member receives three traces that undergo limited branching. Stamens receive a single trace that originates directly from the central cylinder and which in filaments of stamens from bisexual flowers remains undivided along its entire length (fig. 13). The enlarged filaments of stamens from male flowers have a rich vasculature resulting from a basal dichotomy and subsequent three dimensional branching of the stamen trace (figs 11a, b, 12). Stamen traces are surrounded by darkly staining (tanniferous?) cells.

The vascular tissue in the central cylinder becomes organized into a gynoecial venation pattern consisting of one prominent dorsal bundle per carpel and a less obvious ventral supply characterized by the fusion of the two ventral bundles of adjacent carpels (fig. 10). The fused ventrals lie in a plane between the locules of adjacent carpels, and at the same time constitute an interrupted vascular cylinder of the central core. Additional lateral wall bundles are absent. Ovules are vascularized by traces (or procambium) departing from the ventral bundles. In distal regions of the gynoecium the fused ventrals separate resulting in one dorsal and two unfused ventral bundles per carpel. The three carpellary bundles extend to the style apex where they terminate in a massive aggregation of tracheary elements.

Pollen (Plate IV)

Solitary, radially symmetrical, small, tricolporate, semi-angular to more commonly circular in outline in median polar view (Plate IV, 1), spherical to oblate-spheroidal in shape (Plate IV, 1—5), (22.4—)24(—26.5) × (21.5—)22.4(—25) μ m. Ektoaperture elongated meridionally and covered by a granular membrane. Polar index 0.29. Endoaperture slightly elongated meridionally (3 × 5 μm), closed with granular material (Plate IV, 2, 6, 7), and forming a bridge. Intine very prominent under the colpae and forming a plug in the endoaperture. Exine 2—2.5 μm thick in the center of mesocolpium. The exine is stratified into endexine, prominent foot-layer, columellae, and tectum (Plate IV, 6). Endexine (s.s.) is electron dense with the staining method used and forms a very thin layer in the center of the mesocolpium but is rather thick along the margins of the apertures. The boundary between endexine and ektexine is well defined. The foot-layer composes about two thirds of the total exine thickness although it decreases in thickness along the margins

of the ektoapertures. Total exine thickness along the margins of the ektoapertures, however, remains uniform as a result of the corresponding increase in endexine deposition (Plate IV, 6). In our preparations a deposit of unknown origin covers the external surface of the foot-layer. Columellae are short (*c.* 0.3 μm in height), thick, and are distributed in a reticulate pattern in uniseriate rows (Plate IV, 6 & 7). The tectum comprises about one fourth of the total exine thickness. Sculpturing is predominantly reticulate although occasionally it is transitional between reticulate and rugulate (retirugate) in the meso-colpium, becoming finer at the poles and along the colpae. Muri are about 0.4—0.7 μm wide.

Fruit (Plate III, 2)

The fruit is a glabrous, loculicidal capsule that dehisces longitudinally along the ventral suture of each carpel. In order for this to occur each carpel at maturity separates from the central column along its entire ventral margin, although some lateral concrescence among adjacent carpels remains. Although each carpel eventually becomes completely unsealed from the central axis, a distal connection is maintained by two strands apparently representing the lignified ventral carpellary vascular bundles.

Anatomically the fruit is distinguished by a massive sclerification of cells lining the locules (Plate III, 2). This is accompanied by the uniform sclerification of the central axis cells and those ensheathing the vascular bundles. Sclerified cells are extensively pitted, and more or less isodiametric in shape. Remaining ground tissue of the fruit is composed of thin-walled parenchyma. There is no proliferation of vascular tissue in the fruit.

Seed (Plate III, 3)

The number of seeds per fruit locule equals the number of ovules per carpel. Seeds are small, 2.0—2.5 mm in length, compressed, exarillate, and albuminous. The thin seed coat consists of a single cell layer *c.* 12—14 μm thick and is composed of cells with thickened lignified inner walls as viewed in transection. In surface view, cells of the testa have highly undulating anticlinal walls. At maturity the testa becomes extended to form small wings. Endosperm abundant, cellular at maturity, and composed of thin-walled polyhedral cells. A single vascular bundle extends into the dorsal wing of the seed coat for approximately half the length of the seed. In Corner's terminology (1976) the seed of Paracryphia is unitegmic exotestal. Embryo dicotyledonous, straight, c. 0.5.—0.7 mm in length, radicle longer than the cotyledons.

DISCUSSION

General

Paracryphia is distinguished by the following unusual combination of characters: primitive wood structure with extremely long vessel members and scalariform perforation plates containing over 100 bars, scalariform intervessel pits, fiber-tracheids, heterogeneous rays; trilacunar, three-trace nodal anatomy; complex petiole vasculation; simple, ex-stipulate, pseudoverticillate leaves; anomocytic stomata; large styloid crystals; secondary phloem with primitive sieve tube elements and abundant fibres; bisexual and less frequently staminate flowers in the same complex inflorescence; undifferentiated, 4-merous decussate perianth; *c.* 8 stamens with basifixed anthers; a gynoecium of numerous completely concrescent carpels accompanied by the fusion of ventral traces of adjacent carpels;

unitegmic ovules and axile placentation; tricolporate, retirugate pollen; and capsular fruits leaving a central column at dehiscence, with small, winged, albuminous, exotegmic seeds. It is remarkable that most characters from vegetative anatomy are distinctly primitive or at least unspecialized, whereas those of the reproductive organs can be regarded as advanced or specialized.

The fact that *Paracryphia* produces both bisexual and male flowers within the same inflorescence was noted by Bausch (1938). Swamy (1953), however, apparently concluded that only bisexual flowers were formed. The genus clearly produces inflorescences containing predominantly bisexual flowers although a small number of entirely staminate flowers are also present. Examination of male floral buds has shown the stamen filaments to be expanded laterally prior to anthesis. Associated with the enlarged condition of the filaments is the presence of a three-dimensionally branched vascular system. The functional significance of these features with regard to the reproductive biology of the plant is unclear. Pollen produced in anthers from male flowers appears normal.

Another aspect of floral morphology about which some disagreement exists concerns the number and interpretation of the floral envelopes. Both Baker (1921) and Bausch (1938) referred to the presence of two imbricate, caducous perianth segments. Airy Shaw (1965) described *Paracryphia* flowers as having no perianth but one bract and two bracteoles subtending the androecium and gynoecium. Preserved flowers we have examined have two opposing pairs of accessory segments, one of which is distinctly larger than the others. We see no compelling reason not to refer to these structures as perianth members.

Placement of Paracryphia in the General System

In this discussion the putative, previously suggested, allies of *Paracryphia* are examined in the light of available evidence. This is followed by comparisons between *Paracryphia* and additional families that for various reasons we feel deserve consideration as possible relatives. Comparative data were gleamed from the literature or obtained from original observation.

1. *Magnoliales—Piperales.* The presence of unitegmic ovules in *Paracryphia* severely weakens arguments that the genus should be included among the woody families of the subclass *Magnoliidae* (*sensu* Cronquist, 1968). Ovules in the *Magnoliales* are apparently uniformly bitegmic. Unitegmic ovules do occur sporadically in a few families of the *Ranunculales* (*Ranunculaceae, Menispermaceae, Circeasteraceae*) and *Saururaceae* and *Piperaceae* of the *Piperales* (Philipson, 1974). All of these unitegmic *Magnoliidae*, however, have no relationship to *Paracryphia* as demonstrated both morphologically and anatomically. Salient features of *Winteraceae* such as vessseless xylem; bitegmic ovules; pollen grains always anaulcerate (*i.e.*, aperture located distally), semitectate, reticulate, and consistently shed in permanent tetrads (rarely monads); etherial oil cells; and a pattern of leaf venation in which secondary veins have an irregular course and intercostal areas lack uniform size and shape (primitive first rank leaves, *sensu* Hickey, 1971) negate a close alliance with *Paracryphia*. The regular course of the major veins in addition to the well developed pattern of areolation in *Paracryphia* leaves are structurally advanced features according to the interpretations of Hickey (1971). *Illicium*, despite a somewhat similar appearance and having xylem with exceedingly primitive vessel members, is clearly distinguished morphologically and anatomically from *Paracryphia* by unilacunar nodes; specialized stomatal structure; ethereal oil cells; leaf margins with 'Chloranthoid teeth' having a medial vein

'braced' by two prominent laterals which join it distally (see Hickey & Wolfe, 1975); tricolpate pollen in which the three colpi join at the poles resulting in an unusual syncolpate condition; fruit a single whorl of follicles; and a simple carpellary vasculation consisting of only a single dorsal and ventral strand that is more comparable to members of the Lauraceous assemblage (Keng, 1965). *Paracryphia* diverges from the *Chloranthaceae* by the possession of trilacunar nodes, tricolporate pollen, and anatropous ovules, as opposed to the unilacunar nodes, monosulcate and monosulcate derived pollen, and orthotropous ovules of *Chloranthaceae*. The very distinctive type of Chloranthoid tooth is absent in *Paracryphia* leaves.

2. *Trochodendraceae*. Suggestions of a close affinity between *Paracryphia* and *Trochodendraceae*, e.g. by Airy Shaw (1965), appear equally unlikely even though the two taxa have a rather similar pollen morphology and a very superficial resemblance in gross morphology. Although it would be theoretically possible to derive most *Paracryphia* character states from those present in *Trochodendron*, in our opinion the differences outlined below make a close relationship between these taxa improbable.

Paracryphia	*Trochodendraceae*
Vessels present	Vessels absent
Node trilacunar	Node multilacunar (mature)
Petiole vasculation complex	Petiole vasculation simple
Chloranthoid teeth absent	Chloranthoid teeth present
Astrosclereids absent	Astrosclereids present
Styloid crystals present	Styloid crystals absent
Inflorescence paniculate	Inflorescence cymose
Perianth present	Perianth absent
Stamens few	Stamens numerous
Axial tissue present in gynoecium	Axial tissue absent in gynoecium
Simple floral vasculation	Complex floral vasculation
Styles sessile	Styles elongate
Ovules unitegmic	Ovules bitegmic
Ovules few per carpel	Ovules numerous per carpel
Fruit a capsule	Fruit a follicetum

3. *Eucryphiaceae*. Inclusion of *Paracryphia* in or near the *Eucryphiaceae*, as done in a tentative manner by Bausch (1938), also cannot be supported. The large number of significant differences are compared below.

Paracryphia	*Eucryphiaceae*
Vessel elements extremely long	Vessel elements moderately long
Vessel perforations scalariform, many-barred	Vessel perforations simple or scalariform, usually few-barred
Xylem parenchyma diffuse, scanty	Xylem parenchyma terminal, scanty diffuse
Stipules absent	Stipules present
Stomata anomocytic	Stomata paracytic
Styloids present	Styloids absent
Inflorescence paniculate	Flowers solitary

Perianth undifferentiated, caducous	Perianth differentiated, persistent
Ovules unitegmic	Ovules bitegmic
Floral vasculature simple	Floral vasculature ± complex
Pollen small, tricolporate	Pollen minute, dicolporate

In addition, although the fruits initially appear similar, the manner of dehiscence is different with regards to the attachment of the valves to the central axis. As pointed out by Bausch, the valves of the mature fruit of *Eucryphia* are attached basally whereas in *Paracryphia* attachment of the valves to the persistent central axis is distal.

The suggestion that *Paracryphia* is related to *Eucryphia* led us to an examination of other *Rosidae*.

Data on wood anatomy indicate a lower level of evolutionary advancement than any extant Rosalean and supports an early divergence of *Paracryphia* before the oldest *Cunoniaceae*, *Brunelliaceae*, or *Rosaceae*. Cronquist (1968) has characterized a hypothetical Rosalean plant combining all the primitive features found in various members of the order to be woody, with alternate, stipulate leaves, regular, hypogynous flowers with five separate petals, numerous centripetal stamens, several separate carpels, and numerous crassinucellate, bitegmic ovules, the ovaries ripening into follicles with endospermous seeds. *Paracryphia* combines few of the above features. Furthermore, the presumably primitive Rosalean five-trace carpellary vascular pattern (Sterling, 1969) is absent in *Paracryphia*.

4. *Comparisons with other families.* A search for possible close relatives of *Paracryphia* resulted in comparisons with numerous families. Attention was concentrated on those groups which retained primitive xylem traits while possessing moderately advanced to advanced floral characters such as unitegmic ovules. The combination of morphological and anatomical features present in *Paracryphia* is reminiscent in varying degrees to families compared in Table 1.

Members of the *Theaceae*, a family generally thought to be derived from *Dilleniales*, have very primitive woods (subfamily *Ternstroemioideae*) that are comparable to *Paracryphia* although pores are never in radial multiples. Theaceous plants also approach *Paracryphia* in foliar venation, having secondary veins brochidodromous often with ascending arches and tertiary veins that are random to weakly percurrent. Placentation is axile in *Theaceae* and up to ten carpels can be present in the syncarpous gynoecium of *Laplacea* (Keng, 1962). Small, unspecialized, tricolporate pollen of the *Paracryphia* type is widespread in several groups of the Theaceous complex (subfamily *Ternstroemioideae* of *Theaceae*). Other similarities are evident in the capsular fruit of the *Camellioideae* in which the valves at maturity separate from a persistent central columella, fibrous endothecium, and sclereids in the perianth parts. A relationship to *Theaceae* is weakened, however, since their nodes are strictly unilacunar, petioles have a simple vasculature, ovules are bitegmic, and as far as is known mechanical cells are poorly developed or entirely lacking in the bark.

Any similarity between gynoecia of *Paracryphia* and *Medusagyne* is quickly negated by the occurrence in the latter genus of a highly advanced xylem, characterized by vessel elements with simple perforations, petioles with numerous separate vascular bundles arranged in an arc, opposite leaves, and flowers with well differentiated perianth parts and numerous stamens (Beauvisage, 1920).

As seen in Table 1, *Paracryphia* shares a number of features with the *Actinidiaceae sensu lato*. Included among these resemblances are primitive vessel elements, styloids, and unitegmic ovules borne on axile placentas. Styloids are of particular interest because they are of

Characters of Pharacryphia	Theaceae	Actinidiaceae (incl. Saurauia)	Ericaceae	Aquifoliaceae	Sphenostemonaceae
Table 1. Occurrence of some characters of Paracryphia in selected families of dicotyledons					
trilacunar nodes	−	(+)	−	+	+
simple, exstipulate leaves	+	+	+	±	+
leaf venation as in Paracryphia	+	−	(+)	(+)	+
complex petiole vasculation	−	(+)	−	(+)	(±)
anomocytic stomata	(+)	+	+	(+)	+
styloids	−	(+)	−	±	+
extremely long vessel elements, scal. p.p. 100 bars	(+)	(+)	(±)	±	+
fiber-tracheids	+	+	+	+	+
undifferentiated perianth	−	−	−	−	+
compound gynoecium	+	+	+	+	+
sessile stigmas	−	−	−	+	+
axile placentation	+	+	+	+	+
anatropous, unitegmic ovules	−	+	+	+	+
small, retirugate, tricolporate pollen	(+)	(+)	(±)	±	−
loculicidal, capsular fruit	(+)	(+)	(+)	−	−
albuminous seeds	+	+	+	+	+
bark fibrous	−	−	−	−	+

Legends: − = character absent; + = character present in most representatives of the family; (+) = character present in a few representatives only; ± = tendency to be similar in this character.

restricted distribution in Dicotyledons. The wood anatomy of some species of *Saurauia* is distinguished by vessel elements with highly oblique scalariform perforation plates containing over 100 bars and scalariform to opposite intervessel pitting, fiber-tracheids, heterogeneous rays of two sizes that contain a high percentage of upright cells and often sheath cells, and diffuse and scanty axial parenchyma. Vessels are solitary, never in long radial multiples. The secondary xylem of *Actinidia* has become modified in structure typical of lianas. A few Saurauias have trilacunar nodes but the majority of species have a unilacunar node more typical of *Ericales*. Medullary bundles are found in petioles of some species and stomata are not surrounded by modified subsidiary cells. Loculicidal, capsular

fruits are known in *Saurauia* and seeds are small, unitegmic exotestal, with cellular endosperm lacking starch. Many species, however, have seeds that are arillate.

The similarities between the *Actinidiaceae* and *Ericales* are impressive as has been previously pointed out by several workers including one of us (Dickison, 1972). Among these resemblances are unitegmic-tenuinucellate ovules, syncarpy, the sclerified nature of cells lining the fruit locules, and seeds that have the outer cells of the testa with thickened inner walls; all features that also occur in *Paracryphia* and when considered in conjunction with wood anatomy lead to the suggestion that the genus may represent an early divergent offshoot of the Dillenialean-Thealean-Ericalean line. Fibrous endothecia and spurless stamens, as found in *Paracryphia*, are not common in *Ericales* but do occur in *Clethraceae*. Our material did not permit an accurate characterization of the ovule of *Paracryphia* as crassinucellate or tenuinucellate, although this is clearly an important consideration (see Philipson, 1974; Palser, 1975) that needs clarification.

Paracryphia differs significantly from the above assemblage, and particularly *Actinidiaceae*, in possessing an undifferentiated perianth, sessile stigmas, and in having a comparatively simple floral vasculation. *Paracryphia* also lacks the complex trichome morphology, raphides, and craspedodromous leaf venation with rigidly percurrent tertiaries that are so typical of *Actinidiaceae*. The large number of carpels in *Paracryphia* is also nonericalean although this condition is seen in *Actinidia* and up to ten carpels may occur in some *Ericaceae* (*e.g.*, *Arctostaphylos*, *Gaylussacia*). Although the floral vasculature of *Paracryphia* offers few obvious clues regarding the relationships of the genus, flowers of *Saurauia* are richly vascularized and characterized by numerous fusions of floral bundles in contrast to the pattern in *Paracryphia*. The occurrence of septal bundles in the gynoecium of *Saurauia* is similar to many members of the *Ericales* and unlike *Paracryphia*. *Actinidia*, however, shows an absence of septal bundles accompanied by the fusion of the two ventral bundles of each carpel. Pollen of *Actinidiaceae* is small, tricolporate, and not highly sculptured.

Few similarities are evident between *Paracryphia* and primitive *Dilleniaceae* which have basically pentamerous flowers with a well differentiated perianth, an apocarpous gynoecium containing bitegmic ovules, raphide crystals, and never produce capsular fruits. *Paracryphia* lacks the rigidly percurrent secondary veins so characteristic of all genera of *Dilleniaceae* except various species of *Hibbertia*.

In the course of reviewing the salient morphological and anatomical features of *Paracryphia* our attention became focused again on the large number of similarities between it and the genus *Sphenostemon*, also from New Caledonia, and New Guinea and Queensland. This genus, having a very chaotic taxonomic history, has recently been thoroughly studied by one of us (Baas, 1975) and it was concluded that *Sphenostemon* deserves familial status and has affinities with *Aquifoliaceae* and *Icacinaceae*. *Sphenostemon* is anatomically circumscribed by the following features: hairs if present unicellular, stomata anomocytic, petiole with a simple open or closed vascular system connected with the stem through a trilacunar, three-trace node, cork arising in the subepidermis, secondary phloem with diffuse to tangentially arranged fibers and sieve tubes with compound sieve plates, styloid crystals in the ground tissue of leaf and stem and in the secondary phloem, wood with scalariformly perforated vessels (with 32—185 bars), scalariform intervessel pits, long fibretracheids, diffuse-in-aggregates parenchyma, heterogeneous II rays (Kribs, 1968) of two distinct sizes. All these characters from vegetative anatomy agree remarkably well with those of *Paracryphia*. The differences in petiole vasculation and wood rays is not regarded as significant. In external morphology the 4 decussate perianth parts of *Sphenostemon* also recall *Paracryphia*, as well as the occasionally pseudo-verticillate leaf arrangement. Leaf

venation harmonizes with this pattern since both genera have secondary veins brochido-dromous with marginal arches developed apically; tertiary veins are weakly transverse. The detailed morphology of the reproductive structures: stamens, ovary, and pollen grains are, however, quite different. The pendulous anatropous ovules of *Sphenostemon* are, nevertheless, also unitegmic (Bernardi, 1964). The indehiscent fruit with one or two stony seeds is quite unlike the capsular fruit of *Paracryphia**. Vasculation of the bilocular gynoecium of *Sphenostemon* consists of 8—12 bundles, two of which are fused and extend vertically in the tissue separating the two locules. At the apex of the locules the central strand bifurcates with each branch vascularizing one ovule (Bailey & Swamy, 1953).

In spite of the significant differences in reproductive morphology, we cannot ignore the most striking similarities between *Sphenostemon* and *Paracryphia* in all aspects of vegetative anatomy, supported by general reproductive features such as the 4-merous, decussate, undifferentiated perianth; superior ovary with anatropous, unitegmic ovules; basifixed anthers; and to a lesser extent the sculpturing of the pollen exine (*cf.* Lobreau-Callen, 1975). To explain all these similarities in terms of convergent evolution seems unreasonable and it is our belief that *Sphenostemon* and *Paracryphia* are in some way related. Although one of us (Baas, 1975) concluded that *Sphenostemon* should be treated as a member of the *Celastrales*, this was only based on similarities with *Aquifoliaceae*, *Phellinaceae*, and *Icacinaceae*. However, the inclusion of *Aquifoliaceae* and *Icacinaceae* in the order *Celastrales* appears to be more and more doubtful. Thorne (1968) referred *Aquifoliaceae* to the *Theales*, and although the second author (1975) strongly criticized the placement of this family in an order different from that of the apparently related *Icacinaceae*, there are a fairly large number of anatomical similarities between *Theaceae* and *Aquifoliaceae*, and accordingly, with *Icacinaceae*. According to Corner (1976) the seed structure (unitegmic, exotestal) of *Icacinaceae* and *Aquifoliaceae* is incompatible with a Celastralean alliance and could be more in line with *Theales*, where (exclusive of *Theaceae*) there is a unitegmic tendency.

Recently, Dahlgren (1975) included *Icacinaceae* in *Cornales*, and earlier Huber (1963) favored inclusion of *Aquifoliaceae* in that order. If *Paracryphia* is related to these two families 'through' *Sphenostemon*, then all families included in *Cornales* deserve attention as putative allies, as well as all families of *Celastrales*. Likewise, the similarities between *Paracryphia* and *Actinidiaceae* reported above should invite comparisons with all families of the orders *Theales* and *Ericales* to which that family has been assigned. Such comparisons have been made, taking all four orders in the widest possible sense; that is, including all families that have been assigned to these orders by different workers (Melchior in Engler, 1964; Hutchinson, 1959, 1974; Lanjouw *et al.*, 1968; Cronquist, 1968; Takhtajan, 1973; and Dahlgren, 1975). Just over one-hundred families were considered, as well as all families listed in Metcalfe and Chalk (1950) as possessing scalariform perforations in their wood. Following a comprehensive survey of the anatomical and morphological characters of this large sample of dicotyledons, only the following families emerged, sharing enough characters with *Paracryphia* to merit further considerations as a close relative: *Sphenostemonaceae*, *Actinidiaceae*, *Aquifoliaceae*, *Icacinaceae*, *Theaceae*, *Pentaphylacaceae*, *Clethraceae*, *Cyrillaceae*, and *Escalloniaceae*. Of these *Sphenostemonaceae*, *Theaceae*, and *Actinidiaceae* were discussed above. *Aquifoliaceae* and *Icacinaceae* (*p.p.*) share a fairly large number of anatomical features with *Paracryphia*; the floral morphology is, however, quite different and deviates to a greater degree from *Paracryphia* than either *Sphenostemon* or *Actinidiaceae*. *Pentaphylacaceae*,

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*) In most descriptions the fruits of *Sphenostemon* are referred to as drupes with one or two bony pyrenes. This is, however, erroneous (*cf.* Bailey, 1956): the pericarp remains more or less soft throughout but the seed develops a very thick testa of many layers of sclerified cells.

Clethraceae, *Cyrillaceae*, and *Escalloniaceae* all share a rather primitive wood structure with *Paracryphia*. *Escallonia* has also been reported to possess styloids. Floral morphological characters of these four families still deviate considerably from *Paracryphia*, however, and their affinities with *Paracryphia*, if any, must be rather remote.

Pollenmorphologically the small, unspecialized, tricolporate, reticulated pollen of *Paracryphia* is consistent with the type of pollen grains found in many *Theaceae*, *Actinidiaceae*, *Clethraceae*, and *Cyrillaceae*, *i.e.*, groups transitional between *Theales* and *Ericales* (Walker & Doyle, 1975).

It is noteworthy that many of the families mentioned above have at one time or another been transferred from the *Celastrales* to *Theales* or *Ericales* or vice versa. *Cyrillaceae* have thus been treated in *Ericales* as well as in *Celastrales*, and although the former affinity is favored by most contemporary systematists, there are striking anatomical similarities with *Aquifoliaceae* (*cf.* Baas, 1975). *Actinidiaceae* (including *Saurauia*) are ranked at the base of the *Ericales* or included in *Theales*. Similarly, *Clethraceae* have been moved from *Ericales* to *Theales* by Thorne (1968). *Aquifoliaceae* now also face an uncertain future: retention in *Celastrales* or transferal to *Theales*. *Pentaphylacaceae* can be found under both ordinal headings.

We believe the *Cornales* should be excluded from this discussion in as much as the rather haphazard suggestions of Cornalean affinities of *Icacinaceae* and *Aquifoliaceae* seem to be too much in conflict with the morphological and anatomical tendencies in that order. The fact that for the orders *Ericales*, *Theales*, and *Celastrales* several families seem to be exchangeable makes the problem of assigning *Paracryphia* to an existing ordinal concept very difficult. *Paracryphia* shows affinities, although never very close ones, to some representatives of all three orders. This may well be taken as an argument to support the view that *Paracryphia* represents an independent and early divergence from the *Thealean*, *Ericalean*, and/or *Celastralean* (*pro parte?*) lines of evolution. With the present disagreements about the definition of orders it is not readily apparent which of the three alternatives best reflects the evolutionary relationships of the genus. The families *Actinidiaceae*, *Theaceae*, and *Sphenostemonaceae* appear to us to be the closest extant relatives of *Paracryphia*. The present study fully confirms the view that *Paracryphia* merits familial status.

The emerging synthesis is of a reticulate pattern of relationships between the *Theales*, *Celastrales pro parte*, and *Ericales* through families like *Paracryphiaceae*, *Sphenostemonaceae*, *Actinidiaceae*, *Cyrillaceae*, and *Pentaphylacaceae*. These relationships should present an interesting challenge to contemporary system makers.
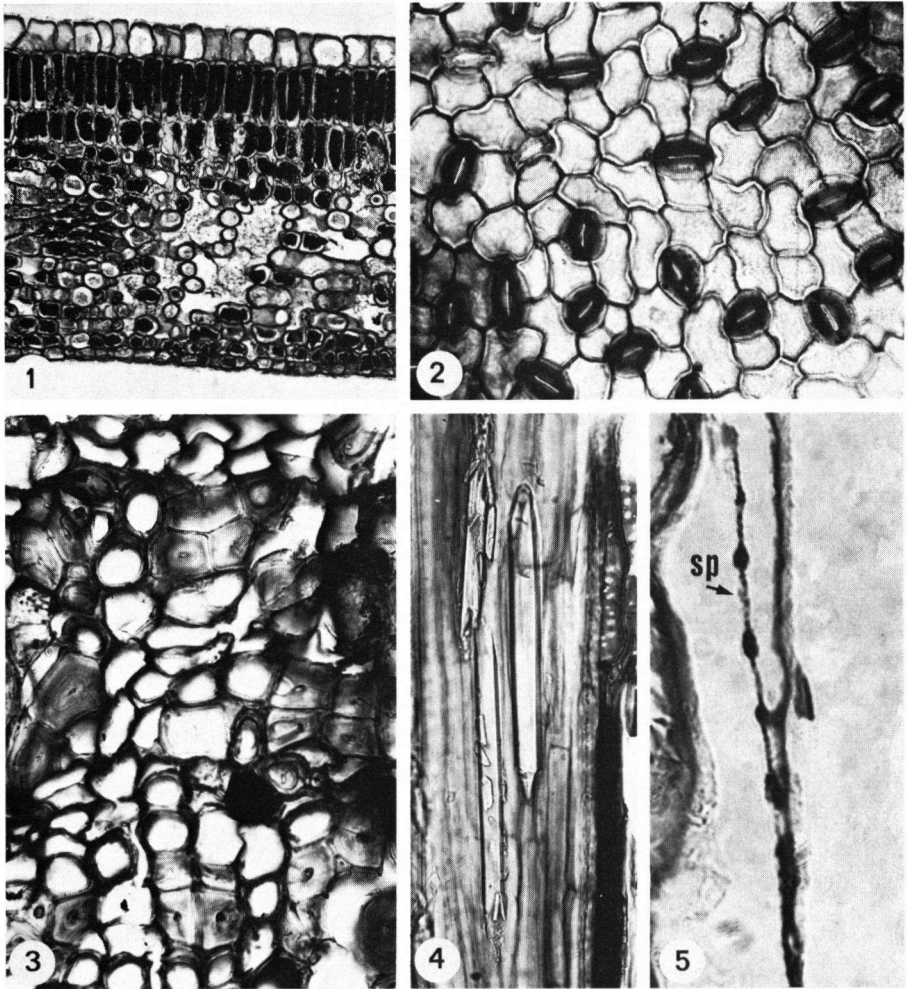
Plate I. Vegetative anatomy of *Paracryphia alticola*. — 1. Transverse section of leaf (*MacKee 4993*), ×220. — 2. Paradermal section of abaxial leaf epidermis showing anomocytic stomata (*McKee 31070*), ×220. — 3. Transverse section of bark showing interrupted bands of fibrous cells (*McKee 31070*), ×530. — 4. Longitudinal section of bark showing styloid crystals (*Schlechter 15326*), ×530. — 5. Longitudinal section through a sieve tube element from the secondary phloem showing a compound sieve plate (sp) (*McKee 31070*), ×870.
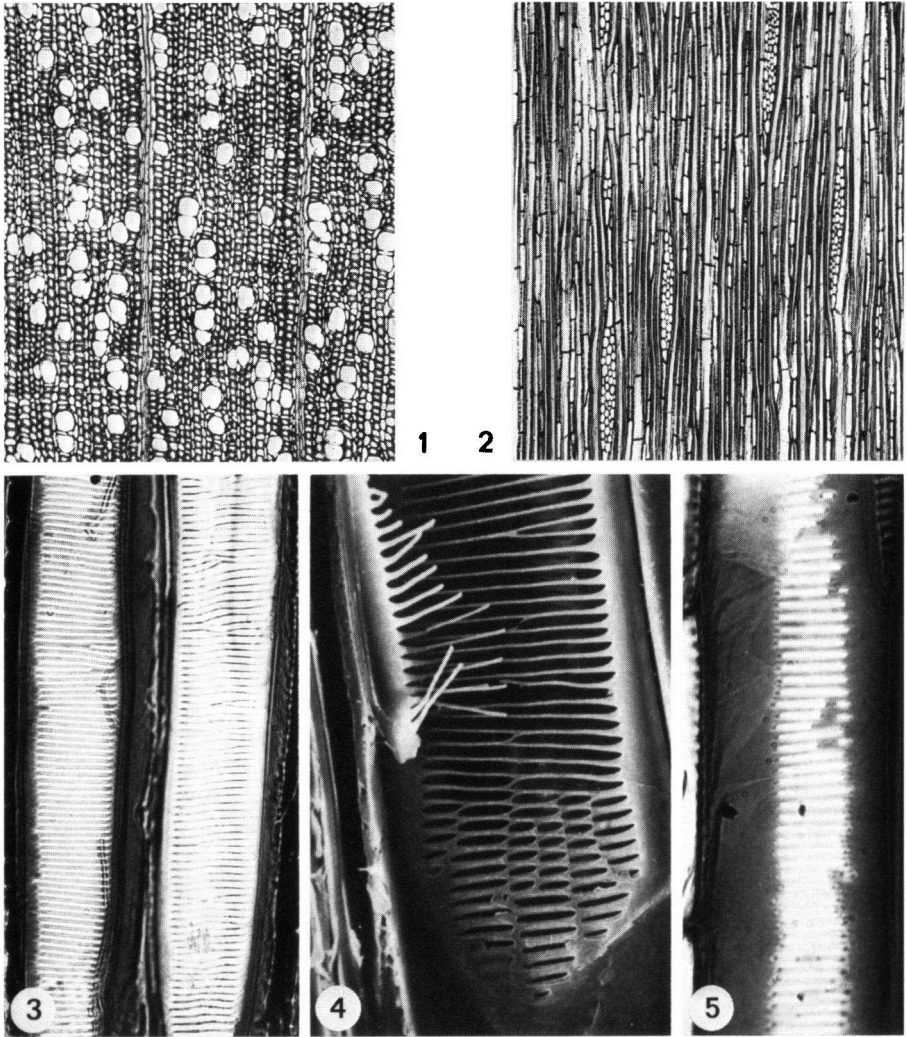
Plate II. Wood anatomy of *Paracryphia alticola* (*McKee 31070*). — 1. Transverse section, ×85. — 2. Tangential section, ×85. — 3. Longitudinal section of vessel elements showing scalariform perforation plates, ×530. — 4. SEM of vessel element scalariform perforation plate showing partial reticulation, ×430. — 5. Longitudinal section of vessel element showing scalariform intervascular pitting, ×530.
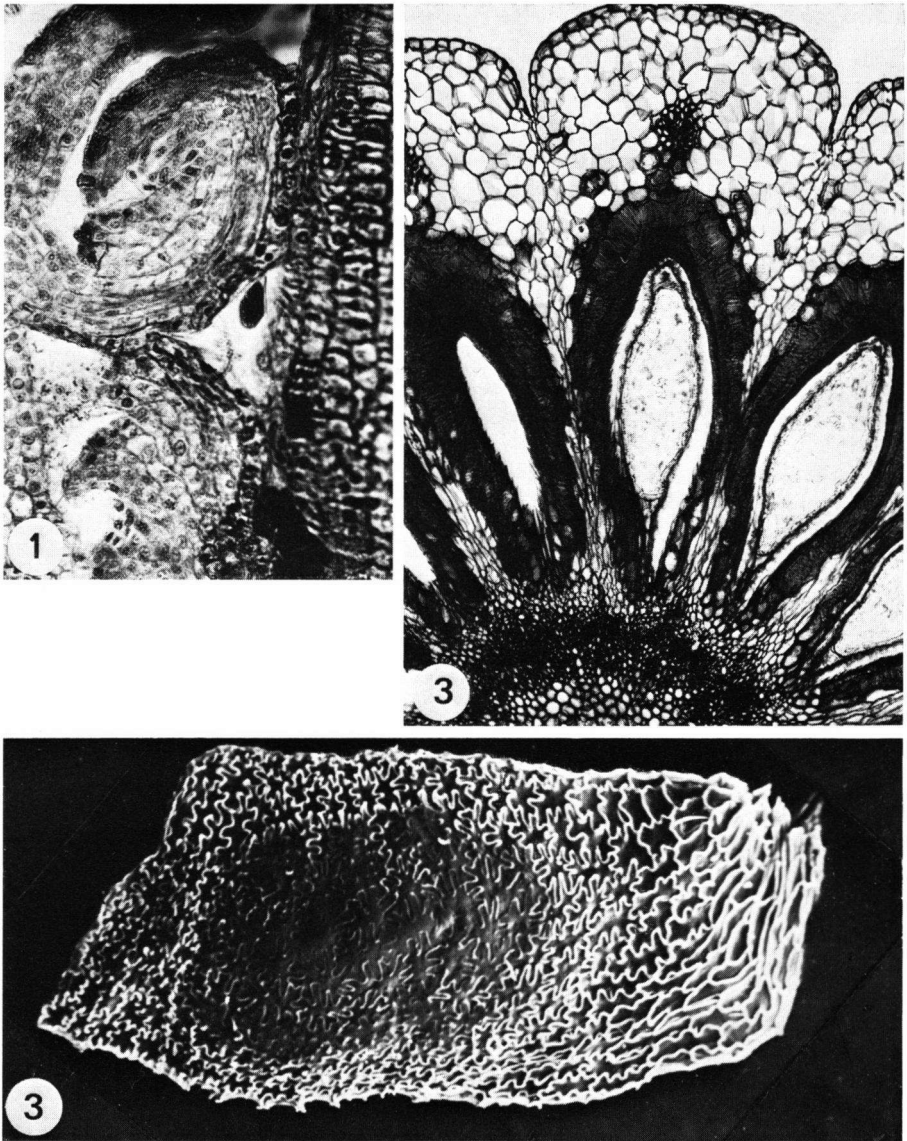
Plate III. Reproductive morphology of *Paracryphia alticola*. — 1. Longitudinal section of ovule illustrating anatropous, unitegmic condition (*McKee 26820*), ×670. — 3 (top). Transverse section of mature fruit showing prominent sclerification of cells lining the locules (*McKee 31070*), × 110. — 3 (bottom). SEM of mature seed showing undulating pattern of the anticlinal walls of epidermal cells (*McKee 31070*), ×50.
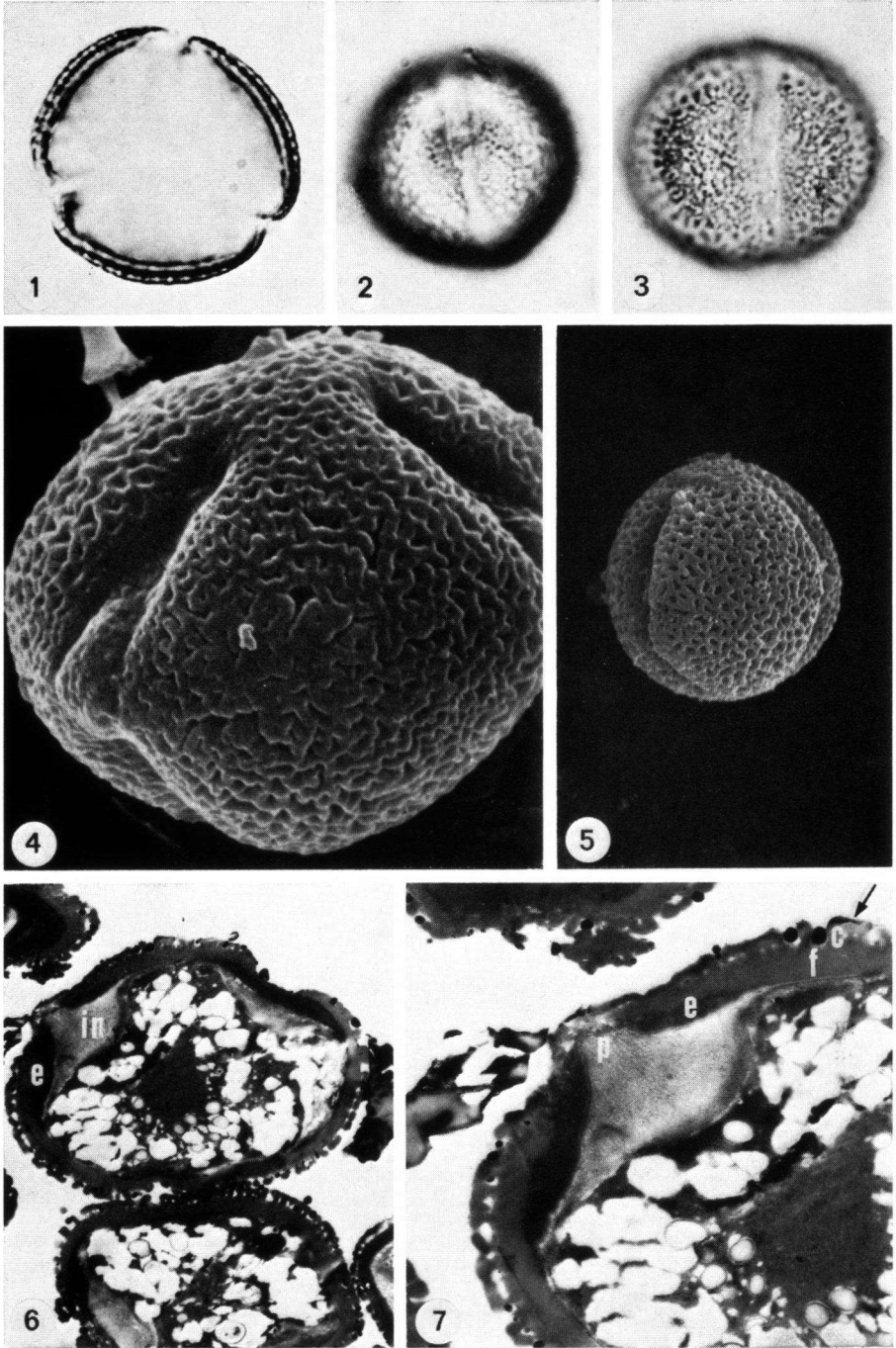
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EXPLANATION OF PLATE IV

Plate IV. Pollen morphology of *Paracryphia alticola* (*McKee 26820*). — 1. Median polar view showing circular outline, ×1330. — 2. Equatorial view, high focal level showing endoaperture and reticulate sculpture, ×1330. — 3. Same grain, equatorial view at lower focal level showing pattern of columellae distribution, ×1330. — 4. SEM of acetolyzed pollen grain as seen in equatorial view. Note the retirugate sculpturing in the mesocolpium, ×3500. — 5. SEM of acetolyzed grain in equatorial view, ×1700. — 6. TEM of FAA preserved, nonacetolyzed grain sectioned obliquely along the equatorial axis. Note the prominent intine (in) under the colpae and the thick endexine (e) along the margins of the apertures, ×4400. — 7. Same grain showing a median section through the endoaperture (p). The exine is stratified into endexine (e), foot-layer (f), columellae (c), and tectum (arrow), ×9900.