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Source: Systematic Botany, 35(4) : 766-782

Published By: The American Society of Plant Taxonomists

URL: <https://doi.org/10.1600/036364410X539853>

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Phylogeny and Recircumscription of Artocarpeae (Moraceae) with a Focus on *Artocarpus*

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Communicating Editor: Anne Bruneau

Abstract—Moraceae is a large (~1,050 species) primarily tropical family with several economically and ecologically important species. While its monophyly has been well supported in recent studies, relationships within the family at the tribal level and below remain unresolved. Delimitation of the tribe Artocarpeae has been particularly difficult. Classifications based on morphology differ from those based on phylogenetic studies, and all treatments include highly heterogeneous assemblages of genera that seem to represent a cross section of the family. We evaluated chloroplast and nuclear DNA sequence data for 60 Moraceae taxa representing all genera that have been included in past treatments of Artocarpeae and also included species from several other Moraceae tribes and closely related families as outgroups. The data were analyzed using maximum parsimony and maximum likelihood methods and indicate that none of the past treatments of Artocarpeae represent a monophyletic lineage. We present the most complete phylogenetic hypothesis for Artocarpeae and the genus *Artocarpus* to date. Inflorescence evolution and pollination are briefly discussed and the phylogenetic reconstructions are used to inform a revised treatment of Artocarpeae and the *Artocarpus* subgenera. The following new combinations are proposed: the genus *Prainea* is reduced to *Artocarpus* subgenus *Prainea*, and the series *Cauliflori* is raised to *Artocarpus* subgenus *Cauliflori*.

Keywords—*Artocarpus*, *Clarisia*, *Hullettia*, *Parartocarpus*, *Prainea*, *Treculia*.

The mulberry family (Moraceae) comprises approximately 37 genera and 1,050 species (Berg et al. 2006) including several economically and ecologically important species such as breadfruit (*Artocarpus altilis* (Parkinson) Fosberg), paper mulberry (*Broussonetia papyrifera* Vent.), and figs (*Ficus* L.). The family is distributed throughout tropical and temperate regions worldwide, but its diversity is centered in the tropics. Based on molecular (Datwyler and Weiblen 2004; Zerega et al. 2005a) and combined morphological and molecular evidence (Clement and Weiblen 2009), the family is strongly supported as monophyletic, but an amazing diversity of complex inflorescence structures, pollination syndromes, breeding systems, and growth forms in the family has complicated its taxonomy at the tribal level and below. Despite the fact that the tribal circumscription of the Moraceae has come under frequent scrutiny by several investigators (Berg 1977a, b; Rohwer 1993; Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006; Clement and Weiblen 2009), tribe Artocarpeae has remained particularly difficult (Table 1). It has long been recognized as a highly heterogeneous and unnatural assemblage of pantropical taxa with no clear morphological synapomorphies and the genera included in the tribe have changed frequently.

The most recent floristic treatment of the tribe recognizes an Artocarpeae including five paleotropical genera (*Artocarpus* J. R. Forst. and G. Forst., *Hullettia* King ex Hook. f., *Parartocarpus* Baill., *Prainea* King ex Hook. f., and *Treculia* Decne ex Trécul) characterized by “pistillate inflorescences mostly formed of connate perianths, many seeded infructescences, and free fruits” (Berg et al. 2006). The results of phylogenetic studies differ from the floristic treatment in that two neotropical genera (*Clarisia* Ruiz & Pavón and *Batocarpus* Karsten) are also included within Artocarpeae, and the tribe is characterized by the reduction of stamen number, peltate interfloral bracts, vitreous silica, and straight filaments (Datwyler and Weiblen 2004; Zerega et al. 2005a; Clement and Weiblen 2009). Unfortunately, the phylogenetic studies did not include *Hullettia* or *Treculia* in their analyses and the place-

ment of *Parartocarpus* was inconsistent (either being placed in Artocarpeae or a polyphyletic Moreae). Earlier floristic treatments also placed *Clarisia* and *Batocarpus* within Artocarpeae as well as additional neotropical (Moraceae Aubl., *Poulsenia* Eggers, and *Sorocea* A. St.-Hil.) and paleotropical (*Antiaropsis* K. Schum. and *Sparattoscyce* Bureau) genera (Rohwer 1993; Berg 2001). *Artocarpus* (~45 species; Berg et al. 2006) is the largest genus in the tribe, and the third largest genus in the Moraceae family (after *Ficus* and *Dorstenia* L.). As the type genus, its inclusion in the tribe is not in question, but what remains unclear is the monophyly of the genus, and exactly what other genera should be included in the tribe.

Artocarpus is distributed from Southeast Asia east into Oceania (Fig. 1A). Additionally, several *Artocarpus* species have been introduced throughout the tropics and are harvested for food (e.g. *A. altilis*, breadfruit; *A. camansi* Blanco, breadnut; and *A. heterophyllus* Lam., jackfruit). *Treculia* Decne. ex Trécul (three species) occurs in Africa and Madagascar, and its seeds are a source of food for humans. The other genera that have most recently been included in Artocarpeae have relatively few species and are of little economic value. *Hullettia* (two species) is restricted to the Malay peninsula and Sumatra. *Parartocarpus* (two species) ranges from Thailand east to the Solomon Islands. *Prainea* (two to four species) ranges from the Malay Peninsula to New Guinea. *Batocarpus* (three species) and *Clarisia* (three species), both range from Central to South America (Fig. 1B).

Artocarpus and the six smaller genera (*Batocarpus*, *Clarisia*, *Hullettia*, *Parartocarpus*, *Prainea*, and *Treculia*) that have been most recently included in Artocarpeae (Datwyler and Weiblen 2004; Clement and Weiblen 2009) all bear unisexual flowers, as do all Moraceae, and typically have unisexual inflorescences. They are either monoecious or dioecious latex-producing trees, or rarely shrubs. Pistillate inflorescences are condensed capitate heads (or rarely uniflorous as in some *Clarisia*), which develop into syncarps and may attain enormous sizes in some species, up to 100 cm × 50 cm

TABLE 1. Comparison of the classification of Artocarpeae according to the four most recent treatments and findings from the present study. Berg (2001) included 12 genera in Artocarpeae and the classification history of these 12 genera is listed below. When Artocarpeae is listed, it indicates the genus is included in Artocarpeae in that treatment. An asterisk means the genus was moved to the indicated tribe. "Maintained" means that in the present study the authors maintain the most recent transfer of the genus to a tribe other than Artocarpeae (Clement and Weiblen 2009).

Berg 2001 (Artocarpeae)	Datwyler and Weiblen 2004	Berg et. al. 2006	Clement and Weiblen 2009	Zerega et al.
<i>Antiaropsis</i> K. Sch.	*Castilleae C. C. Berg	*Antiaropsidae C. C. Berg	*Castilleae	Maintained
<i>Artocarpus</i> J. R. and G. Forster	Artocarpeae R. Br.	Artocarpeae	Artocarpeae	Artocarpeae
<i>Bagassa</i> Aublet	*Moreae Gaudich.	*Soroceae C. C. Berg	*Moreae	Maintained
<i>Batocarpus</i> Karsten	Artocarpeae	*Soroceae	Artocarpeae	Artocarpeae
<i>Clarisia</i> Ruiz & Pavon	Artocarpeae	*Soroceae	Artocarpeae	Artocarpeae
<i>Hullettia</i> King	Artocarpeae	Artocarpeae	Not treated	Unplaced
<i>Parartocarpus</i> Baillon	Artocarpeae	Artocarpeae	Artocarpeae	Unplaced
<i>Poulsenia</i> Eggers	*Castilleae	*Soroceae	*Castilleae	Maintained
<i>Prainea</i> King	Artocarpeae	Artocarpeae	Artocarpeae	Artocarpeae (subg. of <i>Artocarpus</i>)
<i>Sorocea</i> St. Hil.	*Moreae	*Soroceae	*Moreae	Maintained
<i>Sparratosyce</i> Bur.	*Castilleae	*Antiaropsidae	*Castilleae	Maintained
<i>Treculia</i> Decne ex. Trecul	Artocarpeae	Artocarpeae	Artocarpeae	*Dorstenieae Gaudich.

in *A. heterophyllus*, jackfruit (Jarrett 1959c, 1975). Staminate inflorescences are typically spicate or less frequently globose. Both pistillate and staminate inflorescences are typically comprised of numerous small, tightly packed flowers, which either sit upon (*Artocarpus*, *Prainea*, *Treculia*, *Batocarpus*, *Clarisia*) or are embedded in (*Hullettia*, *Parartocarpus*) a fleshy receptacle, and either have (*Artocarpus*, *Prainea*, *Batocarpus*, *Clarisia*, *Treculia*) or lack (*Hullettia*, *Parartocarpus*) a perianth (Jarrett 1959a; Berg 1977b) (Fig. 2). In pistillate inflorescences of *Artocarpus*, the perianths of adjacent flowers are fused together at least apically and medially (leaving syncarps with an even surface) or are fused medially and are free at the apices (leaving syncarps with a spiky or tuberculate surface) (Fig. 3). This allows the entire inflorescence to develop into a highly specialized syncarp formed by the enlargement of the entire female head even if only a portion of the flowers develop seeds (Jarrett 1976). However, in *Prainea* (Fig. 2), *Batocarpus*, and *Clarisia* adjacent pistillate perianths remain free so that only fertilized ovules enlarge. In *Treculia*

adjacent pistillate perianths are not fused, but rather the stalks of the abundant interfloral bracts are fused for about half their length. The flowers are enclosed in cavities between the fused bracts and the entire inflorescence enlarges into a syncarp (Jarrett 1959c).

The smaller genera do not have any recognized infrageneric taxa, but *Artocarpus*, which has been monographed twice (Trécul 1847; Jarrett 1959a, c, 1960a), has been subdivided. Trécul (1847) placed the 15 species of *Artocarpus* recognized at the time into two subgenera. Species with alternate, spirally arranged leaves, amplexicaul stipules, and annulate stipule scars were placed in subgenus *Jaca* Trécul (from the Malayalam word *chakka* given to jackfruit, *A. heterophyllus*). Those species with alternate, distichous leaves, nonamplexicaul stipules, and lateral stipule scars were placed in subgenus *Pseudojaca* Trécul.

Beccari (1902) noted that the only difference between *Artocarpus* and *Prainea* was the degree of fusion among adjacent pistillate perianths (with those in *Artocarpus* being

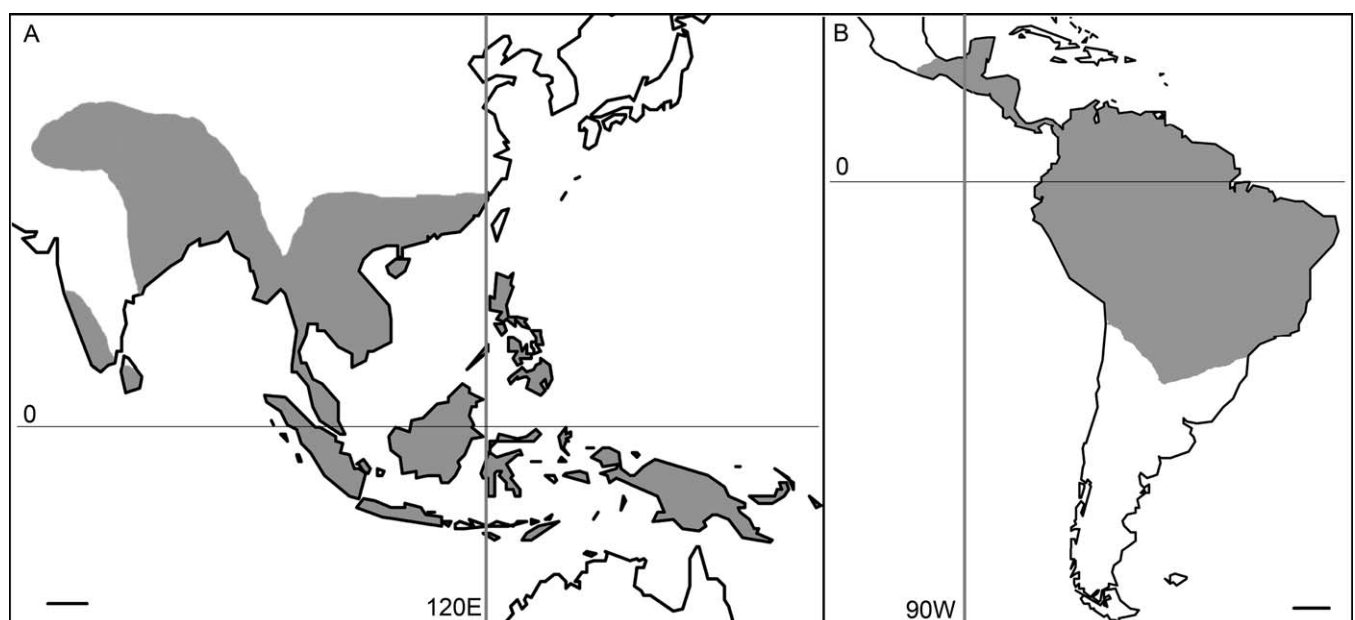


FIG. 1. Distribution of Artocarpeae. This treatment of the tribe Artocarpeae includes: A. one paleotropical genus (*Artocarpus* including *Prainea* as a subgenus) and B. two neotropical genera (*Clarisia* and *Batocarpus*). Several *Artocarpus* species, including *A. altilis*, *A. camansi*, and *A. heterophyllus*, are cultivated throughout the tropics. Scale bar for each map is 500 km.

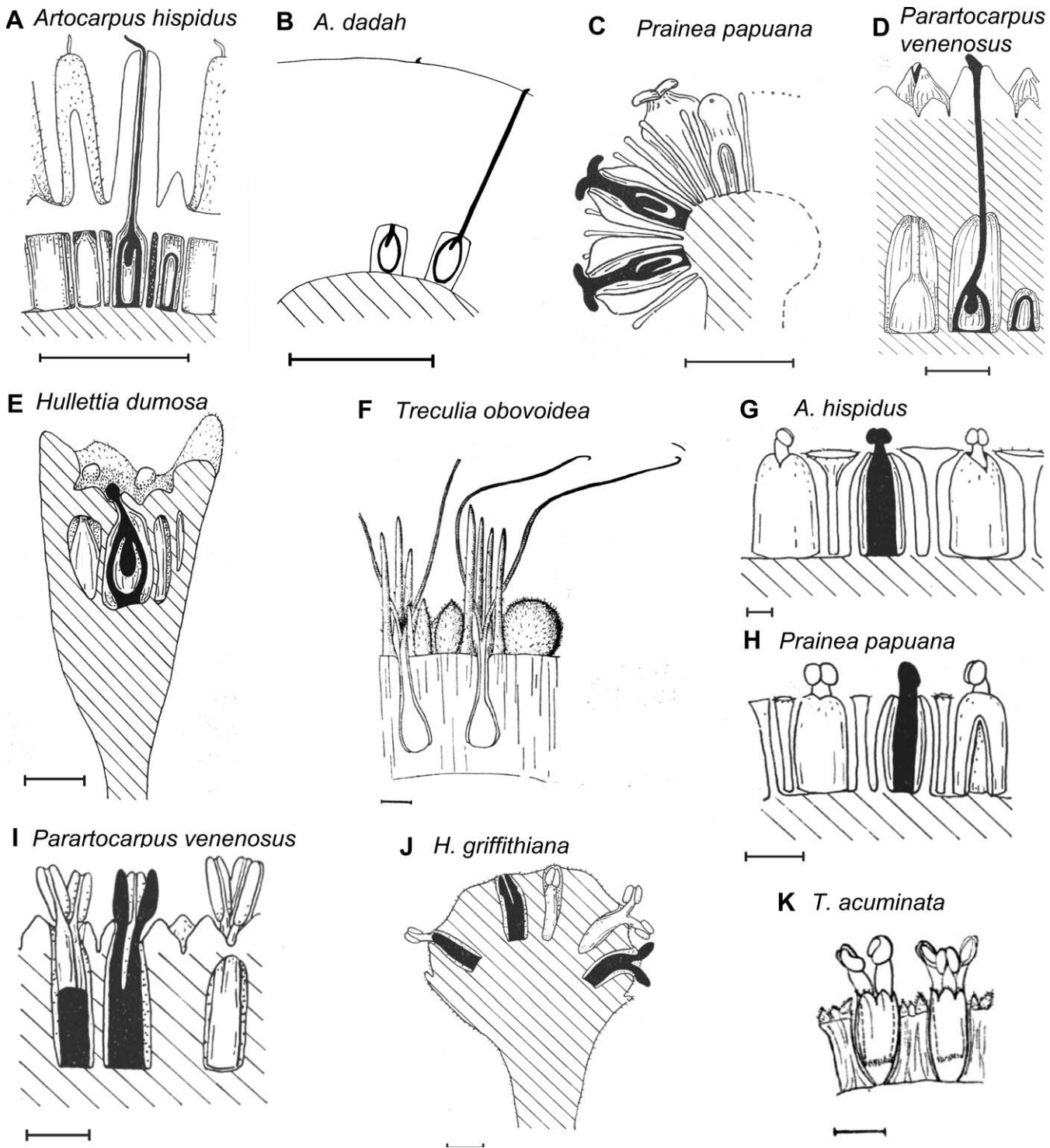


FIG. 2. Inflorescence sections. Longitudinal sections through pistillate (A-F) and staminate (G-K) inflorescences of species of *Artocarpus*, *Prainea*, *Parartocarpus*, *Hullettia*, and *Treculia*. A. *Artocarpus hispidus* (subgenus *Artocarpus*) exhibits medial adjacent perianth fusion. B. *Artocarpus dadah* (subgenus *Pseudojaca*) exhibits complete fusion of perianth apices. C. *Prainea papuana* exhibits no fusion between adjacent perianth apices, but dense interfloral bracts are present. D and E. *Parartocarpus venenosus* and *Hullettia dumosa*, respectively, lack perianths, and flowers are embedded directly in the receptacle. F. Flowers of *Treculia obovoidea* are enclosed in cavities formed by the fusion of the stalks of abundant interfloral bracts. G and H. In *A. hispidus* (G) and *Prainea papuana* (H), adjacent staminate perianths are free and interfloral bracts are present. I and J. Staminate flowers of *Parartocarpus venenosus* ssp. *forbesii* and *H. griffithiana* lack perianths and are embedded in the receptacular tissue. K. Adjacent staminate perianths are free and interfloral bracts are present in *T. acuminata*. The scale bar in A - F is 1 cm, and for G - K is 1 mm. In A - E, and G - J, the diagonal lines indicate receptacular tissue, the black indicates either pistils (A - E) or stamens (G - J), and the white indicates either perianth tissue or interfloral bracts. A, B - E, and G - J have been modified from Jarrett 1959 with permission from the Arnold Arboretum. Copyright © President and Fellows of Harvard College, Archives of the Arnold Arboretum. F and K have been modified from Berg (1977a) with permission from the *Bulletin du Jardin botanique national de Belgique*.

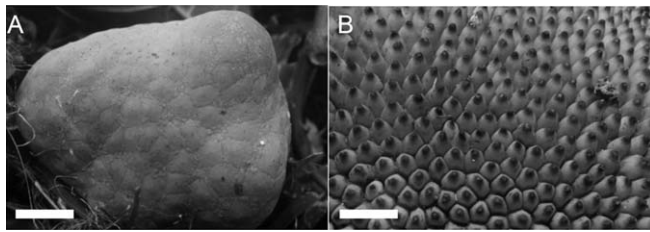


FIG. 3. Surface characteristics of *Artocarpus*. A. Species containing pistillate inflorescences with adjacent perianth apices fused apically have a smooth surface as in *A. nitidus* ssp. *lingnanensis* (NZ4); B. species with perianth apices fused medially but free apically have a spiky surface, like *A. heterophyllus* (NZ6). Scale bar is 1 cm.

completely to partially fused to one another and those in *Prainea* being entirely free) (Fig. 2). Renner (1907) maintained Trécul's (1847) subgeneric sections (*Jaca* and *Pseudojaca*), but reduced the genus *Prainea* to a third section within *Artocarpus*. His treatment was based largely on leaf and stipule char-

acters that *Prainea* shared with the other two subgenera of *Artocarpus*. More recently, Jarrett (1959a, 1959b) rejected Renner's (1907) treatment of *Prainea*, maintained the two subgenera originally created by Trécul (1847), and changed subgenus *Jaca* to subgenus *Artocarpus* (resulting in subgenera *Artocarpus* and *Pseudojaca*). Jarrett (1959c, 1960a) also subdivided both subgenera into several sections and series (Table 2), and proposed for the first time a close affinity between *Hullettia* and *Parartocarpus* based on the shared presence of an inflorescence involucre, absence of a perianth, and pistillate flowers embedded in the receptacle.

Objectives—Historically, Artocarpeae has represented a highly heterogeneous assemblage of genera, and various authors (Rohwer 1993; Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006; Clement and Weiblen 2009) have at one time or another placed its putative members in at least five different tribes (Artocarpeae, Castilleae, Moreae, Soroceae, and Antiaropsidae) (Table 1). Of the competing hypotheses regarding the circumscription of Artocarpeae, only two have

TABLE 2. Characters used to define infrageneric taxa in the genus *Artocarpus* (sensu Jarrett 1959c, 1960a). All species epithets listed under "members of group" heading belong to the genus *Artocarpus*.

Jarrett	Characters of group	Members of group	Zerega et al.
Subgenus <i>Artocarpus</i> (= <i>Jaca</i>)	Adjacent pistillate perianths fused medially, apices free; spirally alternate leaves; large amplexicaul stipules leaving annulate stipule scars; spongy mesophyll cells loose; presence of resin cells in the leaves; epidermal gland hair heads typically multicellular	Sections <i>Artocarpus</i> and <i>Duricarpus</i>	Monophyletic if <i>A. sepicanus</i> and series <i>Cauliflori</i> are excluded
Section <i>Artocarpus</i>	Free pistillate perianth apices fleshy; interfloral bracts infrequent or lacking; long slender staminate inflorescences	Series <i>Angusticarpus</i> , <i>Cauliflori</i> , <i>Incisifolii</i> , <i>Rugosi</i>	Monophyletic if series <i>Cauliflori</i> is excluded
Series <i>Angusticarpus</i>	Unspecialized	<i>A. lowii</i> , <i>A. teysmannii</i>	Not tested
Series <i>Cauliflori</i>	Cauliflorous; absence of resin cells in the leaves	<i>A. heterophyllus</i> , <i>A. integer</i>	Monophyletic if <i>A. annulatus</i> is included
Series <i>Incisifolii</i>	Adult leaves frequently pinnatifid; inflated hairs on syncarp of some species (absent in <i>A. altilis</i> , <i>A. camansi</i> , and <i>A. mariannensis</i>)	<i>A. blancoi</i> , <i>A. treculianus</i> , <i>A. horridus</i> , <i>A. communis</i> (recently spilt into <i>A. altilis</i> , <i>A. camansi</i> , and <i>A. mariannensis</i>), <i>A. pimatisectus</i> , <i>A. multifidus</i>	Not monophyletic
Series <i>Rugosi</i>	Staminate inflorescences with vertically wrinkled surface, continuous hypodermis of isodiametric cells, 4-celled depressed globose epidermal gland hair heads	<i>A. scortechinii</i> , <i>A. elasticus</i> , <i>A. sericicarpus</i> , <i>A. tamaran</i> , <i>A. sumatranus</i> , <i>A. kemando</i> , <i>A. maingayi</i>	Monophyletic if <i>A. lowii</i> is included
Section <i>Duricarpus</i>	Free pistillate perianth apices indurated and woody; interfloral bracts abundant	Series <i>Asperifolii</i> and <i>Laevifolii</i>	Monophyletic
Series <i>Asperifolii</i>	Hypodermis absent; hispid shoots	<i>A. melinoxylum</i> , <i>A. chaplasha</i> , <i>A. odoratissimus</i> , <i>A. hispidus</i> , <i>A. rigidus</i>	Monophyletic
Series <i>Laevifolii</i>	Hypodermis present; glabrous shoots	<i>A. anisophyllus</i> , <i>A. lanceifolius</i>	Monophyletic
Section Anomalous	Characteristics shared with both sections <i>Artocarpus</i> and <i>Duricarpus</i>	<i>A. hirsutus</i> , <i>A. nobilis</i> , <i>A. sepicanus</i>	Not monophyletic
Subgenus <i>Pseudojaca</i>	Adjacent pistillate perianth apices fused to one another; alternate distichous leaves; nonamplexicaul stipules leaving lateral stipule scars; spongy mesophyll cells compact; epidermal gland hair heads typically unicellular	Sections <i>Glandulifolium</i> and <i>Pseudojaca</i>	Not tested
Section <i>Glandulifolium</i>	Leaf base trinerved; glandular crenate leaf margins	<i>A. altissimus</i>	Not tested
Section <i>Pseudojaca</i>	Leaf base pinnately nerved; no glandular crenate leaf margin	Series <i>Clavati</i> and <i>Peltati</i>	Monophyletic
Series <i>Clavati</i>	Interfloral bracts thinly stalked with clavate heads	<i>A. petelotii</i> , <i>A. hypargyreus</i> , <i>A. styracifolius</i>	Not tested
Series <i>Peltati</i>	Interfloral bracts thickly stalked with peltate heads	<i>A. glaucus</i> , <i>A. vrieseanus</i> , <i>A. xanthocarpus</i> , <i>A. longifolius</i> , <i>A. subrotundifolius</i> , <i>A. reticulatus</i> , <i>A. lakoocha</i> , <i>A. gomezianus</i> , <i>A. tomentosulus</i> , <i>A. ovatus</i> , <i>A. tonkinensis</i> , <i>A. fretessii</i> , <i>A. dadah</i> , <i>A. rubrovenius</i> , <i>A. nitidus</i> , <i>A. fulvicortex</i>	Monophyletic

been based on phylogenetic analyses (Datwyler and Weiblen 2004; Clement and Weiblen 2009). Unfortunately, samples from only 3–4 species of *Artocarpus* and none from *Hullettia* or *Treculia* were included in these studies. Using sequence data from the plastid (*trnL* intron and *trnL-F* spacer, *trnL-F*) and nuclear (ITS 1 and 2 and 5.8S rDNA) genomes, this study was designed to create a well-resolved phylogenetic hypothesis with which to: 1) test the monophyly of Artocarpeae, *Artocarpus*, and infrageneric divisions within *Artocarpus* and 2) develop a phylogenetic classification and treatment based on the results and morphological considerations. We present the most complete phylogenetic estimate for Artocarpeae and the genus *Artocarpus* to date, and also consider inflorescence evolution and pollination in the tribe.

MATERIALS AND METHODS

Taxon Sampling—The ingroup included all genera that have been placed in Artocarpeae in the most recent circumscriptions (Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006; Clement and Weiblen 2009). Thus, the ingroup included two species each of *Prairiea*, *Treculia*, *Parartocarpus*, and *Sorocea*, one species each of *Hullettia*, *Bagassa*, *Batocarpus*, *Clarisia*, *Sparattosyce*, *Antiaropsis*, *Poulsenia*, and 34 species and four subspecies of *Artocarpus* representing all subgenera, sections (except the monotypic sect. *Glandulifolium* Jarrett), and series (Appendix 1). Outgroup taxa belong to five other tribes of Moraceae and one species each of *Ficus* (Ficeae), *Dorstenia* and *Brosimum* Sw., (Dorstenieae), *Castilla* Cerv. (Castilleae), *Morus* L. (Moreae), and *Maclura* (Maclureae (sensu Clement and Weiblen 2009), as well as one species each of *Humulus* L. and *Cannabis* L. (Cannabaceae).

Sequence data for the two gene regions (ITS and the *trnL-F* region) were generated by the authors for all taxa with the exception of seven previously published sequences; nine sequences for *trnL-F* are missing (Appendix 1).

DNA Extraction, Amplification, and Sequencing—Leaf samples were collected either in silica gel or from herbarium sheets (Appendix 1). Genomic DNA was extracted from approximately 1 cm² of dried leaf tissue using a modified CTAB (cetyltrimethylammonium bromide) method (Zerega et al. 2002).

DNA amplification for the ITS and *trnL-F* regions were performed in a 25 μ l volume (1 \times Taq buffer with 1.5 mM MgCl₂, (Qiagen, Valencia, California), 1mg/ml BSA (bovine serum albumin), 2.5 mM each dNTP, 20 μ M of each primer, 1 M betaine, 1 unit Taq polymerase (Qiagen), and ~50 ng of genomic DNA). Amplification and cycle sequencing reactions were run on a Gene Amp PCR system 9600 (Applied Biosystems, Foster City, California).

Amplification of the *trnL-F* region utilized external primers “c” and “f,” and the internal primers “d” and “e” were also employed for amplification from herbarium specimens (Taberlet et al. 1991). Thermal cycling conditions for amplification of the *trnL-F* region were: 94°C for 3 min followed by 32 cycles of 94°C for 45 sec, 52°C for 30 sec, 72°C for 1 min 30 sec, and a final extension of 74°C for 7 min. The ITS region was amplified using forward (5'-AACAAAGGTTTCCGTAGGTGA-3') and reverse (5'-TATGCTTAAAYTCAGCGGGT-3') primers, and for some herbarium specimens, internal primers were also employed (5'-GCATCGATGAAGAACGTAGC-3' and 5'-GCTACGTTCTTCATCGATGC-3') (modified from Baldwin 1992; Nickrent et al. 1994; Baldwin et al. 1995). The PCR conditions for amplification of the ITS region were: 97°C for 50 sec, 30 cycles of 97°C for 50 sec, 53°C for 50 sec, 72°C for 1 min 50 sec, and a final extension of 72°C for 7 min.

Amplified products were purified with spin columns from the QIAquick PCR purification kit (Qiagen) following protocols provided by the manufacturer. Purified products were cycle sequenced in 10 μ l reactions using Big Dye sequencing reagents and protocols (Applied Biosystems). Primers for cycle sequencing were the same as those used in the PCR reactions, but the internal primers “d” and “e” were also employed for all samples for the *trnL-F* region. Cycle sequencing conditions were: 95°C for 1 min, 32 cycles of 96°C for 10 sec, 50°C for 5 sec, 60°C for 3 min. Cycle sequencing products were purified on a sephadex column and data were collected on an ABI Prism 377 DNA sequencer (Applied Biosystems) and edited in Sequencher version 3.1.2 (Gene Codes Corporation, Ann Arbor, Michigan).

Sequence Alignment and Phylogenetic Analysis—Sequences from the ITS region were aligned using Clustal W (Chenna et al. 2003) followed

by manual optimization. Sequences from the *trnL-F* region were easily aligned manually. Manual alignment and optimization were performed in Se-AI v2.0a7b (Rambaut 2001). For the *trnL-F* region, indels were coded as additional, unordered characters if they were bordered by stretches of unambiguously aligned nucleotides and were not a single nucleotide repeat. Indels were treated as the same state if they were the same size and their nucleotide sequence did not vary.

Data from ITS and the *trnL-F* regions were analyzed separately. The trees obtained for each region were examined for hard (bootstrap of 70% or higher) or soft (bootstrap below 70%) incongruences based on bootstrap support for nodes in both of the separate analyses. In the case of soft incongruences, conflicts likely reflect insufficient information in one or both of the datasets leading to an unstable position and considerable character evolution and resolution in the other, rather than different branching histories (Seelanan et al. 1997). Combining the data in such a scenario may lead to better resolution and more accurate phylogeny reconstruction, allowing the phylogenetic signal to assert itself over the noise. We did not employ the incongruence length difference test (ILD), as there were no hard incongruences between the datasets, and the ILD test has been shown to be a poor test of the compatibility of separate data partitions (Hipp et al. 2004). Separate and combined maximum parsimony (MP) searches were performed using the ratchet as employed in Winclada 1.00.08 (Nixon 1999–2002) and NONA (Goloboff 1999) and maximum likelihood (ML) searches were performed in PAUP* 4.01b10 (Swofford 2002).

Maximum parsimony searches using the ratchet method were performed with uninformative characters excluded. The ratchet is able to more efficiently estimate phylogeny by randomly varying taxon order, holding fewer trees per replicate, sampling many tree islands, and holding fewer trees per island (Nixon 1999). Five sequential ratchet runs were performed and iterated 1,000 times per replicate, with 10 trees held per replicate. Each ratchet performs two searches, one in which all characters are equally weighted, and one search in which a random percentage of characters (determined by the user, 30% in this case) are weighted, but weights are not assigned to the same characters in each iteration. Trees from the independent searches are used to extract the most parsimonious trees.

For ML analyses, Modeltest version 3.7 (Posada and Crandall 1998) was used to select substitution models that best fit the separate and combined datasets. Heuristic searches were performed under ML with a neighbor joining tree as a starting topology and model parameters obtained with Modeltest under the Akaike Information Criterion (AIC) for model selection (Posada and Buckley 2004).

Clade support for both MP and ML phylogenies were assessed with a bootstrap analysis using 1,000 replicates with 100 random addition sequence replicates, and tree bisection and reconnection (TBR) branch swapping as implemented in PAUP* 4.01b10 (Swofford 2002).

RESULTS

ITS Analyses—The ITS dataset provided a total of 779 aligned nucleotides of which 416 were parsimony informative. The data matrix had 2.6% missing data. Parsimony searches recovered 111 most parsimonious trees (MPTs) of 1,984 steps, consistency index (CI) of 0.43, and retention index (RI) of 0.66. In the strict consensus tree ten nodes collapsed. For ML analyses a total number of 779 characters were used. Modeltest (Posada and Crandall 1998) identified a general time reversible model with a gamma distribution and proportion of invariable sites (GTR + I + G) as the best fitting model of sequence evolution for ITS. The single most likely ITS tree resulting from heuristic searches had a score of $-\ln L = 10917.89138$ with a rate matrix of AC = 0.766900, AG = 1.388800, AT = 1.022600, CG = 0.376200, and CT = 2.729000, gamma = 1.2999, I = 0.1674, and base frequencies of A = 0.22130, C = 0.30450, G = 0.26900, and T = 0.20520. The MP strict consensus tree (not shown) and the ML tree (Fig. 4) revealed Artocarpeae as defined by any past circumscriptions to be polyphyletic. There are only two deep and three tip level relationships that differ between the ML and MP analyses of ITS, and these relationships have no support in either reconstruction. In the MP analysis, *Maclura*

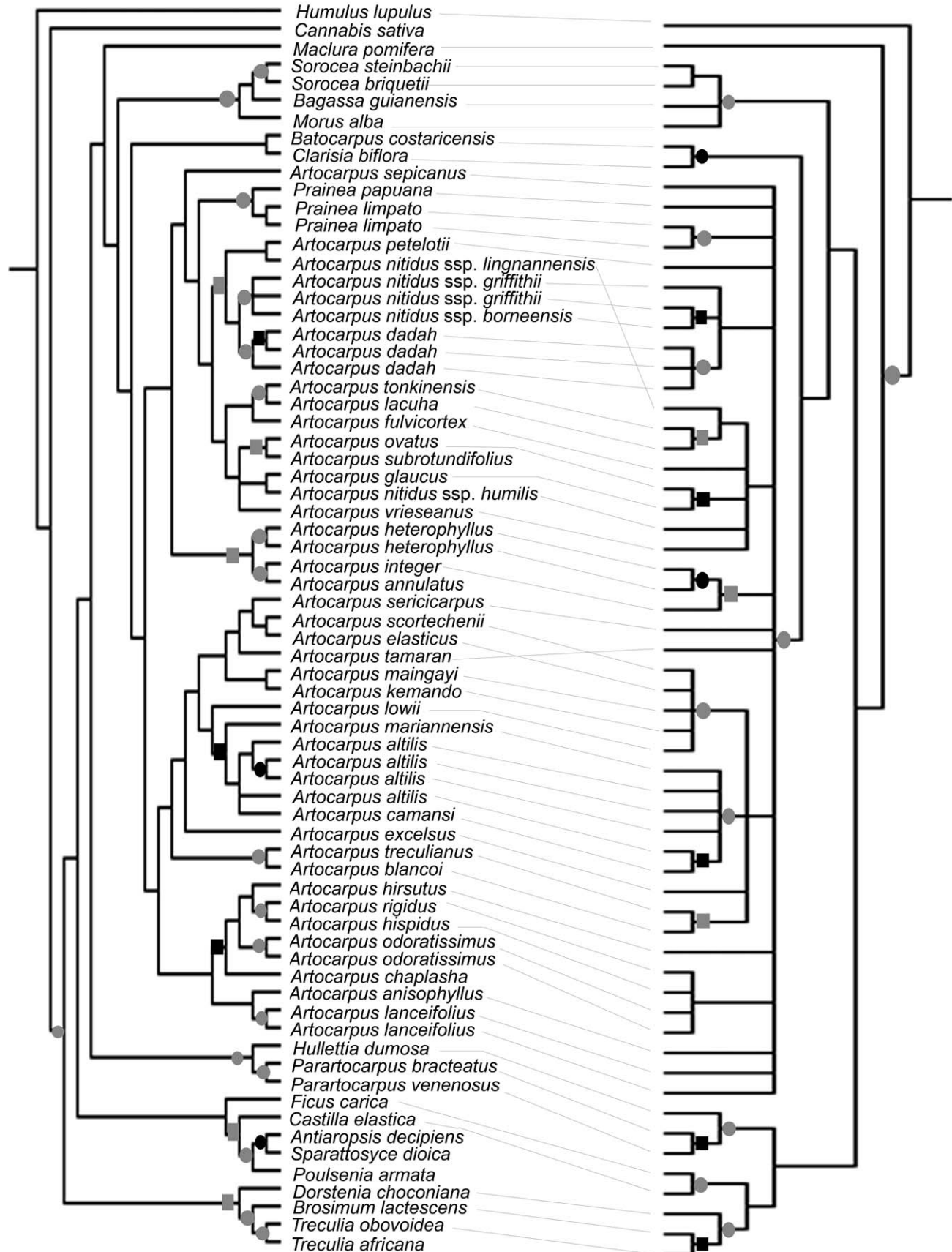
ML tree based on *ITS* dataML tree based on *trnL-F* data

FIG. 4. Maximum likelihood analyses based on separate datasets. A. Tree based on ITS data, B. Tree based on *trnL-F* data. Bootstrap support ranges are indicated by symbols on branches: Gray circles = 90–100%, black circles = 80–89%, gray squares = 70–79%, and black squares = 60–69%.

pomifera is sister to the rest of the Moraceae family, while in the ML analysis, it is sister to a clade comprising only *Artocarpus*, *Prainea*, *Batocarpus*, *Clarisia*, *Morus*, *Sorocea*, and *Bagassa*. In the ML analysis, the following taxa form a grade of three clades: 1) *Dorstenia*, *Brosimum*, and *Treculia*; 2) *Ficus*, *Castilla*, *Poulsenia*, *Antiaropsis*, and *Sparattosyce*; and 3) *Hullettia* and *Parartocarpus*. In the MP analysis, these clades are part of an unresolved and unsupported monophyletic group. The remaining differences between the ML and MP analyses of ITS are near the tips and involve minor rearrangements of *Artocarpus camansi* and *A. petelotii*.

***trnL-F* Analyses**—The *trnL-F* dataset provided 1,140 aligned nucleotides of which 123 were parsimony informative. The data matrix had 13.7% missing data. Additionally, the *trnL-F* region provided five unambiguous parsimony informative indels which were coded as separate characters. Parsimony searches recovered 552 MPTs of 202 steps, CI = 0.75, and RI = 0.89. In the strict consensus tree (not shown) 26 nodes collapsed. For ML analyses, a total number of 1,140 characters were used. Modeltest (Posada and Crandall, 1998) identified a K81uf + G as the best fitting model of sequence evolution for the *trnL-F* dataset. The two most likely *trnL-F* trees resulting from heuristic searches had a score of $-\ln L = 3,905.04799$ with a rate matrix of AC = 1.010600, AG = 1.832000, AT = 0.396900, CG = 0.825400, and CT = 1.832000, gamma = 1.2094, and base frequencies of A = 0.35970, C = 0.16200, G = 0.15900, and T = 0.31930. The ML *trnL-F* topology was more resolved than the MP analysis. In the MP consensus tree the following taxa form a grade of three clades: 1) *Dorstenia*, *Brosimum*, and *Treculia*; 2) *Ficus* and *Castilla*; and 3) *Hullettia* and *Parartocarpus*. In the ML analysis, these taxa form an unsupported monophyletic group (Fig. 4).

Combined Analyses—Comparing the phylogenies based on the separate analyses of ITS and *trnL-F* revealed only minor rearrangements at unsupported tips, with the exception of four instances where one dataset provided strong support for an arrangement of taxa while the other dataset provided weak or no support for an alternate arrangement (Fig. 4). There was 98% support for placement of *Prainea papuana* in a clade with *Prainea limpato* in the ITS tree, while its position was unresolved within the *Artocarpus* + *Prainea* clade in the *trnL-F* tree. *Ficus carica* was strongly supported (95% bootstrap) as sister to *Castilla elastica* (Castilleae) in the *trnL-F* tree, and it was sister to a clade comprising *Castilla elastica*, *Antiaropsis decipiens*, *Sparattosyce dioica*, and *Poulsenia armata* (all members of Castilleae) and *Dorstenia choconiana*, *Brosimum lactescens*, *Treculia obovoidea*, and *T. africana* (all members of Dorstenieae as defined here) in the ITS tree. *Artocarpus lowii* was strongly supported (96%) as part of a clade including members of series *Rugosi* in the *trnL-F* tree and was placed as sister to the breadfruit clade (with no support) in the ITS tree. *Batocarpus* and *Clarisia* were supported (88%) as sister taxa in the *trnL-F* tree, but there was no bootstrap support for their sister relationship in the ITS tree. As no hard incongruencies in relationships were present, the two datasets were combined. Parsimony searches of the combined datasets recovered 16 MPTs of 1,992 steps, CI = 0.43, and RI = 0.65. In the strict consensus tree, seven nodes collapsed (MP tree not shown). Additionally, the number of supported nodes increased in the combined analysis compared to either separate analysis. In the combined analysis, 35 nodes had support of 70% or higher, compared with 25 and 16 nodes in the ITS and *trnL-F* analyses, respectively. For ML analyses of the combined dataset, a

total of 1919 characters (779 from ITS and 1,140 from *trnL-F*) were used. Modeltest (Posada and Crandall 1998) identified a general time-reversible model with a gamma distribution and a proportion of invariable sites (GTR + I + G) as the best fitting model of sequence evolution for the combined ITS and *trnL-F* dataset. The single most likely tree resulting from heuristic searches had a score of $-\ln L = 15,459.66603$ with a rate matrix of AC = 0.674700, AG = 1.243500, AT = 0.557300, CG = 0.558200, and CT = 2.416800, base frequencies of A = 0.29870, C = 0.23990, G = 0.21290, and T = 0.24850, gamma = 0.586, and proportion of invariable sites = 0.2477. The ML and MP trees based on combined datasets differed only in the exact placement of *A. fulvicortex* within subgenus *Pseudojaca* and in whether *Morus* is sister to *Bagassa* + *Sorocea* (MP, 61% bootstrap) or *Bagassa* is sister to *Morus* + *Sorocea* (ML, 100% bootstrap) (Fig. 5). Data matrices and trees for this study are deposited in TreeBASE (study number S2347).

DISCUSSION

This study represents the most complete phylogeny of Artocarpeae and *Artocarpus* to date. Artocarpeae as treated here comprises three genera, which include a small neotropical lineage (*Batocarpus* and *Clarisia*) and a larger Southeast Asian/Malesian lineage (*Artocarpus* including *Prainea*). Previous divergence date estimates for Moraceae suggest that these lineages diverged from one another 65.1 mya (52.2–80.6 mya) and that their split was facilitated via land migration from the Old to the New World across an Eocene North Atlantic Landbridge (Zerega et al. 2005a). The more comprehensive Artocarpeae phylogenetic reconstruction presented here will aid in testing this hypothesis and further understanding the timing and mechanisms for the movement of this group.

Artocarpeae Phylogeny—The delimitation of Artocarpeae has historically been difficult and circumscriptions have been variable. This study tested the monophyly of the tribe by including all genera that have been placed in the tribe in recent treatments (Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006; Clement and Weiblen 2009). Because the two molecular datasets presented here had no significant conflict, and the phylogenies based on the combined datasets for MP and ML analyses varied only in two poorly supported tip relationships, the ML tree based on the combined datasets will be referred to in the following discussion (Fig. 5). The data presented here indicate that none of the previous Artocarpeae classifications represent a monophyletic group, but rather the taxa once placed within the tribe are spread throughout several tribes of the Moraceae (Table 1). Because our results largely agree with the most recent Moraceae treatment of Clement and Weiblen (2009), with only a few differences, their tribal level treatment will be used as the framework within which to discuss the results.

Castilleae—*Antiaropsis*, *Sparattosyce*, and *Poulsenia* have been placed in the tribe Artocarpeae in recent treatments of the Moraceae family (Rohwer 1993; Berg 2001) (Table 1). The present study resolved *Antiaropsis*, *Sparattosyce*, and *Poulsenia* as part of the Castilleae clade and all three genera share the synapomorphies that characterize Castilleae, namely an inflorescence involucre of imbricate bracts that only partially encloses the flowers (as opposed to fully enclosing in Ficeae). As such, we maintain the treatment of Castilleae as proposed by Datwyler and Weiblen (2004) and Clement and Weiblen (2009) (Table 1).

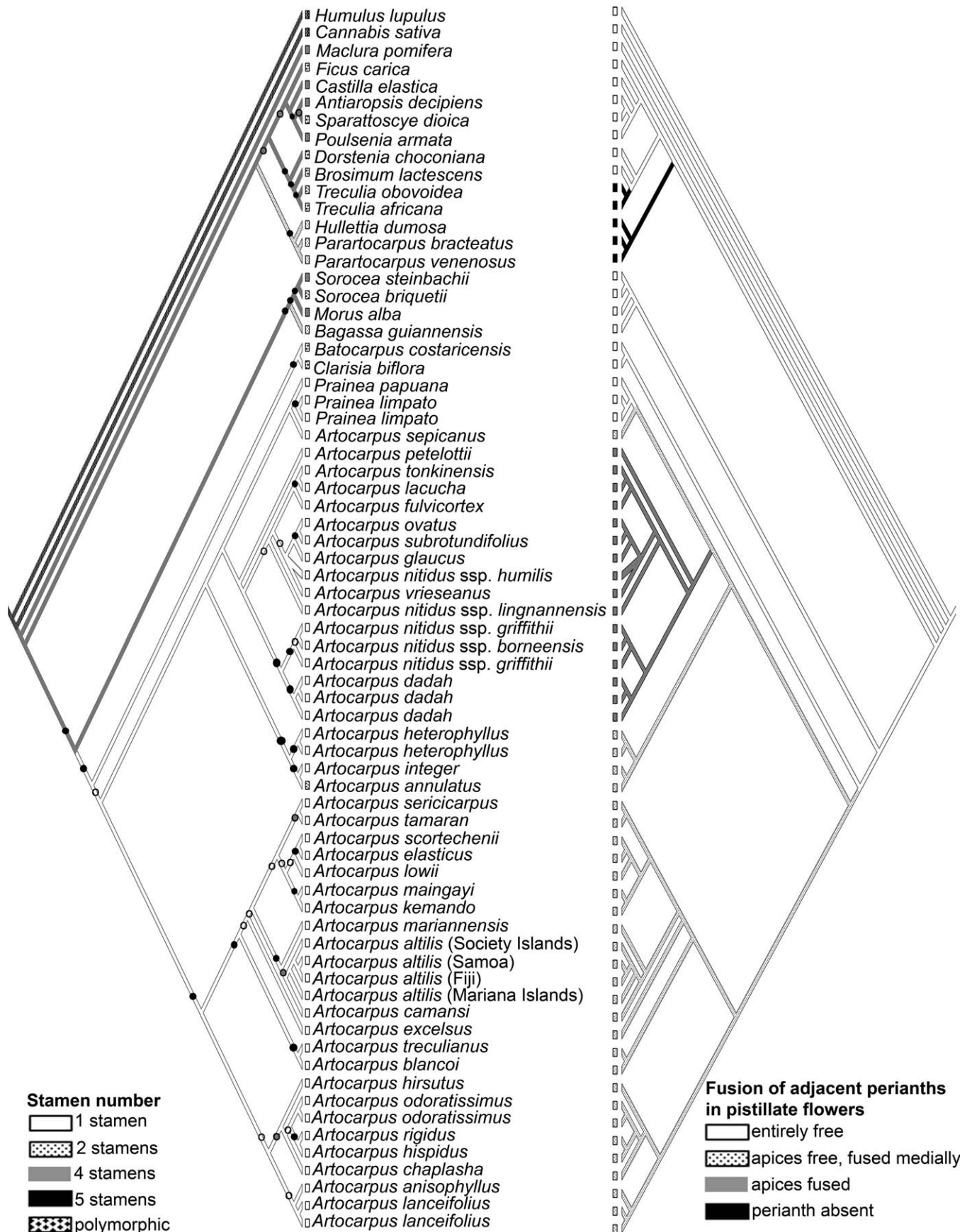


FIG. 5. Maximum likelihood tree based on combined datasets from ITS and *trnL-F*. The tree on the left traces the number of stamens in staminate flowers. The tree on the right traces the degree of fusion among perianths from adjacent flowers in pistillate inflorescences. All species were scored for these characters. Bootstrap support ranges are indicated by symbols on branches: Black circles = 90–100%, gray circles = 80–89%, open circles = 60–69%.

Moreae—*Bagassa* and *Sorocea* have both been placed in the tribe Artocarpeae (Rohwer 1993; Berg 2001). The most recent treatments of Moraceae place these genera in Moreae (Datwyler and Weiblen 2004; Clement and Weiblen 2009) and the present study supports this.

Dorstenieae—*Treculia* was established by Decaisne in Trécul's (1847) monographic treatment of Artocarpeae, and it has been primarily treated in Artocarpeae ever since (Jarrett 1959a; Corner 1962; Rohwer 1993; Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006). However, in his treatment of African Moraceae, Berg (1977b) placed *Treculia* in a Moreae tribe that combined the Artocarpeae and Moreae tribes. Previous phylogenetic studies based on molecular data (Datwyler and Weiblen 2004; Zerega et al. 2005a; Clement and Weiblen 2009) did not include any *Treculia* species. The present study indicates that *Treculia*, the only African taxon included in previous circumscriptions of Artocarpeae, is nested with strong support within the tribe Dorstenieae, a tribe with numerous African and Madagascan members. While Corner (1962) and Berg (1977b) both hypothesized a possible alliance between *Treculia* and *Parartocarpus* based on similarities in inflorescences, infructescences, fruits, and seeds, affinities with Dorstenieae have never before been considered, and this placement is surprising. It is possible that a misinterpretation of character homologies (i.e. confusing flowers embedded in receptacular tissue (e.g. *Hullettia* and *Parartocarpus*) or the fused adjacent pistillate perianths of *Artocarpus* with the fused interfloral bract stalks of *Treculia*) may have led to the placement of *Treculia* in Artocarpeae. The Dorstenieae are quite variable, being the only tribe that exhibits the full range of habits from herbs, to succulent shrubs, to trees (Berg 2001). However, most genera in the tribe have bisexual inflorescences, which are typically not found in other Moraceae tribes apart from Ficeae. *Treculia* is a small genus (three species) and includes both dioecious and monoecious shrub and tree species. However, the female inflorescences of *Treculia* may have numerous abortive male flowers, male inflorescences often have pistillodes, and in one species, *T. africana*, bisexual inflorescences frequently occur (Jarrett 1959a; Berg 1977b). This lineage may represent an incomplete loss of bisexual inflorescences within the tribe Dorstenieae. Further phylogenetic, morphological, and developmental studies should be conducted to help elucidate this intriguing affinity of *Treculia* with Dorstenieae. We recommend that *Treculia* be transferred to Dorstenieae.

Unplaced—*Parartocarpus* and *Hullettia* have been placed in Artocarpeae in recent floristic treatments (Jarrett 1960b; Berg 2001; Berg et al. 2006). Phylogenetic studies have recorded conflicting placements of *Parartocarpus* within either Moreae or Artocarpeae, while *Hullettia* samples have not been included in these studies (Datwyler and Weiblen 2004; Zerega et al. 2005a; Clement and Weiblen 2009). The position of *Hullettia* has been in question since King's (1888) erroneous placement of the genus in the Conocephaleae. Renner (1907) excluded the genus from his treatment of the Artocarpeae and Conocephaleae, and was uncertain about its relationship to the other genera. Jarrett (1959a) first proposed a close relationship between *Hullettia* and *Parartocarpus* (a relationship strongly supported (100% bootstrap) by this study) based in part on the shared absence of perianths and flowers embedded in receptacular tissue. The two genera also share an inflorescence involucre that is absent in *Artocarpus*. The results presented here sug-

gest that *Hullettia* and *Parartocarpus* may be sister to Ficeae + Castilleae + Dorstenieae, but there is no support for this relationship. Based on our results, the strongly supported clade of *Hullettia* and *Parartocarpus* may deserve tribal status. However, given the clade's unstable position in relation to three closely related tribes in this and previous analyses, further studies are warranted.

Artocarpeae—*Batocarpus*, *Clarisia*, *Prainea*, and *Artocarpus* have all been placed in Artocarpeae in one or more recent treatments of the family (Jarrett 1959a; Rohwer 1993; Berg 2001; Datwyler and Weiblen 2004; Clement and Weiblen 2009). This placement is strongly supported (100% bootstrap) in the current study and it is recommended that the limits of Artocarpeae be reduced to comprise the species represented in these four genera. Artocarpeae as defined here are supported by a reduction in stamen number within the family (Fig. 5). *Artocarpus*, *Prainea*, *Clarisia*, and *Batocarpus* all have one (or less frequently two in *Batocarpus* and *A. annulatus*, and one to three in *Clarisia*) stamen per flower as compared to the more typical two to five in other Moraceae. The typical number of stamens per flower in the Moraceae is four, but exceptions exist in all of the tribes.

Batocarpus and *Clarisia* form a well-supported (100% bootstrap) clade that is sister to the more weakly supported (65% bootstrap) clade of *Artocarpus* + *Prainea*. Fosberg (1942) suggested that *Clarisia* and *Batocarpus* have close affinities with one another and that as the species of these two genera become better known, they may prove difficult to maintain as separate genera. Further studies focusing on all species of *Clarisia* and *Batocarpus* will be necessary to determine generic limits.

Artocarpus and Prainea Phylogeny—The relationship between *Artocarpus* and *Prainea* has long been recognized as a close one (Beccari 1902; Renner 1907; Jarrett 1959a). Renner (1907) viewed *Prainea* as an intermediate between *Artocarpus* subgenera *Jaca* (= *Artocarpus*) and *Pseudojaca* and placed it at the subgeneric level within the genus *Artocarpus*, while Jarrett (1959a, 1959b) treated *Prainea* as a separate but closely allied genus. Jarrett (1959a) placed priority on reproductive (lack of fusion among adjacent pistillate perianths in *Prainea* compared to partial to complete fusion in genus *Artocarpus*) over vegetative characters. Renner placed priority on leaf phyllotaxy and stipule characters (which *Prainea* shares with subgenus *Pseudojaca*), and leaf anatomy (which *Prainea* shares with subgenus *Artocarpus*). *Prainea* and subgenus *Artocarpus* both have glandular epidermal hairs with multicellular heads and resin-containing cells in the leaf mesophyll (with the exception of *A. heterophyllus* and *A. integer* which lack the latter), whereas subgenus *Pseudojaca* has unicellular epidermal gland hair heads and no resin-containing cells in the mesophyll. The combined phylogenetic evidence presented here supports Renner's treatment, as *Prainea* (two of four species sampled) is supported as a monophyletic group nested within the genus *Artocarpus*. Given the position of *Prainea* in the combined phylogeny and its morphological intermediacy between other subgenera of *Artocarpus*, it is treated here as a subgenus of *Artocarpus*.

The treatment of *Prainea* as a separate genus (Jarrett 1959a, b) was based primarily on the degree of fusion among adjacent pistillate perianths. Interestingly, Jarrett noted that in young pistillate inflorescences of *A. rigidus* (subgenus *Artocarpus*), adjacent pistillate perianths are entirely free from one another. The thick-walled medial portions of the perianths become

fused only later in development. Moncur (1985) also reported fusion of the medial portion of adjacent pistillate perianths in *A. heterophyllus* only after anthesis. Sharma (1965) studied the anatomy and morphology of eight *Artocarpus* species (seven from subgenus *Artocarpus* and one from subgenus *Pseudojaca*), and reported that adjacent pistillate perianths are free from one another at early stages in all eight species studied. He found that even before anthesis the middle region of the perianth begins to thicken outward due to rapid divisions and subsequent enlargement of the ground tissue. It is possible that *Prainea* represents a lineage within *Artocarpus* that has secondarily lost the ability to undergo delayed fusion. Delayed fusion of neighboring parts is a relatively rare phenomenon among angiosperms (Okimoto 1948, Moncur 1985) and would be of interest for further investigation.

Sister to subgenus *Prainea* is the species *A. sepicanus*, which has been treated as anomalous within subgenus *Artocarpus* because it shares characters with both sections *Artocarpus* (long slender male inflorescences) and *Duricarpus* (presence of well-developed interfloral peltate bracts) (Table 2) (Jarrett 1959b). In the phylogeny based on ITS, *A. sepicanus* is sister to a clade containing subgenus *Prainea* plus subgenus *Pseudojaca*. In the phylogeny based on *trnL-F*, *A. sepicanus* collapses within a clade comprised of subgenus *Prainea* and the rest of the genus *Artocarpus*. In the combined phylogeny, *A. sepicanus* is sister to subgenus *Prainea*. None of these placements have any support and the position of *A. sepicanus* remains problematic. Its leaf arrangement, stipule characters, partial fusion of adjacent pistillate perianths (with apices free), and presence of resin in the spongy mesophyll cells clearly match subgenus *Artocarpus*, rather than subgenera *Pseudojaca* or *Prainea*. *Artocarpus sepicanus* has a wide separation of the subapical style and the ventral hilum, which is unusual in *Artocarpus*, but is consistent with subgenus *Prainea* (Jarrett 1959a). It is possible *A. sepicanus* is of hybrid origin with putative parents in subgenera *Prainea* and *Artocarpus*. Although hybridization is rarely reported in *Artocarpus*, members of the breadfruit clade are known to hybridize (Fosberg 1960; Zerrega et al. 2004b, 2005b). Given its problematic position and the lack of support for its sister relationship to subgenus *Prainea*, it is treated here within subgenus *Artocarpus*, with which it shares the most morphological characters.

Artocarpus has been divided into subgenera, sections, and series (Table 2). The two subgenera, *Artocarpus* (= *Jaca*) and *Pseudojaca*, originally described by Trécul (1847) and maintained by Renner (1907) Jarrett (1959a, c, 1960a), and Berg et al. (2006), are not entirely supported by the combined phylogeny presented here. Additionally, at the sectional and series level there is varying support as discussed below.

Artocarpus Subgenus *Pseudojaca*—Jarrett (1960a) described two sections within subgenus *Pseudojaca*: the monotypic *Glandulifolium* (not included in this analysis) and *Pseudojaca* (Table 2). Section *Pseudojaca* has strong support as a monophyletic group (100% bootstrap). It is well defined within the genus *Artocarpus* by both vegetative and floral synapomorphies (Table 2; Figs. 2, 3). Series *Peltati* is monophyletic, though with no support, while the monophyly of series *Clavati* could not be tested since only one (*A. petelotii*) of three species was included in this analysis. A previous *Artocarpus* phylogenetic analysis based on restriction fragment length polymorphism analyses of 11 species found neither subgenus to be monophyletic (as the position of *A. nitidus* was unresolved and *A. chaplasha* was sister to subgenus *Pseudojaca*) (Kanzaki et al. 1997).

Jarrett (1960a) recognized 19 species (several with numerous subspecies) within subgenus *Pseudojaca* series *Peltati*. In the present study, nine species and four subspecies were included. Among these, several have been subsequently treated differently by Berg et al. (2006), and these differences are addressed in the taxonomic treatment below in light of the present study.

Artocarpus Subgenus *Artocarpus*—Subgenus *Artocarpus* has been defined within the genus by both vegetative and floral synapomorphies (Table 2; Figs. 2, 3). Species in subgenus *Artocarpus* exhibit much greater morphological diversity than those in subgenus *Pseudojaca*, and Jarrett (1959c) described six series within two sections (*Duricarpus* and *Artocarpus*) (Table 2). The data presented here indicate that subgenus *Artocarpus* represents a strongly supported (100% bootstrap) monophyletic group, if series *Cauliflori* and the anomalous *A. sepicanus* are excluded from it.

Section *Duricarpus* is monophyletic with weak support (60% bootstrap), and members of the section share the morphological synapomorphy of indurate, free, pistillate perianth apices (Figs. 3, 5). The series described within section *Duricarpus* (Jarrett 1959c) are monophyletic (*Asperifolii* with 82% bootstrap support and *Laevifolii* with 61% bootstrap support).

In section *Artocarpus*, the free, pistillate perianth apices are flexuous rather than indurate as in section *Duricarpus*. Section *Artocarpus* (with the removal of series *Cauliflori* and *A. sepicanus*) is strongly supported (100% bootstrap) as monophyletic (Figs. 4, 5). Series *Cauliflori* is sister to subgenus *Pseudojaca* + *Prainea*. However, there is no support for this sister relationship. Members of *Cauliflori* are monophyletic (100% bootstrap) and, as the name suggests, share the synapomorphy of cauliflorous inflorescences, though inflorescences may also be axillary. They share the leaf arrangement (spirally arranged with amplexicaul stipules) and perianth fusion characters (adjacent pistillate perianths medially fused but free apically) with subgenus *Artocarpus*. They are allied with subgenus *Pseudojaca* in having compact mesophyll and the absence of resin in the spongy mesophyll cells (absent in *A. heterophyllus* and *A. integer*, not examined in *A. annulatus*). Jarrett (1959c) included *A. heterophyllus* (jackfruit) and *A. integer* (chempedak) in series *Cauliflori*, but *A. annulatus* had not yet been described at the time. The present study indicates that *A. annulatus* is also closely allied with these species with a sister relationship to *A. integer*. *Artocarpus annulatus* is endemic to Sarawak and known only from a few localities. Berg et al. (2006) considered *A. annulatus* to be part of section *Duricarpus*. However, it has flexuous perianth apices, indicative of section *Artocarpus*, rather than the indurated perianth apices of section *Duricarpus*. The inflorescences of *A. annulatus* can be axillary or cauliflorous (Kochummen 2000). In the treatment below, *Cauliflori* is raised to the subgeneric rank and comprises the three species discussed above.

The remaining species that Jarrett (1959c) included in section *Artocarpus* were in series *Rugosi*, *Incisifolii* or classified as anomalous. Series *Rugosi* is weakly supported as monophyletic if *A. lowii* is included within it. Apart from *A. lowii*, all the species in this clade have the synapomorphies listed in Table 2. The position of *A. lowii* in the separate analyses varies, being nested within *Rugosi* based on *trnL-F* and sister to breadfruit and its relatives based on ITS. It is possible that *A. lowii* may be of hybrid origin, with a member of the breadfruit clade serving as the maternal parent and a member

of the *Rugosi* clade serving as the paternal parent. However, additional data and samples should be examined to determine the affinities of *A. lowii*.

Series *Incisifolii* was circumscribed based on the presence of multicellular peltate heads on the glandular hairs of the leaf epidermis (as opposed to either globose or depressed globose heads as in the rest of the genus) and on the occasional to consistent presence of pinnatifid adult leaves (Jarrett 1959c). While *Artocarpus* species outside of this series all have adult leaves with entire margins, several species in both subgenera exhibit pinnately lobed juvenile leaves. One species (*A. anisophyllus*) even has compound leaves, demonstrating the labile nature of leaf shape in this group and throughout the Moraceae family. The present study does not include all members originally included in series *Incisifolii*, but nonetheless indicates it does not represent a natural lineage. Additionally Berg et al. (2006) made several changes to species circumscriptions in this series and they are not maintained here, as described in the taxonomic treatment below.

Within subgenus *Artocarpus* there are three anomalous species (*A. hirsutus*, *A. sepicanus*, and *A. nobilis*) that Jarrett (1959c) did not assign to a section, as each species possesses characters that appear to be intermediate between sections *Artocarpus* and *Duricarpus*. The position of *A. sepicanus* was discussed above. In the case of *A. hirsutus*, it has long, slender, male inflorescences typical of section *Artocarpus*, but has indurate, free, perianth apices typical of section *Duricarpus*. The combined phylogeny strongly supports its placement within section *Duricarpus*. *Artocarpus nobilis* also has long, slender male inflorescences typical of section *Artocarpus*, but well-developed peltate interfloral bracts typical of section *Duricarpus*. The placement of *A. nobilis* is not shown in the phylogenies here as only the *trnL-F* spacer region was successfully sequenced for this species. When *A. nobilis* was included in the analyses, it always occurred within subgenus *Artocarpus*, but caused the resolution of sections *Artocarpus* and *Duricarpus* to collapse, possibly due to missing data or hybrid origin with parents from each section. Examination of additional plant material will be necessary before more definitive conclusions can be reached about this species.

Inflorescence Evolution and Pollination Biology—When writing about Moraceae, Corner (1962) stated that “No family has such small standardized flowers, yet such an astonishing array of infructescences” and that Moraceae “holds many fascinating problems of vestigial features, transference of function, and parallel evolution.” This diversity of inflorescences and infructescences has confounded classification throughout the family, but may be indicative of the diversity in reproductive strategies. In *Ficus*, for example, the syconium inflorescence shows clear adaptations to the specialized mode of wasp pollination, and there are numerous examples of convergent evolution within the genus that continue to confound the efforts toward a phylogenetic classification (Rønsted et al. 2005).

Although pollination in other genera of Moraceae, like *Artocarpus*, has received less attention (van der Pijl 1953; Momose et al. 1998; Sakai et al. 2000; Sakai 2001; Zerega et al. 2004a), the inflorescence structures may provide clues. Within Artocarpeae, only limited data exist on pollination for a few *Artocarpus* species, and the conclusions, even within a species, are mixed (Corner 1962; Singh et al. 1963; Brantjes 1981; Primack 1983; Momose et al. 1998; Sakai et al. 2000). However,

pollination by phytophagous insects, breeding in staminate inflorescences, and visiting pistillate inflorescences through deceit, may be more common than previously realized in *Artocarpus* and other Moraceae (van der Pijl 1953; Sakai et al. 2000; Sakai 2001; Berg 2001; Zerega et al. 2004a; Berg et al. 2006). In *Artocarpus*, staminate inflorescences with numerous tightly packed flowers, and frequently with interfloral bracts, provide a potentially attractive breeding site for insects, with ample pollen for larvae and opportunities of protection from predators. Additionally, the pistillate inflorescences of *Artocarpus* are well protected against phytophagous insects due to the fusion of adjacent perianths (subgenera *Artocarpus* and *Pseudojaca*), or in some cases interfloral bracts (section *Duricarpus* and subgenera *Pseudojaca* and *Prainea*), denying easy access to the ovules. It is clear that pollination syndromes in Artocarpeae are still largely unknown, empirical studies will be necessary for further elucidation, and a phylogenetic classification will be a useful tool to understand and interpret pollination in an evolutionary context.

Taxonomic Treatment of Artocarpeae—Artocarpeae has long been a heterogeneous, ill-defined, and ever-changing tribe within Moraceae (Corner 1962; Jarrett 1959a; Rohwer 1993; Berg 2001; Datwyler and Weiblen 2004; Berg et al. 2006; Clement and Weiblen 2009). Based on evidence from phylogenetic analyses of molecular data, and considering morphological characters, this treatment circumscribes a monophyletic Artocarpeae comprising two neotropical (*Clarisia* and *Batocarpus*) and one paleotropical (*Artocarpus* including *Prainea*) genus. Three genera are removed from recent circumscriptions of Artocarpeae: *Parartocarpus* and *Hulleltia* form a monophyletic group that may warrant tribal status, and *Treculia* is transferred to Dorstenieae. When taxon circumscriptions have changed within the Artocarpeae genera, brief descriptions that highlight the unique characters of the group are included. When circumscriptions have not changed, descriptions are not included as they have been described in detail elsewhere (Jarrett 1959c, 1960a; Berg 2001; Berg et al. 2006).

I. ARTOCARPEAE R. Br. in Tuckey, Narr. Exped. Zaire, App. 5: 454. 1818. *Euartocarpeae* Trécul, Ann. Sci. Nat., Bot. ser. 3(8): 108. 1847, nom. inval. —TYPE: *Artocarpus altilis* (Parkinson) Fosberg.

Members of Artocarpeae can be trees, shrubs, or rarely climbers, and are either monoecious or dioecious. The leaves are simple (rarely compound), spirally alternate or distichous, and have either amplexicaul or nonamplexicaul stipules. The inflorescences are unisexual, and are typically axillary, but are cauliflorous in a few species. Interfloral bracts may be present or absent. The staminate inflorescences have numerous flowers with 2–4 connate tepals, and typically one stamen (occasionally 2–3 may be present) that is straight in bud. The pistillate inflorescences have one to more typically numerous flowers with 2–4 connate tepals, and adjacent perianths may be free or partially to completely fused to one another. The synapomorphy for the tribe is a reduction in stamen number compared to the rest of the family (although several *Ficus* species have also independently evolved a single stamen). The typical number of stamens in Moraceae is 4 or 5, but species in Artocarpeae typically have only one stamen per staminate flower, with a few species occasionally having 1–3 stamens. Members of Artocarpeae also share straight embryos, hypogean germination (semihypogean in *Clarisia* and not examined

in *Batocarpus*), a chalazal that is basal relative to the ovary (not examined in *Batocarpus* and *Clarisia*), little to no endosperm, and large seeds (> 4 × 4 mm) (Jarrett 1959a, b, c, 1960a; Berg 2001).

Distribution—Genera in this tribe are indigenous to the Paleotropics (*Artocarpus*: Asia eastward into Australasia and

Oceania) or the Neotropics (*Batocarpus* and *Clarisia*: Central and South America) (Fig. 1). Three species (*A. altilis*, *A. camansi*, and *A. heterophyllus*) are cultivated throughout much of the tropics.

Genera—*Artocarpus* J. R. & G. Forst., *Batocarpus* Karsten, and *Clarisia* Ruiz & Pavón.

KEY TO THE GENERA AND SUBGENERA OF ARTOCARPEAE

1. Staminate inflorescences spicate with a distinct abaxial sterile strip; staminate flowers crowded in longitudinal rows; leaves alternate and distichous with lateral stipules; neotropical in distribution 2
2. Inflorescences axillary; pistillate inflorescences multiflorous and globose-capitate; fruiting perianth green *Batocarpus*
2. Inflorescences often cauliflorous, or if axillary then the bark at the base of the trunk reddish; pistillate inflorescences uniflorous or multiflorous and discoid-capitate; fruiting perianth red, orange, pale yellow, or greenish yellow) *Clarisia*
1. Staminate inflorescences spicate to globose to obovoid or clavate, lacking a distinct abaxial sterile strip; staminate flowers crowded but not in longitudinal rows; leaves alternate and distichous with lateral stipules or spirally alternate with amplexicaul stipules; paleotropical in distribution (however, some species of *Artocarpus* have been introduced and are cultivated throughout the tropics) 3
3. Perianths of adjacent pistillate flowers entirely free from one another; only fertilized flowers enlarging at maturity *Artocarpus* subgenus *Prainea*
3. Perianths of adjacent pistillate flowers partially to completely fused to form a syncarp; entire pistillate head enlarging at maturity 4
4. Leaves distichous; stipules lateral and nonamplexicaul, less than 1 cm, stipule scar not annulate; pistillate inflorescences with adjacent perianths fused apically, giving the inflorescence and syncarp a smooth/uniform surface *Artocarpus* subgenus *Pseudojaca*
4. Leaves spirally alternate; stipules fully amplexicaul, 1 cm or longer, leaving an annulate stipule scar; pistillate inflorescences with adjacent perianths fused only medially, leaving perianth apices free and giving the inflorescence and syncarp a spiky or bumpy surface 5
5. Inflorescences always axillary *Artocarpus* subgenus *Artocarpus*
5. Inflorescences develop directly from the trunk or branches of previous year's growth (cauli- or ramiflorous). Axillary inflorescences may also be present and male inflorescences may have ring-like constrictions (in *A. annulatus*) *Artocarpus* subgenus *Cauliflori*

A. ARTOCARPUS J. R. & G. Forst., Char. Gen. Pl.: 101, t. 51, 1775, nom. cons.—TYPE: *Artocarpus altilis* (Parkinson) Fosberg.

Sitodium Banks & Sol. ex Parkinson, J. Voy. South Seas 45. 1773.—TYPE: *Rademachia incisa* Thunb (= *Artocarpus altilis* (Parkinson) Fosberg).

Rademachia Thunb., Kongl. Svenska Vetensk. Akad. Handl. 37: 251. 1776 ('*Rademachia*').—TYPE: *Rademachia incisa* Thunb. (= *Artocarpus altilis* (Parkinson) Fosberg).

Polyphema Lour. Fl. Cochinch. 546. 1790.—TYPE: *Polyphema jaca* Lour (= *Artocarpus heterophyllus* Lamarck).

Prainea King ex Hook. f., Fl. Brit. India 5: 546. 1888. *Artocarpus* section *Prainea* Renner, Bot. Jahrb. Syst. 39: 366. 1907.—TYPE: *Prainea scandens* King.

Trees (possible climber in subgenus *Prainea*), monoecious (dioecious in subgenus *Prainea*). Leaves: simple (rarely compound – *A. anisophyllus*), alternate and spiral (subg. *Artocarpus* and *Cauliflori*) or alternate and distichous (subg. *Pseudojaca* and *Prainea*), large fully amplexicaul stipules (subg. *Artocarpus* and *Cauliflori*) or small lateral stipules (subg. *Pseudojaca* and *Prainea*). Inflorescences: unisexual, axillary or cauliflorous (subg. *Cauliflori*), interfloral bracts present or absent. Staminate inflorescences: with numerous tightly packed flowers with 2 (-4) connate tepals, stamens 1(-3), straight in bud. Pistillate inflorescences: with numerous tightly packed tubular flowers, adjacent perianths may be free (subg. *Prainea*) or partially (subg. *Artocarpus* and *Cauliflori*) to completely fused to one another (subg. *Pseudojaca*).

Distribution—Asia (China in the north, India in the west, Malesia in the south) eastward into Australasia, and Oceania. Three species (*A. altilis*, *A. camansi*, and *A. heterophyllus*) are cultivated throughout much of the tropics.

1. ARTOCARPUS subg. ARTOCARPUS. *Artocarpus* subg. *Jaca* Trécul, Ann. Sci. Nat. Bot. III, 8: 110. 1847. *Artocarpus* sect. *Jaca* (Trécul) Renner, Bot. Jahrb. Syst. 39: 363. 1907. *Artocarpus* ser. *Incisifolii* F. M. Jarrett, J. Arnold Arbor. 40: 298. 1959.—TYPE: *Artocarpus altilis* (Parkinson) Fosberg.

Artocarpus sect. *Duricarpus* F. M. Jarrett, J. Arnold Arbor. 40: 137. 1959. *Artocarpus* ser. *Asperifolii* F. M. Jarrett, J. Arnold Arbor. 40: 143. 1959.—TYPE: *Artocarpus rigidus* Blume.

Artocarpus ser. *Laevifolii* F. M. Jarrett, J. Arnold Arbor. 40: 138. 1959.—TYPE: *Artocarpus anisophyllus* Miq.

Artocarpus ser. *Angusticarpus* F. M. Jarrett, J. Arnold Arbor. 40: 338. 1959.—TYPE: *Artocarpus teysmannii* Miq.

Artocarpus ser. *Rugosi* F. M. Jarrett, J. Arnold Arbor. 40: 343. 1959.—TYPE: *Artocarpus elasticus* Blume.

Subgenus *Artocarpus* has been described in detail elsewhere (Jarrett 1959c), and this is an abbreviated and modified description to accommodate the recircumscription to exclude series *Cauliflori*. Leaves: simple (compound in *A. anisophyllus*), alternate and spiral, juvenile and adult leaves may be entire or pinnatifid, hypodermis present or absent, resin cells present, spongy mesophyll cells loose. Stipules: large, amplexicaul, scars annulate. Inflorescences: axillary, interfloral bracts sparse or absent. Staminate inflorescence: cylindrical or clavate, rarely ellipsoid. Syncarp: cylindrical or ellipsoid, rarely

subglobose; free perianth apices either flexuous, indurated, or aerolate.

The circumscription of subgenus *Artocarpus* here includes 31 species and differs from that of Berg et al. (2006) and Jarrett (1959c) in the exclusion of series *Cauliflori*, which is elevated to the subgeneric rank. Berg et al. (2006) made reference to Jarrett's sections and series within subgenus *Artocarpus* but did not maintain them. Due to the lack of monophyly for several of the series, we do not recognize them either. Berg et al. (2006) and Jarrett (1959c) also differed in the treatment of several species level circumscriptions as described below.

Since Jarrett's (1959c, 1960a) treatment of *Artocarpus*, several new species have been described (Jarrett 1975; Kochummen 2000). Among those assigned to subgenus *Artocarpus*, *A. corneri* and *A. jarrettiae* were reduced by Berg et al. (2006) to *A. elasticus*. These new species are endemic to Borneo and known from only a few collections and were not included in the present study, therefore Berg et al.'s (2006) treatment is followed here.

Berg et al. (2006) elevated *A. melinoxylus* subsp. *brevipedunculatus* to *A. brevipedunculatus*. Although *A. melinoxylus* and its subspecies were not sampled here, it is recommended that the changes be maintained. Morphological (leaf and peduncle characters) and geographical distributions support maintaining *A. brevipedunculatus*. *Artocarpus brevipedunculatus* is endemic to Borneo, whereas the rest of the diversity represented in *A. melinoxylus* is endemic to Indochina.

Among the species assigned to Jarrett's (1959c) series *Rugosi*, Berg et al.'s (2006) treatment differed as follows: *A. scortechinii* was included in *A. elasticus*; and *A. maingayi* and *A. sumatranus* were included in *A. kemando*. In the present study, *Artocarpus elasticus* and *A. scortechinii* are strongly supported as sister, but their status as separate species is maintained here due to consistent and easily recognized morphological differences that suggest they are not experiencing gene flow. *Artocarpus scortechinii* has generally smaller parts compared to *A. elasticus*, elongate processes are absent on the syncarp in *A. scortechinii* and present in *A. elasticus*, and the upper surface of the leaves is smooth in *A. scortechinii* and rough in *A. elasticus*. In the present study, *Artocarpus kemando* and *A. maingayi* are strongly supported as sister; *A. sumatranus* was not included. The three species have differently shaped processes (free apical portion of perianths): umbonate in *A. kemando*, truncate in *A. maingayi*, and conical in *A. sumatranus*, and the length of the male peduncles varies: ~0.5 cm in *A. maingayi*, between 0.7 and 1.3 cm in *A. kemando*, and ~3.5 cm in *A. sumatranus*. Additionally, the leaves of *A. sumatranus* are larger and the leaf apices of *A. kemando* are acuminate, whereas they are rounded in *A. maingayi*. Given these differences, they are treated as three separate species here.

Series *Incisifolii*, as circumscribed by Jarrett (1959c), consists of four species endemic to the Philippines (*A. blancoi*, *A. multifidus*, *A. pinnatisectus*, and *A. treculianus*), one species native to the Moluccas (*A. horridus*), and the breadfruit complex which Jarrett (1959c) treats as one highly variable pantropical species, *A. communis*, but has recently been revised to include three species (*A. altilis* – breadfruit, *A. camansi*, and *A. mariannensis*) and hybrids (Zerega et al. 2005b). Berg et al. (2006) has more recently included *A. blancoi*, *A. horridus*, *A. camansi*, *A. mariannensis*, *A. multifidus*, and *A. pinnatisectus* within *A. altilis*, considering them all to represent a range of variation from the wild to cultivated form of breadfruit. The present study does not include all members of the series, but nonethe-

less indicates that series *Incisifolii* does not represent a natural lineage and Berg et al.'s (2006) changes are not maintained. *Artocarpus treculianus* and *A. blancoi* form a well-supported clade (100% bootstrap) that is sister to a clade containing the breadfruit and *Rugosi* clades and *A. excelsus*. *Artocarpus blancoi* and *A. treculianus* may be most closely allied with the unsampled species (*A. pinnatisectus*, *A. horridus*, and *A. multifidus*) as they all share the following characteristics: adult leaves frequently pinnatifid and presence of inflated hairs on syncarp. *Artocarpus altilis*, *A. camansi*, and *A. mariannensis* form a separate, well-supported clade also characterized by the presence of adult pinnatifid leaves, but lack the inflated hairs on the syncarp.

Jarrett (1959c) noted three anomalous species within subgenus *Artocarpus*: *A. hirsutus*, *A. nobilis*, and *A. sepicanus*. The present study indicates that the former two species are part of the subgenus and that the latter remains of uncertain affinity. Given the problematic position and lack of strong evidence detailed in the discussion, *A. sepicanus* is presently maintained here to be part of subgenus *Artocarpus*.

Distribution—Subgenus *Artocarpus* is concentrated in the Malesian region and is distributed in the Philippines, Moluccas, New Guinea, Malaya, Indonesia, Myanmar, Thailand, and the Nicobar Islands, with some species extending westward to Sri Lanka (*A. nobilis*) and the western Ghats of India (*A. hirsutus*), eastward into the uplifted limestone islands of Micronesia (*A. mariannensis*), and into the Asian mainland. The widely cultivated species *A. altilis* was domesticated from *A. camansi* and spreads into Oceania and throughout the tropics (Zerega et al. 2005b), whereas *A. camansi* is cultivated in Indonesia, Malaysia, the Caribbean Islands, tropical Central and South America, and coastal West Africa. *Artocarpus altilis* has also undergone introgressive hybridization with *A. mariannensis* in Micronesia (Fosberg 1960; Zerega et al. 2005b).

Species—There are 31 species included in this subgenus: *Artocarpus altilis* (Parkinson) Fosberg, *A. anisophyllus* Miq., *A. blancoi* (Elmer) Merr., *A. brevipedunculatus* (F. M. Jarrett) C. C. Berg, *A. camansi* Blanco, *A. chaplasha* Roxb., *A. elasticus* Reinw. ex Blume, *A. excelsus* Jarrett, *A. hirsutus* Lamarck, *A. hispidus* Jarrett, *A. horridus* Jarrett, *A. kemando* Miq., *A. lanceifolius* Roxb., *A. lowii* King, *A. maingayi* King, *A. mariannensis* Trécul, *A. melinoxylus* Gagnep., *A. multifidus* Jarrett, *A. odoratissimus* Blanco, *A. nobilis* Thwaites, *A. obtusus* Jarrett, *A. pinnatisectus* Merr., *A. rigidus* Blume, *A. sarawakensis* Jarrett, *A. scortechinii* King, *A. sepicanus* Diels, *A. sericicarpus* Jarrett, *A. sumatranus* Jarrett, *A. tamaran* Becc., *A. teysmannii* Miq., and *A. treculianus* Elmer.

2. **Artocarpus** subgenus **Cauliflori** (F. M. Jarrett) Zerega, stat. nov. *Artocarpus* ser. *Cauliflori* F. M. Jarrett, J. Arnold Arbor. 40: 327. 1959.—TYPE: *Artocarpus integer* (Thunb.) Merr.

Series *Cauliflori* was described by Jarrett (1959c), and it is elevated here to the subgeneric rank, with an abbreviated description. Leaves: simple, alternate and spiral, adult leaves entire, juvenile leaves may be lobed, hypodermis and resin cells absent, spongy mesophyll cells compact. Stipules: large amplexicaul, scars annulate. Inflorescences: solitary in leaf axils, cauliflorous or ramiflorous, interfloral bracts present (*A. annulatus*) or absent. Staminate inflorescence: cylindrical to clavate (surface wrinkled by ring-like constrictions in *A. annulatus*). Syncarp: cylindrical to clavate or ellipsoid, reaching enormous sizes (up to 100 × 50 cm) in *A. heterophyllus* and *A. integer*, free perianth apices flexuous.

Subgenus *Cauliflori* appears to be intermediate between subgenera *Artocarpus* and *Pseudojaca*. It shares the leaf arrangement (spirally arranged with amplexicaul stipules) and perianth fusion characters (adjacent pistillate perianths medially fused but free apically) with subgenus *Artocarpus*. It is allied with subgenus *Pseudojaca* in having compact mesophyll and the absence of resin in the spongy mesophyll cells (absent in *A. heterophyllus* and *A. integer*, not examined in *A. annulatus*).

This subgenus includes three species and is defined primarily by the presence of cauliflorous inflorescences, which are not found in the rest of the genus. Although affinities of *A. annulatus* to *A. heterophyllus* and *A. integer* have not previously been suggested, molecular evidence, as well as the presence of cauliflorous inflorescences, strongly supports the placement of *A. annulatus* in subgenus *Cauliflori*.

Distribution—*Artocarpus heterophyllus* (jackfruit) is thought to be indigenous to the Indian subcontinent and possibly more specifically to the western Ghats of India (Wight 1843). Today it is cultivated throughout much of the tropics and subtropics. *Artocarpus integer* (chempedak) is distributed and cultivated in Thailand, Malaysia, and parts of Indonesia and Myanmar, and is thought to be indigenous to Sumatra, Borneo, Sulawesi, the Moluccas, and western New Guinea. It has been treated as two varieties, *A. integer* var. *integer*, a cultivated form, and the wild form *A. integer* var. *silvestris*. *Artocarpus annulatus* is endemic to Sarawak.

Species—Three species are included in this subgenus: *Artocarpus annulatus* Jarrett, *A. heterophyllus* Lamarck, and *A. integer* (Thunb.) Merr.

3. **Artocarpus** subg. *Prainea* (King) Zerega, Supardi, and Motley, stat. nov. *Prainea* King, in Hook. f., Fl. Brit. Ind. 5: 546. 1888. *Artocarpus* sect. *Prainea* (King) Renner, Bot. Jahrb. Syst. 39: 366. 1907.—TYPE: *Prainea scandens* King (= *Artocarpus scandens* (King) Renner).

Prainea was originally described by King (1888). Renner (1907) reduced it to sectional status within *Artocarpus* and Jarrett (1959b) resurrected it to generic status. It is reduced to subgeneric rank here. Leaves: simple, alternate and distichous, juvenile and adult leaves entire, hypodermis absent, resin cells present, spongy mesophyll cells loose. Stipules: small, nonamplexicaul, scars lateral or intrapetiolar. Inflorescences: axillary, interfloral bracts present. Staminate inflorescence: globose to short obovoid. *Syncarp*: globose, adjacent perianths completely free from one another.

The phylogenetic analysis of molecular data presented here indicates that *Prainea* is nested within *Artocarpus*, although there is no bootstrap support for this relationship. However, this position and the intermediacy of characters, as described above, of *Prainea* compared to other subgenera of *Artocarpus* indicates that *Prainea* represents a monophyletic group within *Artocarpus* that has lost the ability for belated fusion of adjacent pistillate perianths. Previous phylogenetic studies based on chloroplast *ndhF* and 26S rDNA sequences also placed *Prainea* within *Artocarpus* (Zerega et al. 2005a). Analysis of additional characters and all taxa may help to support this relationship further.

Jarrett (1959b) and Berg et al. (2006) recognized four or two species of *Prainea*, respectively. Berg et al. (2006) reduced *P. frutescens* into *P. scandens* and *P. papuana* into *P. limpatu* because only “small” differences separated them. Descriptions of *P. frutescens* and *P. scandens* are based on limited material,

however, *P. scandens* is unique as a climber, and *P. frutescens* and *P. scandens* occupy different niches (*P. scandens* is found in lowland evergreen forests to 2,500 ft. in Malaya, while *P. frutescens* is restricted to lowland evergreen forests to 200 ft. in Borneo). *Prainea limpatu* and *P. papuana* occupy different ranges and the inflorescences of *P. limpatu* are generally larger than those of *P. papuana*. *Prainea limpatu* is found in lowland evergreen forest in Malaya, Sumatra, and Borneo while *P. papuana* is restricted to lowland evergreen forests in the Moluccas and New Guinea. Jarrett’s (1959b) species level circumscription is maintained here.

Distribution—Malay Peninsula, Sumatra, Borneo, and New Guinea.

Species—There are four species included in this subgenus: *Artocarpus frutescens* (Becc.) Renner, *A. limpatu* Miq., *A. papuana* (Becc.) Renner, and *A. scandens* (King) Renner.

4. **ARTOCARPUS** subg. **PSEUDOJACA** Trécul, Ann. Sci. Nat. Bot. III, 8: 117. 1847. *Artocarpus* sect. *Pseudojaca* (Trécul) Renner, Bot. Jahrb. Syst. 39: 368. 1907. *Artocarpus* ser. *Peltati* F. M. Jarrett, J. Arnold Arbor. 41: 83. 1960.—TYPE: *Artocarpus lacucha* Buch.-Ham.

Artocarpus ser. *Clavati* F. M. Jarrett, J. Arnold Arbor. 41: 130. 1960.—TYPE: *Artocarpus hypargyreus* Hance.

Artocarpus sect. *Glandulifolium* F. M. Jarrett, J. Arnold Arbor. 41: 134. 1960.—TYPE: *Artocarpus altissimus* (Miq.) J. J. Smith.

Subgenus *Pseudojaca* contains 24 species and is defined morphologically within the genus *Artocarpus* by its distichous leaf arrangement and complete fusion of adjacent pistillate perianth apices. Jarrett’s (1960a) circumscription of subgenus *Pseudojaca* is upheld with a brief description. Leaves: simple, alternate and distichous, adult and juvenile leaves entire, hypodermis and resin cells absent, spongy mesophyll cells compact. Stipules: small, nonamplexicaul, scars lateral or intrapetiolar. Inflorescences: axillary (or staminate ones may be on short shoots or older wood), interfloral bracts abundant. Staminate inflorescence: globose to obovoid, cylindric or clavate. *Syncarp*: globose or lobed, pistillate perianths fused at least apically and medially to adjacent perianth apices.

Since Jarrett’s (1959c, 1960a) treatment, several new *Artocarpus* species assigned to subgenus *Pseudojaca* have been described from China (*A. gongshanensis*, *A. nanchuanensis*, *A. nigrifolius*, and *A. pithecolobus* (Wu and Chang 1989), Borneo (*A. albobrunneus*; Berg et al. 2006), and Thailand (*A. thailandicus*; Berg 2005). None of these species were included in the present study, however, they all share the typical characters of subgenus *Pseudojaca* and their circumscription in *Pseudojaca* remains untested and unchanged.

Within subgenus *Pseudojaca* Berg et al. (2006) recently combined several species, subspecies, and varieties (*A. dadah*, *A. fretessii*, *A. ovatus*, and *A. vrieseanus* var. *papillosus*, and *A. v. var. refractus*) into *A. lacucha* Buch.-Ham. However, based on morphological characters, biogeographical distributions, and the phylogenetic analysis of molecular data of some of these species, these changes are not maintained. Among these species, the present study included *A. dadah*, *A. ovatus*, and *A. lacucha*. Phylogenetic analyses indicate that these three entities represent three distinct lineages, and that they are not sister to one another. *Artocarpus ovatus* is restricted to the Philippines and does not overlap ranges with the other species. It is also readily distinguished by its long peduncles,

15–40 mm in the staminate inflorescence and 40–80 mm in the pistillate inflorescence (Jarrett 1960a). *Artocarpus dadah* is a common and variable species that has been described under multiple names at different times by the same author (see Jarrett 1960a). The variation within the species occurs chiefly in the length of the peduncles and in the indumentum (Jarrett 1960a). Three individuals of *A. dadah* were included in this study (all from Malaysia) and they are strongly supported (100% bootstrap) as a monophyletic group. While the ranges of *A. dadah* and *A. lacucha* overlap in Thailand and possibly Myanmar, the range of the former extends southward from there into the Malay peninsula and Indonesia, while the range of the latter extends northward and westward into monsoon forests of India, China, Bangladesh, and Indochina. They can be distinguished from one another based on the surface of the syncarp being finely ribbed in *A. dadah*. It is recommended that *A. ovatus*, *A. dadah*, and *A. lacucha* be treated as separate species.

Within subgenus *Pseudojaca* several species are divided into subspecies. Of these, only the subspecies of *A. nitidus* were included in the present study. Variation present in *A. nitidus* has been variously treated as separate species (Trécul 1847; Beccari 1902), separated into several subspecies (Jarrett 1960a), or treated as “informal entities” within *A. nitidus* (Berg et al. 2006). Four of the five *A. nitidus* subspecies described by Jarrett (1960a) were included in this analysis and are polyphyletic. *Artocarpus nitidus* subsp. *griffithii* and *A. n.* subsp. *borneensis* form a well-supported (100% bootstrap) monophyletic group sister to *A. dadah*. These two subspecies are similar, differing only in the indumentum on the syncarp, nearly glabrous in the former and densely pubescent in the latter. *Artocarpus n.* subsp. *borneensis* is restricted to the island of Borneo, while *A. n.* subsp. *griffithii* overlaps this range and extends northward up to Yunnan in southern China. *Artocarpus n.* subsp. *lingnannensis* (extending from Southern China to Thailand) and *A. n.* subsp. *humilis* (restricted to Borneo) appear to represent two separate lineages. Their morphological differences are slight and are primarily leaf venation characters. All subspecies of *A. nitidus* were at one time or another described at the specific rank and subsequently demoted by Jarrett (1960a). Berg et al. (2006) treated four “informal entities” of *A. nitidus* in the Malesian area. The combined phylogeny presented here suggests that *A. n.* subsp. *humilis*, and *A. n.* subsp. *lingnannensis* may warrant resurrection to specific rank (*A. humilis* Becc. (Beccari 1902) and *A. parva* Gagnep. (Gagnepain 1926), respectively). *Artocarpus n.* subsp. *griffithii*, and *A. n.* subsp. *borneensis* could be treated as a single variable species. However, additional data from the fifth subspecies (*A. nitidus* subsp. *nitidus*) is desirable before any action is taken.

Distribution—India, Sri Lanka, Myanmar, Thailand, Indochina, southern China, Malaysia, Indonesia, Australasia, Solomon Islands, Philippines.

Species—There are 24 species included in this subgenus: *A. albobrunneus* Berg, *A. altissimus* (Miq.) J. J. Smith, *A. dadah* Miq., *A. fulvicortex*, *A. glaucus* Blume, *A. gomezianus* Wall ex. Trécul, *A. gongshanensis* S. K. Wu ex C. Y. Wu & S. S. Chang, *A. hypargyreus* Hance, *A. lacucha* Buch.-Ham., *A. longifolius* Becc., *A. nanchuanensis* S. S. Chang, C. Tan, and Z. Y. Liu, *A. nigrifolius* C. Y. Wu, *A. nitidus* Trécul, *A. ovatus* Blanco, *A. petelotii* Gagnep., *A. pithecogallus* C. Y. Wu, *A. reticulatus* Miq., *A. rubrovenius* Warb., *A. subrotundifolius* Elmer, *A. thailandicus* C. C. Berg, *A. tomentosulus* Jarrett, *A. tonkinensis* A. Chev. ex.

Gagnep., *A. vrieseanus* Miq., and *A. xanthocarpus* Teysm. and Binnend.

B. **BATOCARPUS** Karsten, Fl. Columb. 2: 67. 1863.—TYPE: *Batocarpus orinocensis* Karsten.

Annocarpus Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 38. 1922.—TYPE: *Annocarpus amazonicus* Ducke (= *B. amazonicus* (Ducke) Fosberg).

We maintain Berg’s (2001) circumscription of *Batocarpus* with a brief description. Leaves: simple, alternate and distichous, adult and juvenile leaves entire. Stipules: small, non-amplexicaul, scars lateral or intra petiolar. Inflorescences: axillary, interfloral bracts present or absent. Staminate inflorescence: spicate with an abaxial sterile strip. Syncarp: globose, adjacent pistillate perianths free from one another.

Distribution—Costa Rica to Amazonian Bolivia.

Species—There are three species included in this genus: *Batocarpus costaricensis* Standley & L. O. Williams, *B. amazonicus* (Ducke) Fosberg, and *B. orinocensis* Karsten.

C. **CLARISIA** Ruiz & Pavón, Fl. Peruv. Chil. 128. 1794, nom. cons., non *Clarisia* Abat, 1792, nom. rejic.; —TYPE: *Clarisia racemosa* Ruiz & Pavón, typ. cons.

Sahagunia Liebm., Kongel, Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 5 (2): 316. 1851.—TYPE: *Sahagunia mexicana* Liebm. (= *Clarisia biflora* Ruiz & Pavón).

Soaresia Allemão, Revista Brazil. 1: 210. 1857, nom. rejic., non C. H. Schultz-Bip., 1863, nom. conserv. (Asteraceae).—TYPE: *Soaresia nitida* Allemão (= *Clarisia racemosa* Ruiz & Pavón).

Acanthinophyllum Allemão, Revista Brazil. 1: 368. 1858.—TYPE: *Acanthinophyllum strepitans* Allemão (= *Clarisia ilicifolia* (Sprengel) Lanjouw & Rossberg).

Aliteria Benoist, Bull. Mus. Hist. Nat. (Paris), 2 (1): 163. 1929.—TYPE: *Aliteria sagotii* Benoist (= *Clarisia ilicifolia* (Sprengel) Lanjouw & Rossberg).

Berg’s (2001) circumscription of *Clarisia* reflects our phylogenetic findings. Leaves: simple, alternate and distichous, adult and juvenile leaves entire. Stipules: small, nonamplexicaul, scars lateral or intrapetiolar. Inflorescences: axillary or on leafless short shoots, interfloral bracts present. Staminate inflorescence: spicate with an abaxial sterile strip. Syncarp: capitate with adjacent pistillate perianths free from one another or uniflorous.

Distribution—From southern Mexico through Central America into Venezuela, Colombia, Ecuador, Peru, Bolivia, the Guianas, the Brazilian Amazon Basin, and eastern Brazil.

Species—There are three species included in this genus: *Clarisia biflora* Ruiz & Pavón, *C. racemosa* Ruiz & Pavón, and *C. ilicifolia* (Sprengel) Lanjouw & Rossberg.

ACKNOWLEDGMENTS. The authors are grateful for the field assistance of C. Y. Chong, L. Y. Fah, A. Hussin, R. Kiapranis, R. Kiew M. Kostka, S. Lum, V. Novotny, L. Raulerson, and A. Rinehart. We would like to thank W. Clement, N. Cordeiro, H. Ndangalasi, D. Ragone, and G. Weiblen for specimens and DNA samples and two reviewers for helpful comments on the manuscript. Finally, we would like to thank the following institutions and herbaria for access to specimens: BRIT, CHIC, F, FTG, GH, GUAM, KEP, LAE, MIN, NY, PTBG, SAN, SING, US. This research was funded by the Lewis B. and Dorothy Cullman Foundation, NSF grant DEB-0073161, The Garden Club of America Award in Tropical Botany, and The Explorers Club.

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APPENDIX 1. Specimens used in the phylogenetic analyses. Herbarium abbreviations follow Index Herbariorum (Holmgren et al. 1990). For each specimen, the following is listed: sampled taxa, voucher specimen information [collection locality, collection number (herbarium code)], and GenBank accession numbers (ITS, *trnL-F*); — = sequence not obtained. Previously published sequences downloaded for inclusion in our analyses are indicated by an asterisk. Material acquired from herbarium samples, rather than leaf material dried on silica, is indicated by two asterisks.

MORACEAE: *Antiaropsis decipiens* K. Schum., Papua New Guinea, G. Weiblen 1233 (MIN), AY730142* (Rønsted et al. 2005). —. *Artocarpus altilis* (Parkinson) Fosberg, Samoa, D. Ragone 453 (PTBG), FJ917055, FJ917116; Mariana Islands, D. Ragone 311 (PTBG), FJ917056, FJ917056; Fiji, D. Ragone 486 (PTBG), FJ917057, FJ917118; Society Islands, D. Ragone 236 (PTBG), FJ917023, FJ917087. *Artocarpus anisophyllus* Miq., Singapore, N. Zerega 210 (CHIC), FJ917027, FJ917091. *Artocarpus annulatus*** Jarrett, Sarawak, R. Primack 38722 (GH), FJ917046. —. *Artocarpus blancoi*** (Elmer) Merr., Philippines, Ramos s. n. (NY), FJ917021, FJ917085. *Artocarpus camansi* Blanco, Papua New Guinea, N. Zerega 69 (NY), FJ917024, FJ917088. *Artocarpus chaplasha*** Roxb., India, Huq and Mia 10274 (BRIT), FJ917047. —. *Artocarpus dadah* Miq., Malaysia, N. Zerega 245, 247, and 250 (CHIC), FJ917034, FJ917098; FJ917050, FJ917111; FJ917051, FJ917112. *Artocarpus elasticus* Reinw. Ex Blume, Malaysia, N. Zerega 243 (CHIC), FJ917032, FJ917096. *Artocarpus excelsus*** Jarrett, Sabah, J. Beaman et al. 7918 (NY), FJ917017, FJ917081. *Artocarpus fulvicortex* Jarrett, Malaysia, N. Zerega 228 (CHIC), FJ917015, FJ917079. *Artocarpus glaucus* Blume, Malaysia, N. Zerega 263 (CHIC), FJ917040, FJ917104. *Artocarpus heterophyllus* Lamarck, Singapore, Zerega 219 (CHIC), FJ917039, FJ917103. *Artocarpus heterophyllus* Lamarck, Hawaii, U. S. A., N. Zerega 13 (NY), FJ917052, FJ917113. *Artocarpus hirsutus* Lamarck, Florida, U. S. A., Fisher 96–58 (FTG), FJ917016, FJ917080. *Artocarpus hispidus* Jarrett, Malaysia, N. Zerega 258 (CHIC), FJ917031, FJ917095. *Artocarpus integer* (Thunb.) Merr., Malaysia, N. Zerega 227 (CHIC), FJ917041, FJ917105. *Artocarpus kemando* Miq., Malaysia, N. Zerega 257 (CHIC), FJ917043, FJ917107. *Artocarpus lakoocha*** Roxb., Vives s. n. (NY), FJ917018, FJ917082. *Artocarpus lanceifolius* Roxb., Malaysia, N. Zerega 256 and 241 (CHIC), FJ917042, FJ917106; FJ917053, FJ917114. *Artocarpus lowii* King, Malaysia, N. Zerega 246 (CHIC), FJ917033, FJ917097. *Artocarpus maingayi* King, Malaysia, N. Zerega 233 (CHIC), FJ917030, FJ917094. *Artocarpus mariannensis* Trécul, Rota, CNMI, N. Zerega 162 (CHIC), FJ917022, FJ917086. *Artocarpus nitidus* Trécul subsp. *lingnanensis* (Merr.) Jarrett, Hawaii, U. S. A., N. Zerega 4 (NY), FJ917035, FJ917099. *Artocarpus*

nitidus Trécul subsp. *borneensis* (Merr.) Jarrett, Singapore, N. Zerega 270 (CHIC), FJ917036, FJ917100. *Artocarpus nitidus* Trécul subsp. *griffithii* (King) Jarrett, Singapore, N. Zerega 216 (CHIC), FJ917028, FJ917092; Malaysia, N. Zerega 226 (CHIC), FJ917038, FJ917102. *Artocarpus nitidus* Trécul subsp. *humilis* (Becc.) Jarrett, Malaysia, N. Zerega 262 (CHIC), FJ917037, FJ917101. *Artocarpus odoratissimus* Blanco, Malaysia, N. Zerega 261 (CHIC), FJ917025, FJ917089; Singapore, N. Zerega 224 (CHIC), FJ917054, FJ917115. *Artocarpus ovatus* Blanco, Hawaii, U. S. A., N. Zerega 202 (CHIC), FJ917014, FJ917078. *Artocarpus petelotii*** Gagnep., China, Hsiu-Lan Ho 757 (NY), FJ917011, FJ917075. *Artocarpus rigidus* Blume, Malaysia, N. Zerega 248 (CHIC), FJ917026, FJ917090. *Artocarpus scortechenii* King, Singapore, N. Zerega 218 (CHIC), FJ917029, FJ917093. *Artocarpus sepicanus* Diels, Papua New Guinea, G. Weiblen 1701 (MIN), FJ917010, FJ917074. *Artocarpus sericarpus*** Jarrett, Philippines, Burley 69 (NY), FJ917013, FJ917077. *Artocarpus subrotundifolius*** Elmer, Philippines, Madulid 6810 (GH), FJ917045. —. *Artocarpus tamaran* Becc., Singapore, (SING), FJ917019, FJ917083. *Artocarpus tonkinensis*** A. Chev. Ex Gagnep., China, Gillis 10954 (S), FJ917012, FJ917076. *Artocarpus treculianus* Elmer, Hawaii, U. S. A., Zerega 203 (CHIC), FJ917020, FJ917084. *Artocarpus vrieseanus* Miq., Papua New Guinea, G. Weiblen 1229 (MIN), FJ917044, FJ917108. *Bagassa guianensis* Aubl., G. D. Weiblen 1677, French Guiana (MIN), FJ917001, FJ917066. *Batocarpus costaricensis* Standley & L. O. Williams, Peru, G. Weiblen 1463 (MIN), FJ917000, FJ917065. *Brosimum lactescens* (S. Moore) C. C. Berg, Peru, G. Weiblen 1473 (MIN), FJ916996, FJ917061. *Castilla elastica* Sessé, G. Weiblen 1238 (MIN), FJ916997, FJ917062. *Clarisia biflora* Ruiz & Pav., Peru, G. Weiblen 1460 (MIN), FJ917002, FJ917067. *Dorstenia choconiana* S. Watson, Costa Rica, G. Weiblen 1417 (MIN), FJ916995, FJ917060. *Ficus carica* L., New York, U. S. A., N. Zerega 15 (NY), FJ916994, FJ917059. *Hullettia dumosa* King, Malaysia, N. Zerega 242 (CHIC), FJ917006, FJ917070. *Maclura pomifera* (Raf.) C. K. Schneid., New York, U. S. A., N. Zerega 205 (CHIC), FJ916993, FJ917058. *Morus alba* L., New York, U. S. A., N. Zerega 16 (NY), FJ917003, FJ917068. *Parartocarpus bracteatus*** (King) Becc., Papua New Guinea, W. Takeuchi 1518 (GH), FJ917049, FJ917110. *Poulsenia armata* (Miq.) Standley, Panama, G. D. Weiblen 1428 (MIN), AY635565*, —. *Prainea limpato* (Miq.) Beumée ex Heyne, Nutt., Malaysia, N. Zerega 249 and 264 (CHIC), FJ917009, FJ917073; FJ917048, FJ917109. *Prainea papuana* Becc., Papua New Guinea, N. Zerega 61 (NY), FJ917008, FJ917072. *Sorocea steinbachii* C. C. Berg, Peru, G. Weiblen 1501 (MIN), FJ916998, FJ917063. *Sorocea briquetii* J. F. Macbr., Peru, G. Weiblen 1457 (MIN), FJ916999, FJ917064. *Sparattosyce dioica* Bur., AY730141* (Rønsted et al. 2005). —. *Treculia africana* Decne., Tanzania, Ndangalasi and Cordeiro 7 (F), FJ917005. —. *Treculia obovoidea*** N. E. Br., Cameroon, Leeuwenberg 9700 (US), FJ917004, FJ917069.

CANNABACEAE: *Cannabis sativa* L., Y18150* and Y12587* (Siniscalco et al. 1997). —. *Humulus lupulus* L., DQ005990* (Kress et al. 2005), AF501599* (Systema et al. 2002).