

Classification of Convolvulaceae: A Phylogenetic Approach

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ABSTRACT. Because recent molecular studies, based on multiple data sets from all three plant genomes, have indicated mutually congruent, well-resolved, and well-supported relationships within Convolvulaceae (the morning-glory family), a formal reclassification of this family is presented here. Convolvulaceae, a large family of worldwide distribution, exhibiting a rich diversity of morphological characteristics and ecological habitats, are now circumscribed within twelve tribes. A key to these tribes of Convolvulaceae is offered. The group of spiny-pollen bearing Convolvulaceae (forming "Echinoconiae") and tribe Cuscutae are retained essentially in their traditional sense, Cresseae are circumscribed with only minor modifications, Convolvuleae and Erycibae are recognized in a restricted sense, while Dichondreae and Maripeae are expanded. Also, to produce a tribal taxonomy that better reflects phylogenetic relationships, the concept of Poraneae is abandoned as artificial, three new tribes are recognized (**Aniseieae**, **Cardiochlamyaeae**, and **Jacquemontieae**), and a new tribal status is proposed for the Malagasy endemic *Humbertia* (**Humbertieae**). "Merremieae" are tentatively retained even though the monophyly of this tribe is not certain. In addition to the formal classification, we provide clade name definitions for the family as well as for most of the clades recognized presently as tribes. Also, five well-supported clades that are not assigned formal ranks are recognized and their names defined. The reevaluation of traditional taxonomic characters reveals that many homoplasious characters were emphasized in previous classifications, resulting in formal recognition of non-monophyletic groups. Putative morphological synapomorphies for many clades discovered through molecular cladistic analyses are discussed. However, the morphology of several clades that are well-supported by DNA evidence remains poorly understood, creating further challenges for future studies in Convolvulaceae.

Recent advances in understanding of the phylogenetic relationships within Convolvulaceae, the morning-glory family, based on molecular data sets drawn from all three plant genomes, indicate the need for a revised classification of this family (Manos et al. 2001; Miller et al. 2002; Stefanovic et al. 2002; Stefanovic and Olmstead in press).

The morning-glory family comprises approximately 1600–1700 species grouped in 55–60 genera (Mabberley 1987). The family is nearly cosmopolitan in distribution, but its members are primarily tropical plants, with many genera endemic to tropical zones of individual continents (Austin 1998). Uncertainties exist regarding both delimitation of the family and intrafamilial (tribal) circumscription. Currently available classifications within Convolvulaceae rely largely on the work of several earlier workers, including Choisy (1845), Bentham and Hooker (1873), Hallier (1893), Peter (1891, 1897), and Roberty (1952, 1964). An overview of these, including both points of conflict and congruence among them, is presented by Austin (1973; his Table 8). All of these pre-cladistic schemes are based on very few characters considered to be "the most important" by the author. Among the most influential are those of Peter (1891), based upon fruit type, and Hallier (1893), adopted by Peter (1897), based on pollen surface features as well as fruit and styler characters. Hallier divided the family into two groups: "Echinoconiae", with spiny pollen surface, and "Psisloconiae", with smooth pollen. The major outlines of this classi-

fication were subsequently adopted by many authors (but see Roberty 1952, 1964), with modifications concerning mainly the taxonomic ranks.

The most comprehensive traditional work at the family level was offered by Austin (1973) based mainly on chromosome numbers. Austin's treatment (1973, modified 1998) is currently the most widely used traditional classification. Following Austin, the nonparasitic members of the family are circumscribed in nine tribes (Table 1). *Cuscuta*, the only parasitic taxon associated with Convolvulaceae, is treated as a separate monotypic family, Cuscutaceae.

The major traditional synoptic works on flowering plants place Convolvulaceae in the order Solanales (sensibus Cronquist 1988; Dahlgren 1989; Thorne 1992) along with the Polemoniaceae, Hydrophyllaceae, and Solanaceae. Takhtajan (1997) placed this family in its own order, Convolvulales, due to a number of characteristics, such as presence of articulated latex canals and latex cells, intraxylary phloem position, distinct seed structure and pollen morphology, not shared with other Solanales. Results of broad molecular phylogenetic studies of angiosperms in general, and Asteridae in particular, based on limited molecular data for the Convolvulaceae suggested that the family is most closely related to the Solanaceae and Montiniaceae (e.g., Olmstead and Palmer 1992; Olmstead et al. 1992, 1993, 2000; Chase et al. 1993; Soltis et al. 1997, 2000; APG 1998; Savolainen et al. 2000).

Some members of Convolvulaceae, especially *Cus-*

TABLE 1. Synopsis of Convolvulaceae classification—a comparison of the most recent traditional (Austin 1973, 1998) and newly proposed phylogenetic classification. Asterisks (*) indicate genera not sampled in any molecular study of Convolvulaceae (see text), but retained in present classification in their putative respective tribes based on morphology. Pound signs (#) indicate genera found not to be monophyletic as circumscribed traditionally. Quotation marks (“ ”) indicate the tribe not confirmed to be monophyletic (see text).

Austin (1973, modified 1998) Family Tribe Genus	Phylogenetic classification (present study) Family Tribe Genus
Convolvulaceae	Convolvulaceae
Argyreieae	Ipomoeae s.l.
<i>Argyria</i>	<i>Argyria</i>
<i>Blinkworthia</i>	(including <i>Rivea</i>)
<i>Rivea</i>	<i>Astripomoea</i>
Ipomoeae	<i>Blinkworthia</i> *
<i>Ipomoea</i>	<i>Ipomoea</i> #
<i>Astripomoea</i>	<i>Lepistemon</i>
<i>Lepistemon</i>	<i>Lepistemonopsis</i> *
<i>Lepistemonopsis</i>	<i>Paralepistemon</i>
<i>Paralepistemon</i>	<i>Stictocardia</i>
<i>Stictocardia</i>	<i>Turbina</i> #
<i>Turbina</i>	“ <i>Merremieae</i> ”
Merremieae	<i>Merremia</i> #
<i>Merremia</i>	<i>Hewittia</i>
<i>Hewittia</i>	<i>Hyalocystis</i> *
<i>Decalobanthus</i>	<i>Decalobanthus</i> *
<i>Operculina</i>	<i>Xenostegia</i>
<i>Xenostegia</i>	<i>Operculina</i>
<i>Hyalocystis</i>	Convolvuleae
<i>Aniseia</i>	<i>Convolvulus</i>
<i>Iseia</i>	(including <i>Calystegia</i>)
<i>Odonellia</i>	<i>Polymeria</i>
<i>Tetralocularia</i>	Aniseieae
Convolvuleae	<i>Aniseia</i>
<i>Calystegia</i>	(including <i>Iseia</i>)
<i>Convolvulus</i>	<i>Odonellia</i>
<i>Polymeria</i>	<i>Tetralocularia</i>
<i>Jacquemontia</i>	Cuscutaeae
Erycibeae	<i>Cuscuta</i>
<i>Maripa</i>	Jacquemontieae
<i>Dicranostyles</i>	<i>Jacquemontia</i>
<i>Lysiostyles</i>	Maripeae
<i>Erycibe</i>	<i>Dicranostyles</i>
<i>Humbertia</i>	<i>Maripa</i>
Hildebrandtieae	<i>Lysiostyles</i> *
<i>Hildebrandtia</i>	<i>Cresseae</i> s.l.
<i>Sabaudiella</i>	<i>Hildebrandtia</i>
<i>Cladostigma</i>	(including <i>Cladostigma</i> and <i>Sabaudiella</i>)
Cresseae	<i>Seddera</i>
<i>Seddera</i>	<i>Evolvulus</i>
<i>Evolvulus</i>	<i>Cressa</i>
<i>Cressa</i>	<i>Bonamia</i> #
<i>Bonamia</i>	<i>Stylisma</i>
<i>Stylisma</i>	<i>Wilsonia</i>
<i>Wilsonia</i>	<i>Itzaea</i>
<i>Itzaea</i>	<i>Neuropeltis</i>
<i>Neuropeltis</i>	<i>Neuropeltopsis</i> *
<i>Neuropeltopsis</i>	Dichondreae s.l.
Dichondreae	<i>Dichondra</i>
<i>Dichondra</i>	<i>Falkia</i>
<i>Falkia</i>	<i>Nephrophyllum</i> *
<i>Nephrophyllum</i>	<i>Petrogenia</i>

TABLE 1. Continued.

Austin (1973, modified 1998) Family Tribe Genus	Phylogenetic classification (present study) Family Tribe Genus
Poraneae	<i>Porana</i> p.p.
<i>Porana</i>	<i>Metaporana</i>
<i>Metaporana</i>	<i>Calycobolus</i> #
<i>Calycobolus</i>	<i>Dipteropeltis</i>
<i>Dipteropeltis</i>	<i>Rapona</i>
<i>Rapona</i>	Erycibeae
<i>Cordisepalum</i>	<i>Erycibe</i>
<i>Poranopsis</i>	Cardiochlamyaeae
<i>Cardiochlamys</i>	<i>Cordisepalum</i>
<i>Tridynamia</i>	<i>Poranopsis</i>
<i>Dinetus</i>	<i>Cardiochlamys</i>
Cuscutaceae	<i>Tridynamia</i>
Cuscutaeae	<i>Porana</i> p.p.
<i>Cuscuta</i>	<i>Dinetus</i>
	Humbertieae
	<i>Humbertia</i>

cuta and *Ipomoea*, have been used as model systems to address a wide variety of biological questions. Many species of the parasitic genus *Cuscuta* are recognized as pests on a large array of important agricultural crops. A substantial body of literature deals with the life history, ecology, and pest control of *Cuscuta* species (reviewed by Dawson et al. 1994, and references therein). These branch parasites are also frequently used to study haustorial initiation and formation (e.g., Dörr 1987; Heide-Jørgensen 1987; Lee and Lee 1989; Subramaniam and Mahadevan 1994). In addition, *Cuscuta* has been the subject of extensive molecular analyses. The diversity of photosynthetic ability among species prompted several physiological studies of photosynthetic enzymes and molecular evolution studies of the chloroplast genome (Machado and Zetsche 1990; Haberhausen et al. 1992; Haberhausen and Zetsche 1994; Bömmer et al. 1993; Freyer et al. 1995). Species attributed to the genus *Ipomoea* are exceptionally morphologically diverse, varying in habit and vegetative and reproductive morphology. Due to this diversity *Ipomoea* species have been the focus of a broad range of evolutionary and molecular genetic studies including maintenance of floral polymorphisms, mating system evolution, and evolution of flavonoid biosynthetic pathway (reviewed by Miller et al. 1999).

Convolvulaceae have been the subject of only two family-wide molecular phylogenetic studies (Stefanovic et al. 2002; Stefanovic and Olmstead in press). The first study (Stefanovic et al. 2002) was based on sequences from four chloroplast loci: *rbcL*, *atpB*, *psbE-J* operon, and the *trnL-F* region. These sequences were obtained from a broad sample of taxa within the family, including 102 species from all nine traditionally recognized nonparasitic tribes (Austin 1973; 1998), seven *Cuscuta* species, as well as three outgroups. The

chloroplast DNA (cpDNA) results confirmed that Convolvulaceae are sister to Solanaceae, with 100% bootstrap support for each family and the clade comprising both families. Two groups, *Cuscuta* and tribe Dichondreae, that have been proposed as segregate families (Dumortier 1829), were found nested within the Convolvulaceae. The position of *Cuscuta* as sister to the rest of Convolvulaceae, which would be compatible with recognizing it as a separate family, was rejected. This result was further corroborated by the distribution of deletions in the *atpB* gene and *trnL* intron found in all *Cuscuta* species as well as in all other Convolvulaceae, with the exception of *Humbertia*, which is sister to the rest of the family (Stefanovic et al. 2002). The second study (Stefanovic and Olmstead in press) was designed to better address the question of the position of *Cuscuta* within Convolvulaceae. A new molecular data set consisting of mitochondrial (*atpA*) and nuclear (*RPB2*) genes was generated for a subset of species chosen to best represent the diversity of the family, and analyzed together with the existing chloroplast data matrix to which an additional chloroplast gene (*rpl2*) was added. That study confirmed the previously recovered polyphyly of Erycibeae, Poraneae, and Merremieae, the close relationships of tribes Hildebrandtieae with Cresseae, of Ipomoeae with Argyreieae, and of Dichondreae with some members of Poraneae. At least two nonparasitic lineages were shown to diverge within the family before *Cuscuta*. However, the exact sister group of *Cuscuta* could not be ascertained, even though many alternatives were tested and rejected with confidence (Stefanovic and Olmstead in press).

Halliers's (1893) "Echinoconiae" circumscribe species with spiny pollen and include approximately one-half of the species in Convolvulaceae. The results regarding relationships within this group inferred from broader sampling across Convolvulaceae, but more modest sampling of "Echinoconiae" (Stefanovic et al. 2002; Stefanovic and Olmstead in press) are in agreement with the more detailed studies focusing on this clade conducted by Manos et al. (2001) and Miller et al. (2002). Those studies sampled more taxa and used more rapidly evolving nuclear sequences (ITS and *waxy*), and offered a resolved and well-supported phylogeny for the Convolvulaceae with spiny pollen. The paraphyly of tribe Ipomoeae and genus *Argyreia* as well as polyphyly of *Ipomoea* and *Turbina* are first reported and discussed in detail in those studies.

The widespread congruence among independent data sets provides compelling support for the classification proposed here. The main goal of the present study is to develop a comprehensive, phylogeny-based classification, in conjunction with a reevaluation of traditional taxonomic characters. In a phylogenetic classification, only monophyletic groups are recognized and named (Wiley et al. 1991; de Queiroz and Gauthier

1994). Classification based exclusively on monophyletic groups provides a more efficient way to store, communicate, and retrieve information and has greater predictive value (Farris 1979; Donoghue and Cantino 1987; for different opinions see Cronquist 1987; Brummit 2002). Most importantly, phylogenetic classification provides an explicit basis for comparative biological studies (Funk and Brooks 1990). In this way the classification can communicate to the scientific community the currently available phylogenetic information on relationships within Convolvulaceae.

MATERIALS AND METHODS

At present, the best basis for intrafamilial classification of Convolvulaceae is provided by two family-wide molecular cladistic analyses (Stefanovic et al. 2002; Stefanovic and Olmstead in press) combined with two additional studies focusing on species-rich group of Convolvulaceae with spiny pollen (Manos et al. 2001; Miller et al. 2002). A series of goals for the research on Convolvulaceae has been established by Stefanovic et al. (2002) and the first three, to test the monophyly of Convolvulaceae, to circumscribe major lineages within the family, and to develop a well-supported phylogenetic hypothesis of Convolvulaceae, have been addressed in that study. An additional goal, to narrow down the phylogenetic position of *Cuscuta*, the only parasitic genus of Convolvulaceae, was addressed in more detail in a separate study (Stefanovic and Olmstead in press). The questions regarding the monophyly of *Ipomoea* and the relationships among its species and members of tribe Argyreieae were first addressed in depth by Manos et al. (2001) and Miller et al. (2002). A summary of the current evolutionary hypothesis for Convolvulaceae based on all currently available molecular analyses is depicted in Fig. 1. A synoptical overview of our proposed phylogenetic classification and comparison with most recent taxonomic treatment (Austin 1973, 1998) is given in Table 1.

The *PhyloCode* is a rank-free system of classification based on phylogenetic principles (de Queiroz and Gauthier 1992; 1994) that has generated much discussion regarding its advantages (Cantino et al. 1997, 1999; Cantino 1998, 2000; Baum et al. 1998; de Queiroz and Cantino 2001; Lee 2001; Bryant and Cantino, 2002) and disadvantages (Brummitt 1997; Lindén and Oxelman 1996; Lindén et al. 1997; Benton 2000; Nixon and Carpenter 2000; Forey 2001, 2002) with respect to a traditional, or Linnaean, system. It is beyond the scope of this paper to partake in this debate. However, in addition to the formal Linnaean classification, as governed by the *International Code of Botanical Nomenclature* (ICBN), we provide phylogenetic definitions for the family and for most of the clades recognized as tribes according to the rankless phylogenetic nomenclature system (de Queiroz and Gauthier 1992; 1994) as governed by the set of rules published on-line in the draft *PhyloCode* (Cantino and de Queiroz <http://www.ohio.edu/phylocode/>). These definitions follow the discussions of individual groups. Node-based definitions are preferred whenever taxon sampling and/or confidence in given clades allows it. However, we offer stem-based tribe definitions in certain cases due to the uncertainties regarding the exact circumscription of some tribes. In this way the core members of a tribe can be joined eventually by other taxa of unsure position as additional information becomes available. Also, five well-supported clades that are not assigned formal ranks are recognized and defined in this manner. They are distinguished from the traditional taxa by a preceding slash mark (e.g., /Dicranostyloideae, Fig. 1), following Alverson et al. (1999). These additional groups are discussed following the formal taxonomic treatment.

While deciding which clades are well enough supported to warrant naming, the priority was given to the molecular analyses, but

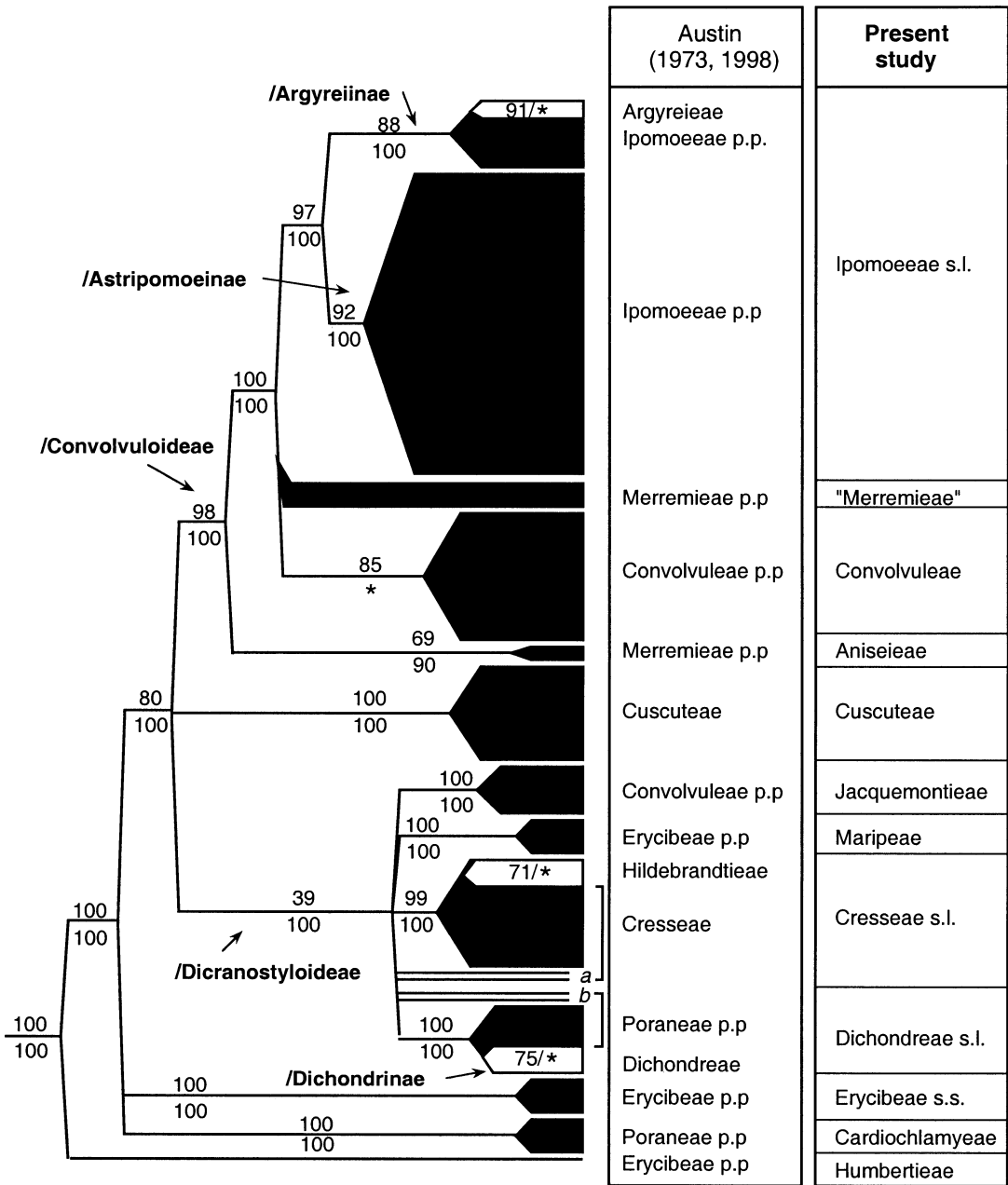


FIG. 1. The summary evolutionary hypothesis for Convolvulaceae derived from sequence data from all three plant genomes and analyzed with a range of analytical methods (Manos et al. 2001; Miller et al. 2002; Stefanovic et al. 2002; Stefanovic and Olmstead in press). Numbers above branches represent bootstrap values for selected clades as reported by Stefanovic et al. (2002); numbers below branches are the Bayesian posterior probabilities for the same clades following Stefanovic and Olmstead (in press). Asterisks (*) indicate nodes for which Bayesian posterior probabilities were not estimated by Stefanovic and Olmstead (in press) due to the reduced taxon sampling. The areas of clades correspond approximately to the number of species found in those clades. Traditional definition of tribes (Austin, 1973, 1998) is indicated in the left column. The formal phylogenetic classification proposed in this paper is indicated in the right column. Compare with Table 1 for the generic circumscription of tribes according to both classifications. Letters a-b represent genera traditionally circumscribed in Cresseae (a = *Itzaea*, *Neuropeltis*, *Neuropeltopsis*, *Wilsonia*) and Poraneae (b = *Dipteropeltis*, *Rapona*, *Calycobolus*) for which molecular data did not ascertain more precise tribal affinities. Rankless names, indicated by a preceding slash mark, are provided for five additional clades (see text for further explanation).

the morphological distinctiveness as well as correspondence with previously named taxa also were taken into consideration. Each named clade was supported by the molecular analyses (Fig. 1). However, different degrees of support were deemed sufficient depending on whether the particular clade was corroborated by other lines of evidence or not. For example, the /*Dicranostyloideae* clade (Fig. 1) was found to be only moderately supported in some molecular analyses but this clade corresponds closely to *Dicranostyleae* sensu Hallier (1893) and is corroborated by morphology (divided style; see below). On the other hand, /*Argyreinae* and /*Astripomoeinae* clades lack defining morphological features uniting all of their respective members and contradict traditional circumscription (see below) but are strongly supported by all molecular analyses (Fig. 1). Also, it is not necessary that all well supported clades be named; hence some clades, albeit well supported, were left unnamed at present due to the lack of known morphological synapomorphies and/or because their respective members do not correspond well to previously named groups.

TAXONOMIC TREATMENT

Given the recently achieved stability of circumscription and relationships within Convolvulaceae (Fig. 1; Table 1), we deem it timely to present a formalized reclassification of the family. Traditionally, the genera of Convolvulaceae have been assigned to tribes, and we follow this tradition by recognizing 12 tribes, three of which are newly described.

CONVOLVULACEAE Juss., Gen. Pl.: 132 (1789), nom. cons.—Type: *Convolvulus* L.

Cressaceae Raf., Ann. Gén. Sci. Phys. Bruxelles 8: 270, 1821

Cuscutaceae Berch. & J. Presl, Prir. Rostlin. 247, 1820

Dichondraceae Dumort., Anal. Fam. Pl. 20: 24, 1829

Erycibaceae Endl. ex Meisn., Pl. Vasc. Gen. Tab. Diagn. 272, Comm. 185, 1840

Humbertiaceae Pichon, Notul. Syst. (Paris) 13: 23, 1947

Poranaceae J. Agardh, Theoria. Syst. Pl. 364, 1858

Plants perennial, rarely annual, herbs, vines or woody lianas, twining always in counterclockwise direction, rarely shrubs or trees, sometimes with little or no chlorophyll and hemi- or holoparasitic; with laticifers and usually milky sap. Stems usually with internal (intraxylary) phloem. Hairs usually present, simple, 2-branched, or stellate. Leaves exstipulate, petiolate, alternate, usually simple, rarely lobed or compound, usually entire, with pinnate or palmate venation, sometimes highly reduced. Stomata usually paracytic. Inflorescences determinate, sometimes reduced to a solitary flower. Flowers actinomorphic, rarely zygomorphic, complete, perfect (except *Hildebrandtia*), hypogynous. Calyx usually polysepalous, composed of five equal or unequal sepals, sometimes accrescent as the fruit matures. Corolla five-parted, strongly gamo-

petalous, often large and showy, frequently funnel-shaped. aestivation usually convolute, with clockwise twist. Stamens five, epipetalous, usually inserted; filaments sometimes of unequal length, straight to dilated at the base, glabrous or pubescent. Pollen tricolpate to multiporate, spiny or relatively smooth in texture. Gynoecium of two united carpels (3 in some *Ipomoea* spp.), unlobed to deeply lobed, forming a two-locular, superior ovary, and axile placentation. Ovules 1–2 per locule (~20 in *Humbertia*), with one integument, tenuinucellate, apotropous. Styles entire or partially to completely divided, terminal to gynobasic. Stigmas 1 or 2 (rarely 3), capitate, flattened, linear to lobed. Fruits usually dry, dehiscent capsule or indehiscent utricle, sometimes fleshy. Embryo straight or curved, with cotyledons folded or reduced. The C3 photosynthesis type recorded directly in several genera. Alkaloids present in many species. Iridoids not detected. $X = 7-15(+)$.

Although the family is best known in temperate regions for its weedy representatives (e.g., *Calystegia*, *Convolvulus*) or crop pests (*Cuscuta*), many tropical and subtropical species, chiefly those found in *Ipomoea*, *Convolvulus*, *Jacquemontia*, and *Dichondra*, are valuable ornamentals, medicinals, and food crops. The sweet potato, *Ipomoea batatas* (L.) Lam., is the world's second most important root crop (>128 million metric tons per year; Simpson and Ogorzaly 1995).

Convolvulaceae are sister to Solanaceae, a mainly New World family (Olmstead et al. 1992, 1993; Chase et al. 1993; Soltis et al. 1997, 2000; APG 1998; Savolainen et al. 2000; Stefanovic et al. 2002). Molecular sequence data strongly support a single origin of Convolvulaceae (Stefanovic et al. 2002), even though there is no evident, unique, and unreversed morphological synapomorphy for all members of the family. Two of the three groups that have been proposed as segregate families (Dumortier 1829), *Cuscuta* and tribe *Dichondreae*, are nested within Convolvulaceae, and the third, *Humbertia*, is the sister group to the other members of the family. Convolvulaceae monophyly also is supported by a structural change in the chloroplast genome of this family. An intron usually found in the *rpl2* gene of angiosperms is deleted in all Convolvulaceae, including *Humbertia* and *Cuscuta* (Stefanovic et al. 2002). This deletion represents a unique event within Asteridae and a synapomorphy for Convolvulaceae.

We provide the following node-based clade definition: Convolvulaceae are the least inclusive clade that contains *Convolvulus arvensis* L. and *Humbertia madagascariensis* Lam.

KEY TO THE TRIBES OF CONVULVULACEAE

1. Plants large trees; many ovules per ovary; flowers zygomorphic 8. Humbertiaceae
1. Plants herbs, vines, lianas, or shrubs (rarely small trees); 1–4(–6) ovules per ovary; flowers actinomorphic (rarely weakly zygomorphic).

2. Plants parasitic, achlorophyllous 5. Cuscutaeae
2. Plants non-parasitic, chlorophyllous.
3. Style 1 or absent and ovary with sessile stigma.
 4. Leaf venation palmate; fruit utricular; calyx accrescent; bracts foliaceous 2. Cardiochlamyaeae
 4. Leaf venation pinnate; fruit capsular, baccate, or dry-baccate; calyx accrescent or not; bracts scale-like.
 5. Style absent; stigma sessile, often conic; corolla lobes bifid 7. Erycibaeae
 5. Style present; stigma on style, not sessile, mostly globose or otherwise not conic; corolla lobes entire or shallowly bifid.
 6. Pollen echinate, pantoporate 9. Ipomoeaeae
 7. Pollen not echinate, colpate (except *Calystegia* & *Xenostegia*, where porate).
 7. Stigmas globose 12. "Merremieae"
 7. Stigmas subulate or ellipsoid and flattened.
 8. Pollen prolate; sepals unequal (except in *Iseia*) 1. Aniseieae
 8. Pollen spheroidal; sepals more or less equal.
 9. Fruits 2–4 valvate; stigma subulate, 2-lobed or dissected (*Polymeria*) 3. Convolvuleae
 9. Fruits 8 valvate; stigma ellipsoid & flattened 10. Jacquemontieae
 3. Styles 2 or at least bifid (if single, then plants lianas; fruits woody-baccate; stigma never sessile).
 10. Fruit dehiscent, capsular; small shrubs, herbs, or less often lianas; filaments usually straight and glabrous 4. Cresseae
 10. Fruits indehiscent (utricle or ligneous baccate); mat-forming herbs or lianas; filaments usually dilated and pubescent.
 11. Fruits utricles; prostrate herbs or lianas 6. Dichondreae
 11. Fruits ligneous-baccate; lianas 11. Maripeae

CIRCUMSCRIPTION OF TRIBES IN CONVULVULACEAE

1. *Aniseieae* Stefanovic & Austin, tribus nov.—Type: *Aniseia* Choisy

Tribus haec, inter tribus familiae Convolvulaceae Juss., habitu generali et morphologia vegetativa ad tribum Ipomoeaeae Hall. f. accedes, sed stigmatibus elongis (raro globosis) et pollenibus laevibus, non echinatis ab ea differt.

Plants herbaceous, vines. Leaf base cordate or cuculate. Flowers actinomorphic, bisexual. Sepals usually unequal, sometimes accrescent. Filaments dilated, pubescent. Stigmas usually elongate, rarely globose. Fruits dehiscent, capsule, pericarp ligneous. Pollen 3- to poly-colpate, prolate, non-echinate.

Included genera: *Aniseia* Choisy (Americas), *Iseia* O'Donell (South America), *Odonellia* K. Robertson (Americas), *Tetralocularia* O'Donell (South America).

This well-defined and supported segregate of Merremieae sensu Austin (1982) is the first lineage diverging within the /Convolvuloideae clade (Fig. 1; Stefanovic et al. 2002; Stefanovic and Olmstead in press), and is recognized here as tribe Aniseieae. This tribe, endemic to the Americas, is composed of taxa that, unlike the rest of "Merremieae," have, with the exception of *Iseia*, unequally enlarged sepals and elongated stigmas. According to cpDNA data (Stefanovic et al. 2002), the monotypic South American genus *Iseia* is nested within *Aniseia*. *Iseia* was recognized by O'Donell (1953) as a separate genus due to several morphological characters (e.g., indehiscent fruit, subequal sepals, globose stigma) all of which appear, in the phylogenetic context, to be autapomorphies of its single species, *I. luxurians* (Morici) O'Donell. *Odonellia* is found to be closely associated with *Aniseia* s.l., as predicted by Robertson (1982) when he removed two *Jacquemontia* species

as this new genus, based on simple rather than stellate trichomes and some additional, mainly palynological, differences. Albeit only moderately supported, the inclusion of monotypic genus *Tetralocularia* within tribe Aniseieae is warranted because it shares the defining combination of morphological features with the other species of this tribe and is recovered as its sister-group by all molecular analyses (Stefanovic et al. 2002; Stefanovic and Olmstead in press).

We provide the following stem-based clade definition: Aniseieae are the most inclusive clade that contains *Aniseia martinicensis* (Jacq.) Choisy and *Odonellia hirtiflora* (Martens & Galeotti) K. Robertson, but not *Convolvulus arvensis* L. or *Merremia peltata* (L.) Merr.

2. *Cardiochlamyaeae* Stefanovic & Austin, tribus nov.—Type: *Cardiochlamys* Oliver

Tribus haec a tribubus familiae Convolvulaceae Juss. aliis combinatione characterum sequente differt: stylus unus, integer, non divisus; venatio foliorum palmata; fructus utriculatus indehiscensque; bractae foliaceae; granula pollinis laevia, non echinata.

Plants usually woody, lianas. Leaf base cordate, venation palmate. Bracts foliaceous. Flowers actinomorphic, bisexual. Sepals equal to unequal, accrescent. Style one, entire. Fruits indehiscent, utricle. Pollen usually 3-colpate (in *Cardiochlamys* pantoporate), non-echinate.

Included genera: *Cardiochlamys* Oliver (Madagascar), *Cordisepalum* Verdc. (SE Asia), *Dimetus* Sweet (Asia), *Poranopsis* Roberty (Asia), *Tridynamia* Gagnepain (India to SE Asia).

Disintegration of Poraneae as defined traditionally was one of the most surprising results of the molecular analyses (Stefanovic et al. 2002; Stefanovic and Olmstead in press). This tribe was first circumscribed by

Hallier (1893) based mainly on a combination of two characters: the accrescent calyx (sepals equally or unequally enlarge as the fruit matures) and utricle (indehiscent, one-seeded fruit with papery pericarp). Many authors have subsequently adopted this tribal concept, with minor changes in circumscription (e.g., Peter 1891; Melchior 1964; Austin 1973). The most recent comprehensive examination of this tribe was done by Staples (1987, 1990). However, Poraneae, in any of the proposed delimitations, is not monophyletic. It comprises essentially two distinct groups. One group, characterized by deeply divided styles and pinnate leaf venation, is found within the /Dicranostyloideae clade (Fig. 1), with most of its members tightly associated with the monophyletic tribe Dichondreae. The other group, consisting of *Cordisepalum*, *Cardiochlamys*, *Poranopsis*, *Tridynamia*, and *Dinetus* is found as the second lineage diverging within Convolvulaceae after *Humbertia* (Fig. 1). We circumscribe here this latter group as tribe Cardiochlamyae. All members of this clade have a single, undivided style. Besides this character, which sets it apart from the /Dicranostyloideae (i.e., "bifid style") clade members, this group is supported by palmate leaf venation and foliaceous, sessile bracts, characters not found in other taxa assigned previously to Poraneae. Staples (1987) was the first to point out the importance of these two morphological characters, style morphology and leaf venation, for the systematics of tribe Poraneae, but he considered Poraneae to be a natural group (Staples 1987, 1990). The genus *Porana* is also not monophyletic. This genus was defined, within the tribe, by having all five sepals equally accrescent. *Porana*, however, splits along the same morphological lines as the tribe, with the type species *P. volubilis* Burm. f., having the bifid style, found in the /Dicranostyloideae clade (Stefanovic et al. 2002). The formal transfers of *Porana* species currently placed in this genus, but found within Cardiochlamyae (e.g., *P. commixta* Staples), await more detailed study with broader taxon sampling.

We provide the following node-based clade definition: Cardiochlamyae are the least inclusive clade that contains *Cardiochlamys madagascariensis* Oliv. and *Dinetus truncatus* (Kurz) Staples.

3. CONVULVULEAE (Choisy) Choisy in DC., Prodr. 9: 325 (1845).—Type: *Convolvulus* L.

Plants usually herbaceous, vines. Leaf base usually cordate, sometimes cuneate, truncate, or obtuse. Flowers actinomorphic, bisexual. Sepals equal, non-accescent. Filaments dilated, pubescent (except in *Polymeria*). Style one, entire. Stigmas elongated, narrow, subulate to clavate (or dissected in *Polymeria*). Fruits dehiscent, capsule, usually 4-valvate. Pollen 3-colpate to pantoporate, non-echinate, spheroidal.

Included genera: *Calystegia* R. Br. (Americas, Europe, Asia), *Convolvulus* L. (worldwide, with most species in the temperate and subtropic regions), *Polymeria* R. Br. (Australia, New Guinea).

We present here a significantly narrowed circumscription of tribe Convolvuleae, comprised of only three genera. Choisy (1845) established this tribe, placing into it *Ipomoea*, *Convolvulus*, *Jacquemontia*, and numerous other genera characterized by dehiscent capsules. This basic alignment was followed by most 19th century treatments, until Hallier (1893) provided his classification of Convolvulaceae. *Convolvulus* and *Jacquemontia* remained included in Convolvuleae sensu Hallier, along with seven other genera, but *Ipomoea* was removed due to its spiny pollen. Austin (1973) further restricted the tribe by placing many of its genera in the informal "merremioid" group (see below), but kept *Jacquemontia* as well as *Evolvulus* and *Wilsonia* within the Convolvuleae. The last two genera were subsequently excluded from the tribe (Austin 1998). The cpDNA analyses (Stefanovic et al. 2002) provided moderate support for tribe Convolvuleae consisting of *Calystegia* and *Convolvulus*, both cosmopolitan in their distribution, and the Australian endemic *Polymeria*. Molecular analyses (Stefanovic et al. in press; Stefanovic and Olmstead in press) also provided strong support for exclusion of *Jacquemontia* from Convolvuleae (Fig. 1). *Calystegia* is well defined morphologically by pantoporate pollen and supported as a monophyletic group. However, according to the molecular data this genus is nested within the bigger genus, *Convolvulus*, rendering this taxon, in its present circumscription, paraphyletic. The transfer of approximately 30 *Calystegia* species to *Convolvulus* (~200 spp.) would be one option to solve this problem. The other would be to split *Convolvulus* into several genera. Neither of these options is warranted at present, until a more significant number of species have been sampled and analyzed under a rigorous phylogenetic framework. However, a rankless clade *Calystegia* could be defined as a part of a more inclusive clade *Convolvulus*, without need for any name changes under the principles of phylogenetic nomenclature (de Queiroz and Gauthier 1992; 1994).

We provide the following node-based clade definition: Convolvuleae are the least inclusive clade that contains *Convolvulus arvensis* L. and *Polymeria pusilla* R. Br.

4. CRESSEAE Benth. & Hook., Gen. Pl. 2: 868 (1873).—Type: *Cressa* L.

Neuropeltidae Roberty, Candollea 14: 24, 1952
Hildebrandtieae Melchior, Engler's Syllabus der Pflanzenfam., ed. 12. 2: 427–429, 1964
Hildebrandtieae Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 19–20, 1891

- Dicranostyleae (Meisn.) Hall. f., Bot. Jahrb. Syst. 16: 569, 1893, pro parte
 Wilsonieae Hallier f., Bot. Jahrb. Syst. 16: 569, 1893
 Wilsonioideae Roberty, Candollea 14: 23, 1952
 Evolvuleae Roberty, Candollea 14: 28, 1952
 Dicranostylineae Ooststr., Fl. Males. 4: 389, 1953
 Wilsoniinae Ooststr., Fl. Males. 4: 389, 1953
 Neuropeltidae Roberty, Boissiera 10: 153, 1964

Plants suffrutescent herbs to shrubs, less often lianas. Leaf base not cordate. Flowers actinomorphic, usually bisexual (unisexual in *Hildebrandtia*). Sepals equal or unequal, usually non-acrescent (acrescent in *Hildebrandtia* female flowers and some *Seddera* spp.). Styles two, or bifid. Stigmas globose, reniform, or lobed. Filaments usually straight, glabrous. Fruit dehiscent, capsular (rarely utricular), 1–4 locular, 1–4 seeded. Pollen 3-colpate or pantocolpate, non-echinate.

Included genera: *Bonamia* DuPetit-Thouars (pantropical), *Cladostigma* Radlk. (Africa), *Cressa* L. (Americas, Africa, Asia, Australia), *Evolvulus* L. (Americas), *Hildebrandtia* Vatke (Africa, Arabian Peninsula, Madagascar), *Sabaudiella* Chiov. (Africa), *Seddera* Hochst. (Africa, Arabian Peninsula), *Stylisma* Raf. (E USA). Tentatively also included: *Itzaea* Standl. & Steyerl. (Mesoamerica), *Neuropeltis* Wall. (Africa, Asia), *Neuropeltopsis* Ooststr. (Borneo), *Wilsonia* R. Br. (Australia).

As circumscribed here tribe Cresseae s.l. consists of members of tribes Hildebrandtieae (sensu Peter 1891) and Cresseae s.s. Hildebrandtieae are characterized by anatomically and/or functionally unisexual flowers, two free styles, and accrescent sepals in female flowers. Dioecy is unique here in the family. Hallier (1893) and Austin (1973) suggested a connection between Hildebrandtieae and genera from tribe Cresseae, which share with Hildebrandtieae branched or free styles and similar habitat. Morphology-based cladistic analyses by Demissew and Austin (1996) and Austin (1998) confirmed this relationship between tribes Hildebrandtieae and Cresseae. They showed that monophyletic Hildebrandtieae are nested within a paraphyletic Cresseae, with *Cladostigma* as a sister group to *Hildebrandtia*. However, given the position of *Cladostigma* inferred from cpDNA data (Stefanovic et al. 2002), this genus, characterized by the complete absence of anthers in female flowers and sepals clawed at the base, is regarded as congeneric with *Hildebrandtia*. Monotypic *Sabaudiella*, the third genus included in Hildebrandtieae by Peter (1891) has been shown previously to share a number of characters with *Hildebrandtia*, and its inclusion in *Hildebrandtia* has been suggested (Demissew and Austin 1996). Molecular data further support the need for this transfer (Stefanovic et al. 2002). Within *Hildebrandtia* defined in this broad sense (~13 spp.) two well-supported groups emerged. One group comprises all species from mainland Africa

and Arabia, monophyly of which is highlighted by presence of two-locular ovaries and capsular fruits. The second group comprises species from Madagascar characterized by unilocular ovaries and utricular fruits (Stefanovic et al. 2002). The African genus *Seddera* (Cresseae s.s.), some species of which also have accrescent sepals, is confirmed to be sister to Hildebrandtieae by the cpDNA data. The Cresseae, as circumscribed here, including *Hildebrandtia* and the majority of genera placed in tribe Cresseae s.s., are well supported by both morphological (Austin 1998) and molecular data (Stefanovic et al. 2002). However, two genera belonging historically to Cresseae, *Itzaea* and *Neuropeltis*, as well as some *Bonamia* species, are found elsewhere in the cpDNA tree (Stefanovic et al. 2002). Inclusion of more molecular data did not resolve the more precise placement of these taxa (Stefanovic and Olmstead in press) within the /Dicranostyloideae (Fig. 1.). Similarly, *Wilsonia*, a small Australian genus usually associated with Cresseae, is found in all optimal trees as part of the Cresseae clade, but support for this position remains weak. Also, *Bonamia* is shown to be polyphyletic (Stefanovic et al. 2002). Two of its species form a clade sister to *Stylisma*, firmly within Cresseae, whereas another species forms a clade with *Itzaea*. Only additional sampling within this variable genus will elucidate the relationships of its members, and enable the proper realignment of *Bonamia* species.

Due to the uncertainty regarding the exact circumscription of Cresseae, we believe it more prudent to offer a stem-based clade definition. In this way the “core” members of the tribe can be joined eventually by other taxa of unsure position as the additional information becomes available. We provide the following stem-based clade definition: Cresseae are the most inclusive clade that contains *Cressa cretica* L. but not *Maripa scandens* Aubl., *Jacquemontia pentantha* (Jacq.) G. Don, or *Dichondra repens* J.R. Forst. & G. Forst.

5. CUSCUTEAE Choisy in DC., Prodr. 9: 452 (1845).—
 Type: *Cuscuta* L.

Plants parasitic, with little or no chlorophyll, attached to hosts by haustoria. Roots absent. Stems twining, slender, pale to bright orange, with no internal phloem. Leaves reduced, scale-like. Flowers actinomorphic, bisexual, with infrastaminal fimbriate scales. Sepals equal, non-acrescent. Styles entire or partially to completely divided. Stigmas elongate, capitate, ovoid. Fruit dehiscent, capsular, 2-locular, 1–4 seeded. Embryo spirally coiled, almost acotyledonous. Pollen 3-colpate or pantocolpate, non-echinate.

Included genus: *Cuscuta* (worldwide).

Cuscutae are a monogeneric tribe, comprising the genus *Cuscuta*. *Cuscuta* consists of some 160–170 species, is nearly cosmopolitan in distribution, and occurs

in a wide range of habitats. Even though vegetative characters of this group are altered in association with parasitism, its floral morphology is similar to that of the Convolvulaceae and the clear association with this family was recognized early on (e.g., Choisy 1845). Traditional classification, for the most part, ignored the question of the broader relationships of *Cuscuta*, mainly due to the lack of useful taxonomic characters (but see Austin 1973). Most classifications recognize a separate tribe (Choisy 1845; Bentham and Hooker 1873; Baillon 1891; Hallier 1893; Peter 1897; Austin 1998) or subfamily (Peter 1891; Melchior 1964) within Convolvulaceae. However, some botanists adopted Dumortier's (1829) view that the genus should be recognized as a separate family (e.g., Roberty 1952, 1964; Austin 1973). This opinion is reflected also in some major synoptic works on flowering plants (e.g., Cronquist 1988; Takhtajan 1997). Subdivisions within the genus were proposed by Engelmann (1859; adopted by Yuncker 1932), based primarily on the morphology of styles and stigmas, which show considerable diversity.

The genus *Cuscuta* is one of the best supported groups in molecular analyses of Convolvulaceae (Stefanovic et al. 2002; Stefanovic and Olmstead in press). The relationships within *Cuscuta* are also fully resolved and well supported. All three subgenera (sensu Yuncker 1932) are found to be monophyletic, with subgenus *Monogyna* as the sister group to subgenus *Cuscuta* plus subgenus *Grammica* (Stefanovic et al. 2002). However, despite intensive efforts to recover the exact position of *Cuscuta*, both in terms of the range of analytical methods and the quantity of molecular data (Stefanovic et al. 2002; Stefanovic and Olmstead in press), its closest non-parasitic relative(s) remain uncertain. Nevertheless, this approach did help to narrow down the position of *Cuscuta*. At least two nonparasitic lineages (Humbertieae and Erycibeae plus Cardiochlamyaeae) are shown to diverge within the family before *Cuscuta* (Stefanovic and Olmstead in press). The *Cuscuta*-Dichondreae s.s. association, implicitly proposed by Austin (1973) based on some unique shared fruit features as well as similarities in the embryo morphology, was rejected with confidence (Stefanovic and Olmstead in press). The consensus places this parasitic genus in the general vicinity of clades /Convolvuloideae and /Dicranostyloideae, without further bearing on exact patterns among these three groups (Fig. 1).

We provide the following node-based clade definition: Cuscuteae are the least inclusive clade that contains *Cuscuta europaea* L. and *Cuscuta japonica* Choisy.

6. DICHONDREAEE (Choisy) Choisy in DC., Prodr. 9: 325 (1845).—Type: *Dichondra* J. R. Forst. & G. Forst. Dichondraceae Dumortier, Anal. Fam. 20: 24, 1829 Poraneae Hallier f., Bot. Jahrb. Syst. 16: 57, 1893, pro parte

Dichondroideae Roberty, Candollea 14: 22, 1952
Nephrophyllaeae Roberty, Candollea 14: 28, 1952
Dipteropeltideae Roberty, Candollea 14: 24, 1952
Prevosteeae Roberty, Candollea 14: 25, 1952
Dichondrinae (Choisy) Ooststr., Fl. Males. 4: 389, 1953
Lepistemonopseae Roberty, Candollea 14: 27, 1952.

Plants prostrate herbs to lianas. Leaf base usually cordate, sometimes cuneate. Flowers actinomorphic, bisexual. Sepals equal, accrescent to non-accrescent. Filaments dilated, pubescent. Styles partially to completely divided. Stigmas globose. Fruits indehiscent, utricles. Pollen 3-colpate, non-echinate.

Included genera: *Dichondra* J. R. Forst. & G. Forst. (Mexico, SW USA, Africa, Australia, introduced into Asia), *Falkia* L. f. (Africa), *Metaporana* N. E. Br. (Africa, Madagascar), *Nephrophyllum* A. Rich. (Ethiopia), *Petrogenia* I. M. Johnst. (Mexico, SW USA), *Porana* Burm. f. (SE Asia). Tentatively also included: *Calycobolus* Willd. (tropical Americas, Africa), *Dipteropeltis* Hall. f. (Africa), *Rapona* Baillon (Madagascar).

We propose here a substantially expended concept of Dichondreae including members of the traditional tribe Dichondreae s.s. and members of Poraneae sensu Hallier (1893) characterized by bifid styles. Dichondreae s.s. is a group frequently removed from the Convolvulaceae due to its deeply divided ovary and gynobasic styles, but is found to be a well-supported, monophyletic group positioned within the family. It occurs in the /Dicranostyloideae clade, as a sister group to the monotypic *Petrogenia* (together forming /Dichondrinae, Fig. 1; see below), and further, the clade including some taxa with divided style assigned traditionally to Poraneae (Stefanovic et al. 2002). Dichondreae s.l. are strongly supported although their exact relationships within the /Dicranostyloideae clade are not resolved (Fig. 1). The close relationship between Dichondreae and Poraneae was first suggested by Austin (1973) but the concept of Poraneae is now known to be artificial. The possible morphological synapomorphy for this otherwise morphologically diverse clade is the utriculate fruit. The indehiscent, one-seeded fruit with papery pericarp (utricle) is inferred to have evolved at least three times independently within Convolvulaceae: in Cardiochlamyaeae, in Dichondreae s.s., as well as in some *Hildebrandtia* species. The same fruit type is shared also with additional genera with divided styles assigned traditionally to Poraneae, *Rapona* plus *Dipteropeltis*, but the precise relationship of this clade is not clear (Stefanovic et al. 2002). Information from additional molecular data did not help to resolve the more precise placement of these taxa (Stefanovic and Olmstead in press) within the /Dicranostyloideae. We tentatively retain the genera *Rapona* and *Dipteropeltis* in the recircumscribed Dichondreae until more decisive information becomes available. Addi-

tionally, *Calycobolus*, also regarded as a member of traditional Poraneae, is not monophyletic (Stefanovic et al. 2002; Stefanovic, unpublished). One species, *C. nutans* (Choisy) D. Austin, is firmly nested within *Porana* s.s. (i.e., excluding members with single style and palmate venation found in Cardiochlamyae). O'Donnell (1960) transferred this species to genus *Porana* [*P. nutans* (Choisy) O'Donnell]. The affinities of the other members of this variable genus with a South American-African disjunct distribution awaits further in-depth examination.

We provide the following stem-based clade definition: Dichondreae are the most inclusive clade that contains *Dichondra repens* J.R. Forst. & G. Forst. but not *Maripa scandens* Aubl., *Jacquemontia pentantha* (Jacq.) G. Don., or *Cressa cretica* L.

7. ERYCIBEA (Endl.) Hall. f., Bot. Jahrb. Syst. 16: 576 (1893).—Type: *Erycibe* Roxburgh
 Erycibea Endl., Enchir. Bot. 3221841, 1841, as “subordo Convolvulaceis affines,” nom. illeg.
 Erycibea (Endl.) Peter in Engler & Prantl, Nat. Pflanzenfam. 4: 36, 1891
 Eryciboideae (Endl.) Roberty, Candollea 14: 22, 1952
 Erycibinae (Endl.) Ooststr., Fl. Males. 4: 389, 1953

Plants woody, lianas. Leaf base not cordate. Flowers actinomorphic, bisexual. Sepals equal, non-acrescent. Corolla lobes deeply divided. Filaments straight, glabrous. Styles absent. Stigmas sessile, conic. Fruits indehiscent, ligneous, baccate. Pollen 3-colpate, non-echinate.

Included genus: *Erycibe* Roxburgh (Asia, N Australia).

The concept of Erycibea has been changing significantly over time since it was first introduced by Endlicher (1841) for the single genus *Erycibe*. Early botanists considered this predominantly SE Asian genus distinct from Convolvulaceae, and some thought it best transferred to Boraginaceae (Choisy 1834, 1845). Hallier (1893) was the first to combine *Erycibe*, *Maripa*, and *Humbertia* in the tribe Erycibea. Most taxonomic treatments of the family since Hallier have either followed his concept (Austin 1973, 1998; Derooin 1992), broadened it by inclusion of *Dicranostyles* and *Lysiostyles* (Bentham 1846), or separated the genus *Humbertia* from the tribe (Pichon 1947; Roberty 1952, 1964). We close the circle here by including only the genus *Erycibe* in the tribe Erycibea following Endlicher (1841). This genus is both well-defined by morphological characters and molecular data (Stefanovic et al. 2002). However, its relationship with other tribes of Convolvulaceae is equivocal (Fig. 1). Regardless whether Erycibea and Cardiochlamyae are confirmed to be successive lineages diverging within the family after Humbertieae (as suggested by cpDNA data; Stefanovic

et al. 2002) or sister-groups (Stefanovic and Olmstead in press), the simplest explanation for one of the most conspicuous features of *Erycibe*, the absence of a style, is the complete reduction of an undivided ancestral style.

We provide the following stem-based clade definition: Erycibea are the most inclusive clade that contains *Erycibe paniculata* Roxb. but not *Cardiochlamys madagascariensis* Oliv., *Cuscuta europaea* L., *Jacquemontia pentantha* (Jacq.) G. Don., *Dicranostyles scandens* Benth., or *Convolvulus arvensis* L.

8. **Humbertieae** (Pichon) Stefanovic & Austin, status nov. Basionym: Humbertiaceae Pichon, Notul. Syst. (Paris) 13: 23 (1947).—Type: *Humbertia* Lam.
 Humbertioideae Roberty, Candollea 14: 22, 1952

Plants large trees. Stems without internal phloem. Secretory cells restricted to flowers. Leaf base not cordate. Flowers zygomorphic, bisexual, single, axillary. Sepals with 5 traces, non-acrescent. Stamens exserted. Filaments bent in buds. Styles entire, exserted. Ovules ∞ (~20 per locule). Fruits baccate, 1- to 4-seeded. Pollen non-echinate.

Included genus: *Humbertia* Lam. (Madagascar).

The monospecific Humbertieae, endemic to Madagascar, are the sister group to the rest of Convolvulaceae. The only species, *H. madagascariensis*, retains several suspected ancestral features of Convolvulaceae. Baillon (1891) first noted the solanaceous character of indefinite number of ovules, and transferred *Humbertia* to the Solanaceae. Hallier (1893) kept this genus within Convolvulaceae (tribe Erycibea) despite the specialized anatomical traits he described, such as the absence of internal phloem and secretory cells, both of which characterize most Convolvulaceae. The most detailed anatomical study of *Humbertia* was done by Derooin (1992), who showed that secretory cells, typical for the family, are present in the corolla, androecium, and gynoecium of *H. madagascariensis*. Furthermore, Derooin pointed out that, with the exception of the absence of internal phloem, a condition also found in most *Cuscuta* species, there are no major anatomical differences between *Humbertia* and the other genera of Convolvulaceae.

The isolated position of *H. madagascariensis* in molecular analyses (Stefanovic et al. 2002; Stefanovic and Olmstead in press) is consistent with either segregating the genus in its own monotypic family, Humbertiaceae (Pichon 1947), or keeping it within the Convolvulaceae. However, our results are not consistent with its placement in tribe Erycibea (Hallier 1893; Austin 1973, 1998; Derooin 1992; see above). Relying on strongly supported relationships inferred from molecular data (Stefanovic et al. 2002) and taking into account well documented similarities between *Humbertia* and

the other genera of Convolvulaceae (Deroin 1992), we retain it in the family and recognize it as tribe Humbertieae (Fig. 1). Retention in the family is further supported by presence of a derived chloroplast structural character, the *rpl2* intron deletion, shared with the rest of the family (Stefanovic et al. 2002).

We do not provide a clade definition, because only one species, *Humbertia madagascariensis* Lam., is included in this tribe.

9. IPOMOEAE Hall. f., Bot. Jahrb. Syst. 16: 583 (1893).—
Type: *Ipomoea* L.

Plants vines or lianas, rarely small trees. Leaf base usually cordate. Flowers actinomorphic, bisexual. Sepals equal, sometimes accrescent. Filaments dilated, pubescent. Style one, entire. Stigmas globose. Fruits dehiscent, capsule, or indehiscent, fleshy. Pollen echinate, pantoporate.

Included genera: *Argyreia* Lour. (SE Asia, N Australia), *Astripomoea* A. Meeuse (Africa), *Blinkworthia* Choisy (SE Asia), *Ipomoea* L. (Americas, Africa, Asia, Australia), *Lepistemon* Blume (Africa, Asia, Australia), *Lepistemonopsis* Dammer (Africa), *Paralepistemon* Lejoly & Lisowski (Africa), *Rivea* Choisy (SE Asia, Australia), *Stictocardia* Hall. f. (Africa, SE Asia), *Turbina* Raf. (pan-tropical).

We adopt here the broad concept of Ipomoeae, as proposed by Manos et al. (2001) based on nuclear DNA sequences and morphological data. Ipomoeae s.l. follows entirely the original Hallier's (1893) idea of subfamily Echinoconiae (nom. illeg.), including all Convolvulaceae genera with echinate, pantoporate pollen. Hallier subdivided this taxon into two tribes: (1) Argyreieae, characterized by indehiscent, fleshy fruit, and (2) Ipomoeae, with dry, capsular fruit. Two major clades, both well supported, are resolved within the spiny-pollen group according to both nuclear (Manos et al. 2001; Miller et al. 2002) and cpDNA data (Stefanovic et al. 2002). However, these clades do not correspond to Hallier's (1893) subdivisions. One clade includes the small African genus *Astripomoea* and, as its sister, a predominantly New World group of more than 500 *Ipomoea* species (Fig. 1; /Astripomoeinae). The other group consists primarily of Old World genera classified traditionally in Ipomoeae such as *Lepistemon*, *Stictocardia*, *Paralepistemon*, and *Turbina* interspersed among some Old World *Ipomoea* species (Fig. 1; /Argyreinae). The monophyletic tribe Argyreieae (sensu Hallier) is nested within the latter group (Fig. 1). However, the genus *Argyreia* is paraphyletic as circumscribed currently, because it includes at least one of the moth-pollinated species of *Rivea* (Wilkin 1999; Manos et al. 2001). A small SE Asian genus *Blinkworthia* was not sampled in any molecular study, but is likely to be associated with Argyreieae based on its

indehiscent fruit with leathery pericarp. Additional information is needed in order to propose formal realignments of species in this group. The two major clades within Ipomoeae are difficult to reconcile with any particular pattern of morphological characters, leading to the hypothesis of a generalized model of morphological evolution derived from an *Ipomoea*-like form in this group (Manos et al. 2001).

The subdivisions within Ipomoeae s.l. pose an additional challenge. It is clear that generic boundaries within Ipomoeae s.l. require extensive redefinition in order for genera to be monophyletic. Options for generic revisions include: (1) retaining the traditional *Ipomoea* in broad sense as the only genus of Ipomoeae and reassigning species of the nine other genera to *Ipomoea*, or (2) splitting the traditional genus *Ipomoea*. The first option is already proposed by Wilkin (1999). He concluded that there was no support for recognizing distinct genera among Ipomoeae and that only a broader *Ipomoea* can be defined based on morphology (Wilkin 1999). The additional advantages of this option are that fewer species in Ipomoeae s.l. would require a name change and all of the intensely studied *Ipomoea* species would retain the name with which they are currently identified. In this scenario, monotypic *Ipomoea* would be synonymous with the Ipomoeae. The primary disadvantages of this option are that nine genera would require name changes (~150 species) and that all the morphological diversity and species-richness contained in Ipomoeae would be assigned to one genus. The second option would result in a higher number of genera in Ipomoeae s.l. and would require as many as 600 name changes, depending on where generic boundaries are drawn. As noted by Manos et al. (2001), the type species for *Ipomoea*, *I. pes-tigridis* L., is found in the /Argyreinae clade (their clade 1), as a part of a grade leading toward the well-supported clade of *Argyreia* plus *Rivea*. This grade also includes some members of *Turbina* and several other *Ipomoea* species of Old World distribution, none of which form a sister group to *I. pes-tigridis*, making the decision of generic limits even more complicated. Also, in this "splitting" scenario, more than 500 New World *Ipomoea* species found in the /Astripomoeinae clade, on which most of the evolutionary and molecular genetics studies were conducted, would have to change names.

Clearly, a conflict exists between phylogenetic and pragmatic considerations in Ipomoeae nomenclature, similar to those encountered in *Caryopteris* (Lamiaceae) (Cantino et al. 1997) and *Phrymaceae* (Beardsley and Olmstead 2002). Within Ipomoeae, many species will need to be re-named to comply with the ICBN rules. A much simpler system would be one in which names were given to well-supported clades representing lineages thought to be taxonomically or evolutionarily important without arbitrary decisions about ranks (de

Queiroz and Gauthier 1992) and one in which species names were more stable (Cantino et al. 1999). As already indicated, redrawing generic boundaries within Ipomoeae is a large and difficult issue, and is beyond the scope of this paper. This task requires much more detailed taxon sampling, especially of Old World *Ipomoea* species, and should be taken into consideration by future treatments of spiny-pollen Convolvulaceae. However, we do provide definitions for two major clades recovered by molecular analyses within Ipomoeae (/Argyreinae and /Astripomoeinae, Fig. 1; see below).

We provide the following node-based clade definition: Ipomoeae are the least inclusive clade that contains *Ipomoea pes-tigridis* L. and *Astripomoea malvacea* (Klotzsch) A. D. J. Meeuse.

10. **Jacquemontieae** Stefanovic & Austin, tribus nov.—
Type: *Jacquemontia* Choisy

Tribus haec, inter tribus familiae Convolvulaceae Juss., habitu generali et morphologia vegetativa ad tribus Convolvuleae (Choisy) Choisy similis, sed fructus 8-valvatus, stigmata lingulata (non subulata), et trichomata stellata ab ea differt.

Plants herbaceous, vines. Leaf base usually cordate. Trichomes stellate. Flowers actinomorphic, bisexual. Sepals equal or unequal, non-acrescent. Filaments dilated, usually pubescent. Style one, entire. Stigmas elongated, flattened, tongue-shaped. Fruits dehiscent, capsule, usually 8-valvate. Pollen polycolpate, non-echinate, spheroidal.

Included genus: *Jacquemontia* Choisy (Americas, a few species in Asia and Australia).

As circumscribed here, the tribe Jacquemontieae is equivalent to *Jacquemontia*. The genus *Jacquemontia* was established by Choisy (1834), who segregated some species from *Ipomoea* and *Convolvulus* based on shapes of stigmatic lobes. This genus was regarded as a member of tribe Convolvuleae in all traditional circumscriptions of this tribe (see above) as well as in the most comprehensive revision of *Jacquemontia* (Robertson 1971) due to its undivided, filiform style with elongated stigmas. Therefore, the inclusion of *Jacquemontia* in the /Dicranostyloideae, the “bifid style” clade (Fig. 1), comes as one of the most unexpected results of the cpDNA study of Convolvulaceae (Stefanovic et al. 2002). Even though the defining morphological character, divided style, is not present in *Jacquemontia*, this genus was found to share a unique molecular synapomorphy with the rest of the /Dicranostyloideae clade, reversion to a nonedited start codon for the *psbL* gene (Stefanovic et al. 2002). This condition is not found anywhere else in Convolvulaceae and its closest relatives that have been sampled to date.

We provide the following stem-based clade defini-

tion: Jacquemontieae are the most inclusive clade that contains *Jacquemontia pentantha* (Jacq.) G. Don. but not *Maripa scandens* Aubl., *Cressa cretica* L., *Dichondra repens* J.R. Forst. & G. Forst., *Wilsonia humilis* R. Br., *Neuropeltis racemosa* Wall., *Itzaea sericea* (Standl.) Standl. & Steyerl., or *Dipteropeltis poranoides* Hall. f. This somewhat cumbersome definition is necessary in order to exclude a number of taxa with unresolved placement found within /Dicranostyloideae, while allowing for all *Jacquemontia* species to be included.

11. **MARIPEAE** Webb. & Berth., Nat. Hist. Can. Isl. 3. 2(3): 27 (1844).—Type: *Maripa* Aublet
Dicranostyleae Meisn. in Mart., Fl. Bras. 7: 205, 1869, pro parte
Dicranostyleae (Convolvuloideae) Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 14–18, 1893, pro parte
Argyreinae (Convolvuloideae) Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 14–18, 1893, pro parte
Lysiostyleae Roberty, Candollea 14: 42, 1952
Dicranostylinae (Meisn.) Ooststr., Fl. Males. 4: 389, 1953, pro parte

Plants woody, lianas. Leaf base not cordate. Flowers actinomorphic, bisexual. Sepals equal, non-acrescent. Filaments dilated, pubescent. Styles partially to completely divided, in some specimens fused all the way. Fruits indehiscent, ligneous baccate. Pollen 3-colpate, non-echinate.

Included genera: *Dicranostyles* Benth. (Central & South America), *Lysiostyles* Benth. (South America), *Maripa* Aublet (Central & South America).

Tribe Maripeae, comprising three genera restricted to Central and South America, includes the bifid-style taxa excluded from Erycibae sensu Austin (1973). Most species of *Dicranostyles* and *Maripa* have divided styles, and are found in the /Dicranostyloideae clade (Fig. 1; Stefanovic et al. 2002). This is also the predicted position for *Lysiostyles* (not sampled) endemic to Guyanas and Venezuela, which is morphologically and geographically close to *Dicranostyles* (Austin 1973). The monophyly of this tribe is strongly supported by available molecular analyses, but its relationship with other tribes and genera of the /Dicranostyloideae clade is uncertain (Fig. 1; Stefanovic et al. 2002; Stefanovic and Olmstead in press).

We provide the following stem-based clade definition: Maripeae are the most inclusive clade that contains *Maripa scandens* Aubl. and but not *Dichondra repens* J.R. Forst. & G. Forst., *Jacquemontia pentantha* (Jacq.) G. Don, or *Cressa cretica* L.

12. “**MERREMIEAE**” Austin, Fl. Venez. 8, Part 3: 16 (1982).—Type: *Merremia* Endl.

Plants herbaceous, vines. Leaf base usually cordate. Flowers actinomorphic, bisexual. Filaments dilated, usually pubescent. Styles entire. Stigmas globose. Fruits dehiscent, capsular, valvate to operculate. Pericarp chartaceous. Pollen 3-colpate or pantoporate, non-echinate.

Genera tentatively included: *Decalobanthus* Ooststr. (Sumatra), *Hewittia* Wight & Arn. (Africa, Asia), *Hyalocystis* Hall. f. (Africa), *Merremia* Dennst. (pantropical), *Operculina* S. Manso (pantropical), *Xenostegia* Austin & Staples (Africa, Asia, Australia).

Merremieae were treated initially as an informal assemblage of taxa, the "merremioids", and were formally recognized only recently (Austin 1982). This reflected the lack of defining morphological characters for this group which was defined as lacking some characters used to circumscribe other tribes (e.g., spiny pollen), rather than by their own putative synapomorphies. The notion of a monophyletic Merremieae sensu Austin (1982) was rejected by cpDNA (Stefanovic et al. 2002). Even after exclusion of a subset of genera circumscribed presently in tribe Aniseieae (see above) the tribe Merremieae s.s. seems not to be monophyletic. Globose stigmas characterize the remaining taxa assigned traditionally to tribe Merremieae but this feature is also found in the members of the Ipomoeae s.l. which appear to be nested within Merremieae s.s. (Fig. 1; Stefanovic et al. 2002). Some clades within this grade are supported. For example, *Xenostegia*, *Hewittia*, and *Operculina* form a moderately supported clade, as well as most of the *Merremia* species sampled (Stefanovic et al. 2002), but the relationships between them, as well as among these two clades and several *Merremia* segregates, are largely unresolved. However, the putative monophyly of Merremieae s.s. cannot be rejected at present. Thus, we retain this tribe, in its narrow sense, in the proposed classification, but we do not provide a clade definition until further data become available.

ADDITIONAL RECOGNIZED CLADES

/Convolvuloideae Clade. We provide the following node-based clade definition: /Convolvuloideae are the least inclusive clade that contains *Convolvulus arvensis* L., *Ipomoea pes-tigridis* L., and *Aniseia martinicensis* (Jacq.) Choisy. Judging from Hallier's (1893) illustration of intrafamilial relationships (his Figure on p. 586), this clade corresponds largely to the family branch composed of Convolvuleae and "Echinoconiae". This clade, comprising about 2/3 of Convolvulaceae species, was recovered as well-supported in both family-wide molecular analyses (Stefanovic et al. 2002; Stefanovic and Olmstead in press). Also, the backbone phylogenetic relationships within this clade are mainly resolved (Fig. 1). Given the size and morphological diversity contained in this large lineage, it is difficult to

find a single unifying morphological character supporting it. However, the following combination of characters is diagnostic for this clade: plants mainly herbaceous (except for the majority of /Argyreinae members, see below); predominantly cordate leaf base; cymes nearly always dichasial; corolla with five interpalpical veins; style single, undivided; and pollen grains of medium to large size ($\geq 50 \mu\text{m}$ in diam.).

/Argyreinae Clade. We provide the following stem-based clade definition: /Argyreinae are the most inclusive clade that contains *Argyria obtusifolia* Lour. but not *Astripomoea lachnosperma* (Choisy) A. D. J. Meeuse or *Ipomoea coccinea* L. The composition of this clade is discussed already (see tribe Ipomoeae), as well as the lack of defining morphological features for all of its members. However, this lineage, one of two major subclades of Ipomoeae s.l., was recovered and strongly supported by both nuclear (Manos et al. 2001; Miller et al. 2002) and chloroplast (Stefanovic et al. 2002) data, and merits, in our opinion, to be recognized and named. In addition, as discussed in more detail by Manos et al. (2001), there is a suite of morphological change associated with this clade. It includes species with diverse fruit type (dehiscent to indehiscent), but mostly with herbaceous sepal texture, uniformly puberulent or glabrous seed, and flat pollen tectum surface (Manos et al. 2001). Also, species found here are of predominantly woody habit. These noteworthy trends are helpful in identifying members of this clade from a morphological standpoint, but are not by any means shared by all of its species. The biogeographical pattern within /Argyreinae is equally complex (Manos et al. 2001), but most of its members are Old World in distribution.

/Astripomoeinae Clade. We provide the following node-based clade definition: /Astripomoeinae are the least inclusive clade that contains *Astripomoea lachnosperma* (Choisy) A. D. J. Meeuse and *Ipomoea coccinea* L. This clade, the second lineage within Ipomoeae s.l. (Manos et al. 2001; Stefanovic et al. 2002), in comparison to /Argyreinae, has a nearly uniform fruit type (2-locular dehiscent capsule), but varies significantly in sepal texture, seed pubescence, and pollen tectum surface (Manos et al. 2001). Members of this clade have a predominantly herbaceous habit, and are of New World distribution (except the small African genus *Astripomoea*).

/Dicranostyloideae Clade. We provide the following node-based clade definition: /Dicranostyloideae are the least inclusive clade that contains *Dicranostyles scandens* Benth., *Cressa cretica* L., and *Dichondra repens* J.R. Forst. & G. Forst. As defined here, this clade comprises taxa that have a more or less deeply divided style, generally following the concept of Dicranostyleae proposed by Hallier (1893). This "bifid style" clade was first explicitly identified by Stefanovic et al. (2002),

but support for its monophyly was not strong. Additional molecular data provided further evidence, not only for the monophyly of this clade, but also its composition (Stefanovic and Olmstead in press). The inclusion of *Jacquemontia* in the "bifid style" clade, although unexpected from a morphological viewpoint, was confirmed. Progressive fusion of styler branches was reported from several genera nested within /Dicranostyloideae. For example, some *Stylisma* species (Myint 1966) and some species of *Maripeae* (Austin 1973) have styles ranging from entirely separate to almost completely fused. However, the ancestral style type is thought to be with two free styler branches, and that from this condition a progressive fusion of branches has occurred (Austin 1973). In some cases this variation is evident within the same species having some flowers with either half-fused or completely fused styler branches. However, a divided style is not reported from any of 100–120 species of *Jacquemontia* (Robertson 1971). In addition, *Jacquemontia* differs from other members of /Dicranostyloideae by dichasial rather than monochasial cymes, cordate instead of mostly cuneate leaf base, and relatively large pollen grains, all of which are predominant characteristics of /Convolvuloideae (see above). However, all sampled *Jacquemontia* species share a unique synapomorphy with the rest of the /Dicranostyloideae, reversion to a nonedited start codon for the *psbL* gene (Stefanovic et al. 2002). This condition is not found anywhere else in Convolvaceae and its closest relatives. Given the strong support for monophyly of /Dicranostyloideae, including *Jacquemontia*, and unresolved relationships within this clade, one possible evolutionary scenario is that this genus is the sister group to the rest of the taxa with a divided style. This would account for a single event of reversion to nonedited *psbL* start codon among Convolvaceae and would explain the above-mentioned morphological differences as retention of plesiomorphic conditions in *Jacquemontia*. The definition of the /Dicranostyloideae clade, by virtue of not mentioning any *Jacquemontia* species, can accommodate such a scenario, and would apply in that case only to taxa with a bifid style. Alternatively, if *Jacquemontia* is found to be nested deeper within /Dicranostyloideae, the present definition would encompass this genus as well.

***Dichondrineae* Clade.** We provide the following node-based clade definition: /Dichondrineae are the least inclusive clade that contains *Dichondra repens* J.R. Forst. & G. Forst. and *Petrogenia repens* I. M. Johnst. This clade consists mostly of species assigned to traditional Dichondreae s.s. with the addition of the monotypic genus *Petrogenia*. Most species of tribe Dichondreae, unlike the rest of Convolvaceae, have deeply 2- or 4-lobed ovaries with the lobes united at the base and with gynobasic styles. This peculiarity was recognized

from the earliest treatments of the family, but the importance given to these features, and their taxonomic implications, differed greatly, ranging from tribe to family (Dichondraceae; Dumortier 1829). This assemblage is monophyletic in its traditional circumscription. The well-supported sister to this clade is *Petrogenia repens* (Stefanovic et al. 2002), an unexpected result given that this species was believed to be more closely related to some Cresseae genera (Johnston 1941) and was transferred to the heterogeneous genus *Bonamia* (Austin and Staples 1985). *Petrogenia* has styles attached terminally (as does *Nephrophyllum*, a traditional member of Dichondreae), but it shares a suite of characters with other Dichondreae s.s. species, otherwise unusual for Convolvaceae: prostrate, mat forming habit, rooting at the nodes, and reniform to elliptic, somewhat thickened, leaves. These features make the /Dichondrineae clade morphologically quite distinct and easily identifiable. Based on morphology (Demissew and Austin 1995), the monotypic East African endemic *Nephrophyllum*, not sampled in any molecular studies, is expected to be included in the /Dichondrineae, a clade with an African-American disjunct distribution.

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