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Phylogenetic Relationships Within Tribe Hibisceae (Malvaceae) Reveal Complex Patterns of Polyphyly in *Hibiscus* and *Pavonia*

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Abstract—The diverse and spectacular Hibisceae tribe comprises over 750 species. No studies, however, have broadly sampled across the dozens of genera in the tribe, leading to uncertainty in the relationships among genera. The non-monophyly of the genus *Hibiscus* is infamous and challenging, whereas the monophyly of most other genera in the tribe has yet to be assessed, including the large genus *Pavonia*. Here we significantly increase taxon sampling in the most complete phylogenetic study of the tribe to date. We assess monophyly of most currently recognized genera in the tribe and include three and thirteen newly sampled sections of *Hibiscus* and *Pavonia*, respectively. We also include five rarely sampled genera and 137 species previously unsampled. Our phylogenetic trees demonstrate that *Hibiscus*, as traditionally defined, encompasses at least 20 additional genera. The status of *Pavonia* emerges as comparable in complexity to *Hibiscus*. We offer clarity in the phylogenetic placement of several taxa of uncertain affinity (e.g. *Helicteropsis*, *Hibiscadelphus*, *Jumelleanthus*, and *Wercklea*). We also identify two new clades and elevate them to the generic rank with the recognition of two new monospecific genera: 1) *Blanchardia* M.M.Hanes & R.L.Barrett is a surprising Caribbean lineage that is sister to the entire tribe, and 2) *Astrohibiscus* McLay & R.L.Barrett represents former members of *Hibiscus caesioides* s.l. *Cravenia* McLay & R.L.Barrett is also described as a new genus for the *Hibiscus panduriformis* clade, which is allied to *Abelmoschus*. Finally, we introduce a new classification for the tribe and clarify the boundaries of *Hibiscus* and *Pavonia*.

Keywords—large genera.

Malvaceae Juss. subfamily Malvoideae Burnett (Malvaceae sensu stricto) has been the subject of considerable attention in molecular phylogenetic studies (e.g. La Duke and Doebley 1995; Alverson et al. 1999; Bayer et al. 1999; Pfeil et al. 2002; Baum et al. 2004; Pfeil and Crisp 2005; Tate et al. 2005; Koopman and Baum 2008; Areces-Berazaín and Ackerman 2016, 2017). As a result, the limits of subfamily Malvoideae (/Eumalvoideae) have been substantially clarified resulting in the recognition of three tribes, Gossypieae Alef., Malveae J.Presl, and Hibisceae Reichenbach s.l., which are respectively monophyletic (Seelanan et al. 1997; Pfeil et al. 2002; Tate et al. 2005). Six tribes have traditionally been recognized, but phylogenetic work has demonstrated that Decaschisteae Fryxell (1975), Kydieae Bates (1968), and Malvavisceae K.Presl (1835; formerly Ureneae Bentham and Hooker) are all embedded in Hibisceae, and indeed within the genus *Hibiscus* L. s.l. (Pfeil et al. 2002; Bayer and Kubitzki 2003; Pfeil and Crisp 2005). The Australasian genera *Camptostemon* Mast., *Howittia* F.Muell., *Lagunaria* (DC.) Rchb., and *Radyera* (F.Muell.) Fryxell & S.H.Hashmi (also African), all previously placed in the Hibisceae tribe, are instead the earliest diverging taxa in/Eumalvoideae (Pfeil et al. 2002; Baum et al. 2004). Relatively

comprehensive summaries now exist for tribe Malveae (Tate et al. 2005) and tribe Gossypieae (Seelanan et al. 1997; Areces-Berazaín and Ackerman 2016). Tribe Hibisceae, however, remains understudied and no phylogenetic work has included dense sampling across the extraordinary diversity of the tribe.

Hibisceae is the second largest tribe in/Eumalvoideae. Fryxell (1968) provided a provisional list of 53 genera belonging to the residual Hibisceae. Workers in the ensuing half-century have brought much clarity to that list (Table 1). Some authors have pared it down, due to some exclusions (e.g. *Alyogyne* Alef., *Camptostemon*, *Cumingia* S.Vidal, *Howittia*, *Lagunaria*, *Macrocalyx* Costantin & Poiss., *Pariti* Adans., *Petitita* Neck., *Radyera*) and extensive synonymizations (Table 2). But the list has also expanded through the addition of newly described genera (e.g. *Roifia* Verdc., *Talipariti* Fryxell, *Thepparatia* Phuph., *Woodianthus* Krapov.) and of genera, old and new, of the former Decaschisteae, Kydieae, and Malvavisceae. While membership in the list remains fluid (Pfeil and Crisp 2005), current estimates suggest that the tribe comprises at least 750 species in about 30 genera (Table 1; our estimates; Bayer and Kubitzki 2003; Areces-Berazaín and Ackerman 2017).

TABLE 1. Current list of genera of Hibisceae. Updated from Fryxell (1968), Bayer and Kubitzki (2003), POWO (2022), and more recent publications. Genera in bold are sampled here, number of species sampled here are in parentheses.

Genus	Year	Species number following Bayer and Kubitzki 2003 or recent update (species sampled here)	Major clade (recovered here)
<i>Abelmoschus</i> Medik.	1787	6–15 (3)	/Trionum
<i>Cenocentrum</i> Gagnep.	1909	1 (1)	/Trionum
<i>Fioria</i> Mattei	1917	1 (1)	/Trionum
<i>Hibiscadelphus</i> Rock	1911	8 (1)	/Calyphylli
<i>Hibiscus</i> L.	1753	300–430 (118)	/Caesius, /Calyphylli, /Clypeati, /Euhibiscus, /Megistohibiscus, /Phylloglandula, /Trionum
<i>Humbertiella</i> Hochr.	1926	6 (4)	/Megistohibiscus
<i>Jumelleanthus</i> Hochr.	1924	1 (1)	/Megistohibiscus
<i>Kosteletzkya</i> C. Presl.	1835	17 (16)	/Trionum
<i>Megistostegium</i> Hochr.	1916	3 (3)	/Megistohibiscus
<i>Papuodendron</i> C.T.White	1946	2	/Phylloglandula
<i>Perrierophytum</i> Hochr.	1916	15 (8)	/Megistohibiscus
<i>Roiffia</i> Verdc.	2009	1	/Trionum
<i>Senra</i> Cav.	1786	3 (1)	/Trionum
<i>Symphyochlamys</i> Gürke	1903	1	/Trionum
<i>Talipariti</i> Fryxell	2001	23 (5)	/Phylloglandula
<i>Thepparatia</i> Phuph.	2019	1	/Trionum
<i>Wercklea</i> Puttner & Standl.	1916	13 (4)	/Trionum
Former Decaschisteae:			
<i>Decaschistia</i> Wright & Arn.	1834	18 (2)	/Phylloglandula
<i>Dicelostyles</i> Benth.	1862	1	/Phylloglandula
<i>Julostylis</i> Thw.	1858	3	/Phylloglandula
<i>Nayariophyton</i> T.K. Paul	1988	1	/Phylloglandula
Former Kydieae:			
<i>Kydia</i> Roxb.	1811	2 (2)	/Phylloglandula
Former Malvavisceae:			
<i>Anotea</i> (DC.) Kunth	1846	1 (1)	/Trionum
<i>Malachra</i> L.	1767	8–10 (6)	/Trionum
<i>Malvaaviscus</i> Fabr.	1759	4 (4)	/Trionum
<i>Pavonia</i> Cav.	1787	300 (51)	/Trionum
<i>Peltaea</i> (C.Presl) Standl.	1916	16 (4)	/Trionum
<i>Phragmocarpidium</i> Krapov.	1969	1	/Trionum
<i>Rojasimalva</i> Fryxell	1984	1	/Trionum
<i>Urena</i> L.	1753	6–8 (3)	/Phylloglandula
Uncertain affiliation:			
<i>Woodianthus</i> Krapov.	2012	1	unknown
<i>Bombycidendron</i> Zoll. & Mor.	1845	3	unknown

TABLE 2. Synonymizations of names included in Fryxell's (1968) list of Hibisceae (or updated more recently).

<i>Bamia</i> R. Br. ex Wall.	=	<i>Abelmoschus</i> Medik.
<i>Bombycella</i> Lindl.	=	<i>Hibiscus</i> L.
<i>Brockmania</i> W.V. Fitzg.	=	<i>Hibiscus</i> L.
<i>Cotylopecta</i> Alef.	=	<i>Hibiscus</i> L.
<i>Erebennus</i> Alef.	=	<i>Abelmoschus</i> Medik.
<i>Furcaria</i> Kostel.	=	<i>Hibiscus</i> L.
<i>Hymenocalyx</i> Zenk.	=	<i>Abelmoschus</i> Medik.
<i>Ketmia</i> Mill.	=	<i>Hibiscus</i> L.
<i>Laguna</i> Cav.	=	<i>Abelmoschus</i> Medik.
<i>Humbertianthus</i> Hochr.	=	<i>Macrostelia</i> Hochr. (see Koopman and Baum 2008; Hanes et al. 2020)
<i>Macrostelia</i> Hochr.	=	<i>Hibiscus</i> L. (see Craven and Pfeil 2004; Hanes et al. 2020)
<i>Neohumbertiella</i> Hochr.	=	<i>Humbertiella</i> Hochr. (see Dorr 1990)
<i>Papuodendron</i> C.T. White	=	<i>Hibiscus</i> L. (see Van Heel 1972)
<i>Pariti</i> Adans.	=	nomen superfluum (see Fryxell 2001)
<i>Pentagonocarpus</i> Parl.	=	<i>Kosteletzkya</i> Presl
<i>Petitita</i> Neck.	=	nom. inval., suppressed name
<i>Polychlaena</i> Garcke	=	<i>Kosteletzkya</i> Presl
<i>Pseudopavonia</i> Hassl.	=	<i>Pavonia</i> Cav.
<i>Sabdariffa</i> Kostel.	=	<i>Hibiscus</i> L.
<i>Solandra</i> Murr. (nom. rej.)	=	<i>Hibiscus</i> L.
<i>Symphyochlamys</i> Gürke	=	<i>Hibiscus</i> L. (<i>S. erlangeri</i> Gürke = <i>H. erlangeri</i> ; see Thulin 1999a)
<i>Triguera</i> Cav.	=	<i>Hibiscus</i> L. (<i>T. acerifolia</i> Cav. = <i>H. lobatus</i>)
<i>Trionum</i> L.	=	<i>Hibiscus</i> L.
<i>Wilhelmia</i> Hochr.	=	<i>Hibiscus</i> L. (see Van Borssum Waalkes 1966)

Though tribe Hibisceae has been resolved as monophyletic, that is where the clarity ends for this large and complex group. Cytological and genomic sequencing efforts in Hibisceae have revealed complex patterns of polyploidy and genome evolution throughout the tribe (Singh and Khoshoo 1970; Menzel et al. 1983; Kim et al. 2017; Eriksson et al. 2021). Furthermore, no morphological synapomorphies exist for Hibisceae (Pfeil et al. 2002). Instead, the plesiomorphic presence of apical teeth on the staminal column (also in Gossypieae) and branching styles (also in Malveae) distinguish species of Hibisceae from Gossypieae or Malveae (Figs. 1–2; Pfeil et al. 2002). Phylogenetic relationships and taxonomy within tribe Hibisceae is made further challenging because the genus *Hibiscus* is non-monophyletic (e.g. Pfeil et al. 2002; Pfeil and Crisp 2005; Koopman and Baum 2008). Some genera that were long suspected to belong in *Hibiscus* are indeed embedded within the genus; e.g. *Abelmoschus* Medik., *Cenocentrum* Gagnep., *Fioria* Mattei, *Kosteletzkya* C.Presl., *Macrostelia* Hochr., and *Talipariti* (Craven and Pfeil 2004; Koopman and Baum 2008; Blanchard 2012; Neubig et al. 2015; Hanes et al. 2020). But other taxa found to be embedded within *Hibiscus* are more surprising, like *Decaschistia* Wight & Arn., *Pavonia* Cav., *Urena* L., and genera endemic to Madagascar like *Humbertiella* Hochr., *Megistostegium* Hochr., and *Perrierophytum* Hochr. (though the genera on Madagascar have been proposed to be excluded from *Hibiscus*, Pfeil and Crisp 2005). The work of Koopman and Baum (2008) suggested that these Madagascar endemic genera (clade/Megistohibiscus) are sister to the remainder of tribe Hibisceae.

Hibiscus is the largest genus in tribe Hibisceae (ca. 300–430 species; Pfeil et al. 2002; Bayer and Kubitzki 2003; POWO 2022) and was last systematically revised as a whole by Hochreutiner (1900). The genus has traditionally been defined by the coincident presence of seven morphological features: 5 apical teeth at the apex of the staminal column, a 5-branched style, calyx and epicalyx (if present) remain after flowering, epicalyx with (7–)8 or more lobes, petals fused to the base of the staminal column, styles that are apically branching, ovary with at least 2 ovules per cell, and 5–10-celled dehiscent, wingless, capsule (Pfeil et al. 2002). The genus currently encompasses about 30 sections (Table 3).

In a study pointedly entitled in part “What to do with *Hibiscus*?” Pfeil and Crisp (2005) further articulated the problem of a polyphyletic *Hibiscus*. They recommended expanding *Hibiscus* to encompass the smallest clade that includes all *Hibiscus* species. In order to minimize nomenclatural changes and at the same time conform to the constraints of their phylogenetic results they proposed a ‘hybrid classification’ in which *Hibiscus* is expanded to absorb all of the genera in the Hibisceae clade except for a group of species from Madagascar (Pfeil and Crisp 2005; Koopman and Baum 2008). This expanded *Hibiscus* was then coarsely subdivided into informal, named, unranked, and subordinate clades. Under this scheme no exclusive morphological synapomorphies remain for the genus: e.g. *Abelmoschus* has a deciduous calyx, *Kosteletzkya* has winged capsules, and *Cenocentrum*, *Decaschistia*, and *Urena* have 8–10 style branches (Fig. 2). While this treatment proposed a potential solution to the issue of polyphyly of *Hibiscus*, it did not create an easy-to-apply taxonomy for the tribe.

Pfeil and Crisp (2005) sampled about 85 species in tribe Hibisceae, including about 70 species nominally belonging to *Hibiscus* and representing a dozen sections of the genus. Five

sampled sections had three or more species represented and the remaining sections one or two. At least eight sections of *Hibiscus* were unsampled. Pfeil and Crisp (2005) further included one or two representative species from fourteen additional genera within the tribe. Of note, their sampling included only two species of *Pavonia*, even though it has been suggested to be one of the largest genera in the family (Fryxell 1999). With about 250–300 species (Grings and Boldrini 2012; POWO 2022), *Pavonia* rivals *Hibiscus* in its species richness and numerically exceeds all other genera in the tribe by an order of magnitude. To our knowledge, only six species of *Pavonia* have ever been sampled in molecular phylogenetic studies (La Duke and Doebley 1995; Alverson et al. 1999; Pfeil et al. 2002; Baum et al. 2004; Koopman and Baum 2008; Areces-Berazaín and Ackerman 2016) and no Old World species have been included. While the phylogenetic hypotheses presented in Pfeil and Crisp (2005) represent an excellent framework, the trees lack both important sampling throughout the tribe and phylogenetic resolution.

The proposal of Pfeil and Crisp (2005) avoided breaking up *Hibiscus* (one of the options that their results offered) in part because the genus includes several popular and cultivated species. Indeed, *Hibiscus* and related genera represent a very iconic group of plants with great horticultural, agricultural, and cultural significance in many parts of the world (Magdalena and San Pascual 2022). Among these are fiber plants (e.g. *Hibiscus cannabinus* L.) and ornamentals (e.g. *Hibiscus rosa-sinensis* L., *H. schizopetalus* (Mast.) Hook.f., *H. moscheutos* L., *H. mutabilis* L., *H. syriacus* L., and *Malvaviscus penduliflorus* DC.). The large, often brightly colored flowers are naturally attractive. A number of horticulturally significant species are readily amenable to cultivation in a wide variety of environments and have been very widely grown for thousands of years (Singh and Nigam 2017). Okra (the fruit of three *Abelmoschus* species) has significant popularity as a vegetable and is cultivated throughout the tropics (Yildiz et al. 2016). Roselle (*Hibiscus sabdariffa* L.) is another important food plant, the fleshy calyxes being used to make jam and beverages, and the green capsules providing a source of pectin (Islam 2019). Many members of tribe Hibisceae are utilized in traditional medicine and there is a vast literature surrounding their uses and applications (Vasudeva and Sharma 2008). With this in mind, taxonomic decisions impacting these names should not be taken lightly.

Pfeil and Crisp (2005) further supported their decision in favor of an expanded *Hibiscus* based in part on an erroneously low species estimate of *Pavonia* (Pfeil and Crisp suggest “somewhat over 200” species of *Pavonia*), as well as their uncertainty about the monophyly of the latter. Additionally, despite the size of the genus, *Pavonia* has only three or four species of minor importance in the horticultural trade and none of major economic importance (Fryxell 1999). Perhaps that is why *Pavonia* was accorded less significance than *Hibiscus*.

Pavonia has centers of diversity both in the New World and in Africa. The genus was revised for the New World by Fryxell (1999; 224 species) and additional novelties since then bring the total to about 245 species (Esteves 1998a, 1998b, 2001; Fryxell 2009; Krapovickas 2010a, 2010b, 2010c, 2012a; Grings et al. 2011; Grings and Boldrini 2012; Wood 2013; González et al. 2017). Old World *Pavonia* was revised (for Africa) by Ulbrich in 1920–21, and workers over the ensuing century have added new species and new interpretations to

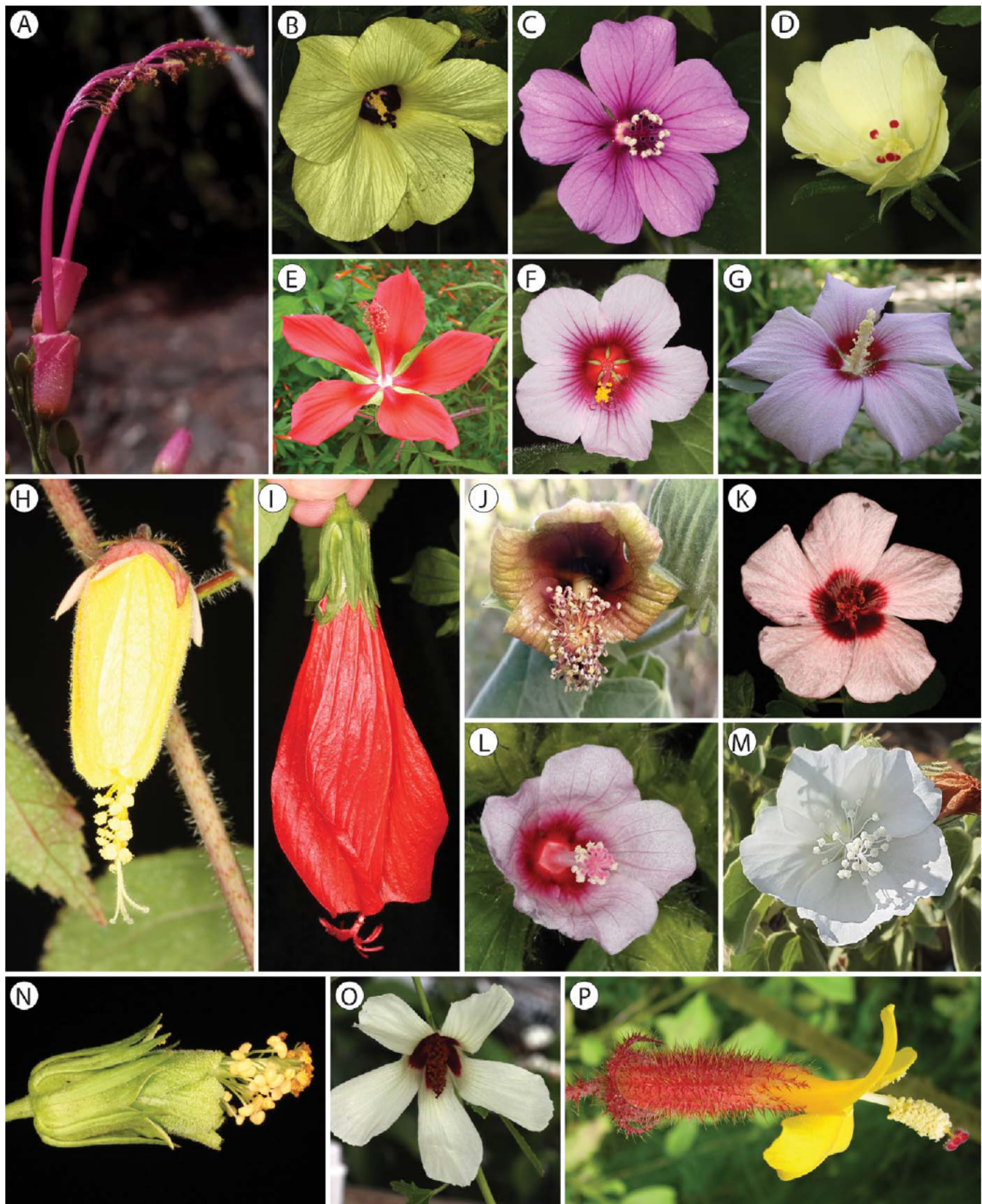


FIG. 1. Diversity of floral morphology in Tribe Hibisceae. A. *Hibiscus microsiphon* Baill. (image F. Rahaingoson; iNat_16988837). B. *Abelmoschus* sp. C. *Perrierophytum macranthum* (Hochr.) M.M. Hanes & Callm. D. *Hibiscus citrinus* Fryxell. E. *Hibiscus coccineus* Walter. F. *Kosteletzkya begoniifolia* (Ulbr.) Ulbr. G. *Hibiscus syriacus* L. H. *Kosteletzkya tubiflora* (Moc. & Sessé ex DC.) O.J. Blanch. & McVaugh. I. *Malva viscus penduliflorus* Moc. & Sessé ex DC. J. *Blanchardia clypeata* (L.) M.M. Hanes & R.L. Barrett [= *Hibiscus clypeatus* L.] (image G. H. Sosa-Tovar; iNat_105036151). K. *Pavonia hastata* Cav. L. *Malachra radiata* (L.) L. M. *Pavonia dentata* Burt Davy (image Joan; iNat_77733207). N. *Pavonia bahamensis* Hitchc. O. *Hibiscus aculeatus* Roxb. P. *Wercklea ferox* (Hook.) Fryxell. All images by K. Neubig unless otherwise stated.

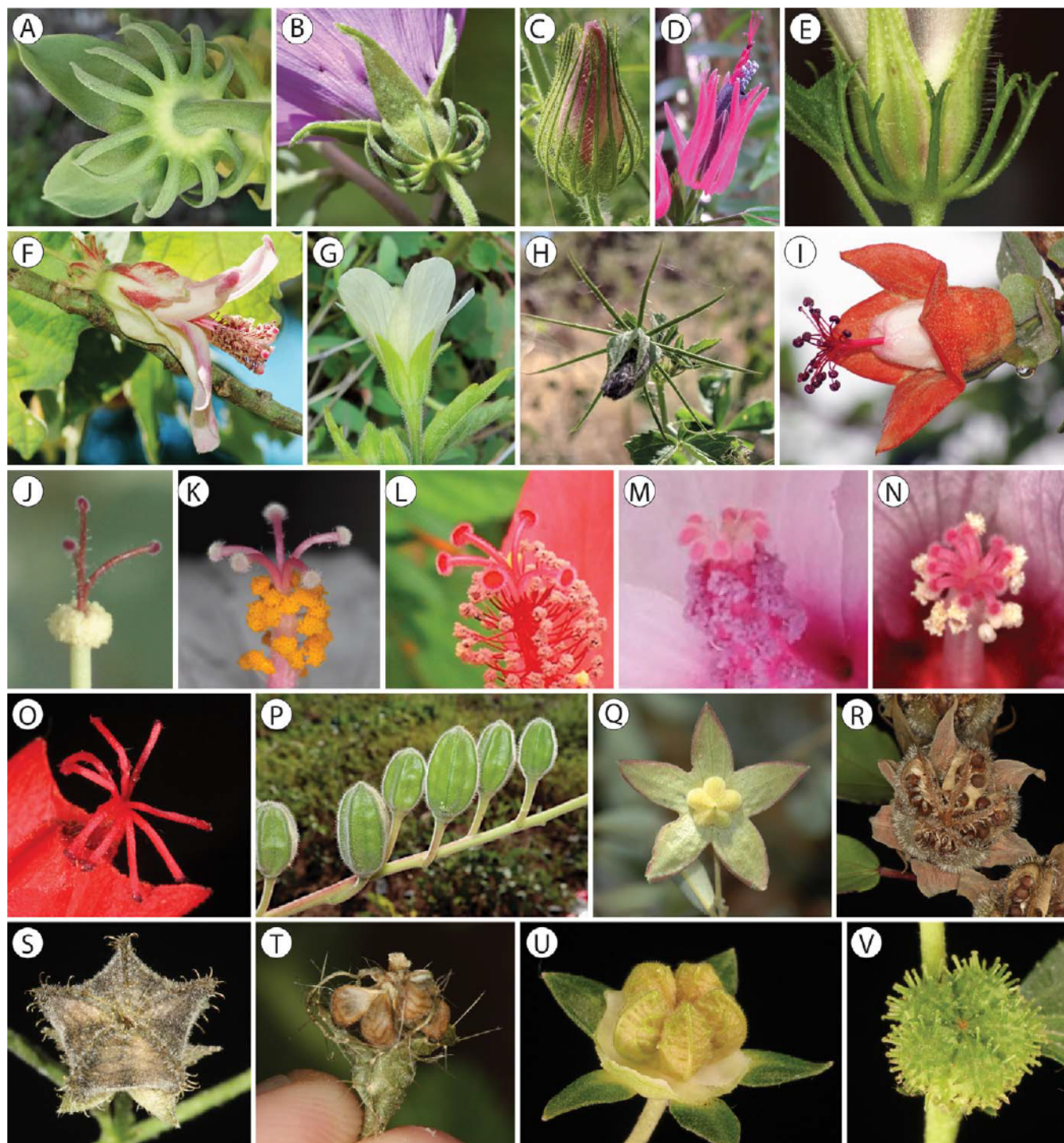


FIG. 2. Diversity in epicalyx features (A–I), style number (J–O), and fruit (P–V) in Tribe Hibisceae. A–F have 10 or more epicalyx lobes. A. *Hibiscus moscheutos* L. (image M. Hanes). B. *Hibiscus leptocladus* Benth. (image K. Brennan). C. *Pavonia clathrata* Mast. (image L. Schwarz; iNat_107754483). D. Highly colored epicalyx: *Pavonia multiflora* A.St-Hil. (image K. Neubig). E. *Hibiscus aculeatus* (image K. Neubig). F. Reflexed epicalyx: *Hibiscus macrogonus* Baill. (image M. Hanes). G. Highly reduced epicalyx lobes: *Hibiscus lobatus* (Murray) Kuntze (image M. Girdhari; iNat_95273564). H. 8–9 filiform epicalyx lobes: *Astrohibiscus caesius* (Garcke) McLay & R.L.Barrett [= *Hibiscus caesius* Garcke.] (image T. McLay). I. Four red epicalyx lobes: *Megistostegium microphyllum* Hochr. (image M. Hanes). J. 3 styles: *Humbertiella quamrubeoides* Hochr. (image M. Hanes). K. 5 styles: *Kosteletzkya begoniifolia* (image K. Neubig). L. 5 styles: *Hibiscus coccineus* (image K. Neubig). M. 10 styles: *Urena lobata* L. (image T. McLay). N. 10 styles: *Malachra radiata* (image K. Neubig). O. 10 styles: *Malva viscosa* (image K. Neubig). P. Fleshy capsule: *Abtelmoschus ficulneus* (L.) Wight & Am. (image M. Fagg, Australian Plant Image Index, <https://www.arb.gov.au/photo/>). Q. Capsule with accrescent calyx: *Humbertiella tormeyana* Dorr. (image M. Hanes). R. Woody capsule: *Hibiscus moscheutos* (image M. Hanes). S. Capsule with prominent hairs/wings on sutures: *Kosteletzkya depressa* O.J.Blanch., Fryxell & D.M.Bates (image K. Neubig). T. Schizocarp: *Malachra urens* Poit. ex Ledeb. (image K. Neubig). U. Schizocarp: *Pavonia hastata* (image K. Neubig). V. Uncinate schizocarp: *Urena lobata* (image K. Neubig).

TABLE 3. Current sectional classification of *Hibiscus* L. Numbers of species currently assigned to each section are shown in parentheses. Sections in bold are sampled here.

<i>Aristivalvus</i> Ulbr. (1)	
<i>Azanzae</i> DC. (35 (23 now in <i>Talipariti</i> ; ~12 <i>Hibiscus</i> on Madagascar))	
<i>Bombicella</i> DC. (c. 130)	<i>Bombicella</i> s.s. Fryxell (70), including subsect. <i>Africanae-lobophyllae</i> Ulbr.
<i>Bombicella</i> segregates	sect. <i>Eubombicella</i> Ulbr. (44)
<i>Bombicella</i> segregates	subsect. <i>Syriaca</i> Ulbr. (17)
<i>Bombicella</i> segregates	
<i>Bombycidendron</i> (Zoll. & Moritz) Borss.Waalk. (3)	
<i>Calyphylli</i> Ulbr. (8)	
<i>Clypeati</i> O.J. Blanch. (1)	
<i>Columnaris</i> Hochr. (2)	
<i>Furcaria</i> DC. (c. 120)	
<i>Gigantocalyx</i> Ulbr. (1)	
<i>Hibiscus</i> L. (3)	
<i>Ketmia</i> (Mill.) DC. (c. 30) =sect. <i>Hibiscus</i>	
<i>Lilibiscus</i> Hochr. (23)	
<i>Panduriformes</i> Ulbr. (7)	
<i>Pterocarpus</i> Garcke (1)	
<i>Solandra</i> (Murr.) Hochr. (9)	
<i>Spatula</i> Hochr. (c. 11)	
<i>Trionastrum</i> Griseb (c. 4)	
<i>Trichospermum</i> Hochr. (5)	
<i>Trionum</i> (L.) DC. (10)	<i>Trionum</i> s.s. (L.) DC. (2)
<i>Trionum</i> segregates	<i>Clypeati</i> O.J. Blanch. (1)
<i>Trionum</i> segregates	<i>Straiti</i> O.J. Blanch. (2)
<i>Trionum</i> segregates	<i>Muenchusia</i> (Heist. ex Fabr.) O.J. Blanch. (5)
<i>Trionum</i> segregates	
<i>Venusti</i> Ulbr. (c. 7)	

arrive at about 50 species (Burt-Davy 1926; Chiovenda 1932; Hauman 1961; Meeuse 1961; Thulin 1985, 1999b; Brummitt and Vollesen 2006; Verdcourt 2007; Verdcourt and Mwachala 2009; Welcome and Victor 2022). Only about seven of the Old World species do not occur in Africa (Ulbrich 1920–21; Abedin 1979; Paul 1993). An overview of the subgenera and sections in *Pavonia*, plus the number of species in each of the sections, is provided in Table 4.

In the present study we bring together 238 species (31%) of Hibisceae, including more than 50 species of *Pavonia*, in an updated molecular phylogeny of the tribe. We also add

samples of five rarely sampled genera of Hibisceae, three sections of *Hibiscus* (*H.* sects. *Clypeati* O.J. Blanch., *Aristivalvus* Ulbr., and *Trionastrum* Griseb.) and over a dozen sections of *Pavonia* that have never been included in a phylogeny. Finally, we add more than 60 previously unsampled species from almost twenty sections of *Hibiscus*. This increased depth of sampling enables firmer conclusions about generic integrity and relationships within the tribe. We also note several significant revelations emerging from this enhanced phylogeny and summarize a new classification for the tribe.

TABLE 4. Current subgeneric and sectional classification of *Pavonia* Cav. Numbers of species currently assigned to each section are shown in parentheses. Sections in bold are sampled here. The African sections *Craspedocarpidium* and *Pterocarpidium*, and the New World sections *Collicolae* and *Lebretonia*, have been further subdivided into subsections that are not shown here.

New World		Old World	
(Fryxell 1999)		(Ulbrich 1920–21, Africa only)	
Subgenus	Section	Subgenus	Section
<i>Pavonia</i>	<i>Pavonia</i> (15) <i>Lopimia</i> (Mart.) Endl. (26) <i>Cancellaria</i> DC. (4) <i>Malvaviscoides</i> A.St.-Hil. (20) <i>Lebretonia</i> (Schrank) Endl. (64)	<i>Pavonia</i>	<i>Afrolopimia</i> Ulbr. (1) <i>Afrolebretonia</i> Ulbr. (10) <i>Columella</i> Ulbr. (1) <i>Praemorsa</i> Ulbr. (1) <i>Callicarpidium</i> Ulbr. (4) <i>Craspedocarpidium</i> Ulbr. (9) <i>Pterocarpidium</i> Ulbr. (10) <i>Pseudohibiscus</i> Ulbr. (3) <i>Afrotyphalea</i> Ulbr. (5)
<i>Typhalea</i> (DC.) Ulbr.	<i>Typhalea</i> (9) <i>Urenoideae</i> A.St.-Hil. (20) <i>Diathericae</i> Fryxell (1) <i>Carcerariae</i> Fryxell (3) <i>Varians</i> Fryxell (1)	<i>Typhalea</i> (DC.) Ulbr.	
<i>Asterochlamys</i> Fryxell	<i>Asterochlamys</i> Fryxell (31) <i>Albae</i> Fryxell (3)		
<i>Malache</i> (B.Vogel) Fryxell	<i>Malache</i> (B.Vogel) Fryxell (4) <i>Collicolae</i> Fryxell (13) <i>Laminares</i> Fryxell (1)		
<i>Goetheoides</i> (Gürke) Ulbr.	<i>Goetheoides</i> Gürke (29)		

MATERIALS AND METHODS

Taxon Sampling—Pfeil et al. (2002) provided a synopsis of sectional classifications of *Hibiscus* s.l. and to the extent that there is overlap with our sampling we have used this and the named major clades (preceded by a/) of Pfeil and Crisp (2005). We further follow conventional sectional and generic names of taxa for the sake of convenience and familiarity. Substantial effort was made to emphasize genera of Hibisceae that have been absent or poorly represented in previous phylogenetic studies, including *Pavonia*, *Malachra* L., *Peltaea* (C.Presl) Standl., *Cenocentrum*, *Wercklea* Pittier & Standl., and *Hibiscadelphus* Rock (but see Areces-Berazaín and Ackerman 2017; Champion 2020). Here we sample all but eleven of 32 genera in the tribe (Table 1); seven of these unsampled genera are monospecific, and the remaining genera have two to three species each. In *Hibiscus* we consider *H.* sects. *Aristivalvus*, *Clypeati*, and *Trionastrium* as newly sampled. Though *H. clypeatus* L. (*H.* sect. *Clypeati*) is included in a general phylogenetic survey of malvaceous fruit types in Areces-Berazaín and Ackerman (2017) and more recently in Champion (2020), this species was not specifically commented upon, so it is treated here as “new” for our much more phylogenetically-focused purposes. *Hibiscus* sects. *Bombycidendron* (Zoll. & Moritz) Borss.Waalk. (3 spp.) and *Gigantocalyx* Ulbr. (1 sp.) remain unsampled by us, and *H.* sect. *Parapavonia* Ulbr. is a superfluous name for *H.* sect. *Adenosiphon* Ulbr., now correctly in *Kosteletzkya*, with both of its species (*K. grantii* (Mast.) Garcke and *K. begoniifolia* Ulbr.) having been sampled by us. In *Pavonia* we sample representatives from all recognized subgenera and 18 (of 25) sections, 13 of these sections and 47 species have never been sampled before.

We further aimed to sample from across the globe and greatly increase sampling from Australia and Africa. Finally, whenever possible, any previously unsampled species of Hibisceae were added. Outgroup taxa were chosen to represent tribes closely related to Hibisceae based on previous phylogenetic work (La Duke and Doebley 1995; Pfeil et al. 2002; Baum et al. 2004; Koopman and Baum 2008) and these include representatives from Gossypieae, Malveae, *Hovittia*, *Lagunaria*, and *Radyera*, along with *Guazuma* Mill. included as a more distant outgroup (Malvaceae subfamily Byttnerioideae Bumett).

Several approaches were used to obtain high quality DNA for this study. First, seeds were obtained from wild-collected plants under appropriate permits or greenhouse-grown descendants of these plants, and then grown for tissue to be used for DNA extraction and vouchers. These samples are represented by extensive collections made by Blanchard (Appendix 1). All freshly collected material, collected with appropriate permits, was preserved in silica gel (Chase and Hills 1991). Second, we sampled directly from herbarium specimens from the following herbaria: Missouri Botanical Garden Herbarium (MO), University of Florida Herbarium (FLAS), Australian National Herbarium (CANB), and Western Australian Herbarium (PERTH).

Our final dataset contains 300 samples in tribe Hibisceae representing 21 genera and includes 118 species in *Hibiscus* (19 sections) and 51 species in *Pavonia* (18 sections).

DNA Extraction, Amplification, and Sequencing—Genomic DNA was extracted using a modified CTAB technique (Doyle and Doyle 1987), scaled to a 1.5 mL volume reaction. Approximately 10 mg of dried tissue were ground in 1.5 mL of CTAB 2 × buffer and 100 µg of proteinase-K. After incubating at 55°C for 2 hr, samples were purified first with 24:1 chloroform/isoamyl alcohol, followed by a silica-column purification directly from the aqueous supernatant using Qiagen DNeasy reagents (Neubig et al. 2014).

Most samples were sequenced with typical Sanger sequences and are indicated as “sanger” in Appendix 1. Several sequences were obtained from GenBank either for particular loci or incorporated from available whole plastomes. The annotated genomes were imported into Geneious Prime (BioMatters, New Zealand), and the relevant loci were extracted from each genome. All of these samples are indicated in Appendix 1 as “from GenBank.” For some samples, chloroplast loci were assembled from genome skim libraries; these samples are identified in Appendix 1 as “skim” (see methods below for details).

Four chloroplast loci were amplified: *matK*, *ndhF*, *trnQ-rps16*, and *ycf1*. These loci were chosen based on previous evidence demonstrating relatively high nucleotide variation (i.e. Shaw et al. 2007; Koopman and Baum 2008; Neubig et al. 2015). Amplification and sequencing primers are listed in Table 5. Amplifications were performed using a Biometra TGradient or an Eppendorf Mastercycler EP Gradient S thermocycler and reagents in 25 µL volumes. All regions were amplified using Jumpstart™ (Sigma) reagents: 0.5–1.0 µL template DNA (~10–100 ng), 17.5 µL water, 2.5 µL 10 × buffer, 2.0–2.5 µL MgCl₂ (25 mM), 0.5 µL of 10 µM dNTPs, 0.5 µL each of 10 µM primers, and 0.5 units *Taq*. For *ycf1*, *matK*, and *ndhF*, samples were amplified with varying primer combinations because of differences in sequence quality and thus amplifiable fragment lengths.

The *trnQ-rps16* intergenic spacer was amplified with the parameters 94°C, 3 min; 30×(94°C, 45 s; 58°C, 45 s; 72°C, 1 min); 72°C, 3 min. All other loci were amplified with the parameters 94°C, 3 min; 8×(94°C, 30 s; 60°C, 1 min, reducing 1°C per cycle; 72°C, 2 min 30 s); 30×(94°C, 30 s; 50°C, 45 s; 72°C, 2 min 30 s); 72°C, 3 min.

Purified cycle sequencing products were directly sequenced on an ABI 3130 automated sequencer according to the manufacturer’s protocols (Applied Biosystems, Foster City, California) at the University of Florida Interdisciplinary Center for Biotechnology Research. All PCRs were sequenced bidirectionally. Electropherograms were edited and assembled using Sequencher 4.9™ (GeneCodes, Ann Arbor, Michigan). All sequences were deposited in GenBank (Appendix 1) and data sets were deposited in Dryad (Hanes et al. 2023).

For the sequences derived from genome-skimming data (“skim”), genomic DNA was extracted using a modified CTAB protocol including a pre-wash buffer with sorbitol (Inglis et al. 2018). Genomic libraries were prepared following the method in Fowler et al. (2020), and sequencing was performed on a NextSeq 500 for 2 × 150 bp paired-end reads (Biological Resource Facility, Canberra, Australia). Reads were trimmed using

TABLE 5. Primers used in this study and the associated papers from which they were obtained.

Locus/primer	Primer sequence	Reference
<i>matK</i>		
–19F	CGTTCTGACCATATTGCACTATG	Molvray et al. (2000)
3F	CGTACAGTACTTTTGTTTACGAG	Fazekas et al. (2012)
1R	ACCCAGTCCATCTGGAAATCTTGGTTC	Fazekas et al. (2012)
<i>trnK2R</i>	ACCTAGTCGGATGGAGTAG	Johnson and Soltis (1994)
<i>ndhF</i>		
1F	GAATATGCATGGATCATACC	Schnabel and Wendel (1998)
757F	TCAGCTATGGTTACCYGATGC	Ibrahim et al. (2009)
1318R	CGAAACATATAAAATGCRGTTAATCC	Olmstead and Sweere (1994)
2110R	CCCCCTATATTTTGATACCTTCTCC	Olmstead and Sweere (1994)
<i>trnQ-rps16</i>		
<i>trnQ</i> UUG	GCGTGGCCAAGYGGTAAGGC	Shaw et al. (2007)
<i>rps16x1</i>	GTTGCTTTTATACCACATCGTTT	Shaw et al. (2007)
<i>ycf1</i>		
<i>ycf1</i> Malv2860F	TTCGTTTTTTGAGCCTATTTTTAAAGAAC	Neubig et al. (2015)
<i>ycf1</i> Malv2970F	TCAAAAGAAACAAAAAATGGATC	Neubig et al. (2015)
<i>ycf1</i> Malv3670F	TCCTCCCTCTCACAAGCATATG	Neubig et al. (2015)
<i>ycf1</i> Malv4400F	GTGATATTGAGTCTGGGTCGATACC	Neubig et al. (2015)
<i>ycf1</i> Malv4565R	GATTGGATGGGACTGAATGAAGAAA	Neubig et al. (2015)
<i>ycf1</i> Malv5050R	TTGAAAACGCAATAACCTTTTATAGGA	This paper
<i>ycf1</i> Malv5600R	AAAGTTCTTTCTTTGGCCCAAT	Neubig et al. (2015)
<i>ycf1</i> Malv5700R	GGTTTAATACTAATAAYGGCAGTCGTT	Neubig et al. (2015)

Trimmomatic (Bolger et al. 2014) with default settings. Assembly was performed with HybPiper v. 1.3.1 (Johnson et al. 2016): bwa (Li and Durbin 2009) was used to map Illumina reads to a set of target sequences including the four chloroplast loci from a range of Malvaceae, contigs were assembled using SPAdes (Bankevich et al. 2012), and the consensus sequences were extracted.

Sequence Alignment—For skimmed loci based on Illumina assemblies, sites with at least 50% missing data were trimmed and put back together using Phyutility (Smith and Dunn 2008). Sequences from each source (Sanger, GenBank, and skim) were combined and alignments were performed separately on each locus in Geneious Prime using the MAFFT v. 7.450 plugin (Katoh and Standley 2013), and manually adjusted by eye.

Refinement of each locus alignment was performed with exploratory phylogenetic analyses using IQ-TREE v. 1.6.12 (Nguyen et al. 2015) with 1000 ultrafast bootstrap replicates (UFBoot; Hoang et al. 2018). This was done to identify issues with individual samples (such as long branches caused by sequencing errors, or very short sequences), and to check the monophyly of the outgroups. For the *trnQ-rps16* alignment, all outgroup sequences were removed as they did not form a monophyletic group in these exploratory phylogenetic analyses. This is likely due to the nature of evolution in the spacer region compared to the genes and the phylogenetic distances between the ingroup and outgroup taxa. The four loci were then concatenated into a single alignment for subsequent analyses.

Phylogenetic Analyses—IQ-TREE v. 1.6.12 was used to perform maximum likelihood (ML) analyses on the concatenated alignment. The analysis was run with the alignment partitioned by each locus (using the -Q flag to account for heterotachy; Crotty et al. 2020) and allowing ModelFinder (Kalyaanamoorthy et al. 2017) to identify the optimal substitution models for each locus. Node support was estimated using 1000 ultrafast bootstrap replicates (UFBoot) and the SH-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010), with -bnni correction to reduce the risk of overestimating branch support with UFBoot.

RogueNaRok (Aberer et al. 2013) was used to check the bootstrap trees for rogue taxa, identified as samples that have unstable positions in bootstrap replicates that can reduce support at multiple nodes of a consensus tree. The 1000 UFBoot replicates were used to test for rogue samples, using default settings on the RogueNaRok server (<https://mrh-its.org/submit>, accessed May 2021). Two samples significantly impacted bootstrap support in the majority-rule consensus tree – *Hibiscus fleckii* Gürke ex Schinz (Seydel 2588) and *H. barbosae* Exell (Brown 302). *Hibiscus fleckii* (Seydel 2588) is sister to a group of seven species of *Pavonia*, with many poorly supported nodes in this part of the tree. This sample failed the composition test performed by IQ-TREE and is morphologically distinct from the *Pavonia* species to which it is sister in the phylogeny, and so it was removed from the alignment. *Hibiscus barbosae* (Brown 302) is part of a well-supported clade of *Euhibiscus* species to which it is likely closely related, and the high rogue score is owing to the uncertain position of this sample within this clade, so it was retained in the alignment. The new alignment with *H. fleckii* removed was rerun with the same IQ-TREE settings used previously and this is the tree we present here.

Bayesian Inference (BI) was performed using MrBayes v3.2.6 (Ronquist et al. 2012), with the alignment partitioned by locus. The best model of substitution for each locus was estimated using jModelTest2 (Darriba et al. 2012). Two runs of four MCMC chains (three 'heated' and one 'cold') were set to run for 30 million generations, or until the standard deviation of split frequencies reached 0.009. Trees were sampled from the chains every 1000 generations and burn-in was set to 25%. Tracer v1.6 (Rambaut et al. 2018) was used to check convergence of the two runs, and that ESS values were over 200 for all parameters. Node support was estimated using posterior probability (PP) on a 50% majority-rule consensus tree. The ML (Figs. 3–9) and BI (Supplemental Fig. S1, Hanes et al. 2023) trees were visualized in FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>, accessed February 2023).

Specimens Examined—All specimens cited in the taxonomic treatment have been seen by at least one of the authors unless indicated by *n.v.* For type specimens, this is further indicated by '!'. In some cases, only digital images have been seen, not original specimens, and these are indicated by '✱'.

RESULTS AND DISCUSSION

The final alignment of the four concatenated loci included 310 samples, was 9001 bp long (with 6.5% missing data) and included 1877 informative sites (see Table 6 for locus information, including substitution models for the two phylogenetic

methods). The two phylogenetic inference methods produced trees with similar topologies (Figs. 3–9; Supplemental Fig. S1; Hanes et al. 2023); most incongruencies between the two topologies were poorly supported (either by UFBoot or PP, or both).

Overall, topologies are congruent with those from previous studies (Pfeil et al. 2002; Baum et al. 2004; Pfeil and Crisp 2005; Koopman and Baum 2008; Neubig et al. 2015) and consistent with the major five lineages outlined in Pfeil and Crisp (2005) (Figs. 3–9), though our work further uncovers two new clades (/Clypeati and/Caesius). Data confirm the extensive non-monophyly of *Hibiscus* (Pfeil et al. 2002; Pfeil and Crisp 2005; Koopman and Baum 2008; Areces-Berazaín and Ackerman 2017; Baker et al. 2022). Notably, with our substantially increased sampling, *Pavonia* is also non-monophyletic. Additionally, we note good agreement between our phylogeny from chloroplast loci and the tree from the phylogenomic nuclear dataset PAFTOL (Baker et al. 2022), although their nuclear phylogeny included many fewer taxa.

Rarely Sampled Genera—The monospecific Southeast-Asian *Cenocentrum* emerges in our phylogeny as sister to *Hibiscus indicus* (Burm.f.) Hochr., a species centered in China (Fig. 4). Our one sampled species from the Hawaiian *Hibiscadelphus*, *H. distans* L.E.Bishop & D.R.Herbst, is embedded in *Hibiscus* sect. *Calyphylli* Ulbr., a group that is otherwise almost exclusively African (Fig. 7). Our four sampled species of the Neotropical genus *Pelteaea* cluster together in a clade that also includes *Malachra radiata* L. (Fig. 5). The four species from the northern Neotropical genus *Wercklea* form a distinct clade that is sister to *Hibiscus* sect. *Striati* (Fig. 6).

Phylogenetic Relationships in Hibiscaceae—We begin with two new major findings. First, *Hibiscus* sect. *Clypeati*, represented by a single polymorphic species (*H. clypeatus*), is sister to the rest of tribe Hibisceae (including/Megistohibiscus). Second, we uncover a previously unnamed, well-supported clade of one never before sampled polymorphic species, *H. caesius* Garcke, as sister to all of the rest of the Hibisceae except *H. sect. Clypeati* and the clade/Megistohibiscus.

The following genera remain monophyletic on our trees, congruent with several recent nomenclatural changes in generic affiliation: *Abelmoschus*, *Decaschistia*, *Humbertiella*, *Kosteletzkya*, *Malvaviscus*, *Megistostegium*, *Pelteaea*, *Perrierophytum*, *Talipariti*, *Urena*, and *Wercklea*, though all of these taxa are embedded within *Hibiscus* and/or *Pavonia*. Samples of the genera *Fioria*, *Hibiscadelphus*, and *Kydia* Roxb. also remain monophyletic, respectively, although represented by only one species each. *Hibiscus*, *Malachra*, and *Pavonia* are not resolved as monophyletic.

Our phylogeny also finds, or confirms, that several previously defined sections of *Hibiscus* (*H. sects. Aristivalvus*, *Clypeati*, *Furcaria* (DC.) Kostel., *Muenchhusia* (Heist. ex Fabr.) O.J.Blanch., *Panduriformes* Ulbr., *Striati* O.J.Blanch., *Trionastrum*, *Trionum* (L.) DC. s.s., and, with caveats, *H. sect. Lilibiscus* Hochr.) are monophyletic. Sampling was sufficient to confirm that five sections of *Pavonia* (*P. sects. Afrolebretonia* Ulbr., *Afrotyphalea* Ulbr., *Asterochlamys* Fryxell, *Pterocarpidium* Ulbr. and *Urenoideae* A.St.-Hil.) are monophyletic.

Here we discuss each of the seven major clades of Hibisceae in turn. For rarely sampled genera and newly sampled species we note their sectional identity in *Hibiscus* or *Pavonia*, when known, and if relevant. Because all seven clades contain species currently called *Hibiscus*, we begin with this genus in our discussion of each clade.



FIG. 3. Three major clades of Hibisceae: /Clypeati, /Megistohibiscus, /Caesius, and outgroups. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

Hibiscus—The type species of *Hibiscus* is *H. syriacus* L. Our results find that two newly sampled species, *H. sinosyriacus* L.H.Bailey and *H. paramutabilis* L.H.Bailey, form a well-supported clade with *H. syriacus* in /Euhibiscus.

/CLYPEATI—Samples of two accessions representing two subspecies of the newly sampled *H.* sect. *Clypeati*, place this section as sister to the remainder of tribe Hibisceae with strong support (Fig. 3). *Hibiscus clypeatus* (Fig. 1J) is a variable

species comprising three subspecies: *H. clypeatus* subsp. *clypeatus* of the region around Tampico on the Gulf Coast of Mexico, the Yucatan Peninsula, and the Greater Antilles exclusive of Cuba; *H. clypeatus* subsp. *cryptocarpus* of Cuba; and *H. clypeatus* subsp. *membranaceus* (Cav.) O.J.Blanch. of the Bahamas and adjacent islands (Areces-Berazaín and Fryxell 2007; Blanchard 2008). The plant is a shrub or small tree of limestone-derived soils and occurs in evergreen or semi-

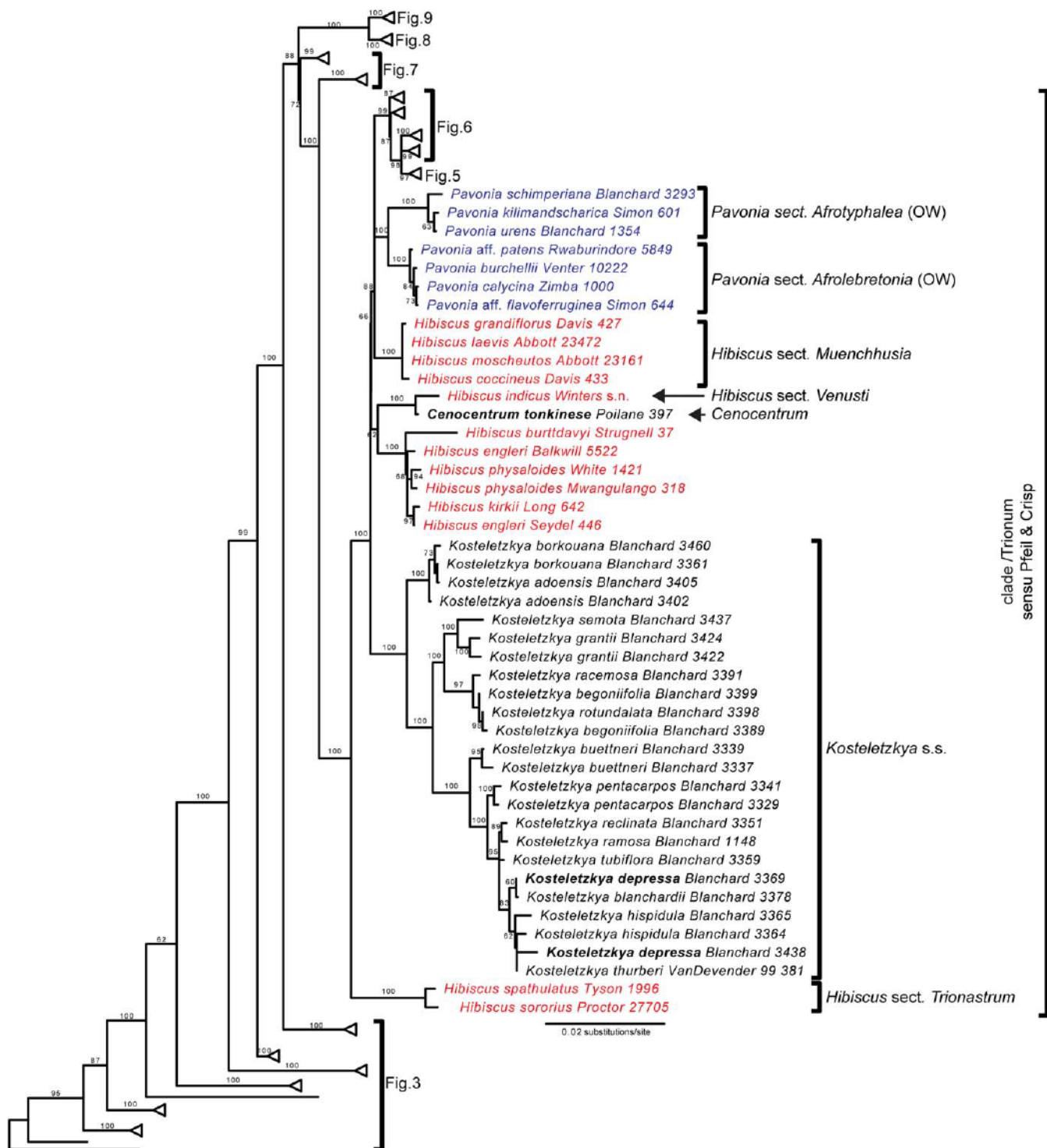


FIG. 4. Clade/Trionum. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (* indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

deciduous scrub. The corolla is bilaterally symmetric, and the staminal column is strongly declinate (Fig. 1j). This species is transferred to a new genus (below). Hummingbirds have been observed visiting the flowers of this species (D. M. Bates pers. comm.; Meerman 1993), but bats are suspected to be the primary pollinators (Blanchard 2015). Its gametic chromosome number of $n = 10$ is the lowest known count in the

Hibisceae (Skovsted 1941; Blanchard 1976; *Pavonia* has a base number of $x = 7$, but no diploid *Pavonia* are known). The sister relationship of *Hibiscus clypeatus* to the remainder of Hibisceae is a result that was hardly expected. Koopman and Baum's (2008) finding that *Megistohibiscus* was sister to the rest of Hibisceae was consistent with the theory of the diversification of Hibisceae in the Indian Ocean basin but our

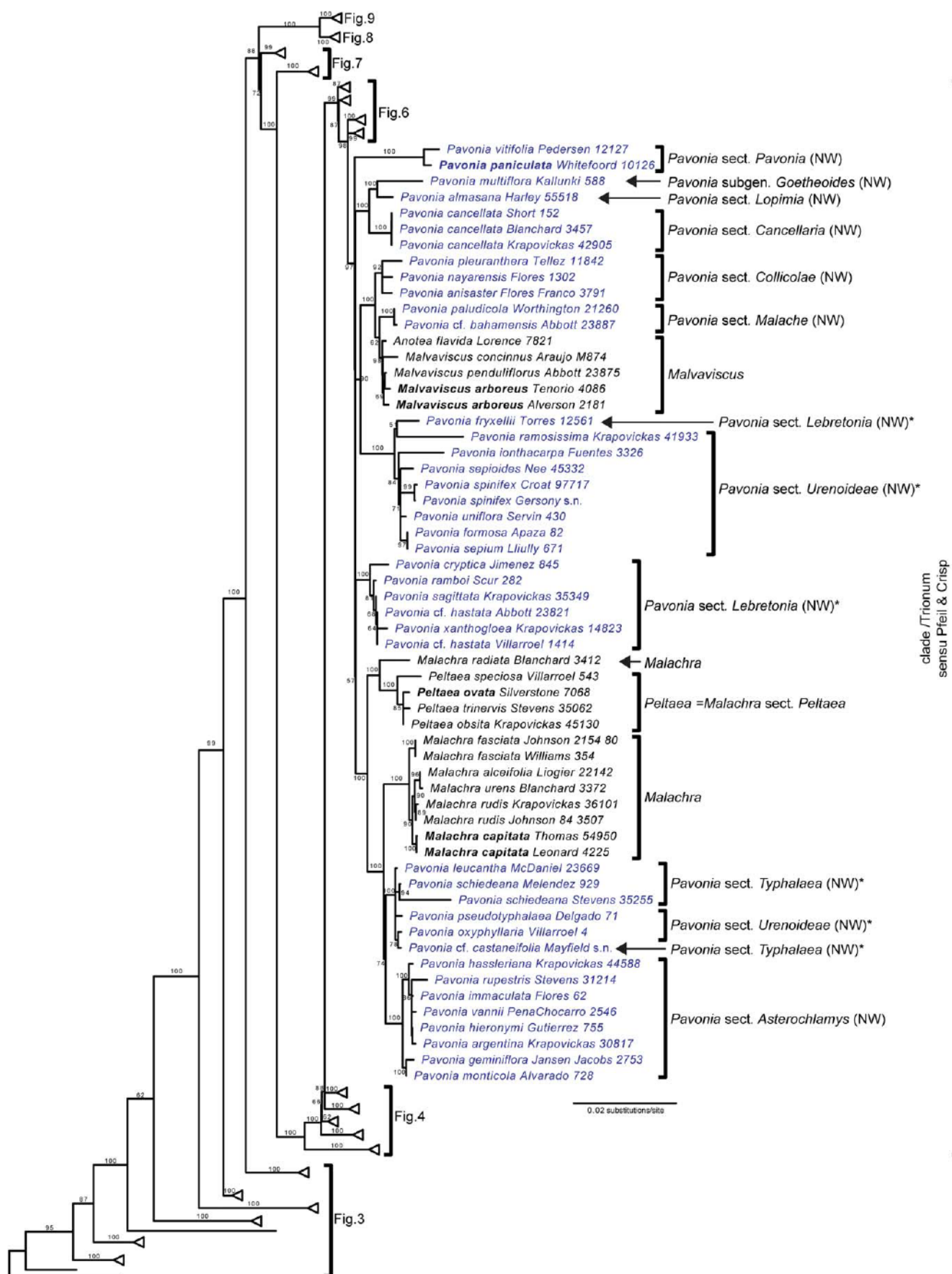


FIG. 5. Clade/Trionum. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

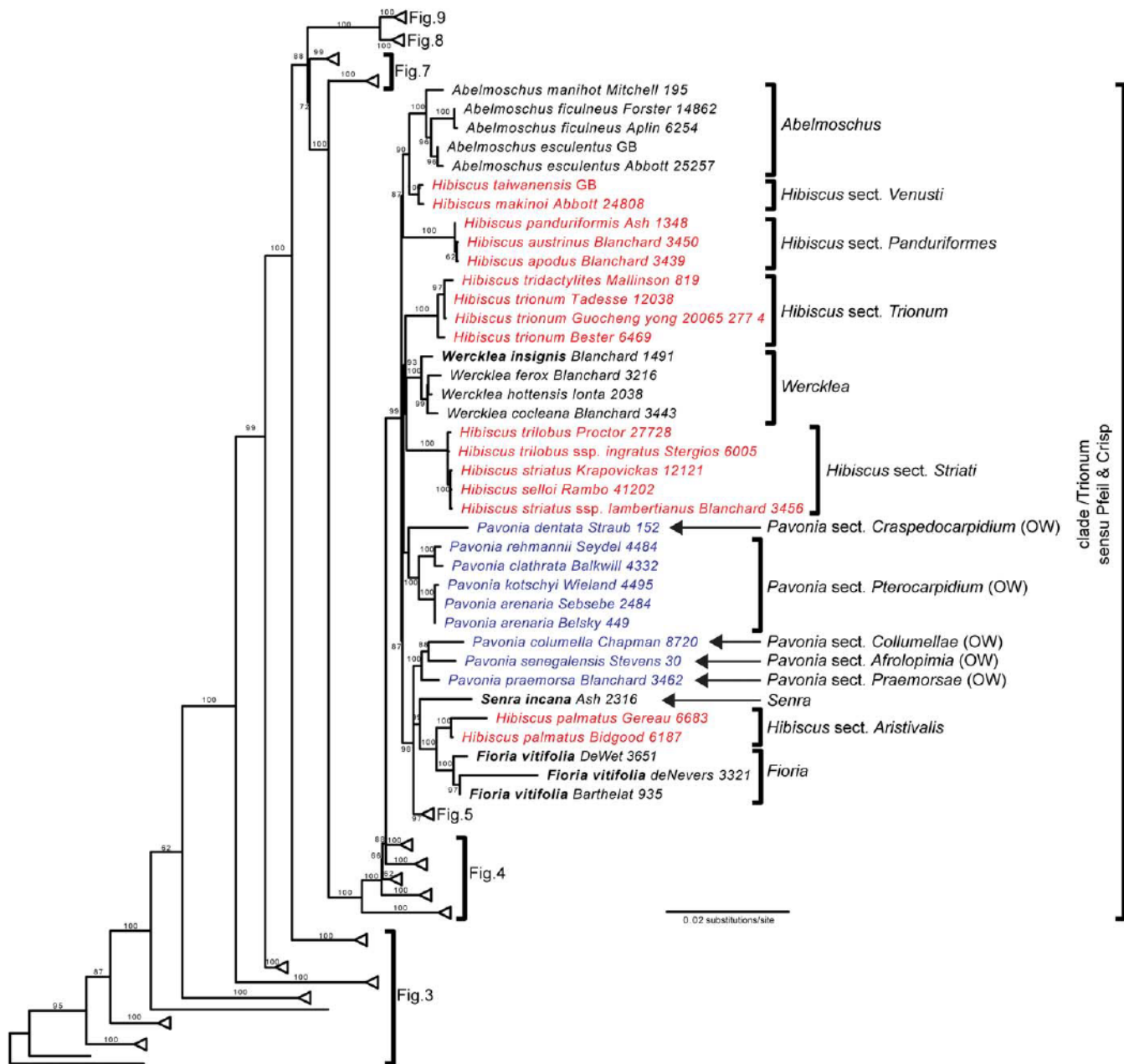


FIG. 6. Clade/Trionum. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

finding that *Hibiscus clypeatus* of the Caribbean basin is now sister to all of the rest of Hibisceae calls into question the former theory.

/MEGISTOHIBISCUS—This Madagascar and Juan de Nova Island endemic clade comprises approximately 41 species. Twenty-two are sampled here and fall into four well-supported clades (Fig. 3). Species of *Hibiscus* sect. *Azanzae* DC. endemic to Madagascar are placed here. Koopman and Baum (2008) speculated that sections other than *H. sect. Azanzae* might belong to the/Megistohibiscus clade, citing *H. lasiococcus* Baill. from *H. sect. Columnaris* Hochr. as a possibility. We did not sample this species, but we did sample the type of the section, *H. columnaris* Cav. This newly sampled species falls squarely in the/Megistohibiscus clade. The addition of

H. columnaris expands the distribution of this clade to the nearby islands of Réunion and (formerly, before extirpation) Mauritius.

Outside of this *Hibiscus* dominated clade, three additional well-delineated genera exist in/Megistohibiscus, and each remains monophyletic (Fig. 3). Koopman and Baum (2008) further documented that *Kosteletzkya* species endemic to Madagascar that correspond broadly to *H. sect. Eukosteletzkya* were embedded in the genus *Perrierophytum*. These species have recently been transferred to *Perrierophytum* (Hanes et al. 2022).

/CAESIUS—This clade corresponds to one polymorphic species, *H. caesius*, and is sister to the remainder of taxa in the tribe (Fig. 3) excluding/Clypeati and/Megistohibiscus.

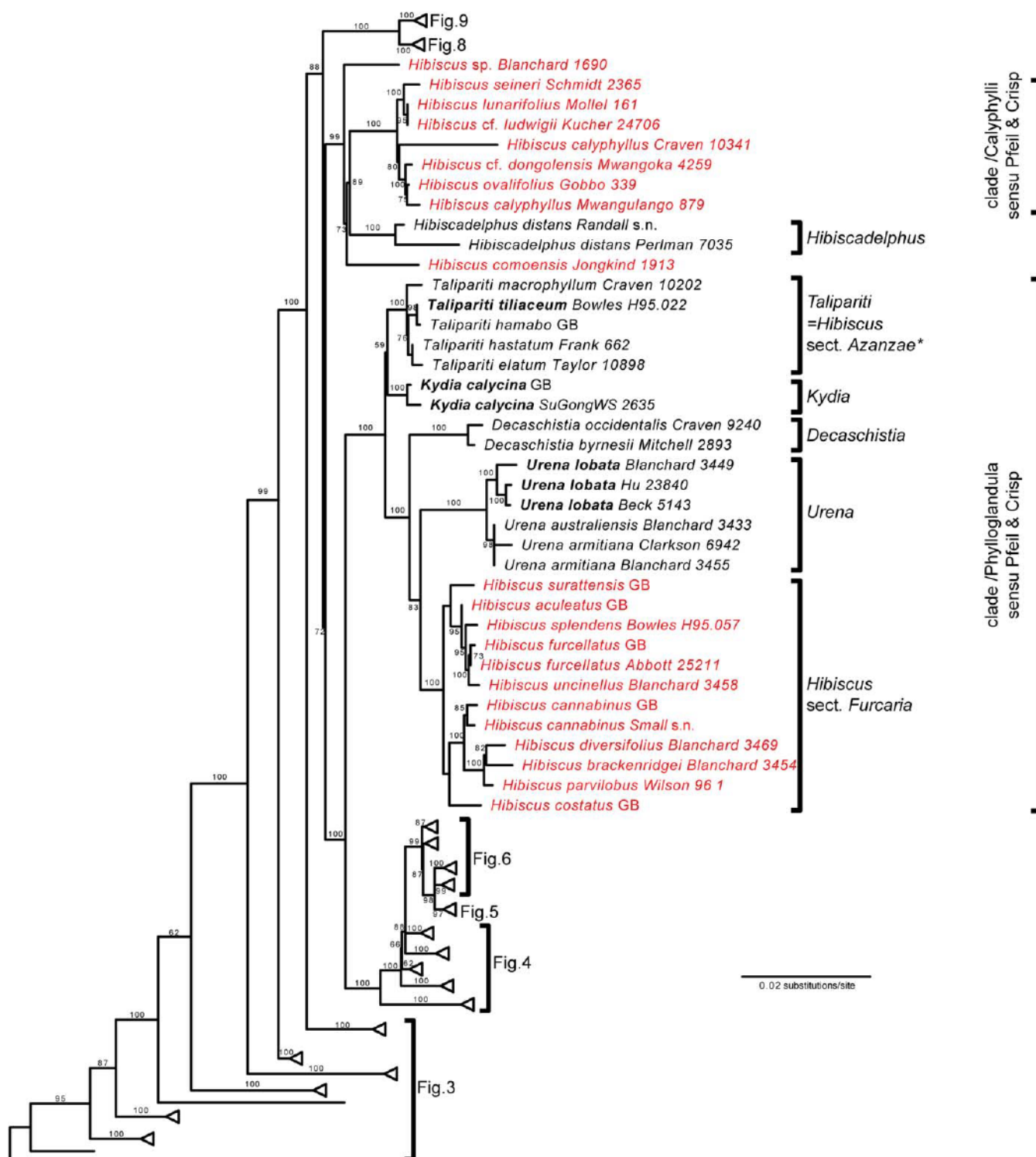


FIG. 7. Clades/Phylloglandula and/Calyphylli. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Hibiscus. Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

Hibiscus caesi was previously placed in *Hibiscus* sect. *Ketmia* (Mill.) DC., (though *H. sect. Ketmia* s.s. is actually a synonym of *H. sect. Hibiscus*, see Fryxell 1988: 195). This species occurs in southern and eastern Africa, India, Pakistan, and northern Australia. *Hibiscus caesi* has a distinctive epicalyx of 7–10 long, narrow lobes that spread in flower and are reflexed in

fruit, and 3–7 deeply lobed leaves. This species is transferred to a new genus (below), and further work is required to determine whether this widely distributed taxon should be considered multiple species. In Australia, this species is referred to as *Hibiscus pentaphyllus* F.Muell., though the use of this name is illegitimate due to the earlier published *H. pentaphyllus*



FIG. 8. Clade/Euhibiscus. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

Roxb. There is some conjecture whether the Australian plants are distinct from *H. caesioides* s.s., but given the lack of resolution in the phylogeny among the five included samples and the absence of morphological characters that clearly distinguish these five samples, we are treating them as a single species.

/TRIONUM—With our sampling, this large clade contains eleven different genera, including all *Pavonia* species sampled and representing at least eight sections of *Hibiscus* (Figs. 4–6).

The newly sampled *Hibiscus palmatus* Forssk. (*H.* sect. *Aristivalvus*), is sister to *Fioria vitifolia* (L.) Mattei (= *Hibiscus vitifolius*, *H.* sect. *Pterocarpus* Garcke), and the monospecific genus *Senra* Cav. is sister to both species (Fig. 6). For the first time we add *H. striatus* Cav. and *H. trilobus* Aubl., which form a clade that solidly confirms the distinctiveness of *H.* sect. *Striati*. Similarly, the monophyly of *H.* sect. *Muenchusia* (Blanchard 1976; Small 2004) is highly supported by the data (Fig. 6). We also confirm the integrity of *H.* sect. *Panduriformes*



FIG. 9. Clade/Euhibiscus. Maximum likelihood phylogenetic tree of the Hibisceae based on four plastid DNA loci. Bootstrap support values are reported on branches. Clade and sectional affiliation are provided (*indicates section in part). *Hibiscus* sect. *Ketmia* is highlighted on the tree to demonstrate previous classification, though it is a synonym of *Hibiscus* sect. *Hibiscus*. *Pavonia* is shown in blue, *Hibiscus* in red. Type species of genera, when sampled, are bolded. Voucher for each accession is provided, GB = sequences obtained from GenBank.

(Fig. 6). *Hibiscus panduriformis* Burm.f., the type species of the section, is an early-described (1764), rather widely distributed species found in tropical Africa, Asia, and Australia. More than two centuries later five additional species were described in Australia (Juswara and Craven 2005), and we have sequenced two of these (*H. apodus* Juswara & Craven and *H. austrinus* Juswara & Craven). This clade is sister to

two other Old World groups: representatives in the genus *Abelmoschus* and a clade that contains *Hibiscus makinoi* Y.Jotani & H.Ohba and *H. taiwanensis* S.Y.Hu (*H. sect. Venusti* Ulbr.). Interestingly, *H. indicus* (also *H. sect. Venusti*) forms a distantly related clade with the genus *Cenocentrum* (Fig. 4). Another distinct clade (unnamed) known from two previously sampled species, *H. engleri* K.Schum and *H. physaloides*

TABLE 6. Summary statistics of the four loci and concatenated alignments, including locus models implemented in IQ-TREE and MrBayes.

Locus	Number of samples	Aligned length (bp)	Informative/invariable	ModelFinder model for IQ-TREE (BIC)	jModeltest for MrBayes (BIC)
<i>matK</i>	309	2653	536/1727	TVM+F+R2	GTR+I+G
<i>ndhF</i>	281	2070	344/1529	TVM+F+R3	GTR+I+G
<i>ycf1</i>	290	3012	642/1992	TIM3 + F+R4	GTR+I+G
<i>trnQ-rps16</i>	263	1266	355/730	TVM+F+R3	HKY+G
Total	310	9001	1877/5978		

Guill. & Perr., is now expanded by the addition of two newly sampled species, *H. burtt-davyi* Dunkley and *H. kirkii* Mast. (Fig. 4).

Hibiscus sororius L. and *H. spathulatus* Garcke are sampled here for the first time and are the first documented representatives of the previously unsampled *H.* sect. *Trionastrum*, which is typified by *H. sororius* (Fig. 4). We speculate that *H. amazonicus* Fryxell, *H. dimidiatus* Schrank, and *H. marioniae* Dorr will also group together here to form a New World clade, ranging from the West Indies and southern Mexico, south throughout tropical South America.

The type species of *Hibiscus* section *Trionum*, *H. trionum*, occurs globally as an agricultural weed (Fig. 6). Taxonomic work on Australian and New Zealand *Hibiscus* has found several segregate species that occur in the region, including *H. tridactylites* (Craven et al. 2011) sampled here. Further work is required to determine the species diversity, distributions, and origins of the *H. trionum* complex.

Cenocentrum—Fryxell (1975) established the tribe Decaschisteae primarily on the basis of it having 10 carpels and 10 stigmas, thereby distinguishing it from both the Ureneae (= Malvaceae; five carpels and 10 stigmas) and the Hibisceae (five carpels and five stigmas). However, Fryxell omitted any reference to *Cenocentrum*, even though, by his primary criterion, it should have been placed in the Decaschisteae. More recently, Pfeil and Crisp (2005) speculated that *Cenocentrum* would turn out to be closely related to, if not in, the genus *Decaschistia*. Our molecular phylogeny disagrees, placing *Cenocentrum tonkinense* and *Hibiscus indicus* together in their own clade and sister to a group of related species (*H. engleri*, *H. physaloides*, etc.) that are also primarily African (Fig. 4). *Decaschistia*, instead, is embedded in the/Phylloglandula clade with *Urena*, *Hibiscus* sects. *Furcaria*, *Talipariti*, and others (Fig. 7), and is thus well separated from *Cenocentrum*.

When Blanchard (1976) broke up *Hibiscus* sect. *Trionum* s.l. into several sections he placed two Chinese species, *H. indicus* and *H. mutabilis*, into *Hibiscus* sect. *Venusti* Ulbr. At the same time, however, he noted that specimens of the first species often had more than five stigmas (in one instance, eight) and he suggested a possible relationship to the monospecific Southeast-Asian genus *Cenocentrum* with ± 10 carpels and stigmas. In 1981, Blanchard (unpublished) grew accessions of *Cenocentrum tonkinense* Gagnep. (Blanchard 3207) and *Hibiscus indicus* (Blanchard 3197) in the greenhouse and obtained seed-set following cross-pollination. The hybrid seed was sown in 2003 (Blanchard 3322) and the resulting hybrid plants were robust and intermediate between the two parents. Since successful experimental intergeneric hybrids are rarely produced in the Hibisceae, the successful progeny suggest that the parents are indeed closely related.

Kosteletzkya—As previously circumscribed, *Kosteletzkya* s.l. was not monophyletic and indeed came out in three

distinct clades. Recent work transferred seven additional nominal *Kosteletzkya* species that are endemic to Madagascar (Hochreutiner 1955) to *Hibiscus* or *Perrieriophytum* (Hanes et al. 2022; see discussion in/Megistohibiscus above).

Kosteletzkya s.s., with 17 species (Blanchard 2015), has a bimodal African-northern Neotropical distribution, although there is also one species in the Philippines. Except for the New World *K. pentacarpos* (L.) Ledeb., which appears to have been introduced into Eurasia and occurs there sporadically, each species is confined to one hemisphere or the other, 8 in the Old World and 8 in the New World (Neubig et al. 2015). We have previously sampled 15 of these species (Neubig et al. 2015), and a 16th species, *K. thurberi* A.Gray, is added here. As defined, *Kosteletzkya* s.s. forms a well-supported clade in the diverse/*Trionum* clade of Pfeil and Crisp (2005) and is sister to all remaining species in the clade (except *Hibiscus* sect. *Trionastrum*) (Fig. 4).

Peltaea—*Peltaea* is a Neotropical genus of about 20 species (Krapovickas and Cristóbal 1965, 1993, 1996; Fryxell 1985; Fryxell and Krapovickas 1990; Fernández and Esteves 2016). Like the similarly Neotropical *Malachra*, *Phragmocarpidium* Krapov., and *Rojasimalva* Fryxell, *Peltaea* has an involucre of $\pm$ modified leaves below the inflorescence or below individual flowers. Cytologically, *Peltaea* has a base number of 25, as does the monospecific *Phragmocarpidium* (Fernández et al. 2003), but the rest of the genera in the former tribe Malvaceae (i.e. *Anotea*, *Malachra*, *Malvaviscus*, *Pavonia*) have base numbers of 7 or 14 (Krapovickas 1969; Krapovickas and Cristóbal 1965). No chromosome count for *Rojasimalva* is yet available.

Our four sampled species of *Peltaea* cluster together in a clade that also includes one of the six sampled *Malachra* species, *M. radiata* L. (Fig. 5). The rest of our sampled species of *Malachra* are sister to some of the New World sections of *Pavonia* and are more distantly related to the *Peltaea* clade. Species in this core *Malachra* clade are unique in the “Malvaceae” in lacking an epicalyx. The one exception, *M. radiata*, possesses an epicalyx, thereby providing a morphological basis for its phylogenetic placement. *Peltaea* is alternatively treated as *Malachra* sect. *Peltaea* C.Presl, reflecting the morphological similarity of these taxa.

Wercklea—*Wercklea* is a northern Neotropical taxon comprising 13 species (Fryxell 1981, 1992) that are highly localized except for *W. ferox* (Hook.) Fryxell (Fig. 1P). The latter is found from Costa Rica to Bolivia but apparently not in Peru. Each of the other 12 species is of highly limited geographical extent in southern Central America (5 species), the Caribbean (4 species), and Colombia and Ecuador (3 species). Our four sampled species (*W. cocleana* (A.Robyns) Fryxell (Panama), *W. ferox* (Panama), *W. hottensis* (Urb.) Fryxell (Haiti), and *W. insignis* Pittier & Standl. (Costa Rica)) form a distinct clade that is sister to *Hibiscus* sect. *Striati* (see Blanchard 1976, 1988; but also see Krapovickas 1999; Fig. 6).

/PHYLLOGLANDULA—This clade (Fig. 7) is characterized by conspicuous foliar nectaries, with few exceptions (e.g. *H. menziesiae* F.D.Wilson & Byrnes, *Hibiscus splendens* C.Fraser ex Graham, *H. superbus* C.A.Gardner) (Wilson 1974). The large, diverse and much-studied *H. sect. Furcaria* (see Wilson 1999, 2006) forms a well-circumscribed clade in our phylogeny based on five previously sampled species plus another five that are newly reported here: *H. aculeatus* Roxb., *H. brackenridgei* A.Gray, *H. diversifolius* Jacq., *H. parvilobus* F.D.Wilson, and *H. uncinellus* Moc. & Sessé ex DC. Along with 14 additional species included in Pfeil et al. (2002) there is no doubt about the global integrity of this group. This element of /Phylloglandula (Pfeil and Crisp 2005) is closely affiliated with the genera *Decaschistia*, *Kydia*, *Talipariti*, and *Urena*, each of which are respectively monophyletic genera in our tree. Also belonging in this clade are three small Asian genera (unsampled here), according to Bayer and Kubitzki (2003) and Tang et al. (2007): *Dicellostyles* Benth., *Julostylis* Thwaites, and *Nayariophyton* T.K.Paul (Table 1). Morphologically, the small Asian genera have distinct foliar nectaries (as determined from online examination of type specimens at JSTOR Global Plants), further supporting our expectation that the three unsampled genera will cluster with *Kydia* as members of the /Phylloglandula clade.

Talipariti—Van Borssum Waalkes' (1966) treatment of the Malesian Malvaceae included 18 mostly poorly known species in *Hibiscus* sect. *Azanzae*. Twenty-two species were published in *Talipariti* (Fryxell 2001) including 12 of Borssum Waalkes' 18, one new species (*T. bowersiae* Fryxell), four species from Borssum Waalkes's subspecies of *H. tiliaceus* L. (i.e. *T. celebicum* (Koord.) Fryxell, *T. crestaense* (Borss.Waalk.) Fryxell, *T. hastatum* (L.f.) Fryxell, *T. simile* (Blume) Fryxell), and five species from outside Malesia and New Guinea (*T. elatum* (Sw.) Fryxell, *T. glabrum* (Matsum. ex Nakai) Fryxell, *T. hamabo* (Siebold & Zucc.) Fryxell, *T. potteri* (O.Deg. & Greenwell) Fryxell, and *T. tortuosum* (Roxb.) Fryxell). In 2010, Bovini raised *T. tiliaceum* var. *pernambucense* (Arruda) I.M.Johnst. to the specific level, bringing the total number of species to 23 (Bovini 2010).

Most species of *Talipariti* occur in southeastern Asia, New Guinea, and the surrounding area, except for the littoral *H. pernambucensis* Arruda (New World) and *H. tiliaceus* (mostly Old World). Fryxell completely ignored and never mentioned (fortunately as it turns out) the several species endemic to Madagascar that Hochreutiner (1900, 1955) had placed in *H. sect. Azanzae*. Our five sampled species, *T. elatum*, *T. hamabo*, *T. hastatum*, *T. macrophyllum*, and *T. tiliaceum*, together form a clade that is sister to *Kydia*. Pfeil and Crisp (2005) called the clade that comprises *Talipariti* the 'Azanzae' clade because their sampling showed it to be a broader group than was accepted by Fryxell's genus. Their data added *H. ellipticifolius* Borss.Waalk. and *Papuodendron lepidotum* C.T.White. Fryxell included the first of these species in *Talipariti* but made no mention of the second; indeed, it was identified as a member of the Bombacaceae by Borssum Waalkes and was excluded from his treatment of the Malesian Malvaceae. Fryxell (2001), as well as Pfeil and Crisp (2005), seem to have overlooked the morphological/anatomical analysis by Van Heel (1972) which shows a clear association between these two species.

Although Hochreutiner (1900) included eight species in *Hibiscus* sect. *Azanzae* from Madagascar and much later (Hochreutiner 1955) included 12 species from the island in

that section, Fryxell (2001) ignored them all, never mentioning them in his *Talipariti* treatment. It turns out that our molecular phylogeny separates these species from Madagascar (Fig. 3) considerably from *Talipariti* species (Fig. 7).

Urena—Early on, the genera comprising the former tribe Ureneae, then called tribe Malvaviscaceae (i.e. *Malachra*, *Malvaviscus*, *Pavonia*, *Peltaea*, *Urena*, and a few smaller genera), were recognized as readily distinguishable from members of the other malvoid tribes by their unique possession of five uniovulate mericarps and ten styles (Kearney 1951; Bates 1968; Fryxell 1968; Bates and Blanchard 1970). Van Heel (1978), studying three species of *Pavonia* and one each of *Malvaviscus* and *Urena*, showed that this condition came about through the early formation of two whorls of five carpels each, the inner of which developed only partially.

Early molecular phylogenetic results (La Duke and Doebley 1995) suggested the distinctness of *Urena* from the rest of the Malvaviscaceae, and more recent DNA evidence moved *Urena* to the /Phylloglandula clade of Pfeil and Crisp (2005). We sequenced two non-glochidiate Australian species (*U. armitiana* F.Muell. and *U. australiensis* Fryxell & Craven), and three accessions of the glochidiate-fruited *U. lobata* L. s.l. and found that together the five form a single, well-supported clade within the /Phylloglandula clade sister to *Hibiscus* sect. *Furcaria* (Fig. 7) and remote from any nominal *Pavonia* (Figs. 4–6). Our results support the view that foliar glands (and other correlated features), not the fruit ornamentation, should guide the circumscription of *Urena*.

Decaschistia—The genus *Decaschistia* comprises about 18 species ranging from India and southern China, irregularly through Indochina to northern Australia, but it does not occur in Malesia and New Guinea (Borssum Waalkes 1966). Fryxell (1975) placed it in a novel tribe Decaschistieae Fryxell, and suggested a relationship with Ureneae. Our results place *Decaschistia* as sister to a clade that includes both *Urena* and *Hibiscus* section *Furcaria*, supporting Fryxell's alliance of the genus with *Urena* (Fig. 7).

/CALYPHYLLI—The mainly African *H. sect. Calyphylli* is represented ostensibly by eight species in our treatment (/Calyphylli of Pfeil and Crisp 2005; Fig. 7), but the group is problematic. Several specimens were not sampled due to inadequate and challenging species identification, and to further complicate matters, intermediate forms have been reported between many pairs of species (see Flora Zambesiaca; Exell 1961, pp. 459–461). While the individual identities of some species remain elusive, their mutual affinities do not. The endangered Hawaiian endemic genus *Hibiscadelphus*, is embedded in *H. sect. Calyphylli*, similar to the results of Champion (2020).

Hibiscadelphus—*Hibiscadelphus* comprises between six and eight species endemic to the Hawaiian Archipelago, all of which are either critically endangered or already extinct (Lorence and Wagner 1995; Bates 1999; Oppenheimer et al. 2014; Price and Wagner 2018). We have two samples of *Hibiscadelphus distans* L.E.Bishop & D.R.Herbst, and they are embedded in a clade that otherwise consists of species in *Hibiscus* sect. *Calyphylli*, a group that is mostly native to Africa. Champion (2020) sampled additional species of *Hibiscadelphus* and found the genus to be monophyletic, and also confirmed the close relationship with *Hibiscus* sect. *Calyphylli*. These results are surprising, as *H. sect. Calyphylli* and *Hibiscadelphus* show no obvious geographical or morphological affinities (e.g. *Hibiscus* sect. *Calyphylli* have foliar nectaries,

Hibiscadelphus does not; *Hibiscadelphus* has circumscissile calyces, *Hibiscus* sect. *Calyphylli* does not). They do, however, share the same base chromosome number, $x = 20$ (Niimoto 1966; Bates 1967; Carr and Baker 1977). Loss of nectaries in a number of Hawaiian plant lineages is a common phenomenon linked to an absence of ants in the archipelago (Keeler 1985) and it is possible that the circumscissile calyces are likewise a localized adaptation within this lineage.

/Euhibiscus—This large clade more or less corresponds to the *Euhibiscus* clade of Pfeil and Crisp (2005) and is made up almost entirely of the large pantropical *Hibiscus* sect. *Bombicella* s.l., but also includes the smaller *H.* sections *Hibiscus*, *Lilibiscus*, *Solandra* (Murr.) Hochr., and *Spatula* Hochr. (Figs. 8–9). Our results suggest two distinct subclades similar to the results of Pfeil and Crisp (2005). In our phylogeny the first subclade (clade 1) includes four distinct groups. The first group comprises 21 New World species that corresponds to *H.* sect. *Bombicella* s.s. (Fryxell 1980) and includes *H. phoenix* Jacq., the type of the section. Of our 12 sampled species in this group only two, *H. coulteri* Harv. ex A.Gray and *H. longifolius* Fryxell, have been sampled previously. A second group corresponds to Ulbrich's (1922) *H.* subsect. *Africanae-lobophyllae* and is represented in our phylogeny by *H. aethiopicus* L., *H. microcarpus* Garcke, and *H. pusillus* Thunb., all newly sampled accessions (*H. marlothianus* K.Schum., which was not sampled here, may also belong here). Sister to this African clade is a third group that comprises Australian species. Our sampling consists of 12 species, all of which, except for *H. geranioides* A.Cunn. ex Benth., have also been sampled elsewhere. *Hibiscus normanii* F.Muell. is confirmed to be in *H.* sect. *Bombicella*, rather than in *H.* sect. *Spatula* as placed by Hochreutiner (1900). *Hibiscus brachysiphonius* F.Muell. is also determined to be in *H.* sect. *Bombicella*. A final group, which corresponds to Ulbrich's (1922) *H.* subsect. *Syriaca* includes the type of *Hibiscus*. It is sister to the New World group of *Bombicella* species and is eastern Asian in distribution. Sister to all taxa in *Hibiscus* sect. *Bombicella* clade 1 is *H. pedunculatus* L.f. ($x = 15$), an annual or perennial shrub from Mozambique to South Africa, and occurring globally as a cultivated plant.

The second of the two major subclades of *Euhibiscus* is composed of mostly African species of *H.* sect. *Bombicella* (= *H.* sect. *Eubombicella* Ulbrich) plus a sister clade that consists of *Hibiscus* sects. *Hibiscus*, *Lilibiscus*, *Solandra*, and *Spatula*, plus the monospecific *Helicteropsis* Hochr. Ulbrich's *Eubombicella* (clade 2) is a species rich and difficult group in Africa as are some of the other African sections, e.g. *Hibiscus* sect. *Calyphylli* (Verdcourt and Mwachala 2009). Understanding this problematic group is confounded by frequently inadequate and/or incomplete specimens and great variability in some species, e.g. *H. micranthus* L.f. It is noteworthy in this context that the relatively short branches of the African *Bombicella* subclade suggest comparatively little genetic diversification among the species. We ultimately sequenced 16 taxa, 13 of which were previously unsampled. Nested within the African diversity is the widely distributed *H. hirtus* L. (occurring in southern North America, India, and Indonesia, potentially dispersed as a weed), and the Australian endemic *H. peralbus* Fryxell which is morphologically very similar.

Hibiscus section *Lilibiscus* includes about 28 species (Cafferty and Cheek 1996; Huppmann 2013; Thomson and Braglia 2019; Thomson and Cheek 2020; Thomson and Mashburn 2022; Thomson et al. 2022, 2023) with a disparate distribution from east Africa, Madagascar, and the Mascarenes to north

and south Pacific Islands. At least two species are of horticultural origin, including *H. rosa-sinensis*. We include seven species in our phylogeny, and two of these species, *H. bernieri* Baill. and *H. boryanus* DC., are sampled for the first time. Koopman and Baum (2008) reported a discordance in their data sets involving two taxa from Madagascar, *Hibiscus grandidieri* Baill. and *Helicteropsis*, which prompted them to exclude these taxa from their combined analysis. We have clarified these clade affiliations here (Fig. 8). Closely affiliated with *Hibiscus* sect. *Lilibiscus*, and sister to *Hibiscus bernieri*, is the sole species of the genus *Helicteropsis*. Though this unique genus continues to be dramatically morphologically different from its neighbors we confirm its phylogenetic placement for the first time. *Hibiscus grandidieri* is in turn sister to the remainder of our sampling in *H.* sect. *Lilibiscus*.

Sister to *Hibiscus* sect. *Lilibiscus* is a clade comprising *Hibiscus* sections *Hibiscus*, *Solandra*, and *Spatula*. We have included two previously-sampled species from sect. *Solandra*, originally characterized by minute or absent involucral bracts, which are widespread in Africa, *H. lobatus* (Murray) Kuntze and *H. sidiformis* Baill. (Fig. 2G). The former species is the type of *H.* sect. *Solandra*, and in addition to Africa it occurs in Pakistan, India, Thailand, Java and Australia. Consistent with the predictions of Koopman and Baum (2008), six species endemic to Madagascar fall here as well, four of which (*H. antanossarum* Baill., *H. erodiifolius* Hochr. & Humbert, *H. oxaliflorus* Bojer ex Baker, and *H. stenophyllus* Baker) are newly sampled. It is noteworthy that members of two additional sections, as designated by Hochreutiner (1955), reside in this clade in our analysis. *H. caeruleus* Baill. and *Hibiscus erodiifolius* were placed in *H.* sect. *Ketmia* (= *H.* sect. *Hibiscus*), whereas *H. humbertianus* Hochr. is in *H.* sect. *Spatula*. *Hibiscus humbertianus* took a brief, mistaken trip into the genus *Cienfuegosia* (Gossypieae; Fryxell 1974, 1997). Koopman and Baum (2008) demonstrated that this species is instead close to *H. caeruleus* and species in *H.* sect. *Lilibiscus* and distant from their sampled Gossypieae; our work confirms this.

Sister to *H.* sects. *Hibiscus*, *Lilibiscus*, *Solandra*, and *Spatula* is where species of *Hibiscus* from Madagascar, previously placed in the genus *Macrostelia* fall (exemplified here as *H. laurinus* Baill.). Seven species of *Hibiscus* belong here, including four newly described species (Callmander et al. 2020; Hanes et al. 2020).

Pavonia—The clear separation of *Urena* from *Pavonia* brings us only a small step closer to clarifying the status of *Pavonia*. As discussed in the introduction, *Pavonia* currently comprises about 300 species. Although we only sampled ~50 of these, we can confirm that *Pavonia*, like *Hibiscus*, is not monophyletic (Figs. 4–6). Old World *Pavonia* species fall into three distinct clades. One large, well-supported clade includes all of the New World *Pavonia* and also includes members of the New World genera *Anotea* (DC.) Kunth., *Malachra*, *Malva viscus*, and *Peltaea* (Fig. 5). Notably this clade does not include any members of *Hibiscus*. Because *Pavonia* has a bimodal distribution with centers in tropical America and Africa, and because, except for one or two introductions, no *Pavonia* species is shared between these two centers, it is convenient to discuss the two geographic groups of *Pavonia* separately.

Ulbrich's (1920–21) revision of African *Pavonia* recognized two subgenera, *Pavonia* (as *Eupavonia*) and *Typhalea* DC., and described eight sections under the first subgenus and one under the second (Table 4). Our molecular phylogeny

includes representatives of eight of the nine sections. All Old World *Pavonia* are found in three, well-supported clades that are not each other's closest relatives. The first Old World clade includes representatives of the Old World *Pavonia* section *Afrotyphalea* Ulbr. (3 of the 5 species in this section are sampled here), *Pavonia* sect. *Typhalea* (DC.) Ulbr., and members of *Pavonia* subg. *Pavonia* sect. *Afrolebretonia* Ulbr. (Fig. 4). The second clade includes species of *Pavonia* sections *Craspedocarpidium* Ulbr. and *Pterocarpidium* Ulbr. (though see Vollesen 1995; Welcome and Victor 2022; Fig. 6). The third Old World clade includes three *Pavonia* sections (*Pavonia* sects. *Afrolopimia* Ulbr., *Columella* Ulbr., and *Praemorsa* Ulbr.; Fig. 6), each of which comprises only a single species, and may be closely related to the likewise Old World *Fioria*+*Senra* and *Hibiscus* sect. *Aristivalvus* (as suggested in Verdcourt and Mwachala 2009).

The New World species of *Pavonia* have been sorted on morphological grounds most recently into five subgenera, four of which are further subdivided into 15 sections (Fryxell 1999; Table 4). A virtually contemporary study, based solely on species from NE and SE Brazil, differs slightly in combining the four previously recognized subgenera into two, merging three of the sections, and resurrecting another (Esteves 1998a, 1998b; see also Fryxell 2000, in which some resulting discrepancies are rectified). Our New World samples (Fig. 5) include representatives of nine of Fryxell's 15 sections (we lack *Albae* Fryxell, *Carcerariae* Fryxell, *Diathericae* Fryxell, *Laminariae* Fryxell, *Malvaviscoides* A.St.-Hil. and *Varians* Fryxell). Together these missing sections comprise only about 29 of the ca. 245 New World species (or about 12%).

One clade is recovered that encompasses all New World *Pavonia* and represents the most species rich sections of the genus (Fig. 5). The following sections are well-supported and remain monophyletic: *Asterochlamys* Fryxell, *Collicolae* Fryxell, *Malache* (B.Vogel) DC., and *Pavonia*. The genus *Pavonia* is typified by the tropical American *P. paniculata* Cav. Our sample of the type section includes *P. paniculata* and one other of the section's 15 species (*P. vitifolia*), and results in a well-supported clade. One species from each of *P. sect. Cancellaria* DC. and *P. sect. Lopimia* (Mart.) Endl. together form a clade with *P. multiflora* A.St.-Hil., our one sampled species from *P. subg. Goetheoides* (Gürke) Ulbr. The New World genera *Anotea* and *Malvaviscus* are closely related to *Pavonia* sections *Collicolae* and *Malache*. Our sample of six species (out of about 60) from *P. sect. Lebretonia* (Schrank) Endl. includes representatives from all four of its subsections. Species from three of these subsections cluster together, but one, *P. fryxellii* Krapov., is placed elsewhere (see below).

The clade containing New World members of *Pavonia* subg. *Typhalea* (DC.) Ulbr. include two larger, sampled sections: *Pavonia* sect. *Typhalea*, comprising nine species, and *P. sect. Urenoideae* A.St.-Hil., comprising 20 species, and three small, unsampled sections that comprise five species in aggregate. Our 13 samples from this subgenus form two clades that are distant from one another in our phylogeny, but the species do not sort cleanly along traditional sectional lines. Instead, four nominally *Pavonia* section *Typhalea* species are joined by three *P. section Urenoideae* species to form one clade. The second, distant clade consists of seven *P. sect. Urenoideae* species plus *P. fryxellii* from *P. sect. Lebretonia* of subg. *Pavonia*.

Pavonia subg. *Asterochlamys* Fryxell comprises two sections. The larger of the two, *P. sect. Asterochlamys* (ca. 31 species),

forms a distinct clade based on our sample of eight species, but we lack samples from *P. sect. Albae*, a small group of three species in the same subgenus. *Pavonia* subg. *Malache* (B.Vogel) Fryxell, with 18 species in three sections, has had five species, representing two of the three sections, sampled by us. Our representatives from *P. subg. Malache* species turn out to be sister to a clade that also includes three sampled species of *Malvaviscus* and *Anotea flavida* (DC.) Ulbr. The single species of *P. sect. Laminariae*, *P. oxyphylla* (Moc. & Sessé ex DC.) Fryxell, that Fryxell placed in this subgenus seems morphologically well apart from the rest. Unfortunately, without a sample we were unable to test this subgeneric assignment.

The base chromosome number of *Pavonia* is apparently $x = 7$ (Fryxell 1999). Chromosome numbers show distinctly different patterns in the two hemispheres. In the New World, where about 10% (27) of the species have been counted, octoploids strongly predominate, whereas in the Old World, where about 25% (12) of the species have been counted, tetraploids strongly predominate (Fryxell 1999). No diploids are known in the genus, and only one hexaploid in each of the hemispheres has been reported (Fryxell 1999).

Genera Incertae—Pfeil and Crisp (2005) list six genera incertae sedis. Subsequent work in the past 20 yr and this paper help the positions of five of these taxa. Our work resolves the phylogenetic positions of *Hibiscadelphus* and *Wercklea*. Champion (2020) further confirms the monophyly of *Hibiscadelphus* and its close affinity with *Hibiscus* sect. *Calyphylli* (Fig. 7). The phylogenetic positions of two monospecific genera restricted to northern Madagascar have remained elusive due to conflicting signals between molecular datasets (Koopman and Baum 2008). We can confirm for the first time that *Helicteropsis*, with small flowers and a style 3–4.5 times the length of the perianth (Fig. 1A), is closely affiliated with *Hibiscus* sect. *Lilibiscus* (/Euhibiscus) (Fig. 8) whereas *Jumelleanthus* Hochr. is supported as a member of the/Megistohibiscus clade (Fig. 1). The monospecific genus *Humbertianthus* Hochr. was described as a taxon in its bud stage and represents unopened flowering collections of *Hibiscus laurinus* Baill. (Hanes et al. 2020; Fig. 8). The last incertae sedis genus of Pfeil and Crisp is *Symphychlamys* Gürke. We have no samples of this genus. Two fairly recent floristic treatments in the rather restricted range of this monospecific African genus (Vollesen 1995, Ethiopia and Eritrea; Thulin 1999a, Somalia), treat the genus differently. The first maintains the genus; the second submerges it in *Hibiscus*, comparing it to *H. socotranus* Lucas from the island of Socotra (Yemen) off the tip of Somalia near the mouth of the Gulf of Aden. We are not persuaded that it is *Hibiscus*, but it and several other Socotran *Hibiscus* endemics remain unsampled and their inclusion in future studies is desirable. The genus *Woo-dianthus* Krapov. was described by Krapovickas (2012b) and its placement remains uncertain. We did not sample this genus though we posit that it is a member of tribe Hibisceae.

Morphology—An obvious next step with this phylogeny will be to begin exploring morphological evolution throughout the tribe. For example, unlobed leaves with reticulate and/or pinnate venation are now known to be represented at least four times in the tribe, twice in/Euhibiscus (e.g. in *Hibiscus laurinus* on Madagascar and *H. tozerensis* Craven & B.E.Pfeil in Australia, both formerly called *Macrostelia*), /Phylloglandula (*Hibiscus papuodendron* Kosterm.; Craven and Pfeil 2004) and /Trionum (*Pavonia* subg. *Goetheoides*; Fryxell 1999).

Tribe Hibisceae is further rich in variation in epicalyx number, style number, carpel number, number of ovules per carpel, and fruit type (Fig. 2). The circumscriptions of *Hibiscus* and *Pavonia* have largely been based on simple fruit classification. However, the capsules of *Hibiscus* and schizocarps of *Pavonia* are clearly homoplasious and highly plastic. Contrary to Areces-Berazaín and Ackerman (2017), who state that schizocarpic fruit has arisen twice in Hibisceae, our data suggest that fruit evolution may be more complex. We find schizocarpy in at least four groups: 1) once to produce a large and diverse schizocarp clade whose earliest derivatives are the African *Pavonia* sects. *Afrolopimia*, *Collumellae*, and *Praemorsae*; 2) once to yield another African group of schizocarpic mallows comprising *Pavonia* sects. *Afrolebretonia* and *Afrotyphalea*; 3) once in another Old World group comprising *Pavonia* sects. *Craspedocarpidium* and *Pterocarpidium*; and 4) once in the genus *Urena* in the otherwise capsular/Phylloglandula clade. Our tree also suggests the first indication that the five carpel-10 style condition has evolved more than once (in/Trionum and/Phylloglandula; Fig. 2M, N).

New Classification for Tribe Hibisceae: “What to do about *Hibiscus* and *Pavonia*?”—The hybrid classification of Pfeil and Crisp (2005) broadly defined *Hibiscus* to include all embedded genera, with the exception of the/Megistohibiscus clade from Madagascar. Because of the new/Clypeati results, the/Megistohibiscus clade, too, is effectively embedded within *Hibiscus*. Our work provides additional insight and paves the way for a necessary taxonomic revision throughout the tribe (Barrett, Hanes, McLay in prep). Here we use our phylogenetic results to briefly introduce a classification scheme for the tribe and to specifically propose new, stricter generic limits for *Hibiscus* and *Pavonia*. See Supplemental Table S1 for a summary of the proposal.

Under the classification of Pfeil and Crisp (2005) we estimate that more than 450 names (including 300 *Pavonia* species) would need to be changed to encompass an expanded *Hibiscus*, as well as the dissolution of a minimum of 15 genera (14 of which remain well delineated on our tree). Here, in contrast, we propose to restrict *Hibiscus* to the/Euhibiscus clade and provide initial guidance on nomenclatural proposals throughout the other clades (Supplemental Table S1). In doing so we estimate that about 164 species will need to be transferred out of *Hibiscus*, the majority to *Sabdariffa* (DC.) Kostel. As about 120 generic names have been published for members of Hibisceae, generic names are already available for many of the additional lineages identified in our study. Therefore, splitting *Hibiscus* and *Pavonia* into a number of segregate genera, many of which already have names, rather than expanding *Hibiscus* to include *Pavonia*, results in fewer nomenclatural changes and a stable classification for tribe Hibisceae.

/CLYPEATI—Because *Hibiscus clypeatus* is sister to all species in tribe Hibisceae we propose a new monospecific genus to encompass this unique taxon outside of *Hibiscus*.

/MEGISTOHIIBISCUS—Following Pfeil and Crisp 2005, members in/Megistohibiscus should not be included in the genus *Hibiscus*. Thus, all species currently called *Hibiscus* in/Megistohibiscus will need to be transferred. The taxonomy of the ca. 13 species involved, including the currently monospecific *Jumelleanthus* whose phylogenetic affinity has remained elusive until now, are under investigation by Hanes and Callmander (in prep.).

/CAESIUS—*Hibiscus caesius* is sister to the remainder of Hibisceae. We propose a new monospecific genus to encompass this polymorphic species outside of *Hibiscus*.

/TRIONUM—This large group currently comprises approximately 425 species in 11 genera. We propose that this clade not be included within the genus *Hibiscus* as only approximately 40 species (from eight sections) of *Hibiscus* (24 of which are sampled here) fall into this clade. We propose instead a revised classification to represent ca. 21 different genera. Of note is our proposition to limit the genus *Pavonia* to New World members for a genus comprising 245 species already called *Pavonia*, but also to include an additional 42 species from the genera *Anotea*, *Malachra*, *Malvaviscus*, and *Peltaea* (and probably *Phragmocarpidium* and *Rojasimalva*, though not sampled here). A proposal to conserve the name *Pavonia* Cav. (1786) over the earlier names *Malvaviscus* Fabr. (1759) and *Malachra* L. (1767) has been published (Barrett et al. 2023).

/PHYLLOGLANDULA—This clade contains members of *Hibiscus* sect. *Furcaria*, *Decaschistia*, *Kydia*, *Talipariti*, and *Urena*. We propose to maintain all of the monophyletic genera in this clade and recognize *Hibiscus* sect. *Furcaria* at generic level as *Sabdariffa*. This represents the largest single-genus change proposed here for the reclassification of the Hibisceae. The genus *Sabdariffa* will consist of over 120 species of erect, often prickly-stemmed herbs and shrubs, found throughout the tropics. This genus is united by nectaries borne on veins on the calyx lobes and the lower portions of the leaves. The lower leaves are typically lobed, often deeply so, and the upper leaves less lobed or unlobed. The bracteoles of the epicalyx are usually forked or with a distinct terminal appendage. There are 10 diploid species (9 African, 1 American) and many polyploid species of hybrid origin, involving those 10, and other, now extinct, diploid species.

It will be important to further investigate the relationships of unsampled *Dicellostyles*, *Julostylis*, and *Nayariophyton*, however we note that the last two genera are both placed near *Kydia* in the published PAFTOL data set (Baker et al. 2022), and *Dicellostyles* has a very strong morphological similarity to *Nayariophyton* (Paul 1988).

/CALYPHYLLI—We propose that this clade also be excluded from *Hibiscus*. Such a change would necessitate name changes to ca. 8 species of *Hibiscus*. This clade, however, remains problematic (as discussed above), and *Hibiscadelphus* is embedded within members of *Hibiscus* sect. *Calyphylli*. More work is warranted to investigate relationships within this group as no obvious geographical or morphological affinities are readily apparent.

/EUIHIBISCUS—We propose to limit the genus *Hibiscus* to this clade. The type of the genus falls here and all 85 samples we provide here are called *Hibiscus* with only one exception: the monospecific genus *Helicteropsis* is embedded in this clade. *Helicteropsis* was described by Hochreutiner (1925) and was based on *Hibiscus perrieri* Hochr. which he later considered as a synonym of *Hibiscus microsiphon* Baill., providing the new combination *Helicteropsis microsiphon* (Baill.) Hochr. (Hochreutiner 1955). *Helicteropsis* should be considered as a synonym of *Hibiscus* and *H. microsiphon* as an accepted species endemic to northern Madagascar (Madagascar Catalogue 2022).

Hibiscus as defined here will encompass approximately 220 species and comprise five currently accepted sections of

Hibiscus (*H. sect. Bombicella* (ca. 130), *H. sect. Hibiscus* s.l. (33), *H. sect. Lilibiscus* (28), *H. sect. Solandra* (9), and *H. sect. Spatula* (11); species from Madagascar previously placed in the genus *Macrostelia*; and other recently described relatives (7; exemplified on the tree by *H. laurinus* Baill.) (Table 3; Supplemental Table S1).

Hibiscus sections *Bombicella* and *Hibiscus* are not monophyletic and clearly need revision. The American clade includes the type of *H. sect. Bombicella*, *H. phoeniceus*, and should be retained as *H. sect. Bombicella*. The smaller African clade (in *Bombicella* clade 1, including *H. aethiopicus*, *H. microcarpus*, and *H. pusillus*) is currently recognized as *H. subsect. Africanae-lobophyllae* Ulbr. Given the geographic patterns and species diversity of the Australian clade, we plan to make additional taxonomic changes at the sectional level for these species. The larger African clade (*Bombicella* clade 2: including *H. ferrugineus* Cav., etc.) was confusingly referred to by Ulbrich (1920–21) as *H. subsect. Eubombycella* Ulbr., implying that he believed this clade to be part of the true sect. *Bombicella*. In light of its distinctiveness, we plan to recognize a distinct section to encompass the species in this clade.

TAXONOMIC TREATMENT

Astrohibiscus McLay & R.L.Barrett, gen. nov. TYPE: *Hibiscus caesius* Garcke (= *Astrohibiscus caesius* (Garcke) McLay & R.L.Barrett)

Herbs, subshrubs or shrubs 0.3–1.5(–2) m high, sometimes sub-scandent. Branchlets commonly with sparse, coarse bristles, 1–2.2 mm long, hairs whitish, yellowish or brownish, or branchlets glabrous. Stipules $\pm$ persistent, or deciduous later, filiform, (3–)5–13(–25) mm long, 0.2–0.5 mm wide, with fine bristles. Mature leaves: petiole 20–80 mm long, indumentum similar or dissimilar to the branchlet; lamina usually lobed to the base, but lobes sometimes partly fused, with 3–7 lobes, the lobes elliptic, (15–)75–100 mm long, (5–)25–45 mm wide, the lobes longer than wide, attenuate, cuneate to obtuse at base, serrulate-serrate margin, acute to obtuse apex, concolorous, adaxial surface indumentum of very sparse simple or 1–3-armed hairs, rays 0.4–1.8 mm in diam, hairs sessile, abaxial surface indumentum of sparse to scattered coarse stellate hairs, mostly 3-armed, sometimes 1- or 2-armed, rays 0.5–2 mm in diam, hairs sessile, the indumentum more dense on the abaxial surface, the abaxial surface with midrib and primary vein indumentum dissimilar to the interveinal regions, indumentum whitish to yellowish. Flowers solitary in leaf axils; pedunculate, the peduncle (20–)30–120(–170) mm long, with coarse bristles and sparse stellate hairs; articulated pedicel very reduced, 2–5 mm long, with coarse bristles, pedicels marginally wider distally; epicalyx with coarse bristles and aculei, 7–10-lobes, the lobes fused at the base for 3–5 mm, straight, linear, held at 90° to the calyx and becoming recurved in fruit, 12–35 mm long at anthesis, ca. 1 mm wide, with sparse, coarse simple hairs persistent in fruit; calyx 5-lobed, 15–25 mm long (to 30 mm in fruit), lobes ovate, free almost to the base but always partly fused, for 1–5 mm, 3–5-nerved, indumentum of moderately dense, simple, whitish, appressed or apically curved hairs on apical half to three quarters of calyx, basally glabrous, nectary absent, calyx in fruit not distinctly inflated or accrescent; petals 18–55 mm long, to 40 mm wide, creamy yellow or yellow (rarely white,

sometimes drying green), with reddish-brown to deep purple petal spot, glabrous adaxially, with sparse stellate hairs abaxially, sometimes with fine simple hairs also, basally with a tuft of simple hairs between each petal, sometimes also with a few hairs on margin of petals; staminal column straight, 10–18 mm long, purple, stamens distributed along the distal 9.5–15 mm of the column, the filaments 1.5–3.0 mm long, anthers red or yellow; style exserted 1.5–3 mm beyond apex of staminal column, sparsely pilose, 5-branched, branches 1.3–2.0 mm long, stigmas entire, 0.7–0.8 mm wide, the hairs 0.1–0.3 mm long. Capsule ovoid, (7–)11–15 mm long, 6–12 mm diam, shortly beaked, sparse to moderately dense $\pm$ erect, simple, coarse hairs all over, glabrescent. Seeds 3 or 4 per cell, black, angular-subreniform, 2.8–5.0 mm long, 2.0–3.5 mm wide, with very short appressed cellular white hairs not all over hairy, hairs whitish, 0–0.1 mm long, with white funiculus. ($x = 18$; Dasgupta and Bhatt 1982; Fryxell and Stelly 1993).

Diagnostic Characters—The slender, radiating epicalyx lobes are found in a few other (unrelated) species, notably *Hibiscus meraukensis* Hochr. and *H. physaloides* Guill. & Perr. Both of these species have only shallowly lobed, or even entire leaves. Sometimes confused with *Hibiscus radiatus* Cav., a purple-red flowered species with shallowly to deeply lobed leaves and $\pm$ flat epicalyx lobes.

Distribution—A single species widely distributed in Southern Africa (Angola, Botswana, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe), Pakistan, India, and northern Australia.

Etymology—From the Greek *Astro-* (star) and *Hibiscus*, a Greek word for mallow, in reference to the stiff, radiating, star-like epicalyx and previous placement in the genus *Hibiscus*.

Astrohibiscus caesius (Garcke) McLay & R.L.Barrett, comb. nov. Basionym: *Hibiscus caesius* Garcke, *Bot. Zeit.* 7: 850 (1849). TYPE: MOZAMBIQUE: Tete, [1840s] *Peters* (holotype: B, destroyed). Neotype (here designated): Mozambique: Tete, ao 5 km, Estrada para Borona, margens do rio Zambeze (Dg), c. 250 m, 23 Mar. 1966, A.R.Torre & M.F.Correia 15,323 (neotype: WAG.1076523*; isoneotype: LISC, n.v.).

Hibiscus heterotrichus E. Mey. ex Harv. in Harv. & Sond., *Fl. Cap.* 1: 172 (1860), *nom. inval., pro syn.*

Hibiscus pentaphyllus F.Muell., *Fragm.* 2: 13 (1860), *nom. illeg., non Roxb.* (1832). TYPE: AUSTRALIA: Northern Territory: Victoria River, 1855–6, F.Mueller s.n. (holotype: K 000659832*).

Hibiscus gibsonii Stocks ex Harv. in Harv. & Sond., *Fl. Cap.* 2: 587 (1862). Type citation: “Hab. Damara land, *Miss Elliott!* (Herb. D., Hk.)” “It is a native of the Deccan and of Afghanistan and was also found by Dr. Kirk in S. E. Africa.” Lectotype (here designated): India: Deccan, J.E.Stocks s.n. (lectotype: L.2362572*; isoelectotypes: M 0211553*, P 06628552*). Residual syntypes: Namibia: Damaraland, *Miss Elliott* s.n. (syn: DBN, K, both n.v.); India: North Deccan, *Gibson* s.n. (syn: K 000659781*); S.E. Africa, *Dr Kirk* s.n. (syn: n.v.).

Hibiscus caesius var. *micropetalus* Gürke, *Abhand. Des Bot. Ver. Brandenburg* 30: 179 (1888), (as *micropetala*); Hochr., *Ann. Conserv. Jard. Bot. Genève* 4, 160 (1900). TYPE: NAMIBIA: Amboland, 1885, *Schinz* 207 (holotype: Z, n.v.).

Hibiscus caesius var. *genuinus* Hochr., *Ann. Conserv. Jard. Bot. Genève* 4: 160 (1900), *nom. inval.* (= the type variety).

Notes—We here designate a neotype for *Hibiscus caesioides* as there is no known original material extant. The majority of Peters' specimens were held at B, with some duplicates at A, BR, CGE, EA, K, and LE (Stafleu and Cowan 1983), but neither we nor previous workers have located any duplicates of *Hibiscus caesioides* to date. We select a recent specimen from the vicinity of the original location of 'Tete,' as cited by Hochreutiner (1900), who examined the type specimen before it was destroyed.

We also designate a lectotype for *Hibiscus gibsonii*, as there is confusion over what constitutes original material for the name. This arises as the name was published in a flora of the Cape Province of South Africa, yet the name was originally proposed as a name written on specimens collected in India and Afghanistan (Harvey and Sonder 1862). We choose to select a sheet collected by Stocks (who originally coined the name) in India, as this choice makes the name available for Indian plants if they are recognized as discrete from *H. caesioides* at some point in the future, and this choice mostly clearly represents Stocks' concept of the taxon.

The World Flora online and Plants of the World Online list *Hibiscus adscendens* G. Don (Aug. 1831) as a synonym of *H. caesioides*, and if correct, then it would be the earliest available name for this taxon. The original description (Don 1831) is relatively brief but appears consistent with *H. caesioides*. The species is recorded from 'Guinea' (West Africa), well outside the known range of *H. caesioides*. Don notes that the 'involucl' is unknown for this species, a curious comment if the species was indeed the same as *H. caesioides* as the epicalyx is prominent and persistent.

A single specimen on JSTOR Plants (accessed Feb. 2023) is retrieved for the name *Hibiscus adscendens*, and the specimen is marked as the type of this name. The specimen is from São Tomé and Príncipe, a large island off the coast of Equatorial Guinea, collected by George Don, and this specimen may reasonably be considered the holotype (BM000645518*), as indicated by Exell (1944), though searches for additional duplicates should be undertaken at other herbaria holding Don collections.

This specimen has short epicalyx lobes, which appears to be an anomaly to this specimen, and it is now identified as *Hibiscus physaloides* Guill. & Perr., a name published just four months before *H. adscendens*. *Hibiscus physaloides* normally has remarkably similar epicalyx lobes to *H. caesioides*, and while not closely related, it appears the two species are sometimes confused, but the leaves of *H. physaloides* are only shallowly lobed. The leaves on the type of *H. adscendens* are small, but the lobes are clearly fused, and we here accept the name as a synonym of *H. physaloides*.

Hibiscus ribesoides Steud., *Nom. Bot.* (edn 2); 1: 760 (1840) is sometimes also listed as a synonym of *H. caesioides*, even though it is an earlier name, but examination of the original publication shows that this is clearly an orthographic variant of *Hibiscus ribesifolia* Guill. & Perr. (= *H. physaloides*).

The type specimen of *Hibiscus pentaphyllus* would have been at MEL at the time it was named, but was subsequently sent to Bentham at K, who retained the material there and it appears that no duplicate remains at MEL.

Due to the wide distribution of *Astrohibiscus caesioides*, it has a range of common names, including dark-eyed hibiscus, five-finger mallow, five-leaflet hibiscus, river hibiscus.

Blanchardia M.M.Hanes & R.L.Barrett, gen. nov. TYPE: *Blanchardia clypeata* (L.) M.M.Hanes & R.L.Barrett (based on *Hibiscus clypeatus* L.).

Muenchhusia Heist. ex Raf., *Sylva Tellur.* 115 (1838), (as *Munchusia*), nom. illeg., non Heist. ex Fabr. (1763). TYPE species: *Muenchhusia tomentosa* Raf., nom. illeg., superfl. (= *Hibiscus clypeatus* L.)

Hibiscus sect. *Clypeati* O.J.Blanch. in Fryxell, *Syst. Bot. Monogr.* 25: 470 (1988). TYPE species: *Hibiscus clypeatus* L.

Shrubs or small trees 2–6 m high, erect. Branchlets with two hair types, with dense, yellowish, short, soft stellate-hairs and sometimes with an obscured line of fine, curved hairs, indumentum obscuring the epidermis. Stipules persistent, subulate, 3–18 mm long, with fine stellate-hairs. Mature leaves: petiole 20–120 mm long, indumentum yellowish, short, soft, stellate-hairy; lamina ovate to orbiculate, palmately 5–7-veined, glands absent, 100–220 mm long, 90–230 mm wide, broadly ovate or ovate-angulate to weakly 3–5(–7)-lobed, the middle lobe the longest and acuminate, lateral lobes acute or obtuse, or less frequently unlobed, base deeply and narrowly cordate to truncate, margins remotely and obscurely denticulate or undulate, apex acute to acuminate, discolorous, adaxial surface indumentum of dense stellate hairs, abaxial surface indumentum of dense stellate hairs, the indumentum more dense on the abaxial surface, the abaxial surface with midrib and primary vein indumentum similar to the interveinal regions, indumentum whitish. Flowers solitary in leaf axils, or sub-corymbose by reduction of internodes and subtending leaves; pedunculate, jointed in the middle, the peduncle 15–50 mm long, with dense fine hairs; obscurely articulated pedicel, 15–50 mm long, stout (3–4 mm diam); epicalyx shorter than the calyx, densely short stellate-hairy, the margins not ciliate, 6–10(–11)-lobed, the lobes free or shortly fused at the base for ca. 1 mm, often randomly incurved (sickle-shaped), remaining incurved in fruit, broadly linear-lanceolate to narrowly triangular, apex acute, base held at 90° to the calyx, unequal in length, (5–)10–30 mm long at anthesis, (1–)3–5 mm wide; calyx at anthesis campanulate, 5-lobed, 25–45 mm long, calyx lobes foliaceous, triangular to cordate-ovate, apex short-acuminate, distinctly 3–5-nerved, fused for one third to two thirds the length of the calyx, indumentum of dense, short stellate hairs on the abaxial surface, more dense towards the base, hairs whitish, nectary absent, calyx in fruit enlarged to 50 mm long, accrescent, ± inflated; corolla funnelform, distinctly zygomorphic; 2 upper petals straight and erect, slightly or not at all recurved, 3 lower petals recurved or their apices revolute, margins apically entire or repand; petals narrowly obovate, 32–55 mm long, 10–20 mm wide, greenish yellow to dull red or dull orange, more rarely pinkish, purple-brown or cream, fleshy, petal spot absent but vertical buttresses between the staminal column and each petal base act as elongated chambers that act as nectar reservoirs, tomentose throughout abaxially, with minute peg-like hairs adaxially; staminal column declinate to recurved, 25–42 mm long, essentially glabrous, pale yellowish to dull orange, stamens distributed in apical 1/3–1/2 of the column, the filaments 4–8(–10) mm long, minutely pubescent, secund and ascending, anthers 1.6–3 mm long, yellow to orange; ovary 5-locular, densely, long, yellowish hairy; style dull red to dull orange, exerted 2–6 mm beyond apex of

staminal column, 5-branched, branches ca. 1 mm long, stigmas entire, dull or dark red to dull orange, ca. 1.3 mm wide, glabrous. Capsule dull orange, ovoid to obovoid, enclosed in calyx, 25–50 mm long, 20–35 mm diam, with a beak 1–2 mm long, externally densely, minutely, coarsely, yellowish, farinose, stellate hairy with longer hispid hairs, hairs orangish, 2–3 mm long, internally pilose, hairs 3–5 mm long. Seeds 5–15 per locule, dark brown to reddish brown or blackish, mottled, subglobose, 3.5–4.5 mm long, ca. 2.0 mm wide, obscurely rugulose or appearing smooth, glabrous. ($x = 10$; Blanchard 1976).

Diagnostic Characters—Our phylogenetic data place this clade sister to all other members of Hibisceae. The strongly zygomorphic flowers, which persist for several days, are distinctive and may be an adaptation to bat pollination (Blanchard 1976).

Distribution—A single species, with three recognized subspecies, distributed from southern USA (Texas), through Mexico, Bahamas, Belize, Cayman Islands, Cuba, Dominican Republic, Guatemala, Haiti, Jamaica, Leeward Islands, Puerto Rico, and Turks-Caicos Islands. Restricted to limestone or limestone-derived rendzina soil in semiarid climates.

Etymology—The generic epithet honors Orland Joseph (Skip) Blanchard, Jr., an expert in *Kosteletzkya* and *Hibiscus*, who studied this group for his Ph.D. and was the first to recognize the distinctiveness of this lineage, recognizing it as a distinct section within *Hibiscus* (Blanchard 1976). He contributed many chromosome counts in Malvaceae and named two additional sections of *Hibiscus* (one of which we also intend to raise to the generic level; Blanchard 1976, 1978, 1988, 2008, 2015).

Conservation Status—*Blanchardia clypeata* (under *Hibiscus clypeatus*) is listed as Least Concern in the IUCN Red List (IUCN 2023).

Notes—Rafinesque (1838) published the name '*Munchusia*' without knowing its origin, and simply 'accepted' it from Heister. The reference to Heister leaves little doubt that the original intention of the name was to honor Otto von Münchhausen, in reference to Heister's original epithet (Fabricius 1763, as *Münchhusia*), variously written as *Muenchhusia* L., *Munchousia* L., or *Muenchhusia* Heist. ex Fabr., with Rafinesque apparently choosing to simplify the spelling further (or possibly even erroneously) to *Munchusia* Heist ex Raf. The spelling of the name is to be corrected to '*Muenchhusia*' and it is therefore a later homonym of *Muenchhusia* Heist. ex Fabr. Rafinesque's name could equally be interpreted as an orthographic variant.

Blanchardia clypeata (L.) M.M.Hanes & R.L.Barrett, comb. nov. Basionym: *Hibiscus clypeatus* L., *Syst. Nat.* (ed. 10): 2: 1149 (1759), non Walter (1788). *Muenchhusia tomentosa* Raf., *Sylva Tellur.* 115 (1838), nom. superfl. TYPE: [Icon] (holotype: C.Plumier, *Pl. Amer. Fasc.* 7, t. 160, Fig. 2, 1758).

Hibiscus tomentosus Mill., *Gard. Dict.* (ed. 8), no. 5 (1768), non Kuntze (1891). TYPE: JAMAICA: 1730, *Houstoun s.n.* (holotype: BM (photo US)).

Hibiscus berlandierianus Moric. ex Ser., *Bull. Bot. (Geneva)* 6: 174 (1830). TYPE: MEXICO: Tamaulipas: Tampico, 1827, *Berlandier* 54 (lectotype: CAS; isolectotypes: G, LE, P, W), designated by Fryxell, *Syst. Bot. Monogr.* 25: 203 (1988).

Hibiscus brachypus Urb., *Repert. Spec. Nov. Regni Veg.* 16: 34 (1919). TYPE: HAITI: Gonaïves, Oct 1901, *Buch* 800 (lectotype: J), designated by Fryxell, *Syst. Bot. Monogr.* 25: 203 (1988).

Blanchardia clypeata subsp. *clypeata*

Blanchardia clypeata subsp. *cryptocarpa* (A.Rich.) M.M.Hanes & R.L.Barrett, comb. nov. Basionym: *Hibiscus cryptocarpus* A.Rich. in R.de la Sagra, *Hist. Phys. Cuba, Pl. Vasc.* 1: 142 (1841 [1845]). *Abelmoschus cryptocarpus* (A.Rich.) Walp., *Repert. Bot. Syst.* 1: 310 (1842). *Hibiscus clypeatus* subsp. *cryptocarpus* (A.Rich.) O.J.Blanch. ex F.Areces & Fryxell, *Fl. Rep. Cuba, Ser. A. Pl. Vasc.* 13: 31 (2007); O.J.Blanch., *Novon* 18(1): 5 (2008). TYPE: CUBA: R.de la Sagra 881 (lectotype: P, *n.v.*; isolectotype: P), designated by O.J.Blanch. in F.Areces & Fryxell, *Fl. Rep. Cuba, Ser. A. Pl. Vasc.* 13: 32 (2007), confirmed by O.J.Blanch., *Novon* 18(1): 5 (2008).

Hibiscus eggersii Urb., *Symbol. Antill.* 5: 421 (1908). TYPE: CUBA: Rio Seco (Oriente Prov.), 200 m, Feb., Eggers 4716 (*n.v.*).

Distribution—Restricted to Cuba.

Blanchardia clypeata subsp. *membranacea* (Cav.) M.M.Hanes & R.L.Barrett, comb. nov. Basionym: *Hibiscus membranaceus* Cav., *Diss.* 3: 159, t. 57, Fig. 2 (1787). *Hibiscus clypeatus* subsp. *membranaceus* (Cav.) O.J.Blanch. ex F.Areces & Fryxell, *Fl. Rep. Cuba, Ser. A. Pl. Vasc.* 13: 31 (2007); O.J.Blanch., *Novon* 18: 5 (2008). TYPE: *s. loc.* [Bahamas], *s. dat.* [pre 1787], *s. coll.* [?M.Catesby] (holotype: P-JU, *n.v.*).

Hibiscus bahamensis Britton, *Bull. New York Bot. Gard.* 4: 120 (1906), nom. illeg., non Mill. (1768). *Hibiscus brittonianus* Kearney, *Leaf. W. Bot.* 7: 121 (1954). TYPE: BAHAMAS: Abaco, California Road, 3 Jan. 1905, L.J.K. Brace 2042 (lectotype: NY 84169; isolectotypes: F, K 000199690, NY 84168, US 98069), designated by O.J.Blanch. in F.Areces & Fryxell, *Fl. Rep. Cuba, Ser. A. Pl. Vasc.* 13: 32 (2007), confirmed by O.J.Blanch., *Novon* 18: 5 (2008).

Distribution—Known from the Bahamas, Caicos Islands and Île de la Tortue, Haiti.

Cravenia McLay & R.L.Barrett, gen. nov. TYPE: *Hibiscus panduriformis* Burm.f. (= *Cravenia panduriformis* (Burm.f.) McLay & R.L.Barrett)

Hibiscus sect. *Panduriformes* Ulbr. in A.Engler (ed.), *Die Pflanzenwelt Afrikas* 3(2): 397 (1921). TYPE SPECIES: *H. panduriformis* Burm.f.

Subshrubs or shrubs 0.4–3(–4) m high, spreading to erect. Branchlets with two or three hair types, with long and/or short soft stellate-hairs and with or without septate glandular hairs, indumentum commonly but not always obscuring the epidermis, long, soft and/or coarse stellate hairs 1.5–4(–5) mm long (when present), short stellate hairs 0.2–1.2 mm long. Stipules deciduous, filiform, 2–12 mm long, 0.1–0.2 mm wide, with fine simple hairs. Leaves: petiole 12–180 mm long, indumentum whitish to yellowish, short, soft, simple and stellate-hairy; lamina broadly elliptic, palmately 6–9-veined, glands absent, 21–185 mm long, 14–160 mm wide, sometimes entire but commonly shallowly to deeply 3–5-lobed, the lobes commonly wider than long, base cordate, margins serrate-dentate to crenate, apex acute to obtuse, discolorous, adaxial surface indumentum of dense simple and stellate hairs, abaxial surface indumentum of dense simple and stellate hairs, the indumentum more dense on the abaxial surface, the abaxial surface with midrib and primary vein indumentum similar to the interveinal regions, indumentum whitish to yellowish. Flowers 1–4 in leaf axils; pedunculate or rarely not, the peduncle (0)2–48 mm long, with dense fine bristles and sparse long hairs; obscurely

articulated pedicel, 3–18 mm long; epicalyx shorter to longer than the calyx, short soft simple and stellate-hairy, 5–9(–10) or 12–19-lobed, the segments shortly fused at the base for 1–2 mm, gently curved, narrowly spatulate to linear-obovate, apex usually obtuse, recurved, held $\pm$ parallel to the calyx, 5–35 mm long at anthesis, 0.5–5 mm wide, with dense, fine simple and stellate hairs on both sides; calyx at anthesis campanulate, 12–34 mm long, calyx lobes ovate, 3.5–13 mm long, 2–7 mm wide, apex acute or obtuse, 3-nerved, fused for ca. half the length of the calyx, indumentum of dense, short, soft simple and stellate hairs on the abaxial surface, hairs whitish or yellowish, nectary absent, calyx in fruit slightly enlarged, but not distinctly inflated or accrescent; petals 15–80 mm long, 8–65 mm wide, yellow, with reddish to deep purple petal spot, glabrous adaxially, with short, coarse stellate hairs abaxially; staminal column straight, 8–80 mm long, white at base, grading to red at apex, stamens distributed along the length of the column, the filaments 0.2–2 mm long, anthers yellow; ovary 5-locular, hairy, style exerted 1–1.5 mm beyond apex of staminal column, 5-branched, branches 0.2–6.5 mm long, stigmas entire. Capsule ovoid to globose, 10–25 mm long, 8–19 mm diam, with a beak 1–2 mm long, sparse to dense $\pm$ erect or antrorse prickles and scattered, short glandular hairs all over. Seeds ca. 6–numerous per cell, brown, angular-reniform, 2.0–3.5 mm long, 2.0–2.5 mm wide, concentrically ribbed, glabrous or sparsely to densely short simple and/or stellate-hairy, hairs brownish to yellowish, to 0.3 mm long. ($x = 12$ for *C. panduriformis*; Fryxell and Stelly 1993).

Diagnostic Characters—Our phylogenetic data place this clade sister to some members of *Hibiscus* sect. *Venusti* and *Abelmoschus*. *Abelmoschus* is readily recognized by the caducous calyx which splits asymmetrically at anthesis, the long, sharp-angled capsules, and smooth, glabrous seeds. *Hibiscus* sect. *Venusti* differs in having filiform (vs. spatulate) epicalyx lobes, relatively thin, papery (vs. $\pm$ leathery) leaves, and petals white (vs. yellow).

Distribution—A single species widely distributed from northern Africa (Benin, Burkina Faso, Cameroon, Chad, Ethiopia, Ghana, Kenya, Malawi, Mali, Mauritania, Nigeria, Senegal, Somalia, Tanzania, The Gambia, Togo, Uganda, Zambia), Yemen, across Asia in Pakistan, India, Myanmar, Indonesia, and the Philippines, to northern Australia, with five species endemic to northern Australia. Introduced in Madagascar and the Comoros, and possibly in Florida (USA) and Mexico.

Etymology—Named in memory of Lyndley (Lyn) Alan Craven (1945–2014), who had a particular passion for Australasian Hibisceae and Gossypieae (e.g. Craven and Fryxell 1989; Fryxell and Craven 1989; Fryxell et al. 1992; Wilson and Craven 1995; Pfeil et al. 2002, 2004; Juswara and Craven 2005; Craven et al. 2011, 2016). Lyn encouraged RLB to undertake further research with the aim of defining monophyletic genera in Hibisceae.

Notes—The genus as defined here was effectively reviewed by Juswara and Craven (2005) as a revision of the *Hibiscus panduriformis* complex in Australia, where all currently recognised species are found. Craven and Fryxell (1993) suggested that *Hibiscus brennanii* Craven & Fryxell belonged here also, but molecular data place that species in *Hibiscus* sect. *Furcaria* (McLay unpubl. data).

Alefeld (1863) published the genus *Triplochiton* Alef. for two species, *T. setosa* Alef. [= *Cravenia panduriformis*] and *T. spathacea* Alef. [= *Talipariti macrophyllum* (Roxb. ex

Hornem.) Fryxell], however this name has been rejected against *Triplochiton* K. Schumann (1900), so it is not available.

Cravenia apoda (Juswara & Craven) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus apodus* Juswara & Craven, *Blumea* 52(2): 391, Fig. 1 (2005). TYPE: AUSTRALIA. Western Australia: 5 km NNE of Broome, 29 May 1985, P.A. Fryxell, L.A. Craven & J. McD. Stewart 4550 (holotype: CANB 377255; isotypes: BRI, MEL, NY, PERTH).

Cravenia austrina (Juswara & Craven) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus austrinus* Juswara & Craven, *Blumea* 52(2): 393, Fig. 2 (2005). *Hibiscus panduriformis* var. *australis* Hochr., *Ann. Cons. Jard. Bot. Genève* 4: 96 (1900), replaced synonym. TYPE: AUSTRALIA. Northern Territory: Port Darwin (Palmerston), Dec. 1891, Herb. Boissier 97 (holotype: G).

Note—*Hibiscus austrinus* var. *occidentalis* Juswara & Craven is not recombined here and is tentatively included as a synonym of *C. calcicola* pending further study by T. McLay.

Cravenia calcicola (Juswara & Craven) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus calcicola* Juswara & Craven, *Blumea* 52(2): 396, Fig. 3 (2005). TYPE: AUSTRALIA. Western Australia: Geikie Gorge National Park, 22 May 1981, J.G. Tracey 13889 (holotype: BRI AQ0403157*; isotypes: CNS QRS81665*, DNA D0058373*, PERTH 03433013*).

?*Hibiscus austrinus* var. *occidentalis* Juswara & Craven, *Blumea* 52(2): 394, Fig. 2 (2005). TYPE: AUSTRALIA. Western Australia: Junction of Stuart and Robinson Rivers, $\pm$ 72 km NNW of Derby, 13 June 1976, A.C. Beauglehole 52782 (holotype: PERTH 3433978; iso: DNA).

Cravenia fluvialis (Juswara & Craven) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus fluvialis* Juswara & Craven, *Blumea* 52: 398, Fig. 4 (2005). TYPE: AUSTRALIA. Northern Territory: Daly River Mission, 22 May 1983, P.A. Fryxell & L.A. Craven 4242 (holotype: CANB; isotypes: AD, BISH, BRI, DNA, K, L, MEL, NY, PERTH, UC, US).

Cravenia multilobata (Juswara & Craven) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus multilobatus* Juswara & Craven, *Blumea* 52(2): 400, Fig. 5 (2005). TYPE: AUSTRALIA. Northern Territory: Kakadu National Park to Koolpin Gorge road, c. 6 km due E of El Sharana, 23 April 1990, A.V. Slee, L.A. Craven, C.R. Dunlop & R. Munns 2784 (holotype: CANB; isotype: DNA, MEL).

Cravenia panduriformis (Burm.f.) McLay & R.L. Barrett, comb. nov. Basionym: *Hibiscus panduriformis* Burm.f., *Fl. Ind.* 151, t. 47, Fig. 2 (1768). *Parita panduriformis* (Burm.f.) Scop., *Intr. Hist. Nat.* 282 (1777), *nom. inval.* *Hibiscus tubulosus* Cav., *Diss.* 3: 161, t. 68, Fig. 2, (1787), *nom. illeg.* *Hibiscus stipularis* Salisb., *Prodr. Stirp. Chap. Allerton*: 384 (1796), *nom. illeg.* *Abelmoschus panduriformis* (Burm.f.) Hassk., *Tijdsch. Natuurl. Gesch. Physiol.* 10: 134 (1843). *Hibiscus panduriformis* var. *tubulosus* (Cav.) Hochr., *Ann. Cons. Jard. Bot. Genève* 4: 96 (1900). TYPE: [Icon] Burm.f., *Fl. Ind.* 151, t. 47, Fig. 2. (1768).

Hibiscus velutinus DC., *Prodr.* 1: 452 (1824). TYPE: TIMOR: Riedlé s.n. (holotype: G-DC).

Hibiscus pilosus Roxb. ex Wall. ex Wall., *Numer. List* [Wallich] n. 1902 (1829), *nom. nud.*, *non* (Sw.) Fawc. & Rendle (1926).

Hibiscus setosus Wall., *Numer. List*: no. 1902 (1829), *nom. nud.*, *non* Roxb. (1832).

Hibiscus senegalensis Guill. & Perr., *Fl. Seneg. Tent.*: 53 (1831), *nom. illeg.*, *non* Cav. (1787).

Hibiscus mollis Zipp. ex Span., *Linnaea* 15: 169 (1841), *nom. inval., pro syn.*
Hibiscus multistipulatus Garke, *Bot. Zeit.* 7: 849 (1849). TYPE: 'East Africa,' no coll. (holotype: B, destroyed).
Triplochiton setosa Alef., *Oesterr. Bot. Z.* 12: 13 (1863). TYPE: INDONESIA: 'Java, Baum. [Burman]' (possible syn: K0001114652).
Hibiscus friesii Ulbr., *Repert. Spec. Nov. Regni Veg.* 13: 521 (1915). TYPE: Northern Rhodesia [Zambia]: near Broken Hill, 7 Aug. 1911, R.E. Fries 239 (holotype: B, destroyed).

Notes—The specific epithet has commonly been mis-spelt as 'panduraeformis.'

As noted by Juswara and Craven (2005), the entity originally named *Hibiscus senegalensis* Guill. & Perr. (nom. illeg., non Cav.) may warrant taxonomic recognition and this should be investigated further.

It is possible that the Chinese species *Hibiscus aridicola* J. Anthony also belongs here (see Tang et al. 2007 for a description), but there are numerous floral differences, and in the absence of molecular data, and first-hand examination of herbarium specimens, we refrain from providing a new combination at this time.

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AUTHOR CONTRIBUTIONS

MMH designed the study and was the primary contributor to the manuscript. OJB designed the study and contributed to the manuscript. JVD edited, curated and analyzed data. TGBM designed the study, generated data, analyzed the data, and contributed to the manuscript. JRA designed the study and contributed to the manuscript. SFM contributed to the manuscript. RLB contributed to the manuscript. SM contributed to the manuscript. KMN designed the study, generated, edited, curated and analyzed data, and contributed to the manuscript.

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APPENDIX 1. Vouchers and GenBank accession numbers of species sampled in this study. Order of data are species, authority, origin, collector and voucher number (herbarium), GenBank accession numbers (*matK*, *ndhF*, *trnQ-rps16*, *ycf1*, — = sequence not obtained), sequence source. Taxa are grouped by major clade and then listed alphabetically by genus and species.

/Caesius: *Hibiscus*. *Hibiscus caesius* Garcke, Smith 2370 (MO), Botswana, MZ394880, MZ419930, MZ542093, MZ612349, sanger; *Stewart* 15084 (MO), India, MZ394912, MZ419960, MZ542234, MZ612386, sanger; *Eichler* 22299 (MO), Australia, MZ394947, MZ419992, MZ542238, MZ612299, sanger; *Harvey* s.n. (CANB), Australia, MZ394948, MZ419993, MZ542206, MZ612144, skim; *Legge* 811 (CANB), Australia, MZ394949, MZ419994, MZ542207, MZ612145, sanger.

/Calyphylli: *Hibiscadelphus*. *Hibiscadelphus distans* L.E. Bishop & Herbst, *Perlman* 7035 (MO), USA, Hawaii, MZ394857, —, MZ542085, MZ612326, sanger; *Randall* s.n. (FLAS), USA, Hawaii, MZ394858, MZ419909, MZ542086, MZ612348, sanger; *Hibiscus*. *Hibiscus calyphyllus* Cav., *Craven* 10341 (CANB), Australia, MZ394881, MZ419931, MZ542205, MZ612138, skim; *Mwangulango* 879 (MO), Tanzania, MZ394882, MZ419932, MZ542087, MZ612235, sanger; *Hibiscus* cf. *dongolensis* Caill. ex Delile, *Mwangoka* 4259 (MO), Tanzania, MZ394884, MZ419934, MZ542089, MZ612236, sanger; *Hibiscus* cf. *ludwigii* Eckl. & Zeyh., *Kucher* 24706 (MO), Tanzania, MZ394885, MZ419935, MZ542090, MZ612238, sanger; *Hibiscus comoensis* A.Chev. ex Hutch. & Dalziel, *Jongkind* 1913 (MO), Ghana, MZ394893, MZ419943, MZ542255, MZ612239, sanger; *Hibiscus lunariifolius* Willd., *Molle* 161 (MO), Tanzania, MZ394928, MZ419974, MZ542091, MZ612366, sanger; *Hibiscus ovalifolius* (Forssk.) Vahl, *Gobbo* 339 (MO), Tanzania, MZ394939, MZ419985, MZ542088, MZ612363, sanger; *Hibiscus seineri* Ulbr., *Schmidt* 2365 (MO), Zambia, MZ394965, MZ420009, MZ542092, MZ612361, sanger; *Hibiscus* sp. *Blanchard* 1690 (FLAS), Kenya, MZ394971, MZ420015, MZ542158, MZ612191, sanger.

/Clypeatus: *Hibiscus*. *Hibiscus clypeatus* L., *Correa* 165 (MO), Mexico, MZ394889, MZ419939, MZ542104, MZ612293, sanger; *Martinez* 29957 (MO), Mexico, MZ394890, MZ419940, MZ542105, MZ612207, sanger.

/Euhibiscus: *Hibiscus*. *Hibiscus acicularis* Standl., *Patterson* 6604 (MO), Mexico, MZ394859, MZ419910, MZ542196, MZ612226, sanger; *Hibiscus aethiopicus* L., *Hull* 172 (MO), South Africa, MZ394861, MZ419912, MZ542111, MZ612314, sanger; *Hibiscus allenii* Sprague & Hutch., *Harder* 4034 (MO), Zambia, MZ394862, MZ419913, MZ542130, MZ612227, sanger; *Hibiscus antanossarum* Baill., *Labat* 3651 (MO), Madagascar, MZ394863, MZ419914, MZ542150, MZ612228, sanger; *Hibiscus arenicola* A.S.Mitch., *Bull* 17.01 (PERTH), Australia, MZ394865, MZ419916, MZ542160, MZ612184, skim; *Hibiscus amottianus* A.Gray, *Lorence* 8171 (MO), USA, Hawaii, MZ394866, MZ419917, MZ542147, MZ612290, sanger; *Hibiscus barbosae* Exell, *Brown* 302 (MO), South Africa, MZ394868, MZ419919, MZ542132, MZ612329, sanger; *Hibiscus barnardii* Exell, *Brusse* 5773 (MO), South Africa, MZ394869, MZ419920, MZ542134, MZ612291, sanger; *Hibiscus bernieri* Baill., *Bardot-Vaucoulon* 1783 (MO), Madagascar, MZ394870, MZ419921, MZ542146, MZ612229, sanger; *Hibiscus biseptus* S.Watson, *Bertelsen* s.n. (MO), USA, Arizona, MZ394871, MZ419922, MZ542117, MZ612230, sanger; *S.Watson*, *Lott* 2098 (MO), Mexico, MZ394872, MZ419923, MZ542118, MZ612231, sanger; *Reina* 98–2136 (MO), Mexico, MZ394873, MZ419924, MZ542119, MZ612232, sanger; *Hibiscus boryanus* DC., *Lorence* 7955 (MO), USA, Hawaii, MZ394874, MZ419925, MZ542149, MZ612315, sanger; *Hibiscus brachychlaenus* F.Muell., *Latz* 7044 (MO), Australia, MZ394875, MZ419926, MZ542113, MZ612233, sanger; *Hibiscus brachysiphonius*

- F.Muell., *Purdie* 7884 (CANB), Australia, MZ394876, MZ419927, MZ542248, MZ612137, skim; *Hibiscus caeruleus* Baill., *Koopman* 233 (MO), Madagascar, EF207265, EF207297, —, —, sanger; *Rahajao* 220 (MO), Madagascar, MZ394879, —, MZ542156, —, sanger; *Hibiscus campanulatus* A.J.Perkins, *Naaykens* 14-8-J420 (PERTH), Australia, MZ394883, MZ419933, MZ542170, MZ612139, skim; *Hibiscus cf. eriospermus* Hochst. ex Cufod., *Mlongwa* 814 (MO), Tanzania, —, —, MZ542131, MZ612237, sanger; *Hibiscus cf. micranthus* L.f., *Blanchard* 1355 (FLAS), Kenya, MZ394886, MZ419936, MZ542143, MZ612298, sanger; *Hibiscus citrinus* Fryxell, *Blanchard* 3431 (FLAS), Mexico, MZ394887, MZ419937, MZ542126, MZ612172, sanger; *Hibiscus clayi* O.Deg. & I.Deg., *Palmer* 800 (MO), USA, Hawaii, MZ394888, MZ419938, MZ542148, MZ612292, sanger; *Hibiscus coulteri* Harv. ex A.Gray, *Nesom* 7383 (MO), Mexico, MZ394894, MZ419944, MZ542121, MZ612240, sanger; *Turner* 93-113 (MO), Mexico, MZ394895, MZ419945, MZ542122, MZ612370, sanger; *Hibiscus debeertii* De Wild. & T.Durand, *Smith* 591 (MO), Zambia, MZ394896, MZ419946, MZ542199, MZ612391, sanger; *Hibiscus denuatus* Benth., *Blanchard* 3436 (FLAS), Mexico, MZ394897, MZ419957, MZ542191, MZ612241, sanger; *Hibiscus elegans* Standl., *Tenorio* 20098 (MO), Mexico, MZ394899, MZ419949, MZ542181, MZ612359, sanger; *Hibiscus elliotiae* Harv., *Burgoyne* 3473 (MO), Namibia, MZ394900, MZ419950, MZ542192, MZ612353, sanger; *Hibiscus erodifolius* Hochr. & Humbert, *Phillipson* 2928 (MO), Madagascar, MZ394903, MZ419953, MZ542154, MZ612343, sanger; *Hibiscus ferrugineus* Cav., *Koopman* 235 (MO), Madagascar, EF207268, EF207300, —, —, sanger; *McPherson* 14939 (MO), Madagascar, MZ394904, MZ419954, MZ542137, MZ612296, sanger; *Phillipson* 3942 (MO), Madagascar, MZ394905, MZ419955, MZ542135, MZ612297, sanger; *Randriatafika* 399 (MO), Madagascar, MZ394906, MZ419956, MZ542133, MZ612310, sanger; *Hibiscus flavifolius* Ulbr., *Blanchard* 1689 (FLAS), Kenya, MZ394907, MZ419957, MZ542191, MZ612244, sanger; *Hibiscus fuscus* Garcke, *Blanchard* 3419 (FLAS), Kenya, MZ394910, MZ419958, MZ542140, MZ612179, sanger; *Hibiscus geranioides* A.Cunn. ex Benth., *Blanchard* 3441 (FLAS), Australia, MZ394911, MZ419959, MZ542252, MZ612245, sanger; *Hibiscus grandidieri* Baill., *Ramanjananahary* 182 (TAN), Madagascar, EF207263, —, —, —, sanger; *Hibiscus hirtus* L., *Craven* 10449 (CANB), Australia, MZ394914, MZ419962, MZ542200, MZ612140, skim; *Hibiscus humbertianus* Hochr., *DuPuy* s.n. (P), Madagascar, EF207266, EF207298, —, —, sanger; *Phillipson* 3952 (MO), Madagascar, MZ394915, MZ419963, MZ542155, MZ612317, sanger; *Hibiscus insularis* Endl., *Blanchard* 3463 (FLAS), Australia, MZ394918, MZ419966, MZ542123, MZ612210, sanger; *Hibiscus kochii* Fryxell, *Koch* 79466 (MO), Mexico, MZ394920, MZ419967, MZ542261, MZ612247, sanger; *Hibiscus laurinus* Baill., *Malcomber* 2806 (MO), Madagascar, EF207267, EF207299, —, —, sanger; *Hibiscus lavateroides* Moric. ex Ser., *Jones* 178 (MO), Mexico, MZ394923, —, MZ542269, MZ612388, sanger; *Hibiscus leptocladus* Benth., *Craven* 6650 (MO), Australia, MZ394924, MZ419970, MZ542265, MZ612330, sanger; *Hibiscus lobatus* (Murray) Kuntze, *Bardot-Vaucoulon* 1628 (MO), Madagascar, MZ394925, MZ419971, MZ542157, MZ612219, sanger; *Russell-Smith* 7998 (CANB), Australia, MZ394926, MZ419972, MZ542171, MZ612141, skim; *Hibiscus longifolius* Fryxell, *Tenorio* 21310 (MO), Mexico, MZ394927, MZ419973, MZ542125, MZ612249, sanger; *Hibiscus macilvraithensis* (Fryxell) Craven & B.E.Pfeil, *Forster* 10626 (CANB), Australia, MZ394929, MZ419975, MZ542161, MZ612142, skim; *Hibiscus martianus* Zucc., *Correll* 32237 (MO), Mexico, MZ394931, MZ419977, MZ542270, MZ612250, sanger; *Fryxell* 1323 (MO), Mexico, MZ394932, MZ419978, MZ542159, MZ612173, sanger; *Hibiscus meyeri* Harv., *Blanchard* 3432 (FLAS), Swaziland, MZ394933, MZ419979, MZ542193, MZ612251, sanger; *Sitoni* 1144 (MO), Tanzania, MZ394934, MZ419980, MZ542141, MZ612252, sanger; *Hibiscus microcarpus* Garcke., *Makwarela* 30 (MO), South Africa, MZ394935, MZ419981, MZ542112, MZ612253, sanger; *Hibiscus microchaetus* F.Muell., *Blanchard* 3448 (FLAS), Australia, MZ394936, MZ419982, MZ542114, MZ612212, sanger; *Hibiscus microsiphon* Baill., *Bardot-Vaucoulon* 1754 (MO), Madagascar, MZ394855, MZ419907, MZ542144, MZ612199, sanger; *Ranaivo-jaon* 468 (MO), Madagascar, MZ394856, MZ419908, MZ542145, MZ612409, sanger; *Hibiscus normanii* F.Muell., *Craven* 10432 (CANB), Australia, MZ394938, MZ419984, MZ542172, MZ612182, skim; *Hibiscus oxaliflorus* Bojer ex Baker, *Harder* 1547 (MO), Madagascar, MZ394940, MZ419986, MZ542151, MZ612254, sanger; *Hibiscus paramutabilis* L.H.Bailey, *Bin* 8533 (MO), China, MZ394944, MZ419989, MZ542254, MZ612257, sanger; *Hibiscus pedunculatus* L.f., *Harder* 42 (CBG), Australia, MZ394946, MZ419991, MZ542210, MZ612143, skim; *Hibiscus peralbus* Fryxell, *RPSConsultants* 488 (PERTH), Australia, MZ394950, MZ419995, MZ542201, MZ612146, skim; *Hibiscus phoeniceus* Jacq., *Stevens* 26928 (MO), Nicaragua, MZ394951, MZ419996, MZ542267, MZ612311, sanger; *Hibiscus poeppigii* (Spreng.) Garcke, *Blanchard* 1746 (FLAS), Mexico, MZ394954, MZ419999, MZ542263, MZ612258, sanger; *Carnevali* 5939 (MO), Mexico, MZ394955, MZ420000, MZ542127, MZ612213, sanger; *Garcia* 1210 (MO), Mexico, MZ394956, MZ420001, MZ542128, MZ612331, sanger; *Stearn* 463 (MO), Mexico, MZ394957, MZ420002, MZ542129, MZ612259, sanger; *Tapia* 1250 (MO), Mexico, MZ394958, MZ420003, MZ542198, MZ612360, sanger; *Hibiscus praeteritus* R.A.Dyer, *Fynn* 49 (MO), South Africa, MZ394959, MZ420004, MZ542142, MZ612260, sanger; *Hibiscus propulsator* Craven & B.E.Pfeil, *Gray* 6856 (CANB), Australia, MZ394960, MZ420005, MZ542163, MZ612147, skim; *Hibiscus pusillus* Thunb., *Glen* 2537 (MO), South Africa, MZ394961, MZ420006, MZ542115, MZ612221, sanger; *Kemp* 1170 (MO), South Africa, MZ394962, —, MZ542223, MZ612372, sanger; *Hibiscus rhodanthus* Gürke, *Gereau* 5207 (MO), Tanzania, MZ394963, MZ420007, MZ542138, MZ612261, sanger; *LaCroix* 4731 (MO), Malawi, MZ394964, MZ420008, MZ542139, MZ612332, sanger; *Hibiscus rosasinensis* L., unknown voucher, unknown origin, MK382984, MK382984, MK382984, GenBank; *Hibiscus shirensis* Sprague & Hutch., *Mwangoka* 3954 (MO), Tanzania, MZ394967, MZ420011, MZ542136, MZ612318, sanger; *Hibiscus sidiformis* Baill., *Harder* 3835 (MO), Zambia, MZ394968, MZ420012, MZ542152, MZ612319, sanger; *Hibiscus sinosyracus* L.H.Bailey, *Lai* 12 (MO), China, MZ394969, MZ420013, MZ542124, MZ612345, sanger; *Hibiscus* sp., *Blanchard* 3440 (FLAS), Australia, MZ394972, MZ420016, MZ542266, MZ612222, sanger; *Hibiscus stenophyllus* Baker, *Labat* 3658 (MO), Madagascar, MZ394974, MZ420018, MZ542153, MZ612264, sanger; *Hibiscus sturtii* Hook., *Latz* 13519 (MO), Australia, MZ394976, MZ420020, MZ542190, MZ612402, sanger; *Nelson* 1461 (MO), Australia, MZ394977, MZ420021, MZ542116, MZ612217, sanger; *Hibiscus syriacus* L., unknown voucher, unknown origin, MH330684, MH330684, MH330684, GenBank; *Hibiscus tozerensis* Craven & B.E.Pfeil, unknown voucher, Australia, EF207269, EF207301, —, —, sanger; *Forster* 9095 (CANB), Australia, MZ394978, MZ420022, MZ542162, MZ612149, sanger; *Hibiscus waimeae* A.Heller, *Koopman* s.n. (WIS), USA, Hawaii, EF207262, AF384654, —, —, GenBank.
- /Megistohibiscus: Hibiscus.** *Hibiscus bojerianus* Baill., *Baum* 383 (MO), Madagascar, EF207275, EF207306, —, —, sanger; *Hibiscus columnaris* Cav., *Lorence* 8504 (MO), USA, Hawaii, MZ394892, MZ419942, MZ542072, MZ612316, sanger; *Hibiscus diplocrater* Hochr., *Noyes* 1026 (MO), Madagascar, MZ395002, MZ420046, MZ542177, MZ612410, sanger; *Hibiscus macrogonus* Baill., *Koopman* 289 (MO), Madagascar, EF207273, EF562456, MZ542073, MZ612399, sanger; *Hibiscus mandrarenensis* Humbert ex Hochr., *Phillipson* 3978 (MO), Madagascar, EF207274, EF207305, MZ542077, MZ612344, sanger; *Hibiscus retrobracteatus* (Hochr.) M.M. Hanes & Callm., *Bardot-Vaucoulon* 1555 (MO), Madagascar, MZ395015, MZ420058, MZ542075, MZ612271, sanger. **Humbertiella.** *Humbertiella decaryi* (Hochr.) Dorr, *Baum* 385 (MO), Madagascar, EF207279, EF207310, MZ542095, MZ612270, sanger; *Humbertiella henrici* Hochr., *Koopman* 236 (MO), Madagascar, EF207281, EF207312, —, MZ612203, sanger; *Humbertiella quarariboides* Hochr., *Baum* 389 (MO), Madagascar, EF207280, EF207311, MZ542097, MZ612389, sanger; *Humbertiella sakamaliensis* (Hochr.) Dorr, *McPherson* 14942 (MO), Madagascar, MZ394989, MZ420033, MZ542096, MZ612338, sanger. **Jumelleanthus.** *Jumelleanthus perrieri* Hochr., *Wohlhauser* 60271 (MO), Madagascar, MZ394990, MZ420034, MZ542074, MZ612377, sanger. **Megistostegium.** *Megistostegium microphyllum* Hochr., *Koopman* 386 (MO), Madagascar, EF207278, MZ420077, MZ542099, MZ612379, sanger; *Schatz* 2967 (MO), Madagascar, MZ395036, —, MZ542100, MZ612396, sanger; *Megistostegium nodulosum* (Drake) Hochr., *Koopman* 308 (WIS), Madagascar, MZ395037, MZ420078, MZ542102, MZ612374, sanger; *Megistostegium perrieri* Hochr., *Koopman* 380 (MO), Madagascar, EF207277, MZ420079, MZ542101, MZ612375, sanger. **Perrierophytum.** *Perrierophytum humbertii* Hochr., *Miller* 6133 (MO), Madagascar, MZ395100, MZ420132, MZ542103, MZ612313, sanger; *Phillipson* 3480 (US), Madagascar, EF207284, EF207315, —, —, sanger; *Perrierophytum macranthum* (Hochr.) M.M. Hanes & Callm., *Blanchard* 3408 (FLAS), Madagascar, MZ395007, MZ420051, —, MZ612159, sanger; *Perrierophytum malvocoeruleum* (Hochr.) M. Hanes & Callm., *Razafindrakoto* 2266 (MO), Madagascar, MZ395008, MZ420052, MZ542189, MZ612218, sanger; *Perrierophytum reflexiflorum* (Hochr.) M.M. Hanes & Callm., *Koopman* 258 (MO), Madagascar, EF207283, EF207314, MZ542109, MZ612371, sanger; *Phillipson* 2898 (MO), Madagascar, MZ395014, —, MZ542110, MZ612214, sanger; *Perrierophytum rubrum* Hochr., *Phillipson*

2543 (MO), Madagascar, EF207285, EF207316, —, —, sanger; *Perrierophytum thoursianum* (Baill.) M.M. Hanes & Callm., *Blanchard* 3453 (FLAS), Madagascar, MZ395018, MZ420061, MZ542268, MZ612183, sanger; *Perrierophytum velutinum* (Garcke) M.M. Hanes & Callm., *Koopman* 215 (MO), Madagascar, EF207282, EF207313, MZ542222, MZ612196, sanger; *Phillipson* 3829 (MO), Madagascar, MZ395021, MZ420064, MZ542232, MZ612272, sanger; *Perrierophytum viscosum* Hochr., *Noyes* 1075 (MO), Madagascar, MZ395101, MZ420133, MZ542098, MZ612342, sanger.

/Phylloglandula: Decaschistia. Decaschistia byrnesii Fryxell, *Mitchell* 2893 (CANB), Australia, MZ394849, MZ419903, MZ542259, MZ612135, skim; *Decaschistia occidentalis* A.S.Mitch. ex Craven & Fryxell, *Craven* 9240 (CANB), Australia, MZ394850, MZ419904, MZ542273, MZ612136, skim. *Hibiscus. Hibiscus aculeatus* Roxb., *Abbott* 22842 (FLAS), USA, Florida, MZ394860, —, —, —, sanger; *Blanchard* 3344 (FLAS), USA, Florida, —, MZ419911, MZ542262, MZ612327, sanger; *Hibiscus brackenridgei* A.Gray, *Blanchard* 3454 (FLAS), USA, Hawaii, MZ394877, MZ419928, MZ542079, MZ612234, sanger; *Hibiscus cannabinus* L., unknown voucher, unknown origin, MK404537, MK404537, MK404537, GenBank; *Small* s.n. (TENN), cultivated, EF207259, EF207290, —, —, GenBank; *Hibiscus costatus* A.Rich., *Fryxell* 740 (MO), Mexico, AY589057, U55323, —, —, GenBank; *Hibiscus diversifolius* Jacq., *Blanchard* 3469 (FLAS), USA, Hawaii, MZ394898, MZ419948, MZ542258, MZ612295, sanger; *Hibiscus furcellatus* Desr., *Abbott* 25211 (FLAS), USA, Florida, MZ394909, —, MZ542243, MZ612223, sanger; *Blanchard* voucher # not yet assigned (FLAS), USA, Hawaii, MZ394986, MZ420030, MZ542249, MZ612269, sanger; *Hibiscus parvifolius* F.D.Wilson, *Wilson* 96-1 (MO), cultivated, MZ394945, MZ419990, MZ542084, MZ612352, sanger; *Hibiscus splendens* C.Fraser ex Graham, *Bowles* H95.057 (CANB), Australia, MZ394973, MZ420017, MZ542169, MZ612148, skim; *Hibiscus surattensis* L., *Small* s.n. (TENN), unknown origin, EF207258, AF384626, —, —, GenBank; *Hibiscus uncinellus* Moc. & Sessé ex DC., *Blanchard* 3458 (FLAS), Mexico, MZ394984, MZ420028, MZ542078, MZ612268, sanger. *Kydia. Kydia calycina* Roxb., *R. Neupaney* s.n., India, EF207261, EF207293, —, —, GenBank; *SuGong* WS-2635 (MO), Laos, MZ395022, —, —, MZ612339, sanger. *Talipariti. Talipariti elatum* (Sw.) Fryxell, *Taylor* 10898 (MO), Puerto Rico, MZ395106, MZ420136, MZ542076, MZ612367, sanger; *Talipariti hamabo* (Siebold & Zucc.) Fryxell, unknown voucher, unknown origin, KR259988, KR259988, KR259988, KR259988, GenBank; *Talipariti hastatum* (L.f.) Fryxell, *Frank* 662 (FLAS), USA, Florida, MZ395107, MZ420137, MZ542276, MZ612404, sanger; *Talipariti macrophyllum* (Roxb. ex Hornem.) Fryxell, *Craven* 10202 (CANB), Australia, MZ395108, MZ420138, MZ542226, MZ612169, skim; *Talipariti tiliaceum* (L.) Fryxell, *Bowles* H95.022 (CANB), Australia, MZ395109, MZ420139, MZ542168, MZ612170, skim. *Urena. Urena armitiana* F.Muell., *Blanchard* 3455 (FLAS), Australia, MZ395110, MZ420140, MZ542080, MZ612208, sanger; *Clarkson* 6942 (CANB), Australia, MZ395111, MZ420141, MZ542264, MZ612171, skim; *Urena australiensis* Fryxell & Craven, *Blanchard* 3433 (FLAS), Australia, MZ395112, MZ420142, MZ542081, MZ612347, sanger; *Urena lobata* L., *Beck* 5143 (MO), Bolivia, MZ395113, MZ420143, —, —, sanger; *Blanchard* 3449 (FLAS), Australia, MZ395114, MZ420144, MZ542082, MZ612202, sanger; *Hu* 23840 (MO), Hong Kong, MZ395115, MZ420145, MZ542083, MZ612356, sanger.

/Trionum: Abelmoschus. Abelmoschus esculentus (L.) Moench, *Abbott* 25257 (FLAS), USA, Florida, MZ394843, MZ419898, MZ542008, MZ612131, sanger; Moench, unknown voucher, unknown origin, KY635876, KY635876, KY635876, GenBank; *Abelmoschus ficulneus* (L.) Wight & Arn., *Aplin* 6254 (CANB), Australia, MZ394844, MZ419899, MZ542164, MZ612132, skim; *Forster* 14862 (CANB), Australia, MZ394845, MZ419900, MZ542165, MZ612133, skim; *Abelmoschus manihot* (L.) Medik., *Mitchell* 1951 (CBG), Christmas Island, MZ394846, MZ419901, MZ542166, MZ612134, skim. *Anotea. Anotea flavida* (DC.) Ulbr., *Lorenz* 7821 (MO), USA, Hawaii, MZ394847, —, MZ542030, MZ612405, sanger. *Cenocentrum. Cenocentrum tonkinense* Gagnep., *Poillane* 397 (MO), Laos, MZ394848, MZ419902, MZ542256, MZ612224, sanger. *Fioria. Fioria vitifolia* (L.) Mattei, *Barthelat* 935 (MO), Mayotte, MZ394851, MZ419905, MZ542062, MZ612225, sanger; *Blanchard* 3331 (FLAS), Australia, MZ394852, MZ419906, MZ542211, MZ612187, sanger; *deNevers* 3321 (MO), Tanzania, MZ394853, —, MZ542063, —, sanger. *Hibiscus. Hibiscus apodus* Juswara & Craven, *Blanchard* 3439 (FLAS), Australia, MZ394864, MZ419915, MZ542208, MZ612309, sanger; *Hibiscus austrinus* Juswara & Craven, *Blanchard* 3450 (FLAS), Australia, MZ394867, MZ419918, MZ542209, MZ612328, sanger;

Hibiscus burtt-davyi Dunkley, *Strugnell* 37 (MO), Malawi, MZ394878, MZ419929, MZ542230, MZ612206, sanger; *Hibiscus coccineus* Walter, *Davis* 433 (FLAS), USA, Florida, MZ394891, MZ419941, MZ542019, MZ612294, sanger; *Hibiscus engleri* K.Schum., *Balkwill* 5522 (MO), South Africa, MZ394901, MZ419951, MZ542188, MZ612242, sanger; *Seydel* 446 (MO), South Africa, MZ394902, MZ419952, MZ542176, MZ612243, sanger; *Hibiscus fleckii* Gürke (removed from trees presented here), *Seydel* 2588 (MO), MZ394908, —, MZ542260, MZ612385; *Hibiscus grandiflorus* Michx., *Davis* 427 (FLAS), USA, Florida, MZ394913, MZ419961, MZ542183, MZ612209, sanger; *Hibiscus indicus* (Burm.f.) Hochr., *Winters* s.n. (MO), cultivated, MZ394916, MZ419964, MZ542231, MZ612246, sanger; *Hibiscus ingratus* Miq., *Stergios* 6005 (MO), Venezuela, MZ394917, MZ419965, MZ542167, MZ612189, sanger; *Hibiscus kirkii* Mast., *Long* 642 (MO), Australia, MZ394919, —, MZ542061, MZ612387, sanger; *Hibiscus laevis* All., *Abbott* 23472 (FLAS), USA, Florida, MZ394921, MZ419968, MZ542020, MZ612364, sanger; *Hibiscus lambertianus* Kunth, *Blanchard* 3456 (FLAS), Mexico, MZ394922, MZ419969, MZ542056, MZ612248, sanger; *Hibiscus makinoi* Jōtani & H. Ohba, *Abbott* 24808 (FLAS), cultivated, MZ394930, MZ419976, MZ542017, MZ612211, sanger; *Hibiscus moscheutos* L., *Abbott* 23161 (FLAS), USA, Florida, MZ394937, MZ419983, MZ542021, MZ612194, sanger; *Hibiscus palmatus* Forssk., *Biggood* 6187 (MO), Tanzania, MZ394941, MZ419987, MZ542064, MZ612255, sanger; *Gereau* 6683 (MO), Tanzania, MZ394942, MZ419988, MZ542240, MZ612256, sanger; *Hibiscus panduriformis* Burm.f., *Ash* 1348 (MO), Ethiopia, MZ394943, —, MZ542235, MZ612398, sanger; *Hibiscus physaloides* Guill. & Perr., *Mwangulango* 318 (MO), Tanzania, MZ394952, MZ419997, MZ542059, MZ612300, sanger; *White* 1421 (MO), Gabon, MZ394953, MZ419998, MZ542060, —, sanger; *Hibiscus selloi* Gürke, *Rambo* 41202 (MO), Brazil, MZ394966, MZ420010, MZ542202, MZ612262, sanger; *Hibiscus sororius* L., *Proctor* 27705 (MO), Jamaica, MZ394970, MZ420014, MZ542224, MZ612263, sanger; *Hibiscus spathulatus* Garcke, *Tyson* 1996 (MO), Panama, MZ394985, MZ420029, MZ542225, MZ612358, sanger; *Hibiscus striatus* Cav., *Krapovickas* 12121 (MO), Argentina, MZ394975, MZ420019, MZ542187, MZ612265, sanger; *Hibiscus taiwanensis* S.Y.Hu, unknown voucher, unknown origin, MK937807, MK937807, MK937807, GenBank; *Hibiscus tridactylites* Lindl., *Mallinson* 819 (CANB), Australia, MZ394979, MZ420023, MZ542227, MZ612150, skim; *Hibiscus trilobus* Aubl., *Proctor* 27728 (MO), Jamaica, MZ394980, MZ420024, MZ542057, MZ612190, sanger; *Hibiscus trionum* L., *Bester* 6469 (MO), South Africa, MZ394981, MZ420025, MZ542022, MZ612266, sanger; *Guocheng-Y* 20065-277-4 (MO), China, MZ394982, MZ420026, MZ542023, MZ612267, sanger; *Tadesse* 12038 (MO), USA, Ohio, MZ394983, MZ420027, MZ542024, MZ612188, sanger. *Kosteletzkya. Kosteletzkya adoensis* (Hochst. ex A.Rich.) Mast., *Blanchard* 3402 (FLAS), Malawi, MZ394991, MZ420035, —, MZ612185, sanger; *Blanchard* 3405 (FLAS), Angola, MZ394992, MZ420036, MZ542217, MZ612181, sanger; *Kosteletzkya begoniifolia* (Ulbr.) Ulbr., *Blanchard* 3389 (FLAS), Kenya, MZ394993, MZ420037, MZ542220, MZ612152, sanger; *Blanchard* 3399 (FLAS), Ethiopia, MZ394994, MZ420038, —, MZ612153, sanger; *Kosteletzkya blanchardii* Fryxell, *Blanchard* 3378 (FLAS), Mexico, MZ394995, MZ420039, MZ542244, MZ612154, sanger; *Kosteletzkya borkouana* Quézel, *Blanchard* 3361 (FLAS), Chad, MZ394996, MZ420040, —, MZ612195, sanger; *Blanchard* 3460 (FLAS), Uganda, MZ394997, MZ420041, MZ542218, MZ612180, sanger; *Kosteletzkya buettneri* Gürke, *Blanchard* 3337 (FLAS), Malawi, MZ394998, MZ420042, MZ542216, MZ612155, sanger; *Blanchard* 3339 (FLAS), Tanzania, MZ394999, MZ420043, —, MZ612156, sanger; *Kosteletzkya depressa* (L.) O.J.Blanch., Fryxell & D.M.Bates, *Blanchard* 3369 (FLAS), Mexico, MZ395000, MZ420044, MZ542245, MZ612188, sanger; *Blanchard* 3438 (FLAS), Peru, MZ395001, MZ420045, —, MZ612176, sanger; *Kosteletzkya grantii* (Mast.) Garcke, *Blanchard* 3422 (FLAS), Nigeria, MZ395003, MZ420047, —, MZ612178, sanger; *Blanchard* 3424 (FLAS), The Democratic Republic of the Congo, MZ395004, MZ420048, MZ542221, MZ612157, sanger; *Kosteletzkya hispida* (Spreng.) Garcke, *Blanchard* 3364 (FLAS), Mexico, MZ395005, MZ420049, MZ542212, MZ612158, sanger; *Blanchard* 3365 (FLAS), Mexico, MZ395006, MZ420050, —, MZ612177, sanger; *Kosteletzkya pentacarpos* (L.) Ledeb., *Blanchard* 3329 (FLAS), Italy, MZ395009, MZ420053, —, MZ612160, sanger; *Blanchard* 3341 (FLAS), USA, Virginia, MZ395010, MZ420054, MZ542219, MZ612161, sanger; *Kosteletzkya racemosa* Hauman, *Blanchard* 3391 (FLAS), Zaire, MZ395011, MZ420055, MZ542247, MZ612162, sanger; *Kosteletzkya ramosa* Fryxell, *Blanchard* 1148 (FLAS), Mexico, MZ395012, MZ420056, MZ542213, MZ612163, sanger; *Kosteletzkya reclinata* Fryxell, *Blanchard* 3351 (FLAS), Mexico, MZ395013, MZ420057, MZ542214, MZ612164, sanger; *Kosteletzkya rotundalata* O.J.Blanch., *Blanchard* 3398 (FLAS), Zaire, MZ395016, MZ420059,

MZ542246, MZ612165, sanger; *Kosteletzkya semota* O.J.Blanch., *Blanchard* 3437 (FLAS), Nigeria, MZ395017, MZ420060, MZ542237, MZ612166, sanger; *Kosteletzkya thurberi* A.Gray, *VanDevender* 99-381 (MO), Mexico, MZ395019, MZ420062, —, MZ612301, sanger; *Kosteletzkya tubiflora* (Moc. & Sessé ex DC.) O.J.Blanch. & McVaugh, *Blanchard* 3359 (FLAS), Mexico, MZ395020, MZ420063, MZ542215, MZ612175, sanger. *Malachra*. *Malachra alceifolia* Jacq., *Lioiger* 22142 (FLAS), Dominican Republic, MZ395024, MZ420066, MZ542039, MZ612273, sanger; *Malachra capitata* (L.) L., *Leonard* 4225 (MO), Haiti, MZ395025, MZ420067, MZ542040, MZ612274, sanger; *Thomas* 54950 (MO), USA, Louisiana, MZ395026, MZ420068, MZ542175, MZ612275, sanger; *Malachra fasciata* Jacq., *Johnson* 2154-80 (MO), Panama, MZ395027, MZ420069, MZ542185, MZ612302, sanger; *Williams* 354 (MO), Philippines, MZ395028, MZ420070, MZ542041, MZ612303, sanger; *Malachra radiata* (L.) L., *Blanchard* 3412 (FLAS), Cuba, MZ395029, MZ420071, MZ542178, MZ612304, sanger; *Malachra rudis* Benth., *Johnson* 84-3507 (MO), Colombia, MZ395030, MZ420072, MZ542174, MZ612276, sanger; *Krapovickas* 36101 (MO), Bolivia, MZ395031, MZ420073, MZ542186, MZ612277, sanger; *Malachra urens* Poit. ex Ledeb., *Blanchard* 3372 (FLAS), USA, Florida, MZ395032, MZ420074, MZ542173, MZ612278, sanger. *Malvaviscus*. *Malvaviscus arboreus* Dill. ex Cav., *Alverson* 2181 (WIS), Mexico, AY589061, AF111718, —, MZ612355, sanger; *Tenorio* 4086 (MO), Mexico, MZ395033, MZ420075, —, sanger; *Malvaviscus concinnus* Kunth, *Araujo* 874 (MO), Bolivia, MZ395034, —, MZ542031, MZ612397, sanger; *Malvaviscus penduliflorus* Moc. & Sessé ex DC., *Abbott* 23875 (FLAS), USA, Florida, MZ395035, MZ420076, MZ542032, MZ612186, sanger. *Pavonia*. *Pavonia* aff. *flavoferruginea* (Forssk.) Hepper & J.R.I.Wood, *Simon* 644 (MO), Tanzania, MZ395039, MZ420080, MZ542025, MZ612279, sanger; *Pavonia* aff. *patens* (Andrews) Chiov., *Ruaburindore* 5849 (MO), Uganda, MZ395040, MZ420081, MZ542026, MZ612320, sanger; *Pavonia almasana* Ulbr., *Harley* 55518 (MO), Brazil, MZ395041, MZ420082, MZ542047, MZ612280, sanger; *Pavonia anisaster* (Standl.) Fryxell, *Flores-Franco* 3791 (MO), Mexico, MZ395042, —, MZ542033, MZ612378, sanger; *Pavonia arenaria* (Murray) Roth, *Belsky* 449 (MO), Kenya, MZ395043, MZ420083, MZ542009, MZ612333, sanger; *Sebebe* 2484 (MO), Ethiopia, MZ395044, MZ420084, MZ542010, MZ612334, sanger; *Pavonia argentina* Gürke, *Krapovickas* 30817 (MO), Argentina, MZ395045, MZ420085, MZ542042, MZ612350, sanger; *Pavonia burchellii* (DC.) R.A.Dyer, *Venter* 10222 (MO), South Africa, MZ395046, MZ420086, MZ542027, MZ612281, sanger; *Pavonia calycina* (Cav.) Ulbr., *Zimba* 1000 (MO), Zambia, MZ395047, MZ420087, MZ542275, MZ612369, sanger; *Pavonia cancellata* (L.) Cav., *Blanchard* 3457 (FLAS), Costa Rica, MZ395048, MZ420088, MZ542049, MZ612215, sanger; *Krapovickas* 42905 (MO), Brazil, MZ395049, MZ420089, MZ542257, MZ612321, sanger; *Short* 152 (MO), Costa Rica, MZ395050, MZ420090, MZ542050, MZ612216, sanger; *Pavonia* cf. *bahamensis* Hitchc., *Abbott* 23887 (FLAS), cultivated, MZ395051, MZ420091, MZ542036, MZ612192, sanger; *Pavonia* cf. *castaneifolia* A.St.-Hil. & Naudin, *Mayfield* s.n. (MO), Costa Rica, MZ395052, —, MZ542051, MZ612376, sanger; *Pavonia* cf. *hastata*, Cav., *Abbott* 23821 (FLAS), cultivated, MZ395053, MZ420092, MZ542011, MZ612193, sanger; *Villarreal* 1414 (MO), Bolivia, MZ395054, MZ420093, MZ542012, MZ612390, sanger; *Pavonia clathrata* Mast, *Balkwill* 4332 (MO), South Africa, MZ395055, MZ420094, MZ542197, MZ612200, sanger; *Pavonia columella* Cav., *Chapman* 8720 (MO), Malawi, MZ395056, MZ420095, MZ542204, MZ612365, sanger; *Pavonia cryptica* Krapov. & Cristóbal, *Jimenez* 845 (MO), Bolivia, MZ395057, MZ420096, MZ542028, MZ612382, sanger; *Pavonia dentata* Burtt Davy, *Straub* 152 (MO), South Africa, MZ395058, MZ420097, MZ542029, MZ612403, sanger; *Pavonia formosa* Fryxell, *Apaza* 82 (MO), Bolivia, MZ395059, MZ420098, MZ542065, MZ612400, sanger; *Pavonia fryxellii* Krapov., *Torres* 12561 (MO), Mexico, MZ395060, MZ420099, MZ542242, MZ612394, sanger; *Pavonia geminiflora* Moric., *Jansen-Jacobs* 2753 (MO), Guyana, MZ395061, MZ420100, MZ542239, MZ612322, sanger; *Pavonia hassleriana* Chodat, *Krapovickas* 44588 (MO), Paraguay, MZ395062, MZ420101, MZ542046, MZ612357, sanger; *Pavonia hieronymi* Gürke, *Gutierrez* 755 (MO), Bolivia, MZ395063, MZ420102, MZ542043, MZ612335, sanger; *Pavonia immaculata* R.E.Fr., *Flores* 62 (MO), Bolivia, MZ395064, MZ420103, MZ542044, MZ612323, sanger; *Pavonia ionthacarpa* Krapov., *Fuentes* 3326 (MO), Bolivia, MZ395065, —, MZ542069, MZ612408, sanger; *Pavonia kilimandscharica* Gürke, *Simon* 601 (MO), Tanzania, MZ395066, MZ420104, MZ542094, MZ612381, sanger; *Pavonia kotschy* Hochst. ex Webb, *Wieland* 4495 (MO), Somalia, MZ395067, MZ420105, MZ542182, MZ612282, sanger; *Pavonia leucantha* Garcke, *McDaniel* 23669 (MO), Peru, MZ395068, MZ420106, MZ542052, MZ612395, sanger; *Pavonia monticola* Fryxell, *Alvarado* 728 (MO), Mexico, MZ395069, MZ420107, MZ542203, MZ612340, sanger; *Pavonia multiflora* A.St.-Hil., *Kallunki* 588

(MO), Brazil, MZ395070, MZ420108, MZ542048, MZ612305, sanger; *Pavonia nayarensis* Fryxell, *Flores* 1302 (MO), Mexico, MZ395071, —, MZ542035, MZ612406, sanger; *Pavonia oxyphyllaria* Donn.Sm., *Villarreal* 4 (MO), Bolivia, MZ395072, MZ420109, MZ542053, MZ612324, sanger; *Pavonia paludicola* Nicolson ex Fryxell, *Worthington* 21260 (MO), Belize, MZ395073, MZ420110, MZ542037, MZ612306, sanger; *Pavonia paniculata* Cav., *Whiteford* 10126 (MO), Belize, MZ395074, MZ420111, MZ542250, MZ612384, sanger; *Pavonia pleuranthera* (DC.) Fryxell, *Tellez* 11842 (MO), Mexico, MZ395075, —, MZ542034, MZ612362, sanger; *Pavonia praemorsa* (L.f.) Cav., *Blanchard* 3462 (FLAS), Australia, MZ395078, MZ420112, MZ542058, MZ612204, sanger; *Pavonia pseudotylphalea* Planch. & Linden, *Delgado* 71 (MO), Ecuador, MZ395076, MZ420113, MZ542055, MZ612341, sanger; *Pavonia ramboi* Krapov. & Cristóbal, *Saur* 282 (MO), Brazil, MZ395077, MZ420114, MZ542016, MZ612368, sanger; *Pavonia ramosissima* (Arechav.) Fryxell & Krapov., *Krapovickas* 41933 (MO), Brazil, MZ395079, —, MZ542241, MZ612412, sanger; *Pavonia rehmannii* Szyszyt, *Seydel* 4484 (MO), South Africa, MZ395080, MZ420115, MZ542015, MZ612401, sanger; *Pavonia rupestris* (Hassl.) Krapov. & Cristóbal, *Stevens* 31214 (MO), Paraguay, MZ395083, MZ420116, —, MZ612220, sanger; *Pavonia sagittata* A.St.-Hil., *Krapovickas* 35349 (MO), Brazil, MZ395081, —, MZ542013, MZ612411, sanger; *Pavonia schiedana* Steud., *Melendez* 929 (MO), Mexico, MZ395082, MZ420117, MZ542054, MZ612336, sanger; *Stevens* 35255 (MO), Nicaragua, MZ395084, MZ420118, —, MZ612205, sanger; *Pavonia schimperiana* Hochst. ex A.Rich., *Blanchard* 3293 (FLAS), Kenya, MZ395085, MZ420119, MZ542179, MZ612283, sanger; *Pavonia senegalensis* (Cav.) Leistner, *Stevens* 30 (MO), South Africa, MZ395086, MZ420120, MZ542018, MZ612284, sanger; *Pavonia sepioides* Fryxell & Krapov., *Nee* 45332 (MO), Bolivia, MZ395087, MZ420121, MZ542068, MZ612285, sanger; *Pavonia sepium* A.St.-Hil., *Liully* 671 (MO), Bolivia, MZ395088, MZ420122, MZ542066, MZ612307, sanger; *Pavonia spinifex* (L.) Cav., *Croat* 97717 (MO), Dominican Republic, MZ395089, MZ420123, MZ542070, MZ612407, sanger; *Cersony* s.n. (MO), unknown origin, MZ395090, MZ420124, MZ542071, MZ612197, sanger; *Pavonia uniflora* (Sessé & Moc.) Fryxell, *Servin* 430 (MO), Mexico, MZ395091, MZ420125, MZ542067, MZ612325, sanger; *Pavonia urens* Cav., *Blanchard* 1354 (FLAS), Kenya, MZ395092, MZ420126, MZ542180, MZ612286, sanger; *Pavonia vaimii* Fryxell, *Peña-Chocarro* 2546 (MO), Paraguay, MZ395093, MZ420127, MZ542045, MZ612337, sanger; *Pavonia vitifolia* Hochr., *Pedersen* 12127 (MO), Brazil, MZ395094, MZ420128, MZ542251, MZ612392, sanger; *Pavonia xanthogloea* Ekman, *Krapovickas* 14823 (MO), Argentina, MZ395095, —, MZ542014, MZ612383, sanger. *Peltaea*. *Peltaea obsita* (Mart. ex Colla) Krapov. & Cristóbal, *Krapovickas* 45130 (MO), Paraguay, MZ395096, MZ420129, MZ542236, MZ612393, sanger; *Peltaea ovata* (C.Presl) Standl., *Silvestone-Sopkin* 7068 (MO), Colombia, MZ395097, MZ420130, MZ542253, MZ612354, sanger; *Peltaea speciosa* (Kunth) Standl., *Villarreal* 543 (MO), Bolivia, MZ395098, —, MZ542272, MZ612380, sanger; *Peltaea trinervis* (C.Presl) Krapov. & Cristóbal, *Stevens* 35062 (MO), Nicaragua, MZ395099, MZ420131, —, MZ612308, sanger. *Senna*. *Senna inana* Cav., *Ash* 2316 (MO), Ethiopia, MZ395104, —, MZ542271, MZ612373, sanger. *Wercklea*. *Wercklea coelestis* (A.Robyns) Fryxell, *Blanchard* 3443 (FLAS), Panama, MZ395116, MZ420146, MZ542194, MZ612351, sanger. *Wercklea ferox* (Hook.) Fryxell, *Blanchard* 3216 (FLAS), Panama, MZ395117, MZ420147, MZ542184, MZ612288, sanger. *Wercklea hottensis* (Helwig ex Urb.) Fryxell, *Ionta* 2038 (FLAS), Haiti, MZ395118, MZ420148, MZ542038, MZ612198, sanger; *Wercklea insignis* Pitier & Standl., *Blanchard* 1491 (FLAS), Costa Rica, MZ395119, MZ420149, MZ542195, MZ612289, sanger.

Outgroups. *Bombax ceiba* L., unknown voucher, unknown origin, MG569974, MG569974, MG569974, GenBank; *Gossypium hirsutum* L., unknown voucher, unknown origin, HQ901196, HQ901196, HQ901196, GenBank; *Guazuma ulmifolia* Lam., *Abbott* 23925 (FLAS), USA, Florida, MZ394854, —, MZ542007, —, sanger; *Howittia trilocularis* F.Muell., *Gilmour* 7849 (CANB), Australia, MZ394987, MZ420031, MZ542229, MZ612151, skim; *Nordenstam* 1263 (MO), Australia, MZ394988, MZ420032, MZ542233, MZ612312, sanger; *Lagunaria patersonia* (Andrews) G.Don, *Keighery* 16961 (CANB), Australia, MZ395023, MZ420065, MZ542274, MZ612167, skim; *Modiola caroliniana* (L.) G.Don, *Abbott* 24188 (FLAS), USA, Florida, MZ395038, —, MZ542107, MZ612174, sanger; *Radyera farragei* (F.Muell.) Fryxell & S.H.Hashmi, *Purdie* 7501 (CANB), Australia, MZ395102, MZ420134, MZ542228, MZ612168, skim; *Radyera urens* (L.f.) Bullock, *Bester* 6723 (MO), South Africa, MZ395103, MZ420135, MZ542106, MZ612201, sanger. *Sida* sp., *Massave* 383 (MO), Tanzania, MZ395105, —, MZ542108, MZ612287, sanger.

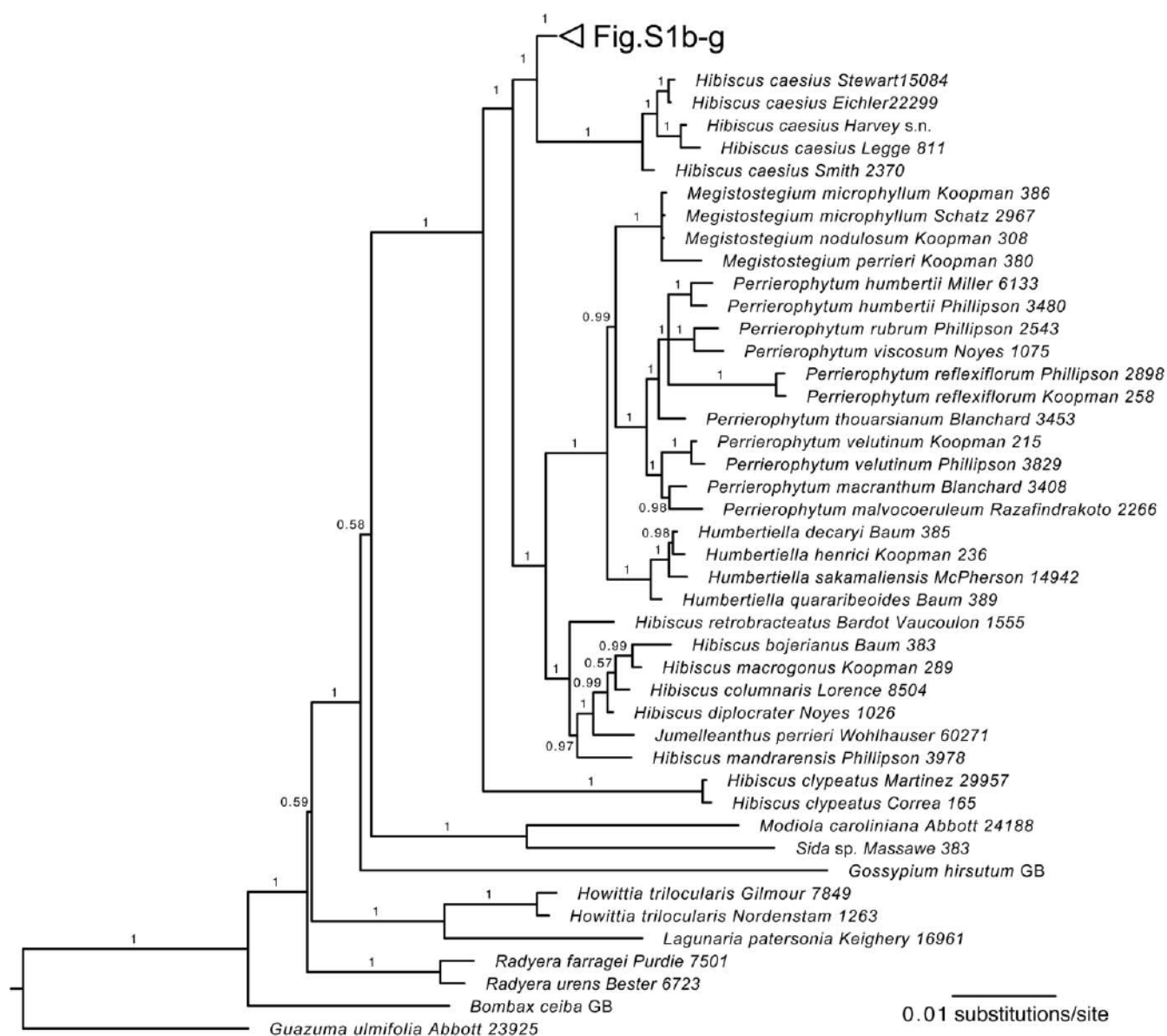


FIG. S1. Bayesian phylogenetic tree of the Hibisceae based on four plastid DNA loci. Support values are posterior probabilities (PP) mapped onto a Bayesian 50% majority rule consensus tree. Voucher for each accession is provided, GB = sequences obtained from GenBank. FIG. S1A. Three major clades of Hibisceae—/Clypeati, /Megistohibiscus, /Caesius, and outgroups. FIGS. S1B–D. Clade/Trionum. FIG. S1E. Clades/Phylloglandula and /Calyphli. FIGS. S1F–G. Clade/Euhibiscus.

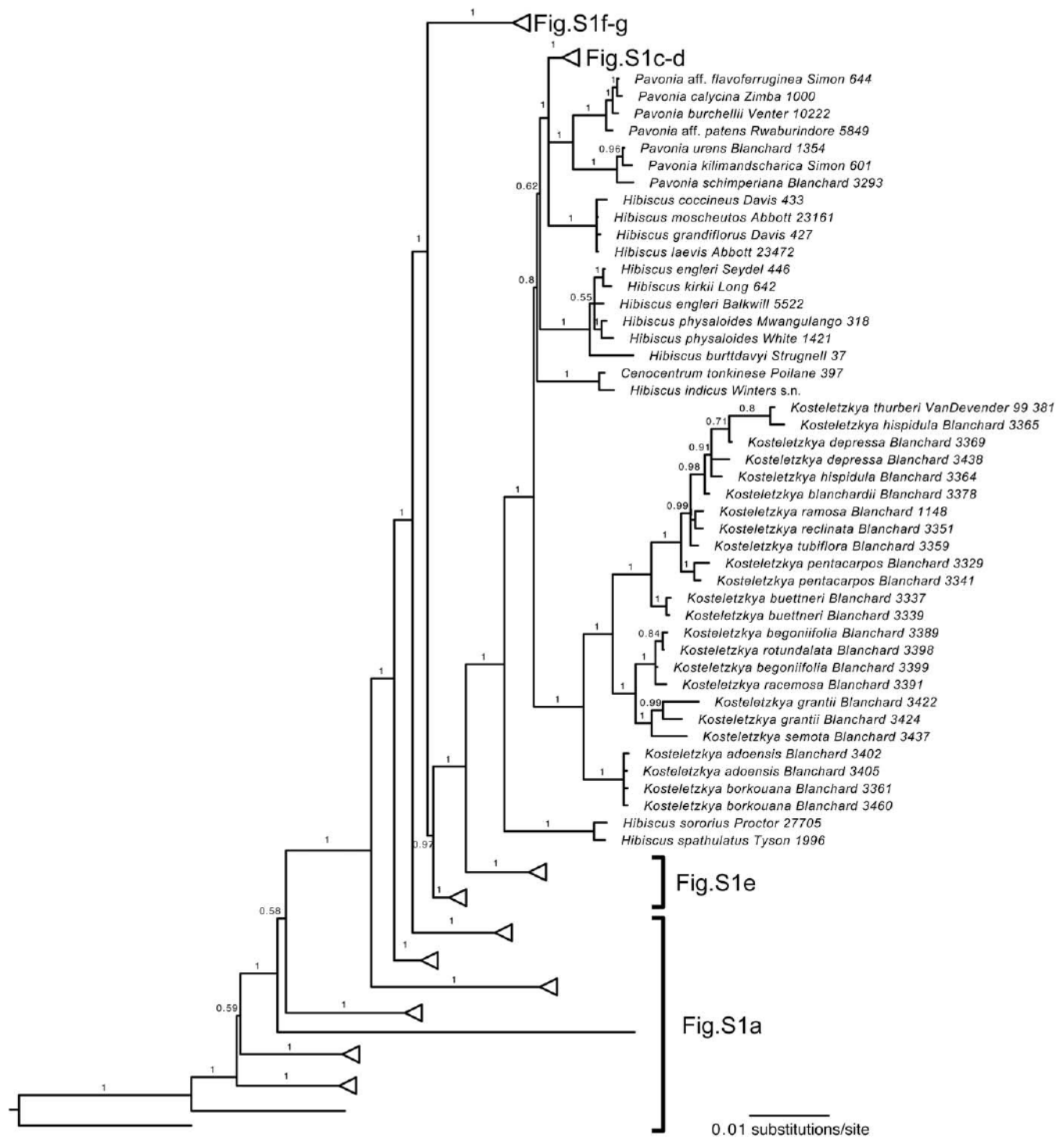


FIG. S1. (CONTINUED).

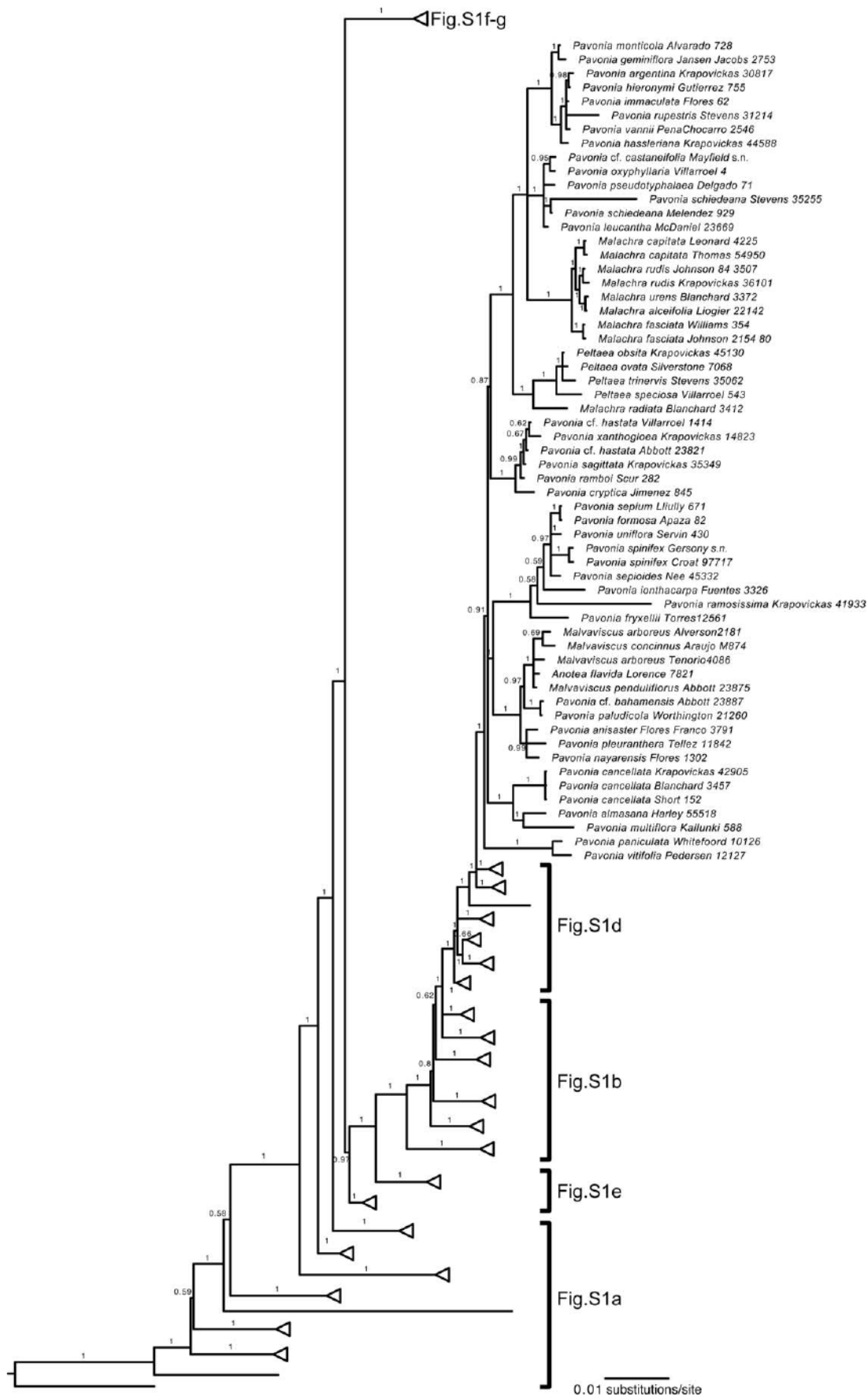


FIG. S1. (CONTINUED).

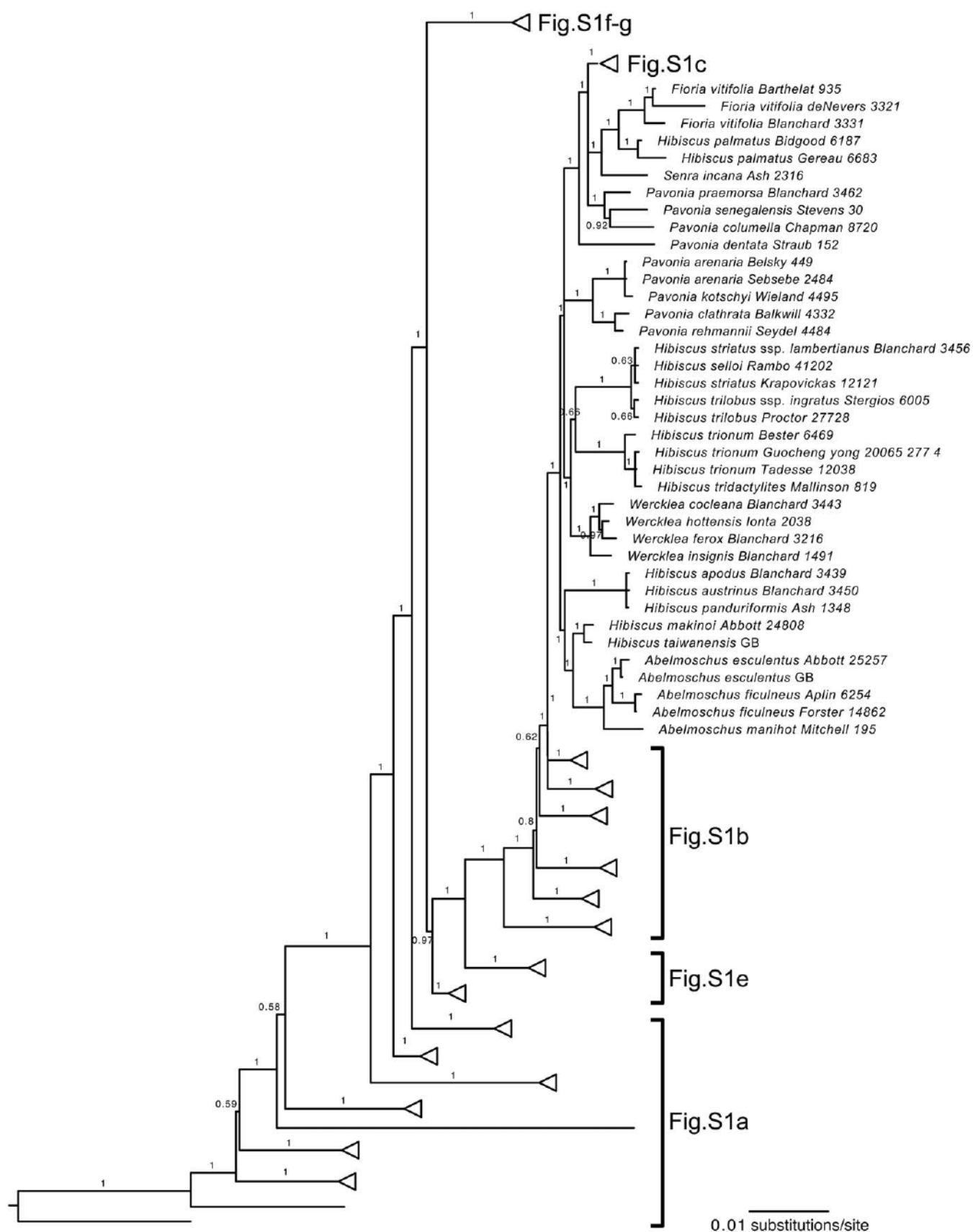


FIG. S1. (CONTINUED).

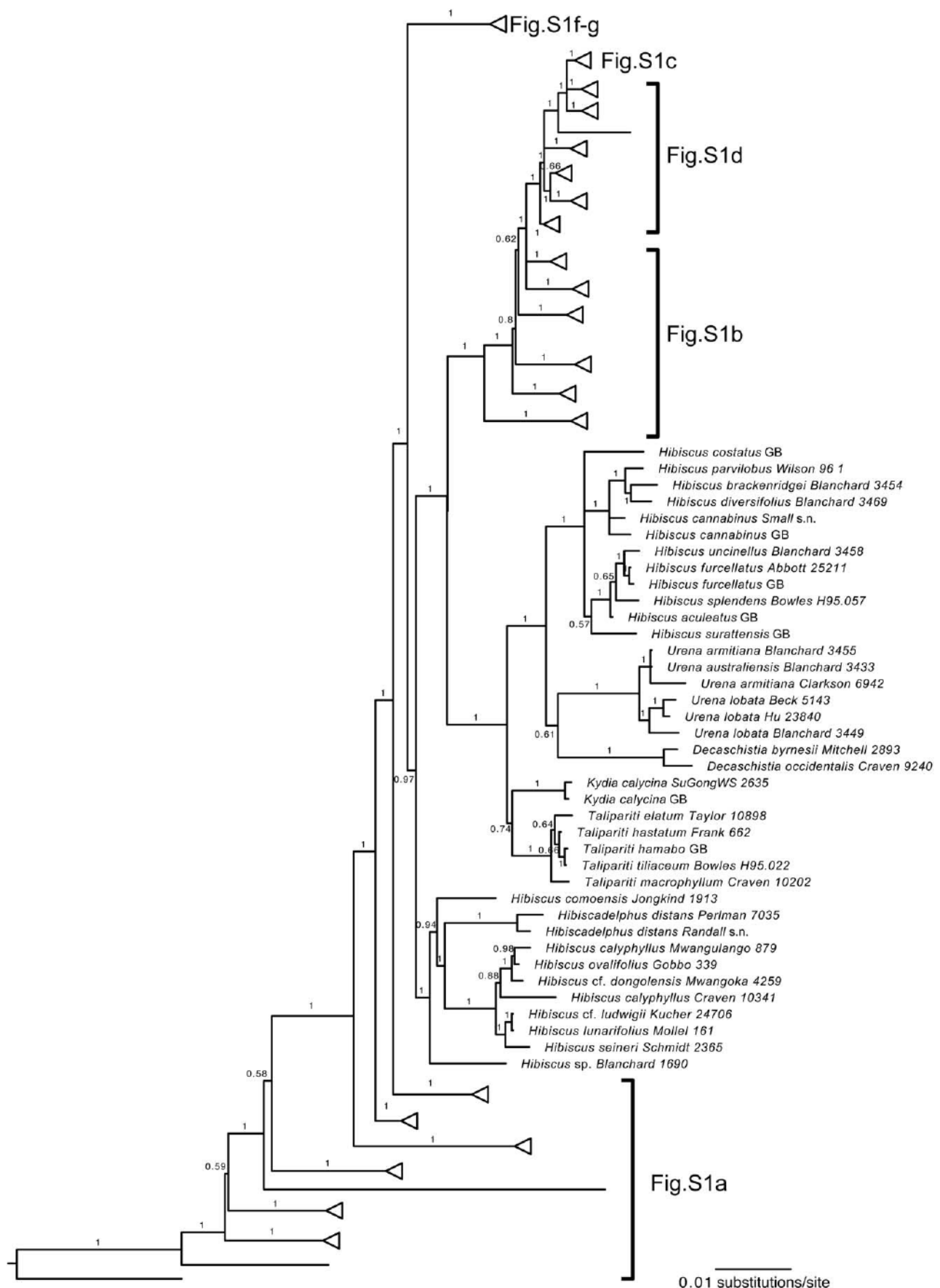


FIG. S1. (CONTINUED).

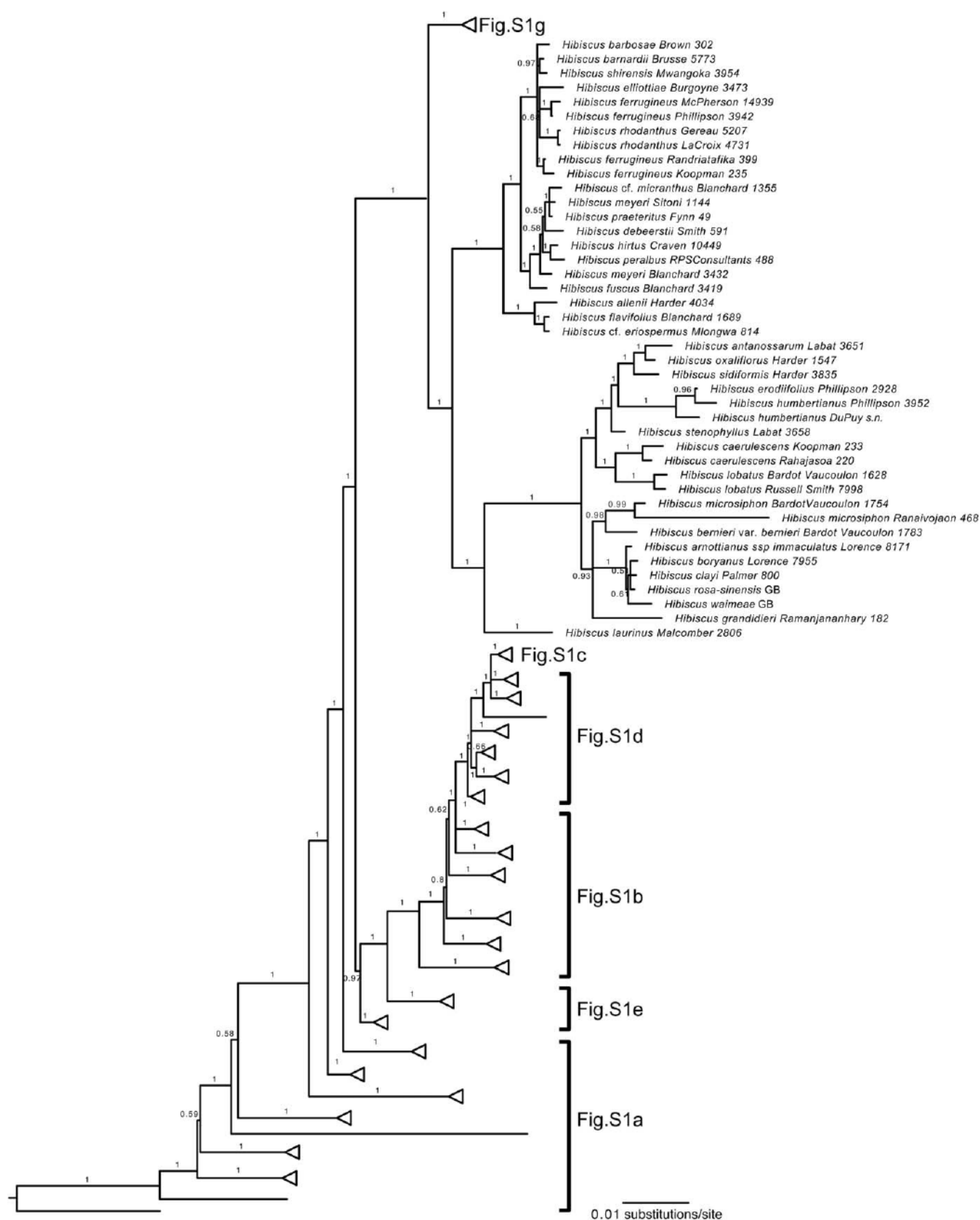


FIG. S1. (CONTINUED).

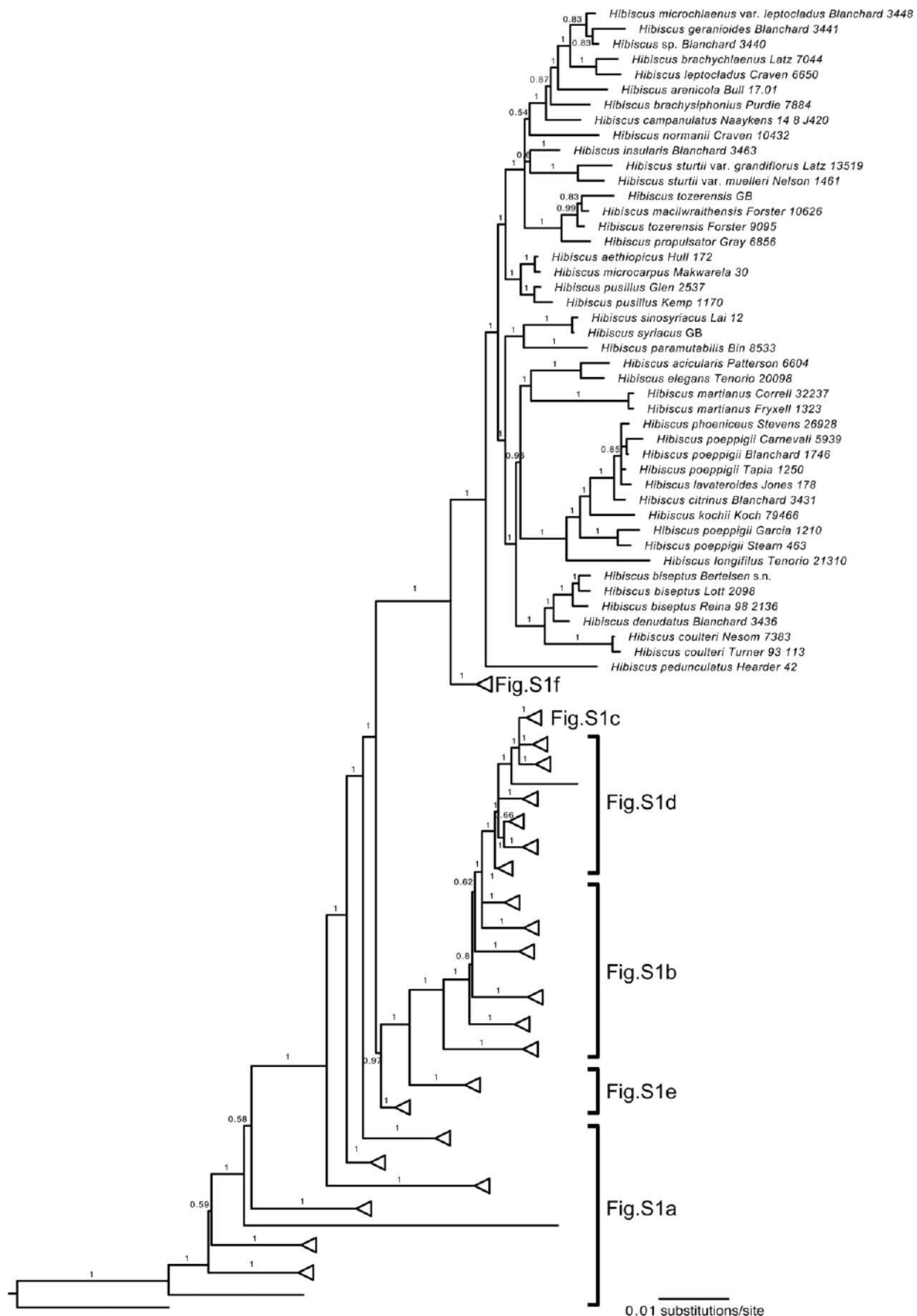


FIG. S1. (CONTINUED).

SUPPLEMENTAL TABLE S1. A new, simplified classification for Tribe Hibisceae.

Major Clade	Species in clade	Genera in clade	Generic status	Generic Names and Proposals	Species in genus	Hibiscus Section(s)	Paronia Section(s)
/Clypeati	1	1	Change required: new name; done here	<i>Blanchardia</i> M.M.Hanes & R.L.Barrett	1	<i>Clypeati</i>	
/Megistohibiscus	ca. 41	5–6	Accepted	<i>Humbertiella</i> Hochr.	6		
			Accepted	<i>Jumelleanthus</i> Hochr.	1		
			Accepted	<i>Megistostegium</i> Hochr.	3		
			Accepted	<i>Perrierophytum</i> Hochr.	15		
			Change required: new name(s)	gen. nov.	at least 13	<i>Azanzae</i> (in part), <i>Columnaris</i>	
/Caesius	1	1	Change required: new name; done here	<i>Astrolibiscus</i> McLay & R.L.Barrett	1	<i>Hibiscus</i> (in part)	
/Trionum	ca. 425	ca. 21	Accepted (Barrett et al. 2023)	<i>Abelmoschus</i> Medik.	6–15		
			Accepted	<i>Cenocentrum</i> Gagnep.	1–2	<i>Venusti</i>	
			Change required: existing name	<i>Fioria</i> Mattei	2	<i>Aristicaltus</i> , <i>Pterocarpus</i>	
			Accepted	<i>Kostyletzkya</i> C.Presl	17		<i>Pterocarpidium</i>
			Change required: existing name	<i>Luederitzia</i> K.Schum.	10		
			Change required: existing name	<i>Muenchusia</i> Heist. ex Fabr.	5	<i>Muenchusia</i>	
			Accepted (Barrett et al. 2023)	<i>Paronia</i> Cav. (all NW members and previous members of <i>Anotea</i> , <i>Malachra</i> , <i>Malva</i> , <i>Peltaea</i> , <i>Phragmocarpidium</i> , <i>Rojasimultra</i>)	275+		all NW <i>Paronia</i> sections: <i>Paronia</i> , <i>Lopimia</i> , <i>Cancellaria</i> , <i>Malva</i> , <i>Urenoidae</i> , <i>Lebretonia</i> , <i>Typhalea</i> , <i>Urenoidae</i> , <i>Diathericae</i> , <i>Carcerariae</i> , <i>Varianis</i> , <i>Asterochlamys</i> , <i>Albae</i> , <i>Malache</i> , <i>Collicolae</i> , <i>Laminariae</i> , <i>Goetheoides</i>
			Accepted	<i>Rofia</i> Verdc.	1		
			Accepted	<i>Serra</i> Cav.	2–3		
			Accepted	<i>Symphyochlamys</i> Gürke	1+		
			Accepted	<i>Tiepparatia</i> Phuph.	1		
			Change required: existing name	<i>Trionum</i> L.	4	<i>Trionum</i>	
			Accepted	<i>Wercklea</i> Puttner & Standl.	13		
			Change required: new name; done here	<i>Cravenia</i> McLay & R.L.Barrett	6	<i>Panduriformes</i>	
			Change required: new name	gen. nov.	3+	<i>Striati</i>	
			Change required: new name	gen. nov.	4+	no sectional affiliation (clade with <i>H. engleri</i>)	
			Change required: new name	gen. nov.	ca. 5	<i>Trionastrum</i>	
			Change required: new name	gen. nov.	2+	<i>Venusti</i>	
			Change required: new name	gen. nov. (1 or 2)	15		<i>Afrotrophalea</i> , <i>Afrolebretonia</i>
			Change required: new name	gen. nov.	9		<i>Craspedocarpidium</i>
			Change required: new name	gen. nov.	5		<i>Columella</i> , <i>Afrolopinia</i> , <i>Praemorsa</i>

(Continued)

SUPPLEMENTAL TABLE S1. (CONTINUED).

Major Clade	Species in clade	Genera in clade	Generic status	Generic Names and Proposals	Species in genus	Hibiscus Section(s)	Paronia Section(s)
Phylloglandula	ca. 151	at least 9	Accepted Accepted Accepted Accepted Accepted Change required: existing name (Barrett et al. in prep) Accepted Accepted	<i>Decaschistia</i> Wight & Arn. <i>Dicelostyles</i> Benth. <i>Julostylis</i> Thw. <i>Kydia</i> Roxb. <i>Nayariophyton</i> T.K.Paul <i>Papuodendron</i> C.T.White <i>Sabdariffa</i> (DC.) Kostel.	15 1 3 2 1 2 ~120+	<i>Furcaria</i>	
Calyphylli	16	4	Change required: existing name Accepted Change required: new name Change required: new name	<i>Talipariti</i> Fryx. <i>Urena</i> L. <i>Cotylopecta</i> Alef. <i>Hibiscadelphus</i> Rock gen. nov.	23 7 7 6-8 1	<i>Azanzae</i> (in part) <i>Calyphylli</i> No sectional affiliation	
Euhibiscus	ca. 220	1	Accepted	<i>Hibiscus</i> L.	ca. 220	<i>Bombicella</i> , <i>Hibiscus</i> (in part), <i>Lilibiscus</i> , <i>Solandra</i> , <i>Spatula</i>	
Uncertain placement	3		Accepted	<i>Bombycidendron</i> Zoll. & Moritz	1		
Total	ca. 857	at least 43	Accepted	<i>Woodianthus</i> Krapov.	1		