Molecular recircumscription of Broussonetia (Moraceae) and the identity and taxonomic status of B. kaempferi var. australis

Kuo-Fang Chung1,2*, Wen-Hsi Kuo1, Yi-Hsuan Hsu1,2, Yi-Hsuan Li1,2, Rosario Rivera Rubite3 and Wei-Bin Xu4

Abstract

Background: Despite being a relatively small genus, the taxonomy of the paper mulberry genus Broussonetia remains problematic. Much of the controversy is related to the identity and taxonomic status of Broussonetia kaempferi var. australis, a name treated as a synonym in the floras of Taiwan and yet accepted in the floras of China. At the generic level, the monophyly of Corner (1962)’s concept of Broussonetia has not been tested. In recent studies of Broussonetia of Japan, lectotypes of the genus were designated and three species (B. kaempferi, Broussonetia monoica, and Broussonetia papyrifera) and a hybrid (B. × kazinoki) were recognized. Based on the revision and molecular phylogenetic analyses, this article aims to clarify these issues.

Results: Herbarium studies, field work, and molecular phylogenetic analyses indicate that all Taiwanese materials identifiable to B. kaempferi var. australis are conspecific with B. monoica of Japan and China. Molecular phylogenetic analyses showed that Broussonetia sensu Corner (1962) contains two clades corresponding to sect. Broussonetia and sect. Allaeanthus, with Malaysia scandens sister to sect. Broussonetia.

Conclusions: Based on our analyses, B. kaempferi var. australis is treated as a synonym of B. monoica and that B. kaempferi is not distributed in Taiwan. To correct the non-monomophyly of Broussonetia sensu Corner (1962), Broussonetia is recircumscribed to contain only sect. Broussonetia and the generic status of Allaeanthus is reinstated.

Keywords: Allaeanthus, Broussonetia × kazinoki, Broussonetia monoica, Dorstenieae, Lectotype, Neotype, Paper mulberry genus, Taxonomy

Background

Prior to Corner (1962)’s circumscription, Broussonetia L’Hér. ex Vent. was known as a genus of three species distributed in East Asia and continental Southeast Asia: the type species Broussonetia papyrifera (L.) L’Hér. ex Vent., Broussonetia kaempferi Siebold, and Broussonetia kazinoki Siebold (Ohwi 1965; Liu and Liao 1976), with a hybrid between B. kazinoki and B. papyrifera known from Japan (Kitamura and Murata 1980; Yamazaki 1989; Okamoto 2006) and Korea (Yun and Kim 2009). Corner (1962) expanded the generic concept by combining Allaeanthus Thwaites as Broussonetia sect. Allaeanthus (Thwaites) Corner, stating that “there are no major differences between these sections (i.e., sect. Broussonetia and sect. Allaeanthus), which are not generically distinct” (Corner 1962). Currently, Broussonetia sect. Allaeanthus comprises four species: B. greveana (Baill.) C.C. Berg of Madagascar, B. kurzii (Hook. f.) Corner of China (Yunnan), India (Assam), Myanmar, and Thailand, B. luzonica (Blanco) Bureau of the Philippines and Sulawesi, and B. zeylanica (Thwaites) Corner of Sri Lanka (Corner 1962; Berg 1977; Zhou and Gilbert 2003; Berg et al. 2006). Based on Corner (1962)’s circumscription, Broussonetia

*Correspondence: bochung@gate.sinica.edu.tw
1 Research Museum and Herbarium (HAST), Biodiversity Research Center, Academia Sinica, 128 Academia Road, Section 2, Nangang, Taipei 11529, Taiwan
Full list of author information is available at the end of the article
© The Author(s) 2017. This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.
is characterized by membranous stipules, globose syncarps, drupes covered by thickly sets of slender stalked bracts of various shapes, crustaceous to ligneous endocarps, and conduplicate to plane cotyledons. Although Corner (1962)’s expanded concept has been followed by most authors (e.g., Berg 1977; Rohwer 1993; Chang et al. 1998; Zhou and Gilbert 2003; Berg et al. 2006) except for Capuron (1972) who sustained the generic status of *Alleaeanthus*, the monophyly of *Broussonetia* sensu Corner (1962) has not yet been tested (Zerega et al. 2005; Clement and Weiblen 2009) and much about the taxonomy of the genus remains unsettled.

Commonly known as paper mulberry, *Broussonetia papyrifera* is renowned as a fibrous tree essential to the development of paper making technique in ancient China around 100 A.D. (Ling 1961; Barker 2002). Long before Linnaeus’ time, paper mulberry had been cultivated widely in European gardens (Barker 2002) and, as documented during Captain James Cook’s circum-Pacific voyages, clonally propagated across Remote Oceanic islands by Austronesian-speaking peoples for making bark cloth (*tapa*), a non-woven textile that is highly symbolic of Austronesian material culture (Matthews 1996; Whistler and Elevitch 2006; Seelenfreund et al. 2010). This fast-growing dioecious weedy tree species is most likely native to China, Taiwan, and continental Southeast Asia (Matthews 1996); however, because of its long history of utilization (Matthews 1996; Barker 2002; Chang et al. 2015), considerable discrepancies exist in the literature regarding distribution ranges of *B. papyrifera* (Table 1). Based on the phylogeographic analysis of chloroplast *ndhF-rpl32* intergenic spacer, Chang et al. (2015) demonstrated that Pacific paper mulberry originated in southern Taiwan, providing the first ethnobotanical support for the “out of Taiwan” hypothesis of Austronesian expansion. Peñailillo et al. (2016) further showed that Pacific paper mulberries are predominately female, consolidating reports on the clonal nature and corroborating Chang et al. (2015)’s inference. In addition to its long-fiber, this fast growing weedy tree has also been introduced for erosion control worldwide (Matthews 1996). Consequently, the multipurpose paper mulberry has been naturalized

| Table 1 Distribution of *Broussonetia papyrifera* in selected literatures |
|---------------------------------|---------------------------------|
| Kanehira (1936)                 | Taiwan, Myanmar, Thailand, Malaysia, Pacific islands, China, Japan |
| Chûjô (1950)                   | Japan, Korea, China, Ryukyus, Taiwan, Philippines, Vietnam, Thailand, Myanmar, India, Malaysia, Java, Borneo, SW Pacific islands, Europe, North America, Australia |
| Liu (1962)                     | Taiwan, India, Thailand, Malaysia, Pacific islands, Japan, China |
| Li (1963)                      | Taiwan, Indo-Malaysia, China, Japan to the Pacific islands, Taiwan |
| Ohwi (1965)                    | Cultivated for making paper in Japan (Honshu, Shikoku, Kyushu); Ryukyus, Formosa, China, Malaysia |
| Liu and Liao (1976)            | China, Japan, the Pacific Islands, Malaysia, Thailand and India |
| Kitamura and Murata (1980)     | Central and southern China, Taiwan, Vietnam, Thailand, Myanmar, India, Malaysia, Pacific Islands |
| Yamazaki (1982)                | S. China, Taiwan, Indochina, Thailand, Burma and Malaysia. Cultivated in Japan |
| Yamazaki (1989)                | Central and southern China, Indochina, Malaysia |
| Liao (1991, 1996)              | Taiwan, Southern China, Japan, the Pacific Islands, Indochina, Malaysia, Thailand, Burma and India |
| Liu et al. (1994), Lu et al. (2006) | Central and southern China, Taiwan, Japan, Malay, Pacific islands |
| Matthews (1996)                | Japan, Korea, northern, central, and southern China, Taiwan, Vietnam, Laos, Thailand, Cambodia, Myanmar, India (Sikkim), islands Southeast Asia (excluding the Philippines and Borneo), Melanesia, and Polynesia islands |
| Florence (1997)                | Native to China and Japan, widely cultivated in South East Asia, Malaysia and the Pacific |
| Shimabuku (1997)               | Cultivated and escaped in Ryukyus. China, Taiwan, Indochina, Malaysia |
| Chang et al. (1998)            | Distributed throughout China from the north to south, also in Sikkim, Myanmar, Thailand, Vietnam, Malaysia, Japan, Korea, wild or cultivated |
| Cao (2000)                     | China (Gansu, Shanxi, Shandong, Chongqing, Anhui, Zhejiang, Fujian, Jiangxi, Hubei, Hunan, Guangdong, Hainan, Guangxi, Guizhou, Yunnan, Sichuan, Xizang), Taiwan |
| Barker (2002)                  | East Asia, China, Japan, and Korea |
| Zhou and Gilbert (2003)        | China, Taiwan, Cambodia, Japan, Korea, Laos, Malaysia, Myanmar, Sikkim, Thailand, Vietnam, Pacific Islands |
| Berg et al. (2006)             | India (Assam, China (incl. Taiwan), Indochina, Japan (introduced in the Ryukyu Islands), Myanmar, Thailand, Polynesia; in Malesia: introduced in Sumatra, Java, Philippines, Celebes, Lesser Sunda Islands (Flores, Timor, Alor, Wetaor), Moluccas, New Guinea |
| Okamoto (2006)                 | Japan (cultivated and naturalized), Taiwan, S. China, Indochina, India, the Malesian region and Pacific islands |
| Whistler and Elevitch (2006)   | Native to Japan and Taiwan; an ancient introduction to many Pacific islands as far east as Hawai’i |
| Yun and Kim (2009)             | Korea, Japan, China, Taiwan, Malaysia, Laos, Myanmar, Thailand, Vietnam |
| LaFrankie (2010)               | China, Japan, naturally occurring as far south as Myanmar and Thailand, cultivated in Java, not found either in Malay or Borneo |
in southern Europe and become invasive in Argentina, Ghana, Uganda, Pakistan, the Philippines, Solomon Islands, and USA. (Matthews 1996; Barker 2002; Morgan and Overholt 2004; Florence and Coladilla 2006; Whistler and Elevitch 2006; Marwat et al. 2010; Bosu et al. 2013).

Although paper mulberry has long been introduced to Europe (Barker 2002), it is Kaempfer (1712)'s plate ("Kampf. amoen. 471. t. 472") depicting paper mulberry (as "Morus papyrifera") in Japan cited by Linnaeus (1753) that was lectotyped (Florence 1997) for Morus papyrifera L., the basionym of Broussonetia papyrifera. In Japan where paper mulberry is known as “Kajino-ki” (Okamoto 2006), B. papyrifera has long been regarded as non-native (Schneider 1917), also introduced for paper making around ca. 610 A.D. (Matthews 1996; Barker 2002). Quite confusingly, the name Kajino-ki was taken by Siebold (1830) for B. kazinoki, a name long applied to a small "monoecious" shrub with 'globose' staminate catkins. 1 cm across known as Hime-kōzo in Japan (Chūjō 1950; Kitamura and Murata 1980; Yamazaki 1989; Okamoto 2006). Elsewhere, B. kazinoki is also widely found in China (Chang et al. 1998; Zhou and Gilbert 2003), Taiwan (Liao 1989, 1991, 1996), and Korea (Yun and Kim 2009). The natural hybrid between Hime-kōzo and Kajino-ki known as Kōzo in Japan (as “Morus papyrifera”) in Japan cited by Linnaeus (1753) that was lectotyped (Florence 1997) for Morus papyrifera L., the basionym of Broussonetia papyrifera. In Japan where paper mulberry is known as “Kajino-ki” (Okamoto 2006), B. papyrifera has long been regarded as non-native (Schneider 1917), also introduced for paper making around ca. 610 A.D. (Matthews 1996; Barker 2002). Quite confusingly, the name Kajino-ki was taken by Siebold (1830) for B. kazinoki, a name long applied to a small "monoecious" shrub with 'globose' staminate catkins. 1 cm across known as Hime-kōzo in Japan (Chūjō 1950; Kitamura and Murata 1980; Yamazaki 1989; Okamoto 2006). Elsewhere, B. kazinoki is also widely found in China (Chang et al. 1998; Zhou and Gilbert 2003), Taiwan (Liao 1989, 1991, 1996), and Korea (Yun and Kim 2009). The natural hybrid between Hime-kōzo and Kajino-ki known as Kōzo in Japan (as B. kazinoki × B. papyrifera; Kitamura and Murata 1980; Okamoto 2006) and Daknamu in Korea (Yun and Kim 2009) has also been long cultivated and favored by Japanese and Korean farmers for traditional paper making for centuries (Yamazaki 1989). In 2009, this natural hybrid was further named B. ×hanjiana M. Kim (Yun and Kim 2009). The third species, B. kaempferi, is a 'dioecious' lianascent climber with 'spicate' staminate catkins ca. 1.5–2.5 cm long distributed in Japan (known as Tsuru-kōzo), central to southern China, and Vietnam (Ohwi 1965; Yamazaki 1982; Zhou and Gilbert 2003; Okamoto 2006), with a controversial record in Taiwan (Suzuki 1934; Kanehira 1936; Liu and Liao 1991, 1996). In the article titled 'A speciograhical revision on Broussonetia kazinoki,' Suzuki (1934) studied a set of highly variable specimens akin to Hime-kōzo, the first identified as B. kaempferi sensu Forbes and Hemsley (1894) from Hayata (1911). After comparing with specimens collected from Japan, Suzuki (1934) concluded that B. kazinoki and B. kaempferi are different species and that all the Taiwanese specimens should be collectively recognized as a distinct taxon, which he named B. kaempferi var. australis T. Suzuki. However, Suzuki (1934)'s treatment was not cited in Kanehira (1936), the most influential pre-World War II work on the woody flora of Taiwan (Li 1963). Instead, Kanehira (1936) followed Hayata (1911)'s treatment, identifying the entity as B. kaempferi and stating that the species is dioecious. Interestingly, although a majority of the treatments of Kanehira (1936)'s 'Formosan Trees' were followed in the first edition of the Flora of Taiwan (Liu and Liao 1976) and its predecessor (Liu 1962), both Liu (1962) and Liu and Liao (1976) treated the species as B. kazinoki, with B. kaempferi var. australis synonymized under B. kazinoki [though mistakenly typed as B. "kazinoki" Sieb. var. australis Suzuki in Liu and Liao (1976)]. Subsequently, Yamazaki (1982) revisited the issue. Yamazaki (1982) emphasized the differences in leaf shapes, adopting Suzuki (1934)'s treatment by circumscribing B. kaempferi var. kaempferi as a variety endemic to Japan and B. kaempferi var. australis a variety distributed in southern China, Taiwan, and Vietnam. Yamazaki (1982)'s treatment was adopted by most treatments of the Chinese floras (e.g., Chang et al. 1998; Zhou and Gilbert 2003; Liu and Cao 2016) with rare exceptions such as Cao (2000) in which B. kaempferi var. australis was treated as a synonym of B. kaempferi. The taxonomic status of B. kaempferi var. australis was further complicated when Liao (1989, 1991, 1996), in addition to B. kazinoki, reported B. kaempferi from Taiwan, with B. kaempferi var. australis again treated as a synonym of B. kazinoki. Liao (1989, 1991, 1996)'s treatment has been followed by all subsequent works of Taiwan (Liu et al. 1994; Yang et al. 1997; Lu et al. 2006) as well as local online blogs (e.g., Nature Campus http://nc.kl.edu.tw/bbs/index.php). In a recent assessment of the conservation status of the flora of Taiwan, B. kaempferi is listed as a 'vulnerable' species with its small and declining populations (Wang et al. 2015).

Given the complicated taxonomy of these names, it is rather surprising that none of the abovementioned authors had attempted to examine and clarify type materials of the two names described by Siebold (1830) as well as B. kaempferi var. australis. After lectotypifying Siebold's Japanese plant names (Akiyama et al. 2013), Ohba and Akiyama (2014) revised the taxonomy of Broussonetia of Japan. Surprisingly, the specimen of Siebold's collections of Japanese plants that matched best to the protologue of B. kazinoki and thus lectotypified (M-0120984) turned out to be Kōzo (Akiyama et al. 2013; Ohba and Akiyama 2014), the natural hybrid between Hime-kōzo and Kajino-ki cultivated for traditional paper making. Consequently, B. monoica Hance, the next valid name long synonymized under B. kazinoki (e.g., Zhou and Gilbert 2003) becomes the correct name for Hime-kōzo (Ohba and Akiyama 2014). For B. kaempferi, the plate of ‘Papyrus spuria’ in Kaempfer (1712) was lectotypified (Akiyama et al. 2013). Based Ohba and Akiyama (2014)'s treatment, the four species of Broussonetia in Japan are B. kaempferi (Tsuru-kōzo), B. ×kazinoki (Kōzo), B. monoica (Hime-kōzo), and B. papyrifera (Kajino-ki).
Because Ohba and Akiyama (2014) dealt only with Japanese materials, this study attempts to clarify the distribution range of *B. papyrifera* and resolve controversies surrounding the name *B. kaempferi var. australis* based on herbarium work, field observation, and molecular data. We also sampled species of *Broussonetia* sect. *Allaeanthus* which thus far has never been sampled (e.g., Zerega et al. 2005; Clement and Weiblen 2009) to test the monophyly of *Broussonetia* sensu Corner (1962).

**Methods**

**Taxon sampling**

Herbarium specimens of A, BM, E, GH, HAST, K, TAI, TAIF, and TNM (herbarium acronyms according to Index Herbariorum; Thiers 2016) were examined. Specimen images of Naturalis Biodiversity Center (http://bioportal.naturalis.nl/?language=en&back), the Chinese Virtual Herbaria (http://www.cvh.org.cn/), and Global Plants on JSTOR (http://plants.jstor.org/) were consulted. Fieldtrips were conducted in Taiwan, China (Zhejiang, Fujian, Guangdong, and Guangxi), and the Philippines. All voucher specimens were deposited in HAST. To expand geographic range of our taxon sampling, herbarium collections were also sampled with the permission from E, HAST, Harvard University Herbaria (A and GH), TAIF, and TNM. The HTTP URIs of the images of important (types and vouchers) specimens examined are listed in Table 2.

**Molecular phylogenetic analyses**

To test the monophyly of *Broussonetia* sensu Corner (1962), Clement and Weiblen (2009)’s aligned DNA matrix of chloroplast *ndhF* and nuclear 26S (TreeBASE Study ID S2229) assembled for phylogenetic analyses of Moraceae was adopted, with morphological characters of the matrix excluded. The analyses of Clement and Weiblen (2009) sampled 76 species representing 32 Moraceae genera and was shown as a sister group to *M. scandens* (Lour.) Planch. in the tribe Dorstenieae. All three species of sect. *Broussonetia*, plus *B. × kazinoki*, and three of the four species of sect. *Allaeanthus* were sampled (Additional file 1) for phylogenetic analyses. Conditions for PCR amplification of *ndhF* and 26S detailed in Clement and Weiblen (2009) were followed. Phylogenetic analyses were performed using MrBayes v3.2.6 (Ronquist et al. 2012) for Bayesian inferences (BI) and GARLIC (Bazinet et al. 2014) for maximum likelihood (ML) analyses. Based on Akaike Information Criterion implemented in jModeltest 2 (Darriba et al. 2012), the models GTR + I+Γ and TVM + Γ, which were chosen in previous study (Zerega et al. 2005), were selected for 26S and *ndhF*, respectively. For both BI and ML analyses, the matrix was partitioned. For ML analysis, five independent searches and 500 replicates of bootstraps were performed and results were summarized by PAUP v. 4.0a150 (Swofford 2002). For Bayesian inferences, all parameters were unlinked and estimated independently for each data partition. Two analyses were performed in parallel, each with 4 chains of 20 million generations with temperature set to 0.1, and posterior distribution was sampled every 500 generations. Model parameters and tree statistics were summarized in MrBayes and posterior probabilities higher than 0.75 were mapped to the maximum likelihood best tree manually.

**Results and discussion**

**Type specimens of *Broussonetia kaempferi var. australis***

In the protologue of *Broussonetia kaempferi var. australis*, Suzuki (1934) designated his own (“ST”) collection No. 8336 as the type (holotype), stating “[*Typus*] ST 8336—in silvis secundaris ad Heikōkô prope Sinten (Suzuki-Tokio Apr. 2, 1933) in Herb. Univ. Imper. Taihoku.” Currently in the Herbarium of National Taiwan University (TAI), successor of the Herbarium of the Taihoku Imperial University, no collection bearing *T. Suzuki 8336* was located. However, a collection of *T. Suzuki 8362* bearing the stamp of “*Typus*” is labeled as the holotype of *B. kaempferi var. australis* T. Suzuki (http://tai2.ntu.edu.tw/Specimen/specimen.php?taiid=118781). Except for the number, all information on the label of *ST 8362*, “*In silvis secundarisis ad Heikōkô prope Sinten, Taihoku-syû, Taiwan. Suzuki-Tokio; 1933.4.2.*”, matches exactly to the protologue. Unfortunately, *ST 8362* is a badly damaged collection, leaving only a branch and a small leaf without diagnosable characters. Following the description of the taxon, Suzuki (1934) wrote “[*Materiae*] Typus-flor. mas. et fem. ST(1) 8337 et ST 4629–fl. fem.; ST 6841 et ST 8952–fruc.; SS(2) 3484 et ST 10829–steril. Fol. non partitis; SS 6042, SS 5998, ST 10827–steril. fol. partitis.” All the materials cited in “*Materiae*” in Suzuki (1934) are thus paratypes and all but two specimens (*ST 8337* and *ST 10829*) are still available in TAI (Table 2). However, after careful examination of these paratypes, all of them should be identified as *B. monoica* sensu Ohba and Akiyama (2014).

**Vouchers of *Broussonetia kaempferi* and *B. kazinoki* cited in Liao (1989, 1991, 1996)**

In the treatments of *Broussonetia*, Liao (1989, 1991, 1996) cited three collections of *B. kaempferi* (Tanaka & Shimada 13557, Yamamoto 37610, and Onizuka 22022) and two collections of *B. kazinoki* (Liao & Wang 12332 and Liao 211714). For *B. kaempferi*, two collections of *Tanaka & Shimada 13557* deposited in PH (Chung et al. 2009) and *Yamamoto 37610* at TAI are available online (Table 2). For *B. kazinoki*, Liao 211714 was located
### Table 2  HTTP URIs of specimens examined (e.g., Hyam et al. 2012)

| Species                  | Collector name and no. (Herbarium barcode) | HTTP URI                                                                 | Type status         | Current identification |
|--------------------------|--------------------------------------------|--------------------------------------------------------------------------|---------------------|------------------------|
| B. kaempferi var. australis | T. Suzuki 8362 (TAI-118781)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=118781                | Holotype?           | B. monoica             |
| B. kaempferi var. australis | S. Suzuki 6042 (TAI-037623)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037623                | Paratype            | B. monoica             |
| B. kaempferi var. australis | T. Suzuki 8952 (TAI-037637)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037637                | Paratype            | B. monoica             |
| B. kaempferi var. australis | T. Suzuki 4629 (TAI-037629)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037629                | Paratype            | B. monoica             |
| B. kaempferi var. australis | T. Suzuki 10827 (TAI-037634)              | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037634                | Paratype            | B. monoica             |
| B. kaempferi var. australis | S. Suzuki 5998 (TAI-037627)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037627                | Paratype            | B. monoica             |
| B. kaempferi var. australis | T. Suzuki 6841 (TAI-037638)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037638                | Paratype            | B. monoica             |
| B. kaempferi var. australis | S. Suzuki 3848 (TAI-037630)               | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037630                | Paratype            | B. monoica             |
| B. kaempferi             | T. Tanaka & Y. Shimada 13557 (PH-00065996) | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=65996                 | Voucher cited in Liao (1989, 1991, 1996) | B. monoica             |
| B. kaempferi             | T. Tanaka & Y. Shimada 13557 (PH-00065997) | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=65997                 | Voucher cited in Liao (1989, 1991, 1996) | B. monoica             |
| B. kaempferi             | Y. Yamamoto s.n. 1929 (TAI-037610)        | http://tai2.ntu.edu.tw/Specimen/specimen.php?taid=037610                | Voucher cited in Liao (1989, 1991, 1996) | B. monoica             |
| B. monoica               | B. C. Henry 21933 (BM-00895739)           | http://plants.jstor.org/stable/10.5555/al.ap.specimen.bm00895739        | Holotype            | B. monoica             |
| B. kazinoki              | P.F. von Siebold s.n. 1842 (M-0120964)    | http://plants.jstor.org/stable/10.5555/al.ap.specimen.m0120964          | Lectotype           | B. × kazinoki          |
| Ampalis greveanus Baill. | Grevé 254 (P-00108324)                   | http://mediaphoto.mnhn.fr/media/1441450681482QFvItbicvY2xWvK            | Lectotype           | Allaeanthus greveanus  |
| Ampalis greveanus Baill. | Grevé 254 (P-00108325)                   | http://mediaphoto.mnhn.fr/media/1441450681502xgnt.lpxEF02J2vX            | Isolectotype        | Allaeanthus greveanus  |
| Ampalis greveanus Baill. | Grevé 254 (P-00108326)                   | http://mediaphoto.mnhn.fr/media/1441450681521Fk9K2W3WQWuDvE             | Isolectotype        | Allaeanthus greveanus  |
| Broussonetia kurzii      | Griffith (Kew Distrb. 4657) (K-000357622) | http://apps.kew.org/herbcat/getImage.do?imageBarcode=K000357622           | Lectotype           | Broussonetia kurzii    |
| Broussonetia luzonica    | F. C. Gates & F. O. Otanes 6663 (Merrill. Species Blancoanae No. 468) (US-00688524) | http://n2t.net/ark:/65665/3ec2ec650-7e9f-4de7-be08-aad13028d806 | Neotype             | Allaeanthus luzonica   |
| Allaeanthus glaber       | O. Warburg 12133 (B-10_0294369)           | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.b_10_0294369 | Holotype            | Allaeanthus luzonica   |
| Allaeanthus glaber       | O. Warburg 12133 (NY-00025190)            | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.ny00025190    | Isotype             | Allaeanthus luzonica   |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (B-10_0294368)         | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.b_10_0294368 | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (FR-0031966)           | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.fr0031966     | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (GH-00034340)          | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.g00034340     | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (K-001050115)          | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.k001050115    | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (K-001050116)          | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.k001050116    | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (L-1583394)            | http://data.biodiversitydata.nl/naturalis/specimen/L.1583394             | Isotype             | Allaeanthus zeylanicus |
| Allaeanthus zeylanicus   | Thwaites—C.P. 2215 (MPU-017376)           | http://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.mpu017376      | Isotype             | Allaeanthus zeylanicus |
TAI. However, despite their determination by Liao (1989, 1991, 1996), all the voucher specimens cited should be identified as *B. monoica* sensu Ohba and Akiyama (2014).

**Identity of Broussonetia kaempferi var. australis**
Over the past few years, we have observed several wild populations in Taiwan that matched to the protologue and paratypes of *B. kaempferi var. australis* described in Suzuki (1934). Figure 1 summarizes their morphological variation and key characteristics. Together with observations of herbarium specimens at A, BM, E, GH, HAST, K, TAI, TAIF, and TNM, we conclude that all Taiwanese materials are monoecious with globose staminate catkins (Fig. 1c–e), the key characteristics of *B. kaempferi* (Ohba and Akiyama 2014). We did not find any living or herbarium collections of Taiwan bearing spicate staminate catkins (Fig. 1n) that are characteristic of *B. kaempferi* (Ohba and Akiyama 2014).

**Molecular phylogenetic analyses**
Topologies of BI and ML analyses were identical with differences in support values. Figure 2 depicts results of ML analysis marked with both BI and ML support values. With the additional samples of *Broussonetia* sensu Corner (1962), the overall phylogenetic relationships of current analyses are congruent with Clement and Weiblen (2009), with samples of *Broussonetia* sensu Corner (1962) placed in tribe Dorstenieae (Fig. 2). However, although the monophyly of *Broussonetia* sect. *Allaeanthus* and sect. *Broussonetia* were each strongly supported, *Malaisia scandens* was placed as the sister clade to sect. *Broussonetia*, rendering *Broussonetia* sensu Corner (1962) paraphyletic. To correct the paraphyly of *Broussonetia* sensu Corner (1962), we propose to reinstate the generic status of *Allaeanthus* Thwaites. Alternatively, an expanded *Broussonetia* by including *M. scandens* would not only necessitate further nomenclatural changes but also generate a genus with no obvious diagnostic character.

With the clade sect. *Broussonetia*, all samples of Taiwanese materials that would be identified as *B. kaempferi* var. *australis* sensu Suzuki (1934), plus the natural hybrid *B. ×kazinoki*, were placed in a strongly supported clade of *B. monoica* (Fig. 2), supporting our observations that all Taiwanese materials are part of the highly polymorphic *B. monoica*. All three samples of *B. kaempferi* formed a strongly supported clade sister to the strongly supported clade of *B. monoica*, with the clade of *B. papyrifera* further sister to the clade composed of *B. kaempferi* and *B. monoica*.

Within the clade sect. *Allaeanthus*, *B. kurzii* and *B. greveana* were successively sister to the clade of *B. luzonica* with strongest supports. Although our sampling did not include *Broussonetia zeylanica* (*≡Allaeanthus zeylanicus*), the type species of *Allaeanthus*, we are confident that our analysis will sustain as morphologically *B. luzonica* and *B. zeylanica* are quite similar (Corner 1962), differing from each other merely by the length of staminate catkins (10–26 cm in *B. luzonica* vs. ca. 6 cm in *B. zeylanica*) and margins of leaves (entire vs. serrate) and stipules (entire vs. denticulate).

**Conclusions**

**Taxonomic treatment**
Our phylogenetic analyses revealed that species of *Broussonetia* sensu Corner (1962) were placed in two clades corresponding to sect. *Allaeanthus* and sect. *Broussonetia*, with *Malaisia scandens* placed sister to the clade of sect. *Broussonetia* with strongest supports. To correct the paraphyly of *Broussonetia* sensu Corner (1962), we propose to reinstate the generic status of *Allaeanthus* Thwaites. Within *Broussonetia* sect. *Broussonetia*,

### Table 2 continued

| Species            | Collector name and no. (Herbarium barcode) | HTTP URI                                           | Type status   | Current identification |
|--------------------|-------------------------------------------|----------------------------------------------------|---------------|------------------------|
| Broussonetia rupicola | F.T. Wang 10884 (PE-00760682)             | http://www.cvh.org.cn/spm/PE/00760682              | Holotype      | Broussonetia monoica   |
| Smithiodendron artocarpioides | H.T. Tsai 53462 (PE-00025031)           | http://www.cvh.org.cn/spm/PE/00025031              | Holotype      | Broussonetia papyrifera |
| Smithiodendron artocarpioides | H.T. Tsai 53462 (P06885709)         | http://plants.jstor.org/stable/10.5555/al.ap.specimen.p06885709 | Isotype       | Broussonetia papyrifera |
| Smithiodendron artocarpioides | H.T. Tsai 53462 (PE-00023979)       | http://www.cvh.org.cn/spm/PE/00023979              | Isotype       | Broussonetia papyrifera |
| Smithiodendron artocarpioides | H.T. Tsai 53462 (PE-1991398)       | http://www.cvh.org.cn/spm/PE/00934142              | Isotype       | Broussonetia papyrifera |
Fig. 1  Broussonetia monoica  Hance (a–j) and  B. kaempferi  Siebold (k–o).  

a, Variation in leaf morphology; b fruiting branch; c flowering branch, showing staminate catkins (d) and pistillate capitula (e); h habit; j leaves and syncarps; k leaves; l habit of  B. kaempferi , a spirally twining liana; m spicate staminate catkins; o syncarps. [a] Shiding, New Taipei City, Taiwan, 7 April 2016, Chung 3332 (HAST); [b] Xianju, Zhejiang, China, 29 May 2016, Chung 3383 (HAST); [c–e] Wulai, New Taipei City, Taiwan, 16 March 2014, Chung 3335; [f, g] Pujiang, Zhejiang, China, 27 May 2016, Chung 3364 (HAST); [h] Xianju, Zhejiang, China, 28 May 2016, Chung 3383 (HAST); [i] Xianju, Zhejiang, China, 29 May 2016, Chung 3384 (HAST); [j] Shiding, New Taipei City, Taiwan, 17 May 2014; [k–m, o] Zong County, Guangxi, China, 18 April 2016, Peng 24753; [n] Yizhang, Hunan, China, 10 March 2004, Xiao 3316 (E)]
Fig. 2 Maximum likelihood tree based on chloroplast ndH and nuclear 26S sequences. Bootstrap percentage ≥50 are labeled above branches. Bayesian posterior probability values ≥0.75 are labeled under branches. Lineages obtained in this study are followed by collection sites (Country: locality), collectors and original collection numbers. All Taiwanese samples of *Broussonetia monoica* (*collection sites in green*) would be identified as *B. kaempferi var. australis* sensu Suzuki (1934).
B. kaempferi var. australis is synonymized under B. monoica. The species B. kaempferi is not distributed in Taiwan.

Allaeanthus Thwaites, Hooker’s J. Bot. Kew Gard. Misc. 6: 302. 1854.—Type: Allaeanthus zeylanica

Allaeanthus zeylanicus Thwaites, Hooker’s J. Bot. Kew Gard. Misc. 6: 303, pl. IX.-B. 1854.—Type: SRI LANKA. Central Province. July 1833, Thwaites.—C.P. 2215 (holotype: PDA; isotypes: B [B 10 0294368 image!], FR [FR-0031966 image!], GH [GH00034340 image!], K [K001050115 image!], L [L. 1583394 image!], MPU [MPU017376 image!]!).—Broussonetia kurzii (Thwaites) Corner, Gard. Bull. Singapore 19: 235. 1962.—Distribution. Sri Lanka.

Allaeanthus luzonicus (Blanco) Fern.-Vill. in Fl. Filip. (ed. 3) 4(15A): 198. 1880; Merrill, Sp. Blancoan. 122. 1918.—Neotype (designated by Merrill 1918, p. 122): PHILIPPINES. Luzon, Laguna Province, Los Baños, 14 March 1914, F.C. Gates & F.Q. Otanes 6663 (holotype: B [B 10 0294369 image!]; isotype: NY [00025190 image!]).—Morus luzonica Blanco, Fl. Filip. 703. 1837.—Broussonetia luzonica (Blanco) Bureau in de Candolle, Prodr. 17: 224. 1873; Merrill, Rev. Blanco Fl. Filip. 78. 1905; Corner, Gard. Bull. Singapore 19: 235. 1962; Berg et al., Fl. Malesiana, Ser. I 3(2–3): 107–109, 1936.—Type. CHINA: Yunnan, the label of this collection contains the most information.

Allaeanthus glaber Warb. in Perkins, Fl. Philipp. 3: 166. 1904.—Type: PHILIPPINES. Luzon Isl., Prov. Cagayan, Enrile, O. Warburg 12133 (holotype: B [B 10 0294369 image!]; isotype: NY [00025190 image!]).—Allaeanthus luzonicus var. glaber (Warb.) Merr., Enum. Philipp. Fl. Pl. 2: 37. 1923.—Broussonetia luzonica var. glabra (Warb.) Corner, Gard. Bull. Singapore 19: 235. 1962.

Distribution. Philippines and Indonesia (Sulawesi). Notes: Type materials of most Blanco’s names, including Morus luzonica Blanco, are not known (Merrill 1918; Nicolson and Arculus 2001). Following Nicolson and Arculus (2001), No 468 of the “illustrative specimen” cited in Merrill (1918)’s Species Blancoanae is here taken as the effective neotypification for Morus luzonica Blanco.

Allaeanthus kurzii Hook. f, Fl. Brit. India 5(15): 490–491. 1888.—Lectotype (designated by Upadhyay et al. 2010, p. 22): MYANMAR (“BURMA”): Herbarium of the late East India Company, Birma, s.d., Griffith (Kew Distribution. 4657) [female plant] (K [K000357622 image!]!).—Broussonetia kurzii (Hook. f.) Corner, Gard. Bull. Singapore 19: 234. 1962; Zhou & Gilbert, Fl. China 5: 27. 2003; Berg et al., Fl. Malesiana, Ser. I 17(1): 1465–1466. 2006.—Type: CHINA: Yunnan, Vietnam, Laos, Thailand, Myanmar, Bhutan, and India (Assam and Sikkim).

Allaeanthus greveanus (Baill.) Capuron, Fiches Bot. Ess. Forest. Madagascar: Fiche 1. 1968; Adansonia, n.s. 12(3): 386. 1972.—Ampalis greveana Baill. in Grandier, Hist. Phys. Madagascar t. 293-A. 1891.—Lectotype (here designated): MADAGASCAR. Bekopaka, near Morodava, H. Grevé 254 (P [P00108324 image!]); isolecotypes: P [P00108325 image!], P [P00108326 image!]!).—Chlorophora greveana (Baillon) Léandri, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 18. 1948.—Maclura greveana (Baillon) Corner, Gard. Bull. Singapore 19: 237. 1962.—Broussonetia greveana (Baillon) C.C.Berg, Bull. Jard. Bot. Belg. 47: 356, fig. 21. 1977.

Distribution. Madagascar.

Notes: Of the three collections of Grevé 254 at P, P00108324 is here designated as the lectotype because the label of this collection contains the most information.

Broussonetia L’Hér. ex Vent., Tabl. Régn. V. 3: 547. 1799, nom. cons.—Type: Broussonetia papyrifera L’Hér. ex Vent.

Papyrius Lam., Tabl. Encycl. 4(2): pl. 762. 1797, nom. illeg.

Smithiodendron H.H. Hu, Sunyatsenia 3(2–3): 106. 1936.

Broussonetia papyrifera (L.) L’Hér. ex Vent., Tabl. Régn. V. 3: 547. 1799.—Morus papyrifera L., Sp. Pl. 2: 986. 1753.—Lectotype (designated by Florence 1997, p. 146): [icon] ‘Morus papyrifera’ in Kaempfer, Amoen. Exot. Fasc., 471, t.472. 1712.

Smithiodendron artocarpioides H.H. Hu, Sunyatsenia 3(2–3): 107–109, pl. 6. 1936.—Type. CHINA: Yunnan, Shih-pin Hsien, 29 May 1933, H.T. Tsai 53462 (holotype: PE [1640641 image!]; isotypes: P [P06885709 image!], PE [P0010834 image!], PE [P0023979 image!], PE [00934142 image!]!).

Distribution. The reported distributions of Broussonetia papyrifera are highly inconsistent across literature (Table 1), confounded by ancient and recent translocations of the species for multiple purposes around the world (Matthews 1996; Barker 2002; Seelenfreund et al. 2010; Chang et al. 2015). The distribution map in Matthews (1996) includes Japan, Korea, China (northern, central, and southern China), Taiwan, Vietnam, Laos, Thailand, Cambodia, Myanmar, India (Sikkim), island Southeast Asia (excluding the Philippines and Borneo), Melanesia, and Polynesia islands. Chang et al. (2015) showed a high chloroplast haplotype diversity in China, Taiwan, and Indochina, suggesting that these regions are likely native range of the species. Zhou and Gilbert (2003) provided a provincial distribution in China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Hebei, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shandong, Shanxi, Sichuan, SE Xizang, Yunnan,
Zhejiang). In Northeast Asia, the non-native status of *B. papyrifera* in Japan has been repeatedly reported (Ohwi 1965; Kitamura and Murata 1980; Okamoto 2006) while this species is regarded as native in Korea (Yun and Kim 2009). Historically, the fibrous *B. papyrifera* had been introduced to Remote Oceanic islands via SE Asian islands (Matthews 1996; Chang et al. 2015); however, its growth and populations in these regions had declined significantly since last century (Matthews 1996). On the other hand, *B. papyrifera* has been introduced and become naturalized and invasive around the world (Florence and Coladilla 2006; Bosu et al. 2013; Rashid et al. 2014; Chang et al. 2015).

**Broussonetia kaempferi** Siebold, Verh. Batav. Genootsch. Kunst. 12: 28. 1830; Akiyama et al., J. Jap. Bot. 89: 127. 2014.—Lectotype (designated by Akiyama et al. 2013, p. 351): [icon] *Papyrus spuria* in Kaempfer, Amoen. Exot. Fasc. t.472, 474. 1712.

*Broussonetia kaempferi* var. *australis* auct. non T. Suzuki: Yamazaki, J. Phytogeogr. Taxon. 30(2): 69. 1982; Chang et al., Fl. Reipubl. Popul. Sin. 23(1): 27, pl. 7(9–13). 1998; Zhou & Gilbert, Fl. China 5: 27. 2003.

Distribution. Documented from Japan (Kitamura and Murata 1980; Okamoto 2006; Ohba and Akiyama 2014) and Korea (Yun and Kim 2009) while introduced to Remote Oceanic islands via SE Asian islands (Matthews 1996; Chang et al. 2015) and Remote Sea Islands. In such features as plant sex (dioecious or monoecious), hairness of young shoots, and leaf shape and texture (Korea J. Pl. Taxon. 39(2): 84, 2009.—Type: KOREA. Province Jeonnam, Is. Gageo, 16 May 2008, syn. nov. KOREA. Province Jeonnam, Is. Gageo, 16 May 2008, syn. nov. KOREA. Province Jeonnam, Is. Gageo, 16 May 2008, syn. nov.

**Broussonetia × kazinoki** Siebold (in Verh. Batav. Genootsch. Kunst. 12: 28. 1830, *nom. nud.*) in Utteridge and Bramley (2015, p. 77, figs. 2 & 6) are a pistillate individual of *B. kaempferi*.

**Broussonetia × xanijiana** M. Kim in Yun and Kim, Korea J. Pl. Taxon. 39: 82. 2009: 82, syn. nov. Type: —KOREA. Province Jeonnam, Is. Gageo, 16 May 2008, *M. Kim 9944* (holotype: JNU).

Distribution. Documented from Japan (Kitamura and Murata 1980; Okamoto 2006; Ohba and Akiyama 2014) and Korea (Yun and Kim 2009).

Notes. Long regarded as *Broussonetia kazinoki × B. papyrifera* (Okamoto 2006), the Japanese *Kōzo Broussonetia × kazinoki* is actually the natural hybrid between *B. monoica* and *B. papyrifera* cultivated for paper making since ancient time in Japan and Korea (Yun and Kim 2009; Ohba and Akiyama 2014). *Broussonetia × kazinoki* is highly variable and “various intermediate forms are known between the parent species (i.e., *B. monoica* and *B. papyrifera*) in such features as plant sex (dioecious or monoecious), hairness of young shoots, and leaf shape and texture” (Ohba & Akiyama 2014) and Korea J. Pl. Taxon. 39: 82. 2009.—Type: CHINA. Guangdong (“prov. Cantonensis”), “Lien chau”, 1881, B. C. Henry 21933 (holotype: BM [BM000895739 image!]).

*Broussonetia kaempferi* auct. non Siebold: Hayata, J. Coll. Sci. Imp. Univ. Tokyo. 30: 273. 1911; Kanehira, For. Trees rev. ed. 146. 1936; Li, Woody Flora of Taiwan 113, fig. 35. 1963; Liao, Quart. J. Exp. Forest. 3(1): 148. 1989; Liu et al., Trees of Taiwan 331. 1994, pro parte; Liao, Fl. Taiwan, 2nd. ed. 2: 140. 1996, pro parte; Lu et al., Trees of Taiwan 2: 95, photos. 2006, pro parte.

*Broussonetia kaempferi* var. *australis* T.Suzuki, Trans. Nat. Hist. Soc. Taiwan 24: 433–435. 1934.—Type: TAIWAN. “In silvis secundris ad Heikoko prope Sinten”, T. Suzuki 8362 (“ST 8336”), 2 Apr 1933 (holotype: TAI [118781 image!]).

*Broussonetia rupicola* FT. Wang & Tang, Acta Phytotax. Sin. 1(1): 128. 1951.—Type: CHINA. “Szechuan” (Sichuan), Nanchuan, F. T. Wang 10884 (holotype: PE [00760682 image!]), syn. nov.

*Broussonetia jiangxiensis* X.W Yu, J. Jiangxi Agric. Univ. (1): 3, fig. 2. 1982.—Type: CHINA. Jiangxi, Nanchang, X.W Yu 1435 (holotype: JXAU), syn. nov.

*Broussonetia kazinoki* var. *ruyangensis* P.H.Liang & X.W.Wei, Bull. Bot. Res., Harbin 2(1): 155–156, fig. 1. 1982.—Type: CHINA. Guangdong: Ruyang, Wu-Zhi-Shan, 600–800 m, 28 Mar 1979, X.-W. Wei 4471 (holotype: CANT).

*Broussonetia kazinoki* form. *koreana* M. Kim, Korean J. Pl. Taxon. 39(2): 84, fig. 1F, 1G. 2009.—Type: KOREA. Province Jeonnam, Is. Gageo, 16 May 2008, *M. Kim 9946* (holotype: JNU), syn. nov.

*Broussonetia kazinoki* auct. non Siebold: Liu, Illustrations of Native and Introduced Ligneous Plants of Taiwan 2: 707, pl. 56f. 1962; Liu & Liao, Fl. Taiwan 2: 120, 122, pl. 234. 1976; Liao, Quart. J. Exp. Forest. 3(1): 148–149. 1989; Liu et al., Trees of Taiwan 331. 1994, pro parte; Liao, Fl. Taiwan, 2nd. ed. 2: 140, pl. 68, photo 59. 1996, pro parte; Chang et al., Fl. Reipubl. Popul. Sin. 23(1): 26, pl. 7(6–8). 1998; Zhou & Gilbert, Fl. China 5: 26–27. 2003; Lu et al., Trees of Taiwan 2: 95, photos. 2006, pro parte; Yun & Kim, Korean J. Pl. Taxon. 39(2): 84, fig. 1C, 1F, 1G. 2009.
Additional file

**Additional file 1. Taxon voucher information** [collector No. (herbarium acronym), Country of origin (Locality), and NCBI accession numbers (26S/nr/dB) of newly collected DNA sequences.]

**Authors’ contributions**

KFC conceived the idea and designed the project, conducted herbarium work, collected plant materials in Taiwan and China, and wrote the article. WHK, YHH, and YHL collected plant materials and molecular data. RRR collected plant material in the Philippines. WBX collected plant materials in China. All authors read and approved the final manuscript.

**Author details**

1 Research Museum and Herbarium (HAST), Biodiversity Research Center, Academia Sinica, 128 Academia Road, Section 2, Nangang, Taipei 11529, Taiwan.
2 School of Forestry and Resource Conservation, National Taiwan University, No. 1, Sec. 4, Roosevelt Rd., Taipei 10617, Taiwan. 3 Department of Biology, College of Arts and Sciences, University of the Philippines Manila, Padre Fauna, 1000 Manila, Philippines. 4 Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China.

**Acknowledgements**

The authors are grateful to the followings for their assistance: Jarearnsak Saewai for providing silica-gel leaves of *Altheafloridana* Kurz from Thailand; Nonryuki Fujii for providing materials from Japan; Yunpeng Chao and Pan Li for assisting collecting *Broussonetia* in Zhejiang, China; A, BM, E, GH, HAST, K, TAI, TAIF, and TNM for access to their collections; A, GH, E, TAI, and TNM for permissions to sample herbarium specimens. KFC’s visit to Harvard University Herbaria was supported by the 2016 Sargent Award for Visiting Scholar, Arnold Arboretum, Harvard University. This study was supported by grants of Biodiversity Research Center, Academia Sinica to KFC.

**Competing interests**

The authors declare that they have no competing interests.

**Received: 28 November 2016 Accepted: 13 February 2017**

**Published online:** 21 February 2017

**References**

Akiyama S, Thijsse G, Esser H-J, Ohba H (2013) Siebold and Zuccarini’s type specimens and original materials from Japan, Part 2. Angiosperms, Dicotyledoneae 1. J Jap Bot 88:346–377.
Barker C (2002) Plate 432. *Broussonetia papyrifera*. Curtis’s Bot Mag 19:8–18. doi:10.1111/1467-8748.00324
Bazinet AL, Zwickl DJ, Cummings MP (2014) A gateway for phylogenetic analysis powered by grid computing featuring GARLI 2.0. Syst Biol 63:812–818. doi:10.1093/sysbio/syu031
Berg CC (1977) Revisions of African Moraceae (excluding Dosteniina, Ficus, Musanga and Mynianthus). Bull Jard Bot Nat Belg 47:267–407.
Berg CC, Corner EJH, Jarrett FM (2006) Moraceae-genera other than Ficus. In: Nooteboom HP (ed) Flora Malesiana, series 1, vol 17. National Herbarium Nederland, Leiden, pp 1–152.
Bosu PP, Apetorgbor MM, Nikumah EB, Bandoh KP (2013) The impact of *Broussonetia papyrifera* (L.) vent. on community characteristics in the forest and forest-savannah transition ecosystems of Ghana. Afr J Ecol 51:528–535. doi:10.1111/aje.12063
Cao Z (2000) Moraceae. In: Fu L, Hong T (eds) Higher plants of China, vol 4. Qingdao Publishing House, Qingdao, pp 27–74.
Capuron R (1972) Contribution à l’étude de lat flore forestière de Madagascar. Adansonia, series 2(13):375–388.
Chang S, Wu C, Cao Z (1998) Moraceae. In: Chang S, Wu C (eds) Flora Reipublcaei Popularis Sinicae, Tomus 23(1). Science Press, Beijing, pp 1–219.
Chang C-S, Liu H-L, Moncada X, Seelenfriend A, Seelenfriend D, Chung K-F (2015) A holistic picture of Austronesian migrations revealed by phylogeography of Pacific paper mulberry. Proc Natl Acad Sci USA 112:13537–13542. doi:10.1073/pnas.1503205112
Chûjô K (1950) Notes on *Broussonetia papyrifera* vent. (Kazinoki), *B. kazinoki* Sieb. (Kôzo) and *B. kaempferi* Sieb. (Turu-Kôzo). J Jap For Soc 32:329–334
Chung K-F, Torke BM, Wu K (2009) Unearthing a forgotten legacy of 20th century floristics: the collection of Taiwanese plant specimens in the herbarium of the Academy of Natural Sciences (PhL). Taiwania 54:159–167
Clement WL, Weiblen GD (2009) Morphological evolution in the mulberry family (Moraceae). Syst Bot 34:530–552. doi:10.1006/syst.2009.2155
Corner EJH (1962) The classification of Moraceae. Gard Bull Singap 19:187–252.
