

## Taxonomic re-assessment of *Kindbergia* (Brachytheciaceae, Bryophyta) in China, with a description of *Pseudokindbergia* gen. nov.

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**Abstract** – The distribution and systematic position of *Kindbergia* Ochyra in China is re-evaluated. The phylogenetic analyses based on nuclear marker (ITS1-5.8S-ITS2) and chloroplastic markers (*rpl16*, *trnG*, and *trnL-F*) show that the alleged species of “*Kindbergia*” in China and Himalayas form a maximally supported clade (1.00 PP and 100 MPBS), which is closely related to the clade of *Brachythecium* Schimp., *Eurhynchiadelphus* Ignatov et Huttunen, and *Myuroclada* Besch., whereas the other *Kindbergia* specimens from Africa, America, Europe, Japan and the Southern Hemisphere form a monophyletic group, which is sister to *Scleropodium* Schimp. The specimens of Chinese species of “*Kindbergia*” are found, both molecularly and morphologically, to be identical with the Himalayan *K. dumosa* (Mitt.) Ignatov et Huttunen, and differ from *Kindbergia* specimens from other regions in the world in the shape of proximal branch leaves, operculum shape and capsule orientation. A new monotypic genus *Pseudokindbergia* M. Li, Y.F. Wang, Ignatov et B.C. Tan, is established to accommodate only the generitype *P. dumosa* (Mitt.) M. Li, Y.F. Wang, Ignatov et B.C. Tan, *comb. nov.* ( $\equiv$  *Hypnum dumosum* Mitt.), and *Bryhnia serricuspis* (Mitt.) Y.F. Wang et R.L. Hu ( $\equiv$  *Eurhynchium serricuspis* Mitt.) is considered synonymous with it.

**Molecular phylogeny / Brachytheciaceae / *Kindbergia* / *Pseudokindbergia* / China**

### INTRODUCTION

The Brachytheciaceae are a moss family within which over 50 genera were recognized, and for a long time they were a point of taxonomic disagreement among different authors. Having an extremely variable morphology and lacking often distinctive taxonomic characters, even in various combination, that are

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specific for one genus, the family has earned the reputation as one of the most taxonomically difficult groups among mosses. The species referred to the genus *Kindbergia* in the middle of 20th century were often placed in *Eurhynchium* Schimp. and frequently confused with species of *Oxyrrhynchium* (Schimp.) Warnst., until the conservation of the latter with the conserved type was introduced (Ignatov & Isoviita, 2003). This action was deemed necessary as *K. praelonga* (Hedw.) Ochyra, the type of the genus *Kindbergia*, had been considered by some authors as the type of the genus *Oxyrrhynchium*. The long history of the misapplication of the species name “*praelongum*” was described in details by Touw & Knol (1978). Noteworthy to mention that in all the current classification systems of the family based on molecular phylogenetic studies (Ignatov & Huttunen, 2002; Vanderpoorten *et al.*, 2005; Huttunen *et al.*, 2007), the three genera, *Kindbergia*, *Eurhynchium* and *Oxyrrhynchium*, belong to three different subfamilies.

The genus *Kindbergia* Ochyra was originally segregated by Robinson (1967) as *Stokesiella* (Kindb.) Robins. Since the name appeared to be an illegitimate later homonym of *Stokesiella* Lemmerm. of 1908, Ochyra (1982) proposed a new replacing name, *Kindbergia*. Many bryologists had followed the suggestion (Giles, 1990; McFarland, 1994; Crosby *et al.*, 1999; Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004; Huttunen *et al.*, 2007; Goffinet & Shaw, 2008; Frey & Stech, 2009). However, the genus was not accepted by Koponen (1987), Buck (1988), Noguchi *et al.* (1991), and Iwatsuki (2004).

In China, the species distribution of the genus *Kindbergia* is not clear and rather controversial. Brotherus (1929) reported *K. praelonga* [as *Eurhynchium stokesii* (Turner) Schimp.] from Hunan Province, which later was proven to be a phenotypic expression of *Bryhnia novae-angliae* (Sull. *et* Lesq.) Grout with longer leaf apex (Ignatov *et al.*, 2005). Several authors reported *K. praelonga* in China successively (Bai, 1997; Zhao & Cao, 1998; Hu & Wang, 2000). *Oxyrrhynchium bifforme* Broth. and *Bryhnia serricuspis* (Müll Hal.) Y.F.Wang *et* R.L.Hu, both endemic to China, were synonymized with *K. praelonga* by Koponen (1987) and Ignatov *et al.* (2005). Redfearn *et al.* (1996) included two species and one variety in the genus *Kindbergia* in China, namely *K. arbuscula* (Broth.) Ochyra, *K. praelonga*, and *K. praelonga* var. *stokesii* (Turner) Ochyra. However, Hu & Wang (2005) and Hu *et al.* (2008) accepted only one species, *K. arbuscula*, for the Chinese moss flora, and put it in the genus *Eurhynchium*.

Recent molecular phylogenetic data provide a lot of evidences for segregation of additional small genera in the family (Huttunen & Ignatov, 2004; Ignatov *et al.*, 2008; Aigoïn *et al.*, 2009a, b; Ignatov *et al.*, 2010). The status of *Kindbergia* as a separate and well-defined genus was confirmed by all the recent studies (Huttunen & Ignatov, 2004; Vanderpoorten *et al.*, 2005, etc.). Notwithstanding, an expanded analysis of the genus was undertaken by Hedenäs (2010) based on the nuclear ITS and chloroplastic tRNA-Gly. His sampling of taxa covered the range of the genus worldwide, showing the very wide distribution of *Kindbergia praelonga* in Europe and Macaronesia, SW Asia, Africa, Australia and New Zealand. The North and South American plants of *K. praelonga* that were morphologically virtually indistinguishable from European plants were found to be somewhat different in their genetic constitution. On the other hand, the morphologically distinct *K. arbuscula* from Japan did not exhibit any differences in the sequence of chloroplastic DNA studied (nuclear marker was not studied). Therefore Hedenäs (2010) suggested that South American plants and most of North American ones are likely to represent another species, which however still awaiting a thorough revision. At the same time, specimens of

Chinese *K. praelonga* (including *Bryhnia serricuspis*) appeared to be even more different in their DNA sequence alignment from the European and American counterparts. Hedenäs (2010) concluded that the Chinese and Himalayan populations of *Kindbergia* may be conspecific and suggested that *K. dumosa* (Mitt.) Ignatov *et* Huttunen, a moss described from the eastern Himalayas (Gangulee, 1978; Vohra, 1983), be used as the proper name of the combined taxon. However, only four sequences of three Chinese samples were involved in the study of Hedenäs (2010), while the Himalayan material of *K. dumosa* was not obtained for the study as the species is not common in distribution. Thus, the necessity of another expanded analysis of the East Asian materials of *Kindbergia* remains and this problem is specifically addressed in the present study.

## MATERIALS AND METHODS

### Morphological investigation

Except for *Kindbergia kenya* (Dixon *ex* Tosco *et* Piovano) O'shea *et* Ochyra, a total of 295 collections of other seven *Kindbergia* species, namely *K. africana* (Herzog) Ochyra, *K. arbuscula*, *K. oedogonium* (Müll.Hal.) Ochyra, *K. oregana* (Sull.) Ochyra, *K. praelonga*, *K. squarriifolia* (Broth. *ex* Iishiba) Ignatov *et* Huttunen, and *K. dumosa* were studied. All these specimens were loaned from BM, DUKE, FH, FI, HIRO, HSNU, JE, KUN, MHA, MO, NY, PE, S, SHNU, SZG, and TNS. A number of characters, such as growth form, leaf shape and dimensions, lamina cell length, shape of proximal branch leaves, shape of operculum, and capsule orientation etc., were investigated. Sporophytes are not common in Chinese plant materials, and only nine samples with capsules were studied. Fortunately, European and American collections with sporophytes were relatively numerous, allowing a reliable observation and evaluation.

### Molecular taxon sampling

Seventy-eight samples belonging to the representative genera of the three subfamilies across the family Brachytheciaceae were used for the molecular analyses (see Appendix). Except for *Brachytheciella* Ignatov, which is known only by the holotype in H and is morphologically quite divergent from *Kindbergia*, all genera of the subfamily Brachythecioideae Engler (including Homalothecioideae Ignatov *et* Huttunen) were included as the in-groups: *Brachytheciastrum* Ignatov *et* Huttunen, *Brachythecium* (including *Bryhnia* Kaurin), *Eurhynchadelphus* Ignatov, Huttunen *et* T.J. Kop., *Eurhynchiastrum* Ignatov *et* Huttunen, *Frahmiella* Ignatov, Vanderpoorten *et* Wang You-fang, *Homalothecium* Schimp., *Kindbergia*, *Myuroclada* Besch., *Sciuro-hypnum* (Hampe) Hampe, *Scleropodium*, and *Unclejackia* Ignatov, T.J.Kop. *et* D.H.Norris (see also Ignatov & Huttunen, 2002; Vanderpoorten *et al.*, 2005; Frey & Stech, 2009; Li *et al.*, 2014). Within the genus *Kindbergia*, four of eight species were sampled: *K. arbuscula*, *K. dumosa*, *K. oregana* (Sull.) Ochyra, and the type species, *K. praelonga*. These are the species studied also by Hedenäs (2010). The remaining four species of the genus could not be included in our study because of no available recent collections.

In our study we sampled twenty specimens of alleged taxa of the genus from China representing different climatic regions of the country and also maximally the differentiated morphotypes. Four specimens of *K. dumosa* from India and Bhutan collected from different altitudinal belts in the Himalayas were sequenced as well. Outgroups include representative members of the other two subfamilies of Brachytheciaceae, Eurhynchioideae Milde (*Rhynchostegium*) and Helicodontioideae M.Fleisch. (*Cirriphyllum* and *Oxyrrhynchium*) (Frey & Stech, 2009). The resulting tree of the family is rooted on one of two analyzed representatives of Meteoriaceae, a sister family to Brachytheciaceae (Huttunen & Ignatov, 2004).

### **Molecular protocols**

DNA extraction followed the protocols described by Sun *et al.* (2000). One nuclear and three plastid markers were chosen: nuclear ribosomal internal transcribed spacer region ITS1-5.8S-ITS2 (hereafter, ITS), ribosomal protein L16 (hereafter, *rpl16*), tRNA (Gly) (UCC) (hereafter, *trnG*) and *trnL-trnF* intergenic spacer (hereafter, *trnL-F*). These four regions have been widely used in phylogenetic analyses of pleurocarpous mosses (eg. Huttunen & Ignatov, 2004; Huttunen *et al.*, 2007; Draper & Hedenäs, 2009; Hedenäs, 2010, 2011a, b, 2012; Li *et al.*, 2014). The following primers were used to amplify the different markers: “18SF” and “26SR” for the ITS region, or sometimes, “18SF” and “5.8SR” for ITS1, and “5.8SF” and “26SR” for ITS2 (Hartmann *et al.*, 2006); “F71” (Jordan *et al.*, 1996) and “antR2” (Hedenäs & Eldenäs, 2007) for *rpl16*; “*trnGF*” and “*trnGR*” for *trnG* (Pacak & Szweykowska-Kulinska, 2000); and “*trnC*” and “*trnF*” for *trnL-trnF* region (Taberlet *et al.*, 1991). For ITS and *trnL-F*, the PCR cycles used an initial denaturation step of 3 minutes at 95°C, followed by 35 cycles of 30 seconds at 95°C, 30 seconds at 50°C, 90 seconds at 72°C, and a final elongation of 5 minutes at 72°C. For *trnG* and *rpl16*, it began with an initial denaturation step of 5 minutes at 80°C, followed by 34 cycles of 1 minute at 95°C, 1 minute at 50°C (58°C for *rpl16*), 4 minutes at 65°C, and a final elongation of 5 minutes at 65°C. PCR products were purified with the Gel Extraction Kit (Cwbio, Shanghai, China) following the manufacturer’s protocol. These purified PCR products were sequenced by Life Technologies Inc., China ([www.lifetechnologies.com](http://www.lifetechnologies.com)).

### **Sequence editing, alignment and phylogenetic analyses**

Sequence chromatograms were compiled using SeqMan II (DNASTAR Inc., Madison, WI, USA) and then aligned manually in PhyDE 0.9971 (Müller *et al.*, 2010). Regions of partially incomplete data at the beginning and end of the sequences were identified and excluded from subsequent analyses. Using simple indel coding as proposed by Simmons & Ochoterena (2000), indels were coded with SeqState (Müller, 2005). Both Maximum parsimony (MP) and Bayesian phylogenetic analyses were conducted as both of them were used by previous authors analyzed this group. For the MP analysis, command files for the parsimony ratchet (Nixon, 1999) were generated using the program PRAP2 (Wall *et al.*, 2008) and executed with the program PAUP 4.0b10 (Swofford, 2003) using TBR branch swapping with character states specified as unordered and unweighted. Bootstrap analysis was performed with 10000 replicates and random taxon addition with 100 replicates. For the Bayesian analysis, after optimal nucleotide substitution models for each region were calculated using MrModeltest v.2.3 (Nylander, 2004)

in PAUP 4.0b10 (Swofford, 2003), the relevant parameters were set accordingly to corresponding values independently derived from each model. Phylogenetic analyses were then conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.2.1 (Huelsenbeck *et al.*, 2001). Four parallel runs, each with four chains, were run for 5000000 generations, with trees being sampled every 1000 generations.

Phylogenetic trees were constructed for the individual loci in each analysis. As some samples studied for phylogenetic analyses have only the sequences of ITS or part of the four markers, the chloroplastic dataset include 59 of the 78 samples representing most of the genera in Brachythecioideae. Topological conflicts were considered significant if two different relationships for the same set of taxa were both supported by Bayesian posterior probability (PP) (> 0.95) and with bootstrap support values from the MP (MPBS) (> 75). When there was no conflict between the nuclear and chloroplast partitions, the phylogenetic analyses were reconstructed based on combined dataset of ITS, *rpl16*, *trnG*, and *trnL-F* regions. TreeGraph 2 (Stöver & Müller, 2010) was used to summarize the topology and support from maximum parsimony and Bayesian analyses.

## RESULTS

### Evaluation of distinguishing morphological characters

Our preliminary evaluation made for a number of characters such as growth form, leaf shape and dimensions, and lamina cell length etc., yielded strong overlapping observation among all seven *Kindbergia* species (not shown). While Chinese *Kindbergia* species and *K. dumosa* from Himalayas are clearly different from extra-Chinese and other species in the shape of proximal branch leaves (previously often called pseudoparaphyllia, but see discussion of Spirina *et al.* (2012) and Ignatov & Spirina (2012)), the shape of operculum, and capsule orientation (Table 1; Figs 1-21). The Chinese + Himalayan species of *Kindbergia* have semi-orbicular to orbicular-triangular, obtuse or truncate proximal branch leaves, conic-apiculate operculum, and an inclined capsule, whereas those of the species of the genus from the rest of the world are ovate-apiculate, ovate-acuminate to triangular proximal branch leaves, long-rostrate operculum, and an subpendent to horizontal capsule.

In addition, the differences shown in the shape of proximal branch leaves, the shape of operculum, and capsule orientation, were found to be rather reliable and congruent among and within the molecularly delimited plant groups (Table 1; Figs 1-24). In all cases, the shape of proximal leaves of a shoot is easy to study and has taxonomic value.

### Phylogenetic reconstruction

Except for the clade of *Sciuro-hypnum* and BME clade which are resolved differently in the nuclear and chloroplastic topologies, the well supported major clades resolved by both dataset were the same, and the combined tree was

Table 1. A morphological comparison among species of *Kindbergia*

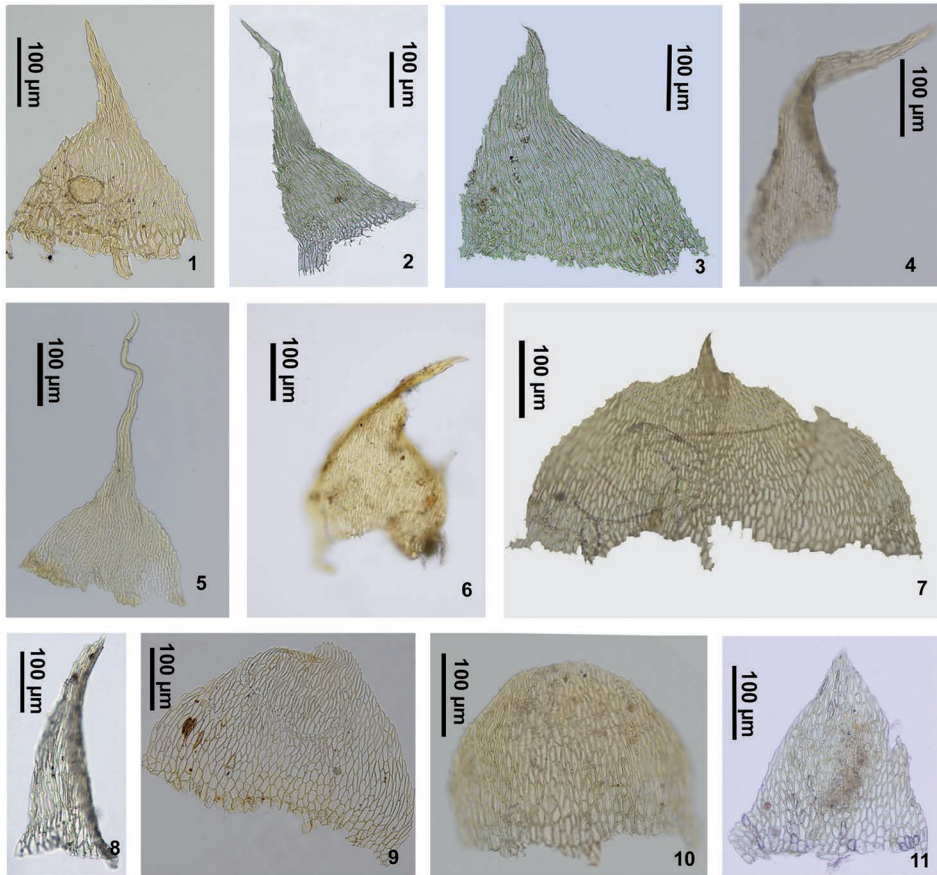
<i>Taxon</i>	<i>Proximal branch leaves</i>	<i>Operculum</i>	<i>Capsule orientation</i>	<i>Distribution</i>
<i>K. africana</i>	triangular-acuminate	not seen	not seen	Uganda, South Africa
<i>K. arbuscula</i>	ovate-apiculate	long-rostrate	subpendent	Japan
<i>K. dumosa</i>	semi-orbicular, truncate	conic-apiculate	inclined	India, Bhutan, Nepal
<i>K. dumosa</i> ("K. arbuscula")	semi-orbicular, truncate	conic-apiculate	inclined	China
<i>K. dumosa</i> ( <i>Bryhnia serricuspis</i> )	triangular, obtuse	not seen	not seen	China
<i>K. oedogonium</i>	ovate-acuminate	long-rostrate	horizontal	Bolivia
<i>K. oregana</i>	ovate-acuminate	long-rostrate	subpendent	Canada, USA
<i>K. praelonga</i>	ovate-acuminate to triangular-acuminate	long-rostrate	subpendent	Africa, Australia, Europe, America, West Asia
<i>K. squarriifolia</i>	triangular-acuminate	not seen	not seen	Japan

Table 2. Numbers of sites in each locus and coded indels based on sequence length (bp), variable (v.) sites, informative (i.) sites, and the models selected for Bayesian analysis

	<i>Gene</i>	<i>Length (bp)</i>	<i>v. sites</i>	<i>i. sites</i>	<i>Model</i>
Nuclear compartment	ITS	872	238	151	GTR+I+G
Plastid compartment	<i>rpl16</i>	707	131	82	GTR+I+G
	<i>trnG</i>	523	76	46	GTR+I
	<i>trnL-F</i>	358	40	18	HKY+I+G
Coded indels		209	215	123	variable
Total		2669	700	420	-----

better resolved than any of the separate trees and the support values were substantially increased as well (Figs 22-24). Thus we used the combined dataset for further analyses.

After the deletion of incomplete regions of the gene sequences at the beginning and end of the alignment for some specimens, the total number of aligned sites of the four loci and coded indels used in the present study contains 2669 bp pairs. Among them, 872 positions belong to the nuclear compartment, 1588 positions for the plastid genes, and 209 for coded indels. The number of sites

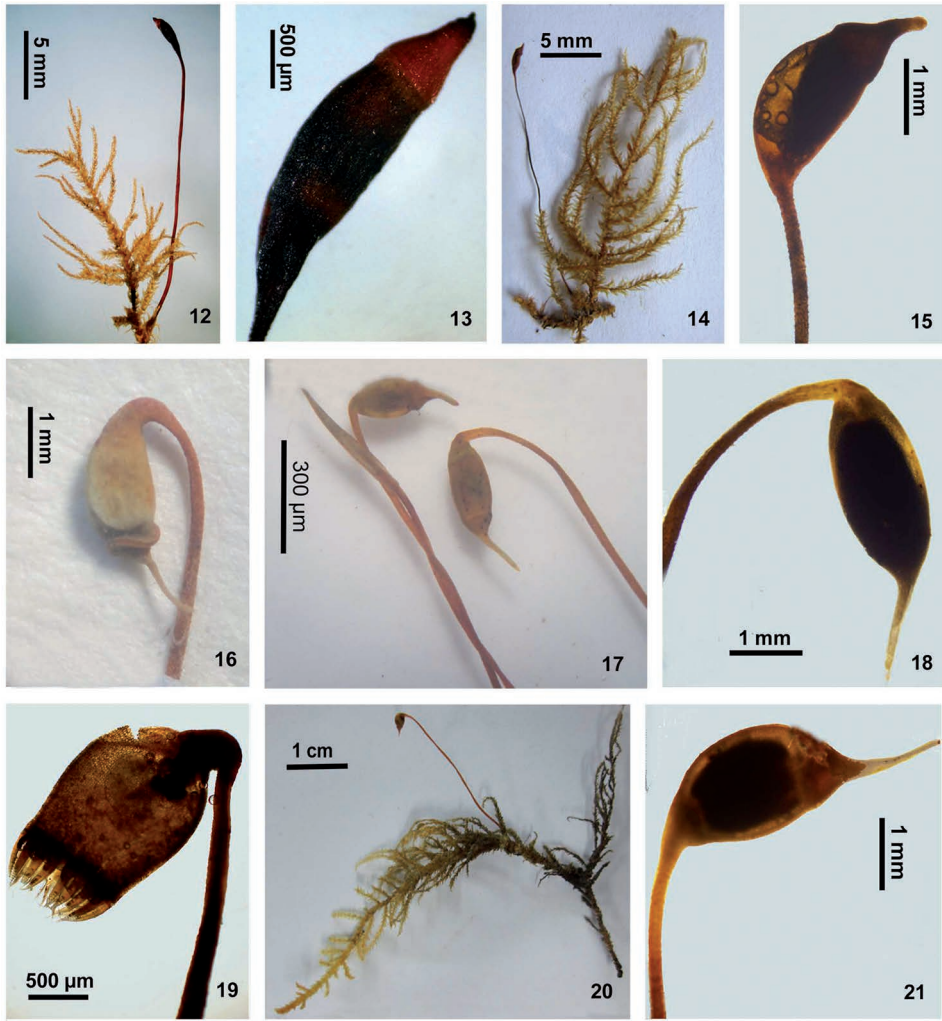


Figs 1-11. The shape of proximal branch leaves in the genus *Kindbergia*

**1.** *K. praelonga* (Canada, W.B. Schofield 12822, MO 5147535). **2.** *K. praelonga* (Australia, H. Streimann 42657, SB96040). **3.** *K. praelonga* (Portugal, Fontinha 2, SB22292). **4.** *K. squarriifolia* (isotype: Japan, H. Sasaoka 13678, TNS 174038). **5.** *K. oregana* (isotype: Oregon, NY 00734140). **6.** *K. oedogonium* (possible type: Germain s.n., NY 01274075). **7.** *K. arbuscula* (Japan, E. Nokubo 31, HIRO). **8.** *K. africana* (isotype: L. Haumann 69, SB82905). **9.** *K. dumosa* (lectotype: India, J.D. Hooker 1041, NY 01179094). **10.** *K. dumosa* (“*K. arbuscula*”) (China, M.Z. Wang 6477, PE). **11.** *K. dumosa* (*Bryhnia serricuspis*) (isotype: China, J. Giraldi s.n., FI).

in each locus and coded indels based on sequence length, variable sites, parsimony informative sites and the optimal substitution models selected for Bayesian analysis are given in Table 2.

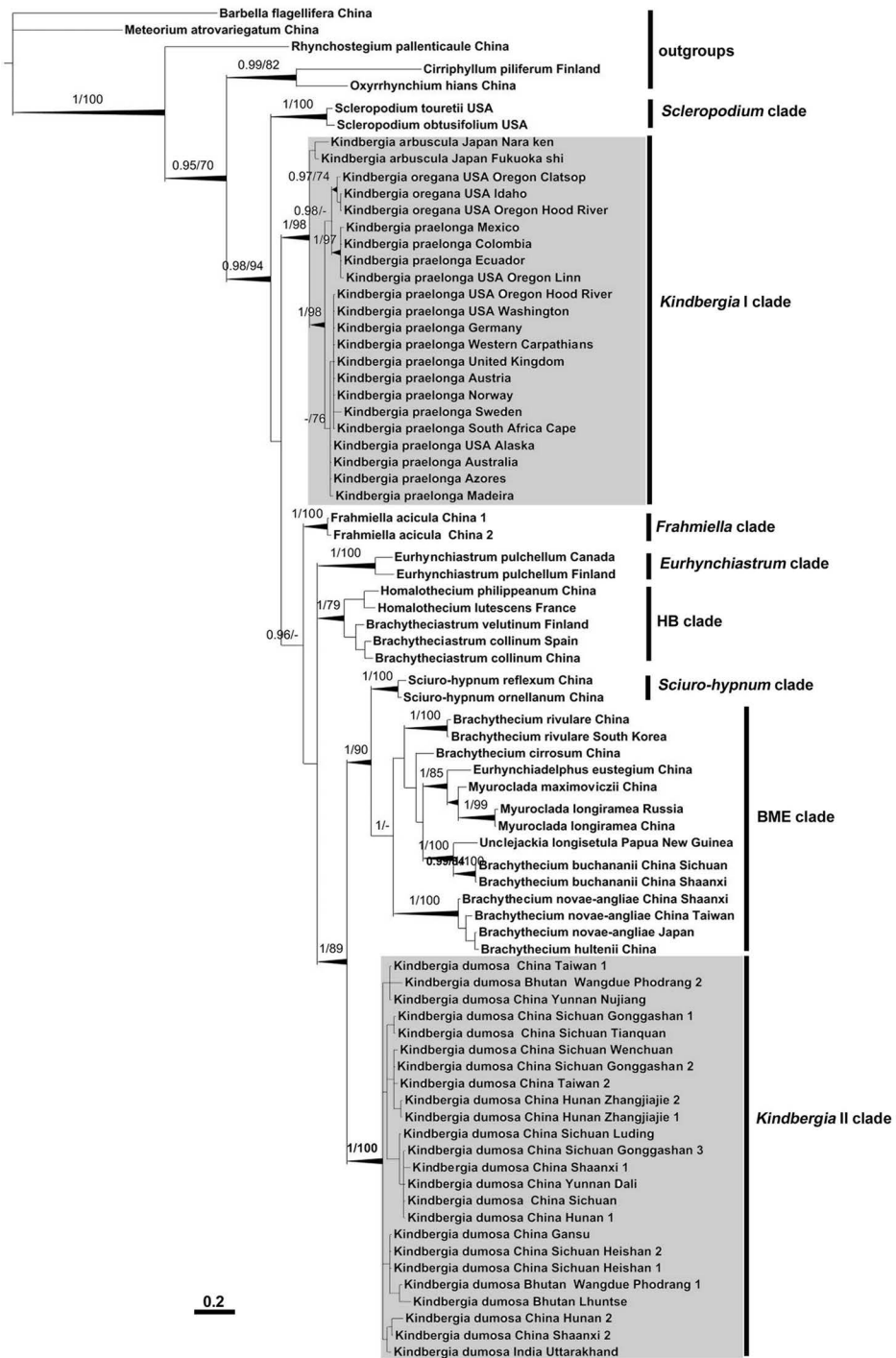
The topologies are mostly identical after a comparison between the MP analysis (number of the most parsimonious trees = 1, length= 1240 steps; Consistency Index = 0.633; Retention Index = 0.842) and the Bayesian analysis (-lnL = 10199.152) (trees not shown). Thus, only the Bayesian consensus tree for the combined dataset is here presented as the main data outline (Fig. 24). The Bayesian posterior probabilities (PP), as well as the bootstrap support values from MP analysis (MPBS), are labeled on the branches respectively.



Figs 12-21. Capsule orientation and the shape of operculum in the genus *Kindbergia*  
**12-13.** *K. dumosa* (“*K. arbuscula*”) (China, *M.Z. Wang* 6477, PE); **14-15.** *K. dumosa* (lectotype: India, *J.D. Hooker* 1041, NY01179094); **16.** *K. arbuscula* (holotype: Japan, JE); **17-18.** *K. praelonga* (Canada, *W.B. Schofield* 12822, MO 5147535); **19.** *K. oregana* (isotype: Oregon, NY 00734140); **20-21.** *K. oedogonium* (possible type: *Germain s.n.*, NY 01274075).

Fig. 22. Fifty percent majority-rule consensus tree from Bayesian analysis of dataset of 78 samples based on ITS. Bayesian posterior probabilities (>0.95) (above) and MP boot-strap support values (>75) (below) are shown on the branches respectively. ▶





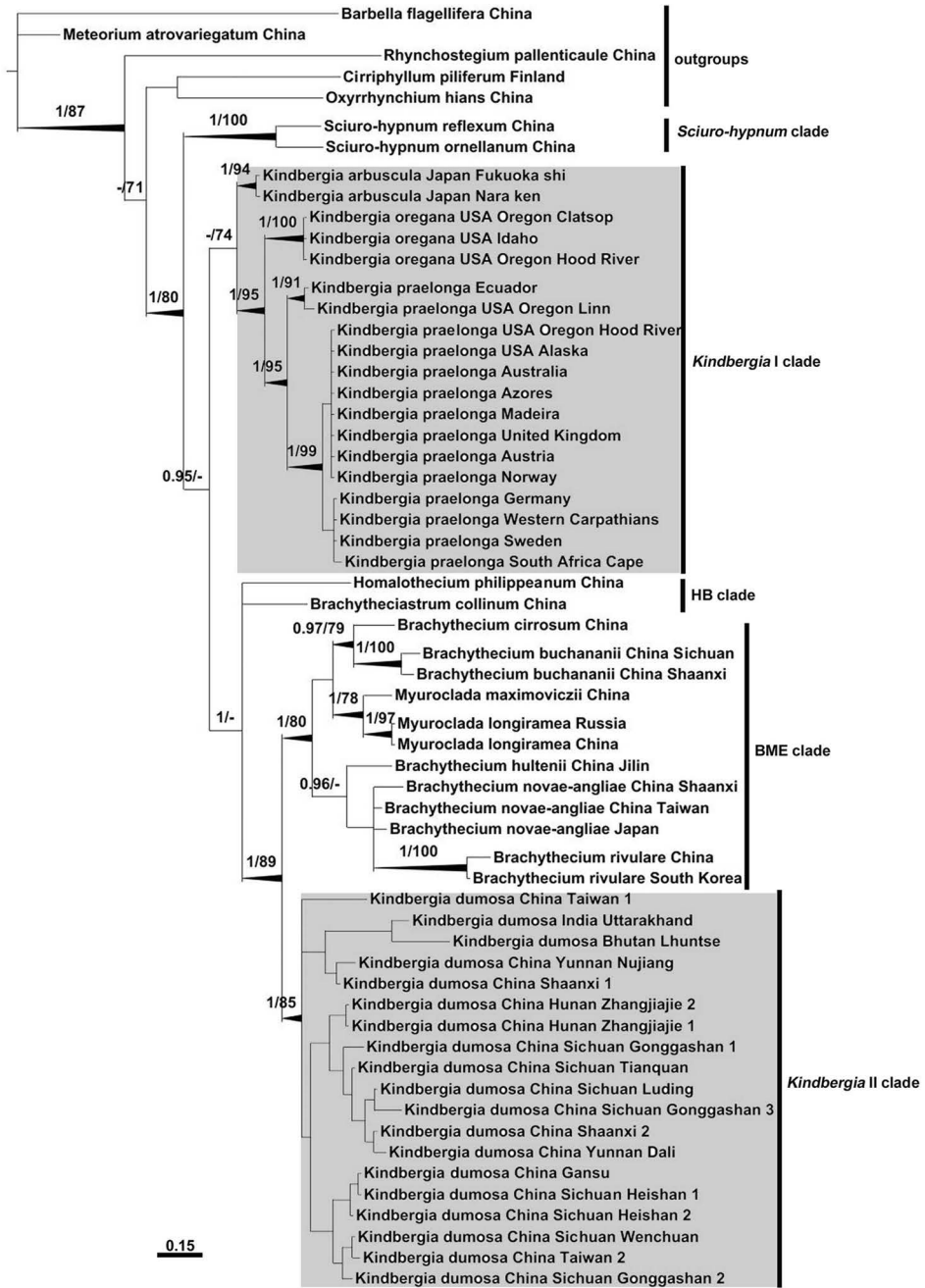


Fig. 23. Fifty percent majority-rule consensus tree from Bayesian analysis of the combined dataset of 59 samples based on *rpl16*, *trnG*, and *trnL-F*. Bayesian posterior probabilities ( $>0.95$ ) (above) and MP boot-strap support values ( $>75$ ) (below) are shown on the branches respectively.

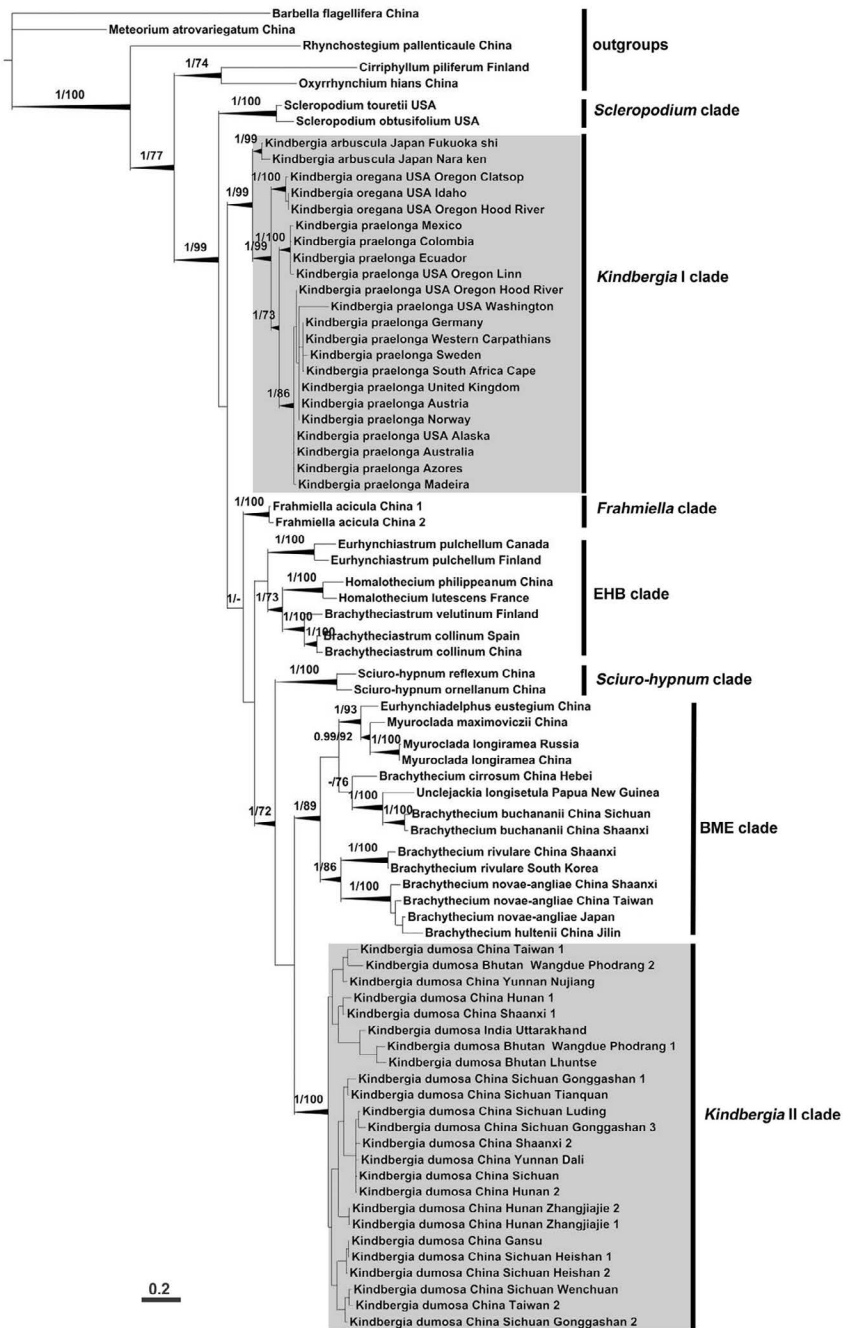


Fig. 24. Fifty percent majority-rule consensus tree from Bayesian analysis of the combined dataset of 78 samples based on ITS, *rpl16*, *trnG*, and *trnL-F*. Bayesian posterior probabilities (>0.95) (above) and MP boot-strap support values (>75) (below) are shown on the branches respectively.

All Chinese “*Kindbergia*” samples, including those identified previously as *K. arbuscula*, *K. praelonga* and *Bryhnia serricuspis*, as well as *K. dumosa* from the Himalayan region, were resolved monophyletically (hereafter, as *Kindbergia* II clade) with a maximal support of 100% (Fig. 24). It forms a sister clade to the *Brachythecium-Myuroclada-Eurhynchiadelphus* clade (hereafter designated as BME clade). The two samples of *Sciuro-hypnum* were resolved as a monophyletic clade as well (1.00 PP and 100 MPBS) and formed the sister clade of the *Kindbergia* II clade, plus the BME clade. No geographic segregation was demonstrated within the *Kindbergia* II clade, and recognition of morphotypes related to the above mentioned names was not supported by any of the performed analyses. *Kindbergia praelonga* from Africa, America, Australia and Europe, *K. oregana* from America and *K. arbuscula* from Japan formed a robust clade (hereafter designated as *Kindbergia* I clade) (1.00 PP and 99 MPBS), which is distantly separated from *Kindbergia* II clade by members of Homalothecioideae, *Frahmiella*, *Eurhynchiastrum*, *Homalothecium* and *Brachytheciastrum*. Two *Scleropodium* samples form a maximally supported clade (1.00 PP and 100 MPBS) which is sister to the rest of Brachythecioideae, including genera *Kindbergia*, *Frahmiella*, *Eurhynchiastrum*, *Homalothecium*, *Brachytheciastrum*, *Sciuro-hypnum*, *Brachythecium*, *Myuroclada*, *Eurhynchiadelphus*, and *Kindbergia* II clade.

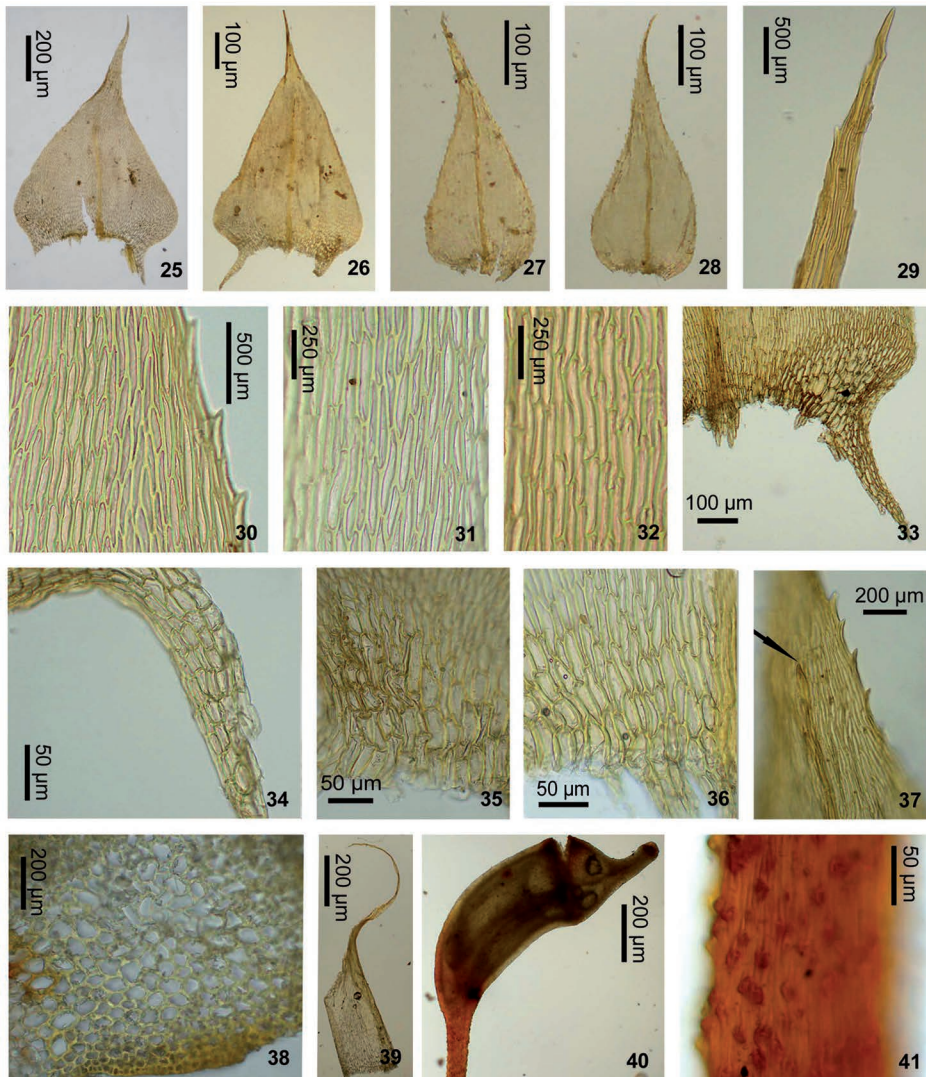
Within the genus, *K. oregana*, *K. arbuscula*, and *K. praelonga* were shown to be monophyletic species (1.00 PP and 73 to 100 MPBS). No subclades within *Kindbergia* I clade got any support. The two subclades of *Kindbergia* I clade have a poor correspondence to the geography of their range. Although all four Himalayan specimens were placed together in one of the two subclades, including samples from Taiwan, Yunnan, Hunan and Shaanxi, and yet, another subclade included also specimens from Taiwan, Yunnan, and Gansu, in addition to samples from Sichuan, Hunan, Shaanxi.

## DISCUSSION

### The general tree topology

Our newly obtained results of the phylogenetic analyses are very similar to what has been found previously by Aigo *et al.* (2009a), Huttunen & Ignatov (2004), Ignatov *et al.* (2008), and Vanderpoorten *et al.* (2005). The Eurhynchioideae (*Rhynchostegium*) occupies a basal position on the tree. The next in the grade is Helicodontioideae, and the terminal clade included representatives of Brachythecioideae *s.l.* Although species referred originally to Homalothecioideae shows in some analyses a segregation of *Homalothecium* plus *Brachytheciastrum* and sometimes also *Frahmiella* plus *Eurhynchiastrum*, the supporting value was low, and the uncertain position of *Kindbergia*, *Sciuro-hypnum* and *Scleropodium* are obviously in favor of treating Brachythecioideae in a broad sense, as suggested by Vanderpoorten *et al.* (2005).

It is interesting to make a comparison of the topology of the phylogenetic trees of Brachytheciaceae generated by our study and that published in Hedenäs (2010). Representatives of Chinese *Kindbergia* were found in both studies to be the most isolated group positioned quite distantly from the taxa of *K. oregana*,



Figs 25-41. *Pseudokindbergia dumosa* (Mitt.) M.Li, Y.F.Wang, Ignatov *et* B.C.Tan  
**25-26.** Stem leaves; **27-28.** Branch leaves; **29.** Cells at apex of stem leaf; **30.** Leaf border in the middle of stem leaf; **31-32.** Median laminal cells of stem leaf; **33.** Leaf base; **34.** Leaf decurrency of the stem leaf; **35.** Basal cells near leaf decurrency; **36.** Basal cells near costa; **37.** End of the costa in stem leaf (arrow pointing at spines on leaf costa); **38.** Cross section of stem; **39.** Inner perichaetial leaf; **40.** Capsule; **41.** Surface of the seta (from lectotype of *Kindbergia dumosa*: India, *J.D. Hooker 1041*. NY 01179094).

American *K. praelonga*, and European+West Asiatic+Africa+Australian *K. praelonga*. However, in contrast to the report of Hedenäs (2010), the position of Japanese *K. arbuscula* was shown in our study to be more isolated from *K. praelonga* than from *K. oregana*. This difference in topology, obviously, is brought by the lacking of ITS data in the dataset of Hedenäs (2010). In our study,

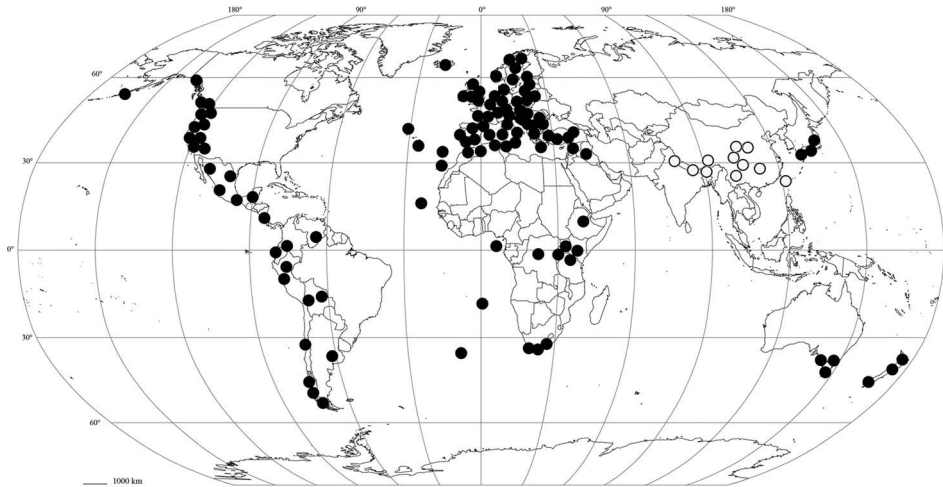


Fig. 42. Schematic map of the world distribution of *Kindbergia* (solid circles) and *Pseudokindbergia* (open circles). Mapping is designed mainly on the country, or in bigger countries, at state/province level, using databases of NY, MO, S, Flora of North America (see Ignatov, 2014), China (Hu *et al.*, 2008), publications on the distribution in Africa (O’Shea, 2006), Europe (Duell, 1984, 1985), West Europe and North Asia (Ignatov *et al.*, 2006), Mediterranean Region (Ros *et al.*, 2013), Middle East (Kürschner & Frey, 2011) and Australia (Hedenäs, 2002), and treatment of genus *Kindbergia* (Hedenäs, 2010.)

the core genera of Brachythecioideae, namely *Brachythecium*, *Sciuro-hypnum*, *Myuroclada*, *Eurhynchiadelphus* form a moderately supported clade which includes also Chinese and Himalayan *Kindbergia* II clade (Fig. 24). Each of the rest of the genera, namely *Kindbergia* (clade I), *Eurhynchiastrum*, *Frahmiella*, *Scleropodium*, *Homalothecium* and *Brachytheciastrum* were shown to be monophyletic. Moderate support was shown for the clade of *Brachytheciastrum* + *Homalothecium* (1.00 PP and 73 MPBS) and maximal support for *Frahmiella* and *Eurhynchiastrum* (1.00 PP and 100 MPBS). Shown in a previous analysis reported by Ignatov *et al.* (2010), the clade of *Frahmiella* and *Eurhynchiastrum* received a poor support in a MP phylogram.

The inclusion in analysis of all the genera of Brachythecioideae (except for the obviously unrelated *Brachytheciella*) and Homalothecioideae brought out another unexpected result. It shows clearly the presence of a topological gap between the Chinese+Himalayan species of “*Kindbergia*” and the populations of the species of this genus from the rest of the world. To witness, this topological gap is filled by a clade that included taxa belonging to the core of Brachythecioideae (see Fig. 24). Furthermore, the set of characters of somewhat dendroid plant habit, dimorphic leaves, strong and nearly percurrent costa and distinctive leaf base decurrency can separate the Chinese+Himalayan of “*Kinbergia*” (*Kindbegia* II clade) from other species of related genera, such as *Brachythecium*, *Eurhynchiadelphus* and *Myuroclada*. Thus, the genus *Kindbergia* in its current circumscription appears to be polyphyletic, suggesting a needed segregation of the Chinese and Himalayan representatives of *Kindbergia* II clade as a separate genus.

***Pseudokindbergia* M. Li, Y.F. Wang, Ignatov et B.C. Tan, gen. nov.**

**Diagnosis:** The new monotypic genus is close in morphology to *Kindbergia* Ochyra, but differs in having semi-orbicular to orbicular-triangular, obtuse or truncate proximal branch leaves (ovate-acuminate, ovate-apiculate to triangular-acuminate in *Kindbergia*), conic-apiculate operculum (long rostrate in *Kindbergia*), and an inclined capsule (subpendent to horizontal in *Kindbergia*) (see Table 1; Figs 1-21).

**Generitype:** *Pseudokindbergia dumosa* (Mitt.) M. Li, Y.F. Wang, Ignatov et B.C. Tan, *comb. nov.* (Figs 25-41)

[Basionym: *Hypnum dumosum* Mitt., *J. Linn. Soc. Bot. Suppl.* 1:80. 1859. **Type:** India, Sikkim, Himalaya orient. reg. temp., *J.D. Hooker* (No. 1041) (Lectotype selected here: NY 01179094! Isotype: S B200108!) = *Kindbergia dumosa* (Mitt.) Ignatov et Huttunen, *Arctoa* 11:263. 2002].

= *Eurhynchium serricuspis* Müll Hal., *Nuovo Giorn. Bot. Ital.*, n.s., 5:197.1898  
= *Bryhnia serricuspis* (Müll Hal.) Y.F. Wang et R.L. Hu, *Acta Phytotax. Sin.* 41: 272. 2003. **Type:** China interior, prov. Shen-si sept., prope In-kia-po, Sept. 1896. [Lectotype (vide Koponen 1987: p.513): H-BR (*non vidi*); isotypes: FI! BM 001030716!), *syn. nov.*]

**Illustrations:** Gangulee, 1978: Fig. 874 (p. 1138); Hu *et al.*, 2008: Fig. 529 (p. 122); Ignatov *et al.*, 2005: Fig. 2 (p. 11).

**Species description:** Plants medium-sized to robust, green to brownish-green. Stem prostrate, dendroid or subpinnately branched, with central strand or not distinct; branches straight densely or moderately densely, julaceously foliate or not. Axillary hairs 3-4-celled, 1-2 basal cells colored, to 80 µm long and 80 µm wide. Proximal branch leaves semi-orbicular to orbicular-triangular, obtuse or truncate. Stem leaves broadly triangular, 1.2-2.2 mm × 0.5-1.2 mm, tapered to lanceolate acumen, at base cordate and longly, broadly decurrent, rarely slightly so; margin serrate above, serrulate below; costa stout, nearly percurrent; median laminal cells rhombic to rhomboidal, 20-52(-70) µm × 3-6(-8) µm, with rounded ends, moderately thick-walled, sometimes prorate; subalar cells hexagonal to shortly rectangular, relatively large and thin-walled, 11-30(-45) µm × 8-15(-20) µm, forming indistinctly delimited group. Branch leaves smaller, triangularly ovate-lanceolate to ovate-lanceolate, 1.0-1.6 mm × 0.6-0.9 mm, acuminate, with more strongly serrate margin. Median laminal cells 24-39(-60) µm × 3-5 µm. Dioicous. Perichaetial leaves lanceolate, ecostate, with reflexed acumen. Seta 2.0-3.0 cm long, blackish when old, twisted, rough in surface texture. Capsule inclined. Annulus present. Operculum conic-apiculate.

**Specimens examined:** Bhutan. Wangdue Phodrang Distr., *G. & S. Miede 00-420-18*, *G. & S. Miede 98-373-9* (MHA); Lhuntse Distr., *G. & S. Miede 00-441-25* (MHA). China. Chongqing, *F.X. Li 1269* (PE); Gansu Prov., *F.X. Li 839*, *Z.T. Zhao & N.N. Yu 20061589*, *20061337*, *20061536*, *20061252* (PE); Hunan Prov., *T. Koponen et al. 52381* (KUN) *T. Koponen et al. 52771*, *52381* (MHA); Shannxi Prov., *P.C. Chen et al. 632*, *649* (PE), *J. Giraldi s.n.* (FI, BM), *M. Wang 553* (KUN), *Y.F. Wang et al. 374*, *37* (HSNU), *Z.P. Wei 6476* (PE); Sichuan Prov., *D.Z. Xie & J.G. Li 0059* (PE), *L.Y. Pei 042*, *265*, *492* (PE), *M.Z. Wang 49995*, *50787*, *50916*, *51066*, *57354*, *58151*, *58158*, *58378*, *58743*, *58749*, *860026c*, *860067e*, *860661*, *860663a*, *860669*, *860678*, *860717*, *860772*, *860840* (PE), *M.Z. Wang & Y. Jia 510846*, *51138* (PE), *X.Y. Hu 0391*, *0414*, *0546*, *0571*, *0752a*, *0762*, *0764* (PE), *P.C. Wu 22218* (PE), *Y. Jia J06811*, *J06958*, *J06966*, *J06849*, *J06823*, *J06824*, *J06825*, *J06833* (PE), *Y. Liu 285*, *515*, *524*, *528*, *536* (PE), *Q. He 663*, *930*, *1095*, *1107*, *1146* (PE), *S.Q. Sun 231* (SHNU), *T. Cao & B.R. Zuo 90592*, *90659*, *91047* (SHNU), *Y.H. Wu s.n.* (HSNU), *X.Y. Li & S.Q. Sun 9* (HSNU); Taiwan, *J.R. Shevock 17918* (MO5219552), *M. Li 203* (HSNU), *S. He 36270*

(MO5355044), Y.F. Wang & M. Li 202 (HSNU); Xizang Prov., S.Y. Ge 1499 (MO3675628); Yunnan Prov., D.G. Long 35981 (KUN), M.Z. Wang 6477 (PE), Q. Liu & Q. Zuo 1290 (HSNU). India. Sikkim, Sinchul, J.D. Hooker 1041 (NY 01179094, S B200108); Uttarakhand, Garhwal Himal, M. Lüth 6643 (MHA).

**Distribution:** Bhutan, China (Taiwan, mainland China), Nepal and India, occurring from low elevation to above 4000 m in Himalayan region.

This species is very polymorphic, which explains its confusion in earlier publications with *Kindbergia* (*Eurhynchium*) *arbuscula* (Redfearn *et al.*, 1996; Hu & Wang, 2005; Hu *et al.*, 2008) and *K. praelonga* (Redfearn *et al.*, 1996; Ignatov *et al.*, 2005; Hu *et al.*, 2008). It is an interesting fact that the distribution of the species of *Pseudokindbergia* does not overlap with that of *Kindbergia* (Fig. 42). The latter genus has a distribution in Northern Hemisphere much similar to that sometimes called Mediterranean disjunctive of the West-West pattern (Schofield, 1988; Ignatov, 1993), which includes western parts of both Eurasia and North America. *Kindbergia* species occur also in western part of South America, East and South Africa. Likely as a result of introduction, *K. praelonga* occurs in Australia and New Zealand. However, *Kindbergia* does not occur in India and China, according to our present study, and this gap is filled by ecologically and morphologically similar plants of *Pseudokindbergia*.

### **Do *Kindbergia arbuscula* and *K. praelonga* occur in China?**

*Pseudokindbergia dumosa* is characterized by a strong branching habit, looking very much like *Kindbergia arbuscula*, another species with also a strong branching habit. The molecular data, however, showed that this character is homoplasious. The very similar subdendroid plants of '*K. arbuscula*' from SW China were shown in the molecular phylogenetic tree to be located within the *Pseudokindbergia* clade (see Fig. 24). Similarly, the weakly branching specimens of *P. dumosa* collected from various parts of China, almost indistinguishable from some phenotypes of European *K. praelonga*, were proven by the DNA sequence analysis to be plants of *Pseudokindbergia*. This conclusion is confirmed further by our study of the proximal branch leaves of the Chinese specimens which always shown to be of the *Pseudokindbergia* type (semi-orbicular to orbicular-triangular, obtuse or truncate), and not the *Kindbergia* type (ovate-acuminate, ovate-apiculate to triangular-acuminate) (Table 1; Figs 1-11).

Based on our study, we conclude that *K. arbuscula* represents a distinct species endemic to Japan. This Japanese endemic is shown by our study to be more distantly related to *K. praelonga* than what was stated in Hedenäs (2010). The signal from the ITS gene sequences indicates that the former species is the basal species of this genus.

Although we included only four specimens from Taiwan in our taxonomic study and DNA analysis, we accept the description of Taiwanese taxon of *K. arbuscula* var. *acuminata* (Takaki) Ochyra, which differs from that of the *K. arbuscula* in having longer and more sharply acuminate leaves, to be within a morphological variation of *Pseudokindbergia*. We conclude therefore that *K. arbuscula* is absent in Taiwan, contrary to the treatment of Takaki (1956).

### **On the identity of Himalayan *Pseudokindbergia dumosa* and Chinese *Bryhnia serricuspis***

*Pseudokindbergia dumosa* is a rare species, treated earlier as an endemic to India and Nepal (Gangulee, 1978; Vohra, 1983). We studied four Himalayan



samples from India and Bhutan collected at different altitudinal belts (alt. 2400 to 4100 m). Superficially, the four Himalayan specimens were quite similar to the European *K. praelonga* in their growth form, leaf shape and dimensions, and lamina cells etc. However, neither specimen was shown to be *K. praelonga* (e.g. a member of *Kindbergia* I clade) in our molecular study, but deeply nested within the clade formed by the Chinese specimens. Hedenäs (2010) had suggested already that *K. dumosa* may be the correct species name for all Chinese specimens called “*K. praelonga*”. By studying the type materials of *K. dumosa*, we found that the species is morphologically quite similar also to *Bryhnia serricuspis* and all Chinese specimens annotated in herbaria as “*K. arbuscula*” and “*K. praelonga*”. Their similarity includes the shape of proximal branch leaves, operculum and capsule orientation (Figs 9-15). The new molecular analyses supported their conspecific identity (Figs 22-24). *Hypnum dumosum* was published in 1859, thus, it has priority over *Eurhynchium serricuspis* (Müller, 1898) in nomenclatural consideration. The latter was lectotypified by Koponen (1987) and accepted by him as a distinct taxon from *K. praelonga*. Based on a study of large collections of specimens, Ignatov *et al.* (2005) came to the conclusion that the character differences seen between these two taxa showed a gradual transition across China in the leaf shape, so they had to be combined as one taxon. At about the same time, Hu *et al.* (2008) accepted this species, but placed it in the genus *Bryhnia*, as *B. serricuspis*. Inferred from molecular data, Li *et al.* (2014) proposed the inclusion of the species recognized in *Bryhnia* (represented by *B. novae-angliae*, *B. hultenii*, and *B. scabrida*) in *Brachythecium* s.str., and further treated *Bryhnia* as a synonym of the latter. While *B. serricuspis* with Chinese and Himalayan “*Kindbergia*” species was nested within another independent clade (*Kindbergia* II clade) (Figs 22-24). The distinction between *B. serricuspis* (actually *Pseudokindbergia*) and other species of *Bryhnia* is not easy as their leaves are similar in appearance, however, plants of the former have more regular pinnate branching, a more abrupt tapering acumen towards the leaf apex, and broader leaf decurrency (Ignatov *et al.*, 2005).

Another opinion on *Bryhnia serricuspis* identity was its conspecificity with *Sciuro-hypnum reflexum* (Qian, 1987), which was thought to occur in southern China (Piippo, 1987). A later study of Hedenäs *et al.* (2012) found, however, that in that area occurs another species, *S. sichuanicum* Ignatov *et* Hedenäs, that have much in common in morphology with *Pseudokindbergia*, being a large plant, although without distinctively regular branching, and with much laxer basal areolation and an autoicous sexual condition (contrary to dioicous condition in *Pseudokindbergia*).

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## APPENDIX

**Details of voucher specimens and Genbank accession numbers used for ITS, *trnG*, *rpl16*, *trnL-F* gene sequence analyses.**

Subfamily: taxon, locality, collector, collectors number or herbarium number, herbarium acronym; Genbank accession numbers ITS (or ITS1/ITS2), *trnG*, *rpl16*, *trnL-F*; Dashes (–) indicate that no sequence was obtained, asterisks (\*) indicate newly generated sequences.

**Brachythecioideae: *Brachytheciastrum collinum*** (Schleich. ex Müll.Hal.) Ignatov et Huttunen, China, Xinjiang Prov., Qinghe Co., *S. Mamtimin 15123* (XJU), KJ605684\*, KJ605759\*, KJ605719\*, KJ605793\*; Spain, Granada, Sierra Nevada, *S.Rams et al.*, 28.VII.2004 (MUB), EU567475, EU567604, EU567538, –. ***Brachytheciastrum velutinum*** (Hedw.) Ignatov et Huttunen, Finland, Regio oboënsis, Karjalohja, *M. Kiirikki s.n.*, 23.VIII.1988 (H), EU567476, EU567539, EU567605, –. ***Brachythecium buchananii*** (Hook.) A. Jaeger, China, Shaanxi Prov., *Y.F. Wang 166* (HSNU), KF434291, KF418126, KF418098, KF434264; China, Sichuan Prov., *Y.F. Wang et al. 102* (HSNU), KF434292, KF418127, KF418099, KF434265. ***Brachythecium cirrosum*** (Schwägr.) Schimp., China, Hebei Prov., Mt. Xiaowutai, *Q. Zuo 711* (HSNU), KF434293, KF418128, KF418100, KF434266. ***Brachythecium hultenii*** (E.B. Bartram) M. Li et *Y.F. Wang*, China, Jilin Prov., *Y.F. Wang 146* (HSNU), KF434278, KF418113, KF418085, KF434251. ***Brachythecium novae-angliae*** (Sull. et Lesq.) A. Jaeger, China, Shaanxi Prov., *Y.F. Wang 174* (HSNU), KF434283, KF418118, KF418090, KF434256; China, Taiwan Prov., *M. Li 203* (HSNU), KF434284, KF418119, KF418091, KF434257; Japan, Hokkaido, Kitahiroshima, *Y.F. Wang 7240* (HSNU), KF434286, KF418121, KF418093, KF434259. ***Brachythecium rivulare*** Schimp., China, Shaanxi Prov., *Y.F. Wang 311* (HSNU), KF434295, KF418130, KF418102, KF434268; South Korea, Cheju-do., *S. He & J.S. Song 34633* (MO), KF434296, KF418131, KF418103, KF434269. ***Eurhynchiadelphus eustegia*** (Besch.) Ignatov et Huttunen, China, Jilin Prov., *T. Koponen 36592* (H), -/AF403602, –, –, AF397790. ***Eurhynchiastrum pulchellum*** (Hedw.) Ignatov et Huttunen, Canada, British Columbia, *Vitt 35808a* (MHA), GQ254298, –, –, –; Finland, Lohja, *T. Koponen & S. Huttunen 1321* (H), FM161101, EF531024, EF530956, –. ***Frahmiella acicula*** (Broth.) Ignatov, Vanderpoorten et *Y.F. Wang*, China, Shaanxi Prov., *Wang 3566* (HSNU, MHA), GU075853, –, –, –; China, Shaanxi Prov., *Wang 4257* (HSNU, MHA), GU075852, –, –, –. ***Homalothecium lutescens*** (Hedw.) H. Rob., France, Cales, *G. Een s.n.*, 9. June 1995 (S), EF617558, –, EF531051, –. ***Homalothecium philippianum*** (Spruce) Schimp., China, Xinjiang Prov., *S. Mamtimin 18706* (XJU), KJ605687\*, KJ605762\*, KJ605722\*, KJ605796\*. ***Kindbergia arbuscula*** (Broth.) Ochyra, Japan, Fukuoka-shi Prov., Sawara-ku, Iiba, Nogouchi-valley, *A. Fujita 65* (dupl. HSNU), KJ605717\*, KJ605791\*, KJ605757\*, –, –; Japan, Nara-ken Prov., Yoshino-gun, Kawakami-mura, *N. Nishimura 12819* (dupl. HSNU), -/KJ605718\*, KJ605792\*, KJ605758\*, KJ605831\*. ***Kindbergia dumosa*** (Mitt.) Ignatov et Huttunen, Bhutan, Lhunse Distr., *G. & S. Miehe 00-441-25* (MHA), KJ659017\*, KJ659023\*, KJ659021\*, KJ659027\*; Bhutan, Wangdue Phodrang Distr. -1, *G. & S. Miehe 00-420-18* (MHA), KJ659018\*, KJ659024\*, –, KJ659028\*; Bhutan, Wangdue Phodrang Distr. -2, *G. & S. Miehe 98-373-9* (MHA), KJ659019\*, KJ659025\*, –, KJ659029\*; China, Gansu Prov., *Z.T. Zhao & N.N. Yu 589* (PE) (*Bryhnia serricuspis*), KJ605685\*, KJ605760\*, KJ605720\*, KJ605794\*; China, Hunan Prov.-1, *T. Koponen et al. 53561* (H) (*Bryhnia serricuspis*), -/AF403590, –, –, –; China, Hunan Prov.-2, *T. Koponen et al. 50467* (H) (“*K. praelonga*”), DQ336907, –, –, –; China, Hunan Prov., Zhangjiajie-1, *T. Koponen et al. 52771* (MHA) (“*K. praelonga*”), KJ605701\*, KJ605775\*, KJ605736\*, KJ605810\*; China, Hunan Prov., Zhangjiajie-2, *T. Koponen et al. 52381* (MHA) (“*K. praelonga*”), KJ605702\*, KJ605776\*, KJ605737\*, KJ605811\*; China, Shaanxi Prov.-1, *Y.F. Wang 374* (HSNU) (*Bryhnia serricuspis*), KJ605686\*, KJ605761\*, KJ605721\*, KJ605795\*; China, Shaanxi Prov.-2, *Y.F. Wang 37* (HSNU) (“*K. arbuscula*”), KJ605688\*, –, KJ605723\*, KJ605797\*; China, Sichuan Prov., *D.Z. Xie & J.S. Lou 172* (H) (“*K. praelonga*”), GQ849704, GQ849617, –, –; China, Sichuan Prov., Gonggashan-1, *S.Q. Sun 231* (SHNU) (“*K. arbuscula*”), KJ605689\*, KJ605763\*, KJ605724\*, KJ605798\*; China, Sichuan Prov., Gonggashan-2, *T. Cao & B.R. Zuo 90592* (SHNU) (“*K. arbuscula*”), KJ605690\*, KJ605764\*, KJ605725\*, KJ605799\*; China, Sichuan Prov. Gonggashan-3, *T. Cao & B.R. Zuo 90659* (SHNU) (“*K. arbuscula*”), KJ605691\*, KJ605765\*, KJ605726\*, KJ605800\*; China, Sichuan Prov., Heishan Co.-1, *Y.F. Wang & M. Li sn-2* (HSNU) (“*K. praelonga*”), KJ605704\*, KJ605778\*, KJ605739\*, KJ605813\*; China, Sichuan Prov., Heishan Co.-2, *Y.H. Wu s.n.* (HSNU) (“*K. praelonga*”), KJ605703\*, KJ605777\*,

KJ605738\*, KJ605812\*; China, Sichuan Prov., Luding Co., *Y. Jia 01821* (PE) ("*K. praelonga*"), KJ605692\*, KJ605766\*, KJ605727\*, KJ605801\*; China, Sichuan Prov., Tianquan Co., *T. Cao & B.R., Zuo 91047* (SHNU) ("*K. praelonga*"), KJ605693\*, KJ605767\*, KJ605728\*, KJ605802\*; China, Sichuan Prov., Wenchuan Co., *Y. Jia 06958* (PE) ("*K. praelonga*"), KJ605694\*, KJ605768\*, KJ605729\*, KJ605803\*; China, Taiwan Prov., Nantou Co.-1, S., *He 36270* (MO) ("*K. praelonga*"), KJ605705\*, KJ605779\*, KJ605740\*, KJ605814\*; China, Taiwan Prov., Nantou Co.-2, *Y.F. Wang & M. Li 202* (HSNU) ("*K. arbuscula*"), KJ605695\*, KJ605769\*, KJ605730\*, KJ605804\*; China, Yunnan Prov., Dali Co., *Q. Liu & Q. Zuo 1290* (HSNU) ("*K. arbuscula*"), KJ605696\*, KJ605770\*, KJ605731\*, KJ605805\*; China, Yunnan Prov., Nujiang Co., Gaoligongshan, *Q. Liu & Q. Zuo 168* (HSNU) ("*K. arbuscula*"), KJ605697\*, KJ605771\*, KJ605732\*, KJ605806\*; India, Uttarakhand, *M. Lüth 6643* (MHA), KJ659020\*, KJ659026\*, KJ659022\*, KJ659030\*. ***Kindbergia oregana*** (Sull.) Ochya, USA, Idaho, Clearwater Co., *K.L. Gray 3941* (MO), KJ605698\*, KJ605772\*, KJ605733\*, KJ605807\*; USA, Oregon, Clatsop Co., *C.E. & D.D. Darigo 3990* (MO), KJ605699\*, KJ605773\*, KJ605734\*, KJ605808\*; USA, Oregon, Hood River Co., *B. Allen 28751* (MO), KJ605700\*, KJ605774\*, KJ605735\*, KJ605809\*. ***Kindbergia praelonga*** (Hedw.) Ochya, Colombia, Dept. Cauca, *S. Churchill et al. 17157* (H), GQ849707, GQ849620, -, -, Ecuador, Azuay Prov., *W.R. Buck 39323* (S), KJ605706\*, KJ605780\*, KJ605741\*, KJ605815\*; Mexico, Estado de México, *A. Cárdenas S. 2675* (H), GQ849696, GQ849608, -, -, Austria, Upper Austria, *R. Krisai, B105472* (S), GQ849746, GQ849660, KJ605751\*, KJ605825\*; Australia, Victoria, *H. Streimann 42657, B96040* (S), GQ849735, GQ849649, KJ605752\*, KJ605826\*; Azores, Sao Miguel, *L. Hedenäs s.n., B42727* (S), GQ849677, GQ849589, KJ605753\*, KJ605827\*; England, Shropshire, *L. Hedenäs s.n., B144669* (S), KJ605707\*, KJ605781\*, KJ605742\*, KJ605816\*; Germany, Badenwürttemberg, *L. Hedenäs s.n., B89252* (S), GQ849685, GQ849597, KJ605754\*, KJ605828\*; Madeira, Tibeira do Moreno, *S. Fontinha 2 B22292* (S), GQ849687, GQ849599, KJ605755\*, KJ605829\*; Norway, Hordaland, *L. Hedenäs s.n., B94298* (S), GQ849713, GQ849626, KJ605756\*, KJ605830\*; South Africa, Cape Prov., *S.L. Williams 1110* (H), GQ849697, GQ849609, -, -, Sweden, Södermanland, Utö., *L. Hedenäs s.n., B175998* (S), KJ605708\*, KJ605782\*, KJ605743\*, KJ605817\*; USA, Alaska, Sitak Co., *N. Darigo 76* (MO), KJ605709\*, KJ605783\*, KJ605744\*, KJ605818\*; USA, Oregon, Hood River Co., *B. Allen 28744* (MO), KJ605710\*, KJ605784\*, KJ605745\*, KJ605819\*; USA, Oregon, Linn Co., *B. Goffinet 7990, B98287* (S), KJ605711\*, KJ605785\*, KJ605746\*, -, USA, Washington, Clark Co., *C.E. & D.D. Darigo 3982* (MO), KJ605712\*, KJ605786\*, -, KJ605820\*; Western Carpathians, Pogorze Slaskie Foothills, *S. Adam., B157666* (S), KJ605713\*, KJ605787\*, KJ605747\*, KJ605821\*. ***Myuroclada longiramea*** (Müll. Hal.) M. Li, Y.F. Wang, M.S. Ignatov et S. Huttunen, China, Hebei Prov., *Y.F. Wang 19* (HSNU), KF434274, KF418109, KF418081, KF434247; Russia, Far East, Sakhalin, Tymovsk Distr., *M.S. Ignatov 06-431* (MHA), KF434277, KF418112, KF418084, KF434250. ***Myuroclada maximoviczii*** (G.G. Borshch.) Steere et W.B. Schofield, China, Shaanxi Prov., *Y.F. Wang 54* (HSNU), KF434299, KF418133, KF418106, KF434271. ***Sciuro-hypnum ornellanum*** (Molendo) Ignatov et Huttunen, China, Xinjiang Prov., *S. Mantimin 15709* (XJU), KJ605714\*, KJ605788\*, KJ605748\*, KJ605822\*. ***Sciuro-hypnum reflexum*** (Starke) Ignatov et Huttunen, China, Sichuan Prov., *Y.F. Wang & M. Li s.n.* (HSNU), KF434300, KF418134, KF418107, KF434272. ***Scleropodium obtusifolium*** (Mitt.) Kindb., USA, CA, Mariposa Co., Yosemite Natl. PK., *Shevock 31752* (UC), HM771748, -, HM772030, -. ***Scleropodium touretii*** (Brid.) L.F. Koch, USA, CA, Obispo Co., Klaw Mine Rd., *S.L. Carter 1288* (UC), HM771722, -, HM772004, -. ***Unclejackia longisetula*** (E.B. Bartram) Ignatov, T.J. Kop. et D.H. Norris, Papua New Guinea, Morobe Prov., *T. Koponen 32496* (H), -/AF395643, -, -, AF397794.

## OUTGROUPS

**Eurhynchioideae:** ***Rhynchostegium pallenticaule*** Müll. Hal., China, Zhejiang Prov., *Y.F. Wang et al. 407* (HSNU), KJ605716\*, KJ605790\*, KJ605750\*, KJ605824\*.

**Helicodontoidae:** ***Cirriphyllum piliferum*** (Hedw.) Grout, Finland, Regio aboënsis, Lohja, *T. Koponen & S. Huttunen s.n., 24.V.1999* (H), EU567479, EU567608, EU567542, -. ***Oxyrrhynchium hians*** (Hedw.) Loeske, China, Zhejiang Prov., *Y.F. Wang et al. 28* (HSNU), KF434301, KF418135, KF418108, KF434273.

**Meteoriaceae:** ***Barbella flagellifera*** (Cardot) Nog., China, Zhejiang Prov. *Y.F. Wang et al. 1051* (HSNU), KJ672398\*, KJ672405\*, KJ672412\*, -. ***Meteorium atrovareiegatum*** Cardot et Thé., China, Zhejiang Prov. *Y.F. Wang et al. 679* (HSNU), KJ672399\*, KJ672406\*, KJ672413\*, KJ672419\*.