A plastid phylogeny and character evolution of the Old World fern genus *Pyrrosia* (Polypodiaceae) with the description of a new genus: *Hovenkampia* (Polypodiaceae)

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ABSTRACT

The Old World fern genus *Pyrrosia* (Polypodiaceae) offers a rare system in ferns to study morphological evolution because almost all species of this genus are well studied for their morphology, anatomy, and spore features, and various hypotheses have been proposed in terms of the phylogeny and evolution in this genus. However, the molecular phylogeny of the genus lags behind. The monophyly of the genus has been uncertain and a modern phylogenetic study of the genus based on molecular data has been lacking. In the present study, DNA sequences of five plastid markers of 220 accessions of Polypodiaceae representing two species of *Drymoglossum*, 14 species of *Platycerium*, 50 species of *Pyrrosia*, and the only species of *Saxiglossum* (subfamily Platycerioideae), and 12 species of other Polypodiaceae representing the remaining four subfamilies are used to infer a phylogeny of the genus. Major results and conclusions of this study include: (1) *Pyrrosia* as currently circumscribed is paraphyletic in relation to *Platycerium* and can be divided into two genera: *Pyrrosia* s.s. and *Hovenkampia* (gen. nov.), with *Hovenkampia* and *Platycerium* forming a strongly supported clade sister to *Pyrrosia* s.s.; (2) Subfamily Platycerioideae should contain three genera only, *Hovenkampia, Platycerium,* and *Pyrrosia* s.s.; (3) Based on the molecular phylogeny, macromorphology, anatomical features, and spore morphology, four major clades in the genus are identified and three of the four are further resolved into four, four, and six subclades, respectively; (4) Three species, *P. angustissima, P. foveolata,* and *P. mannii,* not assigned to any groups by Hovenkamp (1986) because of their unusual morphology, each form monospecific clades; (5) *Drymoglossum* is not monophyletic and those species previously assigned to this genus are resolved in two different subclades; (6) *Saxiglossum* is resolved as the first lineage in the *Niphopsis* clade; and (7) The evolution of ten major morphological characters in the subfamily is inferred based on the phylogeny and various morphological synapomorphies for various clades and subclades are identified.

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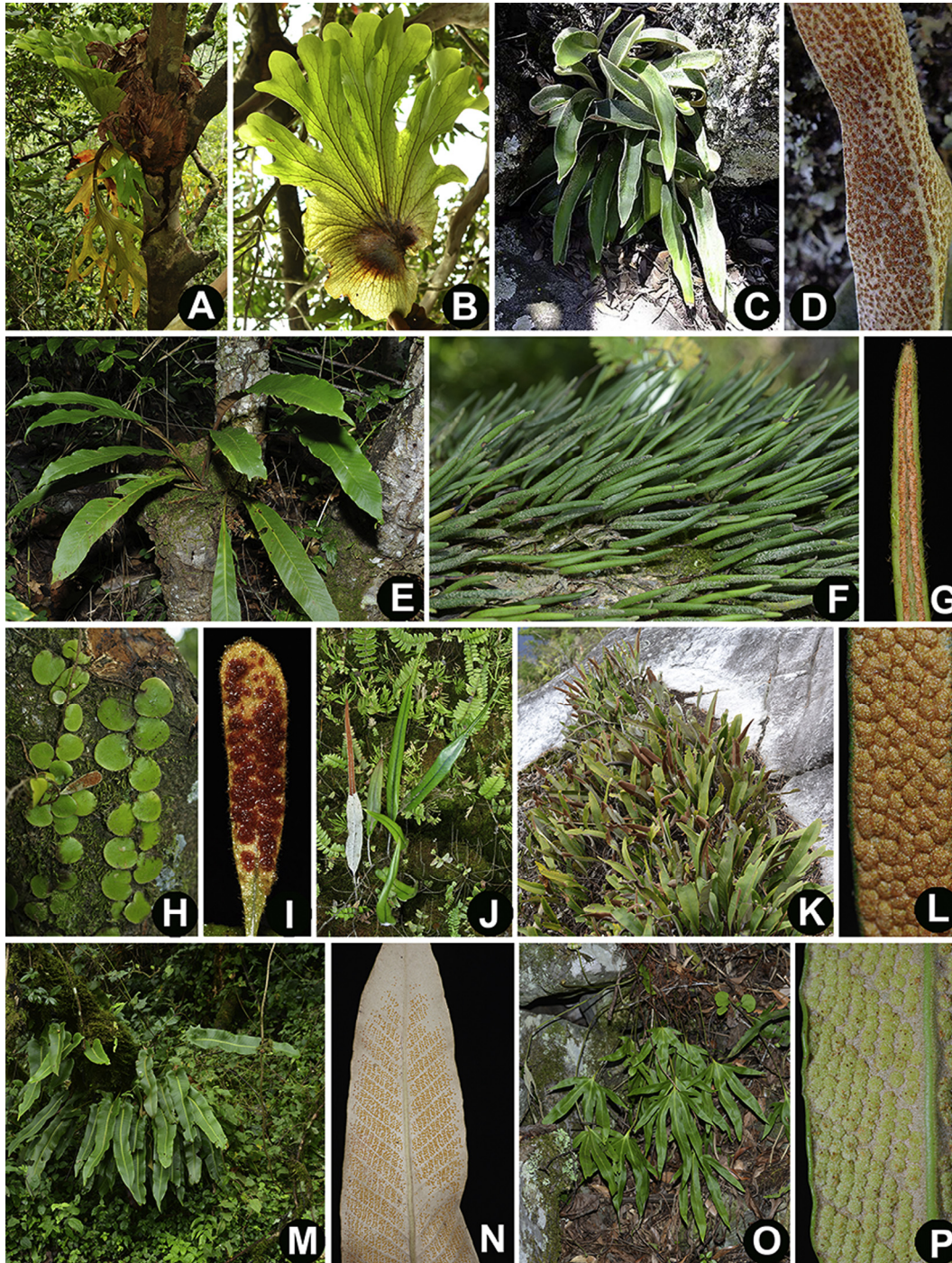 *E-mail addresses:* xfgao@cib.ac.cn (X.-F. Gao), Libing.Zhang@mobot.org (L.-B. Zhang).
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1. Introduction

Pyrrosia Mirb. (Figs. 1 and 2) is a morphologically highly simplified genus in the fern family Polypodiaceae containing 51–100 species (Nayar, 1959; Nayar and Chandra, 1967; Shing, 1983; Hovenkamp, 1986; Shing and Iwatsuki, 1997; Lin, 2000; Lin et al., 2013). Species in the genus are mainly distributed in tropical and subtropical Africa, Asia, and Oceania, and extending north to the Himalaya, central China, and Japan in Asia (Nayar, 1959; Hovenkamp, 1986; Shing and Iwatsuki, 1997; Lin et al., 2013). *Pyrrosia* is characterized by having simple fronds and stellate hairs on the lamina (Shing, 1983; Hovenkamp, 1986; Ravensberg and Hennipman, 1986). Plants are epiphytic or epilithic and have monomorphic to dimorphic fronds (Shing, 1983; Hovenkamp, 1986; Lin et al., 2013).
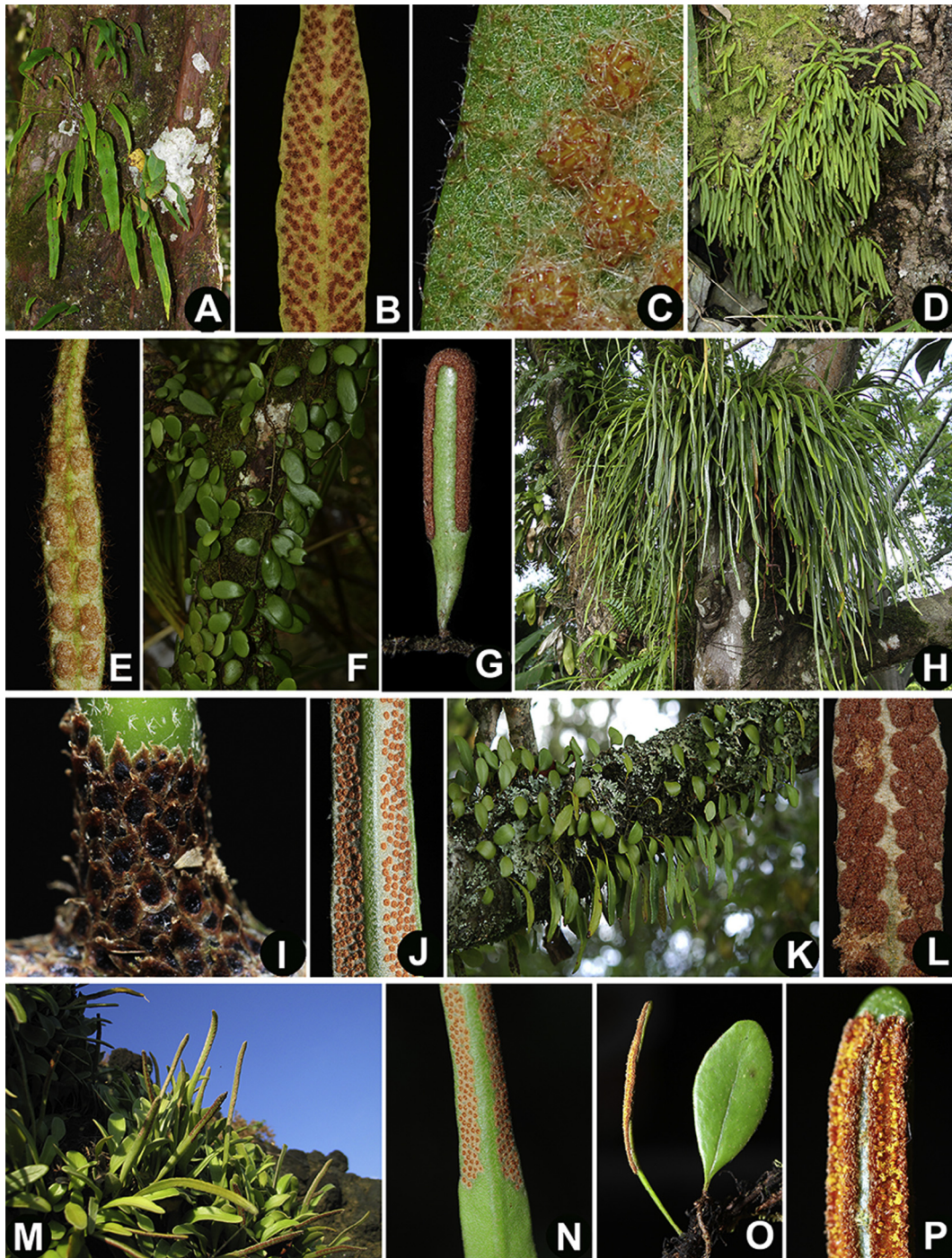
Pyrrosia shares stellate hairs on the lamina with *Drymoglossum* C. Presl (Fig. 2F and G) and *Platycerium* Desv. (Fig. 1A and B), and the three genera had been placed in subfamily Platycerioideae

Fig. 1. Morphology of selected Platyceroideae. **A & B.** *Platycerium.* **C & D.** *Hovenkampia.* **E–P.** *Pyrrosia* (E. The *Pyrrosia* clade. **F–L.** The *Niphopsis* clade. **M–P.** The *Neoniphopsis* clade). **A & B.** Habit and basal frond of *Platycerium coronarium* (O.F. Müll.) Desv. **C & D.** *Hovenkampia schimperiana.* **E.** Habit of *Pyrrosia costata.* **F & G.** Habit and sori of *P. angustissima* (the *Saxiglossum* subclade). **H & I.** Habit and sori of *P. nummulariifolia* (the *Galeoglossa* subclade). **J.** Habit of *P. samarensis* (the *Niphopsis* subclade). **K & L.** Habit and sori of *P. lingua* (the *Heteractides* subclade). **M & N.** *P. sheareri* (the *Drakeanae* subclade). **O & P.** Habit and sori of *P. polydactyla* (the *Polydactyla* subclade). Photo credit: C–D, A. Leonard, Available from www.andrew-leonard.co.uk; F–G & K–P, R. Knapp; H–J, D. L. Nickrent, M. Costea, J. F. Barcelona, P. B. Pelser, and K. Nixon (2006 onwards) PhytoImages. Available from: http://www.phytoimages.siu.edu.

(Nayar, 1970). Additionally, Platycerioideae is characterized by two potential synapomorphies, heavily sclerified rhizomes and lack of pinnate dissection (Hovenkamp, 1986; Hennipman, 1990). Within the subfamily, *Platycerium* is a well-established genus characterized by having basal ("nest") leaves and forked foliage leaves, and pseudo-acrostichoid sorus patches with narrow, linear, densely packed receptacles. Thus, the monophyly of *Platycerium* has not been questioned (Hennipman and Roos, 1982).

However, the monophyly and systematic position of the two other genera in Platycerioideae, *Drymoglossum* and *Pyrrosia*, have been controversial (Hovenkamp, 1986). Based on its monomorphic, linear fronds and linear coenosori, Ching (1933) separated *Pyrrosia angustissima* (Giesenh. ex Diels) Tagawa & K. Iwats. from *Pyrrosia* and established the monotypic genus *Saxiglossum* Ching (Fig. 1F and G). Based on exclusively morphological and anatomical studies, Hovenkamp (1986) and Ravensberg and Hennipman (1986)

Fig. 2. Morphology of *Pyrrosia*. **A–E.** The *Neoniphopsis* clade. **F–O.** The *Niphobolus* clade. **A–C**. Habit, sori, stellate hairs, and sporangia of *Pyrrosia porosa* (the *Dichlamys* subclade). **D & E.** Habit and sori of *P. linearifolia* (the *Dichlamys* subclade). **F & G.** Habit and sori of *P. piloselloides* (the *Drymoglossum* subclade). **H–J.** Habit, scales, and sori of *P. longifolia* (the *Candollea* subclade). **K & L.** Habit and sori of *P. eleagnifolia* (the *Serpens* subclade). **M & N.** Habit and sori of *P. lanceolata* (the *Niphobolus* subclade). **O & P.** Habit and sori of *P. fallax* (the *Fallax* subclade). Photo credit: A–E & M–N, R. Knapp; G, L. Zhang; H–J & O–P, C. -W. Chen; K & L, D. L. Nickrent, M. Costea, J. F. Barcelona, P. B. Pelser, and K. Nixon (2006 onwards) PhytoImages. Available from: http://www.phytoimages.siu.edu.

thought that *Drymoglossum* and *Saxiglossum* should be members of *Pyrrosia*.

Earlier analyses of *Pyrrosia* based on non-molecular data failed to identify any evident synapomorphies uniting the whole genus (Hovenkamp, 1986; Hennipman, 1990). Hovenkamp's (1986) cladogram of Platycerioideae was a trichotomy consisting of *Platycerium*, the *P. africana* group [including two species: *Pyrrosia africana* Ballard and *P. schimperiana* (Mett. ex Kuhn) Alston; Fig. 1C and D], and the remaining 49 species of *Pyrrosia*. All three groups have unique characters and each seemed monophyletic. Particularly, Hovenkamp (1986) noticed that the *P. africana* group

differs from the rest of *Pyrrosia* by anatomical and morphological features including the sclerenchyma sheath, secondary veins, stomata type, and sporangium size. Hennipman (1990) proposed three hypotheses for their relationships: (a) *Platycerium* and *P. africana* group have a close relationship based on their shared polo- and anomocytic stomata; (b) The *P. africana* group and the rest of *Pyrrosia* have a close relationship, because they all have entire fronds; and (c) The *Platycerium* and rest of *Pyrrosia* are more closely related considering the massive sclerification of the rhizomes, which is never found in other species of Polypodiaceae (Hovenkamp, 1986).
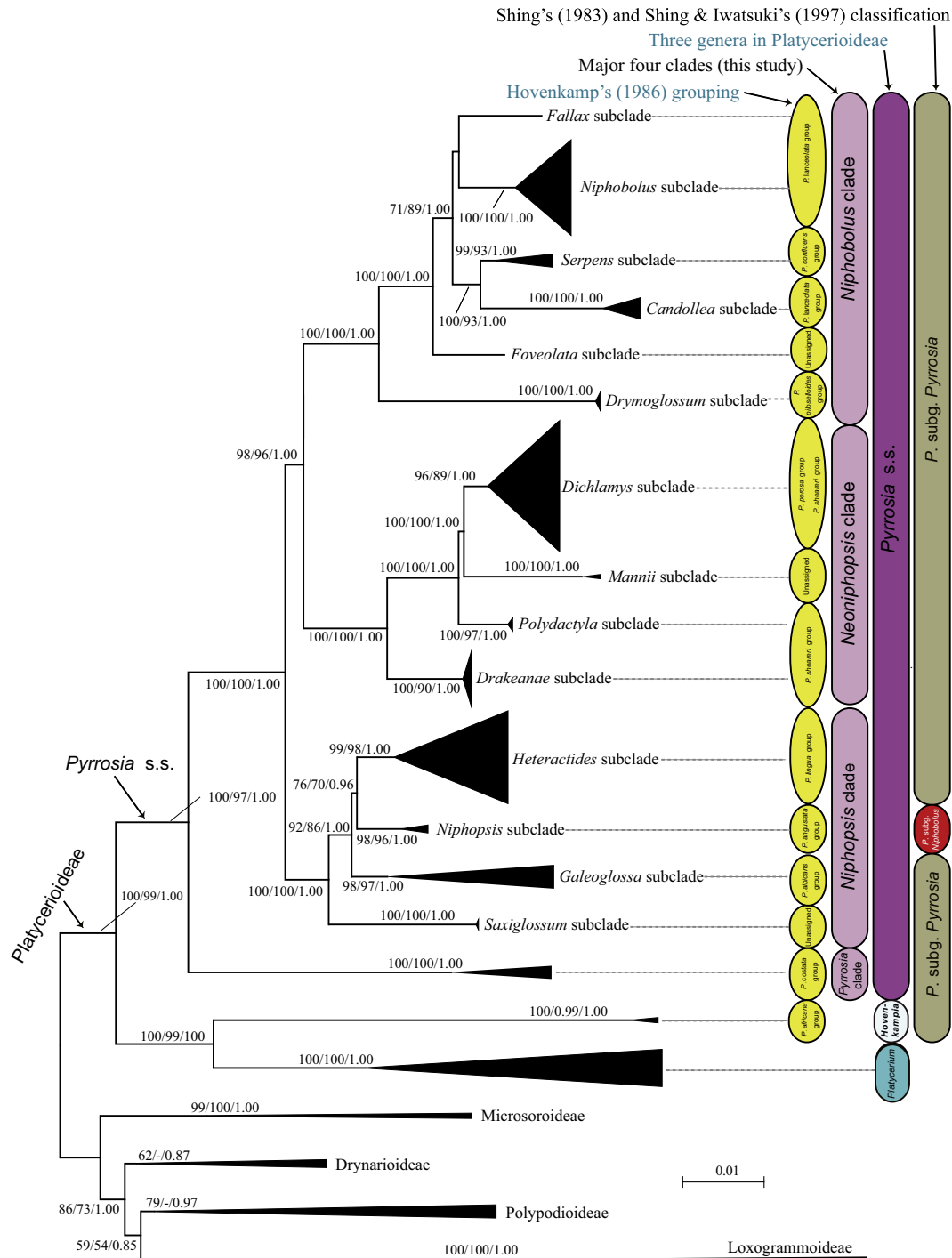

Fig. 3. Simplified maximum likelihood phylogeny of *Pyrrosia* and related taxa based on five plastid markers (*rbcL*, *rps4*, *rps4-trnS*, *trnL*, and *trnL-F*). Maximum likelihood bootstrap support (MLBS), maximum parsimony jackknife support (MPJK), and Bayesian inference posterior probability are along branches.

Fig. 4. Maximum likelihood phylogeny of *Pyrrosia* and related taxa based on five plastid markers (*rbcL*, *rps4*, *rps4-trnS*, *trnL*, and *trnL-F*). Thick lines indicate strong support [maximum likelihood bootstrap support (MLBS) ≥ 80%, maximum parsimony jackknife support (MPJK) ≥ 75%, and Bayesian inference posterior probability (BIPP) ≥ 95%), and thin lines indicate moderate or weak support (either MLBS < 80% or MPJK < 75%). Voucher information is indicated in green. Geographical provenances are indicated in blue. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Red vertical bar indicates the outgroups.
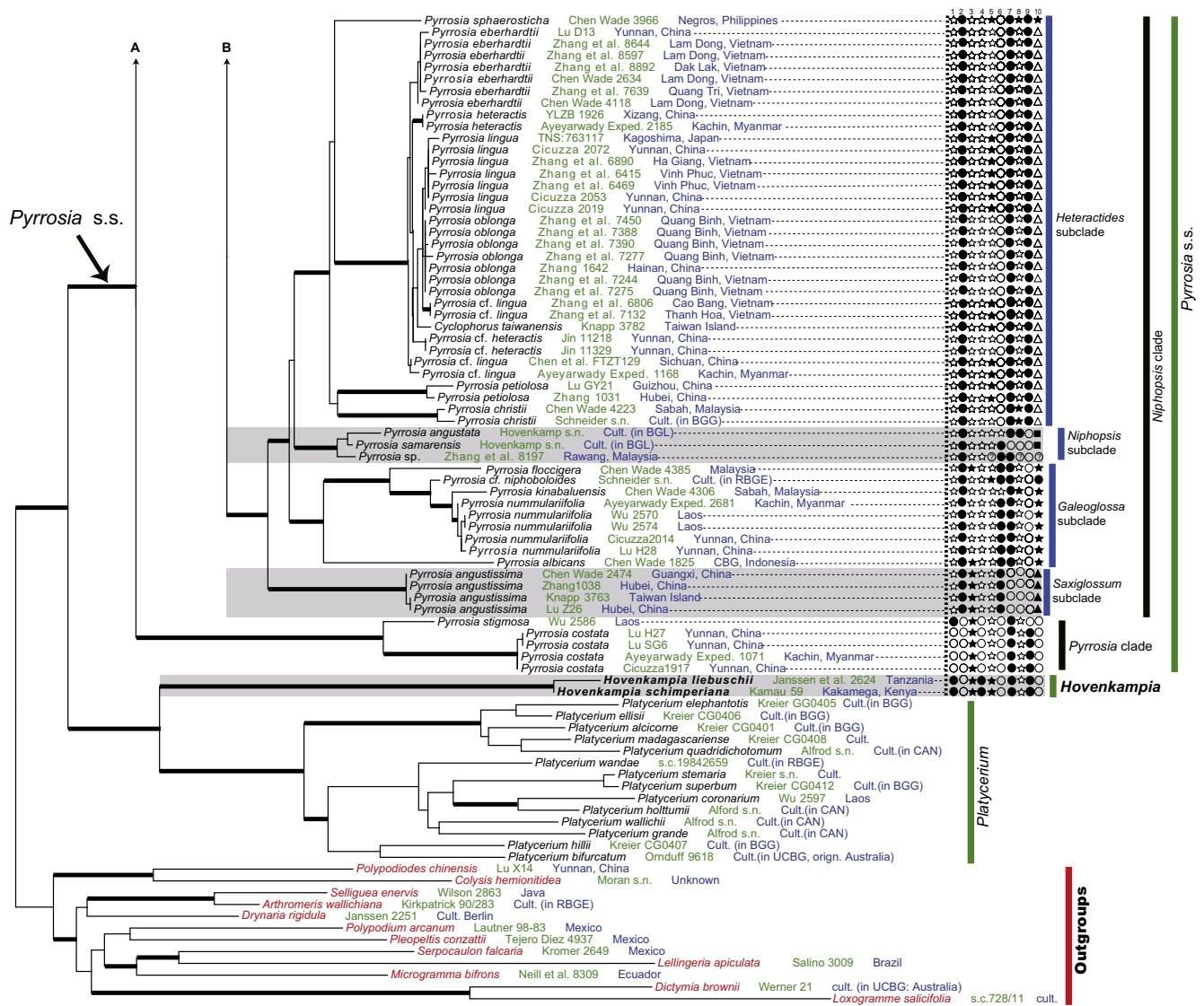
Fig. 4 (*continued*)

Previous molecular studies showed that one species of *Dry-moglossum* (*D. piloselloides* C. Presl) is deeply nested within *Pyrrosia* (Schneider et al., 2004). In addition, the monophyly of Platycerioideae and *Platycerium* was also strongly supported (Kreier and Schneider, 2006; Janssen et al., 2007). Based on the largest sampling so far, including 18 species of *Pyrrosia* and four chloroplast markers, *Pyrrosia* was weakly supported as monophyletic (Janssen et al., 2007). *Pyrrosia liebuschii* (Hieron.) Schelpe, considered a variety of *P. schimperiana* in Hovenkamp's (1986) monograph, was included in the phylogenetic study of Janssen et al. (2007). Their maximum parsimony tree showed that *P. liebuschii* was sister to the remaining species in *Pyrrosia* with weak support. However, their maximum likelihood analysis instead resolved it as sister to the rest of Platycerioideae but with no statistical support. Notably, the only data available for *P. liebuschii* in Janssen et al. (2007) study was a very short region of the *trnL-F* marker.

Spore morphology typically shows high diversity in ferns, making it an important systematic character (e.g., Tryon and Lugardon, 1991; Moran et al., 2010). Spore morphology of *Pyrrosia* has been observed by a number of authors using LM (light microscope) (e.g., Tardieu-Blot, 1966; Welman, 1970; Huang, 1981) and SEM (scanning electron microscopy) (e.g., Liew, 1976; van Uffelen,

1985; van Uffelen and Hennipman, 1985; Tryon and Lugardon, 1991; Yang, 2012). Among these authors, van Uffelen and Hennipman (1985) analyzed the spore morphology of 51 species of *Pyrrosia* recognized by Hovenkamp (1986), and identified five spore types (the *P. christii* type, the *P. nummulariifolia* type, the *P. princeps* type, the *P. rupestris* type, and the *P. subfurfuracea* type) mainly based on perispore morphology. Spore morphology of *Pyrrosia* shows high diversity and has some unique characteristics that are not reported from other homosporous leptosporangiate ferns (van Uffelen and Hennipman, 1985). Spore morphology of the *P. princeps* type and the *P. africana* group with thin perispores is similar to that of most species of *Platycerium* (Hennipman and Roos, 1982; Tryon and Lugardon, 1991). Thus, spore morphology potentially shows the *Pyrrosia africana* group has a closer relationship with *Platycerium* than with the rest of *Pyrrosia*.

Hovenkamp (1986) noticed that the asymmetric leaves in *Pyrrosia africana* (Kunze) F. Ballard are similar to the juvenile fronds in *Platycerium*, suggesting a close relationship between the *Pyrrosia africana* group and *Platycerium*.

Within *Pyrrosia*, Shing (1983) and Shing and Iwatsuki (1997) recognized about 100 species and two subgenera [*P.* subg. *Pyrrosia* and *P.* subg. *Niphopsis* (J. Sm.) Shing]. In their classifications,

P. subg. *Pyrrosia* contained two sections: *P.* sect. *Pyrrosia* and *P.* sect. *Dichlamys* Ching & Shing, and these two sections were further divided into three (*P.* ser. *Pyrrosia*, *P.* ser. *Heteractides* Ching & Shing, and *P.* ser. *Drakeanae* Ching & Shing) and two (*P.* ser. *Costatae* Ching & Shing, *P.* ser. *Molles* Ching & Shing) series, respectively. In contrast, their *P.* subg. *Niphopsis* contained two species only, *P. angustata* (Sw.) Ching, and *P. samarensis* (Mett. ex Presl) Ching, which are different from other species in *Pyrrosia* in having longitudinal ridges on the spore surface. However, Shing's (1983) and Shing and Iwatsuki's (1997) classifications were rarely accepted by other pteridologists. Based on comprehensive studies of morphology, anatomy, and ontogeny of *Pyrrosia*, Hovenkamp (1986) recognized only 51 species, of which 44 species were divided into 10 groups and seven were not assigned to any groups. In his monograph, a number of species recognized previously by various authors were treated as synonyms by Hovenkamp (1986). Following the study of Hovenkamp (1986), Hennipman (1990) tended to divide *Pyrrosia* into two parts, the *P. africana* group and the rest of *Pyrrosia*.

In addition to the *Pyrrosia africana* group, the *P. costata* group proposed by Hovenkamp (1986) appeared also morphologically incompatible with the rest of *Pyrrosia*. This group has a large number of unique characters, such as: (1) basifixed scales; (2) stipes with a central bundle of collenchyma; (3) included veins strongly anastomosing; (4) distinctly lower number (9–14) of indurated cells situated on the apical side of the capsule; (5) each sorus with few (∼10) sporangia; and (6) smooth spores with a thin, tightly adhering perispore. The last character may reflect a close relationship to *Platycerium*. Using plastid data Kim et al. (2013) resolved the *P. costata* group (one species sampled) as sister to the remaining five species of *Pyrrosia* sampled.

Based on previous studies, although the monophyly of subfamily *Platycerioideae* and *Platycerium* is not controversial, that of *Pyrrosia* is questionable. There are a few molecular studies published, but the majority of species of *Pyrrosia* remains unsampled and the most of the earlier hypotheses based on morphology, anatomy, and spore features have never been tested in a modern phylogenetic context.

The goals of this study included: (1) testing the monophyly of *Pyrrosia* and discovering its affinities with *Drymoglossum* and *Saxiglossum*; (2) resolving phylogenetic relationships within *Pyrrosia*, in particular determining how many major evolutionary clades in the genus should be recognized and the phylogenetic placement of the enigmatic *P. africana* group; (3) testing the monophyly of the infrageneric taxa/groups proposed by previous authors; and (4) inferring the evolution of major anatomical and macromorphological characters and spore features in *Platycerioideae*.

2. Materials and methods

2.1. Taxon sampling

Sampling for this study consisted of 220 accessions of Polypodiaceae representing two species of *Drymoglossum*, 14 species of *Platycerium*, ca. 50 species of *Pyrrosia*, the only species of *Saxiglossum* (subfamily Platycerioideae), and 12 species of other Polypodiaceae representing the remaining four subfamilies (Drynarioideae, Loxogrammoideae, Microsoroideae, and Polypodioideae) of Polypodiaceae (Appendix A). Our sampling covered the entire geographical range of *Pyrrosia* and included all infrageneric taxa proposed by Shing (1983) and Shing and Iwatsuki (1997) and all groups recognized by Hovenkamp (1986).

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from silica-dried material or sometimes from herbarium fragments using the TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China) following the manufacturer's protocol.

Five plastid markers (*rbcL*, *rps4*, the *rps4-trnS* intergenic spacer, the *trnL* intron, and the *trnL-F* intergenic spacer) were selected for the phylogenetic study. The *rbcL* sequences were amplified with primers F1 (Fay et al., 1997) and 1379R designed by Zurawski et al. (1984). For some herbarium specimens with degraded DNA, the internal primers of the *rbcL* gene 595F (Le Péchon et al., 2016a, 2016b), 650R, 819R (Zhang et al., 2015; Le Péchon et al., 2016b), and 895R (Le Péchon et al., 2016a) were employed when amplification of the larger region was unsuccessful. The *rps4* gene and *rps4-trnS* intergenic spacer were amplified with primers TRNS (Souza-Chies et al., 1997) and an unnamed primer derived from Li and Lu (2006). The *trnL* intron and *trnL-F* intergenic spacer were amplified together using the primers FERN1 (Trewick et al., 2002) and F (Taberlet et al., 1991). All PCR conditions followed Zhang et al. (2001). PCR products were purified and sequenced by TSINGKE Biological Technology (Chengdu, China). Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble and edit contiguous sequences.

2.3. Sequence alignment and phylogenetic analysis

Sequences obtained for each marker were initially aligned and manually adjusted in BioEdit (Hall, 1999). Partial regions of the *trnL-F* spacer of *Platycerium* and all *trnL-F* spacer and partial regions of the *rps4-trnS* spacer of the outgroups were removed from the analysis because of the difficulty in aligning them to other sequences.

Equally weighted maximum parsimony (MP) analyses for each locus were conducted in PAUP* ver. 4. 0b10 (Swofford, 2002) using 1000 tree-bisection-reconnection (TBR) searches with MAXTREES set to increase without limit. Insertions and deletions were coded as missing data. Parsimony jackknife (JK) analyses (Farris et al., 1996) were conducted using PAUP* with the removal probability set to approximately 37%, and "jac" resampling emulated. One thousand replicates were performed with 10 TBR searches per replicate and a maximum of 100 trees held per TBR search.

For each marker and the simultaneous analysis (Kluge 1989; Nixon and Carpenter 1996) of all nucleotide characters, maximum likelihood (ML; Felsenstein, 1973) tree searches and ML bootstrapping (BS) were conducted using the web server RAxML-HPC2 on TG ver. 7. 2. 8 on the Cipres web server (Miller et al., 2010), with 5000 rapid bootstrap analyses followed by a search for the best-scoring tree in a single run (Stamatakis et al., 2008).

Bayesian inference (BI) was conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) on Cipres (Miller et al., 2010). Two runs of four Markov chain Monte Carlo chains were conducted, each beginning with a random tree and sampling one tree every 1000 generations of 10,000,000 generations. Convergence among chains was checked using Tracer ver. 1.4 (Rambaut and Drummond, 2007), and the first 25% was discarded as burnin to ensure that stationarity in log-likelihood had been reached. The remaining trees were used to calculate a 50% majority-rule consensus topology and posterior probabilities (PP).

2.4. Morphology

Macromorphological data were obtained from field observations, herbarium investigations, and literature studies (e.g., Nayar, 1959; van Uffelen and Hennipman, 1985; Hovenkamp, 1986; Ravensberg and Hennipman, 1986; Shing and Iwatsuki,

1997). Herbarium investigations were carried out mainly by L.Z. at CDBI, and X.-M.Z. and L.-B.Z. at MO (herbarium acronyms follow Index Herbariorum by Thiers, 2015) and using images available through JSTOR (plants.jstor.org). R.K. identified all material from Taiwan, and D.C. helped identify material from Xishuangbanna, China. C.W.C. identified material from the Solomon Islands and a portion of Southeast Asian material. A large sum of the morphological data was derived from Hovenkamp (1986) for *Pyrrosia*. Other data were obtained from the study of Shing and Iwatsuki (1997) for Asian and adjacent Oceanian species, and Ravensberg and Hennipman's (1986) study for those species previously assigned to the genera *Drymoglossum* and *Saxiglossum*. Data of spore morphology were mainly from the studies of van Uffelen and Hennipman (1985), Yang (2012), Liew (1976), and Tryon and Lugardon (1991).

Based mainly on previous works (Hennipman and Roos, 1982; Hovenkamp, 1986; Shing and Iwatsuki, 1997; Lin et al., 2013, etc.) and our own study, a character matrix containing 10 important taxonomic characters was built. The 10 characters and their states are as follows (Fig. 4): (1) Rhizome: short and thick (Fig. 1A, E, M, and O), shortly elongated (Fig. 1C; Fig. 2A), long-creeping (Fig. 1F, H, J, and K; 2D, F, H, K, M, and O); (2) Lateral buds: with buds shifted (the buds bearing from halfway to farther down on the internodia or on the opposite position of phyllopodia on rhizome; Hovenkamp, 1986), buds not shifted (the buds bearing on the base of phyllopodia on the abaxial-lateral position of rhizome; Hovenkamp, 1986); (3) Fronds: dimorphic with distinct sterile and fertile fronds (Fig. 1A, H, and K; Fig. 2F, K, M, and O), monomorphic without distinct sterile and fertile fronds (Fig. 1C, J, M, and O; Fig. 2A, D, and H); (4) Scales on rhizome: basifixed, peltate (Fig. 2I), pseudopeltate; (5) Wooly hairs: present, absent; (6) Rays of stellate hairs: boat-shaped rays, acicular rays (Fig. 2C), boat-shaped to acicular rays (narrowly boat-shaped rays, sometimes nearly acicular); (7) Morphology of sori: confluent in a coenosorus (Fig. 1G and J; Fig. 2G, O, and P), linear, orbicular to oblong or elliptic (Fig. 1D, I, L, N, and P; Fig. 2B, C, E, J, L, and N); (8) Size of sori: extremely large and exceeding areole (Fig. 1G and J; Fig. 2G, O, and P); relatively large; 1, 2 (–3) in each areole (Fig. 2E and L), small and several (>E3) to many in each areole (Fig. 1D, I, L, N, and P; Fig. 2B, C, E, J, L, and N), very small and closely packed and pseudo-acrostichoid when ripe; (9) Placement of hydathodes: absent, constantly scattered over lamina, inconstantly scattered over lamina, in a marginal row on the upper surface of lamina, in a row on the lower surface of lamina; and (10) Spores morphology: the *Pyrrosia angustata* type, the *Pyrrosia angustissima* type, the *P. christii* type, the *P. nummulariifolia* type, the *P. princeps* type, the *P. rupestris* type, the *P. subfurfuracea* type (for the detail, see discussion). Mesquite v.2.75 (Maddison and Maddison, 2011) was used to optimize morphological features on the most likely tree inferred from ML analysis. The ancestral states were estimated based on parsimony criterion.

3. Results

A total of 426 (or 700 when separating *trnL* and *trnL-F*, and *rps4* and *rps4-trnS*) sequences were newly generated for this study (Appendix A). All 220 accessions of samples were represented by

at least one plastid marker. For details concerning the datasets analyzed and statistics for the resulting trees, see Table 1. A comparison of the trees resulting from MPJK analyses of the individual plastid markers and the combined plastid dataset did not identify any well-supported conflicts in MP analyses (MPJK ≥ 70%; Mason-Gamer and Kellogg, 1996; Zhang and Simmons, 2006; Zhang et al., 2015, 2016; Zhou et al., 2016). The five plastid markers were therefore concatenated and analyzed in unison. The MP, ML, and BI trees generally agreed. The ML phylogeny of *Pyrrosia* and related genera based on five plastid markers (*rbcL*, *rps4*, *rps4-trnS*, *trnL*, and *trnL-F*) is presented in Figs. 3 and 4. The monophyly of the subfamily Platycerioideae is strongly supported (MLBS: 100%; MPJK: 99%; BIPP: 1.00). Within Platycerioideae, our data clearly resolved the intergeneric relationships. The monophyly of *Platycerium* is confirmed (MLBS: 100%; MPJK: 100%; BIPP: 1.00). *Pyrrosia* is resolved as paraphyletic in relation to *Platycerium*, with two species of the *Pyrrosia africana* group, *P. liebuschii*, and *P. schimperiana*, forming a monophyletic clade with *Platycerium* with strong support (MLBS: 100%; MPJK: 99%; BIPP: 1.00). Within *Pyrrosia*, the remaining 192 accessions (*Pyrrosia* s.s.) form a strongly supported clade (MLBS: 100%; MPJK: 100%; BIPP: 1.00) which is resolved into four major clades: the *Pyrrosia* clade, the *Niphopsis* clade, the *Neoniphopsis* clade, and the *Niphobolus* clade, each being strongly supported (MLBS: 100%; MPJK: 100%; BIPP: 1.00). The *Pyrrosia* clade is resolved as sister to the remaining accessions of *Pyrrosia* s.s. with strong support (MLBS: 100%; MPJK: 99%; BIPP: 1.00), followed by the *Niphopsis* clade which is sister to a strongly supported clade (MLBS: 98%; MPJK: 96%; BIPP: 1.00) containing the *Neoniphopsis* clade and the *Niphobolus* clade. The *Niphopsis* clade, the *Neoniphopsis* clade, and the *Niphobolus* clade are further resolved into four, five, and six subclades, respectively, with all subclades being strongly supported (MLBS:>96%; MPJK:>90%; BIPP: 1.00; except MPJK: 83% in the *Dichlamys* subclade; Figs. 3 and 4). The paraphyly of *Pyrrosia* s.l. and four major clades resolved in our study are consistent with the results presented by Testo and Sundue (2016) who sampled 27 accessions of *Pyrrosia* only.

4. Discussion

4.1. Resolution of Drymoglossum

Drymoglossum was established by Presl (1836). Earlier authors often recognized about five species in the genus including *Drymoglossum fallax* Alderw., *D. heterophyllum* (L.) Trimen, *D. niphoboloides* (Luerss.) Baker, *D. novo-guinee* Christ (incl. *D. crassifolium* Brause), and *D. piloselloides* (Christensen, 1929; Copeland, 1947; Nayar, 1970; Pichi Sermolli, 1977a, 1977 b). Ravensberg and Hennipman (1986) studied the morphology and anatomy of all five species and related species of *Pyrrosia* and found that *Drymoglossum* is not monophyletic, but three out of the five species, *D. heterophyllum*, *D. niphoboloides* and *D. piloselloides*, did form a monophyletic group. In our present study we included seven accessions of *D. piloselloides* and one accession of *D. fallax*. Our results show that *Drymoglossum* is polyphyletic because the two species are resolved in different subclades in the *Niphobolus* clade with *D. piloselloides* resolved in the *Drymoglossum* subclade and *D. fallax* in the *Fallax* subclade (Figs. 3

Table 1
Data matrices and tree statistics for each of the analyses. Missing data include missing sequences, uncertain bases (N, R, Y, V, etc.) and gaps (−). "PI" = parsimony-informative. "MPT" = most parsimonious trees. "CI" = consistency index. "RI" = retention index.

Matrix	# accessions	# missing	# chars.	# PI chars. (%)[a]	MPT length	CI	RI
Plastid *rbcL* gene	209	10%	1273	225(18)	962	0.4179	0.8499
Plastid *rps4* gene & *rps4-trnS* spacer	200	24%	1060	377(36)	1169	0.5620	0.9117
Plastid *trnL* intron & *trnL-F* spacer	156	55%	1116	302(27)	768	0.6419	0.9392
Simultaneous	220	29%	3449	904(26)	2884	0.5392	0.9051

and 4). Our resolution of *D. piloselloides* in *Pyrrosia* is consistent with that in Schneider et al. (2004). Our resolution of *Drymoglossum* as polyphyletic based on molecular data is consistent with that in Ravensberg and Hennipman (1986) based on morphological and anatomical data.

4.2. Resolution of Saxiglossum

The genus *Saxiglossum* was established by Ching (1933). Normally it is considered as a monospecific genus, although sometimes three species are recognized including *S. angustissimum* (Giesenh. ex Diels) Ching, *S. sasakii* (Hayata) Tagawa, and *P. taeniodes* (C. Chr.) Ching (e.g., Ching, 1965). The placement of this genus was unclear but it was never sampled in previous molecular studies. Four accessions of *S. angustissimum* s.l. are included in our analysis, and our analysis resolved this species as monophyletic within the second major clade, the *Niphopsis* clade, suggesting that *Saxiglossum* is part of *Pyrrosia*. Our resolution of this genus is consistent with that of Ravensberg and Hennipman (1986) based on morphological and anatomical data. Within the *Niphopsis* clade, the *Saxiglossum* subclade is resolved as sister to the remaining three subclades (Figs. 3 and 4).

4.3. Resolution of Pyrrosia

Based on the morphology and anatomy, Hovenkamp (1986) noticed that the *Pyrrosia africana* group is different from the rest of *Pyrrosia* by having the following features: (1) sheath of sclerenchyma completely absent and collenchymatous sheath present; (2) the secondary veins hardly distinct from the other veins; (3) polocytic stomata; and (4) relatively small sporangia. Hennipman (1990) proposed three hypotheses for the relationships among *Platycerium*, the *Pyrrosia africana* group, and the rest of *Pyrrosia* (see above).

Our analysis resolved 194 accessions of *Pyrrosia* s.l. (incl. those of *Drymoglossum* and *Saxiglossum*) into two large clades: one clade containing the *Pyrrosia africana* group and *Platycerium*, which is in turn sister to *Pyrrosia* s.s. *Platycerium* is morphologically very distinct (Kreier and Schneider, 2006a; Janssen et al., 2007) and therefore should not be expanded to include the *Pyrrosia africana* group. A separate genus accommodating the *P. africana* group (*Hovenkampia* gen. nov., see below) must be recognized in order for a monophyletic *Pyrrosia* s.s. to be maintained. Our resolution is not in conflict with that based on morphological and anatomical data by Hovenkamp (1986) who found a trichotomy in Platycerioideae consisting of *Platycerium*, the *P. africana* group, and the remaining 49 species of *Pyrrosia* he recognized.

4.4. Circumscription of Platycerioideae

Platycerioideae is resolved as monophyletic with strong support in our study (MLBS: 100%; MPJK: 99%; BIPP: 1.00). Our study also confirms that *Drymoglossum* and *Saxiglossum* should be synonymized with *Pyrrosia* (see above; Figs. 3 and 4). Importantly, *Pyrrosia* is resolved as paraphyletic with our data and can be divided into two genera, *Pyrrosia* s.s. and *Hovenkampia* gen. nov. Therefore, based on our study Platycerioideae should contain three genera: *Hovenkampia*, *Platycerium*, and *Pyrrosia* s.s. The three genera can be distinguished from one another with the following key:

Key to the genera in Platycerioideae

1. Fronds strongly dimorphic, basal fronds with basal part tightly adpressed to substrate, fertile fronds dichotomously lobed; scales basifixed (except peltate in *P. bifurcatum* (Cav.) C. Chr. *p.p.*)
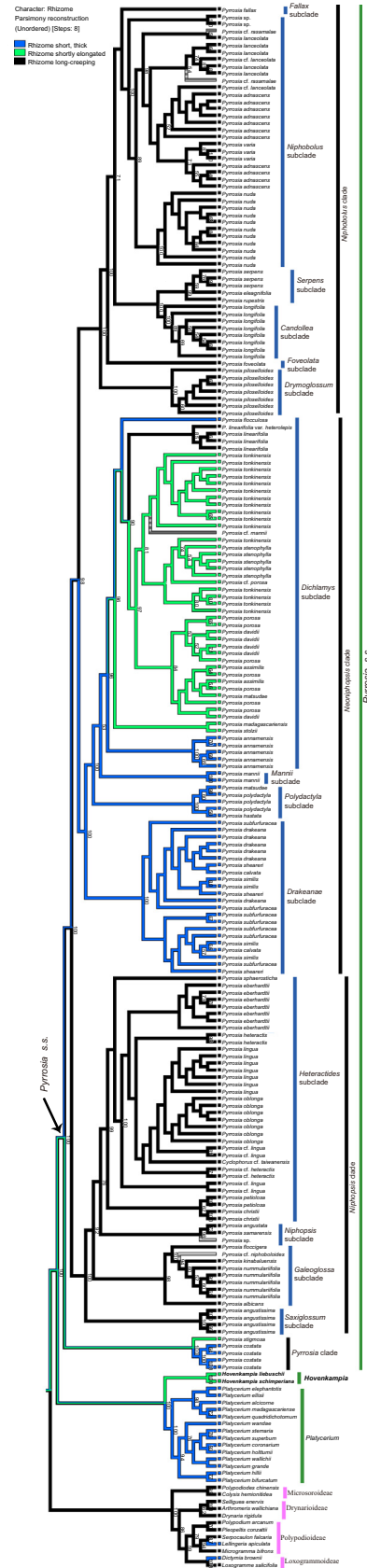
[*Platycerium*]

Fig. 5. Morphological reconstruction: Rhizomes of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s. s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states.

Fig. 6. Morphological reconstruction: Lateral buds on rhizome of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1. Fronds monomorphic or dimorphic, but fronds without adpressed basal part and not dichotomously lobed; scales basifixed (only in the *Pyrrosia* clade of *Pyrrosia*), pseudopeltate or peltate.

2. Rhizomes completely parenchymatous; stomata polocytic; perispore thin, tightly adhering to the exospore surfaces

[*Hovenkampia*]

2. Rhizomes completely sclerenchymatous (in the *Pyrrosia* clade) or differentiated into parenchyma and sclerenchyma; stomata pericytic (except *Pyrrosia manni* and *P. penangiana*); perispore thick and completely covering to the exospore surfaces (except in the *Pyrrosia* clade)

[*Pyrrosia*]

4.5. Infrageneric relationships within Pyrrosia s.s

The 192 accessions of *Pyrrosia* s.s. are resolved into four major clades: the *Pyrrosia* clade, the *Niphopsis* clade, the *Neoniphopsis* clade, and the *Niphobolus* clade. The *Pyrrosia* clade is sister to the rest, followed by the *Niphopsis* clade which is sister to a clade containing the remaining two clades (Figs. 3 and 4). Our overall results are consistent with those presented by Testo and Sundue (2016) who sampled 27 accessions of *Pyrrosia* only.
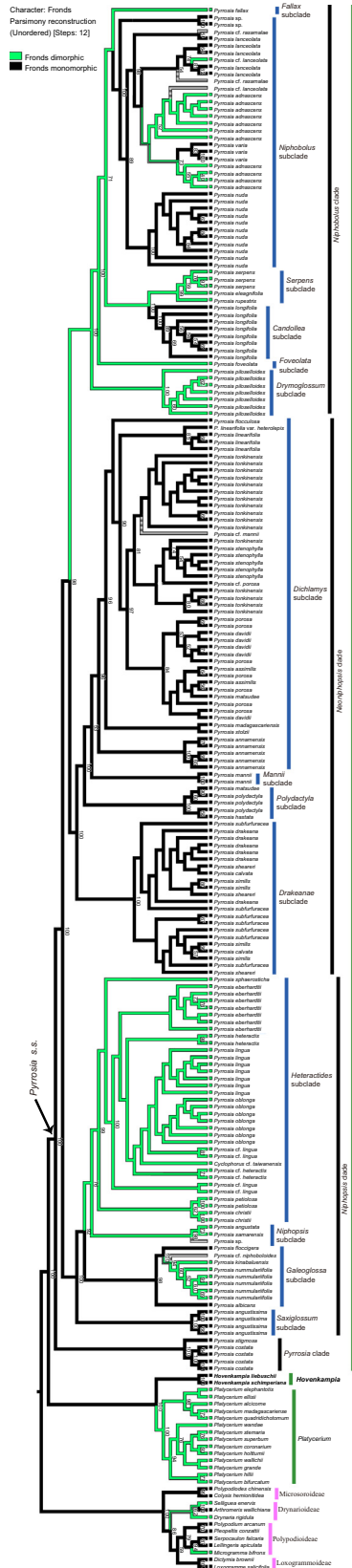
4.5.1. The Pyrrosia clade

Two species, *Pyrrosia stigmosa* (Sw.) Ching, type of the genus, and *P. costata* (Wall. ex C. Presl) Tagawa & K. Iwats., are included in our sampling. The *Pyrrosia* clade corresponds the *P. costata* group in the monograph of Hovenkamp (1986). The *Pyrrosia* clade is morphologically distinct from the rest of *Pyrrosia* s.s. Members of the *Pyrrosia* clade are similar to those of *Hovenkampia* and *Platycerium* in having thin perpispores and basifixed rhizome scales. Meanwhile, the *Pyrrosia* clade also has some unique characters, e.g., distinctly lower number of indurated annulus-cells in sporangia and few sporangia in each sorus. It is tempting to treat the *Pyrrosia* clade as an independent genus in *Platycerioideae* based on its unusual morphology and our resolution. However, the *Pyrrosia* clade contains the type species of the currently circumscribed *Pyrrosia*. Therefore we treat the *Pyrrosia* clade as part of *Pyrrosia* for nomenclatural stability.

Species of the *Pyrrosia* clade were treated in *P.* ser. *Costatae* Ching & K. H. Shing by Shing (1983) and Shing and Iwatsuki (1997) which included *P. costata*, *P. nummularifolia* (Swartz) Ching and *P. strigosa* (Swartz) Ching. Based on morphology and our molecular study, *P.* ser. *Costatae* is not a monophyletic group.

Following Hovenkamp (1986) and our phylogeny, the *Pyrrosia* clade contains about five species: *Pyrrosia costata* (Fig. 1E), *P. platyphylla* Hovenkamp, *P. princeps* (Mett.) C.V. Morton, *P. splendens* (Presl) Ching, and *P. stigmosa*.
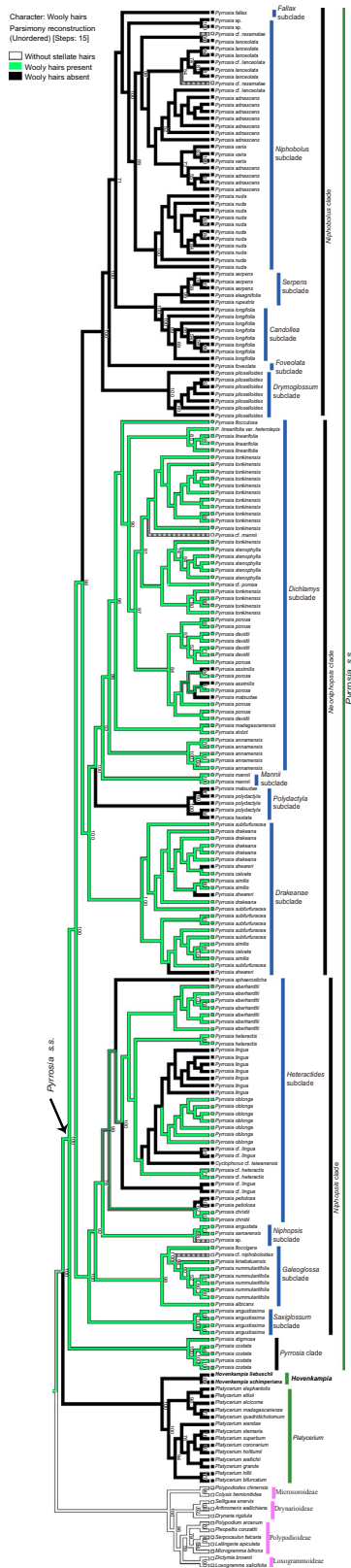
4.5.2. The Niphopsis clade

Monomorphic fronds (Fig. 1F) in the *Niphopsis* clade are a plesiomorphic character state, and dimorphic fronds evolved twice in this clade (Fig. 7). Species of this clade have long-creeping rhizomes (Fig. 1F, H, J, and K) with buds shifted (Fig. 6). Stellate hairs with acicular rays are pleisiomorphic, but those with boat-shaped rays evolved once in the clade, while boat-shaped to acicular rays evolved twice (Fig. 10). This clade is further resolved into four well-supported subclades: the *Galeoglossa* subclade, the *Heteractides* subclade, the *Niphopsis* subclade, and the *Saxiglossum* subclade. The *Saxiglossum* subclade is sister to the rest, followed by the *Galeoglossa* subclade which is sister to a clade containing the *Heteractides* subclade and the *Niphopsis* subclade (Figs. 3 and 4). Relationships among these four subclades are strongly supported
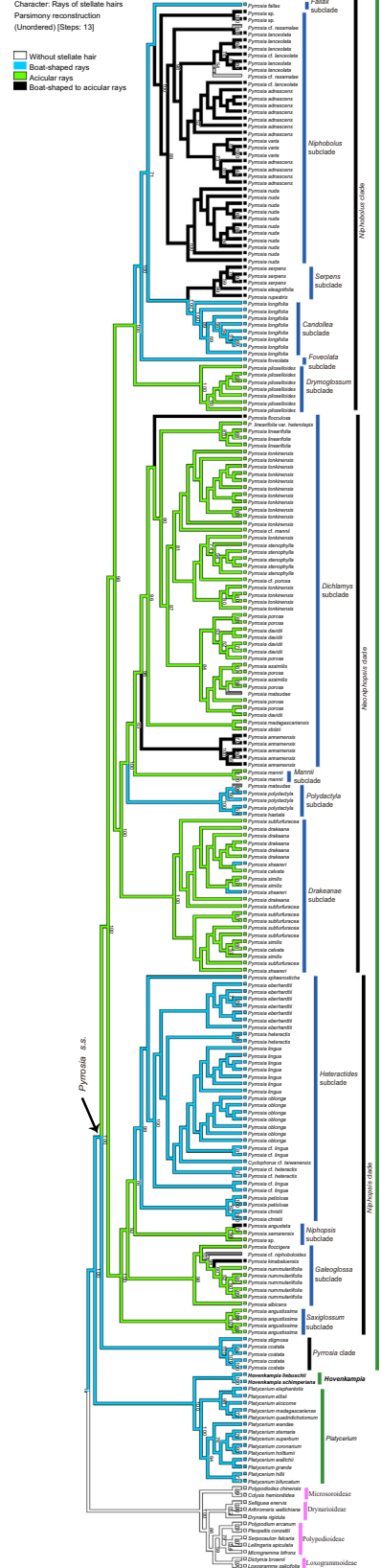
Fig. 7. Morphological reconstruction: Fronds of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 8. Morphological reconstruction: Scales of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
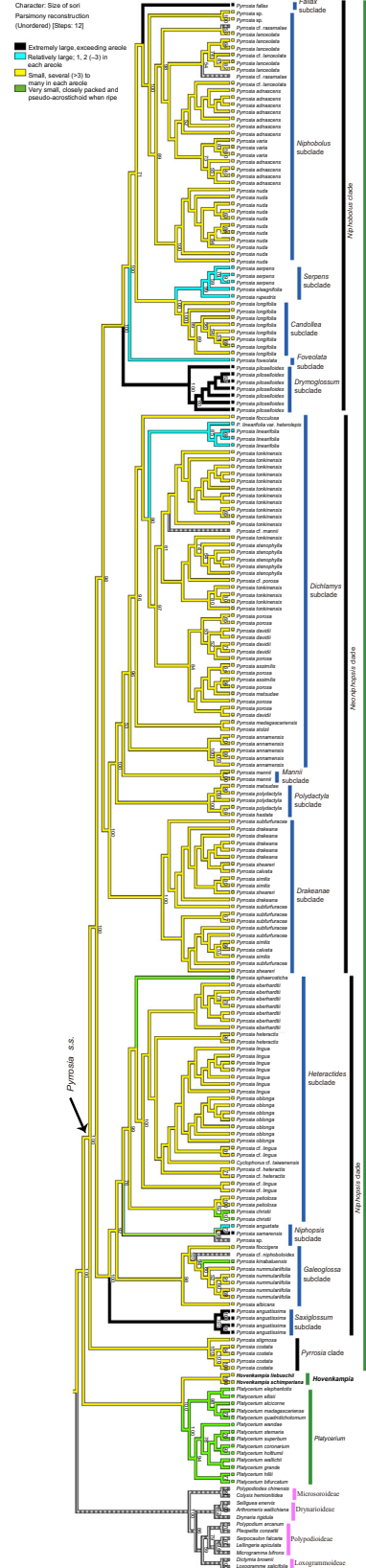
Fig. 9. Morphological reconstruction: The wooly hairs present or absent of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae optimized onto the maximum likelihood tree of Fig. 4. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
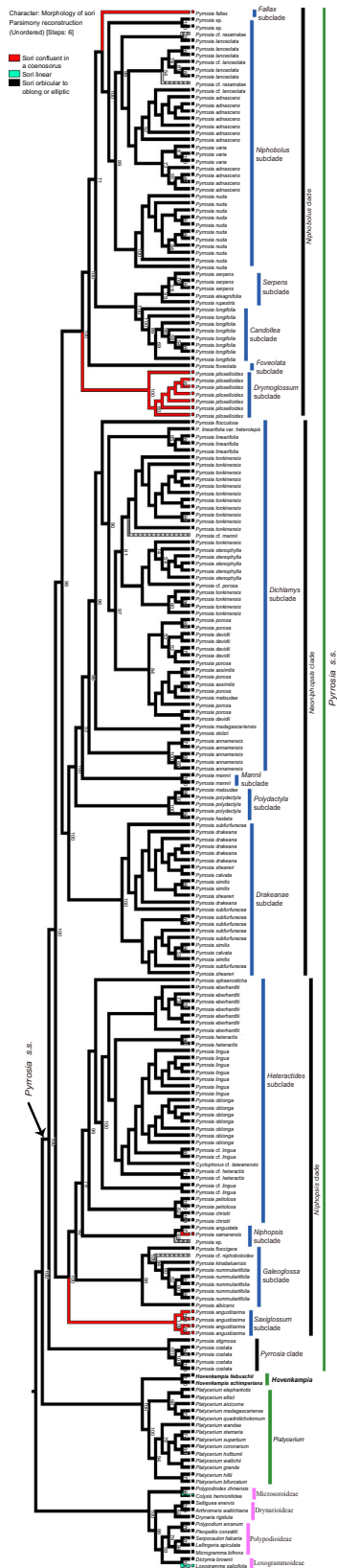
Fig. 10. Morphological reconstruction: Rays of stellate hairs of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 11. Morphological reconstruction: Morphology of sori of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
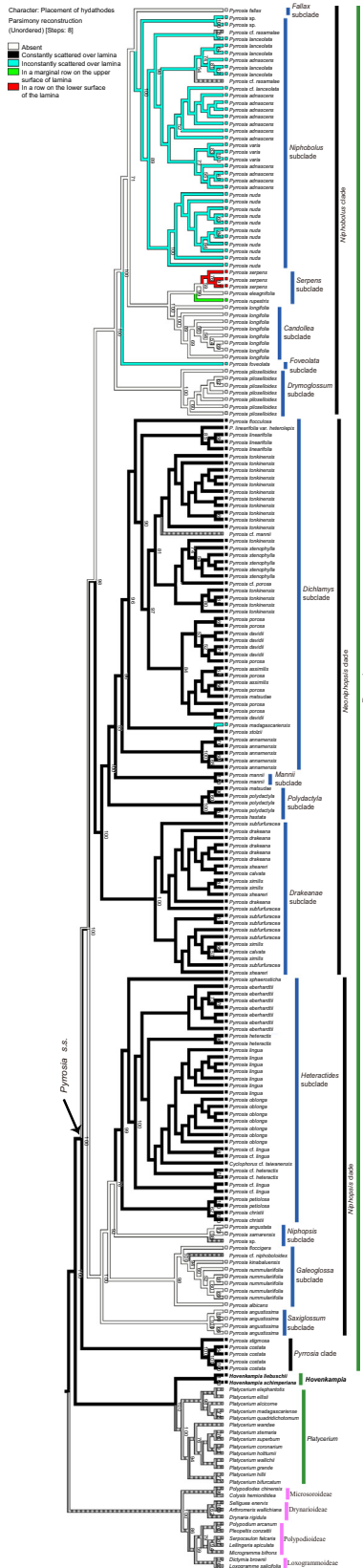
Fig. 12. Morphological reconstruction: Size of sori of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
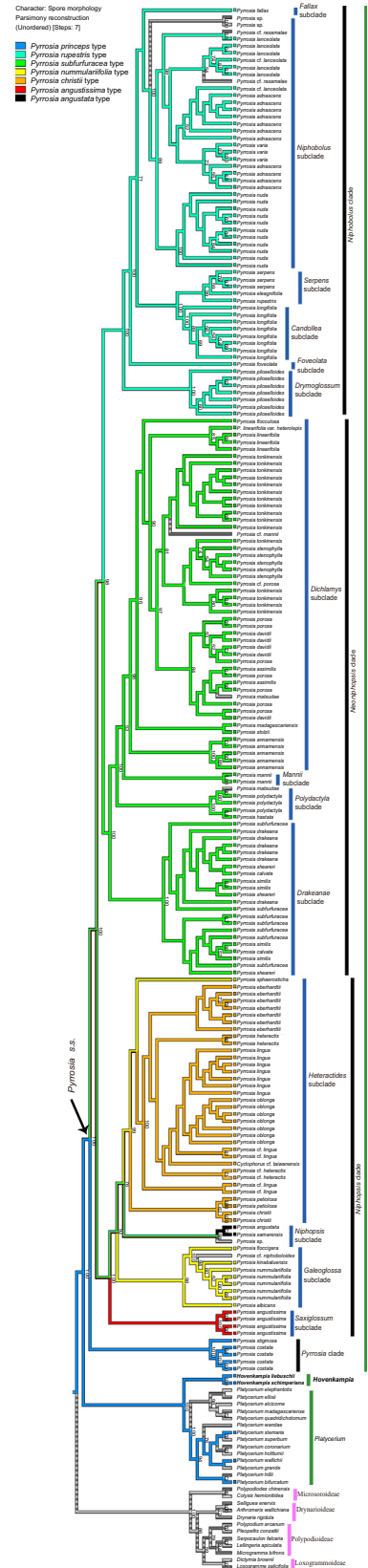
Fig. 13. Morphological reconstruction: Placement of hydathodes of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 14. Morphological reconstruction: Spore morphology of *Pyrrosia* and related taxa optimized onto the maximum likelihood tree of Fig. 4. Green vertical bars indicate genera in Platycerioideae. Black vertical bars indicate four major clades of *Pyrrosia* s.s. Blue vertical bars indicate 14 subclades in *Pyrrosia* s.s. Purple vertical bar indicates the outgroups. Grey clades show these taxa with ambiguity states. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

except the sister relationship between the *Heteractides* subclade and the *Niphopsis* subclade which is moderately to strongly supported (MLBS: 71%; MPJK: 89%; BIPP: 1.00).

Based on spore morphology (van Uffelen and Hennipman, 1985) and macromorphology (Hovenkamp, 1986), *Pyrrosia rasamalae* is a member of our *Galeoglossa* subclade in *Niphopsis* clade. However, two accessions of *P. rasamalae* from GenBank do not form a clade, and are nested within the *Niphobolus* subclade (the *Niphobolus* clade). We doubt the identification of these two accessions from GenBank.

Pyrrosia niphoboloides (Luerss.) M.G. Price was assigned to *Drymoglossum* in previous morphological studies (Copeland, 1947; Pichi Sermolli, 1977a). Janssen et al.'s (2007) analysis of three plastid markers (*rbcL*, *rps4-trnS*, *trnL-trnF*) resolved *P. niphoboloides* as the second earliest lineage in *Pyrrosia* with weak support. We excluded their *rps4-trnS* accession "DQ642207" as it appears to be erroneous (more closely related to accessions of *Platycerium*), and only used *rbcL* and *trnL-F* data for this species in our study. Although our study resolved *P. niphoboloides* as sister to a clade containing *P. kinabaluensis* and *P. nummulariifolia*, such a relationship is not supported by morphology (van Uffelen and Hennipman, 1985; Ravensberg and Hennipman, 1986) which instead suggests that it is a member of the *Niphobolus* clade. More studies on this species are needed.

4.5.2.1. The Galeoglossa subclade. About five species of this subclade are included in our study. Monomorphic fronds in this subclade is the ancestral state, and dimorphic fronds evolved once within this subclade (Fig. 7). The *Pyrrosia nummulariifolia* type of spores might be a synapomorphy of this subclade (Fig. 14). Species of this subclade can be distinguished by long-creeping rhizomes, monomorphic to strongly dimorphic fronds (Fig. 1H and I), peltate scales, succulent lamina with a distinct water-tissue, lack of hydathodes (Fig. 13), and outer surface of perispore with fingerprint patterns (van Uffelen and Hennipman, 1985).

4.5.2.2. The Heteractides subclade. About seven species of the subclade are included in our study. Stellate hairs with boat-shaped rays are a synapomorphy of this subclade (Fig. 10). Dimorphic fronds are a synapomorphy of this subclade + the *Niphopsis* subclade (Fig. 7). It is, however, ambiguous if the *Pyrrosia christii* type of spores is a synapomorphy of this subclade (Fig. 14). Species of the *Heteractides* subclade share long-creeping rhizomes, appressed indumenta with boat-shaped rays, moderately dimorphic fronds with sterile fronds being generally shorter and wider than the fertile ones, usually strongly anastomosing veins (Fig. 1K and L) (Hovenkamp, 1986), and spore surfaces covered with irregularly verrucate to tuberculate ornamentation (van Uffelen and Hennipman, 1985).

This subclade corresponds to the *P. lingua* group of Hovenkamp (1986) who included five species in this group: *P. lingua* (Thunb.) Farw., *P. christii* (Giesenh.) Ching, *P. abbreviate* (Zoll. & Moritzi) Tagawa, *P. petiolosa* (Christ) Ching, and *P. sphaerosticha* (Mett.) Ching. Although Hovenkamp (1986) somewhat questioned the monophyly of his *P. lingua* group because of the wide variation in morphology, it is strongly supported by our molecular data (Figs. 3 and 4). Our study shows that this subclade contains more than these five species.

4.5.2.3. The Niphopsis subclade. Three species of the *Niphopsis* subclade are included in our study. Relatively large sori and 1, 2 (–3) in each areole or sori confluent in a coenosorus is a synapomorphy of this subclade (Fig. 12). This subclade shares dimorphic fronds with the *Heteractides* subclade (Fig. 7). The *Pyrrosia angustata* type of spores is a synapomorphy of this subclade (Fig. 14). Spore surfaces are covered with obviously longitudinal ridges

(Shing, 1983; Hovenkamp, 1988). Species of this subclade have peltate and entire scales, strongly dimorphic fronds with fertile fronds divided into a sterile part and a fertile part with a narrow spike at the apex of the lamina, and laminae without hydathodes (Fig. 13) (Hovenkamp, 1986).

This subclade corresponds to the *Pyrrosia angustata* group of Hovenkamp (1986). Based on morphology (van Uffelen and Hennipman, 1985; Hovenkamp, 1986), a New Guinean species *P. novo-guineae* (Christ) M. G. Price is likely a member of this subclade.

4.5.2.4. The Saxiglossum subclade. This subclade is currently treated as monospecific (*Pyrrosia angustissima* distributed in East Asia), and is resolved as sister to the rest of the *Niphopsis* clade. The *Pyrrosia angustissima* type of spores and the sori confluent in a coenosorus (Fig. 11) are two synapomorphies of this subclade (Fig. 1G).

4.5.3. The Niphobolus clade

Dimorphic fronds in the *Niphobolus* clade is a synapomorphy, while monomorphic fronds evolved at least twice in the clade (Fig. 7). Having no wooly hairs (Fig. 9) and the *Pyrrosia rupestris* type of spores are two synapomorphies of this clade. This clade is further resolved into six well-supported subclades: the *Candollea* subclade, the *Drymoglossum* subclade, the *Fallax* subclade, the *Foveolata* subclade, the *Niphobolus* subclade, and the *Serpens* subclade. The *Drymoglossum* subclade is resolved as sister to the rest, followed by the *Foveolata* subclade, further by the *Candollea* subclade + the *Serpens* subclade which are together sister to a clade containing the *Niphobolus* subclade and the *Fallax* subclade (Figs. 3 and 4). Relationships among these six subclades are mostly strongly supported.

4.5.3.1. The Candollea subclade. This subclade contains only one species, *Pyrrosia longifolia* (Fig. 2H–J), distributed across Asia to Australia. Monomorphic fronds reversed from dimorphic fronds are a synapomorphy of this subclade (Fig. 7). *Pyrrosia longifolia* has especially long laminae (usually >20 cm), long-creeping rhizomes, and completely entire scales on the rhizome, monomorphic indumenta with boat-shaped rays, and spore surfaces covered with irregular verrucae. Hovenkamp (1986) assigned it to the *P. lanceolata* group (our *Niphobolus* subclade), while our analysis resolved it as an independent subclade sister to the *Serpens* subclade. Morphologically, *P. longifolia* is similar to *P. lanceolata*, but the former has completely entire and broadly ovate scales on the rhizome (Fig. 2I), obviously different from those species of the *Niphobolus* subclade.

4.5.3.2. The Drymoglossum subclade. Seven accessions of one species, *Pyrrosia piloselloides* (L.) Price, distributed in N. E. India to Hainan, China, and Vietnam, are included in our study. Stellate hairs with acicular rays are pleisiomorphic in this subclade but this character state distinguishes this subclade from other subclades in the *Niphobolus* clade (Fig. 10). Sori extremely large, exceeding areole (Fig. 2G and 12), and confluent in a coenosorus (Fig. 2G and 11) are a synapomorphy of this subclade. Species of the *Drymoglossum* subclade have strongly dimorphic fronds (Fig. 2F), unique rhizome scales that are strongly ciliate at the base and the apex, and spore surfaces covered with verrucae and conical spine-like protuberances (van Uffelen and Hennipman, 1985).

Based on the morphology, Ravensberg and Hennipman (1986) recognized a group containing *P. heterophylla* (L.) Price, *P. niphoboloides* (Luerss.) Price, and *P. piloselloides*. It is accepted by Hovenkamp (1986) who assigned them to the *P. piloselloides* group.

4.5.3.3. The fallax subclade. Only one species, *Pyrrosia fallax* (Alderw.) Price (Fig. 2O and P), distributed in Ambon eastwards to the Solomon Islands, is included in our study. Sori confluent in

a coenosorus (Fig. 2P and 11) and extremely large, exceeding areole (Fig. 2P and 12) are a synapomorphy of this subclade. The stellate hairs with boat-shaped rays are pleisiomorphic and shared with the *Candollea* and the *Foveolata* subclades (Fig. 10). *Pyrrosia fallax* was often assigned to *Drymoglossum* (Ravensberg and Hennipman, 1986). This relationship is not supported with our data which instead suggest that it can be recognized as an independent subclade as we do here. This species has paraphyses arranged in a central row (Hovenkamp, 1986; Ravensberg and Hennipman, 1986).

4.5.3.4. The foveolata subclade. The subclade currently contains only one species, *Pyrrosia foveolata* (Alston) Morton, distributed in Moluccas, New Guinea, and the Bismarck Archipelago. The relatively large sori in 2(–3) per areole are a synapomorphy of this subclade (Fig. 12). Species of this subclade have long-creeping rhizomes, monomorphic indumenta with boat-shaped rays, and apical sori closely packed but with distinctly separate and deeply sunken paraphyses with short and straight rays mixed with the sporangia. Hovenkamp (1986) did not assign it to any group. Our data resolved *P. foveolata* as the second earliest lineage in the *Niphobolus* clade, contrasting the results by Testo and Sundue (2016) who found *P. foveolata* as sister to *P. serpens*. Although it has deeply sunken sori similar to members of the *Niphobolus* subclade, its paraphyses are completely mixed with sporangia in the sori instead of being in a central bundle in the latter (Hovenkamp, 1986).

4.5.3.5. The Niphobolus subclade. This subclade contains at least five species: *Pyrrosia adnascens* (Sw.) Ching, *P. ceylanica* Sledge (based on morphology only), *P. lanceolata* (L.) Farw., *P. nuda* (Giesenh.) Ching, and *P. varia* Farwell, distributed across Africa, Asia, and Australia. Monomorphic fronds reversed from dimorphic fronds (Fig. 7) and stellate hairs with boat-shaped to acicular rays (Fig. 10) are two synapomorphies of this subclade. Species of this subclade have long-creeping rhizomes (Fig. 2M) and deeply sunken sori (Fig. 2N) with centrally situated paraphyses arranged in a bundle. The *Niphobolus* subclade is similar to the *P. lanceolata* group of Hovenkamp (1986) who included four species in it: *P. ceylanica*, *P. fallax*, *P. lanceolata*, and *P. longifolia*. The *P. lanceolata* group is polyphyletic (see above and below too).

4.5.3.6. The Serpens subclade. Three species are included in our study. Stellate hairs with boat-shaped to acicular rays (Fig. 10) and the relatively large sori in groups of 2(-3) per areole (Fig. 2L) are two synapomorphies of this subclade. Species of this subclade have moderately or distinctly dimorphic fronds (Fig. 2K), hydathodes absent or present (only in the marginal row, or in a row on the lower surface of the lamina; Fig. 13), appressed and monomorphic indumenta with boat-shaped rays, and sori distinctly sunken, and present the tendency toward forming coenosori on the upper part of lamina (Hovenkamp, 1986). This subclade is equivalent to the *P. confluens* group of Hovenkamp (1986). Testo and Sundue (2016) did not recover the monophyly of this subclade.

4.5.4. The Neoniphopsis clade
Short and thick rhizomes (Fig. 5) and the *Pyrrosia subfurfuracea* type of spores (Fig. 14) are two synapomorphies of this clade. The monomorphic fronds of the clade are pleisiomorphic (Fig. 7). This clade is further resolved into four well-supported subclades: the *Dichlamys* subclade, the *Drakeanae* subclade, the *Mannii* subclade, and the *Polydactyla* subclade. The *Drakeanae* subclade is resolved as sister to the rest, and followed by the *Polydactyla* subclade, further (weak support) by the *Mannii* subclade which is sister to the *Dichlamys* subclade (Figs. 3 and 4). Relationships among these four subclades are mostly strongly supported.

4.5.4.1. The Dichlamys subclade. Forty-five accessions representing at least 10 species of this subclade are included in our study. Although well supported as monophyletic (MLBS: 96%; MPJK: 89%; BIPP: 1.00), there are no synapomorphies for this subclade for the seven major morphological characters analyzed. This subclade corresponds the *P. porosa* group and two species [*Pyrrosia annamensis* (Christ) Li Bing Zhang, X.M. Zhou & C.W. Chen (Zhou et al., 2017) and *P. flocculosa* (D. Don) Ching] of the *P. shearer* group of Hovenkamp (1986). Species of the *Dichlamys* subclade have elongated, occasionally short (*P. flocculosa* and *P. annamensis*) or long-creeping (*P. linearifolia* (Hook.) Ching) rhizomes, monomorphic fronds, peltate (occasionally pseudopeltate) scales, and wooly hairs present.

Based on the morphology, geographic distribution, and our molecular data, five lineages within the *Dichlamys* subclade can be identified:

(1) The *Pyrrosia linearifolia* lineage containing only one East Asian species, *P. linearifolia*, which has long-creeping rhizome (Fig. 2D) and sori in a single or two rows between midribs and margins (Fig. 2E) (vs. usually more than three rows).
(2) The *Pyrrosia porosa* lineage containing the most species of the *P. porosa* group of Hovenkamp (1986), e.g., *P. assimilis* (Baker) Ching, *P. davidii*, *P. porosa* (C. Presl) Hovenkamp (Fig. 2A–C), *P. stenophylla* (Bedd.) Ching, and *P. tonkinensis* (Giesenh.) Ching. A potential hybrid species *P. matsudae* related to the *Polydactyla* subclade is resolved in this lineage.
(3) The *Pyrrosia madagascariensis* lineage containing two species, *P. madagascariensis* from Madagascar and *P. stolzii* from Tanzania in our sampling. Morphologically, *P. madagascariensis* is extremely similar to the rest of the *Dichlamys* subclade. However, it is geographically highly isolated. It has a 180 bp long insertion in *trnL-F* region in comparison with other species of *Pyrrosia*.
(4) The *Pyrrosia flocculosa* lineage containing only one species from Kaski, Nepal that is very similar to *P. annamensis*. Hovenkamp (1986) placed it in his *P. shearer* group, but noticed its difference from other members of the *P. shearer* group in having fewer sclerenchyma strands in the rhizome, dentate rhizome scales, and spare granules on the spore surfaces.
(5) The *Pyrrosia annamensis* lineage contains only one species. In the previous study, *P. annamensis* was widely treated as a synonym of *P. flocculosa* (e.g., Hovenkamp, 1986). However, our molecular data resolved these two species in very different clades, suggesting they are apparently different species. Five accessions representing *P. annamensis* from Vietnam and Laos are included in our study.

4.5.4.2. The Drakeanae subclade. About six species are included in our phylogenetic study. The pseudopelate scales (Fig. 8) are the only synapomorphy we found for this subclade. It corresponds to part of the *P. shearer* group of Hovenkamp (1986). This group is found to be polyphyletic with our data and members of this group sensu Hovenkamp (1986) are resolved in three subclades: the *Dichlamys* subclade, the *Drakeanae* subclade, and the *Polydactyla* subclade. Species of the *Drakeanae* subclade have short and thick rhizomes (Fig. 1M), and spore surfaces covered with granules (van Uffelen and Hennipman, 1985).

4.5.4.3. The mannii subclade. Two accessions from India and Nepal of *Pyrrosia mannii* are included in our study. Although well supported as monophyletic (MLBS: 100%; MPJK: 100%; BIPP: 1.00), there are no synapomorphies for this subclade for the 10 major morphological characters analyzed. *Pyrrosia mannii* has short rhizomes, pseudopelate scales, estipitate fronds, polocytic stomata,

and occasionally laciniate fronds. Hovenkamp (1986) thought that this species is closely related with *P. penangiana*, neither of which was assigned to any groups by Hovenkamp (1986). The polocytic stomata occur only in *Hovenkampia* (= the *P. africana* group), *P. mannii*, and *P. penangiana*. We do not include *P. penangiana* in our study.

4.5.4.4. The Polydactyla subclade. Five accessions representing three species are included in our study. Having no wooly hairs (Fig. 9) and the stellate hairs with boat-shaped rays (Fig. 10) are two synapomorphies of this subclade. Species of the *Polydactyla* subclade have short rhizomes, peltate scales, and monomorphic and pedately lobed fronds (Fig. 1O and P), Hovenkamp (1986) assigned species of the *Polydactyla* subclade to his *P. sheareri* group which is resolved as polyphyletic with our data.

4.6. The monophyly of the infrageneric taxa/groups in previous works

Hovenkamp (1986) recognized 51 species in *Pyrrosia* s.l., and divided 44 species into ten groups: the *P. africana* group, the *P. albicans* group, the *P. angustata* group, the *P. confluens* group, the *P. costata* group, the *P. lanceolata* group, the *P. lingua* group, the *P. piloselloides* group, the *P. porosa* group, and the *P. sheareri* group. Because of ambiguous morphological and anatomical characters, seven [*P. angustissima*, *P. foveolata* (Alston) Morton, *P. gardneri* (Mett.) Sledge, *P. laevis* (J. Sm. ex Bedd.) Ching, *P. mannii* (Giesenh.) Ching, *P. pannosa* (Mett. ex Kuhn) Ching, and *P. penangiana* (Hooker) Holttum] out of the 51 species were not assigned to any groups. Our molecular data resolved eight out of his 10 groups as monophyletic, except the polyphyletic *P. lanceolata* group and *P. sheareri* group. Three, *P. angustissima*, *P. foveolata*, and *P. mannii*, out of the seven species not assigned to any groups by Hovenkamp (1986) are included in our study and are resolved in three independent subclades of three different clades in our study (Fig. 4).

Based on their unique spore morphology (the *Pyrrosia angustata* type), two species (*P. samarensis* and *P. angustata*) were assigned to *P.* subg. *Niphopsis* (J. Smith) Shing in the classifications of Shing (1983) and Shing and Iwatsuki (1997), and the rest of species of *Pyrrosia* were assigned into *P.* subg. *Pyrrosia*. Our study shows that *P.* subg. *Niphopsis* is monophyletic and corresponds to the *P. angustata* group of Hovenkamp (1986) and our *Niphopsis* subclade, while *P.* subg. *Pyrrosia* sensu Shing (1983) and Shing and Iwatsuki (1997) is not monophyletic. In addition, none of the series and sections recognized by Shing (1983) based mainly on indumentum morphology are resolved as monophyletic with our data.

4.7. Evolution of major morphological features in Platycerioideae

4.7.1. Rhizomes

The ancestral state of rhizomes of *Pyrrosia* s.s. is ambiguous. Shortly elongated rhizomes are a morphological synapomorphy of *Hovenkampia*, while short and thick rhizomes are a synapomorphy of *Platycerium*. Long-creeping rhizomes evolved independently three times in *Pyrrosia* s.s. in the *Niphopsis* clade, the *Dichlamys* subclade, and the *Niphobolus* clade. Short and thick rhizomes are a synapomorphy of the *Neoniphopsis* clade and evolved to shortly elongated and long creeping rhizomes in about 10 species in the clade (Fig. 5).

4.7.2. Lateral buds on rhizome

Non-shifted buds are the ancestral state in *Pyrrosia* s.s. but a synapomorphy of the *Neoniphopsis* clade (reversed from shifted buds) and evolved to shifted buds twice in the *Dichlamys* subclade. It is ambiguous if the shifted buds evolved three or four times in *Pyrrosia* s.s. Therefore, the shifted buds can be a synapomorphy

of the *Niphobolus* clade and the *Niphopsis* clade, respectively, or a synapomorphy of the whole genus *Pyrrosia* s.s. excluding the *Pyrrosia* clade (Fig. 6).

4.7.3. Fronds

Monomorphic fronds are the ancestral state of the fronds in *Hovenkampia* (Fig. 1C) and *Pyrrosia* (Fig. 1E). Dimorphic fronds are a synapomorphy of *Platycerium* (Fig. 1A and B). Dimorphic fronds evolved twice in the *Niphopsis* clade. Dimorphic fronds are a synapomorphy of the *Niphobolus* clade, but reversed to monomorphic fronds at least twice in the clade. In a few species of the *Niphobolus* clade, dimorphic fronds evolved again from monomorphic fronds (Fig. 7).

4.7.4. Scales

It is ambiguous if basifixed scales in *Platycerium* and the *Pyrrosia* clade are plesiomorphic. Pseudopeltate scales are a synapomorphy of *Hovenkampia* and the *Drakeanae* subclade of the *Neoniphopsis* clade, respectively. Peltate scales are a synapomorphy of the whole *Pyrrosia* s.s. except the *Pyrrosia* clade (Fig. 8).

4.7.5. Wooly hairs

Having wooly hairs is a synapomorphy of *Pyrrosia* s.s., while having no wooly hairs is a synapomorphy of the clade containing *Hovenkampia* and *Platycerium*. Having no wooly hairs is also a synapomorphy of the *Niphobolus* clade and the *Polydactyla* subclade of the *Neoniphopsis* clade, respectively (Fig. 9).

4.7.6. Rays of stellate hairs

Stellate hairs with boat-shaped rays are pleisiomorphic in Platycerioideae. Stellate hairs with acicular rays evolved once in the sister of the *Pyrrosia* clade. Stellate hairs reversed from those with acicular rays to those with boat-shaped rays in the *Niphobolus* clade, and evolved to those with boat-shaped to acicular rays in some species of this clade. Stellate hairs evolved from those with acicular rays to those to boat-shaped to acicular rays in some species in the *Neoniphopsis* clade (Fig. 10).

4.7.7. Morphology of sori

Orbicular to oblong or elliptic sori are the ancestral state in Platycerioideae. Sori confluent in a coenosorus are a synapomorphy of the *Saxiglossum* subclade (Fig. 1G) of the *Niphopsis* clade, and the *Fallax* subclade (Fig. 2O and P) and the *Drymoglossum* subclade (Fig. 2G) of the *Niphobolus* clade, respectively, and evolved once in the *Niphopsis* subclade of the *Niphopsis* clade (Fig. 11).

4.7.8. Size of sori

Small, several to many sori in each areole are the ancestral state in Platycerioideae. Very small sori closely packed and pseudo-acrostichoid when ripe are a synapomorphy of *Platycerium* and evolved once in the *Galeoglossa* subclade and independently evolved twice in the *Heteractides* subclade of *Pyrrosia* s.s. Large sori exceeding areole are a synapomorphy of the *Saxiglossum* subclade (Fig. 1G), the *Fallax* subclade and the *Drymoglossum* subclade of the *Niphobolus* clade, respectively. The relatively large sori in 2(–3) per areole are a synapomorphy of the *Serpens* subclade (Fig. 2L) of the *Niphobolus* clade (Fig. 12).

4.7.9. Placement of hydathodes

Hydathodes inconstantly scattered over lamina are a synapomorphy of the *Niphobolus* subclade of the *Niphobolus* clade. Hydathodes constantly scattered over lamina are a synapomorphy of the *Neoniphopsis* clade and evolved to those inconstantly scattered over lamina in *Pyrrosia madagascariensis*. Having no hydathodes is a synapomorphy of the *Niphopsis* clade and reversed to those constantly scattered over lamina once in the *Heteractides*

subclade. Having no hydathodes might also be a synapomorphy of the *Niphobolus* clade, but this state in this clade independently evolved once each to those in a row on the lower surface of lamina (the *P. serpens* subclade) and those in a marginal row on the upper surface of lamina (the *P. serpens* subclade), respectively, and twice to those inconstantly scattered over lamina (the *P. foveolata* subclade and the *P. Niphobolus* subclade) (Fig. 13).

4.7.10. Spore morphology

Based on van Uffelen and Hennipman (1985), we recognize two more spore types in addition to the five recognized by the original authors: the *Pyrrosia angustata* type (spores with the longitudinal ridges on perispore surfaces; subdivided from the *Pyrrosia nummulariifolia* type) and the *P. angustissima* type (spores with the less obvious verrucae and no spherical bodies on perispore surfaces; subdivided from the *Pyrrosia christii* type). The *P. angustata* type is a synapomorphy of the *Niphopsis* subclade, while the *P. angustissima* type is a synapomorphy of the *Saxiglossum* subclade. The *P. rupestris* type is a synapomorphy of the *Niphobolus* clade, while the *P. subfurfuracea* type is a synapomorphy of the *Neoniphopsis* clade. However, it is ambiguous how the *P. christii* type and the *P. nummulariifolia* type evolved in the *Niphopsis* clade (Fig. 14).

The thin perispores containing spherical bodies in the *Pyrrosia princeps* type (in *Hovenkampia* and the *Pyrrosia* clade) are similar to those in *Platycerium*, suggesting that thin perispores on exospore might be plesiomorphic in Platycerioideae, while thick perispores are a synapomorphy of *Pyrrosia* s.s.

4.8. Hybridization and polyploidization in Pyrrosia s.s

A large number of potential hybridization and polyploidization have been proposed based chromosome numbers (e.g., Manton and Sledge, 1954; Abraham et al., 1962; Patnaik and Panigrahi, 1963; Hovenkamp, 1986), morphology (e.g., Serizawa, 1970; Beppu and Serizawa, 1982), and most recently molecular data (Choi and Park, 2016) in *Pyrrosia*. Notably, previous studies suggest that hybridization and polyploidization are mainly found in the *Neoniphopsis* clade.

In addition, it has been shown that members of the *Niphobolus* subclade of the *Niphobolus* clade are highly varied in chromosome numbers, e.g., 2n = ∼ 74 (*P. lanceolata*; Hovenkamp, 1986), 2n = ∼ 144 [*P. nuda*; Patnaik and Panigrahi, 1963), and 2n = 216 [*P. adnascens*; Abraham et al., 1962). Potentially, species of this subclade might have experienced polyploidization many times in their evolutionary history.

In our study, two accessions of *P. matsudae* from Taiwan, Knapp 3796 and Knapp 3793, are resolved in the *Dichlamys* subclade and the *Polydactyla* subclade, respectively. Two vouchers show no significant morphological variation from each other according to one of us (R. Knapp) who suspects *P. matsudae* to be a hybrid between *P. polydactyla* and *P. porosa*, and it is partially confirmed by nuclear data (Choi and Park, 2016). Our phylogeny discovered additional polyphyletic taxa (although not well supported), which can point to potential hybridization. We need to better resolve the relationships among species using more data, especially nuclear data, in order to well understand the role of hybridization in the evolution of this genus.

4.9. Hovenkampia gen. nov. segregated from Pyrrosia

Based on molecular (our study) and non-molecular (Hennipman and Roos, 1982; van Uffelen and Hennipman, 1985; Hovenkamp, 1986; Tryon and Lugardon, 1991, etc.) characters, a new genus, *Hovenkampia*, is established to accommodate the *Pyrrosia africana* group of Hovenkamp (1986), and it is sister to *Platycerium* (MLBS: 100%; MPJK: 99%; BIPP: 1.00).

Hovenkampia Li Bing Zhang & X. M. Zhou, **gen. nov.** – Type: *Hovenkampia schimperiana* (Mett. ex Kuhn) Li Bing Zhang & X. M. Zhou ≡ *Polypodium schimperianum* Mett. ex Kuhn, Fil. Afr., 152. 1868 ≡ *Niphobolus schimperianus* Giesenh. ex Diels in E. & P., Nat. Pfl. Fam. 1(4): 325. 1899 ≡ *Cyclophorus schimperianus* C. Chr., Ind. Fil. 200. 1906.

Diagnosis: *Hovenkampia* is most similar to *Pyrrosia s.s.*, but the former has completely parenchymatous rhizome, secondary veins hardly distinct from the other veins, polocytic stomata, and relatively small sporangia.

Etymology: In honor of Prof. Peter Hovenkamp, a specialist of *Pyrrosia*, based at the Naturalis Biodiversity Center, Leiden, Netherlands.

Rhizome shortly elongated, lateral buds situated on or close to the phyllopodia. Ground tissue parenchymatous, sclerenchyma sheath and sclerenchyma strands absent (Hovenkamp, 1986). Scales pseudopeltate. Fronds monomorphic, sessile; widest at or above the middle, base gradually narrowed, apex acute to narrowly acuminate. Lateral veins hardly distinct, with the tertiary veins forming irregular areoles; included veins copiously branched and anastomosing. Lamina thick, upper epidermis with distinctly projecting cells with thin walls, hypodermis and water-tissue absent, palisade and spongy parenchyma distinct, lower epidermis with thin cell-walls; stomata polocytic, slightly sunken. Indumenta monomorphic, with appressed, boat-shaped or auricular rays. Sori apical or all over the laminae, closely packed, superficial; several scattered throughout each soriferous areole, occasionally confluent along the veins; developing from the apex downwards. Sporangia small, with 13–15 indurated annulus cells. Paraphyses not differentiated. Spores with thin perispores, covered with less obvious verrucae.

The description largely follows Hovenkamp (1986). The genus contains three African species, *Hovenkampia africana*, *H. liebuschii*, and *H. schimperiana*.

Hovenkampia africana (Kunze) Li Bing Zhang & X. M. Zhou, **comb. nov.** Basionym: ≡ *Niphobolus africanus* Kunze, Linnaea 10: 501. 1836 ≡ *Gyrosorium africanum* (Kunze) C. Presl, Epimel. Bot. 140. 1851 ≡ *Polypodium africanum* (Kunze) Mett., Mus. Senckenberg. 2(1): 131, pl. 3, Figs. 11, 12. 1856. non Desv. (1827: 239) ≡ *Cyclophorus africanus* (Kunze) C.Chr., Ind. Fil. 197. 1905. ≡ *Pyrrosia africana* (Kunze) F. Ballard, Bull. Misc. Inform. Kew 6: 349. 1937.

Niphobolus africanus Kunze f. (β) minor Kunze, Linnaea 10: 501. 1836.

This species is endemic to South Africa (Hovenkamp, 1986; Roux, 2009).

Hovenkampia liebuschii (Hieron.) Li Bing Zhang & X. M. Zhou, **comb. nov.** Basionym: *Cyclophorus liebuschii* Hieron., Bot. Jahrb. Syst. 46(3): 398. 1911 ≡ *Niphobolus liebuschii* (Hieron.) Peter, Feddes Repert., Beih. 40(1): 32. 1929 ≡ *Pyrrosia liebuschii* (Hieron.) Schelpe, J. S. African Bot. 18: 131. f.1(1). 1952 ≡ *Pyrrosia schimperiana* (Mett. ex Kuhn) Alston var. *liebuschii* (Hieron.) Hovenkamp, Blumea 30(1): 208. 1984.

This species is endemic to Tanzania (Hovenkamp, 1986; Roux, 2009).

Hovenkampia schimperiana (Mett. ex Kuhn) Li Bing Zhang & X. M. Zhou (Fig. 1C and D), **comb. nov.** Basionym: *Polypodium schimperianum* Mett. ex Kuhn, Fil. Afr., 152. 1868 ≡ *Niphobolus schimperianus* Giesenh. ex Diels in E. & P., Nat. Pfl. Fam. 1(4): 325. 1899 ≡ *Cyclophorus schimperianus* C. Chr., Ind. Fil. 200. 1906.

Cyclophorus mechowii Brause & Hieron., Bot. Jahrb. Syst. 46(3): 395, 396. 1911; *Pyrrosia schimperiana* var. *mechowii* (Brause &

Hieron.) Schelpe. J. S. African Bot. 18(3): 129, Fig. 1, t. 2, 3. 1928; *P. mechowii* (Brause & Hieron.) Alston, Estudos Ensaios Doc. Junta Invest. Ci. Ultramar. 12: 37. 1954.

This species is distributed across Africa (Hovenkamp, 1986; Roux, 2009).

Appendix A

List of taxa sampled with information related to taxonomy, GenBank accession numbers, references, and voucher information. Herbarium code follow *Index Herbariorum* (Thiers, 2015).

Arthromeris wallichiana (Spreng.) Ching, Kirkpatrick 90/283 (E), Cult. (RBGE): rbcL EU128500 (Schneider et al., 2008), rps4-trnS EU128507 (Schneider et al., 2008).

Colysis hemionitidea C.Presl, Moran s.n. (NY), Unknown: rbcL EU482950 (Kreier et al., 2008), rps4-trnS EU483000 (Kreier et al., 2008).

Cyclophorus taiwanensis (Christ) C.Chr. (*Pyrrosia lingua*) Knapp 3782 (P), Taiwan Island: rbcL KY931028, rps4-trnS KY931179, trnL intron & trnL-F spacer KY931331.

Dictymia brownii Copel., Werner 21 (UC), Cult. (UCBG: Australia): rbcL DQ227292 (Kreier and Schneider, 2006b), rps4-trnS DQ227295 (Kreier and Schneider, 2006b).

Drynaria rigidula (Sw.) Bedd., Janssen 2251 (GOET), Cult. Berlin: rbcL AY529166 (Janssen and Schneider, unpubl. data), rps4-trnS AY529188 (Janssen and Schneider, unpubl. data).

Hovenkampia liebuschii (Hieron.) Li Bing Zhang & X. M. Zhou, Janssen et al. 2624 (P), Tanzania: trnL intron & trnL-F spacer DQ642253 (Janssen et al., 2007). **Hovenkampia schimperiana** (Mett. ex Kuhn) Li Bing Zhang & X. M. Zhou, Kamau 59 (MO), Kakamega, Kenya: rbcL KY931029, rps4-trnS KY931029, trnL intron & trnL-F spacer KY931332.

Lellingeria apiculata (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran, Salino 3009 (UC), Brazil: rbcL AY362343 (Ranker et al., 2004), rps4-trnS AY362690 (Schneider et al., 2004).

Loxogramme salicifolia (Makino) Makino, Coll. Nr. 728/11 (E), Cult. (RBG: China): rbcL DQ227294 (Kreier and Schneider, 2006 b), rps4-trnS DQ227297 (Kreier and Schneider, 2006b).

Microgramma bifrons (Hook.) Lellinger, Neill et al. 8309 (UC), Ecuador: rbcL AY362582 (Schneider et al., 2004), rps4-trnS AY362654 (Schneider et al., 2004).

Platycerium alcicorne Desv., Kreier CG0401 (GOET), Cult. (BGG): rbcL DQ164445 (Kreier and Schneider, 2006a), rps4-trnS DQ164476 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164509 (Kreier and Schneider, 2006a). **Platycerium**
bifurcatum (Cav.) C.Chr., Ornduff 9618 (UC), Cult. (UCBG: Australia): rbcL AF470341 (Haufler et al., 2003), trnL intron & trnL-F spacer AY083644 (Haufler et al., 2003). **Platycerium coronarium** (O.F. Müll.) Desv., Wu 2597 (KUN), Laos: rbcL JX103711 (Kim et al., 2013), rps4-trnS JX103753 (Kim et al., 2013), trnL intron & trnL-F spacer JX103795 (Kim et al., 2013). **Platycerium elephantotis** Schweinf., Kreier GG0405 (GOET), Cult. (BGG): rbcL DQ164449 (Kreier and Schneider, 2006a), rps4-trnS DQ164480 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164513 (Kreier and Schneider, 2006a). **Platycerium ellisii** Baker, Kreier GG0406 (GOET), Cult. (BGG): rbcL DQ164450 (Kreier and Schneider, 2006a), rps4-trnS DQ164481 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164514 (Kreier and Schneider, 2006a). **Platycerium grande** J.Sm., Alfrod s.n. (GOET), Cult. (CAN): rbcL DQ164451 (Kreier and Schneider, 2006a), rps4-trnS DQ164482 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164515 (Kreier and Schneider, 2006a). **Platycerium hillii** T. Moore, Kreier CG0407 (GOET), Cult. (BGG): rbcL DQ164452 (Kreier and Schneider, 2006a), rps4-trnS DQ164483 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164516 (Kreier and Schneider, 2006a). **Platycerium holttumii** de Jonch. & Hennipman, Alford s.n. (GOET), Cult. (CAN): rbcL DQ164453 (Kreier and Schneider, 2006a), rps4-trnS DQ164484 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164517 (Kreier and Schneider, 2006a). **Platycerium madagascariense** Baker, Kreier CG0408 (GOET), Cult.: rbcL DQ164454 (Kreier and Schneider, 2006a), rps4-trnS DQ164485 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164518 (Kreier and Schneider, 2006a). **Platycerium quadridichotomum** (Bonap.) Tardieu, Alfrod s.n. (GOET)., Cult. (CAN): rbcL DQ164455 (Kreier and Schneider, 2006a), rps4-trnS DQ164486 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164519 (Kreier and Schneider, 2006a). **Platycerium stemaria** (P. Beauv.) Desv., Kreier s.n. (GOET), Cult.: rbcL EF463257 (Schuettpelz and Pryer, 2007). **Platycerium superbum** de Jonch. & Hennipman, Kreier CG0412 (GOET), Cult. (BGG): rbcL DQ164459 (Kreier and Schneider, 2006a), rps4-trnS DQ164490 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164523 (Kreier and Schneider, 2006a). **Platycerium wallichii** Hook., Alfrod s.n. (GOET), Cult. (CAN): rbcL DQ164461 (Kreier and Schneider, 2006a), rps4-trnS DQ164492 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164525 (Kreier and Schneider, 2006a). **Platycerium wandae** Racif., s. c. 19842659 (E), Cult. (RBGE): rbcL DQ164462 (Kreier and Schneider, 2006a), rps4-trnS DQ164493 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164526 (Kreier and Schneider, 2006a).

Pleopeltis conzattii (Weath.) R.M. Tryon & A.F. Tryon, Tejero Diez 4937 (GOET), Mexico: rbcL EU650103 (Otto et al., 2009), rps4-trnS EU650142 (Otto et al., 2009).

Polypodiodes chinensis (Christ) S.G. Lu, Lu X14 (NPA), Yunnan, China: rbcL DQ078630 (Lu and Li, 2006), rps4-trnS DQ078637 (Lu and Li, 2006).

Polypodium arcanum Maxon, Lautner 98–83 (BGUG), Mexico: rbcL AY362586 (Schneider et al., 2004), rps4-trnS AY362659 (Schneider et al., 2004).

Pyrrosia adnascens (Sw.) Ching, [1] Lu I38 (NPA), Yunnan, China: rbcL KY931031, rps4-trnS KY931181; [2] Lu V2 (NPA), Hainan, China: rbcL KY931032, rps4-trnS KY931182; [3] TNS:764058 (TNS), Taiwan Island: rbcL AB575294 (Ebihara et al., 2010); [4] Zhang et al. 6319 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rps4-trnS KY931183, trnL intron & trnL-F spacer KY931333; [5] Zhang et al. 6342 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931033, rps4-trnS KY931184, trnL intron & trnL-F spacer KY931334; [6] Zhang et al. 6683 (CDBI, MO, VNMN), Bac Kan, Vietnam: rbcL KY931034, rps4-trnS KY931185, trnL intron & trnL-F spacer KY931335; [7] Zhang et al. 6930 (CDBI, MO, VNMN), Ha Giang, Vietnam: rbcL KY931035, rps4-trnS KY931186, trnL intron

& trnL-F spacer KY931336; [8] Zhang et al. 7064 (CDBI, MO, VNMN), Thanh Hoa, Vietnam: rbcL KY931036, rps4-trnS KY931187, trnL intron & trnL-F spacer KY931337; [9] Zhang et al. 7272 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931037, rps4-trnS KY931188, trnL intron & trnL-F spacer KY931338; [10] Zhang et al. 7378 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931038, rps4-trnS KY931189, trnL intron & trnL-F spacer KY931339; [11] Knapp 3770 (P), Taiwan Island: rbcL KY931030. **Pyrrosia albicans** Ching, Chen Wade 1825 (TAIF), Cibodas Botanical Garden, Indonesia: rbcL KY931040, rps4-trnS KY931191, trnL intron & trnL-F spacer KY931341. **Pyrrosia angustata** (Sw.) Ching, Hovenkamp s. n. (L), Cult. (BGL): rbcL DQ642165 (Janssen et al., 2007), rps4-trnS DQ642204 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642250 (Janssen et al., 2007). **Pyrrosia angustissima** (Giesenh. ex Diels) Tagawa & K. Iwats;, [1] Chen Wade 2474 (TAIF), Guangxi, China: rbcL KY931041, rps4-trnS KY931192, trnL intron & trnL-F spacer KY931342; [2] Lu Z26 (NPA), Hubei, China: rbcL KY931043, rps4-trnS KY931194; [3] Zhang1038 (CDBI), Hubei, China: rbcL KY931044, rps4-trnS KY931195, trnL intron & trnL-F spacer KY931343; [4] Knapp 3763 (P), Taiwan Island: rbcL KY931042, rps4-trnS KY931193. **Pyrrosia annamensis** (Christ) Li Bing Zhang, X.M.Zhou & C.W.Chen, [1] Chen Wade 2571 (TAIF), Lam Dong, Vietnam: rbcL KY931045, rps4-trnS KY931196, trnL intron & trnL-F spacer KY931344; [2] Wu 2310 (KUN), Laos: rbcL JX103712 (Kim et al., 2013), rps4-trnS JX103754 (Kim et al., 2013), trnL intron & trnL-F spacer JX103796 (Kim et al., 2013); [3] Zhang et al. 6328 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcLKY931046, rps4-trnS KY931197, trnL intron & trnL-F spacer KY931345; [4] Zhang et al. 7395 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931048, rps4-trnS KY931199, trnL intron & trnL-F spacer KY931347; [5] Zhang et al. 7032 (CDBI, MO, VNMN), Thanh Hoa, Vietnam: rbcL KY931047, rps4-trnS KY931198, trnL intron & trnL-F spacer KY931346. **Pyrrosia assimilis** (Baker) Ching, [1] Chen Wade 2475 (TAIF), Guangxi, China: rbcL KY931049, rps4-trnS KY931200, trnL intron & trnL-F spacer KY931348; [2] Sino-Amer.Bot.Exped. 1980 (E), Cult. (RBGE): rbcL DQ164464 (Kreier and Schneider, 2006a), rps4-trnS DQ164495 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164528 (Kreier and Schneider, 2006a). **Pyrrosia calvata** (Baker) Ching, [1] Lu QC15 (NPA), Sichuan, China: rbcL KY931050, rps4-trnS KY931201; [2] Zhang et al. 6372 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931051, rps4-trnS KY931202, trnL intron & trnL-F spacer KY931349. **Pyrrosia christii** (Giesenh.) Ching, [1] Chen Wade 4223 (TAIF), Sabah, Malaysia: rbcL KY931058, rps4-trnS KY931210, trnL intron & trnL-F spacer KY931355; [2] Schneider s.n. (GOET), Cult. (BGG): rbcL DQ164465 (Kreier and Schneider, 2006a), rps4-trnS DQ164496 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164529 (Kreier and Schneider, 2006a). **Pyrrosia costata** (Wall. ex C.Presl) Tagawa & K. Iwats., [1] Xia et al.1071 (CDBI), Kachin, Myanmar: rbcL KY931059, rps4-trnS KY931211, trnL intron & trnL-F spacer KY931356; [2] Lu H27 (NPA), Yunnan, China: rbcL KY931061, rps4-trnS KY931213; [3] Lu SG6 (NPA), Yunnan, China: rbcL KY931062, rps4-trnS KY931214; [4] Cicuzza1917 (CDBI; HITBC), Yunnan, China: rbcL KY931060, rps4-trnS KY931212, trnL intron & trnL-F spacer KY931357. **Pyrrosia davidii** (Giesenh. ex Diels) Ching, [1] Lu C44 (NPA), Yunnan, China: rbcL KY931063, rps4-trnS KY931215; [2] Lu YL3 (NPA), Yunnan, China: rbcL KY931064, rps4-trnS KY931216; [3] Lu YP82 (NPA), Yunnan, China: rbcL KY931065, rps4-trnS KY931217; [4] Lu ZD9 (NPA), Yunnan, China: rbcL KY931066; [5] Zhang 1086 (CDBI), Hubei, China: rbcL KY931067, rps4-trnS KY931218, trnL intron & trnL-F spacer KY931358. **Pyrrosia drakeana** (Franch.) Ching, [1] Gao et al.12242 (CDBI), Xizang, China: rbcL KY931069, rps4-trnS KY931220, trnL intron & trnL-F spacer KY931360; [2] Gao et al.12417 (CDBI), Xizang, China: rbcL KY931070, rps4-trnS KY931221, trnL intron & trnL-F spacer

KY931361; [3] Lu YL4 (NPA), Yunnan, China: rbcL KY931072, rps4-trnS KY931223; [4] Lu Z25 (NPA), Hubei, China: rbcL KY931073, rps4-trnS KY931224; [5] Lu B8 (NPA), Yunnan, China: rbcL KY931071, rps4-trnS KY931222; [6] Chen et al., FTZT299 (CDBI), Sichuan, China: rbcL KY931068, rps4-trnS KY931219, trnL intron & trnL-F spacer KY931359. **Pyrrosia eberhardtii** (Christ) Ching, [1] Chen Wade 2634 (TAIF), Lam Dong, Vietnam: rbcL KY931074, rps4-trnS KY931225, trnL intron & trnL-F spacer KY931362; [2] Zhang et al. 7639 (CDBI, MO, VNMN), Quang Tri, Vietnam: rbcL KY931077, rps4-trnS KY931228, trnL intron & trnL-F spacer KY931364; [3] Zhang et al. 8597 (CDBI, MO, PHH), Lam Dong, Vietnam: rbcL KY931078, rps4-trnS KY931229, trnL intron & trnL-F spacer KY931365; [4] Zhang et al. 8644 (CDBI, MO, PHH), Lam Dong, Vietnam: rbcL KY931079, rps4-trnS KY931230, trnL intron & trnL-F spacer KY931366; [5] Zhang et al. 8892 (CDBI, MO, PHH), Dak Lak, Vietnam: rbcL KY931080, rps4-trnS KY931231, trnL intron & trnL-F spacer KY931367; [6] Chen Wade 4118 (TAIF), Lam Dong, Vietnam: rbcL KY931075, rps4-trnS KY931226, trnL intron & trnL-F spacer KY931363; [7] Lu D13 (NPA), Yunnan,China: rbcL KY931076, rps4-trnS KY931227. **Pyrrosia eleagnifolia** (Bory) Hovenkamp, Schneider s.n. (E), Cult. (RBGE): rbcL DQ642166 (Janssen et al., 2007), rps4-trnS DQ642205 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642251 (Janssen et al., 2007). **Pyrrosia fallax** (Alderw.) M.G. Price, Chen et al., SITW10494 (TNM), San Jorge island, Solomon Islands: rbcL KY931081, rps4-trnS KY931232, trnL intron & trnL-F spacer KY931368. **Pyrrosia flocculosa** (D. Don) Ching, Fraser-Jenkins FN27 (TAIF), Kaski, Nepal: rbcL KY931083, rps4-trnS KY931234, trnL intron & trnL-F spacer KY931370. **Pyrrosia foveolata** (Alston) C.V. Morton, Schneider s.n. (E), Cult. (RBGE): rbcL DQ642167 (Janssen et al., 2007), rps4-trnS DQ642206 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642252 (Janssen et al., 2007). **Pyrrosia hastata** (Houtt.) Ching, TNS:763873 (TNS), Shizuoka, Japan: rbcL AB575296 (Ebihara et al., 2010). **Pyrrosia heteractis** (Mett. ex Kuhn) Ching, [1] Ayeyarwady Exped. 2185 (CDBI), Kachin, Myanmar: rps4-trnS KY931235, trnL intron & trnL-F spacer KY931371; [2] Xu and Zhou YLZB1926 (CDBI), Xizang, China: rbcL KY931084, rps4-trnS KY931236, trnL intron & trnL-F spacer KY931372. **Pyrrosia cf. heteractis** [1] Jin 11218 (CDBI), Yunnan, China: rbcL KY931052, rps4-trnS KY931203, trnL intron & trnL-F spacer KY931350; [2] Jin 11329 (CDBI), Yunnan, China: rps4-trnS KY931204. **Pyrrosia kinabaluensis** Hovenkamp, Chen Wade 4306 (TAIF), Sabah, Malaysia: rbcL KY931085, rps4-trnS KY931237, trnL intron & trnL-F spacer KY931373. **Pyrrosia lanceolata** (L.) Farw., [1] Cranfill BF10 (UC), Malay Penninsula: rbcL DQ164467 (Kreier and Schneider, 2006a), rps4-trnS DQ164498 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacerDQ164531 (Kreier and Schneider, 2006a); [2] Zhang et al. 9071 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931086, rps4-trnS KY931238, trnL intron & trnL-F spacer KY931374; [3] Zhang et al. 9104 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931087, rps4-trnS KY931239, trnL intron & trnL-F spacer KY931375; [4] Zhang et al. 9118 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcLKY931088, rps4-trnS KY931240, trnL intron & trnL-F spacer KY931376; [5] Zhang et al. 9122 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931089, rps4-trnS KY931241, trnL intron & trnL-F spacer KY931377. **Pyrrosia cf. lanceolata,** [1] Jaman 5836 (UC), Malaysia: rps4-trnS AY362622 (Schneider et al., 2004). [2] Zhang et al. 8834 (CDBI, MO, PHH), Dak Lak, Vietnam: rbcL KY931039, rps4-trnS KY931190, trnL intron & trnL-F spacer KY931340. **Pyrrosia linearifolia** (Hook.) Ching, [1] Cranfill TW101 (UC), Taiwan Island: rbcL DQ164468 (Kreier and Schneider, 2006a), rps4-trnS DQ164499 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164532 (Kreier and Schneider, 2006a); [2] TNS:763877 (TNS), Ehime, Japan: rbcL AB575297 (Ebihara et al., 2010); [3] Knapp 3762 (P), Taiwan

Island: rbcL KY931090, rps4-trnS KY931242, trnL intron & trnL-F spacer KY931378. **Pyrrosia linearifolia**var. **heterolepis** Tagawa, TNS:736789 (TNS), Okinawa, Japan: rbcL AB575298 (Ebihara et al., 2010). **Pyrrosia lingua** (Thunb.) Farw; [1] Cicuzza 2072 (CDBI; HITBC), Yunnan, China: rbcL KY931093, rps4-trnS KY931245; [2] Cicuzza 2053 (CDBI; HITBC), Yunnan, China: rbcL KY931092, rps4-trnS KY931244; [3] Cicuzza 2019 (HITBC), Yunnan, China: rbcL KY931091, rps4-trnS KY931243, trnL intron & trnL-F spacer KY931379; [4] TNS:763117 (TNS), Kagoshima, Japan: rbcL AB575299 (Ebihara et al., 2010); [5] Zhang et al. 6415 (CDBI, MO, VNMN), Vinh Phuc, Vietnam: rbcL KY931094, rps4-trnS KY931246, trnL intron & trnL-F spacer KY931380; [6] Zhang et al. 6469 (CDBI, MO, VNMN), Vinh Phuc, Vietnam: rbcL KY931095, rps4-trnS KY931247, trnL intron & trnL-F spacer KY931381; [7] Zhang et al. 6890 (CDBI, MO, VNMN), Ha Giang, Vietnam: rbcL KY931096, rps4-trnS KY931248, trnL intron & trnL-F spacer KY931382. **Pyrrosia cf. Lingua** [1] Chen et al., FTZT129 (CDBI), Sichuan, China: rbcL KY931054, rps4-trnS KY931206, trnL intron & trnL-F spacer KY931351; [2] Ayeyarwady Exped., 1168 (CDBI), Kachin, Myanmar: rbcL KY931053, rps4-trnS KY931205; [3] Zhang et al. 7132 (CDBI, MO, VNMN), Thanh Hoa, Vietnam: rbcL KY931056, rps4-trnS KY931208, trnL intron & trnL-F spacer KY931353; [4] Zhang et al. 6806 (CDBI, MO, VNMN), Cao Bang, Vietnam: rbcL KY931055, rps4-trnS KY931207, trnL intron & trnL-F spacer KY931352. **Pyrrosia longifolia** (Burm. f.) C.V. Morton, [1] Chen et al., SITW11026 (TNM), Vanikoro island, Solomon Islands: rbcL KY931097, rps4-trnS KY931249, trnL intron & trnL-F spacer KY931383; [2] Schneider s.n. (GOET), Cult. (BGG): rbcL DQ164469 (Kreier and Schneider, 2006a), rps4-trnS DQ164501 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164533 (Kreier and Schneider, 2006a); [3] Zhang et al. 9077 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931101; [4] Zhang et al. 7949 (CDBI, MO, VNMN), Quang Nam, Vietnam: rbcL KY931098, rps4-trnS KY931250, trnL intron & trnL-F spacer KY931384; [5] Zhang et al. 7977 (CDBI, MO, VNMN), Quang Nam, Vietnam: rbcL KY931099, rps4-trnS KY931251, trnL intron & trnL-F spacer KY931385; [6] Zhang et al. 9032 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931100, rps4-trnS KY931252, trnL intron & trnL-F spacer KY931386; [7] Zhang et al. 9086 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931102, rps4-trnS KY931253, trnL intron & trnL-F spacer KY931387; [8] Zhang et al. 9088 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcL KY931103, rps4-trnS KY931254, trnL intron & trnL-F spacer KY931388. **Pyrrosia madagascariensis** (C.Chr.) Schelpe, Ravelonarivo 3000 (MO), Madagascar: rbcL KY931104, rps4-trnS KY931255, trnL intron & trnL-F spacer KY931389. **Pyrrosia mannii** (Giesenh.) Ching, [1] Fraser-Jenkins FN10 (TAIF), Bheri Zone, Nepal: rbcL KY931105, rps4-trnS KY931256, trnL intron & trnL-F spacer KY931390; [2] Fraser-Jenkins FN118 (TAIF), Sikkim, India: rbcL KY931106, rps4-trnS KY931257, trnL intron & trnL-F spacer KY931391. **Pyrrosia cf. mannii**, Wu 2571 (KUN), Laos: rbcL JX103715 (Kim et al., 2013), rps4-trnS JX103757 (Kim et al., 2013), trnL intron & trnL-F spacer JX103799 (Kim et al., 2013). **Pyrrosia matsudae** (Hayata) Tagawa, [1] Knapp 3793 (P), Taiwan Island: rps4-trnS KY931258; [2] Knapp 3796 (P), Taiwan Island: rbcL KY931107, rps4-trnS KY931259. **Pyrrosia cf. niphoboloides**, Schneider s.n. (E), Cult. (RBGE): rbcL DQ642168 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642254 (Janssen et al., 2007). **Pyrrosia nuda** (Giesenh.) Ching, [1] Deng 3217 (CDBI), Kachin, Myanmar: rbcL KY931110, rps4-trnS KY931262, trnL intron & trnL-F spacer KY931394; [2] Xu and Zhou YLZB2141 (CDBI), Xizang, China: rbcL KY931115, rps4-trnS KY931266, trnL intron & trnL-F spacer KY931397; [3] Fraser-Jenkins FN111 (TAIF), Sikkim, India: rbcL KY931111, rps4-trnS KY931263, trnL intron & trnL-F spacer KY931395; [4] Fraser-Jenkins FN28 (TAIF), Kaski, Nepal: rbcL KY931112, trnL intron & trnL-F spacer KY931396; [5] Lu H26 (NPA), Yunnan, China: rbcL KY931113, rps4-trnS KY931264; [6] Lu SG5 (NPA), Yunnan, China: rbcL KY931114, rps4-trnS KY931265; [7] Cicuzza1638 (HITBC), Yunnan, China: rbcL KY931108, rps4-trnS KY931260, trnL intron & trnL-F spacer KY931392; [8] Cicuzza 2062 (CDBI; HITBC), Yunnan, China: rbcL KY931109, rps4-trnS KY931261, trnL intron & trnL-F spacer KY931393; [9] Lu C26 (NPA), Yunnan, China: rbcL DQ078623 (Lu and Li, 2006), rps4-trnS DQ078634 (Lu and Li, 2006); [10] Zhang et al. 6295 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931116, rps4-trnS KY931267, trnL intron & trnL-F spacer KY931398. **Pyrrosia nummulariifolia** (Sw.) Ching, [1] Lu H28 (NPA), Yunnan, China: rbcL KY931118, rps4-trnS KY931270; [2] Cicuzza2014 (HITBC), Yunnan, China: rbcL KY931117, rps4-trnS KY931269; [3] Ayeyarwady Exped. 2681 (CDBI), Kachin, Myanmar: rps4-trnS KY931268, trnL intron & trnL-F spacer KY931399; [4] Wu 2570 (KUN), Laos: rbcL JX103713 (Kim et al., 2013), rps4-trnS JX103755 (Kim et al., 2013), trnL intron & trnL-F spacer JX103797 (Kim et al., 2013); [5] Wu 2574 (KUN), Laos: rbcL JX103714 (Kim et al., 2013), rps4-trnS JX103756 (Kim et al., 2013), trnL intron & trnL-F spacer JX103798 (Kim et al., 2013). **Pyrrosia oblonga** Ching [1] Zhang 1642 (CDBI), Hainan, China: rbcL KY931119, rps4-trnS KY931271, trnL intron & trnL-F spacer KY931400; [2] Zhang et al. 7275 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931121, rps4-trnS KY931273, trnL intron & trnL-F spacer KY931402; [3] Zhang et al. 7244 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931120, rps4-trnS KY931272, trnL intron & trnL-F spacer KY931401; [4] Zhang et al. 7277 (CDBI, MO, VNMN), Quang Binh, Vietnam: rps4-trnS KY931274; [5] Zhang et al. 7388 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931122, rps4-trnS KY931275, trnL intron & trnL-F spacer KY931403; [6] Zhang et al. 7390 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931123, rps4-trnS KY931276, trnL intron & trnL-F spacer KY931404; [7] Zhang et al. 7450 (CDBI, MO, VNMN), Quang Binh, Vietnam: rbcL KY931124, rps4-trnS KY931277, trnL intron & trnL-F spacer KY931405; **Pyrrosia petiolosa** (Christ) Ching, [1] Lu GY21 (NPA), Guizhou, China: rbcL KY931125, rps4-trnS KY931278; [2] Zhang 1031 (CDBI), Hubei, China: rbcL KY931126, rps4-trnS KY931279, trnL intron & trnL-F spacer KY931406. **Pyrrosia piloselloides** (L.) M.G. Price, [1] Chen Wade 1346 (TAIF), Bu Gia Map National Park, Vietnam: rbcL KY931127, rps4-trnS KY931280, trnL intron & trnL-F spacer KY931407; [2] Chen Wade 1409 (TAIF), Dong Nai,Vietnam: rbcL KY931128, rps4-trnS KY931281, trnL intron & trnL-F spacer KY931408; [3] Lu T4 (NPA), Yunnan, China: rbcL KY931129, rps4-trnS KY931282; [4] Cranfill BF-7 (UC), Malay Peninsula: rps4-trnS AY096223 (Schneider et al., 2002); [5] Zhang et al. 7667 (CDBI, MO, VNMN), Thua Thien-Hue, Vietnam: rbcL KY931130, rps4-trnS KY931283, trnL intron & trnL-F spacer KY931409; [6] Zhang et al. 8276 (CDBI, MO, PHH), Dong Nai, Vietnam: rbcL KY931131, rps4-trnS KY931284; [7] Zhang et al. 9121 (CDBI, MO, PHH), Kien Giang, Vietnam: rbcLKY931132, rps4-trnS KY931285. **Pyrrosia polydactyla** (Hance) Ching, [1] Ranker 2080 (COLO), Taiwan: rbcL EF463259 (Schuettpelz and Pryer, 2007); [2] Schneider s.n. (GOET), Cult. (BGG): rbcL DQ164470 (Kreier and Schneider, 2006a), rps4-trnS DQ164502 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164534 (Kreier and Schneider, 2006a); [3] Knapp 3801 (P), Taiwan Island: rbcL KY931133, rps4-trnS KY931286, trnL intron & trnL-F spacer KY931410. **Pyrrosia porosa** (C.Presl) Hovenkamp, [1] Gao et al.12643 (CDBI), Sichuan, China: rbcL KY931137, rps4-trnS KY931290, trnL intron & trnL-F spacer KY931414; [2] Fraser-Jenkins FN97 (TAIF), Tamil Nadu, India: rbcL KY931136, rps4-trnS KY931289, trnL intron & trnL-F spacer KY931413; [3] Cicuzza 2079 (CDBI; HITBC), Yunnan, China: rbcLKY931135, rps4-trnS KY931288, trnL intron & trnL-F spacer KY931412; [4] Cranfill TW094 (UC), Taiwan Island: rbcL DQ164466 (Kreier and Schneider, 2006a), rps4-trnS DQ164497 (Kreier and Schneider, 2006a), trnL intron & trnL-F spacer DQ164530 (Kreier and Schneider, 2006a);

[5] Knapp 3483 (Private herbarium of Ralf Knapp), Taiwan Island: rbcL KY931138, rps4-trnS KY931291, trnL intron & trnL-F spacer KY931415; [6] Lu D12 (NPA), Yunnan, China: rbcLKY931139, rps4-trnS KY931292; [7] Cicuzza1687 (HITBC), Yunnan, China: rbcL KY931134, rps4-trnS KY931287, trnL intron & trnL-F spacer KY931411. **Pyrrosia cf. porosa**, Fraser-Jenkins FN3 (TAIF), Kathmandu, Nepal: rbcL KY931057, rps4-trnS KY931209, trnL intron & trnL-F spacer KY931354. **Pyrrosia rasamalae** (Racib.) K.H. Shing, Chen Wade 4385 (TAIF), Malaysia: rbcL KY931082, rps4-trnS KY931233, trnL intron & trnL-F spacer KY931369. **Pyrrosia cf. rasamalae**, [1] Tsutsumi et al. IN81, Indonesia (BBG): rbcL AB232412 (Tsutsumi & Kato, 2012); [2] Tsutsumi INB1 (TI), Java, Indonesia: rbcL DQ642169 (Janssen et al., 2007), rps4-trnS DQ642208 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642255 (Janssen et al., 2007). **Pyrrosia rupestris** Ching, O' Brien s.n. (UC), Australia: rbcL AY362558 (Schneider et al., 2004), rps4-trnS AY362623 (Schneider et al., 2004), trnL intron & trnL-F spacer DQ991141 (Schneider et al., 2004). **Pyrrosia serpens** (G.Forst.) Ching, [1] Ranker 1933 (COLO), Moorea, French Polynesia: rbcL EF463260 (Schuettpelz and Pryer, 2007); [2] Nitta 1358 (UC), Moorea, French Polynesia: rbcL KY931140, rps4-trnS KY931293, trnL intron & trnL-F spacer KY931416; [3] Nitta 2844(UC, GH), Moorea, French Polynesia: rbcL KY931141, rps4-trnS KY931294, trnL intron & trnL-F spacer KY931417. **Pyrrosia samarensis** (C. Presl) Ching, Hovenkamp s.n. (L), Cult. (BGL): rbcL DQ642170 (Janssen et al., 2007), rps4-trnS DQ642209 (Janssen et al., 2007), trnL intron & trnL-F spacer DQ642256 (Janssen et al., 2007). **Pyrrosia sheareri** (Baker) Ching, [1] Unknow (NPA), Unknow: rbcL KY931143, rps4-trnS KY931296; [2] Zhang 1110 (CDBI), Anhui, China: rbcL KY931144, rps4-trnS KY931297, trnL intron & trnL-F spacer KY931419; [3] Knapp 3938 (Private herbarium of Ralf Knapp), Taiwan Island: rbcL KY931142, rps4-trnS KY931295, trnL intron & trnL-F spacer KY931418. **Pyrrosia similis** Ching, [1] Chen Wade 2492 (TAIF), Guangxi, China: rbcL KY931145, rps4-trnS KY931298, trnL intron & trnL-F spacer KY931420; [2] Zhang et al. 6365 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931146, rps4-trnS KY931299, trnL intron & trnL-F spacer KY931421; [3] Zhang et al. 7040 (CDBI, MO, VNMN), Thanh Hoa, Vietnam: rbcL KY931147, rps4-trnS KY931300, trnL intron & trnL-F spacer KY931422; [4] Zhang et al. 9204 (CDBI,), Guizhou, China: rbcL KY931148, rps4-trnS KY931301, trnL intron & trnL-F spacer KY931423. **Pyrrosia sp1.**, [1] Zhang et al. 8197 (CDBI), Rawang, Malaysia: rbcL KY931151, trnL intron & trnL-F spacer KY931426. **Pyrrosia sp2.**, [1] Chen et al., SITW11099 (TNM), Guadalcanal island, Solomon Islands: rbcL KY931149, rps4-trnS KY931302, trnL intron & trnL-F spacer KY931424; [2] Chen Wade 2818 (TNM), Ranongga, Solomon Islands: rbcL KY931150, rps4-trnS KY931303, trnL intron & trnL-F spacer KY931425. **Pyrrosia sphaerosticha** (Mett.) Ching, Chen Wade 3966 (TAIF), Negros, Philippines: rbcL KY931152, rps4-trnS KY931304, trnL intron & trnL-F spacer KY931427. **Pyrrosia stenophylla** (Bedd.) Ching, [1] Deng et al., 1274 (CDBI), Kachin, Myanmar: rps4-trnS KY931305, trnL intron & trnL-F spacer KY931428; [2] Gao and Li YLZB0245 (CDBI), Xizang, China: rbcL KY931153, rps4-trnS KY931306, trnL intron & trnL-F spacer KY931429; [3] Jin 11521 (CDBI), Yunnan, China: rbcL KY931154, rps4-trnS KY931307, trnL intron & trnL-F spacer KY931430; [4] Xu and Zhou YLZB2059 (CDBI), Xizang, China: rbcL KY931155, rps4-trnS KY931308, trnL intron & trnL-F spacer KY931431; [5] Xu and Zhou YLZB2114 (CDBI), Xizang, China: rbcL KY931156, rps4-trnS KY931309, trnL intron & trnL-F spacer KY931432. **Pyrrosia stigmosa** (Sw.) Ching, Wu 2586 (KUN), Laos: rbcL JX103716 (Kim et al., 2013), rps4-trnS JX103758 (Kim et al., 2013), trnL intron & trnL-F spacer JX103800 (Kim et al., 2013). **Pyrrosia stolzii** (Hieron.) Schelpe, Kayombo 2711 (MO), Iringa, Tanzania: rbcL KY931157, rps4-trnS KY931310, trnL intron & trnL-F spacer KY931433. **Pyrrosia subfurfuracea** (Hook.) Ching, [1] Xu

and Zhou YLZB2028 (CDBI), Xizang, China: rbcL KY931159, rps4-trnS KY931313, trnL intron & trnL-F spacer KY931435; [2] lu B6 (NPA), Yunnan, China: rps4-trnS KY931312; [3] Cicuzza 2126 (HITBC), Yunnan, China: rbcL KY931158, rps4-trnS KY931311, trnL intron & trnL-F spacer KY931434; [4] Lu B6 (NPA), Yunnan, China: rbcL DQ078622 (Lu and Li, 2006), rps4-trnS DQ078635 (Lu and Li, 2006); [5] Smith 2883 (UC), China: trnL intron & trnL-F spacer DQ642257 (Janssen et al., 2007); [6] Smith 2885 (UC), China: rbcL AY362559 (Schneider et al., 2004), rps4-trnS AY362624 (Schneider et al., 2004); [7] Zhang et al. 6613 (CDBI, MO, VNMN), Lang Son, Vietnam: rbcL KY931160, rps4-trnS KY931314, trnL intron & trnL-F spacer KY931436. **Pyrrosia tonkinensis** (Giesenh.) Ching, [1] Ayeyarwady Exped. 4013 (CDBI), Kachin, Myanmar: rps4-trnS KY931315, trnL intron & trnL-F spacer KY931437; [2] Lu GLQ50 (NPA), Yunnan, China: rbcL KY931161; [3] Lu T5 (NPA), Yunnan, China: rbcL KY931162; [4] Lu V6 (NPA), Hainan, China: rbcL KY931167; [5] Cicuzza1808 (HITBC), Yunnan, China: rbcL KY931164, rps4-trnS KY931317, trnL intron & trnL-F spacer KY931439; [6] Cicuzza1926 (HITBC), Yunnan, China: rbcL KY931165, rps4-trnS KY931318, trnL intron & trnL-F spacer KY931440; [7] Zhang et al. 6314 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931169, rps4-trnS KY931321, trnL intron & trnL-F spacer KY931443; [8] Zhang et al. 9168 (CDBI), Guizhou, China: rbcLKY931175, rps4-trnS KY931327, trnL intron & trnL-F spacer KY931449; [9] Zhang et al. 7539 (CDBI, MO, VNMN), Quang Tri, Vietnam: rbcL KY931174, rps4-trnS KY931326, trnL intron & trnL-F spacer KY931448; [10] Zhang et al. 6960 (CDBI, VNMN), Ha Giang, Vietnam: rbcL KY931173, rps4-trnS KY931325, trnL intron & trnL-F spacer KY931447; [11] Zhang et al. 6309 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcL KY931168, rps4-trnS KY931320, trnL intron & trnL-F spacer KY931442; [12] Zhang et al. 6380 (CDBI, MO, VNMN), Hoa Binh, Vietnam: rbcLKY931170, rps4-trnS KY931322, trnL intron & trnL-F spacer KY931444; [13] Zhang et al. 6697 (CDBI, MO, VNMN), Bac Kan, Vietnam: rbcL KY931171, rps4-trnS KY931323, trnL intron & trnL-F spacer KY931445; [14] Zhang et al. 6939 (CDBI, MO, VNMN), Ha Giang, Vietnam: rbcL KY931172, rps4-trnS KY931324, trnL intron & trnL-F spacer KY931446; [15] Cicuzza1802 (HITBC), Yunnan, China: rbcL KY931163, rps4-trnS KY931316, trnL intron & trnL-F spacer KY931438; [16] Cicuzza2011 (HITBC), Yunnan, China: rbcL KY931166, rps4-trnS KY931319, trnL intron & trnL-F spacer KY931441. **Pyrrosia varia** (Kaulf.) Farw., [1] Chen Wade 1878 (TAIF), Cibodas Botanical Garden, Indonesia: rbcL KY931176, rps4-trnS KY931328, trnL intron & trnL-F spacer KY931450; [2] Zhang et al. 7583 (CDBI, MO, VNMN), Quang Tri, Vietnam: rbcL KY931177, rps4-trnS KY931329, trnL intron & trnL-F spacer KY931451; [3] Zhang et al. 8026 (CDBI, MO, VNMN), Quang Nam, Vietnam: rbcL KY931178, rps4-trnS KY931330, trnL intron & trnL-F spacer KY931452.

Selliguea enervis (Cav.) Ching, Wilson 2863 (UC), Java: rbcL AY096200 (Schneider et al., 2002), rps4-trnS AY096218 (Schneider et al., 2002).

Serpocaulon falcaria (Kunze) A.R. Sm., Kromer 2649 (GOET), Mexico: rbcL EF551069 (Kreier et al., 2008), rps4-trnS EF551093 (Kreier et al., 2008).

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.06.020.

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