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Lilium yapingense (Liliaceae), a new species from Yunnan, China, and its systematic significance relative to *Nomocharis*

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We describe and illustrate *Lilium yapingense sp. nova* (Liliaceae) and show its position within the *Lilium–Nomocharis* complex (Liliaceae). It is similar in appearance to *L. nanum* but differs by (1) having no spots on the tepal bases, instead possessing symmetric stripes; (2) nectaries lacking fimbriate projections on the surfaces, but having two dark grooves; and (3) an orange-colored instead of a white bulb. Phylogenetic analyses using nuclear ITS showed that *L. yapingense* merits specific rank and that it is more closely related to *Nomocharis* than to *Lilium*. However, the morphological synapomorphies thought to distinguish *Nomocharis* from *Lilium* are absent from the new species. The morphology and phylogeny of *L. yapingense* support previous studies, which show that *Nomocharis* and *Lilium* have intergrading morphologies and that *Lilium* is paraphyletic with respect to *Nomocharis*.

Introduction

The genus *Lilium* is comprised of approximately 110 species that are widely distributed in the boreal and temperate northern hemisphere (Liang 1995, Liang & Tamura 2000, Patterson & Givnish 2002). It is widely accepted that *Lilium* is sister to *Fritillaria*, a genus roughly equal in size and with a similar geographic distribution (Rønsted *et al*. 2005). *Lilium* is also considered closely related to *Nomocharis*, a lesser known genus of eight species that are endemic to the Hengduan Mountain region of southwestern China and adjacent areas (Sealy 1983, Liang 1984, Liang & Tamura 2000, Gao *et al*. 2012). The relationship of *Nomocharis* to *Lilium* and *Fritillaria* has generated ongoing debate since *Nomocharis* was established by Franchet in 1889 based on several specimens collected in southwestern China (Sealy 1950). In particular, the intermediate position of *Nomocharis* between *Lilium* and *Fritillaria* in several aspects of floral morphology has been the basis of numerous re-circumscriptions (Balfour 1918, Evans 1925, Sealy 1950, 1983, Liang 1984). New delimitations of *Nomocharis* have been proposed mainly by either integrating species into or removing them from *Lilium* and *Fritillaria*.

Molecular studies that focused on the *Lilium–Nomocharis* complex showed that the species of *Nomocharis* are nested within *Lilium* and support uniting the two genera under the latter name (Nishikawa *et al*. 1999, 2001, Hayashi & Kawano 2000, Rønsted *et al*. 2005, Peruzzi *et al*. 2009, Gao *et al*. 2012). However, *Lilium* and *Nomocharis* have been regarded as being morphologically distinct (Sealy 1983, Liang 1984). Specifically, *Nomocharis* has been distinguished from *Lilium* on the basis of (1) having a widely opened perigone, (2) tepals having dark blotches at the bases forming a showy "eye" in the center of the flower, (3) outer tepals not channeled or nectarial, (4) the dark "eye" being occupied by low ridges of flabellately arranged nectarial tissue on both sides of a short median channel, and (5) having fleshy, cylindrical filaments with an awn at the top (Sealy 1950). However, morphological intermediacy between the two genera was recently demonstrated by Gao *et al*. (2012) in *N. gongshanensis*. The affinity of *N. gongshanensis* to other species of *Nomocharis* is evidenced by its saucer-shaped flower and filaments with acute apices. However, its dark tepal bases, the absence of nectary processes, and its yellow flowers resemble *Lilium*. Gao *et al*. (2012) concluded that *Lilium* and *Nomocharis* may be morphologically intergrading, but thought that evidence from additional species was needed to support that notion.

In a recent expedition to Mt. Gaoligongshan in the central part of the Hengduan Mountains in China, we discovered a population of a liliaceous plant, which appeared to represent an undescribed species. The primary goals of the present study were to (1) determine the status of the putative new species based on morphology and provide a description if necessary, (2) determine the phylogenetic position of the putative new species within the *Lilium–Nomocharis* complex, and (3) provide further evidence supporting a morphological continuity between *Lilium* and *Nomocharis*.

Material and methods

Taxonomic methods and morphological analysis

To infer the taxonomic status of the putative new species, we performed an extensive literature survey and examined herbarium specimens. In the literature survey, we concentrated on *Flora Reipublicae Popularis Sinicae* (Liang 1980), *Flora of China* (Liang & Tamura 2000), and monographs on lilies of the world (Haw 1986, Jefferson-Brown 1995, McRae 1998). To examine herbarium specimens, we visited PE, KUN, CDBI, SZ in China and accessed images of additional specimens through the Chinese Virtual Herbarium (CVH, http://www.cvh.org.cn/), and digitization projects at P, K and E. Preliminary results showed strong resemblance between the putative species and *Lilium nanum* on the basis of alpine slope habitat and solitary nodding flower with pink-purple tepals. Thus, to verify the independence of the new species, we compared its tepal morphology, bulb structure and nectaries with those of *L. nanum*, because those features have long been considered important within *Lilium* (Comber 1949, Sealy 1950, Liang 1984, Liang & Tamura 2000).

Taxon sampling for phylogenetic analysis

In order to infer the phylogenetic position of the putative new species, we collected accessions for molecular analyses. Our taxonomic sampling was conducted broadly and thoroughly within the *Lilium–Nomocharis* complex and included especially the morphologically similar species, *L. nanum* and all species placed in *Nomocharis*. Some accessions of *Lilium–Nomocharis* species were obtained from GenBank. Those that were newly sampled in this study were collected by the authors in the field except three species: *Lilium longiflorum* var. *scabrum* was collected from cultivated material in Hainan Province, and samples of *L. rosthonii* and *L. papiferum* were obtained from herbarium specimens (SZ). Their leaves were placed in silica gel while in the field, allowed to dry, and stored at –80 °C until analysed. The voucher specimens were deposited in the Herbarium of Sichuan University (SZ).

In total, we sampled 38 of the 55 species of *Lilium* from China based on the classification presented in *Flora of China* (Liang & Tamura 2000). They represent all four sections recog-

nized in *Flora Reipublicae Popularis Sinicae* (Liang 1980) as well as five of Comber's (1949) seven sections native to China. We also sampled six of the seven species of *Nomocharis* accepted by Sealy (1950) and in *Flora of China* (Liang & Tamura 2000), as well as the recently described species *N. gongshanensis* (Gao *et al*. 2012). Thus, our sampling included all *Nomocharis* native to China, and excluded only *N. synaptica*, which is endemic to India. For seven *Nomocharis* species, we sampled 14 accessions, of which three were new. Seven species of *Notholirion*, *Cardiocrinum* and *Fritillaria* were included as outgroups based on previous studies indicating a close relationship between these groups and the *Lilium–Nomocharis* complex (Patterson & Givnish 2002, Tamura *et al*. 2004, Fay *et al*. 2006).

DNA extraction, amplification and sequencing

For most samples, total DNA was isolated from silica-dried leaf tissue using a modification to the cetyltrimethyl-ammonium bromide (CTAB) protocol of Doyle and Doyle (1987). In several cases, the DNAQuick Plant System (TIANGEN Biotech, Beijing, China) or Plant Genomic DNA Kit (TIANGEN Biotech, Beijing, China) was used following manufacturer protocols.

The ITS marker, including 5.8S, was amplified using the ITS4 and ITS5 primers (5´-TCCTCCGCTTATTGATATGC-3´ and 5´-GGAAGTAAAAGTCGTAACAAGG-3´, respectively) of White *et al*. (1990). PCR reactions were performed with 50 ng genomic DNA in 20 μl reactions in a GeneAmp PCR System 9700 (Applied Biosystems, USA) with initial denaturation at 94 °C for 2 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 60 s, and a final extension of 72 °C for 10 min. The PCR products were sent to Invitrogen Biotech Co. Ltd. (Shanghai, China) for purification and sequencing, which was carried out using an ABI-3730XL DNA sequencer (Applied Biosystems). For each PCR amplicon, forward and reverse sequencing reactions were performed for 2× coverage. All sequences new to this study are deposited in GenBank (accession numbers in Appendix).

Data analysis

The ITS sequences for all samples were aligned using ClustalX (Thompson *et al*. 1997) and adjusted by eye in MEGA 4.0 (Tamura *et al*. 2007) following the guidelines of Morrison (2009). Gaps were positioned to minimize nucleotide mismatches, and were treated as missing data in the phylogenetic analyses. The boundaries of ITS were determined by comparing the aligned sequences with previously published *Lilium* sequences (Nishikawa *et al*. 1999, Nishikawa *et al*. 2001) and sequences were trimmed accordingly. Sequence lengths and G + C content were calculated using MEGA 4.0 (Tamura *et al*. 2007).

Bayesian phylogenetic analyses of the ITS dataset were conducted using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003). We applied the GTR + I + G model of nucleotide substitution, which was selected under the Akaike information criterion (AIC, Akaike 1974) by MrModeltest ver. 2.2 (Nylander 2004). We performed two simultaneous Bayesian analyses using three hot chains and one cold chain starting from a random tree. Temperature increments between chains were adjusted to 0.2 based on mixing in preliminary analyses. Analyses were run for 10 million generations with sampling every 100 generations. Variation in likelihood scores was examined graphically for each independent run using the program Tracer 1.4 (http://beast.bio.ed.ac.uk/Tracer) to determine apparent stationarity, and the program output from MrBayes was used to assess convergence between simultaneous runs. The first 25% (or 25 000) trees were discarded as the "burn-in" and posterior probabilities were estimated using the 50% majority-rule consensus of the post burn-in trees.

Maximum parsimony (MP) analyses of ITS were carried out using PAUP* (Swofford 2003). Characters were treated as unordered and unweighted. A heuristic search was performed with 1000 replicate analyses, random stepwise addition of taxa, TBR branch swapping, and a maximum trees set to 20 000. Resulting equally parsimonious topologies were summarized using majority-rule consensus. Bootstrap values for clades present in the consensus topology were calculated from 1 million replicate analyses using fast stepwise addition of taxa.

Results and discussion

Comparison with morphological resemble species

A unique suite of morphological features sets the putative new species apart from the described species of *Lilium* and *Nomocharis*. Superficially, it appears similar to *L. nanum* because both species have solitary (rarely two) nodding flowers. However, *yapingense* lacks tepal spotting, which is present in *L. nanum*. Instead, all tepals of the former have purple stripes that become darker from tepal tip to base (Fig. 1Ab and 1Ac). The inner tepals possess strips similar to those of the outer ones, but the bases of the strips of the inner tepals are darker. These tepal features bear striking resemblance to features of *Nomocharis*, rather than to *L. nanum* or any other *Lilium* species. Unlike either *Nomocharis* or *L. nanum*, the new species exhibits swellings on either side of its nectaries instead of a series of thin flanges of tissue found in *Nomocharis*, or projections, as in *L. nanum*. Nectary swellings are found elsewhere in unrelated and otherwise dissimilar species of *Lilium* (e.g., *L. lophophorum*). The orange-red color of the bulb of the putative new species is rare in both *Lilium* and *Nomocharis*. The morphological distinctiveness of the taxon described here supports its recognition as a new species.

Taxonomic treatment

Lilium yapingense Y.D. Gao & X.J. He, *sp. nova* (Fig. 1)

Type: China. Yunnan: Fugong, Lumadengxiang, Yaping Pass, 3200 m, Gaoligongshan Range, sunny grassy and bushy slopes on limestone soils, 9 July 2010 *Yun-dong Gao G2010070903* (holotype SZ).

Bulb ovoid, ca. 2 cm in diameter; scales orange-red, ovate-lanceolate. Stem green, sometimes with purple-red spots at the apex, 20–40 cm. Leaves scattered, linear, 2.5–7 cm × 3–4 mm, 1-veined, margin sparsely papillose. Flower solitary, sometimes with two flowers, nodding. Tepals pale purple, with deep purple stripes toward base, oblanceolate-oblong, 4.5–5 cm × 7–9 mm, revolute distally; nectaries neither papillose nor with fimbriate projections. Filaments ca. 2 cm, glabrous, apex shapely acute. Ovary green, cylindric, 1.5–2 cm × ca. 3 mm. Style subequal to ovary. Capsule brown, oblong or ellipsoid, 2–2.5 × 1.5–2 cm. Flowering in July.

Lilium yapingense is similar to *L. nanum* in the dwarf habit, solid and nodding flower, and pale purple or purplish red tepals. The former differs by the unspotted tepals that have purple stripes, and by the nectaries being neither papillose nor with fimbriate projections, and by the bulbs being orange-red instead of white.

Lilium yapingense is endemic to Fugong County of northwestern Yunnan, China. It is only known from the type locality, but is fairly common there. The roughly 200 to 300 individuals may comprise two to three populations. The name "*yapingense*" is derived from the name of the type locality, Yaping Pass.

Phylogenetic position of *L. yapingense* and its systematic significance

The final ITS dataset consisted of 129 accessions and 118 taxa, including the seven outgroup accessions (Appendix). The total ITS sequence alignment with gaps was 663 bp long and consisted of 361 variable sites (54%) and 245 potentially parsimony-informative characters (37%). Parsimony analyses resulted in the maximum number of trees, 50 000, of equal length (L = 1093, consistency index, CI = 0.4437, retention index, RI = 0.7898). Bayesian and parsimony summary topologies were generally congruent. Therefore, the further discussion is based on the Bayesian trees.

Lilium nanum was resolved in a phylogenetically distant clade (Fig. 2). The species status of *L. yapingense* is also supported by the analyses of plastid DNA (Gao *et al*. 2013). The phylogenetic analyses indicate that *L. yapingense* has a closer relationship to *Nomocharis* than to *Lilium* species. Specifically, our ITS results show that the new species is embedded within a clade comprised of all sampled *Nomocharis* accessions plus two species placed in *Lilium*, *L. nepalense* and *L. saccatum* (Fig. 2). Therefore, there is considera-

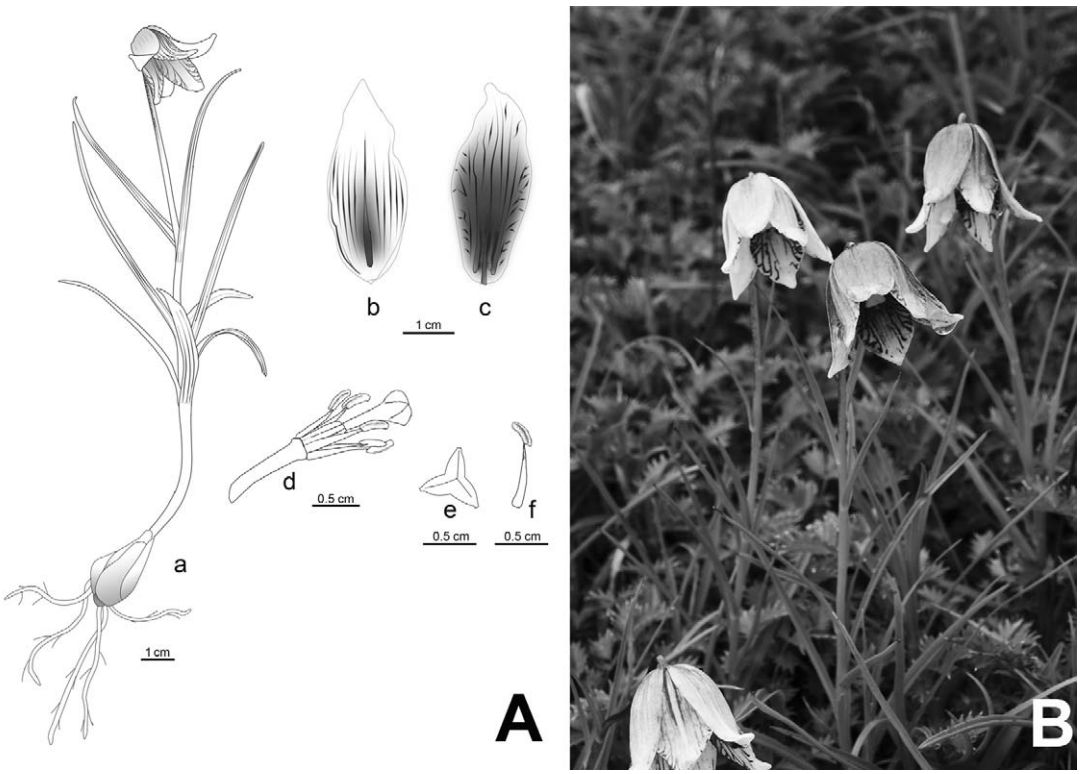

Fig. 1. *Lilium yapingense* (from the holotype). — **A**: Habit (**a** = plant, **b** = inner tepal, **c** = outer tepal, **d** = gynoecium and five stamens, **e** = stigma in top view, **f** = stamen). — **B**: Flowers.

ble phylogenetic distance between *L. yapingense* and its morphologically similar allies. Similar results showing a mismatch between morphology and phylogeny are supported by the analyses of plastid DNA (Gao *et al*. 2013). Thus, our data suggest that *Lilium–Nomocharis* may have been traditionally distinguished from one another on the basis of superfluous morphological similarities and homoplasies.

Lilium yapingense is closer to the *Nomocharis* species than to the other included species. The *Lophophorum* species (including *L. lophophorum*, *L. nanum*, *L. fargesii*, *L. matangense*, and *L. xanthellum*) are "nomocharis-like" plants (Haw 1986, Jefferson-Brown 1995) and some of them were once placed in *Nomocharis* (e.g. *Lilium nanum* as *Nomocharis nana*). Our data indicated that *L. yapingense* and two other *Lilium* species very close to *Nomocharis* instead of *Lophophorum* (Fig. 2).

Our results thus support the notion that *Nomocharis* should be accommodated within *Lilium* since more and more *Lilium*-like taxa became nested within the *Nomocharis* clade (*sensu* Gao *et al*. 2012), so that in fact the latter is totally nested within the former (Gao *et al*. 2012; own results).

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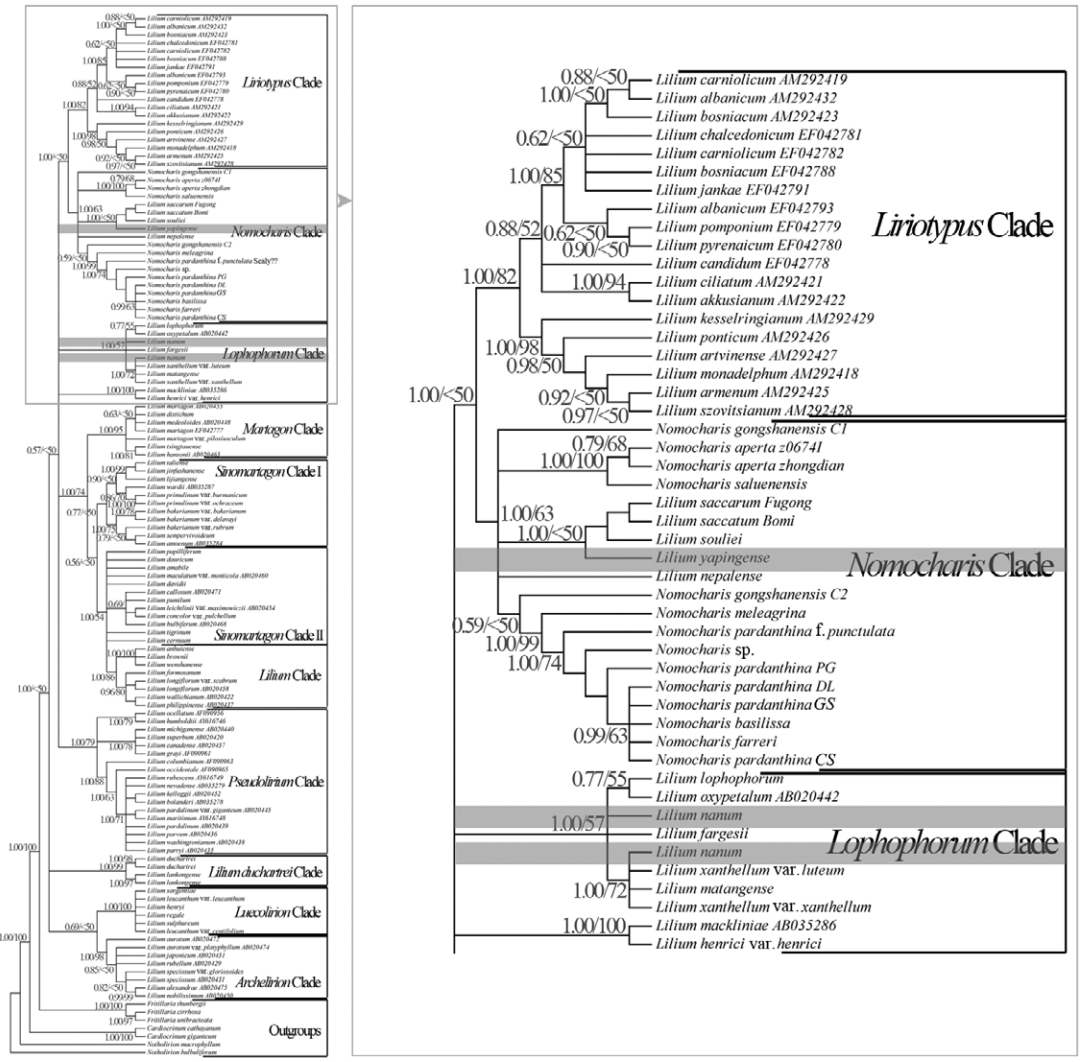

Fig. 2. Phylogenetic tree resulting from a Bayesian analysis of the ITS sequences of *Lilium*, *Nomocharis* and seven outgroup species. A subgeneric classification according to Comber (1949) is indicated by the boxes, and updated cluster names based on Comber (1949) and Liang (1980) are labeled in the right-hand side part. Bayesian posterior probabilities (PP) and parsimony bootstrap (BS), respectively, are shown on branches (left-hand side: the backbone of the phylogenetic framework resolved; right-hand side: the part of the backbone within the box is enlarged to show *Lilium yapingense*, *Nomocharis* clade and *Lophophorum* clade. *Lilium nanum* and *L. yapingense* are on the dark-grey background.

the Ministry of Education of China (20090181110064), and the specimen platform of China, teaching specimens subplatform (http://mnh.scu.edu.cn/).

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Appendix. ITS sequences used in the present study.

Cardiocrinum cathayanum, HM045474; *Cardiocrinum giganteum*, HM045473; *Fritillaria cirrhosa*, HM045469; *Fritillaria thunbergii*, HQ448863; *Fritillaria unibracteata*, HQ448866; *Lilium akkusianum*, AM292422; *Lilium albanicum*, AM292432; *Lilium albanicum*, EF042793; *Lilium alexandrae*, AB020475; *Lilium amabile*, HQ456828; *Lilium amoenum*, AB035284; *Lilium anhuiense*, HM045454; *Lilium armenum*, AM292425; *Lilium artvinense*, AM292427; *Lilium auratum*, AB020472; *Lilium auratum* var. *platyphyllum*, AB020474; *Lilium bakerianum*, HM045428; *Lilium bakerianum* var. *rubrum*, HQ456829; *Lilium bakerianum* var. *delavayi*, HM045468; *Lilium bolanderi*, AB035278; *Lilium bosniacum*, AM292423; *Lilium bosniacum*, EF042788; *Lilium brownii* var. *viridulum*, HQ692117; *Lilium bulbiferum*, AB020468; *Lilium callosum*, AB020471; *Lilium canadense*, AB020457; *Lilium candidum*, EF042778; *Lilium carneolicum*, AM292419; *Lilium carneolicum*, EF042782; *Lilium cernuum*, HM045427; *Lilium chalcedonicum*, EF042781; *Lilium ciliatum*, AM292421; *Lilium columbianum*, AF090963; *Lilium concolor* var. *pulchellum*, HM045460; *Lilium dauricum*, HM045446; *Lilium davidii*, HQ692078; *Lilium distichum*, HM045451; *Lilium duchartrei*, HQ692064; *Lilium duchartrei*, HQ448864; *Lilium fargesii*, HM045459; *Lilium formosanum*, AB020470; *Lilium grayi*, AF090961; *Lilium hansonii*, AB020465; *Lilium henrici*, HM045456; *Lilium henryi*, HM045462; *Lilium humboldtii*, AY616746; *Lilium jankae*, EF042791; *Lilium japonicum*, AB020451; *Lilium jinfushanense*, HQ692157; *Lilium kesselringianum*, AM292429; *Lilium lankongense*, HQ692145; *Lilium lankongense*, HM045430; *Lilium leichtlinii* var. *maximowiczii*, AB020454; *Lilium leucanthum*, HM045466; *Lilium leucanthum* var. *centifolium*, HM045463; *Lilium lijiangense*, HM045424; *Lilium longiflorum*, AB020458; *Lilium longiflorum* Thunberg var. *scabrum* Masamune, HM045447; *Lilium lophophorum*, HQ692099; *Lilium mackliniae*, AB035286; *Lilium maculatum* var. *monticola*, AB020460; *Lilium maritimum*, AY616748; *Lilium martagon*, AB020455; *Lilium martagon*, EF042777; *Lilium martagon* var. *pilosiusculum* , HM045452; *Lilium matangense*, HM045457; *Lilium medeoloides*, AB020448; *Lilium michiganense*, AB020440; *Lilium monadelphum*, AM292418; *Lilium nanum*, HQ687289; *Lilium nanum* var. *flavidum*, HM045458; *Lilium nepalense*, HQ687293; *Lilium nevadense*, AB035279; *Lilium nobilissimum*, AB020450; *Lilium occidentale*, AF090965; *Lilium ocellatum*, AF090956; *Lilium oxypetalum*, AB020442; *Lilium papilliferum*, HQ687262; *Lilium pardalinum*, AB020439; *Lilium pardalinum*, AB020452; *Lilium pardalinum* var. *giganteum*, AB020445; *Lilium parryi*, AB020435; *Lilium parvum*, AB020436; *Lilium philippinense*, AB020437; *Lilium pomponium*, EF042779; *Lilium ponticum*, AM292426; *Lilium primulinum* var. *burmanicum*, HM045449; *Lilium primulinum* var. *ochraceum*, HM045450; *Lilium pumilum*, HQ692084; *Lilium pyrenaicum*, EF042780; *Lilium regale*, HQ692090; *Lilium rubellum*, AB020429; *Lilium rubescens*, AY616749; *Lilium saccatum*, HQ687291; *Lilium saccatum*, HQ687292; *Lilium sargentiae*, HQ692112; *Lilium sempervivoideum*, HM045467; *Lilium souliei*, JQ724631; *Lilium speciosum* var. *clivorum*, AB020431; *Lilium speciosum* var. *gloriosoides*, HM045461; *Lilium sulphureum*, HQ692124; *Lilium superbum*, AB020420; *Lilium szovitsianum*, AM292428; *Lilium taliense*, HQ692109; *Lilium tigrinum*, HQ692093; *Lilium tsingtauense*, HQ687259; *Lilium wallichianum*, AB020422; *Lilium wardii*, AB035287; *Lilium washingtonianum*, AB020438; *Lilium wenshanense*, HM045453; *Lilium xanthellum*, HQ692154; *Lilium xanthellum* var. *luteum*, HQ692152; *Lilium yapingense*, HQ687290; *Nomocharis aperta*, JQ724632; *Nomocharis aperta*, HM045433; *Nomocharis basilissa*, HQ687260; *Nomocharis farreri*, HM045437; *Nomocharis gongshanensis*, HM045438; *Nomocharis gongshanensis*, HM045442; *Nomocharis meleagrina*, HM045436; *Nomocharis pardanthina*, HM045432; *Nomocharis pardanthina*, JQ724635; *Nomocharis pardanthina* f. *punctulata*, HM045435; *Nomocharis pardanthina* f. *punctulata*, JQ724633; *Nomocharis pardanthina*, HM045431; *Nomocharis saluenensis*, HM045434; *Nomocharis* sp., JQ724634; *Notholirion bulbuliferum*, HQ448856; *Notholirion macrophyllum*, HM045475.