**Taxonomic Revision of Quercus serrata subsp. mongolicoides**

**MINEAKI AIZAWA**¹,** KAYA MAEKAWA**¹, **HIROKO MOCHIZUKI**² AND **KAZUYA IIZUKA**³

¹Department of Forest Science, School of Agriculture, Utsunomiya University 350, Mine-machi, Utsunomiya, Tochigi 321-8505, Japan; ²Department of Forest Science, Graduate School of Agriculture, Utsunomiya University 350, Mine-machi, Utsunomiya, Tochigi 321-8505, Japan; ³Utsunomiya University Forests, School of Agriculture, Utsunomiya University, 7556 Funyu, Shioya, Tochigi 329-2441, Japan

*Quercus serrata* subsp. *mongolicoides* of the Tokai and northern Kanto districts of Honshu, Japan, is similar to *Q. mongolica* var. *mongolica* in leaf morphology. Its taxonomic treatment has been long debated, and yet its genetic differentiation from three related taxa, *Q. serrata* subsp. *serrata*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica* has remained unresolved. Genetic differentiation among the four taxa using 11 nuclear microsatellite loci and comparison of leaf morphology was used to revise the taxonomic treatment of *Q. serrata* subsp. *mongolicoides*. The genetic data and leaf morphology support the transfer of *Q. serrata* subsp. *mongolicoides* from *Q. serrata* to *Q. mongolica*. Within the latter, it is treated as a separate intraspecific taxon distinct from *Q. mongolica* var. *crispula* in leaf, acorn, and cupule morphology. Additionally, it is geographically well separated from *Q. mongolica* var. *mongolica* on the Asian continent and shows significant genetic and leaf differences from the typical variety. Thus, *Q. mongolica* var. *mongolicoides* is proposed as a new combination.

Keywords: leaf morphology, nuclear microsatellite, *Quercus mongolica* var. *crispula*, *Quercus mongolica* var. *mongolica*, *Quercus mongolica* var. *mongolicoides*, *Quercus serrata* subsp. *serrata*

*Quercus mongolica* Fisch. ex Ledeb. is common in temperate deciduous forests of the Asian continent [northeast China, northern China, Russia (Far East) and the Korean peninsula], Japan and adjacent islands (southern Sakhalin and the southern Kuril Islands) (Miyabe & Kudo 1925, Kitamura & Horikawa 1951). *Quercus mongolica* has been considered to comprise both a large-leaved arborescent group and a small-leaved arborescent to shrubby group (Kitamura & Horikawa 1951, Ohba 1989); the former consisting of two varieties: *mongolica* on the Asian continent and *crispula* (Blume) H. Ohashi [*Q. mongolica* var. *groseserrata* (Blume) Rehder & E. H. Wilson] in the Japanese archipelago and the adjacent Kuril Islands and Sakhalin (Ohashi 1988). The two varieties have often been considered to be distinct species (*e.g.* Ohba 2006), but here we follow Ohashi (1988) for nomenclature. The arborescent to shrubby group comprises var. *liaotungensis* (Koidz.) Nakai [syn.: var. *undulatifolia* (H. Lev.) Kitam. & T. Horik.] and *Q. crispu* var. *horikawae* H. Ohba (there is no combination under *Q. mongolica*). Var. *liaotungensis* was recognized as a separate species, *Q. liaotungensis*, based on genetic differences and reproductive isolation from var. *mongolica* (syn: *Q. wutaishanica* Mayr; Zeng *et al.* 2010, Chen *et al.* 2017, Liao *et al.* 2019), a treatment we follow.

In Japan, in addition to *Quercus mongolica* var. *crispu* of the arborescent group, plants, which are characterized by rounded leaf serrations similar to *Q. mongolica* var. *mongolica* from the Asian continent, have been reported to occur on low-lying hills in impoverished areas of the Tokai and northern Kanto districts in Honshu (Inami 1966, Satori *et al.* 1981; Fig. 1). Ohba (2006), based on the morphology and possibly following the unpublished data in Kanno *et al.* (2004), described those plants as *Q. serrata*

Previous studies explored the genetic and morphological delimitation of *Quercus serrata* subsp. *mongolicoides*. Mochizuki et al. (2013) analyzed five nuclear microsatellite loci and leaf morphology of populations of *Q. serrata* subsp. *mongolicoides*, *Q. serrata* subsp. *serrata*, and *Q. mongolica* var. *grosseserrata* (*Q. mongolica* var. *crispula*) in Tochigi Prefecture and proposed that *Q. serrata* subsp. *mongolicoides* should not be treated as an intraspecific taxon of *Q. serrata*, but rather as an intraspecific taxon of *Q. mongolica*. Mochizuki et al. (2013) did not analyze or compare *Q. serrata* subsp. *mongolicoides* with *Q. mongolica* var. *mongolica* from the Asian continent. Later, Aizawa et al. (2018) analyzed 11 nuclear microsatellite loci and the leaf morphology of *Q. serrata* subsp. *mongolicoides* (two populations in Tochigi and Aichi prefectures), *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica* across northeast Asia and concluded that *Q. serrata* subsp. *mongolicoides* may have originated from an admixture between *Q. mongolica* var. *crispula* and *Q. mongolica* var. *mongolica*. They (Aizawa et al. 2018) analyzed only a small sample of *Q. serrata* subsp. *serrata*. The genetic differentiation among the four taxa, *Q. serrata* subsp. *serrata*, *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica* (Fig. 1) has therefore remained unknown.

In our study, we analyzed the samples of the four taxa, comprising the populations used in the study by Mochizuki et al. (2013), the genotype data collected by Aizawa et al. (2018) and an additional population of *Quercus serrata* subsp. *serrata* using 11 nuclear microsatellite loci. We also compared the leaf morphology of the four taxa. Based on the results, we here revise the taxonomy of *Q. serrata* subsp. *mongolicoides*.

### Materials and Methods

#### Samples

Details of the four taxa sampled for analysis of the genetics and leaf morphology are shown in Table 1. For the genetic analyses, 144 trees, comprising 54 of *Quercus serrata* subsp. *serrata*, 34 of *Q. serrata* subsp. *mongolicoides*, 23 of *Q. mongolica* var. *crispula*, and 33 of *Q. mongolica* var. *mongolica* were used (Table 1). Samples of *Q. serrata* subsp. *serrata* from sites S1 and S2 and of *Q. mongolica* var. *crispula* from sites S2 and S3, which were originally collected by Mochizuki et al. (2013), and samples of *Q. serrata* subsp. *serrata* from site T, collected for the present study, were analyzed using 11 nuclear microsatellite loci. Genotype data obtained by Aizawa et al. (2018) for *Q. serrata* subsp. *mongolicoides*, based on samples from sites S1 and T and *Q. mongolica* var. *mongolica* from sites S2 and S3, were reused in our analyses.

Two hundred and six trees, comprising 62 of *Quercus serrata* subsp. *serrata*, 30 of *Q. serrata* subsp. *mongolicoides*, 75 of *Q. mongolica* var. *crispula* and 39 of *Q. mongolica* var. *mongolica* were used to analyze leaf morphology (Table 1). Data for *Q. serrata* subsp. *serrata* from sites S1 and S2 were reused from Mochizuki et al. (2013) and supplemented with data on the density of simple hairs collected for the present study. All morphological data for *Q. serrata* subsp. *serrata* from site T were collected for the present study. Data for the remaining taxa, including *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica*, were reused from Aizawa et al. (2018).

*Quercus serrata* subsp. *serrata* occurs sympatrically with *Q. serrata* subsp. *mongolicoides* at sites S1 and T and with *Q. mongolica* var. *crispula* at site S2. The natural distribution of *Q. aliena* Blume and *Q. dentata* Thunb., which are close relatives of the four taxa used in the present study, do not occur around these sites.
New Name: Quercus mongolica var. mongolicoides

Table 1. Taxa, sampling location, and number of samples (N) used for genetic (G) and leaf morphological (M) analyses.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>N</th>
<th>Data†</th>
</tr>
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<tbody>
<tr>
<td>Quercus serrata subsp. serrata</td>
<td></td>
<td></td>
<td>G  M</td>
</tr>
<tr>
<td>S1 University Forest Funyu, Shioya, Tochigi, Japan</td>
<td></td>
<td>24</td>
<td>23 1 3</td>
</tr>
<tr>
<td>S2 Prefectural forest, Yaita, Tochigi, Japan</td>
<td></td>
<td>20</td>
<td>24 1 3</td>
</tr>
<tr>
<td>T  Prefectural forest, Toyota, Aichi, Japan</td>
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<td>15 1 1</td>
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<td>62</td>
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<td>Q. serrata subsp. mongolicoides</td>
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<td>G  M</td>
</tr>
<tr>
<td>S1 University Forest Funyu, Shioya, Tochigi, Japan</td>
<td></td>
<td>16</td>
<td>15 2 2</td>
</tr>
<tr>
<td>T  Prefectural forest, Toyota, Aichi, Japan</td>
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<td>18</td>
<td>15 2 2</td>
</tr>
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<td></td>
<td></td>
<td>34</td>
<td>30</td>
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<tr>
<td>Q. mongolica var. crispula</td>
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<td></td>
<td>G  M</td>
</tr>
<tr>
<td>S2 Prefectural forest, Yaita, Tochigi, Japan</td>
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<td>14</td>
<td>– 1 –</td>
</tr>
<tr>
<td>S3 Mt. Takahara, Shioya, Tochigi, Japan</td>
<td></td>
<td>9</td>
<td>– 1 –</td>
</tr>
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<td>G  M</td>
</tr>
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<td>8 2 2</td>
</tr>
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<td>DO Dongjingcheng, Heilongjiang, China</td>
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<td>7 2 2</td>
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<td>Blagoverschensk, Amur, Russia</td>
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<td>33</td>
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<tr>
<td></td>
<td></td>
<td>144</td>
<td>206</td>
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</tbody>
</table>

† Data source: 1, data obtained in this study; 2, data obtained from Aizawa et al. (2018); 3, data obtained from Mochizuki et al. (2013), but density of short hairs (≤ 1 mm) and long hairs (> 1 mm) on main vein was assessed in this study.

§ Planted trees in plantation of Uryu Experimental Forest, Hokkaido University, were used as representatives of Q. mongolica var. mongolica in China.

Fig. 1. Leaves of Quercus serrata subsp. serrata, Q. serrata subsp. mongolicoides, Q. mongolica var. crispula, and Q. mongolica var. mongolica used in this study. Scale bar = 5 cm. Collection site IDs in parentheses correspond to those in Table 1.
Cultivated trees from the plantation of the Uryu Experimental Forest, Hokkaido University, were used as representatives of *Quercus mongolica* var. *mongolica* (Aizawa et al. 2018).

### Nuclear microsatellite analyses

Previous DNA analyses of species of *Quercus* indicated that chloroplast DNA was not ideal for discriminating species because of the extensive sharing of chloroplast DNA variants among different species. Such sharing is thought to have resulted from hybridization and introgression owing to their propensity for species of *Quercus* to cross and/or from preservation of ancestral polymorphism (Petit et al. 2003, Muir & Schlötterer 2005, Matsumoto et al. 2009). In contrast, the use of nuclear microsatellites is useful for species discrimination among species of *Quercus* (Muir et al. 2000, Zeng et al. 2010, Jose-Maldia et al. 2017, Nagamitsu et al. 2019). We therefore utilized the 11 nuclear microsatellite loci that had been used by Aizawa et al. (2018) (Table 2). Analysis using the 11 nuclear microsatellite loci for the samples was conducted with multiplex polymerase chain reaction following the methodology described by Aizawa et al. (2018).

The total number of alleles detected ($N_a$) and expected heterozygosity ($H_e$) in each taxon and measures of genetic differentiation among the four taxa ($F_{ST}$, $G_{ST}$, and $G'_{ST}$) were assessed at each locus using GenAlEx v.6.503 (Peakall & Smouse 2006, 2012). The statistical significance of the genetic differentiation measures was also tested using GenAlEx. The genetic structure was explored using principal coordinate analysis (PCoA) implemented in GenAlEx based on the genetic distance matrix among individual trees (Smouse & Peakall 1999). The genetic structure was also analyzed using STRUCTURE v.2.3.4 (Pritchard et al. 2000, Falush et al. 2003, Hubisz et al. 2009) by estimating the allele frequencies of each gene pool (cluster) and the population membership of each individual. We used an admixture model and a correlated allele frequency model. The sampling location information was used as a prior. STRUCTURE was run 10 times independently for each number of clusters ($K$) (ranging

<table>
<thead>
<tr>
<th>Loci</th>
<th>QSS ($N = 54$)</th>
<th>QSM ($N = 34$)</th>
<th>QMC ($N = 23$)</th>
<th>QMM ($N = 33$)</th>
<th>Genetic differentiation</th>
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<tr>
<td></td>
<td>$N_a$</td>
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<td>CcC00610</td>
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<td>0.910</td>
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<tr>
<td>CcC00660</td>
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<td>0.837</td>
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<td>0.874</td>
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<td>CcC01513</td>
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<td>11</td>
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<td>QmC00419</td>
<td>5</td>
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<td>5</td>
<td>0.458</td>
<td>4</td>
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<tr>
<td>QmC00716</td>
<td>10</td>
<td>0.529</td>
<td>16</td>
<td>0.891</td>
<td>12</td>
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<td>QmC00898</td>
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<td>0.722</td>
<td>10</td>
<td>0.759</td>
<td>10</td>
</tr>
<tr>
<td>QmC00932</td>
<td>12</td>
<td>0.800</td>
<td>15</td>
<td>0.889</td>
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<tr>
<td>QmC01368</td>
<td>8</td>
<td>0.605</td>
<td>8</td>
<td>0.504</td>
<td>7</td>
</tr>
<tr>
<td>QmC01794</td>
<td>2</td>
<td>0.088</td>
<td>8</td>
<td>0.821</td>
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</tr>
<tr>
<td>QmC02052</td>
<td>9</td>
<td>0.778</td>
<td>9</td>
<td>0.797</td>
<td>10</td>
</tr>
<tr>
<td>QmC02269</td>
<td>8</td>
<td>0.766</td>
<td>10</td>
<td>0.806</td>
<td>10</td>
</tr>
</tbody>
</table>

| 9.8 | 0.660 | 11.3 | 0.772 | 10.7 | 0.759 | 12.3 | 0.775 | 0.088 | **0.076** | **0.388** |

† Averaged over loci; **$P < 0.001$
from 1–6) using 100,000 Markov chain Monte Carlo iterations after a burn-in period of 100,000 iterations. The optimal number of clusters, $K$, was determined using two methods based on the change of mean log likelihoods of the data, $\ln P(D)$ (Pritchard et al. 2000) and the rate of change in $\ln P(D)$, $\Delta K$ (Evanno et al. 2005). The results of 10 independent runs for the optimal $K$ were summarized using STRUCTURE HARVESTER (Earl & vonHoldt 2012), CLUMPP v.1.1 (Jakobsson & Rosenberg 2007), and DISTRUCT v.1.1 (Rosenberg 2004). The genetic differentiation measure ($F_{ST}$; Weir & Cockerham 1984) and 95% confidence interval (CI) among the four taxa was assessed using hierfstat (Goudet 2005) in R (R Core Team 2018). The statistical significance of the $F_{ST}$ values was tested with 1,000 bootstraps.

Morphological analysis of leaves

Based on Mochizuki et al. (2013) and Aizawa et al. (2018), eight leaf characteristics were compared among the four taxa: blade (lamina) length (BL), maximum blade width (BW), distance to the widest point from the apex (DWP), petiole length, number of lateral veins on one side of the main vein of a leaf (NLV), their ratios BW/BL, DWP/BL, and NLV/BL, shape of leaf serrations (Appendix 1), density of stellate hairs on the abaxial leaf surface (0, none; 1, 1–10; 2, 11–100; 3, >100) within a 6 mm diameter circle and density of short hairs (≤1 mm) and long hairs (>1 mm) on the main vein (0, none; 1, 1–10; 2, 11–100; 3, >100) within a 6 mm diameter circle. The median was calculated for each taxon based on Aizawa et al. (2018) and the range was determined for each leaf characteristic. The Steel-Dwass test in R was used for nonparametric multiple comparisons between the four taxa.

Results

Nuclear microsatellite analyses

The nuclear microsatellite loci used in the present study were highly variable ($N_A = 9.8–12.3$ and average $H_E = 0.660–0.775$; Table 2). The overall values of the genetic differentiation measures $F_{ST}$, $G_{ST}$, and $G'_{ST}$ were 0.088, 0.076, and 0.388, respectively, among the four taxa (Table 2). The results of the PCoA indicated that *Quercus serrata* subsp. *serrata* was clearly distinguishable from the other three taxa, *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica* (Fig. 2), whereas the latter three taxa were not separated from each
other in the PCoA plot. The STRUCTURE analysis indicated that an optimal number of clusters (K) would be two on the ΔK method and three based on the change of mean lnP(D). At K = 2, *Quercus serrata* subsp. *serrata* was clearly distinguished from the other three taxa and at K = 3, *Q. mongolica* var. *crispula* exhibited a gene pool in light gray at an average rate of 83–93% in each population and was separated from *Q. mongolica* var. *mongolica*, which exhibited a gene pool in light gray at an average rate of 1–2% in each population (Fig. 3). *Quercus serrata* subsp. *mongolicoides* exhibited a gene pool in light gray at an average rate of 34–65% in each population, suggesting genetic admixture between *Q. mongolica* var. *crispula* and *Q. mongolica* var. *mongolica*.

The pairwise $F_{ST}$ values among the four taxa significantly deviated from zero at all loci examined ($P < 0.001$), denoting a significant genetic differentiation (Table 3). The pairwise $F_{ST}$ values between *Quercus serrata* subsp. *serrata* and the other three taxa (0.162–0.192) were significantly higher than those among the other three taxa (*Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica*; 0.012–0.029; Table 3), based on the non-overlap of

**Table 3.** Pairwise genetic differentiation measure ($F_{ST}$; Weir & Cockerham 1984) and 95% confidence interval (within parentheses) based on 11 nuclear microsatellite loci for *Quercus serrata* subsp. *serrata* (QSS), *Q. serrata* subsp. *mongolicoides* (QSM), *Q. mongolica* var. *crispula* (QMC), and *Q. mongolica* var. *mongolica* (QMM).

<table>
<thead>
<tr>
<th></th>
<th>QSS</th>
<th>QSM</th>
<th>QMC</th>
<th>QMM</th>
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</thead>
<tbody>
<tr>
<td>QSS</td>
<td></td>
<td>0.162 (0.071–0.280) ***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>QSM</td>
<td>0.192 (0.078–0.331) ***</td>
<td>0.012 (0.005–0.020) ***</td>
<td></td>
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</tr>
<tr>
<td>QMC</td>
<td>0.171 (0.061–0.320) ***</td>
<td>0.020 (0.011–0.033) ***</td>
<td>0.029 (0.011–0.049) ***</td>
<td></td>
</tr>
</tbody>
</table>

*** $P < 0.001$
95% CI between the lower limits of the former (0.061–0.078) and the upper limits of the latter (0.020–0.049; Table 3). Among the three taxa, the pairwise $F_{ST}$ value between *Quercus serrata* subsp. *mongolicoides* and *Q. mongolica* var. *crispula* ($F_{ST} = 0.012$) was smaller than between the former and *Q. mongolica* var. *mongolica* ($F_{ST} = 0.020$) and between *Q. mongolica* var. *crispula* and *Q. mongolica* var. *mongolica* ($F_{ST} = 0.029$). Those values, however, were not significantly different because their 95% CIs overlapped (Table 3).

**Morphological analysis of leaves**

The comparison of leaf morphology of the four taxa indicated that *Quercus serrata* subsp. *serrata* was distinguished from the other three taxa, particularly in having a longer petiole, mucronate serrations (= 1.0; Table 4) and dense stellate hairs on the abaxial surface of the leaf (Table 4). *Quercus serrata* subsp. *mongolicoides* was more similar to *Q. mongolica* var. *mongolica* than to *Q. serrata* subsp. *serrata* and *Q. mongolica* var. *crispula*, particularly in having leaves with a more rounded serrations (= 5.0; Table 4) and lack of, or few, stellate hairs on the abaxial surface of the leaf. However, *Q. serrata* subsp. *mongolicoides* was distinguished from *Q. mongolica* var. *mongolica* in having a higher NLV and simple hairs less dense on the main vein (Table 4).

**Discussion**

The taxonomic treatment of *Quercus serrata* subsp. *mongolicoides* has long been debated (Serizawa 2008, Suda & Hoshino 2008, Hiroki 2017). Our study, which concurred with the results of Mochizuki et al. (2013), showed that genetic data and leaf morphology of *Q. serrata* subsp. *mongolicoides* do not support its placement within *Q. serrata*, but rather as an intraspecific taxon of *Q. mongolica* (Figs. 2 & 3; Tables 3 & 4). We also found a low level of genetic differentiation among *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica* ($F_{ST} = 0.012–0.029$; Table 3). The $F_{ST}$ values were much lower than those based on nuclear microsatellite loci between species of *Quercus* on Hokkaido (Table S1 in Nagamitsu et al., 2019), $F_{ST} = 0.133$ (*Q. mongolica* var. *crispula* vs. *Q. dentata*), $F_{ST} = 0.153$ (*Q. mongolica* var. *crispula* vs. *Q. serrata* var. *serrata*) and $F_{ST} = 0.211$ (*Q. dentata* vs. *Q. serrata* var. *serrata*). The pairwise $F_{ST}$ values among the above three taxa ($F_{ST} = 0.012–0.029$; Table 3) were also lower than those observed between *Q. petraea* (Matt.) Liebl. and *Q. robur* L. in Europe ($F_{ST} = 0.050$; Muir & Schlötterer 2005) and between *Q. mongolica* and *Q. liaotungensis* in China ($F_{ST} = 0.069$; Zeng et al. 2010). The results from our study therefore do not support treating *Q. serrata* subsp. *mongolicoides* as a distinct species (*Q. mongoloides*; Hiroki 2017), and also do not support the species status of *Q. crispula* and the inclusion of *Q. serrata* subsp. *mongolicoides* as a variety within *Q. crispula* (*Q. crispula* var. *mongolicoides*; Serizawa 2008).

*Quercus serrata* subsp. *mongolicoides* and *Q. mongolica* var. *mongolica* are similar in leaf morphology (Table 4; Aizawa et al. 2018), ovoid acorns and cupules with prominently humped scales (Iizuka et al. 2008, Suda & Hoshino 2008, Kobayashi 2012, Hiroki 2017). However, our study and the study of Aizawa et al. (2018) indicate that *Q. serrata* subsp. *mongolicoides* is genetically closer to *Q. mongolica* var. *crispula* than to *Q. mongolica* var. *mongolica*, although their pairwise $F_{ST}$ values were not significant based on the 95% CIs (Table 3). The morphological and genetic similarity of *Q. serrata* subsp. *mongolicoides* to both var. *mongolica* and var. *crispula* may be attributed to a potential admixture between var. *crispula* and var. *mongolica*, the latter of which may represent relict populations from the Late Pleistocene in and around Japan (Aizawa et al. 2018). We therefore propose that *Q. serrata* subsp. *mongolicoides* should be treated as an intraspecific taxon of *Q. mongolica* because it differs in leaf, acorn, and cupule morphology from *Q. mongolica* var. *crispula* (Table 4; Ohba 2006, Suda & Hoshino 2008). There is also low but significant genetic differentiation between *Q. serrata* subsp. *mongolicoides* and *Q. mongolica* var. *mongolica* (Table 3). The two
taxa are separated geographically and differ in some morphological traits, such as NLV and density of simple hairs on the main vein (Table 4). We therefore propose the new combination *Quercus mongolica* var. *mongolicoides* for these plants.

We and Aizawa *et al.* (2018) did not analyze *Quercus mongolica* (var. *mongolica* and/or var. *crispula*; Nakai 1915, Kitamura & Horikawa 1951) on the Korean Peninsula, except in comparing the *Q. mongolica* chloroplast DNA haplotypes from South Korea by Aizawa *et al.* (2018). We and Aizawa *et al.* (2018) also did not analyze the morphology of the southern Sakhalin populations in which genetic admixture between *Q. mongolica* var. *crispula* and *Q. mongolica* var. *mongolica* was postulated. Further comparative studies of *Q. mongolica* from these regions is needed to fully understand species delimitation of *Q. mongolica* in northeast Asia.

Trees with rounded leaf serrations similar to *Quercus mongolica* var. *mongolica* in the coastal regions of northern Hokkaido (Miyabe & Kudo 1925, Shimizu 1997) are considered to be hybrids between *Q. mongolica* var. *crispula* and *Q. dentata* (e.g., Ohba 2006). The origin of those plants have remained obscure, but Nagamitsu *et al.* (2019, 2020) showed that such plants were derived through introgression from *Q. dentata* to *Q. mongolica* var. *crispula*. Therefore, this taxon, *Q. ×angustilepidota* Nakai, should be distinguished from *Q. mongolica* var. *mongolicoides* by the more or less dense stellate hairs on the abaxial surface of the leaves (Fig. S4 of Aizawa *et al.* 2008, Nagamitsu *et al.* 2019; Table 4) and cupules at least partly covered by elongate, linear or subulate involucre scales with an acute apex, a distinct characteristic observed in cupules of

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**Table 4.** Median and range of each leaf morphological characteristic in *Quercus serrata* subsp. *serrata*, *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica*.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>N</th>
<th>Blade length (BL, cm)</th>
<th>Maximum blade width (BW, cm)</th>
<th>Petiole length</th>
<th>Distance to the widest point from the top (DWP, cm)</th>
<th>Number of lateral veins (NLV)</th>
<th>BW/BL</th>
<th>Data Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Q. serrata</em> subsp. <em>serrata</em></td>
<td>62</td>
<td>10.3 (7.4–13.5) a</td>
<td>4.9 (3.3–6.8) a</td>
<td>1.3 (0.8–1.9) a</td>
<td>4.6 (3.2–5.9) a</td>
<td>13.0 (10.3–16.3) a</td>
<td>0.5 (0.4–0.7) a</td>
<td>Mochizuki <em>et al.</em> (2013); this study</td>
</tr>
<tr>
<td><em>Q. serrata</em> subsp. <em>mongolicoides</em></td>
<td>30</td>
<td>15.2 (10.3–25.0) b</td>
<td>9.7 (7.1–16.0) b</td>
<td>0.5 (0.3–0.7) b</td>
<td>6.2 (4.3–10.5) b</td>
<td>14.0 (10.0–18.0) a</td>
<td>0.6 (0.5–0.8) b</td>
<td>Aizawa <em>et al.</em> (2018)</td>
</tr>
<tr>
<td><em>Q. mongolica</em> var. <em>crispula</em></td>
<td>75</td>
<td>14.1 (9.9–17.7) c</td>
<td>7.7 (5.5–10.4) c</td>
<td>0.3 (0.1–0.7) c</td>
<td>6.0 (4.4–7.9) b</td>
<td>16.0 (12.0–21.0) b</td>
<td>0.5 (0.4–0.7) c</td>
<td>Aizawa <em>et al.</em> (2018)</td>
</tr>
<tr>
<td><em>Q. mongolica</em> var. <em>mongolica</em></td>
<td>39</td>
<td>13.1 (9.0–18.6) d</td>
<td>8.1 (4.3–11.0) c</td>
<td>0.5 (0.2–0.8) b</td>
<td>5.0 (3.3–7.0) a</td>
<td>10.0 (6.0–12.0) c</td>
<td>0.6 (0.4–0.8) b</td>
<td>Aizawa <em>et al.</em> (2018)</td>
</tr>
</tbody>
</table>

The ranges from minimum to maximum values are shown in parentheses. Different letters in each characteristic indicate significant differences between taxa based on Steel-Dwass multiple comparison tests (*P* < 0.05).

† See Appendix 1.

§ Dense short hairs (≤1 mm) with sparse or somewhat dense long hairs on the main vein in *Q. serrata* subsp. *serrata* and various densities of long hairs (>1 mm) without short hairs on the main vein in *Q. serrata* subsp. *mongolicoides*, *Q. mongolica* var. *crispula*, and *Q. mongolica* var. *mongolica*.
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Q. dentata (Nakahara & Nishikawa 2009).

**Taxonomic Treatment**

Quercus mongolica Fisch. ex Ledeb. var. mongolicoides (H. Ohba) M. Aizawa, comb. nov.


**Typus.** Japan, Aichi Pref., Seto city, Kaisho, 35°10′93″ N, 137°06′78″ E, 130 m alt., T. Miyazaki, 512004, 8 Dec. 2005, (Holo-, TI03125; Iso-, TI03127!).


**Japanese name.** Fumoto-mizunara (Ohba 2006)

**Distribution.** Japan. Kanto district (Tochigi and Gunma prefectures) and Chubu district (Nagano, Aichi, and Gifu prefectures). Details are shown in Hiroki (2017).

Key to arborescent varieties of Quercus mongolica and an allied hybrid taxon.

1a. Leaf margin serrate with acute teeth .......................................................... var. crisupla

1b. Leaf margin crenate-dentate with rounded to widely obtuse teeth .......................................................... 2

2a. Abaxial surface of leaves with more or less dense stellate hairs; involucral scales of cupule at least partly linear or subulate, apex acute .................................................................................................................. Q. ×angustilepidota

2b. Abaxial surface of leaves without or nearly without stellate hairs, involucral scales of cupule triangular-ovate, appressed and prominently humped, apex subacute to obtuse .......................................................... 3

3a. Lateral veins of leaves (10–)13(–16); abaxial main vein glabrous or glabrescent ............................ var. mongolicoides

3b. Lateral veins of leaves (6–)10(–12); abaxial main vein glabrescent or sparsely hairy ................................ var. mongolica

Remarks: Quercus crisupla var. horikawae is variable in leaf shape (Noshiro 1984; Ohba 1989), but is well recognizable by its shrubby habit, bent trunk often decumbent near the ground and by smaller leaves (Ohba 2006). Its identity and nomenclature will be treated in another paper.

We would like to thank Dr. Takahide Kurosawa for help with the taxonomic treatment. We also thank the prefectoral forestry offices for permitting sampling, Dr. Ichiro Tamaki and Dr. Teruyoshi Nagamitsu for sharing information on their Quercus studies, and Dr. Hiroshi Ikeda of TI for permission to examine specimens. We acknowledge the editor and anonymous reviewers for their valuable suggestions.

**References**


Peakall, R. & P. E. Smouse. 2006. GENALEX 6: genetic...


Received June 2, 2020; accepted November 9, 2020

APPENDIX 1. Shape of leaf serrations (as proposed in Mochizuki et al. 2013) used in this study.