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Teuvoa, a new lichen genus in *Megasporaceae* (Ascomycota: *Pertusariales*), including *Teuvoa junipericola* sp. nov.

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Abstract: The relationship of *Aspicilia uxoris* within *Megasporaceae* is assessed within a phylogenetic context. '*Aspicilia*' *uxoris* and other related species are recovered as sister to the genus *Lobothallia* s. str. and described here as a new genus. *Teuvoa* (Ascomycota, *Megasporaceae*) is erected based on nuclear ITS and LSU sequence data and morphological characters. In addition to *Teuvoa uxoris*, a second species, *T. junipericola,* is added to the new genus based on material collected from North America. *Teuvoa junipericola, T. uxoris* and *T. tibetica* form a group with 8-spored asci, absence of extrolites, rather short-sized conidia and ascospores, lack of a subhypothecial algal layer, and different substratum preferences (on organic substratum) with a sister relationship to genus *Lobothallia* s. lat. (*Aspicilia* subgenus *Pachyothallia* Clauzade & C. Roux). Based on spore measurements of the holotypes, *Lecanora ferganensis* Tomin from central Asia (Kyrgyzstan, Tajikistan and Uzbekistan), *Lecanora atrodiscata* Gintovt, from Tajikistan and *Lecanora takyroides* Dzhur. from Turkmenistan are new synonyms to *T. uxoris*. A lectotype for *Lecanora ferganensis* is designated, expanding the known distribution of *T. uxoris* from Algeria, Morocco and Spain, into Central Asia.

Key words: *Aspicilia*, *Juniperus*, lignicolous, *Lecanora*, *Lobothallia*, *Pachyothallia*, substratum preference, terricolous

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Introduction

The lichen-forming ascomycete genus *Aspicilia* s. lat. includes a diverse assemblage of 200–250 species (Owe-Larsson *et al.* 2007; Sohrabi *et al.* 2010*b*) within *Megasporaceae* (Schmitt *et al.* 2006; Lumbsch *et al.* 2007; Nordin *et al.* 2010; Sohrabi *et al.* 2013). Recent taxonomic studies incorporating molecular sequence data have supported the monophyly of *Megasporaceae*, while calling for major generic and species-level revisions (Nordin *et al.* 2010; Sohrabi *et al.* 2013). To accommodate major phylogenetic clades identified within the family, Nordin *et al.* (2010) reintroduced the old generic names *Circinaria* Link and *Sagedia* Ach., and redefined *Aspicilia* A. Massal. and *Lobothallia* (Clauzade & Cl. Roux) Hafellner. Although these studies provide a robust working hypothesis of relationships, taxonomic delimitations within this family cannot be regarded as conclusively settled due to limited taxonomic and molecular sampling. Furthermore, unresolved species complexes burdened by complicated nomenclature and taxonomic problems are common within many *Aspicilia* s. lat. lineages (e.g. Clauzade & Roux 1984; Owe-Larsson *et al.* 2007, 2011; Sohrabi & Ahti 2010; Sohrabi *et al.* 2011*a*, *b*, 2013), requiring substantial taxonomic revisions within many groups.

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Species within *Aspicilia* s. lat. (traditional sense) show a wide range of substratum preference and ecological adaptation. While the majority of species are saxicolous, several taxa are terricolous (including vagrant species – see Rosentreter 1993; Sohrabi *et al.* 2011*b*, 2013) or epiphytic (corticolous and lignicolous). In some cases, species that are normally saxicolous, occurring mainly on acidic rocks, are also occasionally found growing on hard lignum, conifers and worked timber, often with morphological characters deviating somewhat from saxicolous forms (Rico *et al.* 2007; Owe-Larsson *et al.* 2007).

Currently, the relationships of epiphytic *Aspicilia* s. lat. species to major groups within *Megasporaceae* remain unclear. The corticolous taxon *Aspicilia uxoris* was originally studied from material collected in Algeria, Morocco and Spain (Rico *et al.* 2007). However, recent collections of corticolous/lignicolous specimens of *Aspicilia*, particularly on *Juniperus* spp. in Iran and western North America (Shrestha & St. Clair 2009), indicated that *A. uxoris* s. lat. probably has a much broader geographical distribution than originally assumed. Furthermore, a particularly puzzling specimen was recently collected on plant debris on soil in an open *Juniperus* forest in southern Anatolia in Turkey (*M. G. Halici* s. n. – hb. M.G. Halici). This specimen showed morphological similarities to both the epiphytic taxon *A. uxoris* and some terricolous species, such as *A. tibetica* Sohrabi & Owe-Larss., *Aspicilia mansourii* Sohrabi (see Lumbsch *et al.* 2011) and *A. crespiana* V. J. Rico (Rico 1999), suggesting the potential for increased morphological variability and substratum preference within *A. uxoris* s. lat. A literature search revealed the existence of several other epiphytic *Aspicilia* species described from Central Asia: *Lecanora ferganensis* Tomin (Fig. 2D) described from Uzbekistan (Tomin 1950) growing on *Juniperus* trees and also recorded from some localities in Kyrgyzstan (Baĭbulatova 1988), Tajikistan (Kudratov 1984, 1985; Kudratov & Mayrhofer 2002) and Uzbekistan (Tomin 1950; Shafeev 1953); *Lecanora atrodiscata* Gintovt (Fig. 2E) from Tajikistan growing on *Populus* bark (Gintovt 1959); and *Lecanora takyroides* Dzhur. from Turkmenistan growing on Turkmen juniper (Dzhuraeva 1974). As part of an ongoing study of the systematics of *Megasporaceae*, we investigated the relationships of the epiphytic species *Aspicilia uxoris* to other previously recognized groups by using DNA sequence data from the nuclear ribosomal ITS and LSU markers. Our objectives were to 1) identify the phylogenetic position of *A. uxoris* and related species within *Megasporaceae*, 2) assess biogeographical and morphological patterns within *A. uxoris* s. lat, and 3) re-evaluate relationships within *Megasporaceae*. In this study, phylogenetic analyses recovered species within the *A. uxoris* group as a well-supported monophyletic clade, sister to *Lobothallia*, within *Megasporaceae*. Since this species group cannot be included in any of the existing genera within this family, the new genus *Teuvoa* is formally described here. Additionally, morphological, biogeographical, and molecular sequence data support the distinction of a previously unrecognized species within the *A. uxoris* group, described here as *Teuvoa junipericola*.

Materials and Methods

Taxon sampling

In the present study a total of 77 specimens were included in order to assess the phylogenetic position of the *Aspicilia uxoris* group within *Megasporaceae* (Table 1). Specimens were selected to represent genera currently circumscribed within *Megasporaceae*, including *Aspicilia*, *Sagedia*, *Lobothallia*, *Megaspora*, and *Circinaria* (*sensu* Nordin *et al.* 2010). For the nomenclature of *Circinaria affinis, C. aschabadensis, C fruticulosa*, and *C. hispida,* see Sohrabi *et al.* (2012). The focal group was represented by 13 specimens of *A. uxoris* s. lat. and a single representative of *A. tibetica*. We were unable to obtain fresh material corresponding to *Lecanora ferganensis*, *L. atrodiscata* and *Lecanora takyroides* from Central Asia for molecular analyses, although a single collection of *A. uxoris* s. lat. was made from Iran. Representatives of *Aspilidea*, *Ochrolechia*, and *Pertusaria* were used as outgroup taxa (Nordin *et al.* 2010). Voucher specimen information and GenBank accession numbers for sequences produced for this study are listed in Table 1, together with sequences obtained from GenBank. For *Circinaria contorta* and *Megaspora verrucosa*, we combined nuclear ITS and LSU data from different individuals in order to represent important lineages with both loci sampled in this study. Additional specimens from the *Aspicilia uxoris* group investigated for this study are deposited in B, BRY, GZU, H, IRAN, LE, MAF, MSK, the herbarium of M. G. Halici (hb. M. G. Halici)

TABLE 1. *Material used in this study. Vouchers, their geographical origin, and herbaria where vouchers are deposited are also listed. GenBank accession numbers of the newly obtained sequences are in bold.*

Species	Locality and collector number (Herbarium)	nrITS	nrLSU
Aspicilia cinerea 1	Austria, Styria, *Hafellner* 40563 (GZU)	AF332110	–
A. cinerea 2	Sweden, Uppland, *Hafellner* 37308 (GZU)	AF332111	–
A. cinerea 3	Austria, *Kocourkova & Hafellner* 46364 (GZU)	AF332112	–
A. cinerea 4	Sweden, Östergötland, *Nordin* 5542 (UPS)	HQ406799	HM060734
A. cinerea 5	Sweden, Dalarna, *Hermansson* 13275 (UPS)	EU057899	HM060733
A. cyanescens	USA, California, *Owe-Larsson* 9151 (UPS)	–	HM060745
A. dendroplaca 1	Sweden, Torne Lappmark, *Nordin* 5952 (UPS)	HQ259259	HM060744
A. dendroplaca 2	Finland, Enontekiön Lappi, *Nordin* 6366 (UPS)	HQ259260	HM060758
A. dudinensis	Sweden, Torne Lappmark, *Nordin* 6036 (UPS)	EU057906	HM060748
A. epiglypta	Sweden, Västergötland, *Nordin* 6303 (UPS)	EU057907	–
A. haeyrenii	Sweden, Torne Lappmark, *Nordin* 5997 (UPS)	–	HM060755
A. indissimilis	Sweden, Torne Lappmark, *Nordin* 5943 (UPS)	EU057909	HM060746
A. laevata	Sweden, Uppland, *Tibell* 23659 (UPS)	EU057910	HM060730
A. mashiginensis	Sweden, Hälsingland, *Nordin* 5790 (UPS)	EU057912	HM060732
A. permutata	Sweden, Torne Lappmark, *Nordin* 6027 (UPS)	EU057918	HM060747
A. rivulicola	Sweden, Torne Lappmark, *Nordin* 5957 (UPS)	EU057922	HM060753
A. supertegens 1	Norway, Troms, *Owe-Larsson* 9002 (UPS)	EU057936	HM060742
A. supertegens 2	Sweden, Torne Lappmark, *Nordin* 6023 (UPS)	EU057938	HM060751
A. verruculosa 1	Norway, Troms, *Owe-Larsson* 9007 (UPS)	EU057940	–
A. verruculosa 2	Norway, Troms, *Owe-Larsson* 9003 (UPS)	EU057941	–
Aspilidea myrinii	Sweden, Jämtland, *Nordin* 6205 (UPS)	–	HM060754
Circinaria affinis	Russia, Astrakhan Region, *Kulakov* 1408 (M)	HQ171237	–
C. aschabadensis	Turkmenistan, Kopet-Dagh Mt., *Borisova* s. n. (LE)	GU289916	–
C. calcarea	Sweden, Öland, *Nordin* 5888 (UPS)	EU057898	HM060743
C. contorta 1	Austria, Styria, *Wilfling* s.n. (GZU) = nrITS	AF332108	
	Finland, Southern Helsinki, *Pykälä* 30701 (H) = nrLSU		JQ797499
C. contorta 2	Finland, Karjalohja, *Pykälä* 28872 (H) = nrLSU		JQ797500
	Austria, Styria, *Hafellner* 43516 (GZU) = nrITS	AF332109	
C. crespiana	Spain, Madrid, *Rico* 1249/1 & *Florido* (H)	**JX306733**	**JX306752**
C. cupreogrisea	Sweden, *Nordin* 6046 (UPS)	EU057903	–
C. emiliae 1	Kazakhstan, Atyrau, *Kulakov* 3798 (UPS)	–	HM060729
C. emiliae 2	Kazakhstan, Atyrau, *Kulakov* 3702 (UPS)	JQ797512	HM060728
C. fruticulosa 1	Russia, Astrakhan Region, *Kulakov* s. n. (M)	HQ171227	–
C. fruticulosa 2	China, Xinjiang, *Abbas* 940001(H)	HQ171229	–
C. gibbosa	Sweden, Uppland, *Nordin* 5878 (UPS)	EU05790	HM060740
C. gyrosa	Spain, Soria, *Barreno & Crespo* 2041 (MRDS115818)	**JX306734**	–
C. hispida 1	USA, Wyoming, *Muscha* & *Rosentreter* 121 (SRP)	HQ171234	–
C. hispida 2	Russia, Kalmyk Region, *Ochirova* (LE)	HQ171235	–
C. hispida 3	Spain, *Lumbsch* 2 vi 2003 (F)	–	DQ780305
C. hispida 4	Turkey, Malatya, *Candan* 11 (ANES)	HQ406806	HM060722
C. leprosescens	Sweden, Uppland, *Nordin* 5906 (UPS)	EU05791	HM060749
C. mansourii 1	Iran, Golestan, *Sohrabi* 15077 (hb. M. Sohrabi)	**JX306735**	–
C. mansourii 2	Iran, East Azerbaijan, *Sohrabi* 10097 (hb. M. Sohrabi)	**JX306736**	–
Lobothallia alphoplaca 1	USA, Utah, *Leavitt et al.* 743 (BRY – C54919)	**JX306738**	KC667059
L. alphoplaca 2	Iran, East Azerbaijan, *Sohrabi* 3677 (hb. M. Sohrabi)	JQ797516	–
L. alphoplaca 3	USA, Nevada, *Leavitt & Leavitt* 849 (BRY – C54920)	**JX306739**	KC667060
L. alphoplaca 4	USA, Utah, *Leavitt et al.* 447 (BRY – C54921)	**JX306737**	KC667061
L. alphoplaca 5	Iran, East Azerbaijan, *Sohrabi* 4362 (H)	JQ797515	–
L. melanaspis	Sweden, Jämtland, *Nordin* 6622 (UPS)	HQ259272	HM060726
'*Lobothallia*' *recedens*	Sweden, *Nordin* 6035 (UPS) = nrITS	HQ406807	
	Sweden, Dalarna, *Nordin* 6582 (UPS) = nrLSU		HM060762
'*Lobothallia*' sp. 1	France, *C. Roux* 25856 (hb. C. Roux)	KC667063	–
'*Lobothallia*' sp. 2	France, *C. Roux* 25868 (hb. C. Roux)	KC667064	–
Megaspora verrucosa 1	Austria, Styria, *Trinkaus* (GZU)	AF332121	–
M. verrucosa 2	Austria, Styria, *Hafellner* 48544 & *Ivanova* (GZU)	AF332122	–
M. verrucosa 3	USA, Colorado, *St. Clair* 18429 (BRY – C54042)	KC667053	KC667062

TABLE 1. *Continued*

Species	Locality and collector number (Herbarium)	nrITS	nrLSU
Ochrolechia oregonensis	Canada, *Schmitt* 11 vi 2004 (F)	–	DQ780308
O. parella	France, Brittany, *Feige* (ESS 20864)	–	AF274097
O. tartarea	Scotland, *Coppins* s.n. (ESS 21493)	–	AY300848
Pertusaria albescens	Czech Republic, Bohemia, *Schmitt* (ESS 20967)	–	AF329176
P. amara	Germany, Rheinland-Pfalz, *Killmann* (ESS 20865)	–	AF274101
Sagedia mastrucata 1	Norway, Troms, *Nordin* 5708 (UPS)	EU057913	HM060736
S. mastrucata 2	Norway, Troms, *Nordin* 5481 (UPS)	EU057914	HM060737
S. simoënsis	Norway, Troms, *Owe-Larsson* 9000 (UPS)	EU057926	HM060701
S. zonata 1	Norway, Troms, *Owe-Larsson* 8942 (UPS)	EU057946	HM060738
S. zonata 2	Sweden, *Nordin* 5949 (UPS)	EU057953	–
S. zonata 3	Sweden, *Nordin* 6006 (UPS)	EU057952	–
Teuvoa aff. *junipericola*	Iran, Golestan, *Sohrabi* 9507B (hb. M. Sohrabi)	**JX306740**	**JX306756**
T. aff. *uxoris*	Turkey, Konya, *Halici* s.n. (hb. Halici)	**JX306742**	–
T. junipericola 1	USA, Utah, *Rosentreter* 14521 (H, isotype)	**JX306741**	–
T. junipericola 2	USA, Utah, St. Clair et al. 742 (BRY – C54922)	**JX306744**	KC667054
T. junipericola 3	USA, Utah, *St. Clair et al.* 767 (BRY – C54923)	**JX306747**	KC667055
T. junipericola 4	USA, Utah, *Leavitt & Felix* 843 (BRY – C54924)	**JX306748**	KC667056
T. junipericola 5	USA, Utah, *Leavitt & Felix* 844 (BRY – C54925)	**JX306749**	–
T. junipericola 6	USA, Utah, *Leavitt & Felix* 845 (BRY – C54926)	**JX306750**	–
T. junipericola 7	USA, Utah, *Leavitt & Leavitt* 850 (BRY – C54927)	**JX306751**	–
T. tibetica	China, Tibet, *Obermayer* 04386 (H, isotype)	GU289915	–
T. uxoris 1	Spain, Castilla – La Mancha, *Rico & Pizarro* 3622 (H)	**JX306743**	**JX306757**
T. uxoris 2	Spain, Castilla – La Mancha, *Rico & Pizarro* 3622A (BRY – C54928)	**JX306745**	KC667057
T. uxoris 3	Spain, Castilla – La Mancha, *Rico & Pizarro* 3622B (BRY – C54929)	**JX306746**	KC667058

in Erciyes University and the herbarium of the first author. Specimens, including *Lecanora atrodiscata*, *L. ferganensis* and *L. takyroides*, were examined under a light microscope and a stereomicroscope, and tested with the usual reagents (K, C, KC, P, N and KOH/I). Thin-layer chromatography (TLC) followed Orange *et al.* (2001), using solvent systems A, B and C. For spore shape terminology, see Bas (1969: 321–332).

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted from herbarium specimens (e.g., *A. crespiana*, *A. tibetica*), recent collections of *A. uxoris*, and the newly described species *A. mansourii* Sohrabi (see Lumbsch *et al.* 2011) following Sohrabi *et al.* (2010*a*) or Leavitt *et al.* (2011). DNA sequence data were generated from the nuclear ribosomal ITS (ITS1, 5.8S, ITS2) and LSU regions via the polymerase chain reaction (PCR). The complete ITS region was amplified using the primers ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). A fragment of the LSU was amplified using AL2R (Mangold *et al.* 2008) and LR3 (Vilgalys & Hester 1990). Standard PCR reactions were used to amplify targeted loci. PCR cycling parameters for amplifying the ITS loci included an initial denaturation for 1 min 25 s at 94°C, followed by 35 cycles of 35 s at 95°C, 55 s at 55°C, 45 s at 72°C, with a 4 s increase per cycle, terminating with a final elongation at 72°C for 10 min. Cycling parameters for the LSU fragment followed Blanco *et al.* (2004). Purification and sequencing of PCR products were performed by Macrogen Inc. (www.macrogen.com) or followed Leavitt *et al.* (2011).

Sequence alignment and phylogenetic analyses

Sequences were assembled and edited using Sequencher version 4.6.1 (Gene Codes Corporation, Ann Arbor, MI) and sequence identity was confirmed with a 'megaBLAST' search in GenBank (Wheeler *et al.* 2005). The program SATé has been shown to improve alignment accuracy compared to other currently available programs (Liu *et al.* 2009, 2012), including lichen-forming fungi (Leavitt *et al.* 2012). Therefore, ITS and LSU sequences were aligned seperately in SATé version 2.2.5 using the following options: 'Aligner' = MAFFT, 'Merger' = MUSCLE, 'Tree Estimator' = RAxML, and 'RAxML Model' = GTRGAMMA. Each alignment was run for 500 iterations following the final improvement under the remaining default SATé settings. Ambiguously aligned positions were removed from the aligned ITS dataset using the program Gblocks v. 0.91b, implementing settings which allow for smaller final blocks, gap positions within the final blocks, and less strict flanking positions (Castresana 2000). Gblocks provides an objective and repeatable method to exclude difficult to align regions within a multiple sequence alignment, a procedure that has been shown to improve phylogenetic accuracy in some cases (Talavera & Castresana 2007). The Gblocks-modified ITS matrix and LSU alignment were combined for subsequent phylogenetic anlyses.

Phylogenetic hypotheses were constructed under both maximum likelihood (ML) and Bayesian inference (BI) criteria. ML searches were conducted using the program RAxML v. 7.2.8, allowing separate GTRGAMMA models with unique parameter values for each locus (Stamatakis 2006; Stamatakis *et al.* 2008). A search combining 200 separate maximum likelihood searches to find the optimal tree and 1000 'fastbootstrap' replicates to evaluate nodal support was conducted using the combined ITS/LSU dataset.

Bayesian phylogenetic inference was estimated from the combined dataset using the program MrBayes v. 3.1.2 (Huelsenbeck *et al.* 2001; Ronquist & Huelsenbeck 2003), using default priors. MrModeltest was used to identify the best-fitting model of evolution for each marker using the Akaike Information Criterion (AIC; Posada & Crandall 2001; Posada & Buckley 2004) and each marker was treated as a separate partition using unique parameter values for shared parameters and proportional partition rates. Four independent runs were executed with four chains; each run started from randomly generated trees and sampling every 1000 generations for 10 000 000 generations. To evaluate stationarity and convergence between runs, log-likelihood scores were plotted using the program Tracer v. 1.5 (Rambaut & Drummond 2005). Effective sample size (ESS) statistics were all ≫200 and the average standard deviation in split frequencies was below 0·01 (=0·0063) (Hall 2007). The first 250 000 generations were discarded as burn-in, and the results were summarized in the form of a maximum clade credibility tree using Tree Annotator (http://beast.bio.ed.ac.uk/TreeAnnotator).

Results and Discussion

The morphological analyses and comparison with the type material from Spain indicated that all the available epiphytic specimens were morphologically similar to *Aspicilia uxoris* s. lat. (Rico *et al.* 2007), including type material of three epiphytic species described from Asia: *Lecanora atrodiscata*, *L. ferganensis* and *L. takyroides*. Consequently, the three epiphytic species described from Asia become heterotypic synonyms for *Aspicilia uxoris*: *Lecanora ferganensis* (Fig. 2D), known from Kyrgyzstan, Tajikistan and Uzbekistan (Tomin 1950; Shafeev 1953; Kudratov 1984, 1985; Baibulatova 1988; Kudratov & Mayrhofer 2002); *Lecanora atrodiscata* (Fig. 2E), from Tajikistan growing on *Populus* sp. bark (Gintovt 1959); and *Lecanora takyroides* from Turkmenistan, growing on Turkmen juniper (Dzhuraeva 1974).

A total of 127 ambiguously aligned nucleotide positions were removed from the initial multiple sequence ITS alignment made in SATé, resulting in a combined ITS/LSU matrix consisting of 1191 aligned bp (ITS = 457 bp; and LSU = 706 bp). The ML and BI topologies from the combined dataset were identical at all well-supported nodes, and we chose to present the BI topology (Fig. 1). The '*Lobothallia*' group received moderate ML bootstrap support (BS = 64) and strong support in the BI topologies (posterior probability = 1·0) (Fig. 1). The '*Lobothallia* group' included *Lobothallia* s. str., '*Pachyothallia*' *sensu* Clauzade & C. Roux, and '*Aspicilia*' *uxoris*; however, relationships among these lineages were unresolved. Specimens representing '*Aspicilia*' *uxoris* s. lat. formed a well-supported monophyletic clade within the '*Lobothallia*' group (Fig. 1) and are hereafter referred to as the '*Teuvoa*' group, corresponding to the new genus *Teuvoa*. Specimens identified as '*Aspicilia*' *uxoris* s. lat. were recovered in two well-supported lineages within the *Teuvoa* group. One clade included isotype material from '*Aspicilia*' *uxoris* collected from Spain, labelled here as '*Teuvoa uxoris*' (Fig. 1). The specimen found on plant debris on soil in southern Anatolia ('*T.* aff. *uxoris*') was also recovered within the epiphytic '*T. uxoris*' clade, and was not related to the terrestrial species *A. mansourii* and *A. crespiana* (Fig. 1). The second well-supported lineage within the *Teuvoa* group contained *T. uxoris* s. lat. specimens collected in western North America and Iran. All specimens from western North America were recovered within a single well-supported lineage ('*T. junipericola*'), sister to a single specimen collected in Iran ('*T.* aff. *junipericola*'). *Teuvoa tibetica* was recovered as sister to the '*T. junipericola*' clade, with weak statistical support.

Relationships of major lineages within *Megasporaceae* are similar to results reported in Nordin *et al.* (2010) (Fig. 1). However, relationships among genera within *Megasporaceae* were generally only weakly supported in the present study.

In this study, a substantial number of ambiguous nucleotide characters were excluded from the nuclear ribosomal ITS marker. Although our results are largely congruent with previous phylogenetic hypotheses of *Megasporaceae* (Nordin *et al.* 2010), the impact of removing difficult to align regions,

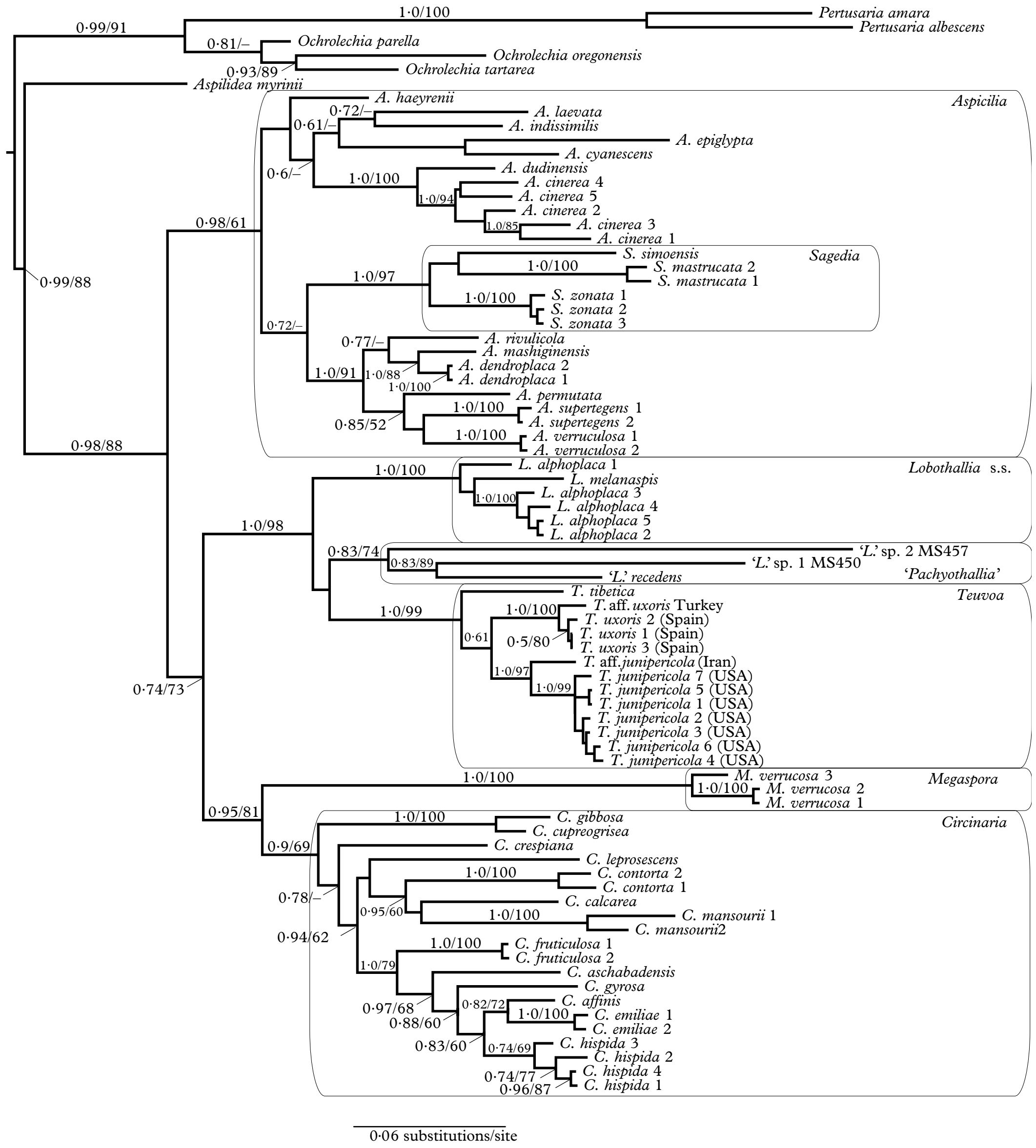

FIG. 1. Phylogenetic relationships within *Megasporaceae*, including the new genus *Teuvoa*, derived from Bayesian inference of nuclear ribosomal ITS and LSU sequence data. Values at each node indicate non-parametric bootstrap support (BS)/posterior probability (PP). Only support indices ≥ PP 0·50/ BS 50 are indicated. With the exception of the newly described genus in this study, *Teuvoa*, generic concepts within *Megasporaceae* follow Nordin *et al.* (2010) and Sohrabi *et al.* (2012).

which are often the most rapidly evolving regions and contain valuable phylogenetic signals (Lee 2001), is uncertain. These results highlight the importance of including additional loci for establishing a well-supported hypothesis of relationships within the family (Schoch *et al.* 2012). Current molecular sampling supports the distinction of *Lobothallia* s. str., '*Pachyothallia*' and *Teuvoa* as three monophyletic clades. Relationships within the *Lobothallia* s. str., '*Pachyothallia*' clades are currently under investigation using a multi-loci phylogenetic framework and will be presented in a subsequent paper (M. Sohrabi, S. D. Leavitt, A. Nordin & B. Owe-Larsson, unpublished).

According to Sohrabi *et al.* (2010*b*), *Teuvoa tibetica* (syn: *Aspicilia tibetica*) is a terricolous species, growing on plant debris at a high altitude in the Tibetan region of China. *Teuvoa uxoris* s. lat. is a predominantly lignicolous species, mainly reported on conifers from North America to Pakistan in the Holarctic (see Ecology and distribution). Both *T. tibetica* and *T. uxoris* s. lat. show morphological and chemical similarities: 8-spored asci, baciliform conidia, absence of extrolites (secondary substances) and a subhypothecial algal layer (Rico *et al.* 2007; Sohrabi *et al.* 2010*b*). However, specimens within *T. uxoris* s. lat. have larger non-globose spores, moniliform paraphyses, pruinose lecanoroid apothecia and it rarely develops rhizomorph-like extensions. Phylogenetic analyses revealed that *T. tibetica* and *T. uxoris* s. lat. are not conspecific, but are both nested in the new genus *Teuvoa*.

Taxonomy

Teuvoa Sohrabi & S. Leavitt gen. nov.

MycoBank No.: MB 800659

Type: *Teuvoa uxoris* (Werner) Sohrabi, V. J. Rico & S. Leavitt (BC hb. Werner! s. n.)

Thallus crustose, verrucose, distinctly areolate, rimose, contiguous, margin indistinct to distinct; *prothallus* absent. *Surface* white to grey, dull. Cephalodia absent. *Pseudocyphellae* absent. *Cortex* one layer, paraplectenchymatous. *Medulla* white, I−. *Photobiont Trebouxia* or other chlorococcoid genera; cells ± globose. *Ascomata* apothecial, aspicilioid. *Disc* black to brown-black, flat, rarely concave or convex. Thalline margin ± elevated, prominent; concolorous with thallus. True exciple thin, distinct, ± I+. *Epihymenium* green to olive-brown, N± light green, K± brown; *paraphysoids* (sub) moniliform to non moniliform, with (1–8) uppermost cells ± globose to subglobose. *Subhymenium* and hypothecium hyaline, I+ blue. *Asci* clavate, *Aspicilia*-type, wall and apical dome I−, outer coat I+ blue, with 8 spores. *Ascospores* hyaline, simple, globose to ellipsoid, I−. Conidiomata pycnidial, immersed, single or aggregated; ostiole dark, punctiform to elongated; conidiogenous cells sessile or on short conidiophores.

Conidia hyaline, simple, more or less filiform, straight.

Chemistry. Spot tests: cortex and medulla K−, C−, P−. Secondary metabolites: none detected.

Etymology. The generic epithet honours Professor Teuvo Ahti, one of the prominent lichen taxonomists of the 20th century.

Distribution. Mostly found in the temperate regions of the Holarctic, growing mainly on wood or plant debris.

Comments. *Teuvoa* is distinguished from *Aspicilia* by its small ascospores and conidia size (5–8 µm), and the absence of extrolites (secondary metabolites). It is also distinguished from *Lobothallia s. str.* by the lack of lobate, radiating thalli, a subhypothecial algal layer (in some), absence of extrolites [norstictic, constictic (9′-*O*-methylsalazinic acid) and salazinic acids], and having organic substrata corticolous/terricolous, on bark, wood and dead plant debris (non-saxicolous thalli). *Teuvoa* is separated from '*Aspicilia* subgenus *Pachyothallia* Clauzade & C. Roux' by the lack of a subhypothecial algal layer, lecanoroid apothecia, absence of extrolites (norstictic and constictic acids) and growing on organic substrata and a different ecological amplitude.

The Species

Teuvoa junipericola Sohrabi & S. Leavitt sp. nov.

MycoBank No.: MB 800661

Morphologically similar to Eurasian *T. uxoris* but differs somewhat by having larger ascospores (10–16 × 13–22 µm) and a different geographical distribution which is so far restricted to the arid continental regions of the western USA.

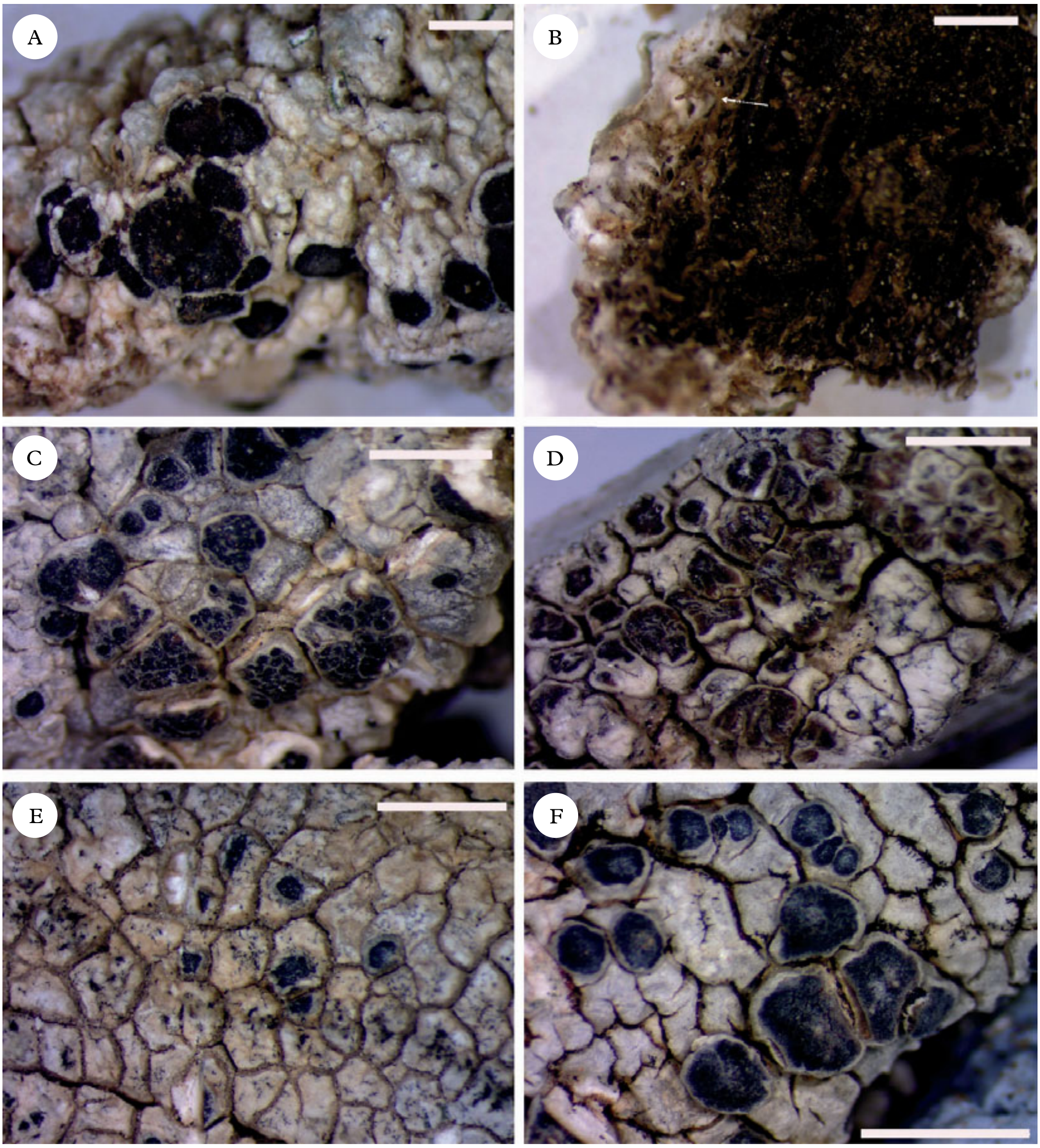

FIG. 2. A & B *Teuvoa uxoris*, habit, arrow indicates rhizomorph-like extensions (Turkey; *Halici* s. n.); C, *Lecanora atrodiscata* (LE L314—holotype); D, *Lecanora ferganensis* (H—isolectotype); E, *Lecanora takyroides* (LE L358—holotype); F, *Teuvoa junipericola*, Utah, USA (*Rosentreter* 14521, H—isotype). Scales: A–F = 1 mm. In colour online.

Type: USA, Utah, Kane County, East of Kanab, Five Mile Road area, off Hwy #89, 37°2′N / 112°14′W, pinyon-juniper woodland with *Artemisia tridentata* subsp. *wyomingensis*, *Hilaria jamesii*, mixed with *Artemisia nova* and *Oryzopsis hymenoides*, 1650 m, on *Juniperus* sp., 24 January 2001, *R. Rosentreter* 14521 (BRY—holotype; H, MAF—isotypes).

(Fig. 1F)

Thallus corticolous to lignicolous, on conifers. *Areoles* irregular, flat to convex, rather thick, opaque, angular to rounded. *Surface* grey to whitish grey, with a greenish shade, slightly roughened, ± pruinose, up to 2 mm wide.

Apothecia numerous, cryptolecanorine or ± urceolate when young, becoming lecanoroid or lecideoid when mature, orbicular to slightly angular, simple to frequently composite, up to 1·0–2·5 mm wide. *Disc* concave to plane or slightly convex when mature, brown to brownish black, but whitish to bluish grey by pruine. *Thalline exciple* ± well-developed, concolorous with thallus, thin, smooth, not flexuous. *True exciple* up to 160 µm wide laterally, variable in development and thickness, of ± paraplectenchymatous tissue. *Epihymenium* dark to olive brown, rarely light brownish, pigment N+ green to fairly blue-green, K+ brown to green, up to 30(–40) µm tall, with granular surface, partially soluble in N and K. *Hymenium* hyaline, I+ persistently blue, (80–)90–145(–160) µm tall, conglutinated. *Subhymenium* and hypothecium pale, I+ persistently blue. *Paraphyses* moniliform, usually simple, rarely branched in lower parts and anastomosed, with 1–7 globose to subglobose cells apically. *Asci* clavate, (65–)70–120(–135) × 18–30(–35) µm, 8-spored, apical apparatus thick, K/I−. *Ascospores* hyaline, simple, (10–)11[12·9]14(–16) × (13–)16[17·9]19(–22) µm, ($n = 81$), ellipsoid to elongate (-cylindrical).

Pycnidia usually very common, 1–3(–5) per areole, immersed, often indistinct, occasionally with a white rim, and aggregated, 100–300 µm diam.; with a brownish or black ostiole, 40–100(–190) µm diam. *Conidia* 5–8 × 0·75–1·00(–1·70) µm, bacilliform, straight.

Chemistry. Spot test: cortex and medulla K−, C−, KC−, I−, and PD−. Secondary metabolites: no lichen substances detected.

Etymology. The specific epithet refers to the substratum (*Juniperus* tree) on which this new species was found.

Distribution and ecology. Widespread in the arid continental regions of the western USA, largely restricted to the Colorado Plateau and Great Basin.

Comments. *Teuvoa junipericola* has the habit of *T. uxoris*, growing on juniper trees, and prefers arid climates. Previously, it was reported by Shrestha & St. Clair (2009) as *Aspicilia uxoris*, new to the USA, but detailed morphological investigations of the American and Eurasian specimens of *A. uxoris* showed that American species generally have a larger ascospore than the Eurasian specimens (see also Fig. 3). To assess this difference, molecular sequence data were obtained from several American and Eurasian specimens. The results show that all American specimens were included within a single well-supported lineage *T. junipericola*, sister to a single Eurasian specimen collected in Iran ('*T.* aff. *junipericola*'). Detailed morphological studies showed that the Iranian specimen has an intermediate ascospore size compared to other American and Eurasian specimens. Therefore, we refrain from including the Iranian specimen within the new species *T. junipericola* until additional specimens from Central Asia are investigated.

Additional specimens examined. **USA:** *Colorado*: Moffat County, Dinosaur National Monument, Deerlodge Park, Plug Hat Picnic Area, 40°17·584′N / 108°57·991′W, 2073 m, in pinyon-juniper woodland, on lignum of *Juniperus osteosperma*, 5 v 1992, *L. St. Clair, C. Newberry & K. St. Clair* (BRY – 35721). *Utah*: Duchesne County, Pinyon Ridge Rest Area, along US Highway 40°12·231′N / 110°42·777′W, 2055 m, in *Pinion-Juniper* woodland, 2009, *L. St. Clair, S. Leavitt* 742 *& G. Shrestha* (BRY); San Juan County, vicinity of Moonhouse Ruin, 37°25·855′N / 109°47·823′W, 1761 m, in pinyon-juniper woodland, 2009, *S. Leavitt* 850 *& J. Leavitt* (BRY); Uintah County, Brush Creek Drainage of Coyote Gulch near US Route 191, 40°35′15·7′N / 109°28′32·2′W, 1786 m, in pinyon-juniper woodland, 15 vii 2009, *L. St. Clair, S. Leavitt. G. Shrestha & C. Newberry* [Leavitt 767 (BRY)]; Wayne County, vicinity of Upper Muley Twist Trailhead, 37°51·647′N / 111°02·414′W, 1773 m, on *Juniperus* lignum in pinyon-juniper woodland, 2008, *Leavitt* 843, 844 & 845 *& M. Felix* (BRY).—**Iran:** *Golestān*: Gorgān district, Shahkuh-e-Bala, *c.* 33 km S of Gorgān along minor road to Shahrud, 36°33·69′N / 54°33·68′E, 2600 m, *Astragalus* steppe with scattered *Juniperus excelsa* on steep mountain slope in valley, on decorticated wood of *J. excelsa*, 2007, *M. Sohrabi* 9507B, *H. Sipman, U. Søchting & R. Zare* (hb. M. Sohrabi, IRAN, B, H, MAF-Lich. 16248, here as *Teuvoa* aff. *junipericola*).

Teuvoa uxoris (Werner) Sohrabi, V. J. Rico & S. Leavitt comb. nov.

MycoBank No.: MB 800660

Lecanora uxoris Werner, *Bull. Soc. Sci. Nat. Maroc* **18**(2): 130–131 (1938) [basionym, as "*Lecanora* (*Zeora*) *uxoris*"]; type: [Morocco: Ifrane: road from Azrou to Midelt,] Ad

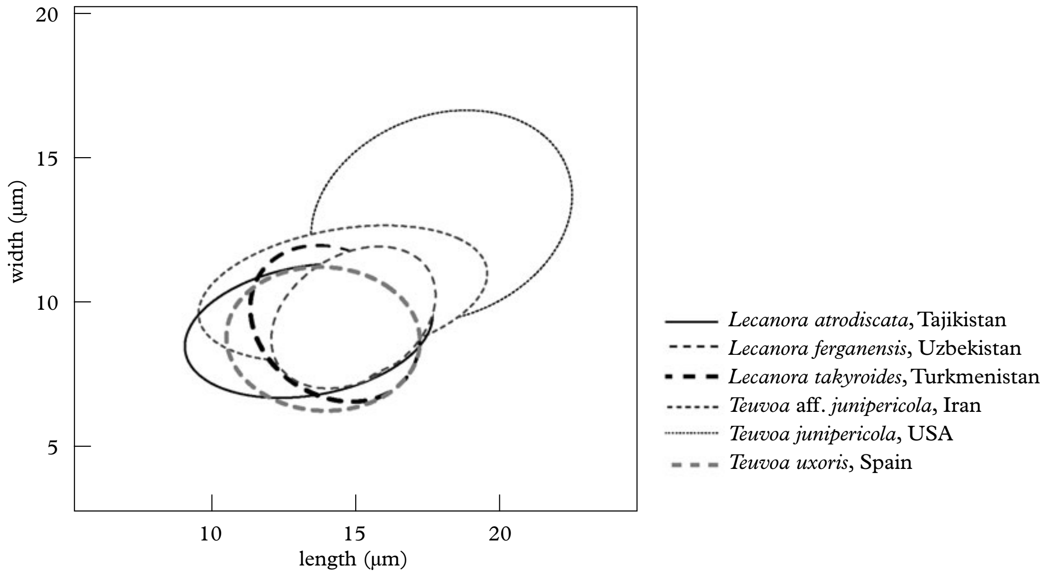

FIG. 3. Relationship between ascospore length and width within the Eurasian and North American species of the genus *Teuvoa* with 95% confidence ellipses obtained from ascospore measurements of 30 ascospores per specimen. The graph was implemented in the R program using boxplot and ellipse packages (see R Development Core Team 2008).

corticem *Juniperi thuriferae* cum *Parmelia jacquesii* prope lacum Si[di] Ali-ou-Mohand dictum in Atlante Medio ad alt. 2100 m, [33°05′N, 05°00′W,] 30 viii [19]34 (BC hb Werner! s. n.—lectotype and isolectotype).—*Aspicilia uxoris* (Werner) V. J. Rico, Aragón & Esnault, *Lichenologist* **39:** 110 (2007).

New heterotypic synonyms:

Lecanora ferganensis Tomin, *Sborn. Naučn. Trudov Inst. Biol. Akad. Nauk Belorussk. SSR [Minsk]* **1:** 82 (1950); type: “In promontoriis jugi Alaiensis, Ad lignum nudum Juniperi, Dzhajlau Schaid”, Uzbekistan, Ferganskaya Oblast’, close to the Alai Range, Shand summer pastures, on lignum of old *Juniperus* sp., 26 November 1946 [?8], *N. Shafeev* s. n. (MSK s. n.!—lectotype, designated here; H s. n.!—isolectotype; LE L328!—isolectotype).—*Aspicilia ferganensis* (Tomin) Baĭbul. *ad int.*

Lecanora atrodiscata Gintovt, *Uzbeksk. Biol. Žurn.* **4:** 72 (1959); type: Tajikistan, Leninobod, between Panjakent and Urmetan, south-western slope of the Dashtikazy canyon, on the bark of *Populus* sp., 7 June 1956, *E. A. Gintovt* (LE L314—holotype).

Lecanora takyroides Dzhur., *Novosti Sist. Nizšh. Rast.* **11:** 294 (1974); type: Turkmenistan, Akhal’skaya Oblast’, central Khrebet Kopet Dag Mountains, Dushak summit, 2290 m, on dry twigs of Turkmen juniper [*Juniperus polycarpos* K. Koch.], 2 June 1967, *Z. Dzhuraeva* s. n. (LE L358—holotype).

(Figs 1A–E)

A full description is provided in Rico *et al.* (2007); an actualized short description, with ecological data, is included here. *Thallus* corticolous to lignicolous, on conifers or rarely on deciduous trees (*Populus* sp.), areolate to rimose-areolate or slightly verrucose. Sometimes the thalli become partially detached from the phorophyte, forming holes between the lichen and the bark or wood, finally become detached portions and fall to the ground, carrying bark portions on the lower surface and developing whitish to yellow-brown rhizomorph-like hypothalline extensions, 1–3 mm long.

Distribution and ecology. Based on the results of this study, it appears that *T. uxoris* represents an element with typical Madrean-Thethyan disjunction (Raven 1971; Wen & Ickert-Bond 2009). *Teuvoa uxoris* belongs to a Mesogean contingent (cf. Quézel 1978), widely distributed in large isoclimatic continental Mediterranean areas of the Mediterranean, Irano-Turanian and Saharo-Sindian phytogeographical regions, as was suggested for some terricolous lichens by Barreno (1991). Pending additional data, it appears that some other lichen species, including terricolous (such as vagrant *Circinaria*), epiphytic and saxicolous species, with similar distributional and ecological ranges could be included in this Mesogean lichen contingent (e.g. Follmann & Crespo 1974; Crespo & Barreno 1978; Barreno 1991; Egea & Alonso 1996; Martínez *et al.* 2003; Rico *et al.* 2007). Furthermore, several bryophytes exhibit a similar type of distribution (cf. Moya *et al.* 1995).

Teuvoa uxoris has been collected on various coniferous trees and shrubs: *Cedrus atlantica* (Endl.) Manetti, *Juniperus oxycedrus* L., *J. phoenicea* L., *J. thurifera* L. and *Pinus halepensis* Miller (Rico *et al.* 2007). Taking into account that all these phorophytes are conifers, which have a very acid bark, and that bark acidity is one of the most important and selective chemical factors for epiphytic lichens (Barkman 1958), it can be expected that *T. uxoris* may also occur on other coniferous species, such as *Juniperus excelsa* M.-Bieb., *J. osteosperma* (Torr.) Little, *J. polycarpos* K. Koch. and *J. sabina* L. All these *Cupressaceae* have a largely relictual distribution in the Holarctic, from western Mediterranean mountains (*J. sabina*) or the eastern Mediterranean (*J. excelsa* and *J. polycarpos*) to Minor Asia, Central Asia (e.g. Iran, Uzbekistan), Pakistan (Baluchistan) and India (Himachal Pradesh), where they form open forest ± confined to semi-arid regions (Vidakovic 1991; Farjon 1992, 2005). The preference of *Teuvoa uxoris* for conifers forming ± open forest and growing on calcareous substrata, with continental influences (never near the coast) in a contrasted seasonal climate (cold-hot, ± semi-arid), suggests that the range of *T. uxoris* may extend still further in view of the availability of suitable host trees and climate conditions. Furthermore, within *T. uxoris*, two records appear to have a deviating substratum preference: a collection from Turkey was found on debris on soil under *Juniperus* trees; and the type collection of '*Lecanora*' *atrodiscata* was on *Populus* bark in Tajikistan. These specimens indicate that *T. uxoris* is not restricted to conifers.

Comments. The taxonomy of epiphytic *Teuvoa uxoris* populations in Central Asia, including '*Lecanora*' *atrodiscata*, '*L.*' *ferganensis* and '*L.*' *takyroides*, remains uncertain. All three species are morphologically and chemically similar to *T. uxoris*. Type collections corresponding to '*L.*' *atrodiscata* and '*L.*' *takyroides* were found in LE herbarium. One of three specimens of '*L.*' *ferganensis* found in MSK herbarium (with collecting date "26.XI.1946[?8]") is clearly identifiable with the original description in Tomin (1950) and consequently is designated here as a lectotype. However, the relationship of these collections with other epiphytic species within *Teuvoa* remains unclear. The only specimen from Central Asia, included in the phylogenetic portion of this study, *T.* aff. *uxoris*, is morphologically and chemically indistinguishable from *T. uxoris* s. str., but appears to be more closely related to *T. junipericola* from western North America. Ultimately it appears likely that molecular phylogenetic studies will be required to accurately resolve the taxonomy of these epiphytic populations from Central Asia.

Additional specimens examined. **Spain:** *Castilla-La Mancha*: Guadalajara, Zaorejas, carretera de Villanueva de Alcorón a Zaorejas, cruce a Huertapelayo, sabinar en calizas, sobre *Juniperus thurifera*, 40°43′58·57″N / 2°12′35·92″W, 2006, *V. J. Rico* 3622 *& J. Pizarro* (BRY 765, 766, H, MAF-Lich. 14275).—**Turkey:** Konya, *G. Halici* s. n. (hb. Halici, here as *Teuvoa* aff. *uxoris*).

Teuvoa tibetica (Sohrabi & Owe-Larss.) Sohrabi comb. nov.

MycoBank No.: MB 800667

Aspicilia tibetica Sohrabi & Owe-Larss., *Mycological Progress* **9:** 492 (2010); type: China, Tibet (Xizang), Himalaya Range, 135 km SSW of Lhasa, SSE of Pomo Tso (=Puma Yumco), near the pass into the Kuru valley, way from the pass-road to the glacier, 28°28′N, 090°37′E, alt. 5100–5300 m, *Kobresia* meadows and slopes covered with rock debris, on soil, 18 July 1994, *Obermayer* 04386 (GZU s. n.!—holotype; H s. n.!—isotype).

New combinations on *Circinaria*

As a consequence of our analysis, the following new combinations are proposed:

Circinaria mansourii (Sohrabi) Sohrabi comb. nov.

MycoBank No.: MB 800662

Aspicilia mansourii Sohrabi, *Phytotaxa* **18:** 17 (2011); type: Iran, Golestan National Park, Mirzabaylou towards Almeh valley, 37°21′N, 56°12′E, 1300 m, May 2008, *Sohrabi* 15077 & *Ghobad-Nejhad* (IRAN MS015088!—holotype; H MS016188!, GZU MS016189!, hb. M. Sohrabi MS016192!—isotypes).

Circinaria crespiana (V. J. Rico) Sohrabi & V. J. Rico comb. nov.

MycoBank No.: MB 800663

Aspicilia crespiana V. J. Rico, Aragón & Esnault, *Lichenologist* **31:** 130 (1999); type: Spain, Madrid, San Martín de Valdeiglesias, road from Cadalso de los Vidrios to Pelayos de la Presa, km 3, Corcobada, 740 m, overgrowing *Grimmia* sp. on horizontal sun-exposed granitic rocks, 30TUK843668, 12 February 1988, *V. J. Rico* 1249/1 & *M. A. Florido* (MAF-Lich. 4221!—holotype; MA-Lich. 3274!—isotype).

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