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# Taxonomy of the genus *Athallia* and its diversity in Turkey

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**Abstract:** Molecular analyses of ITS nrDNA, using 42 new and 56 GenBank sequences, revealed 12 supported lineages of *Athallia* consistent with phenotype data. We regard these lineages as species. Eight of them were previously recognized as species in *Athallia*, and here we make three new combinations: *A. baltistanica*, *A. brachyspora*, and *A. necator*. Eight of these species have been recorded in Turkey; of them, *A. baltistanica* and *A. saxifragarum* are new to the country. The former is also new to Greece. *Athallia baltistanica* is recorded for the first time outside the Karakoram Mountains (N Pakistan). We propose a broader species concept for *A. holocarpa*, and we include *A. vitellinula* and *Caloplaca alcarum* within it. (The name *Caloplaca alcarum* has also been used incorrectly in the past for morphs of *A. scopularis* with reduced lobes.) *Athallia nesodes* includes two traditionally recognized taxa: *Caloplaca inconnexa* var. *nesodes* and *Caloplaca inconnexa* auct., non (Nyl.) Zahlbr. Our observations of type specimens show *Caloplaca necator* to be distinct from *A. nesodes*. We consider *Athallia saxifragarum* and *Caloplaca schoeferi* to be conspecific. The position of "*Caloplaca*" *raesaenenii* is ambiguous based on ITS data, being placed within or outside *Athallia* depending on the type of analysis.

**Key words:** *Athallia baltistanica*, *Caloplaca alcarum*, *inconnexa*, *nesodes*, *raesaenenii*, ITS nrDNA, phylogeny, species concept, Teloschistaceae

## 1. Introduction

*Athallia* was recently established to accommodate a monophyletic group of crustose lichens of Teloschistaceae that were formerly placed in the large genus *Caloplaca*. It is closely related to another newly established genus, *Flavoplaca* (Arup et al., 2013). Most (but not all) species of *Athallia* have a strongly reduced thallus. Unfortunately, some of the small genera that have been split from *Caloplaca* are difficult to delimit on morphological grounds alone. Some crustose members of Teloschistaceae with a strongly reduced thallus, and scarcely distinguishable from species of *Athallia* in that character, are now placed in other genera. On the other hand, a few *Athallia* species have well-developed yellow-orange areolate or lobate thalli and resemble various species now placed elsewhere. Because it can be difficult to place some *Athallia*-like specimens by morphological appraisal alone, ITS fingerprinting is useful to confirm their identities.

During our project we collected thousands of Teloschistaceae crusts from some 700 localities distributed throughout Turkey. At least one specimen of each morphotype was selected for ITS fingerprinting. Our ITS sequence data revealed many *Athallia* specimens in our dataset. Some placements were surprising, e.g., we had not anticipated that "*Caloplaca inconnexa*" specimens would be placed into *Athallia*. This paper combines four species into *Athallia*; provides new concepts of *A. holocarpa*, *A. nesodes*, and *A. saxifragarum*; and provides distributional data for all *Athallia* taxa occurring in Turkey.

## 2. Materials and methods

### 2.1. Sampling and phenotype appraisal

Most of our samples are from Turkey, but in the molecular analyses we also included some from Mediterranean and Central Europe (Appendix 1). Specimens collected by Halıcı (CL) are deposited in ERC (Kayseri, Turkey) and specimens collected by Vondrák (JV) in PRA (Průhonice, Czech R.). The locality details of the specimens examined are given in Appendix 2. We have previous experience recognizing most formerly known *Athallia* taxa from their phenotypes. Although the number of diagnostic characters is limited (Arup, 2009; Vondrák et al., 2012), most of the

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taxa are recognizable using a few simple morphological characters in combination with their ecology, and so we did not spend time searching for further minute characters.

**2.2. Genotype appraisal**

DNA was extracted by simple NaOH extraction (Werner et al., 2002). Primers for PCR amplification of ITS were ITS1F (Gardes and Bruns, 1993) and ITS4 (White et al., 1990); PCR cycling parameters for ITS follow Ekman (2001).

ITS nrDNA sequence data are used in our study for practical reasons: they are easily generated, the GenBank database includes a number of ITS sequences for reasonable fingerprinting, and ITS one-locus genealogies are usually consistent with phenotypic data (seen in numerous ITS-based studies on Teloschistaceae). Sequences of all "species" (or, more accurately, morphotypes) of recorded Turkish Teloschistaceae crusts were taken into the Nucleotide BLAST at http://blast.ncbi.nlm.nih.gov/Blast.cgi to obtain better information about their placement. Our sequences related to GenBank sequences of *Athallia* were aligned and analyzed as follows: our own sequences (42) were manually aligned with 56 GenBank sequences in BioEdit software; most of the GenBank data used are from Gaya et al. (2008), Arup (2009), Vondrák et al. (2012), and Arup et al. (2013). Newly obtained sequences are given Appendix 1. We used sequences of the closely related genera *Calogaya*, *Flavoplaca*, and *Solitaria* as an outgroup. Maximum likelihood (ML) phylogenetic analysis was run in the application PHYLOGENY.FR (Dereeper et al., 2008) with 250 bootstraps and a default substitution model; ML reconstruction is shown in Figure 1 (left). Maximum parsimony (MP) analysis was done in TNT (Goloboff et al., 2000) via the PHYLOGENY.FR application, with 250 bootstrap replicates and the "jackknife" setting (Figure 1, right). MrBayes analysis was also run via the PHYLOGENY.FR application, with the GTR likelihood model and Monte Carlo permutation test with 10,000 generations and 25% tree burning. Neighbor-joining analysis was performed with BioEdit software. The Bayesian tree showed the same topology as the ML tree, and the neighbor-joining tree showed almost identical topology to that of the MP tree (their reconstructions are not shown).

## 3. Results

**3.1. Molecular analyses**

The ITS alignment has 590 positions including numerous in-del positions. The alignment has 250 variable positions, but 172 positions are variable in the ingroup containing 85 sequences. We recognized 13 species in the ITS phylogeny reconstruction as seen in Figure 1 (maximum likelihood on the left, parsimony on the right). The genus *Athallia* forms a supported clade (BS = 0.86 in ML; 0.9 in MP tree). The numbers of nucleotide positions characterizing each *Athallia* species against the others are given in Table 1. Species *A. alnetorum*, *A. cerinella*, *A. cerinelloides*, *A. holocarpa*, *A. saxifragarum*, and *A. scopularis* are closely related, which is shown in Table 1. *Athallia alnetorum*, *A. cerinella*, *A. holocarpa*, and *A. scopularis* form a crown group of the *Athallia* tree in Figure 1. Species clades in the crown group are on short branches with bootstrap supports between 0.9 and 1.0 in ML, but *A. holocarpa* and *A. scopularis* do not form supported clades in the MP analysis. In the ML analysis, an unknown taxon, *A.* aff. *holocarpa* (thermomediterranean epiphyte), is placed into the *A. holocarpa* clade (Figure 1, left), but it forms a tight group of three almost identical sequences distinguished from *A. holocarpa* by 18 diagnostic nucleotide positions (Table 1); in the MP tree, it forms a well-supported clade in polytomy with other crown-group taxa (Figure 1, right). No closely related taxa are known for *A. baltistanica*, *A. brachyspora*, *A. nesodes*, *A. pyracea*, and *A. skii*. These taxa are well resolved on long branches in the ML tree, with bootstrap support of >0.97.

We cannot resolve the position of "*Caloplaca*" *raesaenenii*, which is a part of *Athallia* in the MP tree (Figure 1, right) and the neighbor-joining tree (not shown), but it is placed outside *Athallia* in the ML analysis (Figure 1, left) and in the Bayesian tree (not shown). Thus, *C. raesaenenii* is probably the closest outgroup taxon to *Athallia* or perhaps a part of it. The relations of *C. raesaenenii* to all definite *Athallia* species are shown in Table 1.

**3.2. New combinations**

***Athallia baltistanica* (Poelt & Hinter.) Halıcı & Vondrák, comb. nov.**

[MycoBank number: MB812685]

**Basionym:** *Caloplaca baltistanica* Poelt & Hinter., in Biblthca Lichenol. 50: 82 (1993).

**Type:** Pakistan, Karakoram Mts., Gilgit, Rakaposhi Range, Baghrot, 36°03′N, 74°35′E, on wood, 1991, coll. J. Poelt (GZU, holotype; GZU (K91-646), paratype!, Figure 2).

Its apothecia and pale gray/yellowish thallus resemble *Athallia alnetorum* or *A. pyracea*, but the presence of yellow to gray blastidia/granules on the thallus is diagnostic (Figure 2). It is the only epiphytic blastidiate/granulate *Athallia*. Granules are sometimes present in the saxicolous *Athallia necator*, but that species usually has a well-developed yellow-orange thallus that is lichenicolous on epilithic lichens. *Athallia alnetorum*, sometimes occurring together with *A. baltistanica*, and *Gyalolechia flavorubescens* are similar, but they have flat yellow thalli without isidia (Giralt et al., 1992). *Blastenia coralliza* with delicate coralloid gray to yellow blastidia/isidia differs in its red apothecia and C+ purple apothecial margin containing chlorinated anthraquinones (Arup and Åkelius, 2009).

*Gyalolechia juniperina* (synonyms: *Caloplaca laricina* and *C. juniperi*) has a somewhat similar blastidiate/

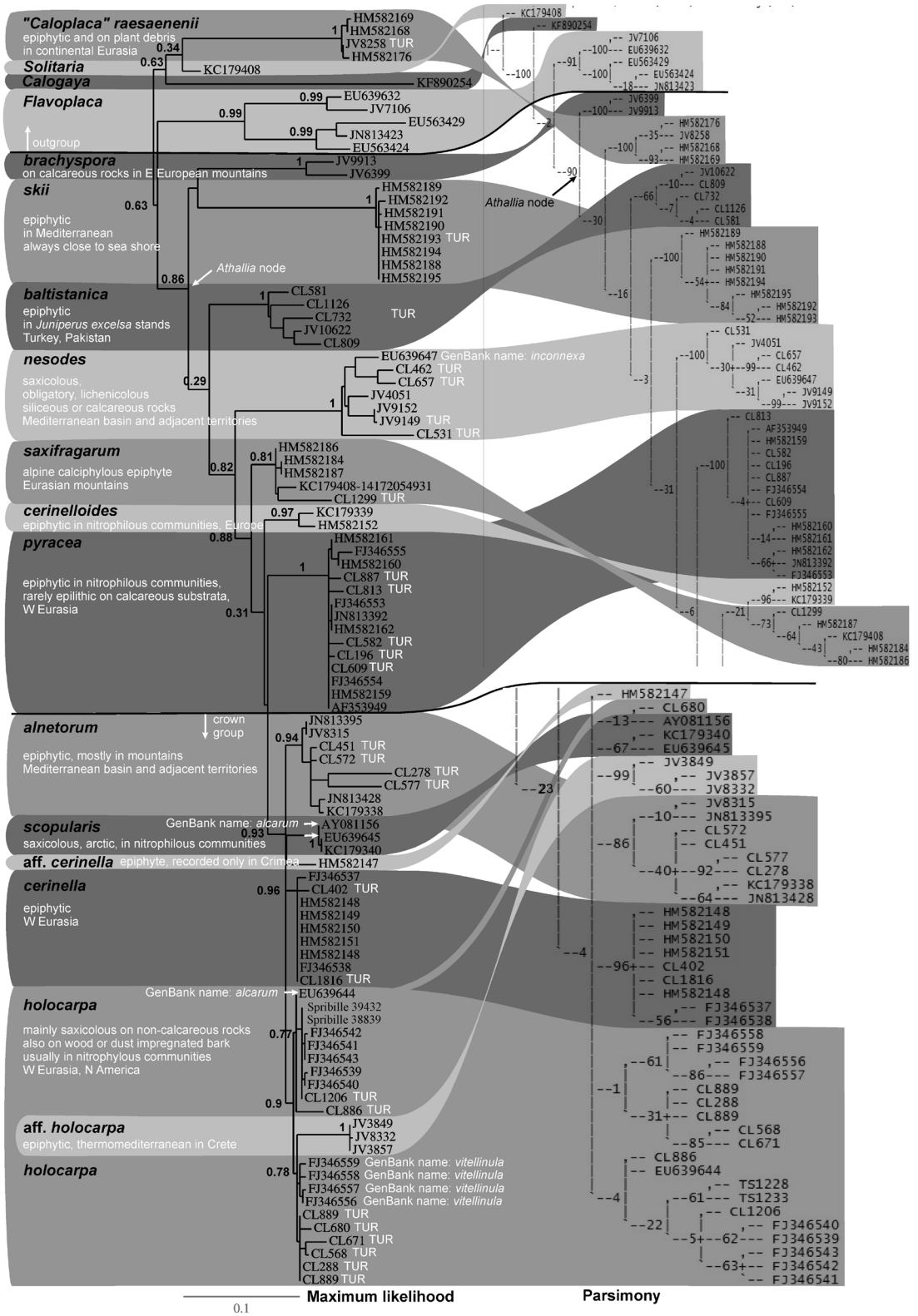


**Figure 1.** Phylogenetic reconstruction of the ITS nrDNA region for the genus *Athallia*. Maximum likelihood approach (left tree) and parsimony (right tree); both trees with bootstraps.

**Table 1.** Differences in ITS sequences among species in *Athallia*. Numbers of characters, i.e. nucleotide positions characterizing each *Athallia* species against the others, are shown. Each diagnostic in-del position is considered equal to a single nucleotide character.

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| aff. holocarpa | 20 | 38 | 59 | 25 | 31 | 18 | 32 | 31 | 90 | 27 | 28 | 56 |
| | alnetorum | 34 | 52 | 11 | 19 | 7 | 31 | 29 | 83 | 15 | 15 | 59 |
| | | baltistanica | 43 | 37 | 32 | 34 | 43 | 41 | 70 | 34 | 37 | 59 |
| | | | brachyspora | 66 | 51 | 54 | 52 | 52 | 64 | 52 | 58 | 69 |
| | | | | cerinella | 17 | 7 | 34 | 33 | 83 | 15 | 15 | 60 |
| | | | | | cerinelloides | 16 | 23 | 24 | 75 | 16 | 23 | 64 |
| | | | | | | holocarpa | 31 | 29 | 82 | 16 | 11 | 62 |
| | | | | | | | nesodes | 38 | 99 | 32 | 45 | 63 |
| | | | | | | | | pyracea | 80 | 26 | 27 | 66 |
| | | | | | | | | | raesaenenii | 75 | 84 | 96 |
| | | | | | | | | | | saxifragarum | 20 | 51 |
| | | | | | | | | | | | scopularis | 66 |
| | | | | | | | | | | | | skii |

isidiate thallus; it commonly grows on *Juniperus excelsa* in continental Eurasia (Tomin, 1953; Poelt and Hinteregger, 1993). It differs from *A. baltistanica* in its red and C+ purple apothecia and pycnidia containing chlorinated anthraquinones (B3 chemosyndrome in Søchting, 2001). Some other sorediate/isidiate species of *Gyalolechia* (e.g., *G. oxneri* and *G. persimilis*) are somewhat similar but they have distinct chemistry with chlorinated anthraquinones and large amounts of fragilin (chemosyndrome B in Søchting, 2001). These epiphytic *Gyalolechia* species are not known from Turkey.

We found *Athallia baltistanica* only on the bark of *Juniperus excelsa* at altitudes of 850–1750 m in Turkey, in rather dry *Juniperus excelsa*-dominated forests, usually on calcareous bedrock. Our records are mostly from the Taurus Mountains in southern Turkey, but two records are from the continental parts of Aegean Turkey. Our Greek record is from unidentified tree bark in dry Cretan mountains, Orosira Dikti. It is probably common in continental Eurasian mountains with *Juniperus excelsa* forests, but it was previously known only from a few sites in the Karakoram Mts. (Poelt and Hinteregger, 1993), on bark of *Juniperus* and on wood. Only one *A. baltistanica* sample is currently available in GZU (no. K91-646, paratype). Except for its deeper orange apothecial discs (Figure 2) we found it morphologically very similar to our specimens.

***Athallia brachyspora* (Mereschk.) Halıcı & Vondrák, comb. nov.**

[MycoBank number: MB812681]

**Basionym:** *Caloplaca brachyspora* Mereschk., in Lich. Flor. Ross. Occid. Exsicc.: no. 22 (1913).

**Type:** Crimean Yayla Mountains, from the monastery of Kosma and Demian (Mereschkowsky: Lichenes Rossiae Exsiccati 276; BP 27078, lectotype!).

This taxon was long forgotten until Vondrák et al. (2010) resurrected it. Malíček et al. (2014) reported it as common in the (sub)alpine belt of the Slovakian Carpathians. As it was described from southern Crimea (Mereschkowsky, 1913), it probably occurs in Turkey, though it is not yet reported for the country. Its position within *Athallia* is shown in Figure 1.

***Athallia nesodes* (Poelt & Nimis) Halıcı & Vondrák, comb. nov.**

[MycoBank number: MB812682]

**Basionym:** *Caloplaca inconnexa* var. *nesodes* Poelt & Nimis 1987.

**Type:** Sardinia, Nuoro, Catena delle Margine, Punta Palai, coll. Nimis & Poelt, 1985, GZU 292657, holotype!);
≡ *C. inconnexa* subsp. *nesodes* (Poelt & Nimis) Cl. Roux

= *Caloplaca inconnexa* auct. p.p., non (Nyl.) Zahlbr.

**Non** *Caloplaca necator* Clauzade & Poelt in Poelt, Planta 51: 302 (1958); type: France, Provence, Rochers de la Chapelle de Notre Dame des Anges, Rustrel, Vaucluse, alt. 350 m, 1957, coll. G. Clauzade and J. Poelt (M 163557, holotype!).

This *Athallia* is usually recognizable in the field by its tiny areolate to granular yellow-orange thallus, usually spread on thin crusts of other lichens or squeezed between areoles of thicker crusts. *Athallia* areoles are smaller

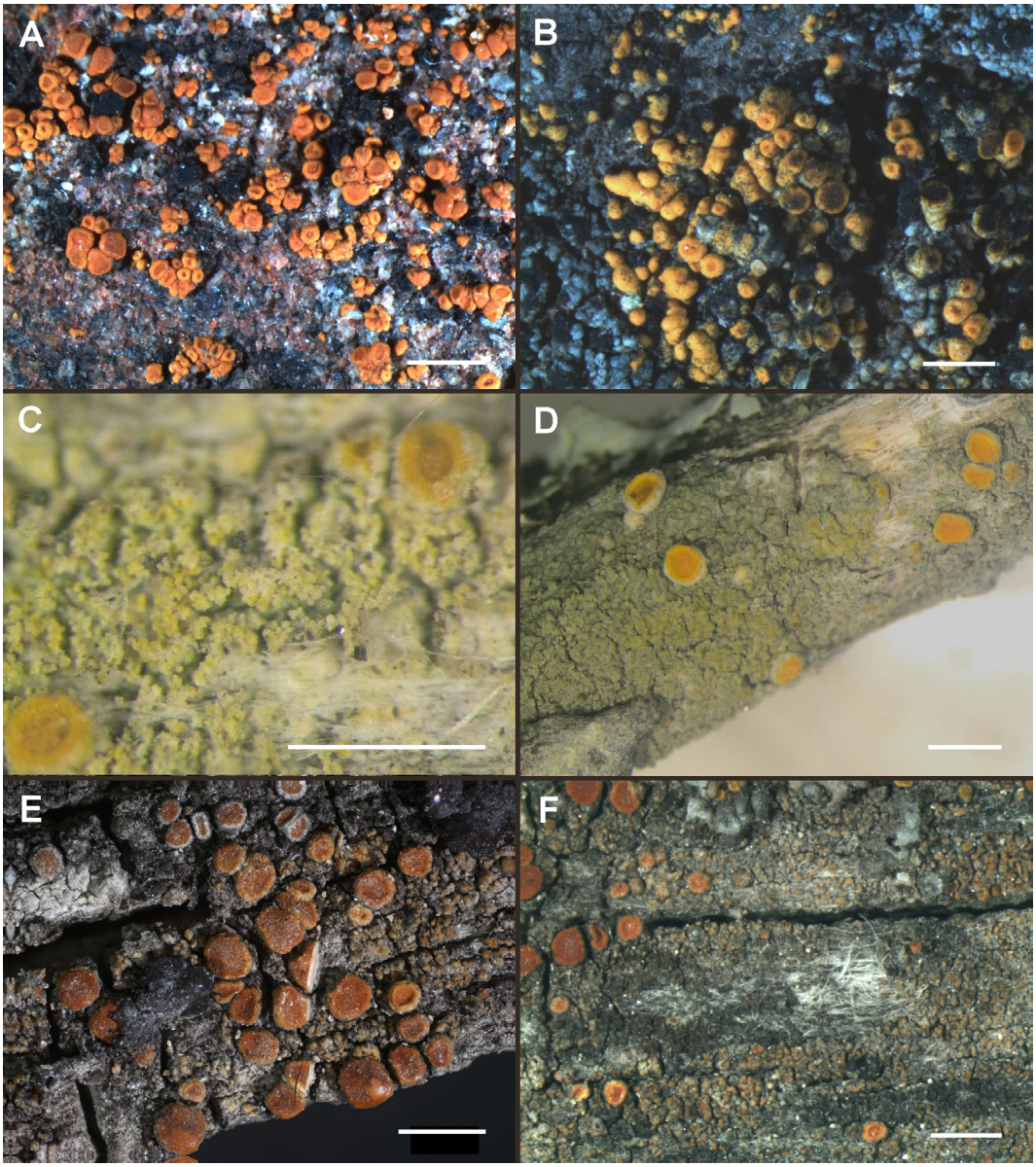


**Figure 2.** A) *Caloplaca alcarum* holotype (=*Athallia holocarpa*); B) *Caloplaca alcarum* auct., Island, *Kristinsson 9556* (=*Athallia scopularis*, form with reduced lobes); C–F) *Athallia baltistanica*; C) CL 1.126, morphotype with tiny granules; D) CL 0.732; E, F) paratype, *Poelt K91-646* (GZU), with *Caloplaca cerina* s.lat. in E; bars - 1 mm.

than those of *Variospora velana* and larger than granules in *Flavoplaca coronata*. Both of the latter species often occur together with *Athallia inconnexa*, but they are only facultatively lichenicolous.

To our understanding, *A nesodes* includes two traditionally recognized taxa: (1) What has been called (incorrectly) "*Caloplaca inconnexa*" by some authors, usually growing on calcareous substrata and lichenicolous on various lichen crusts, especially *Acarospora cervina* (Figure 3), *Aspicilia calcarea*, and *Lecanora saxicola* (Vondrák et al., 2007; Halıcı and Aksoy, 2009; Urbanavichus and Ismailov, 2013; Vondrák and Wirth, 2013; Kocakaya et al., 2014); and (2) *Caloplaca inconnexa* var. *nesodes*, occurring on coastal or inland siliceous rocks and lichenicolous on *Aspicilia* spp. (Figure 3) (Nimis and Poelt, 1987; Vondrák and Slavíková-Bayerová, 2006; Vondrák et al., 2008; Roux, 2014).

*Caloplaca necator* Clauzade & Poelt is also lichenicolous on *Aspicilia* and similar to *A. nesodes*, but it has been said to have smaller ascospores (Nimis and Poelt, 1987). Roux et al. (2014) suggested that some French specimens called *C. necator* are probably identical to *C. inconnexa* var. *nesodes* and we suspected that *C. necator* and *A. nesodes* were conspecific. After studying the type specimens of both taxa,

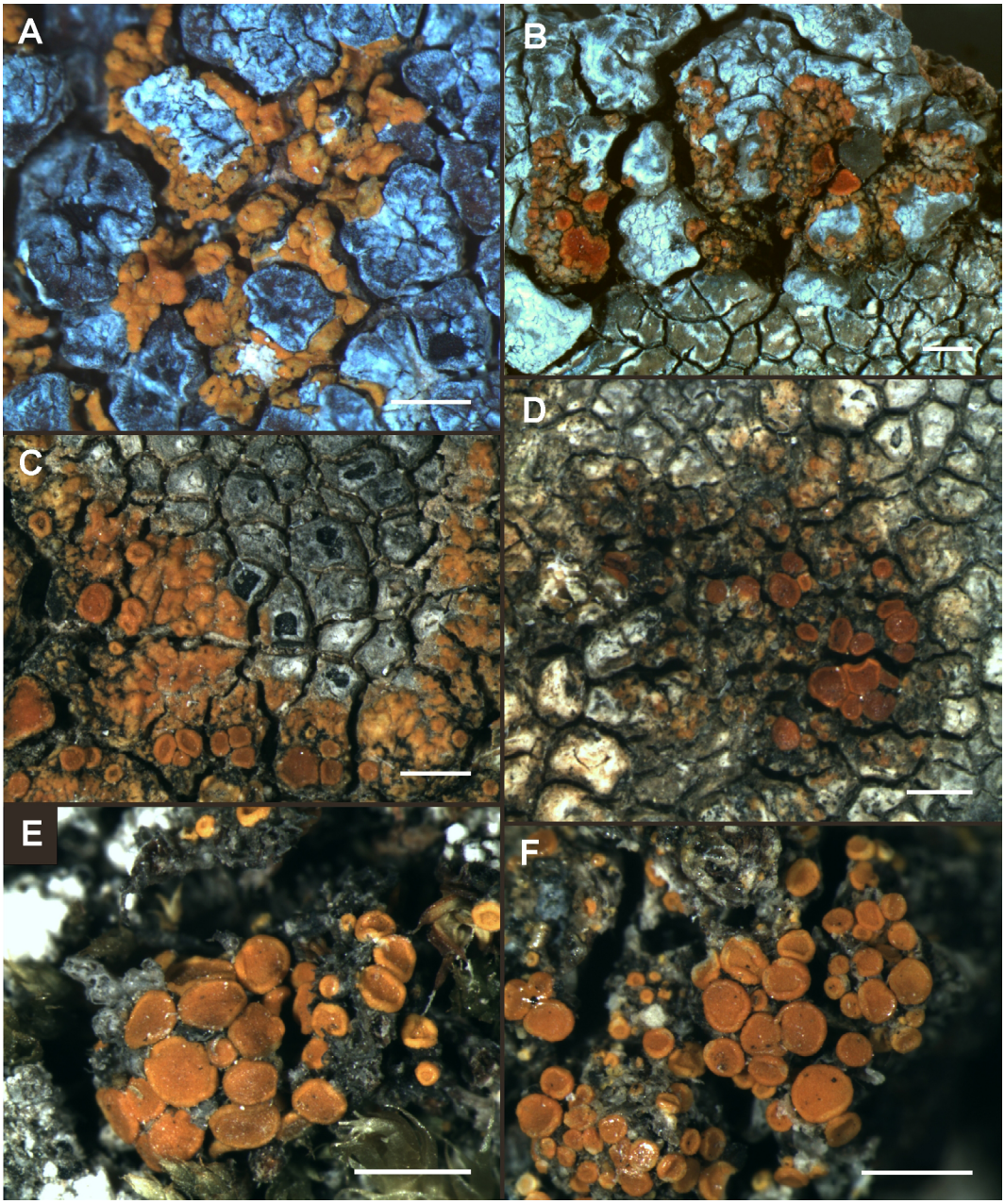


**Figure 3.** A–C) *Athallia nesodes*; A) *JV8526*, common calcicolous morphotype on *Acarospora cervina*; B) *JV5951*, silicicolous morphotype on *Aspicilia* on siliceous rocks; C) holotype (*Caloplaca inconnexa* var. *nesodes*, GZU 292657); D) *Caloplaca necator*, holotype (M-0163557); E) *Athallia saxifragarum*, holotype (M-0258103); F) *Caloplaca schoeferi* (=*Athallia saxifragarum*), holotype (M-00250018); bars - 1 mm.

we confirm the differences of both samples in ascospore characters. Ascospore size of the holotype of *Caloplaca necator* is smaller (Table 2), but observed ascospores are wider than the 8–9 × 5–6 µm of the protologue of *C. necator* (Poelt, 1958: 302). The holotype of *Caloplaca necator* has darker orange and smaller apothecia, thinner exciple, and smaller thallus; thus, we consider it different from *A. nesodes*. Both types are photographed here (Figure 3).

We consider that calcicolous and silicicolous populations belong to a single species, because samples of both ecotypes form together a well-defined ITS-based clade (Figure 1) without clear differences between ecotypes. At any rate, we have no evidence at present for recognizing the two ecotypes as distinct at any taxonomic level, though we realize that some ecologically based allopatric speciation might be occurring here.

**Table 2.** Results from phenotype appraisal of type specimens included in *Athallia necator* and *A. saxifragarum*.

| Taxon | "*Caloplaca*" *necator* | *Athallia nesodes* | *Athallia saxifragarum* | |
|---|---|---|---|---|
| Appraised holotype | *Caloplaca necator* | *Caloplaca inconnexa* var. *nesodes* | *Caloplaca saxifragarum* | *Caloplaca schoeferi* |
| Apothecia, diam. | (0.4–)0.45 ± 0.07(–0.6)* | (0.4–)0.63 ± 0.14(–0.9) | (0.4–)0.54 ± 0.13(–0.8) | (0.4–)0.50 ± 0.67(–0.6) |
| Disc, color | Orange | Pale orange | Orange | Orange |
| Exciple, color | Concolorous with disc | Concolorous to orange-yellow, but outer part often yellow | Concolorous with disc | Yellow-orange or concolorous with disc |
| Paraphyses tips, width (µm) | (3.5–)4.50 ± 0.67(–5.5) | (4.5–)4.85 ± 0.34(–5.5) | (3.0–)4.20 ± 0.79(–5.5) | (3.0–)4.05 ± 0.68(–5.0) |
| Ascospore size (µm) | (9.0–)10.05 ± 0.90(–11.0) × (5.0–)6.95 ± 1.14(–8.5) | (11.0–)12.45 ± 0.90(–14.0) × (6.0–)6.70 ± 0.73(–8.0) | (10.0–)11.20 ± 1.08(–13.0) × (5.0–)6.90 ± 0.96(–8.5) | (10.0–)11.4 ± 1.03(–13.0) × (5.0–)6.80 ± 1.11(–8.0) |
| Ascospore septum, width (µm) | (4.0–)5.15 ± 0.58(–6.0) | (5.0–)5.45 ± 0.55(–6.5) | (4.5–)5.05 ± 0.43(–6.0) | (4.0–)4.90 ± 0.61(–6.0) |
| Substrate | Lichenicolous on *Aspicilia* on quartzite | Lichenicolous on *Aspicilia* on noncalcareous schist ($HCl^-$) | Dead plant tufts | Cushions of *Grimmia anodon* (det. J. Kučera, Czech R.) |

* (minimum) mean ± standard deviation (maximum).

Although *Caloplaca inconnexa* var. *nesodes* belongs in *Athallia*, *Caloplaca inconnexa* itself does not, even though the name *Caloplaca inconnexa* has commonly been used for calcicolous specimens of *Athallia nesodes*. Its type (*Lecanora inconnexa*, France, Montpellier, H-Nyl. 29575!) probably belongs to the genus *Variospora*.

### 3.3. *Athallia holocarpa* includes morphotypes previously recognized at species level

***Athallia holocarpa*** (Hoffm.) Arup, Frödén & Søchting

**Basionym:** *Lichen holocarpus* Hoffm. ≡ *Caloplaca holocarpa* (Hoffm.) A. E. Wade.

**Type:** Germany, Herrenhausi. Ehrhart, Plantae Cryptogamae, no. 284 (GOET, lectotype selected by Arup 2009).

= *Caloplaca alcarum* Poelt, s.str. (non *C. alcarum* auct.)

**Type:** Novaya Zemlya, Goosebay, 5 July 1921, Lynge (M, Holotype!).

= *Caloplaca vitellinula* (Nyl.) H. Olivier ≡ *Athallia vitellinula* (Nyl.) Arup, Frödén & Søchting

**Type:** Russia, Murmansk Region, Lapponia tulomensis: "ad alnos in Lapponia orientali", *N.-I. Fellman* (*Lecanora vitellinula* Nyl., H-NYL 29940, lectotype selected by Arup 2009).

Based on our ITS sequence data from Turkish and a few other temperate to arctic specimens, we conclude that morphotypes that have commonly been called "*Caloplaca alcarum*", "*C. holocarpa*", and "*C. vitellinula*" should not be considered as distinct species.

Arup (2009) recognized *C. holocarpa* and *C. vitellinula* as two distinct species based on morphological differences and ITS sequence data almost exclusively from Scandinavian material. Although a few morphological characters (spore size, width of septa, color of thallus) were congruent with Arup's sequence data, those characters do not fit the sequence data when various Turkish and two Alaskan sequences are added into the alignment (Figure 4). Current data do not support recognition of these two species, and we synonymize them. However, it appears that the two genotypic groups recognized by Arup in Scandinavia may be two lineages without gene flow and with fixed morphological characters. These genotypes presumably dispersed throughout Scandinavia independently, from two source genotypes, after glaciation.

*Caloplaca vitellinula* was reported from Turkey (Bozcaada, Çanakkale) by Öztürk (1999), but its voucher specimen stored in BULU was examined by the second author and it actually belongs to *Candelariella vitellina*.

The name *Athallia alcarum* has been used for two different taxa. Some authors (e.g., Hansen et al., 1987; Søchting et al., 2008; Gaya, 2009) use it for poorly developed thalli of *A. scopularis* with reduced lobes (Figure 2), but the type specimen has no lobes at all (Figure 2) and is morphologically identical to specimens of *A. holocarpa* that we studied from Alaska and the Turkish mountains (Figure 4).

### 3.4. *Athallia saxifragarum* and *Caloplaca schoeferi* are conspecific

***Athallia saxifragarum*** (Poelt) Arup, Frödén & Søchting

**Basionym:** *Caloplaca saxifragarum* Poelt.

**Type:** Germany, the Alps, Wettersteingebirges, "grossen Kalkblöcken am Fusse des Kleinen Waners gegen den Hohen Kamm", coll. Poelt, 1953 (M 258103, holotype!).

= *Caloplaca schoeferi* Poelt

**Type:** Germany, the Alps, Wettersteingebirges, "auf Blöcken am Hohen Kamm am Fusse des Kleinen Wanners", coll. Poelt, 1953 (M 25018, holotype!).

This species is very similar to *A. holocarpa* but has different ecology. It is epiphytic or muscicolous in alpine habitats (Poelt, 1955; Vondrák and Slavíková-Bayerová, 2006; Vondrák et al., 2012).

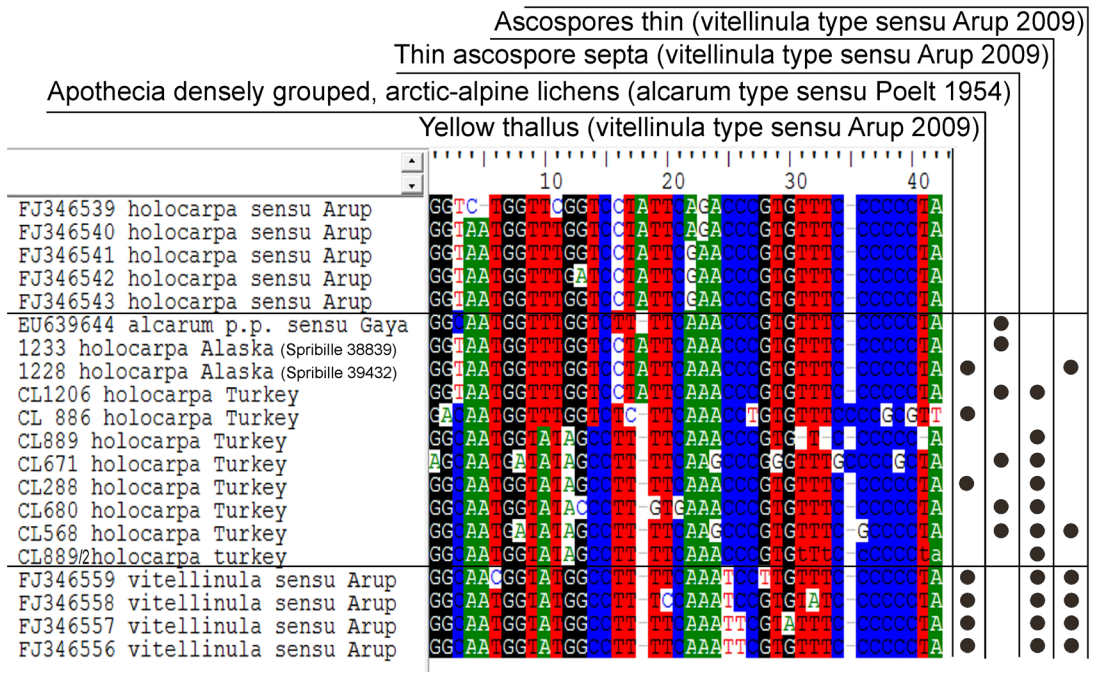


**Figure 4.** Shortened ITS alignment, including only variable positions, of 20 sequences of *Athallia holocarpa*. It demonstrates inconsistency between characters in the ITS region and phenotype diagnoses of *Athallia vitellinula* and *Caloplaca alcarum*. Diagnostic phenotypic characters for taxa *A. holocarpa*, *A. vitellinula*, and *C. alcarum* plotted in the right show their incongruences with ITS characters.

Poelt (1955) described *Caloplaca saxifragarum* and *C. schoeferi* as similar but distinct species. He wrote as follows for *C. schoeferi*: "Unter den muscicolen Arten ähnelt ihr am meisten *C. saxifragarum*, die sich durch kleine Apothecien von mehr rötlicher Färbung, gleichfarbigen Rand und anatomische Daten unterschiedet" ["among muscicolous lichens the most similar is *C. saxifragarum*, which differs in having smaller apothecia of more red color, concolorous apothecial disc, and apothecial margin, and in other anatomical characters" (not specified)]. He gave brief morphological and anatomical characters for *C. schoeferi*, but almost no phenotype information is present in the protologue of *C. saxifragarum*. We examined the holotypes of both names and found them to be conspecific (Table 2; Figure 3). The difference of substrates between the holotypes we consider unimportant, because numerous Teloschistaceae species (e.g., *Blastenia ammiospila* and *Caloplaca stillicidiorum*) occur on all following substrata: twigs of alpine shrubs, plant debris, or bryophytes.

### 3.5. Other *Athallia* species in Turkey

***Athallia alnetorum*** (Giralt, Nimis & Poelt) Arup, Frödén & Søchting

Locality information of all studied specimens is given in Appendix 2.

It may be confused in the field with *Gyalolechia flavorubescens*, but *Athallia alnetorum* has smaller ascospores and shorter and ellipsoid conidia (Giralt et al., 1992).

***Athallia cerinella*** (Nyl.) Arup, Frödén & Søchting

Diagnostic phenotype characters and ecology: Arup (2009), Vondrák et al. (2012).

***Athallia pyracea*** (Ach.) Arup, Frödén & Søchting

Diagnostic phenotype characters and ecology: Arup (2009), Vondrák et al. (2012).

***Athallia skii*** (Khodos., Vondrak & Šoun) Arup, Frödén & Søchting

**Diagnostic phenotype characters and ecology:** Vondrák et al. (2012).

## 4. Discussion

### 4.1. Phenotypic diagnosis of *Athallia*

We agree with Arup et al. (2013) that some species of *Athallia* cannot be distinguished with confidence from some species of the genus *Flavoplaca* using phenotype characters alone. We also found the same problem for some *Athallia* species and some species of *Calogaya*, *Polycauliona*, and *Variospora* and some other Teloschistaceae. However, *Athallia* as a whole does display some clear characters or tendencies: (1) chemosyndrome A in all species (=absence of chlorinated anthraquinones); (2) a tendency to reduce the thallus; (3) broad ascospores with rather broad septa; (4) a tendency to occur on noncalcareous rocks or as an epiphyte; (5)

small and inconspicuous pycnidia or pycnidia absent; (6) a preference for nutrient-rich substrata, e.g., bird-perching rock sites and nitrophilous bark communities; (7) a center of diversity in western Eurasia.

### 4.2. Species recognition in *Athallia* versus other Teloschistaceae genera

All the *Athallia* ITS clades considered species by us have rather few morphological characters, but they occur on various substrates and in various habitats, and most of them are easily recognizable by their niche. In other words, a single microhabitat does not usually contain more than one species of *Athallia*. This suggests simple allopatric speciation with strong reduction of gene flow among ecologically separated lineages. Thus, our rather well-supported ITS clades are well characterized, but they are characterized ecologically or geographically, rather than morphologically. It seems entirely justified to call them species. Similar situations occur in other genera of Teloschistaceae: e.g., *Blastenia*, *Calogaya*, and *Gyalolechia* (Vondrák, unpublished data).

On the other hand, some Teloschistaceae genera prefer only one type of habitat, e.g., calcareous rocks, and various infrageneric populations occur side by side in the same localities. They exhibit numerous morphotypes (often recognized as morphospecies) and numerous alleles in sequenced loci. Their large genetic variability is distributed within numerous clades that often do not have distinct morphological or other phenotypic characters. Examples are *Pyrenodesmia* (Frolov, unpublished data), *Rufoplaca* (Arup, unpublished data), or *Xanthocarpia* (Vondrák, unpublished data). This kind of situation probably calls for a new taxonomic concept, not one focused on "searching for congruencies between phenotypic and genotypic groups of specimens".

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**Appendix 1.**

***Flavoplaca oasis* JV7106**: CZECH REPUBLIC, České Budějovice, alt. c. 400 m, on concrete [**KR902658**]; ***Athallia aff. holocarpa* JV3849**: GREECE, Crete, Mires, alt. 10–100 m, on bark of *Ceratonia siliqua* [**KR902682**]; ***A. aff. holocarpa* JV3857**: GREECE, Crete, Mires, alt. 10–100 m, on bark of *Pistacia* [**KR902681**]; ***A. aff. holocarpa* JV8332**: GREECE, Ätolia, Astakos, alt. 20 m, on bark of *Olea europea* [**KR902680**]; ***A. alnetorum* CL0.278**: TURKEY, Bolu, Abant, alt. 1420 m, on *Abies nordmanniana* [**KR902685**]; ***A. alnetorum* CL0.451**: TURKEY, Denizli, Honaz Dağı Milli Parkı, alt. 1220 m, on *Pinus nigra* [**KR902685**]; ***A. alnetorum* CL0.572**: TURKEY, Ankara, Kızılcahamam, alt. 1420 m, on *Populus* [**KR902687**]; ***A. alnetorum* JV8315**: GREECE, Peloponnese, Argolis Peninsula, alt. c. 500 m, on *Pistacia lentiscus* [**KR902688**]; ***A. alnetorum* CL0.577**: TURKEY, Manisa, Gördes, alt. 800 m, on *Juglans regia* [**KR902689**]; ***A. baltistanica* JV4227**: GREECE, Crete, Orosira Dikti Mts., alt. 1100 m, on bark [**KR921581**]; ***A. baltistanica* CL0.581**: TURKEY, Mersin, Çamlıyayla, alt. 1350 m, on *Juniperus* [**KR902661**]; ***A. baltistanica* CL0.732**: TURKEY, Denizli, Honaz Dağı Milli Parkı, alt. 1750 m, on *Juniperus* [**KR902662**]; ***A. baltistanica* CL0.809**: TURKEY, Kütahya, between Kütahya and Eskişehir, alt. 1490 m, on *Juniperus* [**KR902663**]; ***A. baltistanica* CL1.126**: TURKEY, Antalya, Korkuteli, alt. 1350 m, on *Juniperus* [**KR902664**]; ***A. baltistanica* JV10622**: TURKEY, Mersin, Çamlıyayla, alt. 1357 m, on *Juniperus excelsa* [**KR902665**]; ***A. brachyspora* JV6399**: UKRAINE, Zakarpats'ka oblast, Svidovets Mts., alt. 1300 m, on base-rich schist [**KR902697**]; ***A. brachyspora* JV9113**: SLOVAKIA, Malá Fatra Mts., Mt Veľký Kriváň, alt. 1570 m, on limestone [**KR902696**]; ***A. cerinella* CL0.402**: TURKEY, Zonguldak, Devrek, alt. 430 m, on *Quercus* [**KR902684**]; ***A. cerinella* CL1.816**: TURKEY, Kastamonu, Abana, alt. 170 m, on *Platanus orientalis* [**KR902683**]; ***A. holocarpa* CL0.288**: TURKEY, Nevşehir, Uçhisar, alt. 1255 m, on calcareous rock [**KR902677**]; ***A. holocarpa* CL0.568**: TURKEY, Afyon, İhsaniye, alt. 1200 m, on siliceous rock [**KR902679**]; ***A. holocarpa* CL0.671**: TURKEY, Afyon, Sandıklı, alt. 1895 m, on siliceous rock [**KR902676**]; ***A. holocarpa* CL0.680**: TURKEY, Afyon, Sandıklı, alt. 1895 m, on siliceous rock [**KR902678**]; ***A. holocarpa* CL0.886**: TURKEY, Erzurum, Narman, alt. 1950 m, on *Pinus sylvestris* [**KR902674**]; ***A. holocarpa* CL0.889**: TURKEY, Erzurum, Şenkaya, alt. 1807 m, on *Pinus sylvestris* [**KR902675**]; ***A. holocarpa* CL1.206**: TURKEY, Bayburt, Bayburt-Çaykara, alt. 2400 m, on siliceous rock [**KR902673**]; ***A. holocarpa* TS39432**: USA, Alaska, Glacier Bay National Park, alt. 900 m, on argillite in alpine zone [**KR9026072**]; ***A. holocarpa* TS38839**: USA, Alaska, Glacier Bay National Park, alt. 920 m, on argillite (bird perch.) in alpine zone [**KR902671**]; ***A. nesodes* CL0.462**: TURKEY, İçel, Erdemli, alt. 830 m, on calcareous rock [**KR902690**]; ***A. nesodes* CL0.531**: TURKEY, Bolu, Gerede, alt. 1325 m, on calcareous rock [**KR902691**]; ***A. nesodes* CL0.657**: TURKEY, Afyon, Bolvadin, alt. 980 m, on moss [**KR902692**]; ***A. nesodes* JV4051**: GREECE, Crete, Agii Deka, alt. 700 m, on lime-rich sandstone [**KR902693**]; ***A. nesodes* JV9149**: CZECH REPUBLIC, Český kras karst, Beroun, alt. 350 m, on limestone [**KR902695**]; ***A. nesodes* JV9152**: CZECH REPUBLIC, Český kras karst, Beroun, alt. 350 m, on limestone [**KR902694**]; ***A. pyracea* CL0.196**: TURKEY, Ordu, Center, alt. 42 m, on *Populus* [**KR902669**]; ***A. pyracea* CL0.582**: TURKEY, Amasya, Borabay, alt. 1480 m, on calcareous rock [**KR902670**]; ***A. pyracea* CL0.609**: TURKEY, Kastamonu, Ilgaz Mountain, alt. 1495 m, on *Populus tremula* [**KR902666**]; ***A. pyracea* CL0.813**: TURKEY, Kırşehir, Mucur, alt. 1125 m, on *Salix* [**KR902668**]; ***A. pyracea* CL0.887**: TURKEY, Erzurum, Narman, alt. 1950 m, on *Populus tremula* [**KR902667**]; ***A. saxifragarum* CL1.299**: TURKEY, Karaman, Ayrancı, alt. 2050 m, on *Juniperus* [**KR902660**]; ***Caloplaca raesaenenii* JV8258**: TURKEY, Tekirdağ, Şarköy, alt. 20 m, on bark of *Platanus* [**KR902659**].

**Appendix 2.**

***Athallia baltistanica* (Poelt & Hinter.) Halıcı & Vondrák, comb. nov.**

**Specimens examined: Greece, Crete,** Orosira Dikti Mts., Ano Viannos, S slope of Mt. Troulou, alt. c. 1100 m, on bark, 08 May 2005 [**JV4227, PRA**]. **Turkey, Antalya,** Korkuteli, Karaman Beli Pass, 36°56′672″N, 30°09′629″E, alt. 1350 m, on *Juniperus excelsa*, 09 June 2013 [**CL 1.126**]; **Denizli,** southeast of Honaz Dağı Natural Park, northwest of Tavas, on *Juniperus* sp., 37°41′0″N, 29°15′3″E, alt. 1750 m, 05 July 2012 [**CL 0.710; CL 0.732**]; **İçel,** Çamlıyayla, north of Çamlıyayla, on *Juniperus excelsa*, alt. 1357 m, 37°10′52.3″N, 34°37′47″E, 25 February 2012 [**CL 0.326; CL 0.581**]; **İçel,** Erdemli, Avgadı Village, on *Juniperus* sp., 36°45′285″N, 34°07′519″E, alt. 1325 m, 17 June 2013 [**CL 1.164**]; **Karaman,** Ermenek, Ermenek-Gülnar highway, southwest of Mora Pass, on *Juniperus* sp., 36°30′489″N, 33°00′894″E, alt. 1505 m, 15 June 2013 [**CL 1.422**]; **Konya,** Beyşehir, on the highway of Yenişarbademli, southwest coast of Beyşehir Lake, north of Damla Village, on *Juniperus excelsa*, 37°37′371″N, 31°27′152″E, alt. 1135 m, 07 June 2013 [**CL 1.136**]; **Kütahya,** Kütahya-Eskişehir highway, southwest of Soğukyayla Village, northeast of Ürünçiftliği Village, on *Juniperus* sp., 39°22′30″N, 30°16′30″E, alt. 1490 m, 29 June 2012 [**CL 0.809**]; **Manisa,** on the highway of Akhisar, southwest of Dağdere Köyü, on *Juniperus* sp., 38°58′24″N, 28°01′49″E, alt. 855 m, 30 June 2012 [**CL 0.772**].

***Athallia nesodes* (Poelt & Nimis) Halıcı & Vondrák, comb. nov.**

**Specimens examined: Turkey, Afyon,** Emirdağ, southeast of Emirdağ, north of Dereköy, on siliceous and calcareous mixed rocks, 38°58′03″N, 31°11′25″E, alt. 1080 m, 28 June 2012 [**CL 0.620**]; Bolvadin, north of Eber Lake, southwest of Büyükkarabağ Village, on calcareous rocks, 38°43′50″N, 31°13′41″E, alt. 980 m, 28 June 2012 [**CL 0.657, CL 0.664**]; **Ankara,** Beypazarı, Çayırhan, east of Davutoğlan Village, on calcareous rocks, 40°06′54″N, 31°39′24″E, alt. 535 m, 22 July 2012 [**CL 0.309, CL 0.318**]; **Antalya,** Alanya, Gevne Valley, on the highway to Sarıveliler, on calcareous rocks, 36°42′38″N, 32°28′39″E, alt. 1650 m, 01 October 2011 [**CL 0.057**]; **Antalya,** Alanya, Gevne Valley, on calcareous rocks, 36°45′20″N, 32°27′44″E, alt. 1300 m, 30 September 2011 [**CL 0.058**]; **Artvin,** Camili, Borçka-Camili highway, southwest of Atanoğlu, 41°24′359″N, 41°46′379″E, alt. 700 m, 27 July 2013 [**CL 1.822**]; **Balıkesir,** Bigadiç, Alaçam Mounts, east of Yağcıbedir Village, on calcareous rocks, 39°25′12″N, 28°12′46″E, alt. 425 m, 25 May 2012 [**CL 0.571**]; **Bilecik,** Gölpazarı, southeast of Büyüksusuz Village, on calcareous rocks, 40°15′04″N, 30°12′17″E, alt. 480 m, 24 July 2012 [**CL 0.606**]; **Bolu,** Abant, Nature Park, *Fagus orientalis*, *Abies nordmanniana* forest, on calcareous rocks, 40°36′11″N, 31°16′58″E, alt. 1360 m, 25 July 2012 [**CL 0.274**]; **Bolu,** Gerede, north of Ahmetler Village, on calcareous rocks, 40°47′17″N, 32°08′35″E, alt. 1325 m, 25 July 2012 [**CL 0.527, CL 0.531**]; **Çanakkale,** Lapseki, Şevketiye'nin doğusundaki kıyı serpantin kayalıkları, 40°23′43″N, 26°53′00″E, alt. 30 m, 27 May 2012 [**CL 0.468**]; **Çanakkale**, between Küçükkuyu-Ayvacık, west of Küçükkuyu, on calcareous rocks, 39°33′18″N, 26°33′22″E, alt. 330 m, 26 May 2012 [**CL 0.631**]; **Denizli,** southeast of Honaz Dağı National Park, northwest of Tavas, on calcareous rocks, 37°41′00″N, 29°15′30″E, alt. 1750 m, 05 July 2012 [**CL 0.704**]; **Eskişehir,** Muttalip, northwest of Ahılar Village, on calcareous rocks, 39°51′24″N, 30°38′02″E, alt. 1130 m, 23 July 2012 [**CL 0.643**]; **Eskişehir,** Mihalgazi, northwest of Demirciler Village, on calcareous rocks, 40°01′41″N, 30°30′42″E, alt. 280 m, 23 July 2012 [**CL 0.755**]; **Gaziantep,** Nurdağı, Şehit Kamil, north of Durnalık Village, on calcareous rocks, 37°08′964″N, 37°10′719″E, alt. 1225 m, 02 September 2014 [**CL 1.654**]; **Gaziantep,** Nurdağı, on calcareous rocks, Şahin Bey Village, 37°07′519″N, 37°06′415″E, alt. 1300 m, 02 September 2014 [**CL 2.155**]; **Isparta,** Eğirdir, western coast of Eğirdir Lake, Kayağa, on calcareous rocks, 38°08′139″N, 30°46′206″E, alt. 920 m, 07 June 2013 [**CL 1.662**]; **İçel,** Erdemli, Esenpınar Village, on schist, 36°35′26″N, 34°06′31″E, alt. 830 m, 26 February 2012 [**CL 0.462**]; **İçel,** Erdemli, Avgadı Village, on calcareous rocks, 36°45′285″N, 34°07′519″E, alt. 1325 m, 17 June 2013 [**CL 1.159**]; **İçel,** Mut, between Mut-Ermenek, Çaltılıgöl position, on calcareous rocks, 36°34′418″N, 33°13′917″E, alt. 950 m, 15 June 2013 [**CL 1.292**]; **İçel,** Kırobası, east of Kayalıkaynak position, on calcareous rocks, 36°42′116″N, 33°54′101″E, alt. 1420 m, 16 June 2013 [**CL 1.495**]; **İçel,** Bolkar Mountains, Meydan plateau, on calcareous rocks, 37°24′51″N, 34°33′55″E, alt. 2342 m, 23 September 2011 [**CL 0.075**]; **Konya,** Gevne Valley, Şeker Pınarı position, Antalya-Konya province border, on calcareous rocks, 36°45′19″N, 32°27′69″E, alt. 1350 m, 25 September 2009 [**CL 0.045**]; **Konya,** Taşkent, Gevne Valley, Beyreli Village, on calcareous rocks, 36°52′34″N, 32°20′74″E, alt. 1575 m, 29 July 2011 [**CL 0.067**]; **Konya,** Seydişehir, between Seydişehir-Beyşehir, northwest of Nohuttaş position, on calcareous rocks, 37°29′135″N, 31°49′730″E, alt. 1200 m, 14 June 2013 [**CL 1.104**]; **Konya,** Beyşehir, on the highway to Yenişarbademli, southwest coast of Beyşehir Lake, north of Damla Village, on calcareous rocks, 37°37′371″N, 31°27′152″E, alt. 1135 m, 07 June 2013 [**CL 1.133**]; **Malatya,** Akçadağ, Levent-Malatya 10 km, 38°23′34″N, 37°55′13″E, alt. 1430 m, 28 August 2003 [**CL 0.413**]; **Manisa,** on the highway to Akhisar, southwest of Dağdere Village, on calcareous rocks, 38°58′24″N, 28°01′49″E, alt. 855 m, 30 June 2012 [**CL 0.682**]; **Nevşehir,** Avanos, south of Özkonak Village, on tuff, 38°44′52″N, 34°50′38″E, alt. 1175 m, 18 July 2012 [**CL 0.298**]; **Sivas,** Gürün, between

Pınarbaşı-Gürün, northwest of Kaynarca Village, on calcareous rocks, 38°46′120″N, 36°58′462″E, alt. 1675 m, 25 June 2014 [**CL 2.012**]; **Şanlıurfa,** Suruç, northwest of Suruç, east of Yanaloba, Ezgil Village, on calcareous rocks, 37°03′140″N, 38°18′776″E, alt. 590 m, 03 July 2013 [**CL 1.145**]; **Uşak,** Ulubey, Ulubey Canyon, on calcareous rocks, 38°25′06″N, 29°18′14″E, alt. 745 m, 05 July 2012 [**CL 0.427**].

***Athallia holocarpa*** (Hoffm.) Arup, Frödén & Søchting

**Specimens examined: Turkey, Afyon,** İhsaniye, southeast of Kadımürsel Village on siliceous rocks, 39°06′01″N, 30°19′24″E, alt. 1200 m, 29 June 2012 [**CL 0.568**]; Emirdağ, southeast of Emirdağ, north of Dereköy, on siliceous rocks, 38°58′03″N, 31°11′25″E, alt. 1080 m, 28 June 2012; Sandıklı, Çakmaktepe Pass, on siliceous rocks, 38°28′25″N, 30°23′17″E, alt. 1895 m, 29 June 2012 [**CL 0.671; 0.680**]; **Ardahan,** Çıldır, northeast of Ölçek Village, on siliceous rocks, 41°08′191″N, 42°53′305″E, alt. 1870 m, 30 July 2013 [**CL 1.439**]; southeast of Çamgeçit, highway between Ardahan-Şavşat, west of Çataldere Village, on siliceous rocks, 41°12′160″N, 42°33′691″E, alt. 2250 m, 30 July 2013 [**CL 1.506**]; **Artvin,** Şavşat, Yalnızçam Mountains, southwest of Karaköy, on siliceous rocks, 41°13′641″N, 42°27′045″E, alt. 1890 m, 30 July 2013 [**CL 1.236**]; **Bayburt,** highway between Bayburt-Çaykara, province border of Bayburt-Rize, Soğanlı Pass, on siliceous rocks, 40°30′736″N, 40°14′763″E, alt. 2400 m, 26 July 2013 [**CL 1.203; 1.206**]; **Bilecik,** İnhisar, northwest of İnhisar, on siliceous rocks, 40°03′39″N, 30°22′19″E, alt. 250 m, 23 July 2012 [**CL 0.118**]; Söğüt, Bilecik-Eskişehir highway, southeast of Söğüt, on siliceous rocks, 40°00′32″N, 30°11′50″E, alt. 820 m, 24 July 2012 [**CL 0.115**]; **Elazığ,** Sivrice, north of Koçdağı Pass, on siliceous rocks, 38°30′062″N, 39°14′393″E, alt. 1120 m, 08 July 2013 [**CL 1.866**]; **Erzurum,** Narman, Narman Forest, city forest, on bark of *Pinus sylvestris*, 40°13′311″N, 41°52′504″E, alt. 1950 m, 29 July 2013 [**CL 0.886**]; Şenkaya, Narman-Göle (Ardahan) highway, north of Değirmenlidere Village, on bark of *Pinus sylvestris*, 40°44′164″N, 42°31′487″E, alt. 1807 m, 29 July 2013 [**CL 0.889, CL 0.891**]; **Gümüşhane,** Torul, Zigana Pass, Kadırga Plateau, on siliceous rocks, 40°38′507″N, 39°24′188″E, alt. 2040 m, 25 July 2013 [**CL 1.401**]; Torul, Trabzon-Gümüşhane highway, TBMM 90. Yıl Forest, southwest of Eskiköy Village, on siliceous rocks, 40°38′506″N, 39°23′109″E, alt. 1810 m, 25 July 2013 [**CL 1.412**]; Kelkit, Erzincan-Gümüşhane highway, southeast of Kömür Village, on siliceous rocks, 39°55′010″N, 39°24′517″E, alt. 1775 m, 24 July 2013 [**CL 1.462, CL 1.464**]; **İçel,** Erdemli, northwest of Toros Village, south of Çocuklar Tomb, on calcareous rocks, 36°54′531″N, 34°06′051″E, alt. 1675 m, 17 June 2013 [**CL 1.407**]; **Kütahya,** southwest of Akoluk Village, on tuff, 39°18′08″N, 30°15′28″E, alt. 1125 m, 29 June 2012 [**CL 1.896**]; **Nevşehir,** Uçhisar, Göreme Historical National Park, on siliceous rocks, 38°38′07″N, 34°48′25″E, alt. 1255 m, 18 July 2012 [**CL 0.288**]; Ürgüp, old highway between Nevşehir-Kayseri, northwest of Dörtyol, on siliceous rocks, 38°30′26″N, 35°07′54″E, alt. 1265 m, 18 July 2012 [**CL 0.782**]; **Samsun**, Bafra, Kızılırmak Delta, north of Gernek Lake, on siliceous rocks, 41°40′42″N, 36°03′53″E, alt. 0 m, 27 August 2012 [**CL 1.809; 1.811**]; **Sinop,** northeast of peninsula, on siliceous rocks, 42°01′56″N, 35°11′31″E, alt. 160 m, 27 August 2012 [**CL 0.191**]; **Tokat,** Center, Geyras, on siliceous rocks, 40°14′54″N, 36°32′47″E, alt. 790 m, 29 August 2012 [**CL 1.563**]; **Yozgat,** Eymir, northwest of Yaylalık Village on siliceous rocks, 40°03′12″N, 35°13′56″E, alt. 1400 m, 25 August 2012 [**CL 1.599**].

***Athallia saxifragarum*** (Poelt) Arup, Frödén & Søchting

**Specimens examined: Turkey, Afyon,** Sandıklı, Çakmaktepe Pass, on soil, 38°28′25″N, 30°23′17″E, alt. 1895 m, 29 June 2012 [**CL 0.675**]; **Kahramanmaraş,** Nurhak, Elbistan-Nurhak highway, Bakış Village, Karadere Plateau, on plant debris, 38°02′41″N, 37°24′79″E, alt. 2000 m, 31 August 2014 [**CL 2.123**]; **Karaman,** Ayrancı, Bolkar Mounts, west of Ebekarıyurdu Position, on bark of *Juniperus* sp., 37°03′69″N, 33°55′12″E, alt. 2050 m, 17 June 2013 [**CL 1.299**]; **Kayseri,** southeast of Himmetdede, northwest of Kalkancık Village, on mosses on soil, 38°53′43″N, 35°07′01″E, alt. 1170 m, 25 August 2012 [**CL0.940**]; **Kırşehir,** Mucur, Kızılağıl Village, on plant debris, 39°54′16″N, 34°17′15″E, alt. 910 m, 19 July 2012 [**CL 0.106**]; **Nevşehir,** Topaklı, southwest of Çalış Village, on *Thymus* sp., 38°57′08″N, 34°50′30″E, alt. 1330 m, 18 July 2012 [**CL 0.105**]; **Sivas,** Gürün, İncesu Village, on mosses on soil, 38°45′71″N, 37°07′04″E, alt. 1745 m, 25 June 2014 [**CL 2.021**]; **Tokat**, Çamlıbel, southeast of Tekreli Village, on *Astragalus* sp., 40°10′37″N, 36°30′55″E, alt. 1450 m, 29 August 2012 [**CL 0.686**].

***Athallia alnetorum*** (Giralt, Nimis & Poelt) Arup, Frödén & Søchting

**Specimens examined: Turkey, Ankara,** Kızılcahamam, Çamkoru National Park, on bark of *Populus tremula*, 40°34′43″N, 32°29′48″E, alt. 1420 m, 21 July 2012 [**CL 0.572**]; **Antalya**, Alanya, Gevne Valley, on bark of *Pinus nigra*, 36°32′22″N, 32°23′52″E, alt. 1140 m, 01 October 2011 [**CL 0.066**]; Kemer, south of Beycik Village, on bark of *Juniperus* sp., 36°29′92″N, 30°25′84″E, alt. 730 m, 11 June 2013 [**CL 0.833, CL 0.844**]; Alanya, Sarıveliler highway, east of Yalçı Village, on bark of *Pinus brutia*, 36°33′23″N, 32°18′69″E, alt. 1200 m, 13 June 2013 [**CL 1.122**]; Akseki, north of Akseki, on bark of *Quercus* sp., 37°06′87″N, 31°45′76″E, alt. 1270 m, 12 June 2013 [**CL 1.209**]; Termessos Natural Park, on bark of *Quercus* sp., 36°59′31″N, 30°28′10″E, alt. 870 m, 12 June 2013 [**CL 1.269**]; **Bilecik,** Söğüt, Çaltı Municipality, north of Dudaş

Village, on bark of *Quercus* sp., 40°01′37″N, 30°14′15″E, alt. 560 m, 23 July 2012 [**CL 0.420**]; Gölpazarı, southeast of Büyüksusuz Village, on bark of *Pistacia* sp., 40°15′04″N, 30°12′17″E, alt. 480 m, 24 July 2012 [**CL 0.596**]; **Bolu,** Abant, south of Natural Park, northeast of Örencik Village, on bark of *Abies nordmanniana*, 40°35′31″N, 31°16′51″E, alt. 1420 m, 25 July 2012 [**CL 0.278**]; Bolu-Bilecik highway, northeast of Belkarağaç Village on bark of *Quercus* sp. 40°37′46″N, 31°26′55″E, alt. 925 m, 25 July 2012 [**CL 0.575**]; Abant, Nature Park, on bark of *Fagus orientalis*, 40°36′11″N, 31°16′58″E, alt. 1360 m, 25 July 2012 [**CL 2.233**]; **Denizli,** Çameli, north of İmamlar Village, on bark of *Juniperus* sp., 37°07′36″N, 29°23′33″E, alt. 1500 m, 04 July 2012 [**CL 0.252**]; Honaz Dağı Natural Park, Cankurtaran position, southwest of Natural Park, on bark of *Pinus nigra*, 37°39′38″N, 29°15′00″E, alt. 1220 m, 05 July 2012 [**CL 0.451**]; **Düzce,** Yığılca, west of Güney Village, on bark of *Quercus* sp., 40°56′58″N, 31°24′28″E, alt. 315 m, 26 July 2012 [**CL 0.143**]; **Eskişehir,** Mihallıccık, north of Sorkun Village, on bark of *Juniperus* sp., 39°57′08″N, 31°23′19″E, alt. 1260 m, 22 July 2012 [**CL 0.405**]; **Isparta,** Sütçüler, Aksu, southeast of Aksak, on bark of *Platanus orientalis*, 37°43′259″N, 31°01′592″E, alt. 1150 m, 08 June 2013 [**CL 0.867**]; Eğirdir, northwest of Balkırı Village, on bark of *Salix* sp., 37°48′180″N, 30°50′012″E, alt. 1170 m, 08 June 2013 [**CL 0.871**]; **İçel,** Gülnar, Gülnar-Silifke highway, west of Kurtini Position, on bark of *Juniperus* sp., 36°20′33″N, 33°28′85″E, alt. 1010 m, 16 June 2013 [**CL 0.100**]; Erdemli, northwest of Toros Village, south of Çocuklar Tomb, on bark of *Abies cilicica*, 36°54′53″N, 34°06′05″E, alt. 1675 m, 17 June 2013 [**CL 1.405**]; **Kahramanmaraş,** Andırın, Dilek Mountain, north of Çokak Village, on bark of *Pinus* nigra, 37°45′44″N, 36°19′80″E, alt. 1585 m, 01 September 2014 [**CL 2.156, CL 2.224**]; **Kars,** Arpaçay, Ardahan-Susuz highway, northeast of Kümbet Village, on *Thymus* sp., 40°51′99″N, 43°10′20″E, alt. 1680 m, 30 July 2013 [**CL 0.949**]; **Kastamonu,** Devrakani, Yaralıgöz Pass, on bark of *Populus tremula*, 41°46′17″N, 34°02′50″E, alt. 1450 m, 30 July 2012 [**CL 0.487**]; north of Ilgaz Dağı Natural Park, on bark of *Populus* sp., 41°06′00″N, 33°44′40″E, alt. 1495 m, 31 July 2012 [**CL 0.610**]; Şenpazar, southeast of Dağlı Village, on bark of *Populus* sp., 41°47′11″N, 33°08′22″E, alt. 690 m, 30 July 2012 [**CL 1.814**]; **Kayseri,** Erciyes Mountain, Hisarcık, on bark of *Salix* sp., 38°36′51″N, 35°30′48″E, alt. 1725 m, 03 September 2012 [**CL 0.418**]; **Konya,** Taşkent, Gevne Valley, on bark of *Pinus nigra*, 36°46′33″N, 32°27′07″E, alt. 1300 m, 30 September 2011 [**CL 0.112**]; Akşehir, Cankurtaran, on bark of *Juniperus* sp., 38°15′61″N, 31°24′11″E, alt. 1670 m, 06 June 2013 [**CL 1.188**]; Beyşehir, Kurucuova-Yeşildağ highway, on bark of *Prunus domestica*, 37°33′20″N, 31°27′34″E, alt. 1140 m, 07 June 2013 [**CL 1.192**]; Hadim, Hadim-Bozkır highway, south of Demirtaş Plateau, 36°58′59″N, 32°22′50″E, alt. 1815 m, 13 June 2013 [**CL 1.454**]; **Kütahya,** Kütahya-Eskişehir highway, southwest of Soğukyayla Village, northeast of Ürünçiftliği Village, on bark of *Quercus* sp., 39°22′30″N, 30°16′30″E, alt. 1490 m, 29 June 2012 [**CL 0.801**]; **Manisa,** Gördes, Dağdere Village, on bark of *Juglans regia*, 39°00′03″N, 28°04′55″E, alt. 800 m, 30 June 2012 [**CL 0.577**]; **Muğla,** Marmaris-Muğla highway, south of Kızılağaç Village, on bark of *Laurus nobilis*, 37°04′05″N, 28°21′40″E, alt. 580 m, 03 July 2012 [**CL 0.454, CL 0.456**]; **Zonguldak,** Kozlu, Ereğli-Akçakoca highway, on bark of *Morus nigra*, 41°25′26″N, 31°43′11″E, alt. 0–10 m, 27 July 2012 [**CL 0.478, CL 0.480**].

***Athallia cerinella*** (Nyl.) Arup, Frödén & Søchting

**Specimens examined: Turkey, Ankara,** Güdül, south of Sorgun Municipality, on bark of *Abies nordmanniana*, 40°18′37″N, 32°15′43″E, alt. 1500 m, 21 July 2012 [**CL 0.342**]; **Antalya,** Korkuteli, Denizli-Antalya highway, southwest of Kızılyar position, on bark of *Pinus brutia*, 37°01′98″N, 30°06′61″E, alt. 1255 m, 09 June 2013 [**CL 1.058**]; **Burdur,** Karacaören, on bark of *Pinus brutia*, 41°38′66″N, 36°30′69″E, alt. 400 m, 18 July 2012 [**CL 0.722**]; **Çanakkale,** Bayramiç, Ezine-Bayramiç highway, on bark of *Quercus* sp., 39°46′26″N, 26°26′21″E, alt. 30 m, 26 May 2012 [**CL 0.534**]; **Eskişehir,** Mihalgazi, north of Bozdağ Village, on bark of *Salix* sp., 39°56′31″N, 30°36′08″E, alt. 1130 m, 23 July 2012 [**CL 0.475**]; **Gaziantep,** Nurdağı, Terken Village, on bark of *Quercus coccifera*, 37°06′21″N, 37°02′17″E, alt. 950 m, 02 September 2014 [**CL 2.215**]; **İzmir,** Nifdağı, southwest of Yenikurudere Village, on bark of *Platanus orientalis*, 38°22′04″N, 27°36′11″E, alt. 350 m, 01 July 2012 [**CL 0.174**]; **Kastamonu,** Daday, west of Kasaba Village, on bark of *Prunus domestica*, 41°28′42″N, 33°36′53″E, alt. 800 m, 29 July 2012 [**CL 0.425**]; Devrakani, Yaralıgöz Pass, on bark of *Populus tremula*, 41°46′17″N, 34°02′50″E, alt. 1450 m, 30 July 2012 [**CL 0.485**]; Abana, west of Kuğu Village, on bark of *Platanus orientalis*, 41°57′46″N, 34°06′21″E, alt. 170 m, 30 July 2012 [**CL 1.816**]; **Kırşehir,** Mucur, south of Seyfe Lake, Yazıkınık Village, on bark of *Salix* sp., 39°09′44″N, 34°24′28″E, alt. 1125 m, 19 July 2012 [**CL 0.812**]; **Konya,** Taşkent, Gevne Valley, on bark of *Abies cilicica*, 36°46′33″N, 32°27′07″E, alt. 1300 m, 30 September 2011 [**CL 0.113**]; Beyşehir, Kurucuova-Yeşildağ highway, on bark of *Prunus domestica*, 37°33′20″N, 31°27′34″E, alt. 1140 m, 07 June 2013 [**CL 1.193**]; Beyşehir, Yenişarbademli highway, east of Kayapınar Position, on bark of *Salix* sp., 37°33′73″N, 31°31′72″E, alt. 1210 m, 07 June 2013 [**CL 1.350**]; **Kütahya,** Simav, Kütahya-Manisa province border, south of Hacı Hüseyin Efendi Village, on bark of *Platanus orientalis*, 39°07′04″N, 28°43′26″E, alt. 950 m, 30 June 2012 [**CL 0.726**]; **Nevşehir,** Uçhisar, southwest of Göreme Historical National Park, on bark of *Prunus* sp., 38°38′07″N, 34°48′25″E, alt. 1255 m, 18 July 2012 [**CL 0.290**]; **Sinop,** Durağan, northeast of Yassıalan Village, on

bark of *Quercus* sp., 41°29′01″N, 35°07′42″E, alt. 795 m, 26 August 2012 [**CL 1.318**]; **Trabzon,** Vakfıkebir, on bark of *Populus* sp., 41°02′54″N, 39°14′52″E, alt. 0 m, 31 August 2012 [**CL 0.247**]; **Zonguldak,** Ereğli, Göktepe, on bark of *Populus* sp., 41°13′22″N, 31°25′00″E, alt. 135 m, 26 July 2012 [**CL 0.330**]; Devrek, Devrek-Ereğli highway, west of Nizamlar Village, on bark of *Quercus* sp., 41°13′39″N, 31°54′57″E, alt. 430 m, 28 July 2012 [**CL 0.402**].

***Athallia pyracea*** (Ach.) Arup, Frödén & Søchting

**Specimens examined: Turkey, Amasya,** Borabay, north of Kocabey Lake, on calcareous rocks, 40°09′06″N, 36°08′20″E, alt. 1480 m, 28 August 2012 [**CL 0.582**]; **Ankara**, Çamlıdere, west of Muzrupahaçın Village, on bark of *Quercus* sp., 40°27′20″N, 32°28′35″E, alt. 1180 m, 21 July 2012 [**CL 0.138**]; Bala, north of Bala, Hamidiye on bark of *Quercus* sp., 39°33′48″N, 33°07′21″E, alt. 1300 m, 20 July 2012 [**CL 0.818**]; **Antalya,** Kemer, south of Beycik Village, on bark of *Quercus* sp., 36°29′92″N, 30°25′84″E, alt. 730 m, 11 June 2013 [**CL 0.838**]; Alanya, on the highway to Sarıveliler, east of Yalçı Village, on bark of *Quercus* sp., 36°33′23″N, 32°18′69″E, alt. 1200 m, 13 June 2013 [**CL 1.121**]; Akseki, north of Akseki, on bark of *Quercus* sp., 37°06′87″N, 31°45′76″E, alt. 1270 m, 12 June 2013 [**CL 1.213**]; Termessos National Park, on bark of *Prunus* sp., 36°59′31″N, 30°28′10″E, alt. 870 m, 12 June 2013 [**CL 1.273**]; **Artvin,** Yusufeli, Bostancı Village, Kaçkar Mountain National Park, 40°58′88″N, 41°27′77″E, alt. 975 m, 27 July 2013 [**CL 1.931**]; **Bartın**, Kümesler Village, on bark of *Populus* sp., 41°34′25″N, 32°21′36″E, alt. 130 m, 27 July 2012 [**CL 0.401**]; **Bayburt,** Aydıntepe, on the highway to Araklı, south of Salmankaşı Pass, 40°28′54″N, 39°58′60″E, alt. 1975 m, 26 July 2013 [**CL 1.385**]; **Bayburt,** Bayburt-Gümüşhane province border, east of Vauk Mountain Pass, on bark of *Populus* sp., 40°21′75″N, 39°50′61″E, alt. 1865 m, 25 July 2013 [**CL 1.461**]; **Bilecik,** Söğüt, Çaltı Municipality, north of Dudaş Village, on bark of *Quercus* sp., 40°01′37″N, 30°14′15″E, alt. 560 m, 23 July 2012 [**CL 0.419**]; Gölpazarı, southeast of Büyüksusuz Village, on bark of *Juniperus* sp., 40°15′04″N, 30°12′17″E, alt. 480 m, 24 July 2012 [**CL 0.598**]; **Bingöl,** Solhan, Muş-Bingöl highway, northwest of Karan Village, on bark of *Populus* sp., 38°54′87″N, 40°53′86″E, alt. 1330 m, 03 August 2013 [**CL 1.443**]; **Bitlis,** Tatvan, on the highway to Van, Çayırönü Village, on bark of *Juglens regia*, 38°27′75″N, 42°19′17″E, alt. 1770 m, 06 July 2013 [**CL 1.043**]; **Bitlis,** Siirt-Bitlis highway, Ünaldı Village, on bark of *Acer* sp., 38°19′06″N, 42°01′18″E, alt. 1310 m, 06 July 2013 [**CL 1.231**]; **Bolu,** Göynük, southwest of Bozcaarmut Village, on bark of *Juniperus* sp., 40°26′07″N, 30°52′29″E, alt. 930 m, 24 July 2012 [**CL 0.140**]; **Bolu,** Bolu-Bilecik highway, northeast of Belkarağaç Village, on bark of *Quercus* sp., 40°37′46″N, 31°26′55″E, alt. 925 m, 25 July 2012 [**CL 0.589**]; Mengen, south of Çukurca Village, on bark of *Pistacia* sp., 40°54′39″N, 32°03′46″E, alt. 570 m, 25 July 2012 [**CL 0.789**]; **Burdur,** Bucak, Çentikçi Pass, Sarıova Village, on bark of *Populus* sp., 37°36′02″N, 30°24′70″E, alt. 1350 m, 08 June 2013 [**CL 1.307**]; **Bursa,** Orhangazi, Orhangazi-Hamzalı highway, northwest of Orhangazi, on bark of *Quercus* sp., 40°33′33″N, 29°18′16″E, alt. 125 m, 22 May 2012 [**1.838**]; **Çanakkale,** Bayramiç, Ezine-Bayramiç highway; 15 km west of Bayramiç, on bark of *Quercus* sp., 39°46′26″N, 26°26′21″E, alt. 30 m, 26 May 2012 [**CL 0.532**]; **Çankırı,** Ilgaz Mountain, Derbent Hotel, on bark of *Abies nordmanniana*, 41°03′52″N, 33°44′35″E, alt. 1795 m, 31 July 2012 [**CL 0.586**]; **Denizli,** southwest of Honaz Dağı National Park, Cankurtaran position, on bark of *Pinus nigra*, 37°39′38″N, 29°15′00″E, alt. 1220 m, 05 July 2012 [**CL 0.452**]; **Düzce,** Yığılca, west of Güney Village, on bark of *Quercus* sp., 40°56′58″N, 31°24′28″E, alt. 315 m, 26 July 2012 [**CL 0.142**]; **Erzurum,** Şenkaya, Narman-Göle (Ardahan) highway, north of Değirmenlidere Village, 40°44′164″N, 42°31′48″E, alt. 1807 m, 29 July 2013 [**CL 0.890**]; Narman, Picnic area, Narman City Forest, on bark of *Populus tremula*, 40°13′31″N, 41°52′50″E, alt. 1950 m, 29 July 2013 [**CL 0.887**]; Oltu, Narman-Oltu highway, northwest of Ünlükaya Village, on bark of *Artemisia* sp., 40°28′68″N, 41°58′32″E, alt. 1370 m, 29 July 2013 [**CL 1.330**]; **Gümüşhane,** Şiran, Kelkit-Şiran highway, Çilhoroz Pass, southwest of Kazanpınar Village, on bark of *Quercus* sp., 40°10′45″N, 39°16′20″E, alt. 1670 m, 25 July 2013 [**CL 0.902**]; **Gümüşhane,** Kelkit, north of Kelkit, northwest of Gökçepınar, on bark of *Quercus* sp., 40°17′23″N, 39°29′37″E, alt. 1680 m, 25 July 2013 [**CL 1.400**]; **Gümüşhane,** Kelkit, Erzincan-Gümüşhane highway, southeast of Kömür Village, on bark of *Rosa* sp., 39°55′01″N, 39°24′51″E, alt. 1775 m, 24 July 2013 [**CL 1.469**]; **İçel,** Mut, southeast of Sertavul Pass, on bark of *Juniperus* sp., 36°51′28″N, 33°17′72″E, alt. 1420 m, 14 June 2013 [**CL 1.095**]; **İzmir,** Spil Mount, northwest of National Park, on bark of *Acacia* sp., 38°33′31″N, 27°24′01″E, alt. 1250 m, 30 June 2012 [**CL 0.266**]; **Karabük,** Eflani, northwest of Ulugeçit Village, on bark of *Malus* sp., 41°24′01″N, 32°53′50″E, alt. 885 m, 29 July 2012 [**CL 0.449**]; **Karabük**, Safranbolu, southwest of Ağaçköse Village, (Karabük-Eflani highway), on bark of *Alnus* sp., 41°20′20″N, 32°42′34″E, alt. 965 m, 29 July 2012 [**CL 0.540**]; **Kars,** Arpaçay, Ardahan-Susuz highway, northeast of Kümbet Village, on bark of *Astragalus* sp., 40°51′99″N, 43°10′20″E, alt. 1680 m, 30 July 2013 [**CL 1.049**]; **Kastamonu,** Devrakani, Yaralıgöz Pass, on bark of *Populus tremula*, 41°46′17″N, 34°02′50″E, alt. 1450 m, 30 July 2012 [**CL 0.486**]; **Kastamonu,** Pınarbaşı, Karaağaç Köyü'nün güneybatısı, *Quercus* sp. ormanı, 41°28′42″N, 33°09′11″E, alt. 1050 m, 29 July 2012 [**CL 0.492**]; north of Ilgaz Mountain National Park, on bark of *Populus* sp., 41°06′00″N, 33°44′40″E, alt. 1495 m, 31 July 2012 [**CL**

**0.608, CL 0.609];** Devrakani, northeast of Yolasığmaz Village, on bark of *Pinus sylvestris*, 41°34′10″N, 33°46′33″E, alt. 225 m, 30 July 2012 [**CL 0.571**]**;** Şenpazar, southeast of Dağlı Village, on bark of *Populus*, 41°47′11″N, 33°08′22″E, alt. 690 m, 30 July 2012 [**CL 1.813**]**, Kırıkkale,** Balışeyh, north of Taşyazı Village, on bark of *Quercus* sp., 40°00′31″N, 33°55′40″E, alt. 1250 m, 20 July 2012 [**CL 2.241**]**; Kırklareli,** Center, west of İnece Municipality, on bark of *Salix* sp., 41°32′19″N, 27°06′23″E, alt. 100 m, 29 May 2012 [**CL 0.382**]**; Kütahya,** Ilıca, southwest of Ilıca, on bark of *Salix* sp., 39°35′13″N, 30°03′55″E, alt. 975 m, 29 June 2012 [**CL 0.171**]**;** Kütahya-Eskişehir highway, southwest of Soğukyayla Village, northeast of Ürünçiftliği Village, on bark of *Juniperus* sp., 39°22′30″N, 30°16′30″E, alt. 1490 m, 29 June 2012 [**CL 0.810**]**; Malatya,** Malatya-Kayseri highway, Akçadağ, southeast of Sarıhacı Village, on bark of *Quercus* sp., 38°22′59″N, 37°54′05″E, alt. 1440 m, 10 July 2013 [**CL 1.046**]**; Mardin,** Midyat, north of Danin Pass, northeast of Yemişli Village, on bark of *Prunus* sp., 37°19′99″N, 41°21′22″E, alt. 925 m, 05 July 2013 [**CL 1.290**]**; Muğla,** Köyceğiz, southwest of Hamit Village, near Köyceğiz Lake, on bark of *Alnus* sp., 36°56′30″N, 28°36′31″E, alt. 55 m, 04 July 2012 [**CL 1.768**]**; Niğde,** northwest of Altunhisar, Küçük Hasan Mount., on bark of *Hippophae rhamnoides*, 38°04′77″N, 34°15′767″E, alt. 1630 m, 05 June 2013 [**CL 1.151**]**; Ordu,** Center, City tomb, on bark of *Platanus orientalis*, 40°58′15″N, 37°53′36″E, alt. 42 m, 30 August 2012 [**CL 0.196**]**; Samsun,** Havza, northwest of Salur Village, on bark of *Populus* sp., 41°00′25″N, 35°52′47″E, alt. 840 m, 28 August 2012 [**CL 1.345**]**;** Ladik, east of Akdağ Ski Center, on bark of *Juglans regia*, 40°54′14″N, 35°53′38″E, alt. 960 m, 28 August 2012 [**CL 1.578**]**; Siirt,** Eruh, northwest of Eruh, south of Gölgelikanat Village, on bark of *Pistacia* sp., 37°45′80″N, 42°07′788″E, alt. 950 m, 05 July 2013 [**CL 2.106**]**; Sinop,** Durağan, northeast of Yassıalan Village, on bark of *Quercus* sp., 41°29′01″N, 35°07′42″E, alt. 795 m, 26 August 2012 [**CL 1.320**]**; Tokat,** Çamlıbel, southeast of Tekreli Village, on *Astragalus* sp., 40°10′37″N, 36°30′55″E, alt. 1450 m, 29 August 2012 [**CL 0.685**]**; Tokat,** Center, Geyras, on bark of *Pistacia* sp., 40°14′54″N, 36°32′47″E, alt. 790 m, 29 August 2012 [**CL 1.564**]**; Trabzon,** Vakfıkebir, on calcareous rocks, 41°02′54″N, 39°14′52″E, alt. 0 m, 31 August 2012 [**CL 0.255**]**; Yozgat,** Akdağmadeni, İnönü Village, on bark of *Populus* sp., 39°28′48″N, 35°47′00″E, alt. 1470 m, 10 April 2012 [**CL 0.265**]**; Zonguldak,** Ereğli, Göktepe, on bark of *Populus* sp., 41°13′22″N, 31°25′00″E, alt. 135 m, 26 July 2012 [**CL 0.331**].

***Athallia skii*** (Khodos., Vondrak & Šoun) Arup, Frödén & Søchting

**Specimens examined: Turkey, Hatay,** between Arsuz-Samandağ, on *Erica* sp., 36°19′27″N, 35°47′36″E, alt. 220 m, 03 September 2014 [**CL 2.132**]**; İzmit,** Kandıra, east of Cebeci, on the shrubs in the seashore, 41°12′00″N, 30°19′47″E, alt. 0 m, 31 May 2012 [**CL 0.172**].