Molecular phylogeny and taxonomy of Eurasian Neoerysiphe species infecting Asteraceae and Geranium

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Key words
28S rDNA
Asteraceae
Erysiphales
Japan
Mediterranean region
new species
rDNA ITS region
systematics

Abstract Because Eurasian samples of Neoerysiphe collected on the Asteraceae were not identical in morphology, the molecular and morphological differences among these specimens were compared with those of the American N. cumminsiana. Neoerysiphe on Asteraceae was found to consist of at least four different species. Three of them are described as new species, viz. N. hiratiae, N. joerstadii, and N. nevoi. Neoerysiphe hiratiae is a Japanese species parasitizing hosts belonging to the genera Cacalia and Ligularia (tribe Seneconaeae). Neoerysiphe joerstadii was found in Israel on Phragmalon rupestrae (tribe Graphealaeae). Neoerysiphe nevoi was recorded in Israel and Ukraine on a number of hosts in different genera but all belonging to tribe Cichorieae. Thus, Eurasian Neoerysiphe species infecting the Asteraceae are strongly specialised to particular tribes of this family. Phylogenetic analyses indicated that the three new species were not closely allied. Neoerysiphe hiratiae is related to the American N. cumminsiana and species belonging to Oidium s.str. (Conidiom. Neoe.) Neoerysiphe nevoi is sister to N. geranii, and N. joerstadii is allied to N. gallii. In addition, Ukrainian Neoerysiphe samples on Geranium were phylogenetically and morphologically identical to Japanese samples of N. geranii, and this fungus seems to be an invasive species in Ukraine.

Article info Received: 9 September 2009; Accepted: 5 March 2010; Published: 8 April 2010.

INTRODUCTION

Based on the anamorph type, Heluta (1988) proposed to divide the genus Erysiphe into two separate genera, viz. Erysiphe s.str. and Golovinomyces. The former included all species with an anamorph of the Pseudoidium type (conidia formed singly on conidiophores), whereas the latter consisted of species with an anamorph of the Oidium s.str. type (= Euoiudium; conidia catenate). Species belonging to two Erysiphe sections introduced by Braun (1978, 1981), namely Golovinomyces and Galeopsidis, were included in the genus Golovinomyces sensu Heluta (1988). Only one species, E. galeopsidis, was contained in sect. Galeopsidis. This species differed from other Erysiphe representatives by its lobed appressoria and matura

from Turkey (Bahcecioglu et al. 2006). In addition, Takamatsu et al. (2008) revealed that Oidium alosiae on Alosia citridera, O. baccharidis on Baccharis linearis and B. racemosa, and O. maquii on Aristotelia chilensis are anamorphs of Neoerysiphe. Thus, at present this genus combines six teleomorph and three anamorph species, viz. N. chelones on the Scrophulariaceae, N. cumminsiana and O. baccharidis on the Asteraceae, N. gallii and N. rubiae on the Rubiaceae, N. geranii on the Geraniaceae, O. alosiae on the Verbenaceae, O. maquii on the Elaeocarpaceae, and N. galeopsidis parasitizing many hosts of Lamiaceae as the main host family but also a few species in Acanthaceae, Bignoniaceae, Dipsacaceae, and Malvaceae (Liu et al. 2005, Takamatsu et al. 2008). Each of these species has a quite different distribution. Neoerysiphe galeopsidis is nearly circumglobal, known from all Europe, Asia, Africa, North America, and New Zealand (Braun 1987). Distributions are rather limited for the remaining species. Neoerysiphe chelones is known from the USA, N. rubiae only from Turkey. Neoerysiphe gali is a Eurasian species. Neoerysiphe geranii was known from Japan and probably from New Zealand (Amano 1986, Nomura 1997). Heluta (2001) also reported this fungus from Ukraine. Some questions regarding the distributions of certain Neoerysiphe species have still to be answered. For instance, N. geranii seems to have a more disjunctive distribution. Furthermore, it is also possible that another species morphologically close to N. geranii is distributed in Ukraine. Braun (1983) described N. cumminsiana on Senecio seemannii from the USA and later reported it from North America and Japan on hosts belonging to Cacalia, Eupatorium, Heliopsis, and Ligularia (Braun 1987). Heluta (1989, 1999) first recorded a powdery mildew of Crepis and Taraxacum in Ukraine as Golovinomyces gali, and later changed it to G. cumminsianus. Voytyuk et al. (2004, 2006) reported N. cumminsiana from Israel on hosts of many genera of the Asteraceae, viz. Carthamus, Crepis, Filago, Hedynpois, Phaglam, Rhagadiolus, Senecio, Thrinacia, and Topis. According to Voytyuk et al. (2004), N. cumminsiana has a unique distribution being the only representative of the Erysiphales

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Persoonia 24, 2010: 81–92
www.persoonia.org
DOI: 10.3767/003158510X501696

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which must be classified as an American-African-Eurasian South Holarctic species. However, this does not correspond to the set of probable geographic and mycoflorogenetic units of powdery mildews proposed by Heluta (1993, 1995). These units consist of species having many factors in common, mainly their probable time and place of origin and current habitats. It is also not in accordance with Heluta’s (1992) hypothesis on the ways of powdery mildew migration. Therefore, Voytyuk et al. (2004) assumed that this hypothesis was either not fully correct or N. cumminsiana is a species with complex similar morphological characteristics. In the latter case ‘N. cumminsiana’ might be descended from an ancestor such as N. galapensis and might have emerged independently in several regions of North and South America, Africa, or Eurasia. In addition, specimens of Israeli ‘N. cumminsiana’ are morphologically not uniform. Voytyuk et al. (2004, 2006) reported that collections on Phagnalon rupestre had much larger chasmotheca and smaller peridial cells than those on other host plants. Furthermore, the taxonomic status of Eurasian ‘N. gerani’ and ‘N. cumminsiana’ was never examined with molecular methods. The goal of this study was to clarify the origin of the European populations of N. gerani and the Eurasian biotypes of ‘N. cumminsiana’, using mainly molecular methods.

MATERIALS AND METHODS

Molecular phylogenetic studies

The fungal species, host plants, location of collection, and accession numbers for the nucleotide sequence databases (DDBJ, EMBL and GenBank) are provided in Table 1. Isolation of whole-cell DNA was performed using the chelex method (Walsh et al. 1991) as described in Hirata & Takamatsu (1996). The 5′-end of the 28S rDNA, including the domains D1 and D2, and ITS region, including the 5.8S rDNA, were amplified by polymerase chain reaction (PCR) and then sequenced using direct sequencing as described in Takamatsu et al. (2004).

The sequences were initially aligned using the Clustal X package (Thompson et al. 1997). The alignment was then visually refined with MacClade v4.08 (Maddison & Maddison 2005). The alignments were deposited in TreeBASE (www.treebase.org). Phylogenetic trees were obtained from the data using the maximum parsimony (MP) method in PAUP* 4.0 (Swofford 2001) and Bayesian analysis in MrBayes 3.1.1 (Huelsenbeck & Ronquist 2001). MP analyses were performed with the heuristic search option using the ‘tree-bisection-reconstruction’ (TBR) algorithm with 100 random sequence additions to find the global optimum tree. All sites were treated as unordered and unweighted, with gaps treated as missing data. The strength of the internal branches of the resulting trees was tested with bootstrap (BS) analyses (Felsenstein 1985) using 1 000 replications with the stepwise addition option set as simple and maximum tree number as 100. BS values 70 % or higher are provided.

For Bayesian phylogenetic analyses, the best-fit evolutionary model was determined for each dataset by comparing different evolutionary models via the Akaike information criterion (AIC) using PAUP* and MrModeltest 2.2 (Nylander 2004). MrBayes was launched with random starting trees for 2 × 10^6 genera-

Table 1 Sources of Neoerysiphe material used for molecular analyses and their accession numbers in DNA databases.

| Fungal species       | Host             | Location; year | Voucher no. | Accession no. |
|----------------------|------------------|----------------|-------------|---------------|
| N. galapensis        | Galeopsis sp.    | Ukraine, Volynian region; 2004 | KW 33697F / MUMH4657 | AB498940  |
| Lamium amplexicaule  | Ukraine, Crimea; 2004 | KW 58375F / MUMH 4673 | AB498941  |
| Lamium purpureum     | Ukraine, Crimea; 2004 | KW 33682F / MUMH 4658 | AB498942  |
| Marrubium praecox    | Ukraine, Donetsk region; 2004 | KW 58376F / MUMH 4674 | AB498943  |
| Phlomis pungens      | Ukraine, Donetsk region; 2004 | KW 58398F / MUMH 4659 | AB498944  |
| Phlomis pungens      | Ukraine, Donetsk region; 2004 | KW 58377F / MUMH 4675 | AB498945  |
| Phlomis tuberosa     | Ukraine, Cherkasy region; 2005 | KW 33700F / MUMH 4680 | AB498946  |
| Phlomis tuberosa     | Ukraine, Donetsk region; 2004 | KW 58399F / MUMH4651 | AB498947  |
| Phlomis tuberosa     | Ukraine, Donetsk region; 2004 | KW 58378F / MUMH 4676 | AB498948  |
| Prasium majus        | Israel, Tel-Aviv; 2004 | HAI 4322 / MUMH 4680 | AB498949  |
| Stachys distans      | Israel, Carmel Mt.; 2004 | HAI 4327 / MUMH 4681 | AB498950  |
| N. galli             | Galium aparine    | Israel, Jordan Valley; 2004 | HAI 445 / MUMH 4682 | AB498951  |
| Geranium sibiricum var. popovii | Ukraine, Kyiv; 1998 | KW 28118F / MUMH 4662 | AB498952  |
| Geranium sibiricum var. popovii | Ukraine, Kyiv region; 1998 | KW 28121F / MUMH 4663 | AB498953  |
| Geranium sibiricum var. popovii | Ukraine, Kyiv region; 1998 | KW 28123F / MUMH 4664 | AB498954  |
| Geranium thunbergii  | Japan, Hokkaido; 2004 | KW 34781F / MUMH 3555 | AB498955  |
| Geranium sp.         | Ukraine, Kyiv; 2007 | KW 33701F / MUMH 4665 | AB498956  |
| N. hiratae           | Cacalia delphinifolia | Japan, Ehime; 1998 | KW 34784F / MUMH 567 | AB498957  |
| Cacalia hastata spp. farfarifolia | Japan, Nagano; 2004 | KW 34785F / MUMH 3504 | AB498958  |
| Liguaria fischeri    | Japan, Okayama; 2006 | KW 34786F / MUMH 4471 | AB498959  |
| Liguaria stenocephala| Japan, Mie; 2004 | KW 34789F / MUMH 3611 | AB498960  |
| Liguaria stenocephala| Japan, Nagano; 2004 | KW 34788F / MUMH 3505 | AB498961  |
| Liguaria stenocephala| Japan, Shiga; 2004 | KW 34787F / MUMH 3442 | AB498962  |
| N. joerstadii        | Phagnalon rupestre | Israel, Golan Heights; 2004 | HAI 4239 / MUMH 4668 | AB498976  |
| N. nevii             | Chondrella sp.    | Ukraine, Crimea; 2004 | KW 58373F / MUMH 4672 | AB498963  |
| Crepis aspera        | Israel, Carmel Mt.; 2004 | HAI 4184 / MUMH 4667 | AB498964  |
| Crepis aspera        | Israel, Northern Negev; 2004 | KW 34790F / MUMH 4683 | AB498965  |
| Crepis rhoeasfolia   | Ukraine, Crimea; 1982 | KW 11755F / MUMH 4655 | AB498966  |
| Crepis rhoeasfolia   | Ukraine, Crimea; 1982 | KW 11756F / MUMH 4654 | AB498967  |
| Hedypnois cretica    | Israel, Northern Negev; 2004 | KW 34793F / MUMH 4675 | AB498968  |
| Picris andreanata     | Israel, Mi’ilya; 2004 | HAI 4114 / MUMH 4669 | AB498969  |
| Rhagadiolus stellatus| Ukraine, Northern Negev; 2004 | KW 34797F / MUMH 4670 | AB498970  |
| Rhagadiolus stellatus| Ukraine, Crimea; 2004 | KW 58374 / MUMH 4677 | AB498971  |
| Taraxacum sp.        | Ukraine, Crimea; 1981 | KW 11777F / MUMH 4656 | AB498972  |
| Thrincia tuberosa    | Israel, Lower Galilee; 2004 | HAI 4123 / MUMH 4678 | AB498973  |
| Tolpis virgata       | Israel, Upper Galilee; 2004 | HAI 4296 / MUMH 4679 | AB498974  |
| N. nevii var. scolymi| Scolythus hispanicus | Israel, Carmel Mt.; 2005 | HAI 5195 / MUMH 4671 | AB498975  |

1 Sources: HAI = Haifa University, Herbarium of the Institute of Evolution, Israel; KW = National Herbarium of the M.G. Khodoyr Institute of Botany, Kiev, Ukraine; MUMH = Mie University, Mycological Herbarium, Japan.

2 The nucleotide sequence data will appear in the DDBJ, EMBL, and GenBank databases under the respective accession number.
tions and the Markov chains were sampled every 100 generations, which resulted in $2 \times 10^4$ sampled trees. To ensure that the Markov chain did not become trapped in local optima, we used the MCMC-MC algorithm, performing the estimation with four incrementally heated Markov chains. Bayesian posterior probability (PP) values 0.95 or higher are shown.

**Morphological analysis**

Powdery mildew specimens involved in the morphological analysis are listed after each description of new taxa. Morphological features of the specimens were examined and photographed using light microscopes MBI-6 (LOMO, Russia) with objectives ×16 and ×40 (Carl Zeiss, Germany) in phase contrast and Primo Star (Carl Zeiss, Germany) with objectives ×10 and ×40. Photographs were prepared by the digital cameras EOS 350D and PowerShot A640 (both Canon, Tokyo, Japan), accordingly. Shrivelled conidiophores, conidia, and superficial hyphae were restored by heating to start of boiling in 40 % lactic acid. Only dry chasmothecia on host leaves were measured. For each morphological feature 30 structures were measured and the data processed statistically. Limits of variation were determined as $M \pm 1.96\sigma$, where $M$ is a simple average and $\sigma$ is a standard deviation. The SEM micrographs were obtained with a Jeol JSM–6060LA (Tokyo, Japan) SEM microscope. Dry pieces of leaf with mycelium, conidia, and ascomata were glued to metallic stubs and gold coated under vacuum. The specimens examined are deposited at HAI, HUJ, KW, MUMH, and TNS (abbreviations according to Holmgren et al. (1990)).

**RESULTS**

**ITS phylogeny**

Thirty-five ITS sequences of Neoerysiphe spp. were newly determined in this study (Table 1). These sequences were aligned with 30 sequences of Neoerysiphe spp. and three sequences of Arthrocladiella mougeotii used as an outgroup taxon. The dataset consisted of 68 sequences and 523 characters. All characters were aligned unambiguously. Of the 523 characters, 119 were variable and 104 characters were phylogenetically informative for parsimony analysis. A total of 58 100 equally parsimonious trees with 187 steps (CI = 0.775, RI = 0.961, RC = 0.745) were generated by the MP analysis, when it had to be terminated due to the limit of memory size of the software. One of the trees is shown in Fig. 1. We also performed parsimony ratchet analysis (Nixon 1999) using PAUP* and PAUPRat v1 (Sikes & Lewis 2001) and confirmed the generation of almost identical tree topologies with the same tree length. Thus, we concluded that the tree shown in Fig. 1 is not the result of a local optimum. MrModeltest selected SYM+I+G model as the best for this dataset. Bayesian analysis was performed using this evolution model and yielded 2 $\times 10^4$ trees. Of the trees, the first 14 130 were discarded (burn-in) because the average standard deviation of the split frequencies (ASDSF) dropped below 0.01. The remaining 5 870 trees were summarised in a majority-rule consensus tree, yielding the probability of each clade being monophyletic. The tree topology by the Bayesian analysis was almost identical to the MP tree, and thus the former tree is not shown.

The 65 sequences of Neoerysiphe analyzed in this study were divided into three large clades (A, B and C) clearly defined by their geographical distributions and host plants. Clade A consisted of a single species, *N. galeopidis*, and is supported strongly with both BS and PP values ($BS = 90\%$; $PP = 0.90$). Hosts of this species mostly belong to the Lamiaceae, but Acanthus (*Acanthaceae*) and Catalpa (*Bignoniaceae*) are also included in this clade as hosts. Maximum genetic divergence within this clade is only 0.8 %, which suggests that *N. galeopidis* diverged on the Lamiaceae and sporadically infected other plant families recently. Clades B and C formed a larger clade ($BS = 80\%$; $PP = 0.99$). Clade B ($BS = 75\%$; $PP = 1.0$) consists of hosts of the Asteraceae, and one specimen from both Aloysia (*Verbenaceae*) and Aristotelia (*Elaeocarpaceae*) collected in North and South America and Japan. This clade is further divided into four subclades. B1 contains Oidium *baccharidis* on Baccharis (tribe Asteraceae, Asteraceae) and B3 contains *O. aloysiae* on Aloysia, both collected in Argentina. B2 consists of *O. maquii* on Aristotelia, *N. cumminsiana* on Bidens (tribe Heliantheae, Asteraceae) and Eupatorium (tribe Eupatorieae, Asteraceae), and Oidium sp. on Galinsoga (tribe Millerieae, Asteraceae) obtained from the USA and South America ($BS = 91\%$; $PP = 0.99$). B4 ($BS = 99\%$; $PP = 1.0$) comprises seven sequences of Neoerysiphe on Cacalia and Ligularia (tribe Senecioneae, Asteraceae) collected in Japan. These seven sequences are identical to each other. This fungus has been identified as *N. cumminsiana* (Nomura 1997, Takamatsu et al. 2008), but the present analysis indicates that the fungus forms an independent lineage different from *N. cumminsiana* collected in North and South America. Clade C ($BS = 74\%$; $PP = 0.89$) comprises Neoerysiphe spp. collected in Eurasia, especially in Mediterranean and circum Mediterranean areas like the north part of Israel and the south part of Ukraine, and is further divided into four subclades. C1 consists of a single sequence of a fungus on *Phagnalon rupestre* (tribe *Graphieae*, Asteraceae) collected in Israel. The same sequence was obtained when the sequencing of the DNA extraction from this specimen was repeated. Subclades C2 and C3 consisted of *N. galii* on *Galium* spp. (*Rubieaeae*) and *N. geranii* on *Geranium* spp. (*Geranieaeae*), respectively. Both clades were strongly supported by BS and PP values ($BS = 100\%$; $PP = 1.0$ in both C2 and C3). All these specimens were collected in Europe, except for specimens of *N. geranii* collected in Japan and one sample of *N. galii* from Israel. C4 consisted of 13 sequences from fungi on tribe *Cichorieae* of the *Asteraceae*, collected in Israel and Ukraine. There was some genetic divergence within this clade. Subclades C3 and C4 formed a clade with strong support ($BS = 56\%$; $PP = 1.0$).

**28S phylogeny**

Thirty-one 28S rDNA sequences including D1/D2 domains of Neoerysiphe spp. were newly determined in this study (Table 1). These sequences were aligned with 21 sequences of Neoerysiphe spp. and two sequences of *Arthrocladiella mougeotii* used as an outgroup taxon. The dataset consisted of 54 sequences and 650 characters. All characters were aligned unambiguously. Of the 650 characters, 65 were variable and 51 characters were phylogenetically informative for parsimony analysis. A total of 14 equally parsimonious trees with 87 steps ($CI = 0.770$, $RI = 0.944$, $RC = 0.727$) were generated by the MP analysis. Of these 14 trees, a tree with the highest likelihood value is shown in Fig. 2. MrModeltest selected GTR+I model as the best for this dataset. Bayesian analysis using this evolution model yielded $2 \times 10^4$ trees. Of these, the first 7 020 were discarded (burn-in) because ASDSF dropped below 0.01. The remaining 12 980 trees were summarised in a majority-rule consensus tree, yielding the probability of each clade being monophyletic. The tree topology by the Bayesian analysis was almost identical to the MP tree, and thus the former tree is not shown.

The tree constructed by the 28S rDNA dataset strongly supported the phylogeny of Neoerysiphe shown in the ITS tree. Neoerysiphe sequences analysed in this study were divided...
into three large clades (A, B, and C), although clade B was collapsed in the strict consensus tree. Subclades B1, B2, B3, B4, C1, C2, C3, and C4 are also supported in the 2S tree, although BS and PP supports were lower than those in ITS tree. Subclades C3 and C4 formed a clade with strong support (BS = 85%; PP = 0.99).

**Morphology**

Mycelium of samples belonging to subclade B4 was well developed, especially along the veins of the leaves (Fig. 3a). Primary hyphae had distinct appressoria. The secondary mycelium appeared simultaneously with chasmothecium initials immediately following the sexual reproduction. This mycelium consisted of thin hyaline hyphae that later surrounded chasmothecia as an

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**Fig. 1** Phylogenetic analysis of the nucleotide sequences of the ITS region including 5.8S rDNA for 68 sequences from Neoerysiphe with Arthrocladiella used as outgroup taxon. The tree is a phylogram of one of the 58 KMP trees with 178 steps obtained by a heuristic search employing the random stepwise addition option of PAUP*.

Gaps were treated as missing data. Horizontal branch lengths are proportional to the number of nucleotide substitutions that were inferred to have occurred along a particular branch of the tree. Percentage BS support (1 000 replications; ≥ 70%) and PP (≥ 0.95) are shown on and under branches, respectively. Nodes with asterisks (*) denote that the nodes collapsed in the strict consensus tree.

A Global

B New World & East Asia

C Eurasia

D fremontii

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**Table 1**

| Species | Accession Number | Location |
|---------|------------------|----------|
| N. nevoi ex Chondrilla sp. | KW58373 UKR | Europe |
| N. nevoi ex Crepis aspera | KW34790 ISR | Europe |
| N. nevoi ex Crepis rheoedfolia | KW11753 UKR | Europe |
| N. nevoi ex Crepis rheoedfolia | KW11755 UKR | Europe |
| N. nevoi ex Rhagadiolus stellatus | HA14329 ISR | Americas |
| N. nevoi ex Rhagadiolus stellatus | KW58374 UKR | Americas |
| N. nevoi ex Taraxacum sp. | KW11777 UKR | Eurasia |
| N. nevoi ex Hedyopnis cretica | KW34793 ISR | Asia |
| N. nevoi ex Picris amalcticana | HA14114 ISR | Asia |
| N. nevoi ex Thrinca tuberosa | HA1423 ISR | Asia |
| N. nevoi ex Tolpis virgata | HA4296 ISR | Asia |
| N. nevoi ex Crepis aspera | HA14164 ISR | Asia |
| N. nevoi ex scolyomi ex Scylmus hispanicus | HA5195 ISR | Europe |
| N. galeopsis ex Chondrilla sp. | KW58373 UKR | Europe |
| N. galeopsis ex Crepis aspera | KW34790 ISR | Europe |
| N. galeopsis ex Crepis rheoedfolia | KW11753 UKR | Europe |
| N. galeopsis ex Crepis rheoedfolia | KW11755 UKR | Europe |
| N. galeopsis ex Rhagadiolus stellatus | HA14329 ISR | Americas |
| N. galeopsis ex Rhagadiolus stellatus | KW58374 UKR | Americas |
| N. galeopsis ex Taraxacum sp. | KW11777 UKR | Eurasia |
| N. galeopsis ex Hedyopnis cretica | KW34793 ISR | Asia |
| N. galeopsis ex Picris amalcticana | HA14114 ISR | Asia |
| N. galeopsis ex Thrinca tuberosa | HA1423 ISR | Asia |
| N. galeopsis ex Tolpis virgata | HA4296 ISR | Asia |
| N. galeopsis ex Crepis aspera | HA14164 ISR | Asia |
| N. galeopsis ex scolyomi ex Scylmus hispanicus | HA5195 ISR | Europe |
| N. galeopsis ex Chondrilla sp. | KW58373 UKR | Europe |
| N. galeopsis ex Crepis aspera | KW34790 ISR | Europe |
| N. galeopsis ex Crepis rheoedfolia | KW11753 UKR | Europe |
| N. galeopsis ex Crepis rheoedfolia | KW11755 UKR | Europe |
| N. galeopsis ex Rhagadiolus stellatus | HA14329 ISR | Americas |
| N. galeopsis ex Rhagadiolus stellatus | KW58374 UKR | Americas |
| N. galeopsis ex Taraxacum sp. | KW11777 UKR | Eurasia |
| N. galeopsis ex Hedyopnis cretica | KW34793 ISR | Asia |
| N. galeopsis ex Picris amalcticana | HA14114 ISR | Asia |
| N. galeopsis ex Thrinca tuberosa | HA1423 ISR | Asia |
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| N. galeopsis ex Taraxacum sp. | KW11777 UKR | Eurasia |
| N. galeopsis ex Hedyopnis cretica | KW34793 ISR | Asia |
| N. galeopsis ex Picris amalcticana | HA14114 ISR | Asia |
| N. galeopsis ex Thrinca tuberosa | HA1423 ISR | Asia |
| N. galeopsis ex Tolpis virgata | HA4296 ISR | Asia |
interlacing delicate or somewhat denser web (Fig. 3b, g). It should be noted that both mycelia are pure white without any yellowish or brownish tints. In contrast to these fungi, samples of subclade C4 had yellowish primary mycelium which gave rise to white secondary mycelium occasionally with somewhat yellowish hyphae. Mycelium of the fungus on Phagnalon rupestre (C1) was very weakly developed, almost invisible, greyish and only confined to primary mycelium. *Hyphal appressoria* in all groups were variable, of similar size, unlobed or somewhat lobate (Fig. 3c, d and 5a–c). Anamorphs were observed only in subclades B4 and C4. *Conidiophores* were very similar morphologically, with straight, cylindrical foot-cells, frequently increasing from...
base to top, 24–45.5 × 9.5–12.5 µm, followed by 1–2 shorter cells and conidium initials (Fig. 3e, h and 5e). However, in subclade C4 the foot-cells were occasionally very long, up to 100 µm. Conidia in subclade B4 were catenate, mainly cylindrical with rounded ends, often oblong ellipsoidal, long, up to 48 µm (Fig. 3f), whereas in C4 they were mainly ellipsoidal or short cylindrical with rounded ends, often almost limoniform, short, up to 36 µm (Fig. 5f); the length/width ratios were 1.9–3.5 (average 2.7) and 1.5–2.5 (average 1.9), respectively. Chasmothecia of all specimens studied were hemispherical, depressed or even concave in the lower part (Fig. 3i, 4c, and 5i) but on Phagnalon rupestre (C1) they were more flattened and distinctly larger, up to 200 µm diam. This contrasted with the other specimens, e.g. subclades B4 and C4 having chasmothecial diameters...
mainly up to 157 μm and 148 μm, respectively. The fungus on *Phagnalon* also had a rather transparent peridium, enabling the number of ascis to be easily viewed and counted whilst still within the chasmothecium (Fig. 4d). Peridial ascis of this fungus were obscure, polygonal or irregular in shape and small, 11–17(–33) × 10–14(–16) μm. The peridial surface was indistinctly close-meshed or knobby (Fig. 4b, c), whilst in subclades B4 and C4 the peridium was less transparent with ascis invisible within the chasmothecium. Peridial ascis in subclade B4 were, however, more visible and more regular in shape than those of the *Phagnalon* parasite, but similarly small. Peridial ascis in subclade C4 were distinguished from those in C1 and B4 by being distinct and perceptibly larger, up to 30 × 17 μm. The peridial surface also differed in being distinctly meshed and similar to the other samples in this group (Fig. 5i, j) with the exception of the fungus on *Scolymus hispanicus*. This fungus has chasmothecia with a deeply pitted peridium where cell junctions formed conspicuous ridges (Fig. 5k).

Appendages of all specimens studied were well developed but very short and hyaline in chasmotheca on *Phagnalon rupestre*. In subclade B4 appendages were also hyaline and only in one specimen they were somewhat yellowish. All those in C4 were more or less pigmented. Ascis in all three clades B4, C1, and C4 were similar in shape, mainly obovate, stipitate, and immature in the current season but they were more oblong on *Phagnalon* and more numerous, 16–32 per chasmothecium, in contrast to subclades B4 and C4 where the number of ascis did not exceed 12 (compare Fig. 4g with Fig. 3n and 5n–q).

Morphological analysis indicated that the fungi belonging to subclades B4, C1 and C4 had obvious differences and must be treated as separate species. This conclusion fully agreed with the results of our phylogenetic analysis. The type specimen of *N. cumminsiana*, another *Neoerysiphe* species parasitizing the Asteraceae, was also included in the morphological analysis. In this specimen secondary mycelium was also formed, but it is barely visible and appressed to the substrate. Chasmothecia were large like those on *Phagnalon* but differed in having a unique structure, characterised by a clearly visible basal evagin.

ation up to 27 μm height (Fig. 4h–j). Such a feature is unknown in any other *Neoerysiphe* species. Although the peridium of *N. cumminsiana* was also transparent and the chasmothecia were large like those on *Phagnalon*, the ascis were fewer, mainly 10, and notably larger, 50–57 × 31–35.5 μm. Thus, all the studied samples of Eurasian *Neoerysiphe* parasitizing *Asteraceae* differed from *N. cumminsiana* morphologically and so do undoubtedly not belong to this species. An attempt to sequence the type specimen of *N. cumminsiana* failed.

Results of the phylogenetic analysis indicated that subclades C4 and C3 (N. geranii) were sister groups. Their propinquity was confirmed by morphological examinations of these fungi, including the type specimen of *N. geranii*. However, subclade C4 had a more developed secondary mycelium, a conidial surface with larger number of lengthwise striations, a less transparent peridium, and ascis more ellipsoidal than obpyriform (compare Fig. 5h–q with 4i–o).

*Neoerysiphe* on *Phagnalon* (C1) differs strongly from all known *Neoerysiphe* species, first of all, by its large chasmothecia with numerous somewhat elongated ascis. Powdery mildews in subclade B4 are allied to American *N. cumminsiana* but they differ in having smaller fruiting bodies, chasmothecium being concave in the lower half, without evagination and aerial secondary mycelium, not appressed to the substrate. Morphologically, this group seems to be closer to subclade C4 but is distinguished by long cylindrical conidia, white secondary mycelium, and a less sculptured chasmothecial surface.

### Taxonomy

Phylogenetic and morphological analyses have indicated that all three groups of Eurasian *Neoerysiphe* specimens parasitizing *Asteraceae* do not correspond to *N. cumminsiana* or any other known species of this genus, i.e. they have to be considered separate, new species, which are described as *N. hiartae* from Japan, *N. joerstadii* from Israel, and *N. nevoi*, including its variety *scolymin*, mainly from the Mediterranean region.

**Neoerysiphe hiartae** Heluta & S. Takam., sp. nov. — Myco-

Bank MB513278; Fig. 3

Anamorph. Oidium subgenus Sclerotium.

Species nostra *Neoerysiphe cumminsiana* affinis est tamen mycelio sec-

undario albo et tomentoso, conidiis longis, chasmothecii minoribus et basi chasothecii protuberante carens bene differt.

**Etymology.** Named in honour of the famous Japanese mycologist Koji Amano (Hiarta).

*Mycecum* amphiogenous, often more developed along the veins of leaves, also cauliculous and on petioles, at first forming patches, then confluent. *Primary mycelium* thin, greyish, hyphal diam 5–6(–11) μm. *Secondary mycelium* arising from primary hyphae, pure white, hyphae smooth, without appressoria, 5–6 μm diam, forming a delicate or thick and tomentose web around ascomata. *Hyphal appressoria* very variable in shape and size, distinct, unlobed or slightly lobate, frequently in pairs, 7–10 × 4.5–6.5 μm. *Conidiophores* straight or sometimes arcuate, 112–154 μm, foot-cells cylindrical, 24–41 × 11–12 μm, frequently increasing in width towards the tip, followed by one shorter cell and conidial initials. *Conidia* catenate, mainly cylindrical with rounded ends, often oblong ellipsoidal, 27–48 × 11–17.5 μm, length/width ratio 1.9–3.5 (average 2.7). *Chasmothecia* scattered, hemispherical, depressed in the lower part, with an indistinct close-meshed or often knobby peridial surface, (102–)105–153(–157) μm diam. Peridial cells polygonal or irregular, small, 9–20 × 5–12 μm. *Appendages* numerous, in the basal part of the chasmothecium, meiloid, well developed, 0.5–2 times as long as the chasmothecial diam, 5–6 μm wide, hyaline, rarely somewhat brownish. *Ascis* 7–12 per chasmothecium, immature, oblong ellipsoid, obpyriform, with an irregular outline, wide in the lower part and abruptly narrowed in the upper part, 46–57 × 21–30 μm, short-stalked, ascospores not developed before overwintering.

Specimens examined. JAPAN, Shiga, Mt Ibuki, on *Ligularia stenophoea* (Maxim.) Matsum. & Koidz. (Asteraceae), 7 Nov. 2004, S. Takamatsu, holotype TNS F-25684, isotype KW 34787F, MUMH 3442, DNA sequence ex-type AB498862; Echoine, Mt Ishiduchi, on *Cacalia delphiniifolia* Siebold & Zucc., 9 Nov. 1998, S. Takamatsu, MUMH 552, KW 34783F; Mt Binogamori, on *C. delphiniifolia*, 10 Nov. 1998, S. Takamatsu, MUMH 567, KW 34784F; Nagano, Kamikouchi, on *C. hastata* L. ssp. farfaraefolia, 3 Sept 2004, S. Takamatsu, MUMH 3504, KW 34785F; Okayama, Kagamino Town, Forest Park, on *Ligularia fischeri* Turcz., 2 Nov. 2006, S. Takamatsu, MUMH 4471, KW 34786F; Mie, Mt Nonobori, on *L. stenophoea*, 21 Nov. 2004, S. Takamatsu, MUMH 3611, KW 34789F; Nagano, Kamikouchi, on *L. stenophoea*, 4 Sept. 2004, S. Takamatsu, MUMH 3505, KW 34788F.

**Neoerysiphe joerstadii** Heluta & S. Takam., sp. nov. — Myco-

Bank MB513279; Fig. 4a–g

Anamorph. Not observed.

Species nostra *Neoerysiphe cumminsiana* similis est tamen absentia my-

celii secundarii, numero ascorum majoribus, 16–32 in chasmothecio, ascis longioribus et basi chasmotheci protuberante carens bene differt.

**Etymology.** Named in honour of the famous Norwegian mycologist Ivar Jerstad.

*Primary mycelium* amphiogenous, very sparse, inconspicuous. *Secondary mycelium* absent. *Appressoria* obscure, unlobed or
slightly lobate. *Anamorph* not observed. *Chasmothecia* scattered, hemispherical, very depressed in the lower part, with an indistinct close-meshed or knobly peridial surface, (118–)125–171(–200) µm diam and 92–97 µm high. Peridial cells obscure, polygonal or irregular, small, 11–17(–33) × 10–14(–16) µm. *Appendages* numerous, in the basal part of the chasmothecium, myceloid, 0.5–1 times as long as the chasmothecial diam, 4–6 µm wide, always hyaline, somewhat rough, interfaced with host fibres. *Asci* numerous, 16–32 per chasmothecium, oblong ellipsoid, with irregular outline when immature, increased in the lower part and narrowed in the upper part, 42–60 × 20–31 µm, stalked, ascospores not developed before overwintering.

Fig. 4 Morphology within phylogenetic subclades C1, B2 and C3. a–g: *Neoerysiphe joerstadii* (holotype, KW 35717F, subclade C1) on *Phagnalon rupestre*; h–l: *N. cumminsiana* (isotype, HAL 1462F, subclade B2) on *Senecio seemannii*; m–o: *N. geranii* (KW 34782F, subclade C3) on *Geranium* sp. a. Chasmothecia in reflected light; b, c. chasmothecia viewed by scanning electron microscope: c – side view; d. chasmothecium in transmitted light; e. peridial cells; f. chasmothecial appendages; g. asci; h. chasmothecium with evagination on the lower side, side view; i–k. chasmothecia viewed by scanning electron microscope: i – side view, j – bottom view; l. chasmothecium in transmitted light; m. conidium with longitudinal ridges; n. chasmothecia; o. asci. — Scale bars: a = 200 µm; b–d, h–l, n = 50 µm; e–g, o = 20 µm; m = 5 µm.
Specimens examined. **Israel.** Golan Heights, Yehudiyya, 32°56’N, 35°41’E, on Phagnalon rupestre (L.) DC. (Asteraceae), 17 May 2004, S. Voytyuk, holotype KW 35717F, isotypes HAI 4239, 4245, KW 34794F, 34795F, MUMH 4668, rDNA sequence ex-type AB498976; Upper Galilee, Mt Meron, Nahal Keziv, on Phagnalon rupestre, 18 Mar. 2002, T. Andrianova, KW 35716F; Zefat (= Safed), 22 Aug. 1953, T. Rayss, HUJ 301/111 147S.

**Neoerysiphe nevoi** Heluta & S. Takam., sp. nov. — MycoBank MB513280; Fig. 5

Anamorph. Oidium subgenus Striatoidium.

Species nostra *Neoerysiphe geranii* affinis est tamen mycelio secundario bene evoluto, conidiis magis striatulis, peridio minus translucenti, ascis magis ellipsoideis et minus pyriformibus differt.

Etymology. Named in honour of the famous Israeli biologist Eviatar Nevo.

**Fig. 5** Morphology within phylogenetic subclade C4. a, b, d–g, q: *Neoerysiphe nevoi* (KW 35726F) on Thrincia tuberosa; c, h–j, l–p: *N. nevoi* (holotype, KW 34802F) on Tolpis virgata; k: *N. nevoi* var. scolymi (holotype, KW 34809F) on Scolymus hispanicus. a–c. Hyphae of the primary mycelium with appressoria; d. secondary hypha arisen from the primary hypha; e. conidiophore; f–h. conidia; g. germinated conidium with a hypha extending from a lobed appressorium of the *Striatoidium* type; i–k. chasmothecia viewed by scanning electron microscope; l. chasmothecium viewed by light microscope; m. peridial cells; n–q. asci. — Scale bars: a, f, g, o, p = 10 µm; b, c, h = 5 µm; d, e, l–n, q = 20 µm; i–k = 50 µm.
Mycelium amphigenous, also caulicolous, effuse. *Primary mycelium* thin, yellowish, hyphal diam 4.5–7.5 µm. *Secondary mycelium* arising from primary hyphae, white to brownish, hyphae smooth, without appressoria, 4.5–6.5 µm diam, surrounding aphididae mainly as a delicate web, persistent on or even detached from the leaf. *Hyphal appressoria* on primary mycelium variable in shape and size, distinct, unlobed or slightly lobate, 6.5–8.5 × 4–5 µm. *Conidiophores* straight or somewhat aruncate, 125–165 µm, foot-cells cylindrical, 28.5–45.5–100) × 9.5–12.5 µm, frequently increasing in width towards the tip, followed by 1–2 shorter cells and conidial initials. *Conidia* catenate, mainly ellipsoidal or short cylindrical with rounded ends, often almost limoniform, 23.5–36 × 11–17.5 µm, length/width ratio 1.5–2.5 (average 1.9). *Conidial germ tube* with a lobed appressorium.

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**Specimens examined.** *Israel,* Upper Galilee, near ‘En Kamonnim, on *Tuberosa,* July 1982, *S. Voytyuk,* HAI 4238, KW 34792F, MUMH 4478; Carmel Coast, near Atlit, on *Crepis,* 13 Mar. 2004, *V. Heluta,* anamorph, KW 35721F, HAI 4238, KW 34792F, MUMH 4478; Lower Galilee, near Alonid Abba near Qirat Tiv'on, on *Tuberosa,* Aug. 2004, *S. Voytyuk,* HAI 4123, KW 34801F, MUMH 4478; Carmel Coast, near Atlit, on *Hedyphoiopsis cretica* (L.) Willd., 27 Apr. 2004, *S. Voytyuk,* HAI 4101, 4102, KW 34793F, 35724F, MUMH 4475; Golan Heights, on *Crepis,* 12 July 1982, *S. Voytyuk,* HAI 4110, 4112, KW 34796F, 34797F, MUMH 4475; *Tuberosa,* May 2004, *S. Voytyuk,* HAI 4110, 4112, KW 34796F, 34797F, MUMH 4475; *Tuberosa,* near ‘En Kamonnim, on *Tuberosa,* July 1982, *S. Voytyuk,* HAI 4110, 4112, KW 34796F, 34797F, MUMH 4475; *Tuberosa,* near ‘En Kamonnim, on *Tuberosa,* July 1982, *S. Voytyuk,* HAI 4110, 4112, KW 34796F, 34797F, MUMH 4475; *Tuberosa,* near ‘En Kamonnim, on *Tuberosa,* July 1982, *S. Voytyuk,* HAI 4110, 4112, KW 34796F, 34797F, MUMH 4475.

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**DISCUSSION**

Based on the ITS sequences as well as the 28S rDNA sequences, Takamatsu et al. (2006) reported that *Neoerysiphe* specimens of hosts belonging to the *Asteraceae* are divided into three subgroups, each of which corresponds to different host tribes, viz. *Heliantheae* and *Eupatorieae* (Group 2a), *Senecioneae* (2c), and *Asteraceae* (2d) (see Fig. 2 in Takamatsu et al. (2006) and Table 2). American and Japanese samples of *N. cumminisiana* appeared in different subgroups. Consequently, the authors concluded that *N. cumminisiana* could be divided into two different species. The present study confirmed this assumption. Morphological analysis demonstrated that Japanese samples are uniform, differ clearly from the true *N. cumminisiana,* and belong to a separate species here named *N. hiratae.* This species parasitizes *Cacalia* and *Ligularia* (tribe *Senecioneae,* subfamily *Asteroideae*) and is known only from Japan (East Asia). Other new species analysed here were *N. joerstadii* collected on *Phagnalon rupestre* (tribe *Gnaphalieae* in *Asteraceae*) in Israel (West Asia) and *N. nevo* infecting several hosts belonging to different genera in the tribe *Cichorieae* (in *Cichorieae*), viz. *Chondrilla, Crepis, Hedyphoi, Picris, Rhagadiolus, Scolymus, Taraxacum, Trinia* (= *Leontodon,* and *Tolpis*) (Table 2). Thus, Eurasian *Neoerysiphe* species are clearly connected with specific tribes of the *Asteraceae.* Similar close relationships between powdery mildews and their host tribes of the *Asteraceae* were also reported in *Golovinomyces* (Matsuda & Takamatsu 2003).

As mentioned above, Voytyuk et al. (2004) expressed doubt on the correctness of Heluta’s (1992) hypothesis about migrations...
of powdery mildew fungi because the natural distribution of *N. cumminsiana sensu* Heluta was not in accordance with this hypothesis. However, it is now clear that these authors dealt with a species complex composed of four different species, namely the American genuine *N. cumminsiana*, the Japanese *N. hiratae*, and the Mediterranean taxa *N. joerstadii* and *N. nevoi*. We should note that the description of *N. cumminsiana* in the monograph of Braun (1987) combined characteristics of *N. cumminsiana* and *N. hiratae*. Therefore, only the original description published by Braun (1983) refers to *N. cumminsiana* s.str. *Neoerysiphe nevoi* is currently only known from Israel and Ukraine but this species has probably a much wider distribution. It is very likely that all collections formerly reported as *Erysiphe cumminsiana*, *E. galeopsidis* or *E. gali* on Asteraceae from European countries and Africa (Amano 1986, Braun 1987, Gorter 1987) belong to this species. A few years ago we examined all specimens of powdery mildews from the herbarium of Jerusalem University (HUJ, Israel). Many specimens originally identified as *E. cichoracearum* actually belonged to *N. nevoi*. It is possible that numerous records of *E. cichoracearum* on hosts belonging to the genera *Crepis*, *Filago*, *Hedypnois*, *Hypochoeris*, *Picris*, and *Rhagadiolus* on the Canary and the Balearic Islands (Jørstad 1962a, b), in Portugal (de Mendonça & de Sequeira 1963, de Sequeira & de Mendonça 1965, de Sequeira 1969, 1975, 1978, 1981), Romania (Sandu-Ville 1967, Bontea 1986), Spain (Durrieu & Mercé 1972), and central Europe (Blumer 1967) also belong to *N. nevoi*. De Sequeira (1978) reported that fruiting bodies of *Erysiphe cichoracearum* on *Hedypnois cretica*, *Picris echioides*, *P. hieracioides*, and *Polpis barbata* collected in Portugal were immature, and the descriptions of other characters of these fungi agree well with those of *N. nevoi*.

We collected *N. joerstadii* only on *Phagnalon rupestrum*, but according to Amano (1986), *E. cichoracearum* was recorded on this host and *Ph. saxatile* in France, on the Balearic and the Canary Islands, and in the Spanish Sahara. These specimens very likely belong to *N. joerstadii*. Furthermore, the chasmothecia of this fungus on *Ph. saxatile* from the Balearic and the Canary Islands measured 130–200 µm diam (Jørstad 1962a, b). Such a size range fully conforms to *N. joerstadii*. As explained above, a powdery mildew on hosts belonging to *Geranium* in Ukraine was identified as *N. geranii* by Heluta (2001). However, since this species was known only from Japan and New Zealand (Amano 1986, Nomura 1997), we compared Japanese and Ukrainian samples including the type specimen. Phylogenetically and morphologically, all specimens were found to be uniform. Thus, the true *N. geranii* was correctly recorded in Ukraine as an invasive species.

In conclusion, molecular and morphological evidence revealed that at least four *Neoerysiphe* species, viz. *N. cumminsiana*, *N. hiratae*, *N. joerstadii*, and *N. nevoi*, are able to infect *Asteraceae*. Some of these fungi, above all *N. joerstadii* and *N. nevoi*, are probably common in the Mediterranean region but have been formerly identified and reported mainly as *E. cichoracearum*. Thus, the identity of powdery mildews collected on the *Asteraceae* in the Mediterranean and adjacent regions needs re-examination in the light of these findings.

Acknowledgments We are indebted to Tetiana V. Andrianoa (Ukraine) for kindly donating a specimen of *N. joerstadii*, Nadiya and Sergiej Mosyakin (Ukraine) for specimens of *N. geranii*, Uwe Braun (Germany) for providing the isotype of *N. cumminsiana*, Evital Nevo and Solomon P. Wasser (Israel) for appreciable support of our field work in Israel. We thank Roger Cook (Great Britain) for help with the English and valuable comments on the manuscript. We also gratefully acknowledge the late Mr. D. Diomenko, for his help with scanning electron microscopy.

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Table 2 Neoerysiphe and Oidium subgenus Striatoidium species aligned with their hosts in the Asteraceae and their geographical regions.

| Fungal species     | Subfamily       | Tribe            | Genus            | Geographical region            |
|--------------------|-----------------|------------------|------------------|-------------------------------|
| *Neoerysiphe*      |                 |                  |                  |                               |
| *cumminsiana*      | Asteroideae     | Coreopsisae      | Bidens           | North America                 |
|                    |                 | Eupatoriase      | Eupatorium       | South America                 |
| hiratae            | Asteroideae     | Senecioniase     | Senecio          | North America                 |
| joerstadii         | Asteroideae     | Senecioniase     | Cassalia (=Parasenecio), Ligularia | Eastern Asia |
| nevoi              | Cichorioidae    | Gnaphaliaceae    | Phagnalon        | Mediterranean                 |
|                    |                 | Coreiaceae       | Chondrilla, Crepis, Hedyopnios, Poiris, Rhagadiolus, Scolymus, Taraxacum, Thrinicia (= Leontodon), Tolpis | Mediterranean |
| Oidium             |                 | Astereae         | Baccharis         | South America                 |
| baccharidis        |                 | Milleriace       | Galinsoga        | South America                 |

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