Phylogeny of *Hyaloperonospora* based on nuclear ribosomal internal transcribed spacer sequences

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Phylogenetic relationships in *Hyaloperonospora* (Oomycetes) were investigated by molecular analyses using internal transcribed spacer (ITS) sequences and collections from different host plants. Trees were inferred with Bayesian Markov chain Monte Carlo, neighbor-joining and maximum parsimony methods and rooted with *Perofascia*. The results are discussed with respect to host taxonomy and species concepts of downy mildews from the literature. Molecular data mainly support the use of narrow species delimitations and host range as a taxonomic marker. *Hyaloperonospora brassicae* turns out to be a non-monophyletic assemblage of different species. New combinations are proposed in accordance with the phylogenetic trees.

Taxonomic novelties: *Hyaloperonospora crispula* (Fuckel) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora arabidopsis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora cardaminopsis* (Gustavsson) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora cochleariae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora galligena* (Blumer) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora berteroae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora iberidis* (Gäumann ex Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora isatidis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora hesperidis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora thlaspeos-arvensis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora cheiranthi* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler; *Hyaloperonospora barbareae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler.

Probably the most difficult problem in the taxonomy of the plant parasitic Oomycetes or downy mildews (Peronosporaceae) is species definition and delimitation. Hence, debate about the different species concepts in use is controversial (see SKALICKY 1964 or HALL 1996 for a more recent survey). These difficulties are reflected by the numerous principal changes in the species concepts applied in *Peronospora* from the very beginning of its taxonomy.

Peronospora represents the largest genus of downy mildews; CONSTANTINESCU (1991) lists about 600 binomials which were correctly ascribed to it. According to the view presented in the seminal work of DE BARY (1863), *Peronospora* specimens from the same family of host plants should be ascribed to a single species. Most students of Peronosporaceae following DE BARY adopted his concept. However, oospore morphology, which was regarded to be especially useful in *Peronospora* taxonomy by SCHROETER (1886) and FISCHER (1892), contradicts specialization on host families in some cases (GUSTAVSSON 1959b, VOGLMAYR 2003).

A major shift in *Peronospora* taxonomy came through the work of GÄUMANN (1918, 1923) who carried out extensive series of conidial measurements. In cases where he considered differences in conidial length and width as significant, new species were erected. Although GÄUMANN (1918, 1923) performed cross-infection experiments in relatively few cases, he concluded that specialization on host species or genera rather than host families should be used for delimiting species in *Peronospora*.

SAVULESCU (1948) mainly followed GÄUMANN'S treatment. On the other hand, GÄUMANN'S concept was criticized by GUSTAVSSON (1959b) for underestimating the amount of variance in conidial size and shape between collections from different sites. According to his opinion, such morphological characters were much less reliable than ecological ones. However, GUSTAVSSON (1959b) accepted GÄUMANN'S (1918, 1923) principle to take the host range as a basis for species delimitation in *Peronospora* and advocated a narrow species concept, too. Another tendency in *Peronospora* taxonomy was to totally reject GÄUMANN'S (1918, 1923) ideas and to return

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to DE BARY'S (1863) original concept of merging all *Peronosporas* parasitizing members of the same host family. This was exemplified by YERKES & SHAW (1959), who ascribed all *Peronospora* specimens on Brassicaceae to a single species, *Peronospora parasitica*.

Recently, CONSTANTINESCU & FATEHI (2002) presented molecular and morphological evidence to split the genus *Peronospora* into three genera, *Peronospora* s. str., *Hyaloperonospora*, and *Perofascia*. Within *Hyaloperonospora*, six species were accepted due to differences in morphology of conidia and conidiophores, *H. lunariae*, *H. floerkeae*, *H. lepidii-perfoliati*, *H. niessleana*, *H. tribulina*, and *H. parasitica*. As far as the latter should comprise the vast majority of *Brassicaceae*-infecting *Peronospora*s, the concept of these authors is somewhat similar to that of YERKES & SHAW (1959). On the other hand, CONSTANTINESCU & FATEHI (2002) stated that the phenetic approach may suffer from limitations and that the taxonomy of *Peronospora* „will be better tackled by using molecular techniques".

CONSTANTINESCU & FATEHI'S (2002) proposal to divide *Peronospora* into three genera was confirmed by the molecular studies of GÖKER et al (2003) and VOGLMAYR (2003). These authors found sequence differences within *H. parasitica* as large as between the different *Hyaloperonospora* species recognized by CONSTANTINESCU & FATEHI (2002) and concluded that *H. parasitica* s. l. should be split up according to the phylogenetic relationships inferred from molecular results. However, these molecular studies included a relatively small sample of *Hyaloperonospora* species.

To get a more comprehensive picture, the present work focuses on *Hyaloperonospora* and *Perofascia*. More taxa and, as far as possible, several specimens from the same host species were included. The internal transcribed spacer (ITS) region of the nuclear rDNA was used to estimate phylogenetic relationships. Suitability of ITS for clarifying infrageneric relationships was demonstrated by FÖRSTER, CUMMINGS & COFFEY (2000) and COOKE et al (2000) for *Phytophthora*, MATSUMOTO et al (1999) for *Pythium*, and VOGLMAYR (2003) for *Peronospora*.

Material and methods

Sample sources, DNA extraction, PCR, and sequencing

The organisms included in this study are listed in Table 1. The nomenclature followed CONSTANTINESCU & FATEHI (2002), but we used the narrow species concept of GÄUMANN (1918, 1923, 1926) for the species ascribed to *Hyaloperonospora parasitica*. In these cases we applied CONSTANTINESCU'S (1991) nomenclature, including the changes proposed by GÖKER et al. (2003). Samples which could not unequivocally be assigned to any of GÄUMANN'S species were named *Hyaloperonospora parasitica* s. l. Microscopical examination of specimens was carried out as previously described (GÖKER et al. 2003).

DNA extraction, PCR, and cycle sequencing procedures were performed acccording to RIETHMÜLLER et al. (2002). We used the PCR and cycle sequencing primers described in COOKE et al. (2000) and additionally ITS4-H (5'-TCC TCC GCT TAT TAA TAT GC), a modification of ITS4. In case very similar sequences were obtained from different host species or strikingly different sequences were found on specimens from the same host species, the whole procedure was repeated, starting with DNA extraction.

Data analysis

ITS sequences were assembled, checked and edited with Se-Al version 2.0 (RAMBAUT 1996. Available from http://evolve.zoo.ox.ac.uk/software). The corresponding nexus file was edited in PAUP* version 4.0b10 (SWOFFORD 2002). The computer program MrBayes (version 3.0B; HUELSENBECK & RONQUIST 2001) was used to perform Metropolis-coupled Markov chain Monte Carlo analyses (see HUELSENBECK et al. 2002 for a recent survey) based on the general time reversible model including gamma distributed substitution rates and a portion of invariable sites (GTR+I+G; see SWOFFORD et al 1996). Four incrementally heated simultaneous Markov chains were run over 1 000 000 generations from which every 100th tree was sampled. From these, the first 1000 trees were discarded. MrBayes was used to compute a 50 % majority rule consensus (containing also compatible groupings with lower frequency) of the remaining trees to obtain estimates for the *a posteriori* probabilities of groups of species. Branch lengths were computed as mean values over the sampled trees. This analysis was repeated five times on Macintosh G4 computers, always starting with random trees and default parameter values to test whether the results were reproducible.

For neighbor-joining analysis (SAITOU & NEI 1987), the data were first analysed with Modeltest version 3.04 (POSADA & CRANDALL 1998) to find the most appropriate models of DNA substitution, which were then used for calculation of neighbor-joining trees in the BIONJ version of GASCUEL (1997), using PAUP* (SWOFFORD 2002). Support for internal nodes was estimated by bootstrap analysis (FELSENSTEIN 1985) using 10 000 replicates.

In PAUP* (SWOFFORD 2002), a heuristic search under the maximum parsimony criterion (e.g., FITCH 1971) was performed using 10 000 replicates with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, STEEPEST option not in effect), each replicate being limited to 100 000 rearrangements. A second search strategy followed the parsimony ratchet approach (NIXON 1999) as implemented in PAUPRat (SIKES & LEWIS 2001) using default values. No shorter trees than in the first approach could be obtained. Gaps were treated as fifth state; a cost of 2 was assigned to transversions and a cost of 1 to transitions and gap insertions. Bootstrap analysis with 1000 replicates (FELSENSTEIN 1985) was performed as in the first heuristic search approach mentioned above, but this time using 20 rounds of

random sequence addition and subsequent branch swapping during each bootstrap replicate. To compute Bremer decay indices (BREMER 1988), TreeRot version 2 (SORENSON 1999) was used in conjunction with PAUP* with a search strategy identical to that used for bootstrapping.

Results

Sequence alignment

The final length of the alignment was 1569 bp. However, the total length was partly due to three large insertions in the ITS 2 region. An insertion from positions 650 to 994 in the final alignment was present in the two specimens of *P. lepidii-sativi* and an insertion of similar length (base positions 1147 to 1445) in *P. parasitica* s. str., confirming the results of VOGLMAYR (2003). *Peronospora brassicae* f. sp. *brassicae* and *P. sisymbrii-loeselii* were characterized by an insertion from position 1034 to 1104. All insertions were homologous to parts of the proper ITS 2 (data not shown). After exclusion of these large insertions, 854 bp remained for phylogenetic analysis. The final alignment and the trees obtained have been deposited in TreeBASE (http://www.treebase.org/) as SN1750.

Bayesian analysis

Based on the results of CONSTANTINESCU & FATEHI (2002), the phylogenetic trees were rooted with the three *Perofascia* specimens included in our sample that appeared as a well-separated, monophyletic group. A *Perofascia*-rooted majority-rule consensus tree from Bayesian analysis is shown in Fig. 1. We did not observe significant deviations in other consensus trees obtained from the independent runs of Bayesian analysis.

The basal subdivision into *Perofascia* and *Hyaloperonospora* was highly supported by an *a posteriori* probability of 100 % (Fig. 1). Within *Hyaloperonospora*, *P. arabis-alpinae* and a group containing specimens from *Cardamine*, *Rorippa*, *Barbarea*, and *Arabis* hosts separates basally, the latter group with a support of 100 %. The remaining *Hyaloperonospora* specimens are distributed over a highly supported cluster (95 %). Within the latter group, a sister group relationship of *Hyaloperonospora niessleana* to the other taxa is also highly supported (100 %). For the remaining groups backbone resolution is relatively low, with high support mainly restricted to assemblages of specimens from the same host species. However, two clusters of 13 and 25 specimens, respectively, were highly supported by 100 % *a posteriori* probability and well resolved within. The latter cluster is composed of an assemblage of specimens belonging to *Peronospora dentariae*, supported by 94 %, and a cluster containing *Peronospora diplotaxidis*, *P. teesdaliae*, *P. cochleariae* on *Armoracia*, and *Hyaloperonospora brassicae*, *H. lunariae*, *H. tribulina* and *H. parasitica* s. l. on *Sisymbrium volgense*. The *P. diplotaxidis* and *H. brassicae* specimens, respectively, did not cluster together. The second highly supported cluster is divided into a group comprising *Peronospora crispula*, *P. thlaspeos-alpestris*, *Hyaloperonospora thlaspeos-perfoliati*, and *H. parasitica* s. l. from *Lepidium ruderale*, supported by 100 % *a posteriori* probability, and a poorly (64 %) supported cluster containing *P. arabidopsidis*, *P. erophilae*, a *P. cochleariae* specimen from *Cochlearia danica*, and *P. cardaminopsidis.*

Neighbor joining

The application of Modeltest version 3.04 proposed the models HKY+G or TVM+I+G (see SWOFFORD et al 1996 for a survey of these DNA substitution models) using likelihood ratio tests or the Akaike information criterion, respectively. Most parts of tree topologies resulting from neighbor-joining analysis based on HKY+G or TVM+I+G, respectively, especially branches which obtained high bootstrap support, were in agreement with the results from Bayesian inference (data not shown).

Maximum parsimony

Heuristic maximum parsimony analysis yielded 51 316 most parsimonious trees of length 1551 from 854 islands; the consistency index of these was 0.5152 (0.4987 when uninformative characters were excluded) and the retention index (FARRIS 1989) 0.8764. The strict consensus tree of the most parsimonious trees is shown in Fig. 2. The consensus is topologically similar to the Bayesian tree, and most of the above-mentioned highly supported groups are present in parsimony analysis, too.

Discussion

Relations between parasite phylogeny and taxonomy of brassicacean hosts

In general, specimens from the same host species appeared in the same cluster, displaying only few or no sequence differences. Exceptions were the specimens from horseradish (*Armoracia rusticana*) that clustered together with specimens from *Brassica napus* or *Sinapis arvensis*, respectively, and the specimens of *Diplotaxis tenuis*, which appeared closely related to *Peronospora lobulariae* or *P. brassicae*, respectively. The *Hyaloperonospora* sequence from *Lepidium ruderale* originated from a coinfection together with *Perofascia lepidii*. Both *Hyaloperonospora*- and *Perofascia*-like haustoria and conidiophores were observed on the heavily distorted host stems and leaves (data not shown).

Collections from the same host genus but different host species did not always cluster together. For instance, the specimens from *Cardamine impatiens* and *C. bulbifera* are widely separated from the parasites of *C. flexuosa*, *C. amara*, *C. hirsuta*, and *C. pratensis*. Likewise, the collection from *Sisymbrium volgense* seems to be only distantly related to the specimens from *S. officinale* and *S. loeselii*. The *Hyaloperonospora* specimens from *Arabis alpina* and *A. soyeri* were not revealed as sister groups, either.

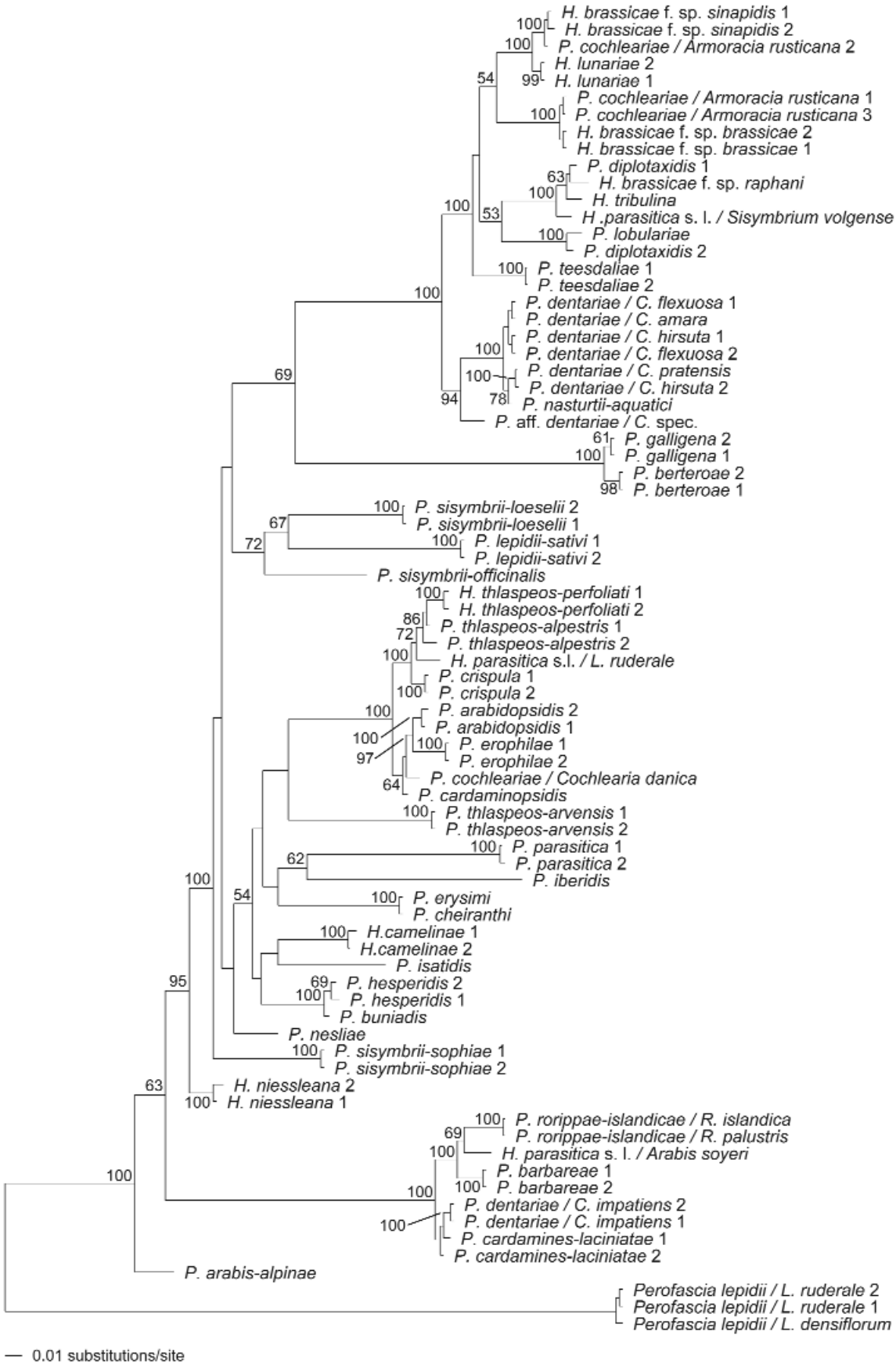

Fig. 1: 50 % majority-rule consensus tree with mean branch lengths including also compatible groupings of lower frequencies from a Bayesian Markov chain Monte Carlo analysis of nuclear ITS data. Numbers on branches represent their respective *a posteriori* probabilities. Probability values below 50 % are not shown. *H.* = *Hyaloperonospora*, *P.* = *Peronospora*, *C.* = *Cardamine*, *R.* = *Rorippa*, *L.* = *Lepidium*.

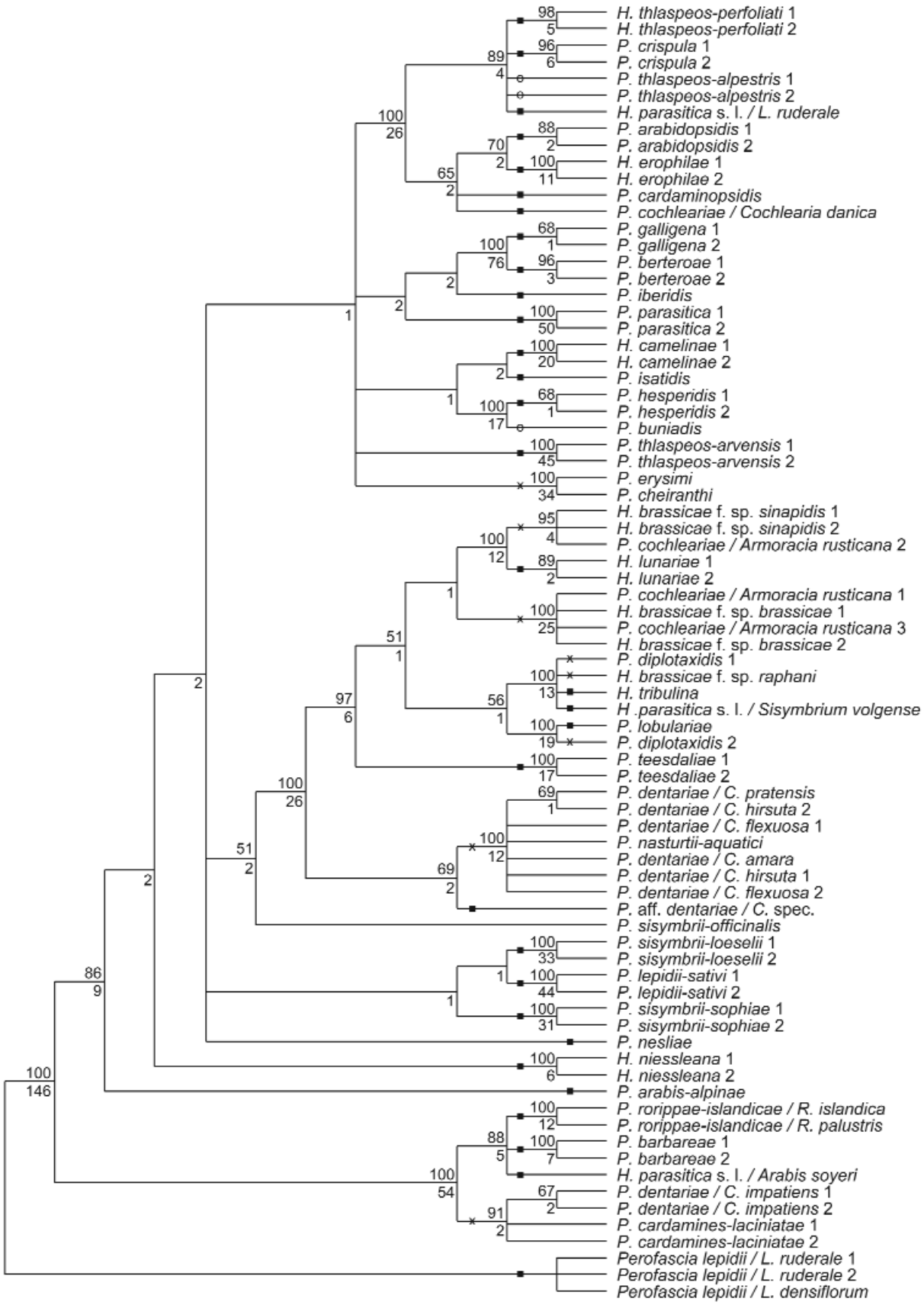

Fig. 2: Maximum parsimony analysis of the ITS data set. A strict consensus tree of 51 316 trees of length 1551 found in heuristic search is shown. Numbers above branches are bootstrap values from 1000 replicates, numbers below branches represent Bremer support indices. Abbreviations are as in Fig. 1. Suggested species boundary in accordance with GÄUMANN'S (1918, 1923) taxonomy (■), suggested species boundary in disagreement with GÄUMANN'S views (×), species delimitations can not be inferred from phylogenetic trees with certainty (○).

Other discrepancies between parasite phylogeny and current host taxonomy may be due to flaws of the latter. For instance, the parasites of *Thlaspi*, *H. thlaspeos-perfoliati* and *P. thlaspeos-alpestris* on the one hand and *P. thlaspeos-arvensis* on the other hand, are not closely related, but *Thlaspi* seems to be a non-monophyletic assemblage (KOCH & MUMMENHOFF 2001). The downy mildew on horseradish had been assigned to *P. cochleariae* as *Armoracia rusticana* was first described as *Cochlearia armoracia,* but already VON HAYEK (1911) doubted whether *Armoracia* and *Cochlearia* are closely related at all. Hence, the loose relationship between the *P. cochleariae* specimens from *Armoracia rusticana* and *Cochlearia danica*, respectively, does not imply incongruence between host and parasite phylogenies (see also GUSTAVSSON 1959a).

Inferring conclusions about relations between host and parasite phylogeny in the *Hyaloperonospora*-Brassicaceae complex is difficult as host taxonomy so far was mainly based on JANCHEN'S (1942) morphological system. Recent molecular studies in Brassicaceae reported striking differences (e.g., MUMMENHOFF, FRANZKE & KOCH 1997, KOCH, BISHOP & MITCHELL-OLDS 1999) between phylogenetic trees inferred from DNA data and classical hypotheses derived from morphology. However, these articles mainly focused on infratribal (e.g., MUMMENHOFF, BRÜGGEMANN & BOWMAN 2001) or interfamiliar relationships (e.g., HALL, SYTSMA & ILTIS 2002). Hypotheses about the degree of congruence between host and *Hyaloperonospora* phylogenetic trees is further complicated by the partial lack of backbone resolution in the latter. However, as high support of terminal branches was achieved in all phylogenetic methods applied, conclusions can be drawn with respect to the different species concepts for *Hyaloperonospora* found in the literature.

ITS phylogenies and species concepts

Considering genetic distances our data do not support the view of DE BARY (1863) to merge all *Peronospora* specimens growing on members of the same host family into a single species. As already demonstrated by VOGLMAYR (2003), *H. tribulina*, a parasite of *Tribulus* (Zygophyllaceae), is nested within Brassicaceae-infecting members of *Hyaloperonospora*. A similar situation is found in *P. crispula* found on *Reseda* (Resedaceae), which is closely related to *Hyaloperonospora* specimens from *Thlaspi* and *Lepidium*. Taxonomic inconsistencies caused by different classifications of *P. crispula* following DE BARY (1863) were already emphasized by GÄUMANN (1918).

Hyaloperonospora parasitica sensu CONSTANTINESCU & FATEHI (2002) is not a monophyletic assemblage. Instead, *H. lunariae*, *H. niessleana* and *H. tribulina*, which were regarded as separate species by these authors are nested within *H. parasitica* s. l. The present results confirm the opinion of VOGLMAYR (2003) and GÖKER et al (2003) that molecular data concur with narrow species delimitations in *Hyaloperonospora*. The lack of morphological differences between several *Hyaloperonospora* specimens (CONSTANTINESCU and FATEHI 2002) does not necessarily imply that they belong to the same species. Our suggestions for species boundaries in accordance with this point of view are depicted in Fig. 2. In the case of *Peronospora buniadis*, genetic distances do not reveal with certainty whether it should be regarded as conspecific with *P. hesperidis*. Similarly, it remains unclear whether or not the two specimens of *P. thlaspeos-alpestris* included in our sampling represent a monophyletic grouping.

At first sight, molecular support for narrow species circumscriptions seems to be in accordance with GÄUMANN'S (1918, 1923) taxonomical proposals. However, several parts of the phylogenetic trees derived from ITS sequences disagree with his arrangements (Fig. 2). For example, GÄUMANN (1918) ascribed *Hyaloperonospora* specimens occurring on *Erysimum crepidifolium* to *P. erysimi*. Instead, the genetic distance between our collection from that host and the *P. cheiranthi* specimen is negligible (FIGS. 1, 2). Molecular trees support the view that the *Hyaloperonospora* specimens from *Cardamine impatiens* do not belong to *P. dentariae* as suggested by GÄUMANN (1923). Instead, the *P. nasturtii-aquatici* sample is nested within the *P. dentariae* cluster. Our results are not necessarily in conflict with presumable host ranges derived from GÄUMANN'S (1918, 1923) cross-infection experiments with *Erysimum* and *Cheiranthus* as host genera, since he did not include *E. crepidifolium*, nor did he use conidia from *C. impatiens* or *Nasturtium officinale* to inoculate other *Cardamine* species. On the other hand, the phylogenetic trees presented here support GUSTAVSSON'S (1959b) opinion that GÄUMANN (1918, 1923) partly overestimated differences in conidial morphology.

In his 1926 work, GÄUMANN recognized three *formae speciales* within *Peronospora brassicae* – a species which was erected by him in 1918 –, namely f. sp. *brassicae*, f. sp. *sinapidis*, and f. sp. *raphani*. Whereas in infection experiments f. sp. *brassicae* seemed to be confined to some members of the genus *Brassica*, f. sp. *sinapidis* and f. sp. *raphani* displayed a limited ability to infect *Brassica* and thus were mainly restricted to *Sinapis* and *Raphanus*, respectively (GÄUMANN 1926). These results were confirmed by HIURA & KANEGAE (1934), MCMEEKIN (1969) and DICKINSON & GREENHALGH (1977) who found a susceptibility of *Brassica* species and varieties to conidia from *Raphanus* but not vice versa. FOSTER'S (1947) experiments revealed high resistance in both mustard and radish varieties after inoculation with conidia from cabbage. These ecological differences are in agreement with our molecular results, since the *Hyaloperonospora* specimens from *Brassica*, *Sinapis*, and *Raphanus*, respectively, show distinct differences in ITS sequences (Fig. 1). Furthermore, strong support is achieved that *H. brassicae* represents a non-monophyletic assemblage. If the narrow species concept advocated here is applied, the *formae speciales* of *H. brassicae* should be regarded as three separate species.

Among the different species concepts in *Hyaloperonospora*, that of GUSTAVSSON (1959b), emphasizing host range and applying narrow species delimitation, is most congruent

with the results from molecular phylogenetic inference. However, the *Hyaloperonospora* specimens from *Diplotaxis tenuis* had marked differences in ITS sequences (Fig. 1). Likewise, horseradish (*Armoracia rusticana*) seems to be susceptible to both *Peronospora brassicae* f. sp. *brassicae* and *P. brassicae* f. sp. *sinapidis.* It may be concluded that *Hyaloperonospora* species are not necessarily confined to closely related host plants and that some host species are susceptible to several *Hyaloperonospora* species. However, further studies are required to reveal whether the molecular results presented here corroborate this hypothesis or whether they represent an example of reticulate evolution (e.g., LEGENDRE 2000) leading to differences between gene trees and species trees.

Taxonomic implications of the current study

For *Hyaloperonospora* species not listed in CONSTANTINESCU & FATEHI (2002), nor in GÖKER et al (2003), nor below, we suggest the use of „*Hyaloperonospora parasitica* s. l.". Whereas molecular analyses support a narrow species concept, sequence data are not always in agreement with the species boundaries proposed by GÄUMANN (1918, 1923; cf. FIG 2). Where such discrepancies occur, further studies are necessary to achieve a natural classification. However, in many cases sequence analysis agrees with classical taxonomy (Fig. 2), and it is appropriate to propose the following new combinations:

***Hyaloperonospora crispula* (Fuckel) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora crispula* Fuckel – Fungi rhenani **23**, 1863 (basionym).

***Hyaloperonospora arabidopsis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora arabidopsidis* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 529, 1918 (basionym).

***Hyaloperonospora cardaminopsis* (Gustavsson) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora cardaminopsidis* Gustavsson – Opera Botanica **3**(1): 105, 1959 (basionym).

***Hyaloperonospora cochleariae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora cochleariae* Gäumann – Beiträge zur Kryptogamenflora der Schweiz **5**(4): 280, 1923 (basionym).

***Hyaloperonospora galligena* (Blumer) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora galligena* Blumer – Mitteilungen der. naturforschenden Gesellschaft Bern 1937: 17-25, 1938 (basionym).

***Hyaloperonospora berteroae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora berteroae* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 521, 1918 (basionym).

***Hyaloperonospora iberidis* (Gäumann ex Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora iberidis* Gäumann ex Gäumann – Annales Mycologici **25**: 176, 1927 (basionym).

***Hyaloperonospora isatidis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora isatidis* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 526, 1918 (basionym).

***Hyaloperonospora hesperidis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora hesperidis* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 525, 1918 (basionym).

***Hyaloperonospora thlaspeos-arvensis* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora thlaspeos-arvensis* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 530, 1918 (basionym).

***Hyaloperonospora cheiranthi* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora cheiranthi* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 524, 1918 (basionym).

***Hyaloperonospora barbareae* (Gäumann) Göker, Riethmüller, Voglmayr, Weiß & Oberwinkler, comb. nov.**
= *Peronospora barbareae* Gäumann – Beihefte zum Botanischen Centralblatt **35**(1): 521, 1918 (basionym).

According to § 32.5 of the International Code of Botanical Nomenclature (GREUTER et al 1999) we adjusted the epithets "arabidopsidis" and "cardaminopsidis" to their correct Latin termination following STEARN (1992) and ZABINKOVA (1968).

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Tab. 1: Collection data of the taxa studied and GenBank accession numbers of the respective ITS sequences. The taxa were grouped taxonomically; the classification follows CONSTANTINESCU (1991) including some changes proposed in CONSTANTINESCU & FATEHI (2002) and GÖKER et al (2003), respectively. Collectors: HJ, H. Jage; WD, W. Dietrich; OF, O. Foitzik; HV, H. Voglmayr; MG, M. Göker. Vouchers: M, Botanische Staatssammlung Munich, TUB, University of Tübingen; WU, University of Vienna. Hosts differing from the type hosts are marked with a star

Taxon	Collection data Host	Origin/source/collector	Collection number/ DNA isolation number	GenBank accession no.
Hyaloperonospora				
H. brassicae (Gäumann) Göker et al. f. sp. *brassicae*	*Brassica napus* L. ssp. *napus* 1	Germany, Sachsen-Anhalt, Prettin; leg HJ	J 3675/01; 24-8 (TUB)	AY531409
H. brassicae f. sp. *brassicae*	*Brassica napus* L. ssp. *napus* 2	Germany, Sachsen-Anhalt, Kohnberg; leg HJ	J 795/01; 26-9 (TUB)	AY531407
H. brassicae f. sp. *raphani*	*Raphanus raphanistrum* L.	Germany, Baden-Württemberg, Tübingen; leg. MG	1858; 14-8 (TUB)	AY531413
H. brassicae f. sp. *sinapidis*	*Sinapis alba* L. 1	Germany, Baden-Württemberg, Tübingen; leg. MG	1866, 14-3 (TUB)	AY531403
H. brassicae f. sp. *sinapidis*	*Sinapis alba* L. 2	Germany, Baden-Württemberg, Niedernhall; leg. MG	1868; 15-4 (TUB)	AY531404
H. camelinae (Gäumann) Göker et al.	*Camelina sativa* (L.) Cr. 1 *	Austria, Upper Austria, St. Willibald; leg. HV	HV 444-447; 21-6 (WU)	AY531456
H. camelinae	*Camelina sativa* (L.) Cr. 2 *	Austria, Burgenland, Kittsee; leg. HV	HV 14 (WU)	AY531457
H. erophilae (Gäumann) Göker et al.	*Erophila verna* (L.) Chev. 1	Germany, Bavaria, Munich; leg. MG	1883; 17-5 (TUB)	AY531439
H. erophilae	*Erophila verna* (L.) Chev. 2	Germany, Baden-Württemberg, Criesbach; leg. MG	1961; 19-4 (TUB)	AY531440
H. lunariae (Gäumann) Constantinescu	*Lunaria rediviva* L. 1	Germany, Bavaria, Munich; leg. MG	1946; 18-10 (TUB)	AY531402
H. lunariae	*Lunaria rediviva* L. 2	Austria, Lower Austria, Lilienfeld; leg. HV	HV 362 (WU)	AY531401
H. niessleana (Berlese) Constantinescu	*Alliaria petiolata* (Bieb.) Cavara & Grande 1	Germany, Baden-Württemberg, Tübingen; leg. MG	1843; 4-1 (TUB)	AY531465
H. niessleana	*Alliaria petiolata* (Bieb.) Cavara & Grande 2	Austria, Vienna; leg. HV	HV 575 (WU)	AY531464
H. parasitica (Persoon: Fries) Constantinescu	*Capsella bursa-pastoris* (L.) Med. 1	Austria, Lower Austria, Pfaffstätten; leg. HV	HV 746 (WU)	AY531451
H. parasitica	*Capsella bursa-pastoris* (L.) Med. 2	Germany, Baden-Württemberg, Criesbach; leg. MG	1964; 19-1 (TUB)	AY531452
H. parasitica s. l.	*Arabis soyeri* Reut. & Huet*	Austria, Carinthia, Flattach; leg. HV	HV 508-510 (WU)	AY531392
H. parasitica s. l.	*Lepidium ruderale* L.*	Germany, Sachsen-Anhalt, Wendelsheim; leg HJ	J 3189/01; 22-8 (TUB)	AY531446
H. parasitica s. l.	*Sisymbrium volgense* Bieb. ex E. Fournier*	Germany, Sachsen-Anhalt, Langenbogen; leg HJ	J 661/01; 24-2 (TUB)	AY531426
H. thlaspeos-perfoliati (Gäumann) Göker et al.	*Thlaspi perfoliatum* L. 1	Germany, Baden-Württemberg, Niedernhall; leg. MG	1882; 17-4 (TUB)	AY531431
H. thlaspeos-perfoliati	*Thlaspi perfoliatum* L. 2	Germany, Baden-Württemberg, Öschingen; leg. MG	1879; 17-9 (TUB)	AY531432
H. tribulina (Passerini) Constantinescu	*Tribulus terrestris* L.	Hungary, Bacs-Kiskun, Lakitelek/Tisza; leg. HV	HV 692 (WU)	AY531414
Peronospora				
P. arabidopsidis Gäumann	*Arabidopsis thaliana* (L.) Heynh. 1	Germany, Baden-Württemberg, Kreßbach; leg. MG	1880; 17-1 (TUB)	AY531441

Tab. 1: Continued

Taxon	Collection data Host	Origin/source/collector	Collection number/ DNA isolation number	GenBank accession no.
P. arabidopsidis	*Arabidopsis thaliana* (L.) Heynh. 2	Germany, Sachsen-Anhalt, Tornau; leg HJ	J 635/01; 24-4 (TUB)	AY531434
P. arabis-alpinae Gäumann	*Arabis alpina* L.	Austria, Lower Austria; leg. HV	HV 408 (WU)	AY531466
P. barbareae Gäumann	*Barbarea vulgaris* R. Br. 1	Austria, Tyrol, Schattwald; leg. MG	1862; 13-6 (TUB)	AY531395
P. barbareae	*Barbarea vulgaris* R. Br. 2	Germany, Saxonia, Wolkenstein; leg. WD	D 21/4/00; 20-10 (TUB)	AY531396
P. berteroae Gäumann	*Berteroa incana* (L.) DC. 1	Germany, Saxonia, Gohlis; leg HJ	J 1165a/01; 23-8 (TUB)	AY531450
P. berteroae	*Berteroa incana* (L.) DC. 2	Germany, Sachsen-Anhalt, Prettin; leg HJ	J 3697/01; 24-6 (TUB)	AY531449
P. buniadis Gäumann	*Bunias orientalis* L.	Austria, Lower Austria, Traismauer; leg. HV	HV 969-971; 27-5 (WU)	AY531453
P. cardamines-laciniatae Gäumann	*Cardamine bulbifera* (L.) Cr. 1	Austria, Lower Austria, Gießhübl; leg. HV	HV 77-80; 21-2 (WU)	AY531399
P. cardamines-laciniatae	*Cardamine bulbifera* (L.) Cr. 2	Austria, Lower Austria, Kaltenleutgeben; leg. HV	HV 151-152; 21-5 (WU)	AY531398
P. cardaminopsidis A. Gustavsson	*Cardaminopsis arenosa* (L.) HAY.	Germany, Saxonia, Plattenthal; leg. WD	D 23/7/97; 20-3 (TUB)	AY531435
P. cheiranthi Gäumann	*Erysimum cheiri* (L.) Cr.	Germany, Sachsen-Anhalt, Plossig; leg HJ	J 3786/01; 22-3 (TUB)	AY531460
P. cochleariae Gäumann	*Armoracia rusticana* G.M. Sch. 1*	Austria, Upper Austria, Raab; leg. HV	HV 1006-1008; 21-11 (WU)	AY531406
P. cochleariae	*Armoracia rusticana* G.M. Sch. 2*	Germany, Sachsen-Anhalt, Deichhaus; leg HJ	J 3914a/01; 23-9 (TUB)	AY531405
P. cochleariae	*Armoracia rusticana* G.M. Sch. 3*	Germany, Baden-Württemberg, Welschingen; leg HJ	J 2520/01; 26-10 (TUB)	AY531408
P. cochleariae	*Cochlearia danica* L.	Germany, Sachsen-Anhalt, Teutschenthal; leg HJ	J 672/01; 24-1 (TUB)	AY531442
P. crispula Fuckel	*Reseda lutea* L. 1*	Austria, Burgenland, Apetlon; leg. HV	HV 1028-1030; 21-12 (WU)	AY531437
P. crispula	*Reseda lutea* L. 2*	Germany, Sachsen-Anhalt, Wittenberg; leg HJ	J 1875/01; 22-12 (TUB)	AY531438
P. dentariae Rabenhorst	*Cardamine amara* L.*	Czech Republic, Krusne Hory, Krystofovy Hamry; leg. WD	D 25/5/99; 20-8 (TUB)	AY531420
P. dentariae	*Cardamine flexuosa* With. 1*	Czech Republic, Krusne Hory, Vejprty; leg. WD	D 24/4/99; 20-4 (TUB)	AY531418
P. dentariae	*Cardamine flexuosa* With. 2*	Germany, Baden-Württemberg, Tübingen; leg HV	HV 833-834; 21-8 (WU)	AY531423
P. dentariae	*Cardamine hirsuta* L. 1*	Germany, Baden-Württemberg, Tübingen; leg. HV	HV 791; 21-7 (WU)	AY531422
P. dentariae	*Cardamine hirsuta* L. 2*	Germany, Nordrhein-Westfalen, Wuppertal; leg. MG	1821; 5-1, 5-8 (TUB)	AY531421
P. dentariae	*Cardamine impatiens* L. 1*	Austria, Tyrol, Schattwald; leg. MG	1840; 13-10 (TUB)	AY531400
P. dentariae	*Cardamine impatiens* L. 2*	Germany, Baden-Württemberg, Tübingen; leg. MG	1939; 18-6 (TUB)	AY531397
P. dentariae	*Cardamine pratensis* L.*	Germany, Baden-Württemberg, Niedernhall; leg. MG	1885; 17-8 (TUB)	AY531417
P. aff. *dentariae*	*Cardamine (Dentaria)* sp.*	USA, Tennessee, Great Smoky Mts Natl. Park; leg. HV	HV 2.4.P.P.; 21-1 (WU)	AY531424

Tab. 1: Continued

Taxon	Collection data Host	Origin/source/collector	Collection number/ DNA isolation number	GenBank accession no.
P. diplotaxidis Gäumann	*Diplotaxis tenuifolia* (L.) DC. 1	Germany, Sachsen-Anhalt, Wittenberg; leg. HJ	J 3073/01; 23-11 (TUB)	AY531412
P. diplotaxidis	*Diplotaxis tenuifolia* (L.) DC. 2	Germany, Sachsen-Anhalt, Dessau; leg HJ	J 4011/01; 26-12 (TUB)	AY531411
P. erysimi Gäumann	*Erysimum crepidifolium*	Germany, Sachsen-Anhalt, Könnern; leg HJ	J 1156/01; 26-8 (TUB)	AY531459
P. galligena Blumer	*Aurinia saxatilis* (L.) Desv. 1	Germany, Bavaria, Munich; leg. MG	1942; 18-3 (TUB)	AY531448
P. galligena	*Aurinia saxatilis* (L.) Desv. 2	Germany, Baden-Württemberg, Eichstetten; leg. MG	2099; 20-12 (TUB)	AY531447
P. hesperidis Gäumann	*Hesperis matronalis* L. 1	Czech Republic, Krusne Hory, Potucky; leg. WD	D 19/5/00; 20-6 (TUB)	AY531455
P. hesperidis	*Hesperis matronalis* L. 2	Germany, Sachsen-Anhalt, Klein-Wanzleben; leg HJ	J 589/01; 23-6 (TUB)	AY531454
P. iberidis Gäumann	*Iberis sempervirens* L.*	Germany, Sachsen-Anhalt, Rachilk; leg HJ	J 3514/01; 22-6 (TUB)	AY531461
P. isatidis Gäumann	*Isatis tinctoria* L.	Germany, Sachsen-Anhalt, Rollesdorf; leg HJ	J 928/01; 22-5 (TUB)	AY531443
P. lepidii-sativi Gäumann	*Cardaria draba* (L.) Desv. 1	Austria, Burgenland, Kittsee; leg. HV	HV 115-116; 21-3 (WU)	AY531462
P. lepidii-sativi	*Cardaria draba* (L.) Desv. 2	Austria, Lower Austria, Guntramsdorf; leg. HV	HV 246 (WU)	AY531463
P. lobulariae Ubriszy & Vörös	*Lobularia maritima* (L.) Desv.	Germany, Sachsen-Anhalt, Arendsee; leg HJ	J 3454/01; 22-10 (TUB)	AY531410
P. nasturtii-aquatici Gäumann	*Nasturtium officinale* R. Br.	Germany, Sachsen-Anhalt, Sülldorf; leg HJ	J 3493/01; 24-3 (TUB)	AY531419
P. nesliae Gäumann	*Neslia paniculata* (L.) Desv.	Austria, Lower Austria, Theresienfeld; leg HV	HV 203 (WU)	AY531458
P. rorippae-islandicae Gäumann	*Rorippa islandica* (Gunnerus) Borbas	Germany, Thüringen, Stadtroda; leg. OF	20-2 (M)	AY531393
P. rorippae-islandicae	*Rorippa palustris* (L.) Bess.*	Germany, Saxonia; Marienberg; leg. WD	D 15/6/97; 20-1 (TUB)	AY531394
P. sisymbrii-loeselii Gäumann	*Sisymbrium loeselii* L. 1	Germany, Sachsen-Anhalt, Köthen; leg HJ	J 73/01; 23-5 (TUB)	AY531428
P. sisymbrii-loeselii	*Sisymbrium loeselii* L. 2	Germany, Sachsen-Anhalt, Heuckewalde; leg HJ	J 243/01; 23-10 (TUB)	AY531427
P. sisymbrii-officinalis Gäumann	*Sisymbrium officinale* (L.) Scop.	Austria, Upper Austria, Raab; leg. HV	HV 1003-1005; 21-10 (WU)	AY531425
P. sisymbrii-sophiae Gäumann	*Descurainia sophia* (L.) Webb ex Prantl 1	Austria, Lower Austria, Weiden; leg. HV	HV 150; 21-4 (WU)	AY531429
P. sisymbrii-sophiae	*Descurainia sophia* (L.) Webb ex Prantl 2	Austria, Lower Austria, Hundsheim; leg. HV	HV 276 (WU)	AY531430
P. teesdaliae Gäumann	*Teesdalia nudicaulis* (L.) R. Br. 1	Germany, Saxonia, Zschepa; leg HJ	J 1186/01; 23-2 (TUB)	AY531415
P. teesdaliae	*Teesdalia nudicaulis* (L.) R. Br. 2	Germany, Bavaria, Markt Pleinfeld; leg HJ	J 1243/01; 23-4 (TUB)	AY531416
P. thlaspeos-alpestris Gäumann	*Thlaspi caerulescens* J. & C. Presl 1	Germany, Saxonia, Ober-ummersdorf; leg HJ	J 450/01; 22-11 (TUB)	AY531436
P. thlaspeos-alpestris	*Thlaspi caerulescens* J. & C. Presl 2	Czech Republic, Krusne Hory, Vejprty; leg. WD	D 24/4/99; 20-5 (TUB)	AY531433
P. thlaspeos-arvensis Gäumann	*Thlaspi arvense* L. 1	Germany, Baden-Württemberg, Niedernhall; leg. MG	1852; 15-1 (TUB)	AY531444

Tab. 1: Continued

Taxon	Collection data Host	Origin/source/collector	Collection number/ DNA isolation number	GenBank accession no.
P. thlaspeos-arvensis	*Thlaspi arvense* L. 2	Austria, Upper Austria, St. Willibald; leg. HV	HV 762 (WU)	AY531445
Perofascia				
Perofascia lepidii (Mac Alpine) Constantinescu	*Lepidium ruderale* L. 1	Germany, Sachsen-Anhalt, Wendelsheim; leg HJ	J 3189/01; 22-8 (TUB)	AY531468
Perofascia lepidii	*Lepidium ruderale* L. 2	Germany, Sachsen-Anhalt, Röden; leg. HJ	J 2068/01; 22-9 (TUB)	AY531467
Perofascia lepidii	*Lepidium densiflorum* Schrader*	GenBank/CONSTANTINESCU & FATEHI (2002)		AF465760