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Authors' contributions

KS conceived and performed the taxonomic research and wrote the manuscript; MG and ŁB performed molecular analyses; AW contributed to the generic description; TC located and described the ATHU syntypes and contributed to the lectotypification; SRD consulted the research and edited the manuscript

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Competing interests

No competing interests have been declared.

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ORIGINAL RESEARCH PAPER

Laserocarpum, a new genus of Apiaceae endemic to Greece

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Abstract

Laserpitium pseudomeum is an endemic umbellifer of Greece occurring in the mountains of Sterea Ellas and northern Peloponnese. Molecular data indicate that it is not related to its putative congeners, but instead constitutes an isolated lineage. The nuclear ribosomal DNA ITS tree places it as a weakly supported sister group to *Portenschlagiella ramosissima*, the sole species in its genus, whereas the tree inferred from three noncoding cpDNA loci does not confirm this relationship. *Portenschlagiella ramosissima* is sometimes placed in *Athamanta*, an affinity supported neither by molecular data nor by fruit morphology. *Laserpitium pseudomeum* notably differs from *P. ramosissima* in vegetative, flower, and fruit characteristics, and no obvious morphological synapomorphies indicate their close relationship. Therefore, we place *L. pseudomeum* in the newly described genus *Laserocarpum* and lectotypify the species with the specimen *Orphanides 2019* (G00766460) at G-Boiss.

Keywords

Apiaceae; Daucinae; *Laserpitium pseudomeum*; taxonomy; typification, Umbelliferae

Introduction

Laserpitium L., a genus of the angiosperm family Apiaceae, is distributed in western Eurasia and encompasses approximately 20-22(-35) species in its traditional circumscription [1-3]. Based on molecular phylogenetic studies, the genus is now placed in tribe Scandiceae, subtribe Daucinae [4]. A distinctive feature of Daucinae is the presence of fruits with secondary (vallecular) ribs that are spiny (as in Daucus L. and Orlaya Hoffm.) or winged (as in Laserpitium). All species traditionally placed in Laserpitium sensu lato (s. l.) are characterized by the presence of wings at all secondary ribs, whereas in some other "laserpitioid" genera (e.g., Thapsia L.), only the lateral ribs are winged or they are much more prominent than the dorsal wings [5]. However, molecular phylogenetic studies have shown that the traditional delineation of winged-fruited genera of Daucinae was artificial [6,7]. In effect, only six species were retained in *Laserpitium* sensu stricto (s. s.), whereas the remaining species were transferred to Ekimia H. Duman & M. F. Watson, Laser Borkh. ex G. Gaertn., B. Mey. & Scherb., a restored Siler Mill., the newly described Silphiodaucus (Koso-Pol.) Spalik, Wojew., Banasiak, Piwczyński & Reduron, and Thapsia. One species, Laserpitium pseudomeum Orph., Heldr. & Sartori ex Boiss., which in some molecular analyses constituted an isolated lineage close to Laser [7]

rather than to its putative congeners, was provisionally retained in the genus while awaiting more data confirming its placement. *Laserpitium pseudomeum* is endemic to the mountainous regions of Sterea Ellas and northern Peloponnese in Greece [8,9].

Recent fruit morphological and anatomical studies have demonstrated that *Laserpitium* s. s. is distinguished from its former congeners by a suite of characters including the shape of the endosperm in transverse section and the fruit sclerification pattern (i.e., the presence of nonelongated sclerified cells in endocarp and mesocarp tissues [10]). The fruits of *L. pseudomeum* are superficially similar to those of *Laserpitium* s. s., in having wings on both dorsal and lateral secondary ribs, but are more similar to those of *Laser*, in having a distinctly flattened endosperm and a nonsclerified exocarp and mesocarp, thus supporting its position inferred from molecular data [7,10]. However, preliminary molecular analyses using nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) data have identified another relative of *L. pseudomeum*, namely *Portenschlagiella ramosissima* (Port.) Tutin. Here, we further explored the phylogenetic relationships of *L. pseudomeum*, lectotypified this species, and characterized it in the separate, monotypic genus *Laserocarpum*.

Material and methods

To infer the phylogenetic placements of *L. pseudomeum* and *P. ramosissima*, we used molecular data from a previous taxonomically comprehensive study of Daucinae [7] deposited in TreeBASE (No. S18012), which was based on analyses of ITS and plastid *rps16* intron, *rpoC1* intron, and *rpoB-trnC* intergenic spacer sequence variation. We selected accessions for which at least two markers were available. We omitted *Cuminum cyminum* L. and *Ammodaucus leucotrichus* Coss. & Durieu, because the phylogenetic positions of these species were unstable between the analyses and their inclusion decreased bootstrap support for several clades [7]. We supplemented these data with new sequences of ITS and *rps16* and *rpoC1* introns for *P. ramosissima* (sample No. 0252, Montenegro: Lovćen, area around Čekanje, September 26, 1985, M. F. Gardner & S. G. Gardner 3319, E00043191). The laboratory procedures followed have been described previously [7]. GenBank accession numbers for the ITS, *rps16* intron, and *rpoC1* intron sequences of *P. ramosissima* are MN176189, MN181497, and MN176190, respectively. In total, 107 accessions were used for the analyses (Appendix S1).

Phylogenetic trees were inferred using the maximum likelihood (ML) method implemented in RAxML ver. 8.1.18 [11] with the GTR + G substitution model and based on 200 independent searches starting from distinct randomized maximum parsimony trees. Bootstrap support (BS) was estimated based on 1,000 rapid bootstrap replicates. Additionally, a posteriori bootstopping analysis with the extended majority-rule consensus tree as a convergence criterion was performed in order to check whether the number of replicates was sufficient. For the combined analyses, plastid and nuclear data were set as separate partitions.

The description of *L. pseudomeum* was mostly based on the material from ATH and ATHU, supplemented with photographs of the specimens from Boissier's herbarium at G.

Results

The topology of molecular trees was similar to that found in previous molecular studies with the same major clades corresponding to the recognized genera of Daucinae [7,10]. Although these clades usually received high bootstrap support in all analyses, the relationships among them were often ambiguous, with BS < 50%. In the ML tree inferred from ITS data, *L. pseudomeum* and *P. ramosissima* were placed together, but with a low bootstrap support of 55% (Fig. 1). This group was sister to *Siler* (BS < 50%). However, this relationship was not evident in the plastid DNA tree (Fig. S1), where *L. pseudomeum* was sister to a clade of *Daucus* and *Silphiodaucus* (BS < 50%), whereas *Portenschlagiella* formed an unresolved polytomy with *Laser* and *Orlaya* (BS = 51%). In

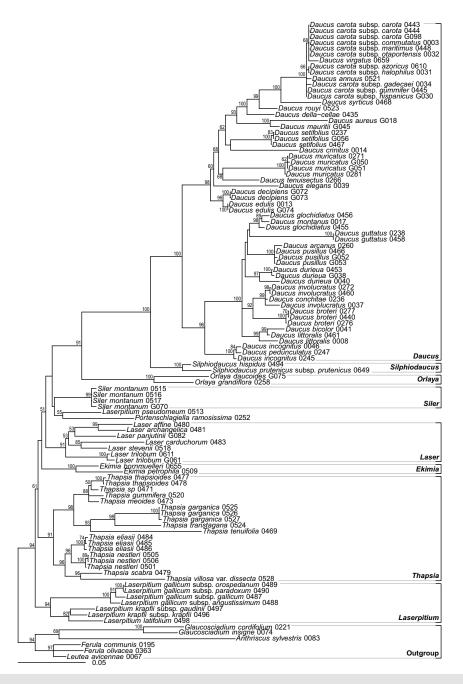


Fig. 1 Maximum likelihood tree inferred from analyses of nrDNA ITS sequences of Apiaceae subtribe Daucinae and outgroups. Bootstrap support values based on 1,000 replicates are given along the branches. Genera of Daucinae recognized by Banasiak et al. [7] are bracketed.

the combined tree (Fig. S2), *L. pseudomeum* and *P. ramosissima* formed a sister group to *Laser*, but these relationships were poorly supported (BS < 50%).

Discussion

Phylogenetic placements of Portenschlagiella ramosissima and Laserpitium pseudomeum

Molecular data indicate that the closest relatives of *L. pseudomeum* include *Daucus*, *Silphiodaucus*, *Orlaya*, *Siler*, *Laser*, and *Portenschlagiella* rather than its congeners, whereas the ITS tree indicates *P. ramosissima* as its sister. *Portenschlagiella ramosissima* was initially described in *Athamanta* L. and some recent studies reinstated it to this genus [2,12];

however, it is more frequently recognized in a monospecific genus [3]. Indeed, apart from hispid fruits and four-five-pinnate leaves with linear-filiform ultimate segments, the similarity of this species to Athamanta is superficial. The fruits of P. ramosissima are slightly dorsally compressed and have filiform secondary ribs, whereas those of Athamanta s. s. are laterally compressed and do not have any secondary ribs [12]. Within tribe Scandiceae, the presence of secondary ribs is a presumed synapomorphy for subtribes Daucinae, Torilidinae, and Artediinae [10], whereas Athamanta s. s. is placed in the subtribe Scandicinae [13]. The affinity of Portenschlagiella to subtribe Daucinae has not been inferred previously. The species occurs along the Dalmatian coast and in Calabria [12,14]. In Dalmatia, it constitutes the coastal chasmophytic association Portenschlagiello ramosissimae-Campanuletum portenschlagianae, with an elevation range between 3 and 770 m a.s.l. [15]. In Campania, Basilicata, and Calabria Apennines, it occurs in inland rocky communities of Campanulo fragilis-Portenschlagielletum ramosissimae at higher elevations, above 600 m a.s.l. [16]. Its presumed sister, Laserpitium pseudomeum, is restricted to the mountains of Sterea Ellas and northern Peloponnese in Greece, in open and semiopen habitats above 1,200 m a.s.l. on calcareous substrates [9].

Given the presumed, albeit weak sister group relationship between *L. pseudomeum* and *P. ramosissima* in the ITS and combined trees, the question is whether they are better recognized in two monospecific genera or whether *L. pseudomeum* should be transferred to *Portenschlagiella*. The taxonomy of Apiaceae has long been inflated with small genera: of the 455 genera recognized by Pimenov and Leonov [1], 41% were monospecific and 26% comprised only two–three species each [13], whereas in the most recent treatment of the family, 187 of the 466 genera (40%) are monospecific [3]. From a practical point of view, monospecific genera are better avoided because such generic names are uninformative. A shared generic name defines a group of closely related and presumably morphologically similar species that may easily be confused. Therefore, it is an important aid to species identification. Apart from being monophyletic, genera should be morphologically distinct, at least regionally, to develop good identification keys. A monospecific genus may be retained if it constitutes an isolated lineage with no close relatives or if its inclusion into the sister genus diffuses the definition of the latter.

Laserpitium pseudomeum and Portenschlagiella ramosissima are not morphologically similar. Portenschlagiella ramosissima is a monocarpic perennial herb with a subglobose rootstock. Laserpitium pseudomeum is a polycarpic perennial herb with a short, branching woody rhizome. Its secondary wood is parenchymatous rather than fibrous, and the rhizome is usually flattened and creased in herbarium specimens. Both species have pinnatisect leaves with narrow linear lobes. This character, however, is highly homoplastic in umbellifers and of poor diagnostic value at the generic level. Inflorescence architecture and fruit morphology also set these two species apart. In L. pseudomeum, there are usually several flowering stems with both lateral and terminal umbels. The former rarely bear fruits. These terminal and lateral umbels consist of four-seven and seven-nine rays, respectively. In some specimens, a single well-developed umbellet is present below one of the terminal umbels. This umbellet may represent a rudimentary primary umbel. Consequently, terminal umbels are secondary, whereas lateral umbels are tertiary in terms of the sequence of inflorescence development. Restriction of the fruit set (or the female reproductive output) to secondary umbels may be an adaptation to the short growing season in mountainous habitats. Portenschlagiella ramosissima also seems to produce only secondary and tertiary umbels, with both setting fruits. The flowering stem is very showy as the umbels are numerous and each has 30-50 rays. The petals of *P. ramosissima* are pubescent underneath and are usually described as yellow [3,12] although they are rather creamy white to yellowish. The flowers of L. pseudomeum are creamy white and without indumentum [9]. The fruits of P. ramosissima are covered with stellate hairs and the primary ribs are stout and prominent, whereas the secondary ribs are filiform [3]. In contrast, the fruits of L. pseudomeum are naked, with primary ribs obsolete and secondary ribs protruding into prominent wings [9,10]. Given the lack of any obvious morphological synapomorphies and a rather low molecular support for the sister-group status of these species, we see no advantage of placing them in one genus. Therefore, we recognize them in two genera: Portenschlagiella and newly described Laserocarpum.

In several references, the authorship of *Athamanta ramosissima* is attributed to C. P. J. Sprengel, who prepared the account on Apiaceae for the sixth volume of *Systema*

vegetabilium edited by J. A. Schultes [17]. However, the protologue of *A. ramosissima* is enclosed in parentheses and annotated Sch., meaning that Schultes rather than Sprengel wrote it (see the footnote on p. 315 [17]). The plant material and diagnosis were sent to Schultes by F. von Portenschlag-Ledermayer as indicated in the protologue ("De Portenschlag in litt.", p. 496 [17]). Therefore, the correct authorship of the basionym is "Port. ex Schult."

Laserocarpum Spalik & Wojew., gen. nov.

TYPE: *Laserocarpum pseudomeum* (Orph., Heldr. & Sartori ex Boiss.) Spalik, Wojew., Constantin. & S. R. Downie, comb. nov. BASIONYM: *Laserpitium pseudomeum* Orph., Heldr. & Sartori ex Boiss., Diagn. Pl. Orient. ser. 2, 2: 95. 1856. LECTOTYPE: Greece, Peloponnese, Mt. Kyllini, July 1851, *Orphanides 2019*, G00766460 (G-Boiss), designated here.

Etymology. Referring to the similarity of its fruits (*karpós* in Greek) to the fruits of *Laserpitium* and *Laser*.

Description. Perennial with two-three-pinnate, glabrous leaves with sessile to shortly stalked primary segments and linear-setaceous lobes. Involucel and involucre present, bracts and bracteoles entire, with broad white margins. Flowers white, not radiant. Mericarps dorsally flattened, primary ribs indistinct, secondary ribs elongated into papery wings. Endosperm distinctly flattened. Monotypic.

Diagnosis. Fruits similar to *Laserpitium* s. s. in having prominent wings on all four secondary ribs, but endosperm distinctly flattened with the ratio of its width to thickness >2 as opposed to <2 in *Laserpitium*. Ring of sclerified cells in endocarp multilayered, mesocarp and exocarp not sclerified (similar to *Laser*), whereas in *Laserpitium* sclerified, nonelongated cells occur in both mesocarp and exocarp.

Distribution area. Greece, Sterea Ellas and northern Peloponnese [8,9]. Endemic.

Representative specimens. STEREA ELLAS. Parnassus Mt, August 9–10, 1852, *Heldreich 2697* (G00766459, ATHU); Parnassus Mt, near Trypios-Vrachos, 6,500 ft., July 13–25, 1854, *Orphanides 358* (G00766461); Iti Mt, Greveno (Simio Vasilissis) summit, 1,900–2,114 m, June 23, 2001, *Constantinidis & Mavrakis 9714* (ATHU); Iti Mt, at the base of E side of Pirgos summit, 1,950–2,000 m, June 15, 1971, *Stamatiadou 12882* (ATH 46829); Giona Mt, Kastro summit, 1,850–1,900 m, July 2, 2005, *Kalpoutzakis 1720* (ATHU); Giona Mt, NE of the summit, 2,100–2,200 m, August 12, 1980, *Baden, Franzén & Strid 921* (ATH 46832); Vardousia Mt, summit area of Korax, 2,000–2,200 m, August 15, 1980, *Baden, Franzén & Strid 763* (ATH 44447). PELOPONNESE. Kyllini Mt, 5,300 ft., June 28 – July 10 1851, *Orphanides 2019* (ATHU, G00766460), Chelmos Mt, Aroania ridge, 3.5 km to SW of Zarouchla, 1,388 m, July 3, 2012, *Zakharova & Ukrainskaya 31* (ATH 60574).

Identification. At the fruiting stage, *L. pseudomeum* can easily be identified by its fruits with prominent secondary ribs protruding into papery wings. Such wings are characteristic of *Laserpitium* s. l. [5,10,18] which is not, however, monophyletic [7]. From among its segregates and relatives, only representatives of *Siler, Laser*, and *Thapsia* occur in Greece [2,7]. *Siler montanum* Crantz (\equiv *Laserpitium siler* L.) also has fruits with its secondary ribs winged, but this robust plant cannot be confused with *L. pseudomeum* at any growing stage due to its stout, thick rootstock, much larger, bipinnate leaves with flat ultimate segments, and large umbels comprising usually more than 20 umbellets. *Laser trilobum* (L.) Borkh. ex G. Gaertn. B. Mey. & Scherb. has characteristic bipinnate leaves with broad, flat trilobate ultimate segments and its umbels always consist of more than ten umbellets. Additionally, its fruits do not have prominent secondary ribs, although they exhibit some anatomical similarities to the fruits of *L. pseudomeum* (as indicated in the protologue of *Laserocarpum*). Two species of *Thapsia – T. garganica* L. and *T. asclepium* L. – occur in Greece and are easy to distinguish from the species

mentioned above owing to their yellow flowers and fruits with wings that develop only on lateral secondary ribs. The genus *Laserocarpum* does not introduce any difficulties for the delineation of genera and identification of umbellifer species in Greece. Due to the limited distribution and distinctive features of its unique species, the impact of the proposed taxonomic change is low.

Typification

Boissier published the description of *Laserpitium pseudomeum* in his *Diagnoses plantarum orientalium novarum* [19] attributing the name to Orphanides, Heldreich, and Sartori. Therefore, these botanists are sometimes regarded as the authors of the name that was published by Boissier, i.e., "ex Boiss." [18], or as the authors of the entire protologue that was published "in Boiss." [8,9]. Accordingly, the lectotype has to be selected either among the material examined by Boissier that is most likely in G-Boiss or among the specimens available to Orphanides, Heldreich, and Sartori, for example, those kept in Orphanides' herbarium (ATHU) or widely distributed by Orphanides and Heldreich as exsiccata. However, because Orphanides and Heldreich never published any plant names together, it is very unlikely that they cooperatively wrote the protologue of this species. Therefore, we are inclined to attribute its authorship to Boissier rather than to Orphanides, Heldreich, and Sartori.

Two collections are cited in the protologue [19]: "in monte Kyllene Peloponnesi Prof. Orphanides anno 1851, *Parnasso* in regione alpinâ Sartori, Heldreich ann. 1852". Collection numbers and exact dates of the gathering are not given. In the account for the *Mountain flora of Greece*, Hartvig indicated that he had examined both syntypes kept at G-Boiss, but he did not choose the lectotype [8]. Kit Tan indicated a specimen "mt Kyllene supra Livadi, ann. 1851, Orphanides Fl. Graec. Exs. no. 358" in G-Boiss as the lectotype of the species [9]. However, there is no such specimen in G-Boiss. The herbarium sheet representing "Fl. Graec. Exs. no. 358" (G00766461) includes plants collected by Orphanides in Parnassus in 1854 rather than in Kyllini in 1851. Therefore, this gathering does not qualify as type material. Moreover, no specimen in G-Boiss is annotated as collected "supra Livadi". Probably, when writing the account of this species, Tan accidentally assembled information from several collections made by Orphanides that were kept in various herbaria.

The syntypes in G-Boiss were correctly identified by M. Pimenov and F. Jacquemoud, but their selection has remained unpublished. The Orphanides syntype is G00766460 and bears the note "2019. Meum? / Mont Kyllene Juillet 1851 / Th. G. Orphanides" with "Laserpitium Pseudo-Meum / B. et Heldr." added in different handwriting. Another specimen from this gathering is extant in the Orphanides herbarium at ATHU and has a more detailed description: "No. 2019 / Laserpitium pseudomeum Heldr Orph et Sart. / Legit in monte Cyllene supra Livadi / 28 Jun/10 Jul 1851 - alt 5500 / Th. G. Orphanides". The locality of Livadi matches that given by Tan [9], while it is not indicated on the G-Boiss duplicate. The gathering of Heldreich is represented in both G-Boiss and ATHU, and annotated as "2697. Elaeoselinum / In monte Parnasso. In reg. alpina / 9–10. Aug. 1852". On both herbarium sheets the determination was later corrected with different handwriting, with the one in G-Boiss identified as that of Reuter. The specimen in G-Boiss (G00766459) was provisionally indicated as the lectotype by Pimenov and Jacquemoud. All specimens mentioned above correspond to Laserocar*pum pseudomeum* (\equiv *Laserpitium pseudomeum*). If we attribute the description of the species to Orphanides, Heldreich, and Sartori, then all qualify as syntypes. However, we have good reasons to believe that Boissier was the sole author of the protologue. In this case, only the specimens at G-Boiss are available for lectotypification. Moreover, this herbarium was indicated as housing the types in earlier accounts [8,9]. To avoid confusion, we also followed the published account of Tan in indicating the Orphanides gathering (albeit with the corrected data) as the lectotype rather than the Heldreich specimen (as preferred by Pimenov and Jacquemoud in their annotations on the specimens). This gathering includes four plants arranged on two herbarium sheets, the main sheet G00766460 and sheet a. We selected the bigger of the two plants on the main sheet as the lectotype of Laserpitium pseudomeum (Fig. 2).

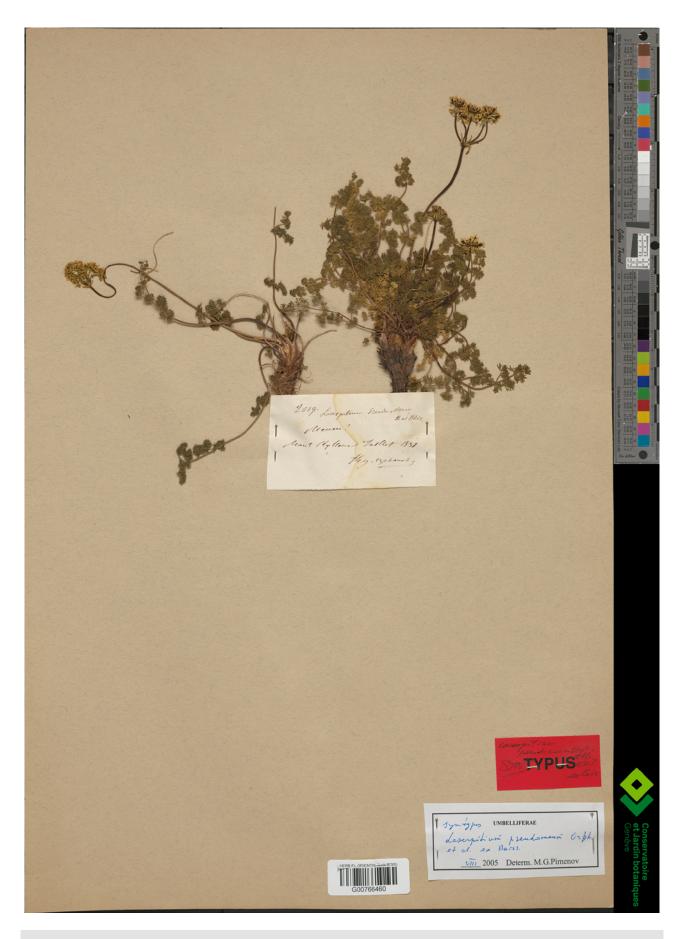


Fig. 2 Lectotype of *Laserpitium pseudomeum* Orph., Heldr. & Sartori ex Boiss., designated here. Photograph © Conservatoire et Jardin botaniques de la Ville de Genève, reproduced with permission.

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3635/0:

Fig. S1 Maximum likelihood tree inferred from analyses of combined sequences of the *rps16* and *rpoC1* introns and the *rpoB-trnC* intergenic spacer for the same accessions as shown in Fig. 1.

Fig. S2 Maximum likelihood tree inferred from analyses of combined nrDNA ITS and cpDNA.

Appendix S1 Accessions of Scandiceae subtribe Daucinae and outgroups used in this study with corresponding accession identifiers and GenBank reference numbers and voucher information.

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