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MOLECULAR SYSTEMATICS OF THE *UMBELLIFERAE*: USING NUCLEAR RIBOSOMAL DNA INTERNAL TRANSCRIBED SPACER SEQUENCES TO RESOLVE ISSUES OF EVOLUTIONARY RELATIONSHIPS

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Phylogenetic relationships among 79 species (58 genera) of *Umbelliferae* (*Apiaceae*), representing all three of its subfamilies, and nine species from outgroup families *Araliaceae*, *Pittosporaceae*, *Sambucaceae* and *Rosaceae*, were inferred from nucleotide sequence variation in the two internal transcribed spacer (ITS1 and ITS2) regions of 18S-26S nuclear ribosomal DNA. Relationships inferred using the neighbour-joining method of tree construction differ drastically from those implied in any existing systems of classification for *Umbelliferae*. While our results support the monophyly of *Umbelliferae* subfamilies *Saniculoideae* and *Apioideae* and their sister-group status, subfamily *Hydrocotyloideae* (represented by only the genus *Hydrocotyle*) allies with *Araliaceae* and not with other *Umbelliferae*. Furthermore, with the exceptions of *Apioideae* tribes *Scandiceae*, *Caucalideae*, and *Tordylieae*, all other previously accepted tribes in the subfamily are not monophyletic. Based on these preliminary analyses, it is evident that the taxonomy of *Umbelliferae* requires radical revision.

The stream of modern molecular phylogenetic publications, based on various DNA structure comparisons, changed considerably the traditional landscape of plant systematics formed during 1970—1980's. These investigations, however, were not adopted by modern classifications due to natural inertion in taxonomic synthesis and predominate interpretation of the results as only phylogenetic, but not taxonomic inferring. The groups obtained by phylogenetic molecular analysis are treated as lineages, and their names (for instance, Saxifragoids, Glucosinolade clade etc.) are not considered as valid taxa names. The plurality of the resulting trees, the discordance between their topologies, when produced basing on different gene sequences, the dependence on the methods of data analysis, as well as a quick change of methodic priorities in DNA-systematics did not promote popularity of molecular approach in practical taxonomy, especially outside of North America. Whether these molecular investigations are truly phylogenetic in traditional term meaning, or they are more and more drawing to comparative, similarity-based approach, being the essence of taxonomy — the matter may be the point of discussion. In any case, they have a clear taxonomic value, and as such they are to be taken into consideration in any up-to-date taxonomic classification. Any dendrogramm-like visualisations of taxa relationships, obtained by both phenetic and cladistic methods, from both morphological and molecular data, are to be regarded, alongside with any other possible representations (factor analysis plots, or even text taxonomic hierarchies), as plausible hypotheses.

The alterations are necessary not only in general phylogenetic arrangement of Angiosperm orders and families (Troitsky et al., 1991; Hamby, Zimmer, 1992; Chase et al., 1993; Olmstead, Palmer, 1994; Боброва и др., 1995; Nickent, Soltis, 1995; Soltis et al., 1997, etc.), but even in particular taxonomy of taxa with a more or less stable classification. Obviously, it's no use talking about such critical families as *Compositae* (*Asteraceae*), *Cruciferae* (*Brassicaceae*) and some others. The *Compositae* studies had

clearly demonstrated a considerable impact of correctly interpreted modern DN information to general systematics and phylogeny of the largest family of flowering plan (Jansen, Palmer, 1987; Jansen et al., 1991; Kim et al., 1992; Baldwin, 1992; Downi Palmer, 1992; Jeffrey, 1995, etc.)

In contrast to the majority of large angiosperm families of mostly tempera distribution, the *Umbelliferae* have no modern classification. The commonly use O. Drude's (1897—1898) classification is not only a century old, but it relies exclusivel upon morphological data. These characters are subject to much homoplasy and, as consequence, have severely confounded the taxonomy of the group. Despite recei intensive multidisciplinary efforts using a variety of phenotypic taxonomic character fundamental disagreements still persist regarding tribal and subtribal designations. As a example of this confusion, we list in Table 1 the 58 genera of *Umbelliferae* considere in this investigation with reference to their classification in the systems by Drud (1897—1898), B. Koso-Poljansky (1916) and M.-T. Cerceau-Larrival (1962). Moreove some large genera (e. g., *Ligusticum*, *Pleurospermum*, *Pimpinella*, *Angelica*, and espec ally *Peucedanum* s. ampl.) are rather problematic in terms of their species number taxonomic limits, and monophyly.

This article presents some of the results of a collaborative research project starte several years ago between Moscow State University and the University of Illinois a Urbana-Champaign in the United States. We are studying the systematics and phylogen of both Old and New World *Umbelliferae*, using primarily molecular evidence i conjunction with data from morphology, anatomy and phytochemistry. In this paper, w use variation in nuclear ribosomal DNA internal transcribed spacer (ITS1 and ITS2 sequences in order to address questions of monophyly and evolutionary relationship within *Umbelliferae*. Among the various chloroplast and nuclear DNA regions routinel used in molecular systematic studies, these ITS regions show sufficient variability t resolve relationships at the ranks of family and below (Baldwin et al., 1995). These tw spacer regions are flanked by the 18S and 26S ribosomal RNA genes. Between these tw spacer regions lies the 5.8S rDNA subunit.

It is of interest to note that the first attempts to use DNA data in inferring taxonomi relationships within *Umbelliferae* began during the late 1970's when DNA—DN hybridization techniques were employed (Вальехо-Роман и др., 1979, 1982). Thes experiments showed a good correlation between the taxonomic placement of taxa in a series with a diminishing similarity (based on morphology and reflected in taxonomy o the time) and their degree of overall DNA similarity. For example, the greates hybridization was observed between DNAs from populations of the same species, and th lowest hybridization occurred between *Eryngium* (subfamily *Saniculoideae*) and an member of subfamily *Apioideae*. When these experiments were expanded to include mor representatives of *Apioideae* the results were astonishing in the sense that they did no correspond with any proposed system of classification for the subfamily. These investi gations were also interpreted (Antonov et al., 1988) as an indication of non-equivalenc of accepted taxa of the same rank (for instance, a genus) in various families (*Iridaceae Compositae*, *Umbelliferae*) and the ambiguity of tribe separation within *Apioideae*. Thes results prompted us to pursue further molecular systematic investigation in order to mor rigorously compare these differences in relationships proposed using molecular an morphological data sets.

Serotaxonomic studies (Шнеер и др., 1991; Shneyer et al., 1992, 1995) also confirme that the groupings of taxa based on immunochemical reactions of seed storage protein differed considerably from those groups recognized in Drude's (1897—1898) widespread and frequently cited classification of *Umbelliferae*. These serological studies clearl showed that many of the tribes and subtribes recognized by Drude are not natural. Thes results were further significant in suggesting that the carpological characters used b Drude and others, recognized previously as being extremely important in delimiting suprageneric groups within the family, may not be adequate to accurately resolv evolutionary relationships.

TABLE 1

Taxonomic position of the genera investigated in the systems of O. Drude, B. Koso-Poljansky, and M.-T. Cerceau-Larrival

Genus	Drude (1897—1898)	Koso-Poljansky (1916)	Cerceau-Larrival (1962)
Aegopodium	*A—Ammineae—Carinae*	*L—Gymnomestomeae—Careae—Carinae* (sub *Carum*)	*Endressioideae—Ammineae*
Aethusa	*A—Ammineae—Seselinae*	*L—Exomestomeae—Aethuseae—Aethusinae*	*Apioideae—Aethuseae*
Anethum	*A—Ammineae—Seselinae*	*L—Exomestomeae—Ligusticeae—Bupleurinae*	—
Angelica	*A—Peucedaneae—Angelicinae*	*L—Gymnomestomeae—Peucedaneae*	*Apioideae—Angeliceae*
Anthriscus	*A—Scandicineae—Scandicinae*	*L—Pachystereomeae—Caucaleae*	*Endressioideae—Scandicineae*
Apium	*A—Ammineae—Carinae*	*L—Gymnomestomeae—Careae—Carinae* (sub *Carum*)	*Apieae—Heteromorpheae*
Arracacia	*A—Smyrnieae*	—	—
Arafoe	—	—	—
Astrantia	*S—Saniculeae*	*L—Cyclocrystalleae—Saniculeae*	*Eryngioideae—Saniculeae*
Bupleurum	*A—Ammineae—Carinae*	*L—Exomestomeae—Ligusticeae—Bupleurinae*	*Bupleuroideae—Bupleureae*
Carlesia	—	—	—
Carum	*A—Ammineae—Carinae*	*L—Gymnomestomeae—Careae—Carinae*	*Endressioideae—Ammineae*
Cenolophium	*A—Ammineae—Seselinae*	*L—Exomestomeae—Aethuseae—Aethusinae*	—
Chaerophyllum	*A—Scandicineae—Scandicinae*	*L—Pachystereomeae—Scandiceae—Scandicinae*	—
Chymsidia	—	*L—Endotaenieae—Crithmeae—Archangelicinae*	—
Coaxana	*A—Ammineae—Seselinae*	—	—
Conium	*A—Smyrnieae*	*L—Endotaenieae—Smyrnieae*	*Apioideae—Conieae*
Coriandrum	*A—Coriandreae*	*L—Pachystereomeae—Scandiceae—Coriandrinae*	*Endressioideae—Coriandreae*
Coulterophytum	*A—Peucedaneae—Angelicinae*	*L—Gymnomestomeae—Peucedaneae*	—
Crithmum	*A—Ammineae—Seselinae*	*L—Endotaenieae—Crithmeae—Crithminae*	*Endressioideae—Endressieae*
Daucus	*A—Dauceae*	*L—Gymnomestomeae—Careae—Daucinae*	*Endressioideae—Dauceae*
Echinophora	*A—Echinophoreae*	*L—Pachystereomeae—Scandiceae—Scandicinae*	*Endressioideae—Echinophoreae*
Enanthiophylla	*A—Peucedaneae—Angelicinae*	—	—
Endressia	*A—Ammineae—Seselinae*	—	*Endressioideae—Endressieae*
Eryngium	*S—Saniculeae*	*L—Cyclocrystalleae—Saniculeae*	*Eryngioideae—Eryngieae*
Falcaria	*A—Ammineae—Carinae*	*L—Pachystereomeae—Scandiceae—Scandicinae*	*Apioideae—Pimpinelleae*
Ferula	*A—Peucedaneae—Ferulinae*	*L—Exomestomeae—Pastinaceae—Pastinacinae*	*Endressioideae—Capnophylleae*
Ferulago	*A—Peucedaneae—Ferulinae*	—	*Apioideae—Pastinaceae*
Hacquetia	*S—Saniculeae*	*L—Cyclocrystalleae—Saniculeae*	*Eryngioideae—Saniculeae*

TABLE 1 (*continuation*)

Genus	Drude (1897—1898)	Koso-Poljansky (1916)	Cerceau-Larrival (1962)
Heracleum	*A—Peucedaneae—Tordyliinae*	*L—Exomestomeae—Pastinaceae—Pastinacinae* (sub *Pastinaca*)	*Apioideae—Heracleae*
Heteromorpha	*A—Ammineae—Carinae*	*L—Exomestomeae—Ligusticeae—Bupleurinae*	*Apioideae—Heteromorpheae*
Hydrocotyle	*H—Hydrocotyleae—Hydrocotylinae*	*Hydrocotyloideae—Centelleae*	*Azorelloideae—Hydrocotyleae*
Imperatoria	*A—Peucedaneae—Ferulinae* (sub *Peucedanum*)	*L—Gymnomestomeae—Peucedaneae* (sub *Angelica*)	—
Komarovia	—	—	—
Laserpitium	*A—Laserpitieae—Thapsiinae*	*L—Gymnomestomeae—Careae—Daucinae*	*Endressioideae—Laserpitieae*
Levisticum	*A—Peucedaneae—Angelicinae*	*L—Gymnomestomeae—Peucedaneae*	*Endressioideae—Capnophylleae*
Lomatium	—	*L—Gymnomestomeae—Peucedaneae*	—
Meum	*A—Ammineae—Seselinae*	*L—Exomestomeae—Ligusticeae—Ligusticinae*	—
Myrrhidendron	*A—Peucedaneae—Ferulinae*	—	—
Myrrhis	*A—Scandicineae—Scandicinae*	*L—Endotaenieae—Crythmeae—Cyithminae*	*Endressioideae—Scandicineae*
Orlaya	*A—Scandicineae—Caucalinae*	*L—Pachystateomeae—Caucaleae*	*Endressioideae—Orlayeae*
Paraligusticum	*A—Ammineae—Seselinae* (sub *Ligusticum*)	—	—
Pastinaca	*A—Peucedaneae—Ferulinae*	*L—Exomestomeae—Pastinaceae—Pastinacinae*	*Apioideae—Pastinaceae*
Peucedanum	*A—Peucedaneae—Ferulinae*	*L—Gymnomestomeae—Peucedaneae*	*Apioideae—Peucedaneae*
Physospermum	*A—Smyrnieae*	*L—Pachystereomeae—Scandiceae—Scandicinae* (sub *Chaerophyllum*)	*Apioideae—Smyrnieae*
Pimpinella	*A—Ammineae—Carinae*	*L—Gymnomestomeae—Careae—Carinae* (sub *Carum*)	*Apioideae—Pimpinelleae*
Prangos	*A—Smyrnieae*	*L—Endotaenieae—Smyrnieae*	—
Prionosciadium	*A—Peucedaneae—Angelicinae*	—	—
Pseudorlaya	—	*L—Pachystereomeae—Caucaleae*	—
Rhodosciadium	*A—Peucedaneae—Angelicinae*	—	—
Sanicula	*S—Saniculeae*	*L—Cyclocrystalleae—Saniculeae*	*Eryngioideae—Saniculeae*
Scandix	*A—Scandicineae—Scandicinae*	*L—Pachystereomeae—Scandiceae—Scandicinae*	*Endressioideae—Scandicineae*
Selinum	*A—Ammineae—Seselinae*	*L—Exomestomeae—Ligusticeae—Ligusticinae*	*Endressioideae—Astydamieae*
Seseli	*A—Ammineae—Seselinae*	*L—Gymnomestomeae—Careae—Carinae*	*Apioideae—Heteromorpheae*
Smyrniopsis	*A—Smyrnieae*	*L—Gymnomestomeae—Careae—Carinae*	—
Smyrnium	*A—Smyrnieae*	*L—Endotaenieae—Smyrnieae*	*Apioideae—Smyrnieae*
Torilis	*A—Scandicineae—Caucalinae*	*L—Pachystereomeae—Caucaleae* (sub *Anthriscus*)	*Endressioideae—Torilineae*
Zizia	*A—Ammineae—Carinae*	*L—Gymnomestomeae—Careae—Carinae*	—

Note. *A* — *Apioideae*, *H* — *Hydrocotyloideae*, *L* — *Ligusticoideae* (Koso-Poljansky, 1916), *S* — *Saniculoideae* (Drude, 1897—1898).

As part of our continuing investigations into the evolutionary relationships of *Umbelliferae*, we use the results of cladistic analysis of the two ITS regions of nuclear rDNA to address questions pertaining to the monophyly of the family and its three commonly accepted subfamilies, and the relationships, if any, among the major tribes and subtribes recognized within *Apioideae*, the largest subfamily of *Umbelliferae*.

Materials and methods

Ingroup and outgroup taxa. In total, 88 species were included in the analysis. Complete ITS1 and ITS2 sequences were compared for 70 species from *Umbelliferae* subfamily *Apioideae*, 6 species from *Umbelliferae* subfamily *Saniculoideae*, 3 species from *Umbelliferae* subfamily *Hydrocotyloideae*, and 9 species from outgroup families *Araliaceae* (*Aralia*, *Eleutherococcus*, *Hedera*), *Pittosporaceae* (*Pittosporum*), *Sambucaceae* (*Sambucus*) and *Rosaceae* (*Aria*, *Spiraea*, *Sorbus*). Within *Umbelliferae*, 58 genera were considered; their classifications in the treatments by Drude (1897—1898), Koso-Poljansky (1916), and Cerceau-Larrival (1962) are presented in Table 1. Of the 70 species of *Apioideae* examined, 40 were included in a previous phylogenetic analysis of ITS sequence variation (Downie, Katz-Downie, 1996) (GenBank accession numbers U27578, U30314, U27589, U30315 and U30522—U30595). One of these 40 accessions was *Daucus carota* L., and its ITS sequences were obtained from Y. Yokota et al. (1989). ITS data for *Sambucus* and the three species of *Rosaceae* were obtained from GenBank accession numbers U41381, U16205, U16185 and U16204, respectively.

The phylogenetic trees were rooted with *Spiraea*, one of the three species of *Rosaceae* included in our study. GenBank accession numbers for the 44 complete ITS1 and ITS2 sequences reported here for the first time, in addition to their source and voucher inrormation, are presented in Table 2.

The ITS regions for the same four species of *Umbelliferae* were sequenced independently in the laboratories at the University of Illinois and at Moscow State University. These species include *Levisticum officinale*, *Prangos pabularia*, *Smyrniopsis aucheri*, and *Astrantia major*. Although each set of species arises together in the trees (described below), minor differences in their sequences are apparent. These different sequences for each species are designated as «1» and «2» in this study.

DNA isolation, amplification, and sequencing. Total genomic DNAs were isolated from fresh or dried leaves or herbarium specimens using the modified CTAB procedure (Doyle, Doyle, 1987). The entire ITS1-5.8S rDNA-ITS2 region was polymerase chain reaction (PCR) amplified using a pair of primers corresponding to conserved areas on the 3′ end of 18S («ITS5» primer) and 5′ end of 26S («ITS4» primer) rDNAs (White et al., 1990). The purified, double-stranded PCR products were then used in cycle sequencing using the Cyclist Exo-Pfu DNA sequencing kit (Stratagene, California, U.S.A.). Sequences were obtained and compared from both DNA strands using the pair of primers indicated above, as well as from primers corresponding to the 3′ and 5′ ends of 5.8S rDNA (these are primers «ITS3» and «ITS2» in: White et al., 1990).

Sequence and phylogenetic analyses. The ITS sequences obtained were aligned using the SED editor of the VOSTORG phylogenetic analysis package (Zharkikh et al., 1990). Aligned DNA sequences of ITS1 and ITS2 of 44 species are provided in fig. 1.

Neighbour-joining (NJ) trees (Saitou, Nei, 1987) were constructed using the TREECON software package (Van de Peer, De Wachter, 1994). It has been shown that this method of tree construction may have a higher level of accuracy than maximum parsimony for estimating phylogenies under a wide range of evolutionary models (see: Kim et al., 1992). Moreover, in the phylogenetic studies of *Umbelliferae* subfamily *Apioideae* both NJ and maximum parsimony trees showed very similar topologies for the same set of taxa (Downie, Katz-Downie, 1996; Katz-Downie et al., 1998). To calculate pairwise distances used in NJ tree construction, two kinds of measures were used: 1) *p*-distances, equal to the observed proportion of differences between pairs of sequences, and 2) evolutionary distances, inferred by applying the two-parameter model of M. Kimura

TABLE 2

Umbelliferae and related taxa for DNA; origin and vouchers

Taxon	Source and vouchers
Aegopodium kashmiricum (R.R. Stewart ex Dunn) Pimenov	Kazakhstan, Dzhungar Alatau Mts., Lepsinsk, 10 VIII 1979, E. V. Kljuykov, N 109.
Angelica sachalinensis Maxim.	Russia, Sakhalin Is., Chekhov Mt., 9 VIII 1983, M. G. Pimenov, E. V. Kljuykov, s. n.
Anthriscus sylvestris (L.) Hoffm.	Botanical Garden of Moscow State University (BG MSU), weed.
Arafoe aromatica Pimenov et Lavrova	Russia, N. Caucasus, Krasnodar terr., Caucasian Reservate, Lagonaki, 19 VII 1976, Pimenov, N 403.
Aralia elata (Miq.) Seem.	BG MSU; origin: Russia, Primorje (Maritime Prov.) K. A. Voskresensky, s. n.
Astrantia major L.	W. Ukraine, Transcarpatia, Volovetz, IX 1988, Ju. V. Daushkevich, s. n.
Bupleurum falcatum L.	BG MSU; seeds from BG Wroclaw (Poland), 1988.
Carum carvi L.	BG MSU; seeds from Komarov Botanical Institute (St. Petersburg).
Cenolophium denudatum (Hornem.) Tutin	Russia, Ryazan prov., Kochemary, 27 VIII 1976, V. S. Novikov, s. n.
Chaerophyllum aromaticum L.	BG MSU; seeds from BG Nancy (France).
C. khorossanicum Czerniak. ex Schischk.	Turkmenistan, Kopet Dagh Mts., Mt. Dalancha, 4 VIII 1978, M. G. Pimenov et al., N 246.
Chymsydia colchica (Albov) Woronow	Georgia, Mt. Kvira, 19 VII 1977, M. G. Pimenov, N 1489.
Echinophora chrysantha Freyn et Sint.	Turkey, Erzurum vill., Bozburun, 11 VII 1994, M. G. Pimenov, E. V. Kljuykov, N 733.
Eleutherococcus senticosus (Rupr. et Maxim.) Maxim.	Main Botanical Garden RAS; origin: Russia, Primorje, railway stat. Okeanskaya.
Eryngium billardieri Delaroche	Armenia, Sachlu, 30 VI 1977; M. G. Pimenov et al., N 1027.
E. campestre L. var. *virens* Link	Turkey, Artvin near Borcka, the mouth of the river Murgul, 4 VII 1994; M. G. Pimenov et al., N 16.
Falcaria vulgaris Bernh.	Russia, Rostov prov., Boguchar distr., Radchenskoye, 26 VI 1977, M. G. Pimenov, N 25.
Ferula tenuisecta Korovin	Uzbekistan, Angren valley, Jertasch, 27 V 1978; M. G. Pimenov et al., N 106.
F. violacea Korovin	Tadzhikistan, Karategin Mts., Obi-Garm. 18 VI 1973, M. G. Pimenov, E. V. Kljuykov, N 893.
Ferulago galbanifera (Mill.) W. D. J. Koch	Ukraine, the Crimea, Oktjabrskoye, 7 IX 1974, M. G. Pimenov, L. P. Tomkovich, N 397.
Hacquetia epipactis (Scop.) DC.	BG MSU: origin unknown (received from an amateur).
Hedera colchica (K. Koch) K. Koch	BG MSU (Arboretum).
Hydrocotyle bonariensis Lam.	BG MSU (greenhouse); origin: BG Bonn, N 54.
H. mexicana Schltdl. et Cham.	BG MSU (greenhouse); origin: BG Nancy (France), N 145.
H. vulgaris L.	BG MSU (greenhouse); origin: BG Caen (France), N 511/215
Imperatoria ostruthium L.	Czech Rep., Krkonoschi Mts. 15 VII 1982; M. G. Pimenov, s. n.
Komarovia anisosperma Korovin	Uzbekistan, Zeravscshtan Mts., Urgut. 30 V 1978, M. G. Pimenov et al., N 178.
Laserpitium hispidum Bieb.	Russia, Krasnodar Terr., Gorjachiy Kljuch, 19 VII 1987, T. A. Ostroumova, N 19.
Levisticum officinale W. D. J. Koch	BG MSU; origin unknown.
Meum athamanticum Jacq.	BG MSU; origin: Karpatian Mts., W. Ukraine.

TABLE 2 (*continuation*)

Taxon	Source and vouchers
Myrrhis odorata (L.) Scop.	BG MSU; seeds from BG Frankfurt/Main (Germany).
Paraligusticum discolor (Ledeb.) V. N. Tichom.	Kazakhstan, Dzhungar Alatau Mts., Lepsinsk, 10 VIII 1979, E. V. Kljuykov, N 119.
Peucedanum morisonii Bess. ex Spreng.	Russia, Altai Mts., Barlak, 1979, T. A. Ostroumova, s. n.
Physospermum cornubiense (L.) DC.	Ukraine, the Crimea, Alikat-Bogaz Pass, 4 IX 1974, M. G. Pimenov, L. P. Tomkovich, s. n.
Pimpinella rhodantha Boiss.	Russia, N. Caucasus, Daghestan, Charami Pass, 2 VII 1976, M. G. Pimenov, s. n.
Pittosporum tobira (Thunb.) Ait.	China, cult. Missouri Botanical Garden, St. Louis, N 801425.
Prangos pabularia Lindl.	Kirghizia, Fergana Mts., Urumbash, 17 VIII 1976, M. G. Pimenov, s. n.
Sanicula rubriflora Maxim.	BG MSU; origin: Primorje.
Seseli krylovii (V. N. Tichom.) Pimenov et Sdobnina	BG MSU; seed from BG Ekaterinburg, 1977.
Smyrniopsis aucheri Boiss.	Armenia, Selim Pass, 11 VII 1977; M. G. Pimenov et al., N 1337.

(1980) to correct superimposed mutations. We also varied the ways in which alignment gaps were considered. First, gaps of any size in any species were counted as one gap. Second, positions with gaps in any taxon were excluded from the analysis. The bootstrap resampling procedure (Felsenstein, 1985) was used to analyze the reliability of branches in the phylogenetic trees. This procedure involves resampling the original data matrix with replacement, in order to create a series of data matrices the same size as the original matrix. The bootstrap values obtained, given as a percentage, describe how often a particular cluster of taxa occurred in these resampled data matrices.

Results and discussion

Despite the availability of 5.8S sequence data for the 44 species sequenced as part of this investigation, only the two spacer regions were included in our analysis. In the study of S. Downie and D. Katz-Downie (1996), sequence data for the 5.8S subunit were incomplete for many taxa, and those that were available were found not to be sufficiently variable to warrant additional sequencing. Indeed the inclusion of available 5.8S data in this study does not change the topology of the inferred trees. This is not surprising as the 5.8S region is extremely conserved (Troitsky, Bobrova, 1986).

In our alignment of 88 ITS sequences from *Umbelliferae* and outgroups *Araliaceae*, *Pittosporaceae*, *Sambucaceae*, and *Rosaceae*, we find both highly conserved and highly variable regions of nucleotides. Although the interspersion of conserved and variable sites facilitates sequence alignability, we admit that several portions of our alignment are ambiguous because of the numerous indels and high sequence divergence that have occurred since the divergence ot these plants.

The NJ tree constructed with *p*-distances and taking alignment gaps into account is shown in fig. 2, with branches having bootstrap values greater than 25 % indicated. With respect to changes in alignment, this topology is rather stable. When several alternative alignments were considered, or questionable regions of alignment excluded from the analysis, only subtle differences in tree topology resulted. Moreover, these changes occurred only in those branches supported by the lowest bootstrap values. When gap positions were excluded from the analysis (thereby eliminating all uncertain areas of the alignment), the resulting tree was almost fully congruent to that seen in fig. 2.

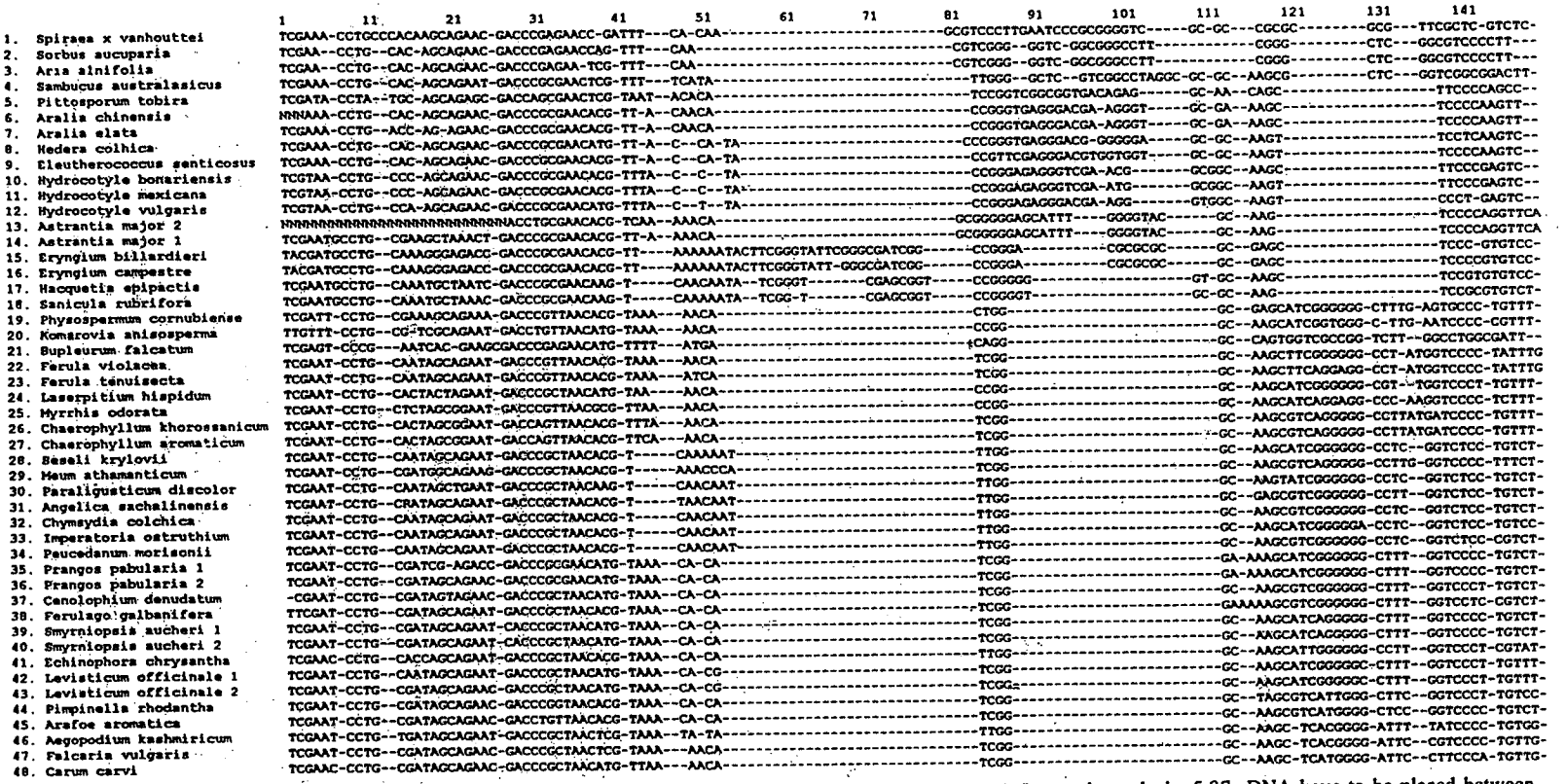

Fig. 1. Aligned sequences of ITS1 + ITS2 regions in ribosomal DNA of 44 species from 84 species used in phylogenetic analysis. 5.8S rDNA have to be placed between positions 377 and 378 of the alignment.

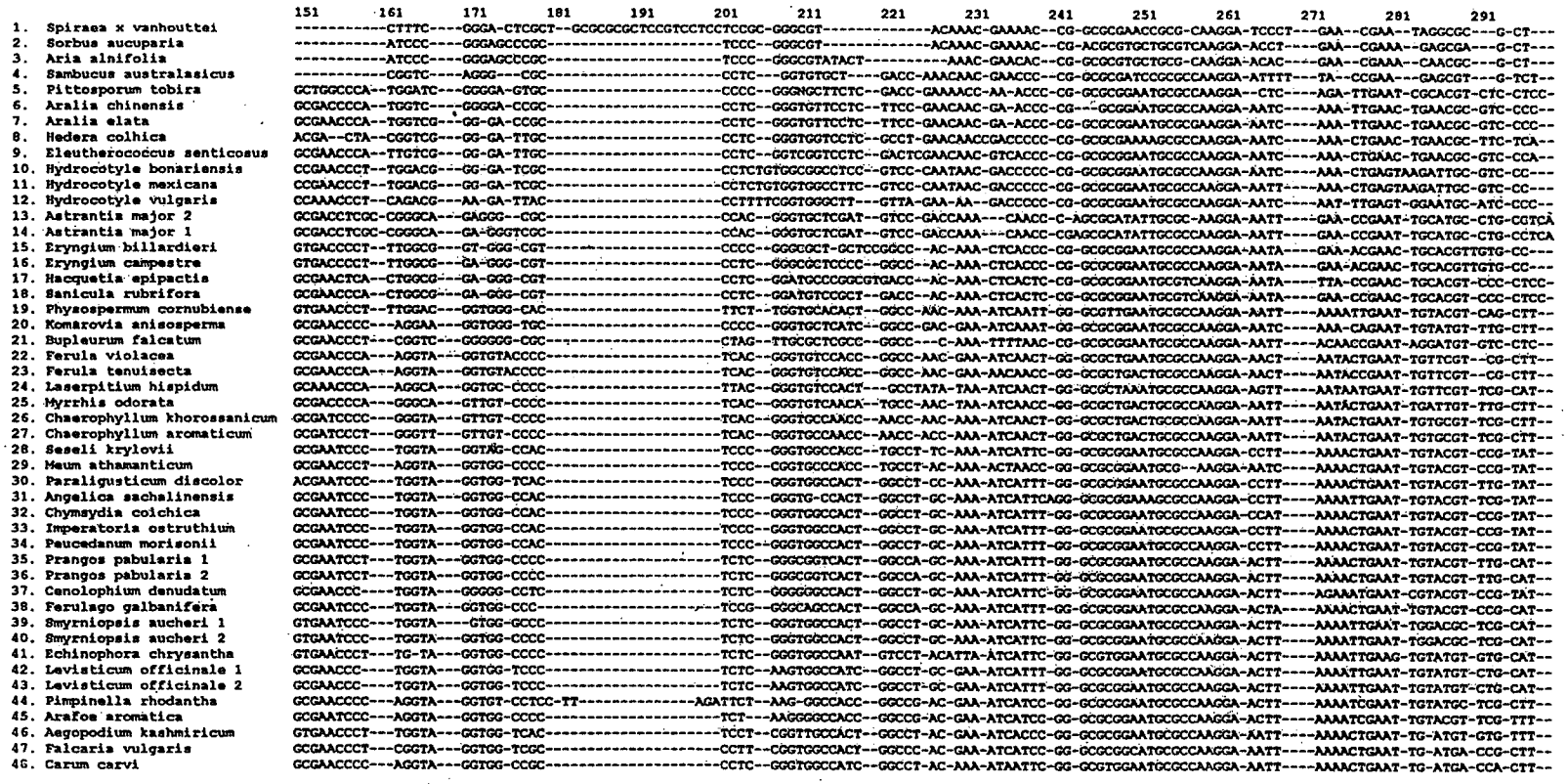

Fig. 1 (*continuation*).

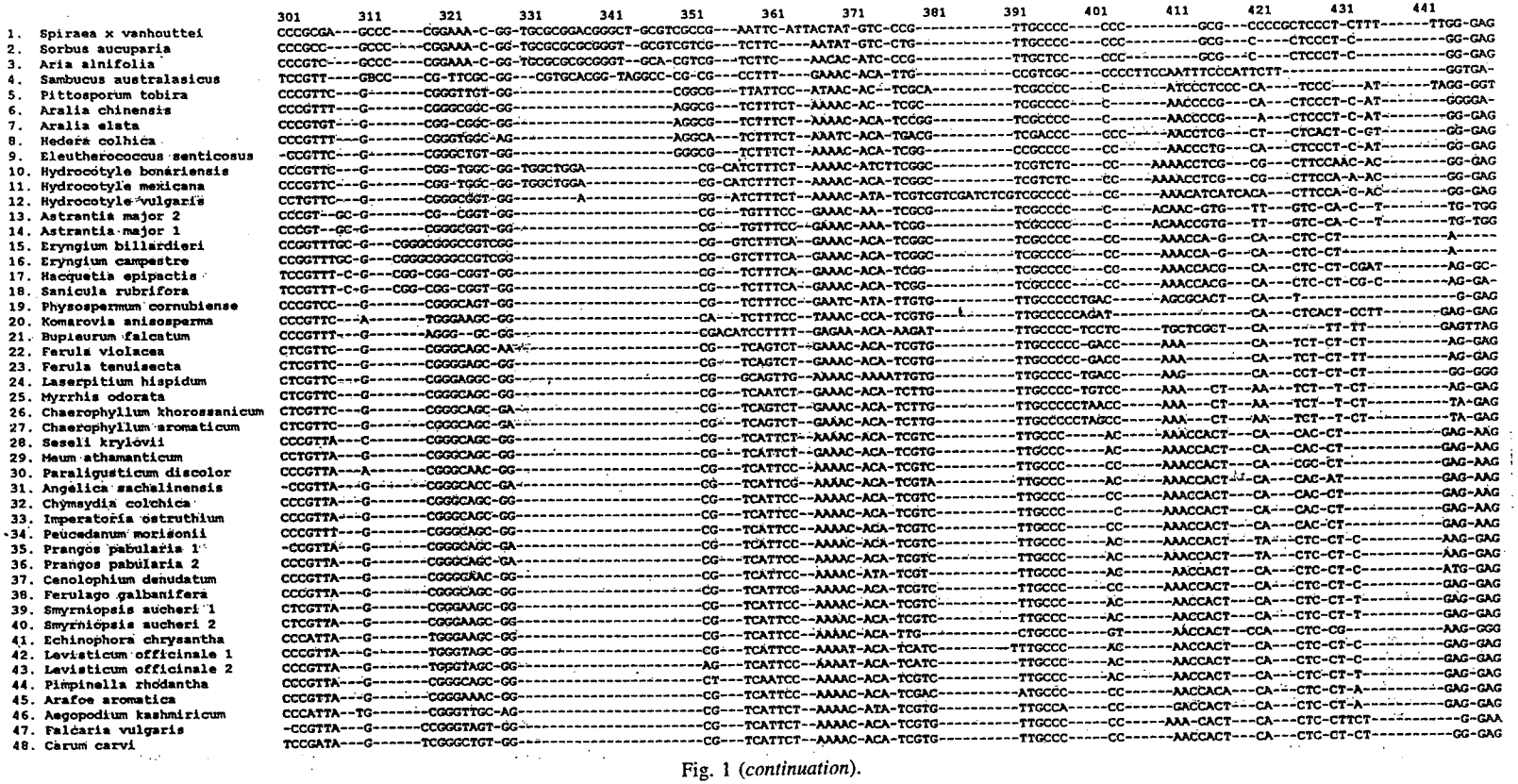

Fig. 1 (*continuation*).

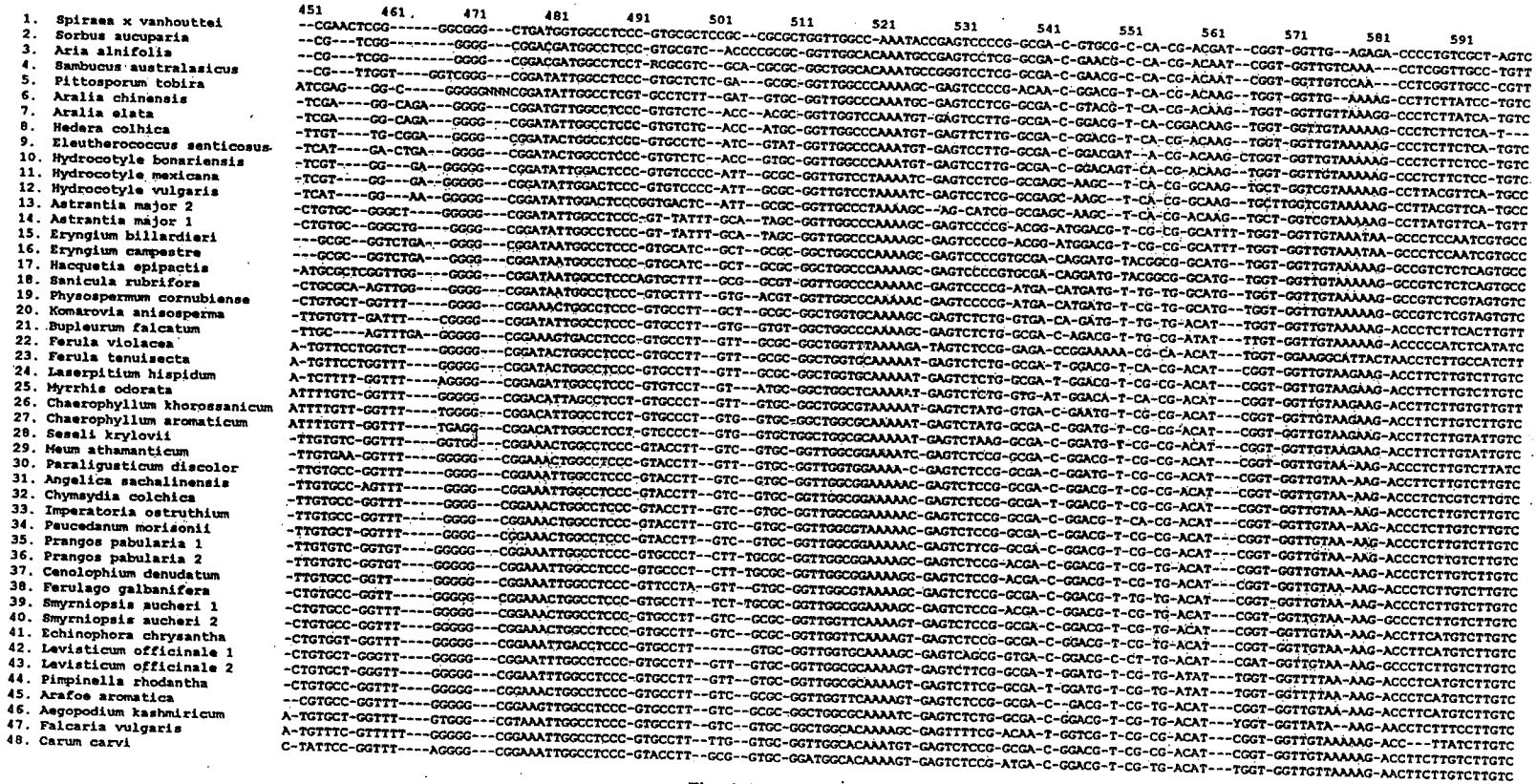

Fig. 1 (*continuation*).

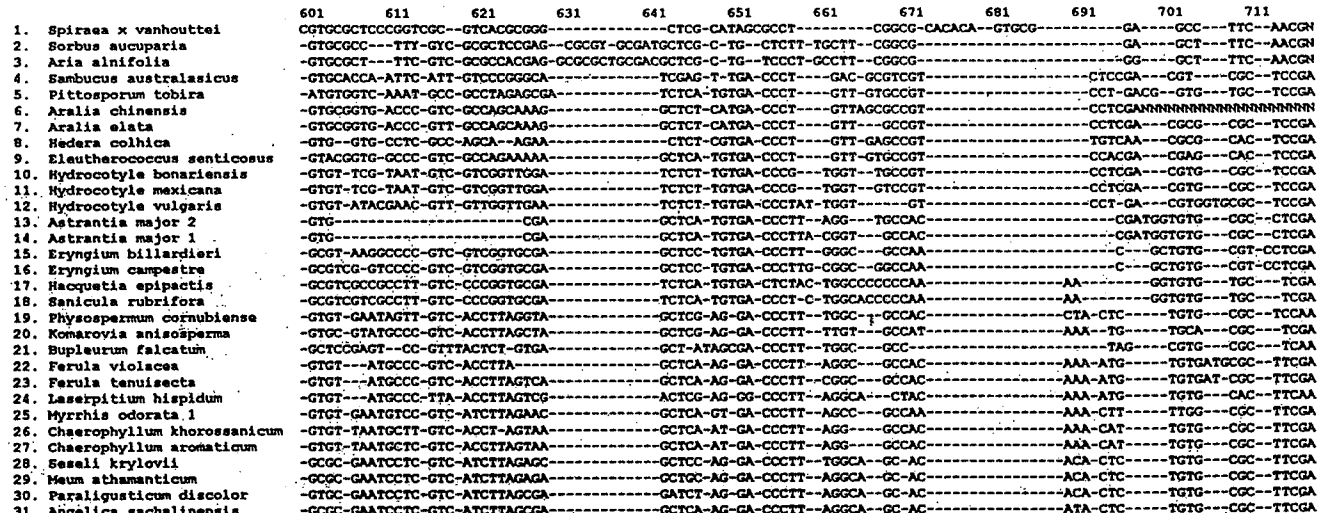

Fig. 1 (*continuation*).

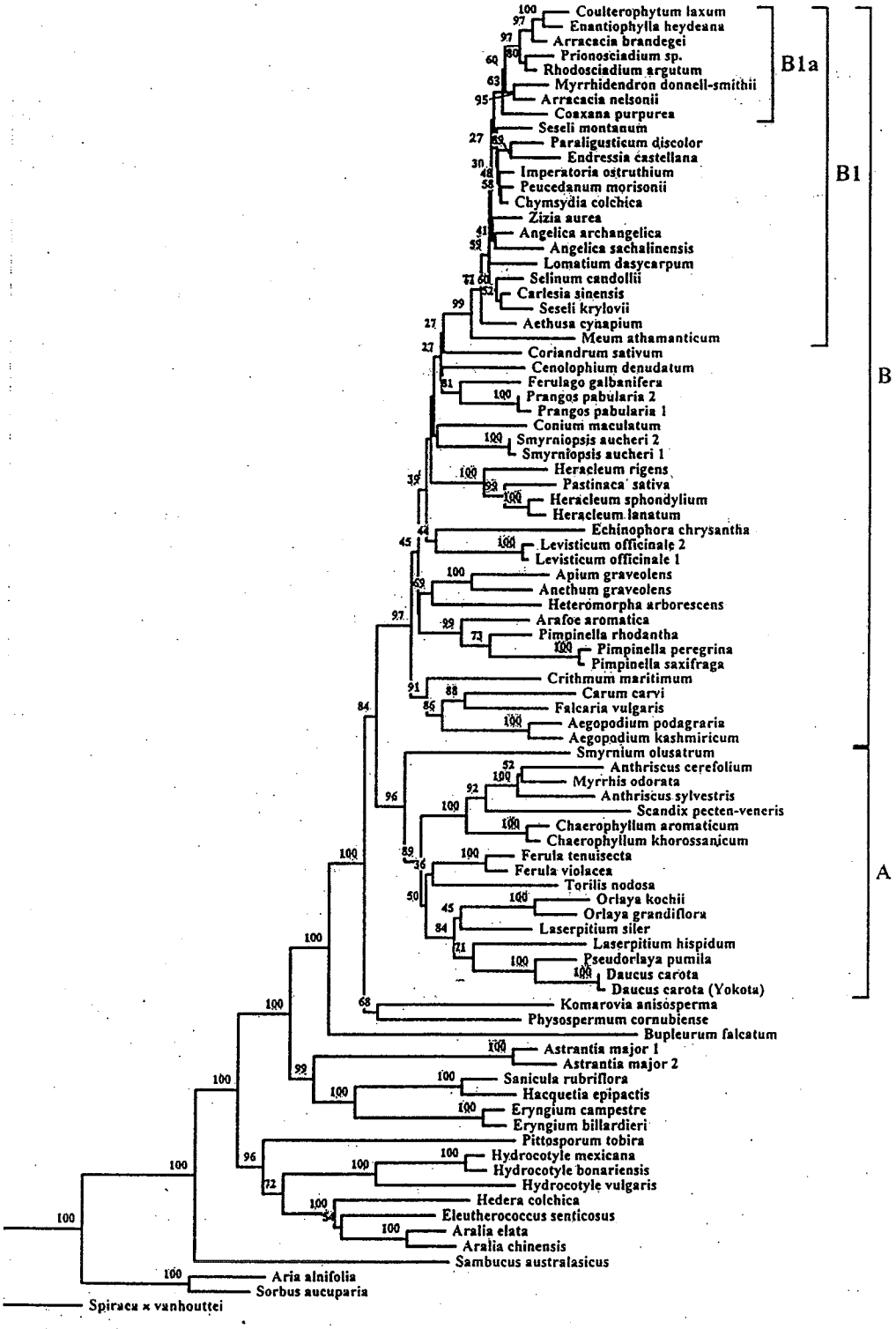

Fig. 2. Neighbour-joining tree of *Umbelliferae* and related groups based on ITS1 + ITS2 sequences.

p-distance matrix with gaps taken into account was used for calculation. Each gap was counted as one nucleotide change irrespective of its length. 100 bootstrap resamplings were used. Bootstrap values greather than 25 % were indicated near the corresponding nodes. *A*, *B*, *B1*, *B1a* — clades in *Apioidaeae* (see explanation in text).

The NJ trees constructed with M. Kimura's (1980) two-parameter method, with ar without gap positions included in the analysis, are also very similar to the tree present in fig. 2. Again, changes in topology occurred only in those regions supported by lo bootstrap values. In general, the branches on these trees had lower bootstrap values th corresponding branches on the tree constructed with *p*-distances and gaps taken in account. Fig. 3 illustrates a strict consensus tree where all branches are supported l bootstrap values greater than or equal to 40 % of the 100 bootstrap replicates carried ou In fig. 2, the branches with the highest bootstrap values (98—100 %) are located at t base of the tree. Using *Spiraea* as the root, the confamilial *Aria* and *Sorbus* arise close as a clade, followed by *Sambucus* (*Sambucaceae*, *Dipsacales*). This close association *Dipsacales* to *Apiales* is consistent with hypotheses of relationships based on morphol gical and anatomical data (Тахтаджян, 1987).

The next deepest branch, sister group to *Umbelliferae* subfamilies *Saniculoideae* a *Apioideae*, combines representatives of *Umbelliferae* subfamily *Hydrocotyloideae*, *Ara aceae*, and *Pittosporaceae*. In this clade, *Pittosporum* is basalmost and *Hydrocotyloide* and *Araliaceae* are sister groups. Many systematists are in agreement that *Umbellifer* and *Araliaceae* are closely related; some have even suggested that they be combin (Thorne, 1983). Similarly, many have suggested an affinity between these two famil and the *Pittosporaceae* (Тахтаджян, 1987).

Subfamily *Hydrocotyloideae* is represented in our study by three species of the sin genus, *Hydrocotyle*. Recent phylogenetic analyses of chloroplast DNA *rbc*L (Plunkett al., 1996a), *mat*K (Plunkett et al., 1997), and *rpo*C1 intron (Downie et al., 1996, 19 sequences also reveal the heterogeneity of this subfamily, with some members allied w *Araliaceae* and others falling as sister to the clade of *Apioideae* + *Saniculoide* Additional species from subfamily *Hydrocotyloideae* must be sampled in order to clar further these issues of relationships.

Our study reveals that subfamilies *Apioideae* and *Saniculoideae* are each monophyle and are sister taxa. Within *Saniculoideae*, all subdivisions are supported by bootst values of 100 %, and of the four genera examined, *Astrantia* is most basal. *Sanicula* sister to *Hacquetia*, and this clade is sister to *Eryngium*.

Of the 70 species we have examined of subfamily *Apioideae*, the genus *Bupleur* occupies the most basal position. Its ITS sequences are highly diverged, and branch leading to *Bupleurum* is the longest in the trees. Indeed, other representati of this genus that have been considered in previous analyses of ITS sequences co not be aligned unambiguously with any included taxon (Downie, Katz-Dow 1996; Katz-Downie et al., 1998). Excluding *Bupleurum* from the data matrix and rerunn the analysis makes no difference; the resulting tree topology is the same as when i included. We cannot offer explanations as to why the ITS region of *Bupleurum* is divergent. It is intriguing to note, however, that this high molecular divergence paral that seen in its morphology. These plants are quite unusual in the subfamily, with m members of the North Temperate zone having grass-like entire leaves with para venation.

Traditionally, *Bupleurum* has been classified in tribe *Apieae* because of its *Carum*-l fruits. C. Sprengel (1820) erected tribe *Bupleureae*, having treated this taxon previo as the separate family *Bupleuraceae* Spreng. (validated by L. Pfeiffer (1873)). M recently, M. T. Cerceau-Larrival (1962) placed *Bupleurum* in its own subfamily, *Bu uroideae*, based on pollen and seedling characters. In the studies of G. Plunkett et (1996a) and Downie et al. (1996, 1998), the genus *Heteromorpha* arises most basal wi *Apioideae*. In Plunkett et al. (1996b, 1997), this position goes to *Bupleurum*, altho *Heteromorpha* is only one node removed. In our study, *Heteromorpha* arises, ra unexpectedly, alongside the genera *Apium* and *Anethum*, well away from the base of subfamily and the genus *Bupleurum*. It is intriguing that the evidence from chlorop DNA suggests a basal position for *Heteromorpha*, whereas the nuclear data suggest this woody species is highly derived. Additional species of *Heteromorpha* will be sam in order to begin to resolve this discrepancy.

The next basal most clade in the subfamily unites, albeit weakly, *Komarovia* with *Physospermum*. These results are similar to those inferred for the subfamily using chloroplast *rpo*C1 intron sequences (Downie et al., 1998), but different to those inferred using ITS sequences when a subset of the datamatrix presented herein is considered (Pimenov et al., 1998).

The remaining members of subfamily *Apioideae* comprise two well-supported major clades, and are identified as sister groups *A* and *B* in figs. 2 and 3. Within each of these clades bootstrap values are generally quite low, although some branches are supported by values over 70 %. In general, many of the relationships inferred do not correspond to any existing system of classification for the subfamily. Few groupings, however, do correspond to traditional tribes or subtribes based on morphological characters. Included here is the group of *Scandix*, *Anthriscus*, *Myrrhis*, and *Chaerophyllum*, conforming with the Sprengel's tribe *Scandiceae* or Tausch's subtribe *Scandicinae*, and the group of *Heracleum* and *Pastinaca*, conforming to the tribe *Pastinaceae* Koso-Pol., revised by I. Mandenova (Манденова, 1959). The correct name for the latter is *Tordylieae* W. D. J. Koch.

Based on these results, we do not see much support for Drude's (1897—1898) system, especially the division of the subfamily into larger tribes, such as *Smyrnieae*, *Peucedaneae*, and *Apieae* (*Ammineae*). These tribes were delimited solely on the basis of morphology, with much emphasis put on carpological characters. Several additional but smaller tribes were separated based on the presence of single, unique characters. For example, *Echinophoreae* Benth. was erected because of its very specialized flower, *Pyramidoptereae* Boiss. — for its pyramidale fruits and fusion of its mericarp ribs with sepals, *Coriandreae* W. D. J. Koch — for its coelospermous seeds and sclerified mesocarp, and *Laserpitieae* Benth. — for its secondary mericarp ribs. Even the three largest tribes within the subfamily (i. e., *Smyrnieae*, *Peucedaneae*, and *Apieae*) were recognized on the basis of a limited number of not very unusual carpological characters. For example, all genera with campylospermous and non-elongate fruits were referred to *Smyrnieae* Spreng., all genera with enlarged marginal mericarp ribs and platyspermous fruits — to *Peucedaneae* Dumort., and all genera with platyspermous fruits with similar dorsal and marginal ribs — to *Apieae*. Drude's system has been criticized by many *Umbelliferae* systematists, and especially by B. Koso-Poljansky (1916). Nevertheless, the Drude's system remains quite popular simply because of the lack of a better alternative.

Tribe *Smyrnieae*, independently recognized by Sprengel (1820) and W. Koch (1824), is one of the largest tribes recognized by Drude (1897—1898). It contains 29 genera distributed in both the Old and New World. When compared with the other two tribes bearing campylospermous fruits, e. g. *Caucalideae* and *Scandiceae*, *Smyrnieae* is quite artificial (Shneyer et al., 1992). Nevertheless, it has been adopted in such great «floras», as «Flora of the USSR» (Шишкин, 1950) and «Flora Reipublicae Popularis Sinicae» (Shan, Sheh, 1979). M. Pimenov and M. Leonov (1993) recognized 52 genera with 330—340 species in the tribe, whereas others, recognized fewer. For example, G. Bentham (1867) transferred *Magydaris*, *Cachrys*, and *Prangos* to tribe *Seseleae* W. D. J. Koch subtribe *Cachrydeae* (*Cachrydinae* Meissn.). Koso-Poljansky (1916), taking an extreme view, recognized only *Prangos*, *Conium*, and *Smyrnium* in *Smyrnieae*, but also erected several new tribes (such as *Lecokieae* Koso-Pol., *Magydareae* Koso-Pol., and *Hippomaranthreae* Koso-Pol.). More recently, K. Rechinger (1987) treated *Smyrnieae* in a narrow sense, including only *Smyrnium* and *Smyrniopsis* (which, according to our data, are not very closely related). Serotaxonomic investigations have shown clearly that the genera of tribe *Smyrnieae* do not form a monophyletic group (Shneyer et al., 1992). In fact, they comprise at least five independent and not very closely related groups, with the largest among them being the *Prangos* group and the *Physospermum—Pleurospermum* group. In our investigation, *Smyrnieae* Spreng. emend Drude were represented by the following taxa: *Prangos pabularia*, *Smyrniopsis aucheri*, *Conium maculatum* L. *Physospermum cornubiense*, and *Smyrnium olusatrum* L. They are widely dispersed in our phylogenetic trees. The closest relative to *Prangos* appears to be *Ferulago*, a result in accordance with

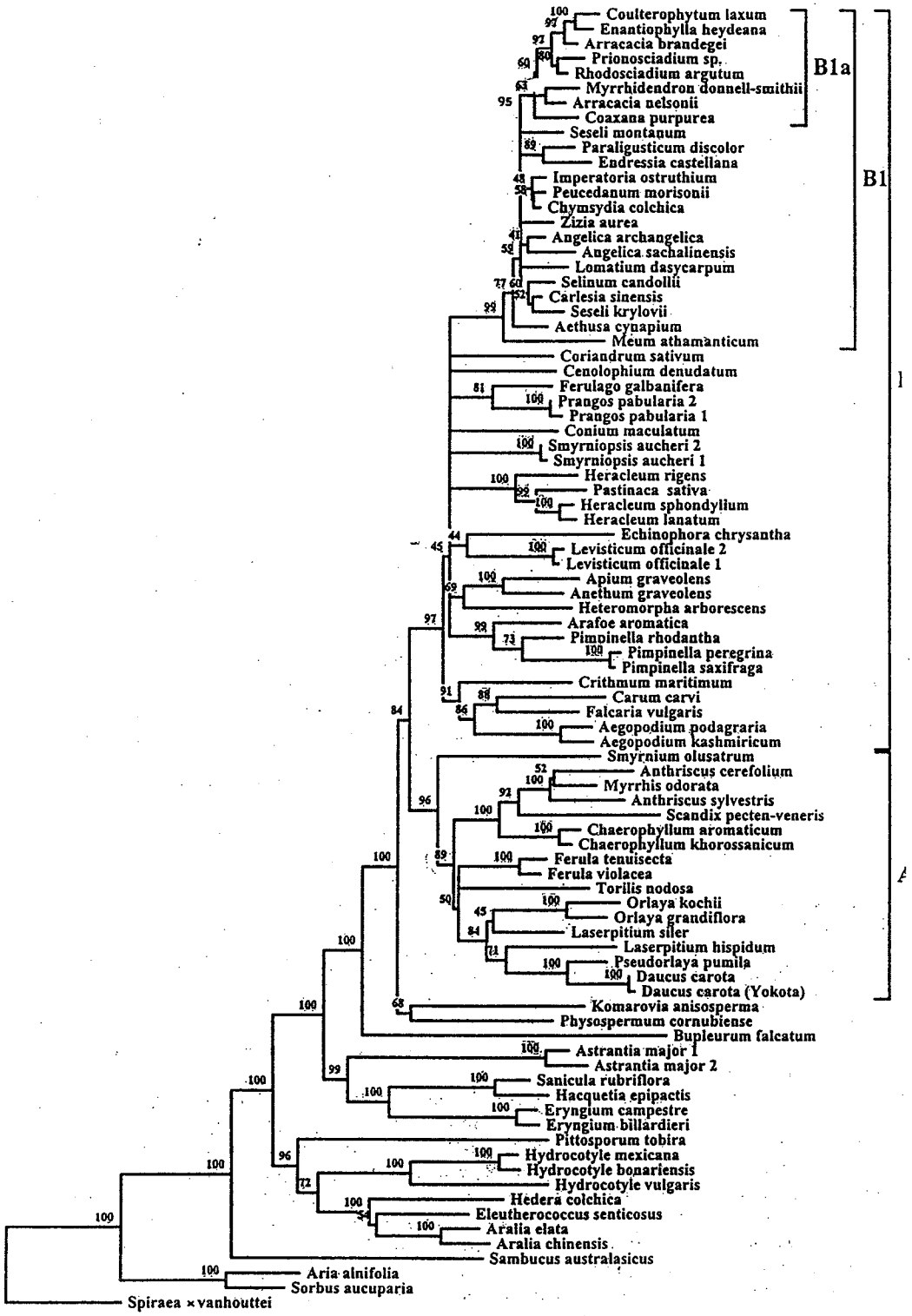

Fig. 3. 40 % bootstap proportion consensus neighbour-joining tree of *Umbelliferae* and related groups based on ITS1 + ITS2 sequences.

p-distance matrix with gaps taken into account was used for calculation. Each gap was counted as one nucleotide change irrespective of its length.

our immunochemical studies (Шнеер и др., 1991; Shneyer et al., 1992). This relationship is also supported, in part, on the basis of coumarin phytochemistry (Пименов, 1971; Murray et al., 1982). Two other members of tribe *Smyrnieae* are *Smyrniopsis* and *Conium*. These taxa form a clade far away from *Smyrnium*, the type genus of the tribe. The separation of *Conium* from *Smyrnium* finds support in earlier classificatory systems. For example, Cerceau-Larrival (1962) erected the independent tribe *Conieae* Cerceau-Larrival but, unfortunately, did not describe it according to the rules of the International Code of Botanical Nomenclature. In the immunochemical studies of V. Shneyer et al. (1992), *Conium* occupied an isolated position. It did however, demonstrate a low similarity with *Coriandrum* and *Bifora* (both *Coriandreae* W. D. J. Koch). This affinity was not confirmed in the present study using ITS sequences.

The genus *Levisticum*, previously referred to *Angelicinae* (Drude, 1897—1898), *Peucedaneae* (Koso-Poljansky, 1916), or *Capnophylleae* (Cerceau-Larrival, 1962), unites with *Echinophora* (fig. 1), albeit its weak bootstrap support. This association is also very surprising. *Echinohora* is a member of the small and isolated tribe *Echinophoreae* Benth., whose members are characterized by possessing an unusual umbel structure with a single sessile, fertille, hermaphrodite, central flower. The fruit is unusual in being enclosed by the hardened bracteoles and stalks of the male flowers. Most taxonomists (Bentham, 1867; Drude, 1897—1898; Cerceau-Larrival, 1962; Hedge, Lamond, 1973, etc.) recognized the tribe as isolated, whereas Koso-Poljansky (1916) referred it, without reason, to *Scandiceae—Scandicinae*. *Echinophoreae* consists of six genera, distributed mainly in the Mediterranean region (Hedge, Lamond, 1973, 1978). Our results indicate that *Echinophoreae* (at least, *Echinophora*, the type of the tribe) allies with representatives from *Smyrnieae*, *Apieae*, and *Peucedaneae*, despite its anomalous morphology. This result demonstrates that by placing undue reliance on some unusual morphological character, the taxonomy of the group can be confused.

The core tribe of *Apioideae*, and of all *Umbelliferae*, is the *Apieae* (*Ammineae* Spreng.). It is the largest tribe in the family. In this tribe, Drude (1897—1898) recognized 89 genera and divided them into two subtribes: *Carinae* Drude and *Seselinae* Tausch. Recently, Pimenov and Leonov (1993) recognized 189 genera and 1330—1400 species in *Apieae*. Because the tribe is so large and our sampling sparse, the relationships within it are unclear. Drude's subtribes are clearly unnatural and have been used infrequently in subsequent treatments of the family. In the past we (Лаврова и др., 1987; Pimenov, Leonov, 1993) recognized the small subtribe *Foeniculinae* Dumort., being approximately equivalent to «*Ligusticum*-Verwandtschaftkreis» of G.-H. Leute (1969, 1970), but now realize that this group cannot easily be separated from other *Apieae* even on the morphological ground. In present studies we have included such genera of subtribe *Foeniculinae* as *Paraligusticum*, *Endressia*, *Cenolophium*, *Arafoe*, *Ligusticum*, and *Meum*. In our study, *Paraligusticum* is allied with *Endressia*, and this clade is related to some *Peucedaneae*. *Cenolophium* occupies a rather isolated position, showing a weak relationship with *Prangos* and *Ferulago*. *Arafoe aromatica* (formerly *Ligusticum arafoe* Albov) appears to be allied closely with *Pimpinella*, and the location of *Meum* in the trees appears to be somewhat isolated. The unnaturalness of subtirbe *Foeniculinae* is demonstrated further using chloroplast DNA *rbc*L sequences (Kondo et al., 1996; Downie et al., 1998), where its members are widely distributed throughout the subfamily and were the genus *Ligusticum* is clearly polyphyletic.

Although we have included 19 genera of *Apieae* in our investigation, this number is quite small compared to the 189 genera listed in the tribe. This sparse sampling does not allow the phylogenetic structure of this tribe to be revealed. Nevertheless, it is clear that the genera we have sampled do not form a monophyletic group, being dispersed widely among other *Apioideae*. This is not surprising; the fruit characters defining this tribe are all rather unspecialized and, therefore, into this group has been placed all those species that cannot be placed comfortably into the other tribes.

It is apparent in figs. 2 and 3 that many *Apieae* genera show close affinities with members of tribes *Smyrnieae* and *Peucedaneae*. Other clades consist of *Apieae* repre-

sentatives only, such as the *Carum—Falcaria —Aegopodium* clade, and the *Pimpinella—Arafoe* clade. The relationships within each of these two clades, however, are surprising. For example, the predicted close relationship between *Aegopodium* and *Pimpinella* was not confirmed by our results.

Tribes *Scandiceae* Spreng. and *Caucalideae* Spreng. are maintained as distinct in our analyses. We have examined members of the former include *Anthriscus*, *Myrrhis*, *Scandix*, and *Chaerophyllum*, and members of the latter unclude *Daucus*, *Pseudorlaya*, *Orlaya*, and *Torilis*. Surprisingly, the genus *Ferula* (or at least, *F. tenuisecta* and *F. violacea*) may occupy a basal position in *Caucalideae*. The genus *Laserpitium* also appears to be nested within *Caucalideae*. In some ways, the relationships seen here in *Caucalideae* are parallel those of Heywood (1978) in showing an affinity between *Dauceae* and *Caucalideae*. In other ways, the relationships support the treatments of Drude (1897—1898) and Tamamschjan (Тамамшян, 1947) in suggesting a close relationship between *Laserpitium* and *Daucus*.

Since the time of E. Boissier (1844, 1872), *Smyrniopsis* was regarded ad belonging to tribe *Smyrnieae*. Rechinger (1987) treated it as the closest relative to *Smyrnium*, almost following Bentham's (1867) inclusion of *Smyrniopsis* into *Smyrnium*. With some hesitation, Koso-Poljansky (1916) places *Smyrniopsis* near *Careae* subtribe *Carinae*, i. e., far away from *Smyrnieae*. S. Tamamschjan (Тамамшян, 1945) used carpological characters to demonstrate the heterogeneity of *Smyrnieae* but did not find an association for *Smyrniopsis* s. str. among Koso-Poljansky's tribes *Smyrnieae* s. str. and *Crithmeae*. She believed that *Smyrniopsis* might best be placed between *Crithmeae* and *Seselinae—Carinae*. This relationships was regarded as doubtful by N. Pervuhina (Первухина, 1947), because of the peculiar secretory system of *Smyrniopsis*, consisting of short cavities. In the immunochemical studies (Шнеер и др., 1991), *Smyrniopsis* appears to be one of the closest relatives to *Prangos*.

In our analysis, *Smyrniopsis* falls into a region of the tree that is poorly resolved (Cluster *B*; fig. 2). This cluster includes representatives of Drude's *Smyrnieae* (*Smyrniopsis*, *Prangos*, and *Conium*) and tribes *Apieae* (including the type genus of the tribe *Apium*), *Peucedaneae*, *Tordylieae*, *Coriandreae* and *Echinophoreae*. These tribes are not regarded traditionally as being closely related to *Smyrnieae*. In contrast, the other campylospermous tribes, *Caucalideae* and *Scandicieae*, are placed in cluster *A*. Our results serve to confirm the heterogeneity of tribe *Smyrnieae*, and the need for its radical reclassification.

From a morphological viewpoint, the members of tribe *Peucedaneae* appear to be more similar to one another than the members belonging to tribe *Smyrnieae*. This was confirmed, in part, by the immunochemical studies of Shneyer et al. (1995). *Peucedaneae* has been accepted by Koch (1824), A.-P. DeCandolle (1830), Bentham (1867) and Drude (1897—1898). Drude treated *Peucedaneae* in its broadest sense, recognizing three subtribes (*Angelicinae* Tausch, *Ferulinae* Drude, and *Tordyliinae* Drude) which were often regarded as independent tribes. We note here that Drude's nomenclature must be corrected. If we consider these three subtribes as separate tribes, their proper names are *Angeliceae* W. D. J. Koch, *Peucedaneae* Dumort., and *Tordylieae* W. D. J. Koch. However, if *Peucedanum* and *Angelica* are referred to the same tribe (as our ongoing studies seem to suggest), the tribal name *Angeliceae* must be given priority over the name *Peucedaneae* (Pimenov, Constance, 1985).

As just stated, the ITS data we have obtained also reveals an affinity between *Angelica* and *Peucedanum* s. str. Both of these genera fall within cluster *B1* (figs. 2 and 3). This cluster is well supported (with a bootstrap value of 99 %) in both this study and the study of Downie and Katz-Downie (1996). Resolution within this clade, however, is weak. In addition to these two genera, this group includes some genera closely related to *Angelica* (*Chymsydia*) or to *Peucedanum* (*Imperatoria*). It also includes a set of genera that has traditionally been treated as members of tribe *Apieae* (e. g., *Seseli* and *Paraligusticum*).

A number of New World genera (*Coaxana*, *Enantiophylla*, *Arracacia*, *Prionosciadium*, *Rhodosciadium*, *Coulterophytum*, and *Myrrhidendron*), endemic to Mexico and neighbo-

uring Central America, comprise a clade (identified as cluster *B1A* in figs. 2 and 3) with moderate bootstrap support. These taxa have been identified as monophyletic in two previous studies (Downie, Katz-Downie, 1996; Katz-Downie et al., 1998).

The genus *Ferula*, represented in our study by two species from different sections, allies unexpectedly with members of *Caucalideae* and *Scandiceae* in cluster *A*. *Ferula* has been traditionally classified in tribe *Peucedaneae*. The isolation of *Ferula* from other members of *Peucedaneae* has already been revealed using immunochemical distance data (Shneyer et al., 1995). In particular, *Ferula* is not close to *Ferulago*, as suggested by Drude (1897—1898), and our results support, in part, Cerceau-Larrival's (1962) placement of these two genera in distantly related tribes from different subfamilies. The placement of *Ferula tenuisecta* and *F. violacea* in cluster *A* is indeed a surprise; we will be studying these relationships further in a subsequent study.

Conclusions

Our analysis of 79 accession of *Umbelliferae*, representing 58 genera from primarily the Old World and from all three subfamilies, reveals the following.

1. Subfamilies *Apioideae* and *Saniculoideae* are each monophyletic and are sister taxa.
2. Subfamily *Hydrocotyloideae*, represented by only the genus *Hydrocotyle*, is more closely allied to *Araliaceae* than to *Apioideae* + *Saniculoideae*. As a result, the monophyly of *Umbelliferae*, as traditionally circumscribed, is dubious.
3. The majority of accepted tribes in subfamily *Apioideae*, including the largest tribes *Smyrnieae*, *Apieae*, and *Peucedaneae*, do not form natural groups.
4. Based on our analysis of these ITS data there is little resolution of relationships within *Apioideae*, with few exceptions. Large polytomies abound within *Apioideae*, resulting in more of a phylogenetic «shrub» than a phylogenetic tree.
5. The carpological characters traditionally used as the basis for *Umbelliferae* taxonomy, such as form of the endosperm ventral surface (campylospermy versus orthospermy) and the general outline of fruit cross section (dorsally compressed verses laterally compressed or not at all compressed), correlate very weakly or not at all to the results of our phylogenetic analysis. These morphological characters cannot be used as indicators of relationships at the tribal and subtribal levels.
6. As also observed in Katz-Downie et al. (1998), there is a good correlation between the results of immunochemical investigations of seed storage proteins and many of the groups inferred herein using ITS data.

Our results, as those of Downie and Katz-Downie (1996), Downie et al. (1996, 1998), Plunkett et al. (1996a, 1996b, 1997), and Katz-Downie et al. (1998), reveal that the taxonomy of *Umbelliferae* requires radical change. Drude's (1897—1898) system of classification for the family, now a century old, needs drastic revision, as do all other existing systems. It is clear that studies of morphology alone cannot serve to resolve relationships within the group; this will have to be achieved by our continued analyses of molecular data.

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РЕЗЮМЕ

Проведено определение последовательностей внутренних транскрибируемых спейсеров (ITS1 и ITS2) 18S-26S ядерной рДНК, выделенной из 79 видов 58 родов *Umbelliferae*, относящихся ко всем трем подсемействам зонтичных. Филогенетические деревья были построены на основании этих данных методом «ближайшего соседа». Полученные схемы отношений таксонов кардинально отличаются от всех ранее предложенных классификаций семейства. В целом филограмма имеет форму, скорее, куста, чем подлинного дерева. Монофилия семейства не подтвердилась из-за значительной дивергенции *Hydrocotyloideae* от подлинных зонтичных. *Hydrocotyloideae* (в настоящей работе представлены одним родом *Hydrocotyle*) ближе к *Araliaceae* и *Pittosporaceae*, чем к *Apioideae* и *Saniculoideae*. Монофилия двух последних таксонов подтверждена, но большинство триб *Apioideae* не оказались монофилетическими. Исключением являются только *Scandiceae*, *Caucalideae* и *Tordylieae*. Систематика семейства нуждается в радикальном пересмотре.