PHYLOGENY AND BIOGEOGRAPHY OF *HAMAMELIS* (HAMAMELIDACEAE)

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Abstract. Interspecific relationships and molecular divergence within *Hamamelis* were studied on the basis of sequences of the internal transcribed spacers (ITS) of nrDNA, *trn*L-*trn*F intergenic spacers and the *mat*K gene of cpDNA, and the nuclear gene GBSSI *(waxy)*. Phylogenies based on the four data sets were congruent, and the combined analysis produced a well-supported pattern of relationship among the species. The North American species, *Hamamelis virginiana*, *H. mexicana,* and *H. vernalis*, formed a robust clade with *H. virginiana* basal. This suggests that *H. vernalis* and *H. mexicana* are not relicts, as previously supposed. The Japanese species, *H. japonica*, is more closely related to the North American species than to the Chinese species, *H. mollis*, which is consistent with leaf morphological characters. This biogeographic pattern is congruent with that seen in several other plant groups and is consistent with a series of vicariance events possibly involving Beringian exchange between Asia and North America.

Keywords: *Hamamelis*, biogeography, phylogeny, ITS, *trn*L-*trn*F spacer, *mat*K, *waxy*.

INTRODUCTION

The Hamamelidaceae includes 31 genera and more than 100 species. *Hamamelis* is one of only two genera in the family that are intercontinentally distributed and exhibit the classic disjunction pattern between eastern Asia and eastern North America (Boufford and Spongberg, 1983).

The monophyly of *Hamamelis* is supported by a suite of probable morphological synapomorphies, such as semi-palmate leaf venation, strictly 4-merous flowers, and strap-shaped petals (Mione and Bogle, 1990), as well as by molecular evidence (Li, 1997). Phylogenetic analyses based on nuclear and chloroplast DNA sequences indicate that *Hamamelis* belongs to the Hamamelidoideae and is sister to a Fothergilleae clade (Li, 1997; Shi et al., 1998; Li et al., 1999).

There are four to six species of *Hamamelis*, depending on taxonomic treatment (Bradford and Marsh, 1977; Chang, 1979). *Hamamelis mollis* is widely distributed in at least seven provinces of central and southern China (Chang, 1979; Zhang and Lu, 1995). *Hamamelis japonica* is common in mountain forests of southern Japan (Sargent, 1890). *Hamamelis virginiana* L., the common witch-hazel, is the most widely distributed *Hamamelis* species in North America. Its distribution ranges from Canada to Florida and the Gulf coast, and from the Atlantic coast to Wisconsin, Iowa, Missouri, eastern Oklahoma, and eastern Texas (Bradford and Marsh, 1977). *Hamamelis vernalis* Sarg. occurs in the interior highlands of Missouri, Arkansas, and eastern Oklahoma (Gleason, 1922; Ernst, 1963; Weaver, 1976; Bradford and Marsh, 1977; Elias, 1980). *Hamamelis mexicana* Standl., which is sometimes treated as a variety of *H. vernalis* (Standley, 1937), has been collected in the mountains of northeastern Mexico.

Disjunct distributions of closely related plant species in the Northern Hemisphere have long attracted the attention of plant systematists and biogeographers (Boufford and Spongberg, 1983; Tiffney, 1985a,b; Crawford and Lee, 1991, 1992; Wen and Jansen, 1992; Wen and

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Zimmer, 1994; Sang et al., 1994, 1995; Xiang et al., 1994; Lee et al., 1996; Wen, 1999). As for *Hamamelis*, Li et al. (1997) studied genetic divergence and interspecific relationships of *Hamamelis* using sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA; they found that the Chinese species *H. mollis* was basal in the genus and that the North American species were closely related to the Japanese species *H. japonica*. However, these relationships were not strongly supported. A similar study was conducted by Wen and Shi (1999), who sampled two individuals each of *H. japonica*, *H. mollis*, and *H. virginiana* and found little intraspecific variation in the nrDNA ITS sequences. The results were largely consistent with Li et al. (1997), but again relationships were poorly resolved. As Wen and Shi pointed out, more evidence is needed to understand the phylogeny and biogeography of *Hamamelis*.

In this study we use four regions of sequences to estimate interspecific relationships in *Hamamelis*. Specifically, we examined two nuclear regions, ITS and GBSSI (globule-bound starch synthesis isomerase, or *waxy*), and two chloroplast regions, *mat*K and the *trn*L-*trn*F spacers.

Materials and Methods

As shown by Wen and Shi (1999),there is little intraspecific ITS sequence variation in *Hamamelis*. The other three markers were all less variable among species than ITS, implying that intrapecific variation should not be an issue (see results); therefore, we used one accession to represent each of the five species.

Fresh leaves of three species of *Hamamelis (H. japonica*, *H. mollis,* and *H. vernalis)* were collected from cultivated plants in the Arnold Arboretum. *Hamamelis virginiana* was collected on the University of New Hampshire (UNH) campus at Durham, New Hampshire, and *H. mexicana* was provided by Rob Nicholson of Smith College in Massachusetts. All vouchers are deposited in the Hodgdon Herbarium (NHA) at UNH (Table 1).

Total genomic DNAs were extracted from fresh leaves or buds according to the protocol of Doyle and Doyle (1987). Polymerase Chain Reaction (PCR) amplification and sequencing of the ITS region, the *mat*K gene, and the

TABLE 1. Species, sources (all vouchers deposited in UNH), and GenBank accession numbers.

SPECIES	COLLECTOR (S)	SOURCE	GENBANK ACCESSION # ITS1/2	*WAXY*	*MAT*K	*TRN*F-*TRN*L
Hamamelis mollis Oliv.	C. Strand/J. Li	Arnold Arboretum, Massachusetts	AF015658	AF248628	AF248619	AF248622 AF015659
Hamamelis japonica Sieb. et. Zucc.	C. Strand/J. Li	Arnold Arboretum, Massachusetts	AF248613	AF248626	AF248617	AF248620 AF248614
Hamamelis virginiana L.	J. Li	University of New Hampshire Campus	AF015656	AF248630	AF013046	AF248624 AF015657
Hamamelis vernalis Sarg.	C. Strand/J. Li	Arnold Arboretum, Massachusetts	AF015655	AF248629	AF013047	AF248623
Hamamelis mexicana Standl.	R. Nicholson	Mexico. Cultivated at Smith College, Massachusetts	AF248615	AF248627	AF248618	AF248621 AF248616
Fothergilla major Lodd.	J. Li	University of New Hampshire Campus	AF015425	AF248631	AF013045	AF248625 AF015426

GBSSI gene are described in detail in Li, Bogle, Klein, and Pan (1997), Li et al. (1998), and Li and Donoghue (1999), respectively. PCR amplification of the *trn*L-*trn*F intergenic spacer was conducted following Taberlet et al. (1991), and sequencing procedures were as described in Li and Donoghue (1999).

All sequences were readily aligned manually, and the resulting data matrix was analyzed using the exhaustive search algorithm in PAUP* (version 4.0b2; Swofford, 1999). Gaps were treated as a fifth state. *Fothergilla* was included in the parsimony analyses for rooting purposes; phylogenetic analyses using both nuclear and chloroplast DNA sequences have shown that *Hamamelis* is sister to the Fothergilleae, within which *Fothergilla* is a basal branch (Li, 1997; Shi et al., 1998; Li et al., 1999). Sequence divergences were calculated using the Kimura-2 parameter method implemented in PAUP*. To evaluate clade support, we conducted 1000 replicates of bootstrap analysis (Felsenstein, 1985) and complete decay analysis (Bremer, 1988; Donoghue et al., 1992) using PAUP*. The aligned sequence matrix is available from the first author and in TreeBASE (http://phylogeny.harvard.edu/treebase; accession number M724). Individual sequences are available in GenBank.

RESULTS

Sequence Characteristics

Internal transcribed spacer 1 (ITS-1) sequences were 270 bases long in all species except *Hamamelis mollis* with 271 bases. Spacer 2 (ITS-2) sequences were 235 bases long in *H. virginiana*, 236 in *H. japonica* and *H. mexicana*, and 237 in *H. vernalis* and *H. mollis*. The aligned sequences were 512 bases long with seven indels, six of one base and one of two bases. ITS sequence divergences ranged from 0.4% to 3.0%. In total, there were 54 variable ITS characters, 11 of which were parsimony informative (Table 2). We note that our ITS sequences differ from Wen and Shi's (1999) in a 55-base indel in the ITS-1 region.

Sequences of the *mat*K gene in all *Hamamelis* species were 1515 bases in length. There were 22 variable characters, only two of which were parsimony informative (Table 2).

The portion of the *waxy* gene sequenced in this study extended from exon 9 to exon 12, including three introns and two exons. The sequence alignment produced a matrix of 734 characters, 34 of which were variable and 4 of which were potentially informative. There were seven indels in the data matrix, none of these parsimony informative. Sequence divergences of *waxy* ranged from 0.28% to 1.4% (Table 2).

TABLE 2. Sequence characteristics of the four DNA regions in *Hamamelis*.

CHARACTERISTIC	NRDNA ITS	PARTIAL WAXY	*MAT*K	*TRN*L-*TRN*F SPACER
Length (bp)	505–508	726–734	1515	381–383
Alignment sites	512	734	1515	385
Indels	7	7	0	4
G + C content average (%)	63	39	35	35
Variable site (%)	8.4	3.4	1.4	2.1
Informative site (%)	1.8	0.5	0.1	0.3
Divergence (%)	0.4–3.0	0.3–1.4	0.1–0.7	0–1.6
Consistency index	0.95	0.97	1.00	1.00

The length of the intergenic spacer between *trn*L and *trn*F ranged from 381 to 383 bases; the alignment produced a data matrix of 385 characters and required four indels, none of which were phylogenetically informative. Sequence divergences ranged from 0% to 1.6%. Among the 13 variable characters only 1 was phylogenetically informative (Table 2).

We also sequenced the *trn*L intron for *Hamamelis* species in accordance with Taberlet et al. (1991) but found no variation.

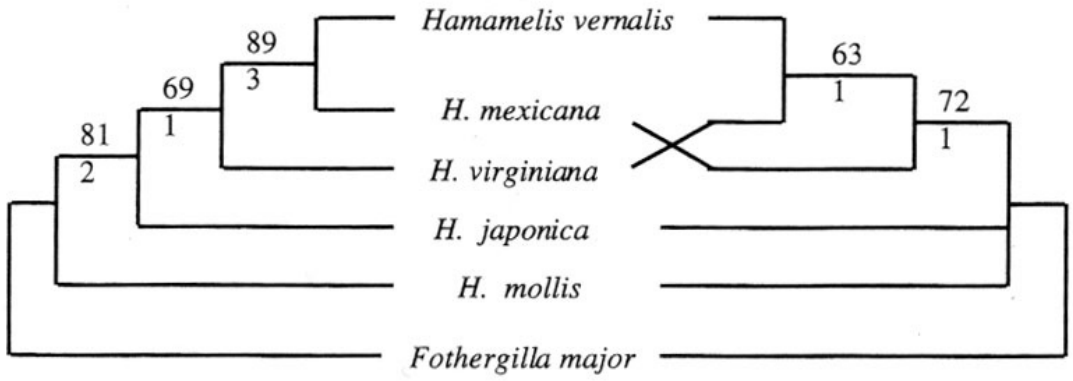
Phylogenetic Relationships

An exhaustive search based on the ITS sequences generated a single most-parsimonious tree of 55 steps with a consistency index of 0.95 (Fig. 1a). *Hamamelis mollis* is basal, followed by *H. japonica*, which is sister to a clade of three New World species. In the New World clade, *H. virginiana* is sister to a clade consisting of *H. vernalis* and *H. mexicana*.

The *waxy* gene sequence analysis produced two most-parsimonious trees of 36 steps and a consistency index of 0.97 (Fig. 1b). This analysis did not resolve relationships among *Hamamelis japonica*, *H. mollis*, and the New World clade. Within the New World clade, *H. vernalis* was weakly united with *H. virginiana*.

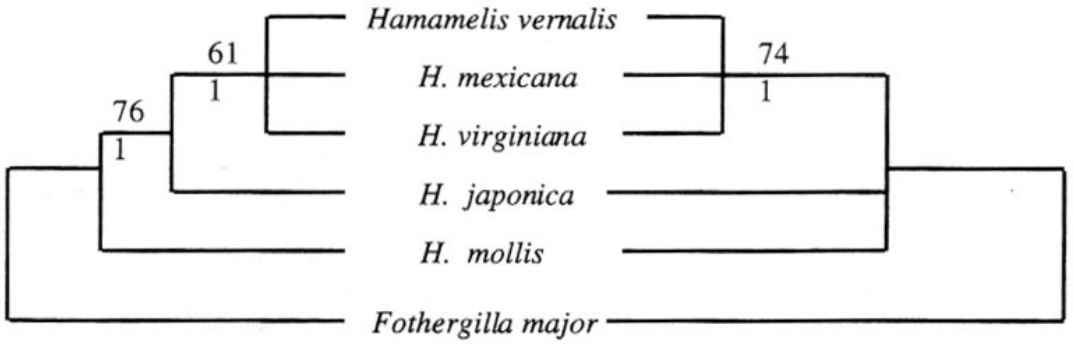
Trees based on the two chloroplast DNA regions were congruent, though the *trn*L-*trn*F spacer phylogeny was less resolved than the *mat*K tree (Fig. 1c,d).

The incongruence length difference (ILD) test (Faris et al., 1994; see Mason-Gamer and Kellogg, 1996) implemented in PAUP* indicated that the four data matrices were congruent with one another (P values from 0.18 to 1.0). A combined analysis was conducted, resulting in a single shortest tree of 127 steps (Fig. 2) and a consistency index of 0.95.



a. ITS (1 tree, 55 steps, CI=0.95)

b. *waxy* (2 trees, 36 steps, CI=0.97)



c. *mat*K (1 tree, 22 steps, CI=1.0)

d. *trn*L-*trn*F spacer (3 trees, 11 steps, CI=1.0)

FIGURE 1. Phylogenetic trees of *Hamamelis* based on analyses of individual data sets. a, ITS; b, *waxy;* c, *mat*K; d, *trn*L–*trn*F spacer. Numbers are bootstrap percentages/decay indices. Clades with bootstrap values <50% are not labeled.

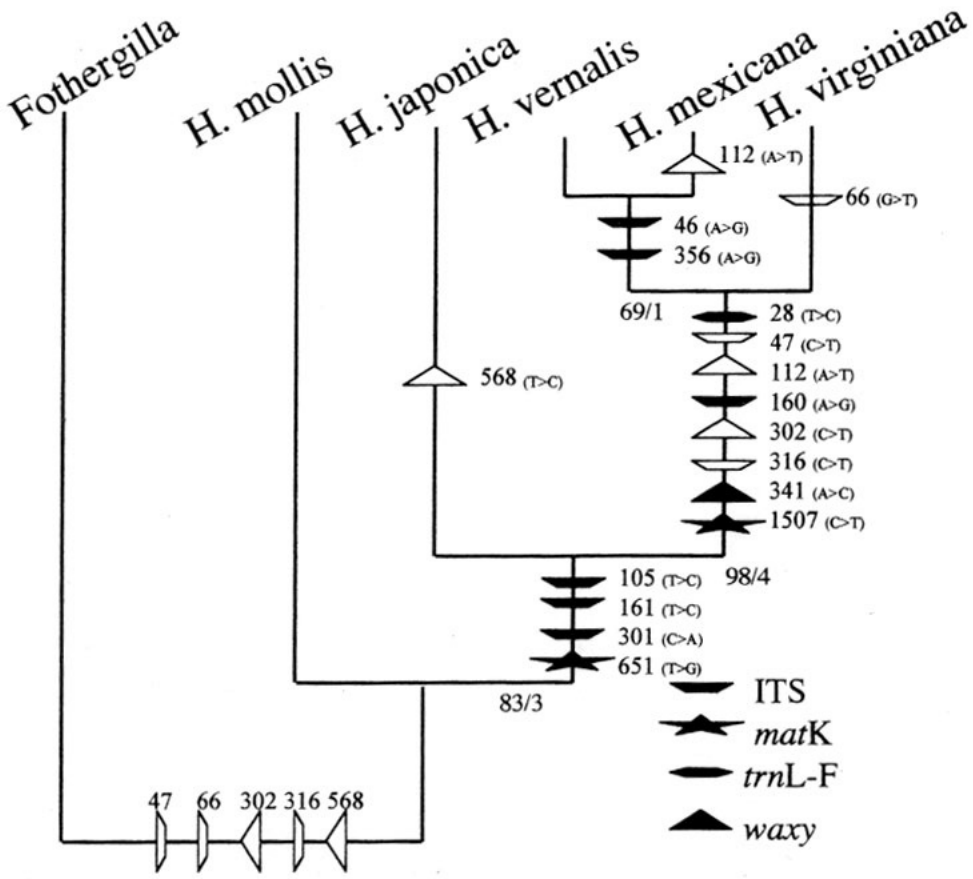


FIGURE 2. The single shortest tree for *Hamamelis* based on combined analyses of the four data sets (127 steps, consistency index = 0.95). Symbols represent ambiguous (open) and unambiguous (solid) informative sites from each data set under ACCTRAN optimization. Bootstrap percentages/decay indices are also given.

Relationships were the same as in the ITS phylogeny but with greater clade support.

DISCUSSION

Hamamelis species are widely cultivated as ornamentals throughout the temperate regions of the Northern Hemisphere, and many hybrids have been produced (Marquard et al., 1997). It is therefore reasonable to consider whether one or more *Hamamelis* species might have been derived through ancient hybridization events. We see no indication of this, since the same relationships are supported by both chloroplast and nuclear DNA sequences (Fig. 1).

The New World *Hamamelis* species form a well-supported clade, even though relationships within this group are not well resolved owing to differences between ITS and *waxy* data sets. The ILD test suggests that the two data sets are congruent (P = 0.18), which presumably reflects weak support for the relationship of *H. vernalis* and *H. virginiana* in the *waxy* gene tree (bootstrap value = 63%). In describing *H. mexicana*, Standley (1937) suggested that it might also be considered a variety of *H. vernalis*. Our ITS data and the combined analysis support the close relationship of these two taxa (Fig. 2).

The two east Asian species, *Hamamelis japonica* and *H. mollis*, do not form a clade; instead, *H. japonica* appears to be more closely related to the New World clade. The same relationships are found in several other groups, including *Viburnum* sect. Pseudotinus (Li and Donoghue, unpublished).

On the basis of the similarities of *Hamamelis vernalis* and *H. mollis* in flowering time and floral fragrance, Bradford and Marsh (1977) suggested that *H. vernalis* was a relict close relative of *H. mollis* and that *H. virginiana* might have been derived from ancestral *H. vernalis*. ITS data suggest a different scenario:

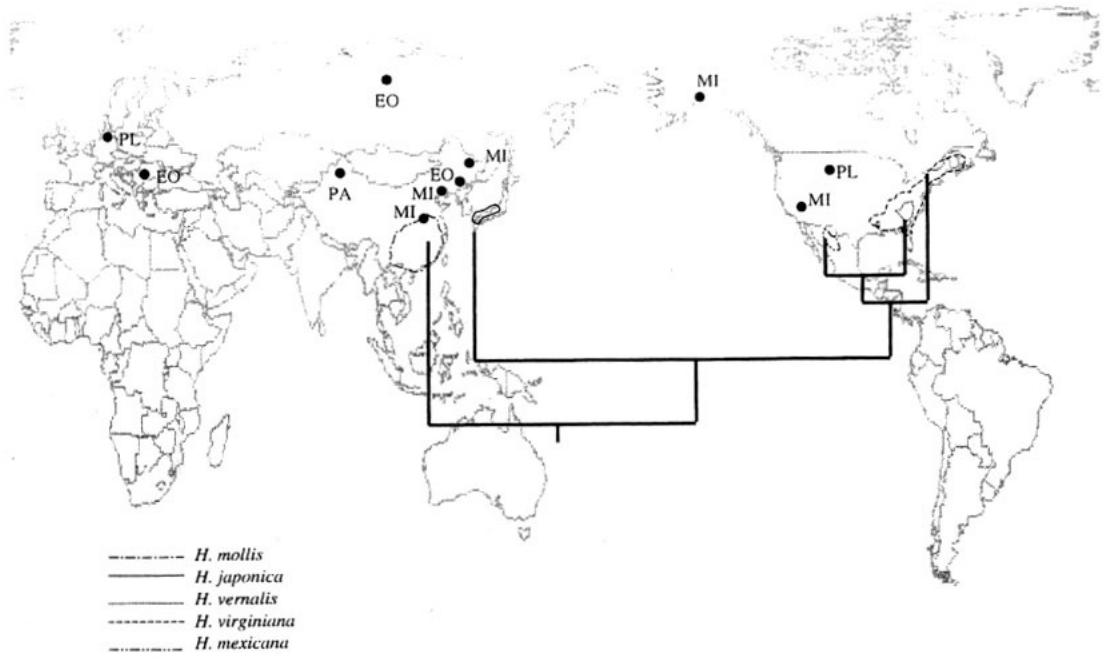


FIGURE 3. Map showing fossil record (solid dots; PA, Paleocene; EO, Eocene; MI, Miocene; PL, Pliocene), modern distribution, and phylogeny of *Hamamelis* species.

H. virginiana is basal among the North American *Hamamelis* and *H. vernalis* is most closely related to *H. mexicana*. Given the wide distribution of *H. virginiana* and the restricted ranges of both *H. mexicana* and *H. vernalis* (Bradford and Marsh, 1977; Standley, 1937), *H. vernalis* might best be interpreted as having adapted to gravelly beds and rocky banks of streams and highlands. Likewise, *H. mexicana* appears to be derived within the North American clade (Wen and Shi, 1999).

Morphological observations of *Hamamelis* species using both herbarium specimens in the Harvard University Herbaria and living collections in the Arnold Arboretum of Harvard University indicate that leaf characters also support a close relationship of *H. japonica* and the North American species. In the Chinese *Hamamelis mollis*, young twigs are grayish tomentose, leaves are orbicular and distinctly serrate, leaf bases are strongly cordate, and abaxial surfaces of mature leaves are heavily tomentose. In contrast, in the other *Hamamelis* species, young twigs are rarely grayish tomentose; leaves are obovate (or rarely orbicular in *H. virginiana*); leaf margins are mostly crenate or slightly wavy; leaf bases are strongly cuneate (*H. vernalis*), slightly cuneate (*H. japonica*, *H. virginiana*), or occasionally asymmetric (*H. virginiana*); and abaxial leaf surfaces are glabrous or only rarely pubescent (*H. virginiana*).

Fossil leaves of *Hamamelis* have been found from the Paleocene in both the Old and New Worlds and appear most similar to the leaves of *H. japonica* and *H. virginiana* (Brown, 1962; Wolfe, 1966; Guo et al., 1984). Therefore, the split between *H. mollis* and the clade including *H japonica* and the New World species had occurred by the Paleocene.

The modern distribution of *Hamamelis* is disjunct and much narrower, as compared with the wide Tertiary distribution implied by the fossil record (Fig. 3) (Berry, 1923; Axelrod, 1966; Hedlund, 1966; CPCEC, 1978; Sun, 1979; Muller, 1981; Smiley and Rember, 1985; Stuchlik and Shatilova, 1987; Gregor, 1990; Taylor, 1990; Endress and Friis, 1991; Li, 1995). This suggests that the modern distribution pattern of *Hamamelis* between eastern Asia and North American is a relict disjunction, which is consistent with previous studies of disjunct plant groups of the two regions (Wood, 1972; Wolfe, 1975; Tiffney, 1985b; Hoey and Parks, 1991; Lee et al., 1996). It has been proposed that there were two main exchange routes of Tertiary plants around the Northern Hemisphere, involving Atlantic and Pacific

land connections (Tiffney, 1985a,b). Reports of *Hamamelis* fossils along the Pacific land bridge suggest a Beringian exchange route between Eurasia and North America (Fig. 3). However, the existence of several fossils in Europe leave open the possibility of exchange across the North Atlantic. Low levels of molecular divergence suggest relatively recent divergences, which favors the Beringian route.

Each of the four data sets provided only a small number of informative sites, among which the ITS sequences contributed the most. Only through the combination of several data sets has it been possible to obtain a robust estimate of phylogenetic relationships. Both the North American clade and the clade that includes the Japanese species and the North American clade are supported by four unambiguous changes (Fig. 2). In each case, support is derived from both chloroplast and nuclear sequences. Until more variable markers are identified, we suspect that the combination of different data sets will be necessary to resolve species relationships in many plant groups.

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