ON THE TAXONOMIC POSITION OF EUCOMMIA ULMOIDES OLIV.  
(EUCOMMIACEAE)  

by  

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1. INTRODUCTION.

During an anatomical examination of *Eucommia ulmoides* Oliv., performed at the request of Dr L. G. M. Baas Becking, on behalf of the Technical Division of the Central Committee for Applied Science, a survey of the literature showed that many divergencies of opinion exist as to the relationship of the monotypical natural order of the *Eucommiaceae* with other families. The anatomical evidence obtained, might, together with morphological characters, shed more light on this relationship.

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*Eucommia ulmoides*, the sole species of the sole genus of the family, is a native of China, where it is found in the provinces of Hupeh, Szechuan, Anhwei and Chekiang. According to the first collector, Henry, the plant is occasionally cultivated in the districts of Chang-Yang and Patung of the province of Hupeh, chiefly because of the alleged medicinal value of the bark. Probably the plant grows wild in the Northern district of Fang. Parges mentions the plant as cultivated in East Szechuan in the district of Tehen-Ke'ou-Tin. Localities in the provinces of Anhwei and Chekiang are given by Hsen-Hsu Hu and Woon-Yung Chun (11). Parkin (18) states that the plant was first introduced in Europe (France) in about 1890. From France the plants arrived at Kew in 1897 and were further distributed from there.

2. TAXONOMIC POSITION.

The taxonomic position of *Eucommia* has, since its first description, undergone many changes. The original material lacked flowers and its
description by Oliver (15) did not lead to a definite placing of the genus, both the Ulmaceae and the Euphorbiaceae being suggested as related. The latter family was again mentioned by Weiss (32), the former by Harms (8).

In 1895, Oliver gives the first description of both the male and the female flowers. The Ulmaceae are not mentioned as a related family, but under the influence of a written communication by Baillon who claimed the identity with Euptelea Davidiana Baillon, Oliver classed Eucommia under the Trochodendraceae (sensu Prantl). Oliver, however, did not recognize the alleged identity of the two genera mentioned, since Euptelea lacked latex and since its flower structure essentially differed from that of Eucommia. Yet, he considered both genera sufficiently related to insert them in the same family.

The Trochodendraceae (sensu Prantl), as segregated from the Magnoliaceae, now contained the genera Trochodendron, Tetracentron, Euptelea, Eucommia and Cercidiphyllum. According to Oliver (16) the first two genera, characterized by their more or less connate carpels and not apiculate anthers, could be combined so as to form a section. The other three genera then should form another section characterized by "free carpels and elongate and apiculate anthers". This classification, however, is in contradiction with Oliver's own words. In his description of 1891 he states "pistillum dimerum syncarpicum" and in 1895: "solitary ovary with bifid stigma, presenting every appearance of a syncarpous dicarpellary pistil". The reasons for Oliver's classification remain, therefore, a mystery.

In his description of the fruit, Oliver in 1891 mentions the words "in the cell of the fruit, which survives and includes the solitary seed", by which it is suggested that one of the carpels is abortive. This indeed appeared to be true.

Harms (7) proposed the segregation of Tetracentron from the Trochodendraceae. For the remaining four genera he followed Oliver's erroneous classification, in which Eucommia was placed in the Eupteleoideae, the carpels of which were regarded to be free. Eucommia should possess a gynoeceum which is bifid at the top.

The error was first discovered by Solereder (28) who re-investigated the gynoeceum and showed it to consist of two connate carpels, one of which is abortive. The reason for Solereder's investigation was probably the supposed relationship of Euptelea, Eucommia and Cercidiphyllum with the Hamamelidaceae (cf. Oliver 16) as claimed by Baillon. Accordingly, Solereder transferred Cercidiphyllum and Eucommia to the Hamamelidaceae.

Van Tieghem (29) could not entirely agree with Solereder's point of view. Not only Eucommia and Cercidiphyllum but also Euptelea should be segregated from the Trochodendraceae. The three genera should belong to three separate families, having little in common.

In the recent handbooks mainly two opinions exist as to the relationship of the Eucomniaceae.

1. The Hamamelidaceae are still considered the closest ally, as is in accordance with the views of Baillon and Solereder, to whom may be
added the names of Schneider (26), Wettstein (33a), Hutchinson (12), Engler (3 and 4), Engler-Diels (5) and Komarow (13).

2. Oliver’s original suggestion, according to which the Ulmaceae should be the nearest of kin, was supported by Harms (8), although he did not mention the source of this opinion. Wettstein (33b), referring to Harms (8) and finally also Pulle (23) agree with this conclusion. Additionally, a paper by Tippo (30) on the comparative anatomy of the secondary xylem and the phylogeny of the Eucommiaceae may be mentioned, although this was unaccessible under the present circumstances.


In order to re-examine the relationship of the Eucommiaceae, morphological and anatomical characters of the family were again compared with those of supposedly related families. Part of these characters are taken from the literature, part of them are founded on my own observations. A survey of these characters is given in the accompanying table. By means of the keys in Engler-Prantl’s "Natürliche Pflanzenfamilien", genera were looked for, which showed the closest relation with Eucommia. As far as possible, dried material of these genera was examined. Concerning the classification of the orders, Von Wettstein’s "Handbuch der Systematischen Botanik" (33b) was followed.

4: Explanation of certain characters of the Eucommiaceae mentioned in the table.

The phyllotaxis is mentioned by Oliver (15) as distichous. We find the same opinion in the monograph by Harms (8) and in various handbooks. The accompanying figure (Fig. 1), representing a cross-section through a terminal bud a little above the level of the vegetation point, shows, however, that the phyllotaxis is originally rather alternate, viz. $\frac{2}{5}$ with an inclination towards $\frac{3}{5}$. On full-grown lateral shoots, the leaves often seem to be distichous. Close inspection of the position of the axillary buds, however, shows that these buds are actually arranged in a spiral so that this is a case of plagiotropic shoots rather than of a truly distichous phyllotaxis.

Harms gives for the length of the leaves 6—8 cm. This is only true for the small fertile shoots. For full-grown leaves Oliver mentions 15—17.5 cm. In sterile branches I observed leaves as long as 19.5—25 cm.

The male inflorescence is most probably a cyme. However, this can only be conclusively stated by an ontogenetic study.

The getah-percha containing latex elements of Eucommia are treated in another paper (lit. 31). It may suffice to mention here that they are unbranched and that they start as unicellular tubes below the stem vegetation point. They originate in about the same way as mentioned by Zander (34) for latex elements of other plants, although they are differing from these in many respects.
The possibility of this relation has been brought forward by Oliver in 1891. This author states that "The fruit and the general aspect of the specimens at once suggest Ulmaceae". Harms (8) mentions these arguments anew and draws the attention to the similarity of the leaf venation. From the table appear, moreover, several other characters Eurcommia has in common with the Ulmaceae, such as: flowers in axillary cymes or the female flowers solitary in the leaf axils; flowers mostly unisexual; the syncarpous gynoeceum consists of two carpels, only one cell of which being developed, the other being usually abortive; the stigmata papillate on the inner surface; shrubs or trees from the tropics of subtropics also occurring in China, with simple, often asymmetrical and serrate leaves; leaf epidermis often with cuticular folds and the stomata sometimes with auxiliary cells; collenchyma often occurs in the bark, suberization subepidermal e. g. in Ulmus, epidermal in Eurcommia; secondary phloem often interspersed by selerenchyma bands.

Important anatomical characters are further the presence of nearly exclusively simple vascular perforations, of libriform with bordered pits and of unicellular conical hairs, the wall of which may be either calcified or silificied in toto or may possess calcified thickenings.

On the other hand, there are important objections to combine
Eucommia with the Ulmaceae. Oliver has already mentioned that Eucommia shows no trace of a perianth even in the very young stages in the winter buds. The leaves possess no stipules. The Ulmaceae have only one ovule in the sole cell, while Eucommia possesses a collateral or nearly lateral pendulous abortive second ovule.

To this we may add the following differing characters. In Ulmus the leaves are claimed in literature to be distichous, as is already shown by the first set of leaves developing after the cotyledons (Lubbock, 14); however, the topmost leaves of the flowering branches are often placed in a spiral; the styles are linear and albumen is mostly absent; the Ulmaceae do not show latex; cells containing mucilage occur in the leaf and in the bark of e.g. Ulmus fulva Michx., the "Slippery Elm" of Canada. Priemer (22) studied the ontogeny of these cells and showed their cystolith nature in the foliar epidermis. In the mesophyll and in the bark they are apparent by their size but they are never tubiform. Neither in their contents, nor in their ontogeny, these cells, therefore, show much relation to latex elements.

Particularly the following genera were compared with Eucommia: of the Ulmoideae, Ulmus and Holoptelea and of the Celtioideae, Celtis, Pteroceltis, Zelkowa and Aphananthe.

Of these genera, Ulmus is undoubtedly the closest relative, as appears from the characters mentioned above. Moreover, the embryo is straight and the cotyledons are flat. On the other hand, Ulmus is characterized by bisexual flowers, possessing a perianth, while Eucommia has unisexual flowers without a perianth. Of the dried material examined, it appeared that Ulmus parvifolia Jacq. shows the closest resemblance. The specimen available was hailing from Sikkim, but according to the literature this species is also found in China and Japan. Our common Ulmus campestris L. was also compared, but of this the fruit is distinctly smaller.

Holoptelea is more different from Eucommia by its entire leaves, the cotyledons are longitudinally folded and the area is India and Ceylon. This genus has, like Ulmus, mostly bisexual flowers, but unisexual ones are also known. The fruit, however, shows a strong resemblance with that of Eucommia. Aphananthe agrees with Eucommia in its unisexual flowers, the male ones arranged in cymes, the females solitary. The seed is provided with a thin layer of endosperm and the cotyledons are narrow. The leaves are pinnately nervet and serrate. Triplinerve leaves, however, are occurring likewise and so are stipules which are lacking in Eucommia. The fruit possesses two sessile stigmata but for the rest it is different in that it is not winged and in that its pericarp is fleshy. In addition, the cotyledons are rolled up. Some slight general similarity with Eucommia was found in dried material of Aphananthe aspersa (Thunb.) Engler from China (Kwantung).

With Zelkowa, a genus represented in southern China, Eucommia has the unisexual flowers in common, as well as the serrate pinnately nervet leaves which are, however, not acuminate in Zelkowa. On the other hand, Zelkowa possesses a perianth. The fruit is drupaceous and has a short excentric style. Endosperm is wanting and the cotyledons are broad and lobed. Finally, stipules are found in this genus.
In *Pteroceltis* and *Celtis* triplinerve leaves are still more common than in *Aphananthe*. They are, moreover, characterized by thorns. Both genera have the flowers either unisexual or bisexual; a perianth is extant and the cotyledons are broad. As to the fruit, *Celtis* has an unwinged drupe; in *Pteroceltis* the fruit is winged and, according to the literature, it is recalling that of *Ulmus*. No material of the last-named genus, however, was available for examination.

6. Relation with the Moraceae.

*Eucommia* agrees with the Moraceae in the following points. In the last-named family the flowers are often dioecious, and in unisexual flowers which are often arranged in cymose inflorescences, the perianth is sometimes lacking. The pistil consists of two connate carpels both or one of which may be developed. The ovary is usually 1-celled, more exceptionally 2-celled. The stigmates are papillate. Albumen may be extant or wanting. The Moraceae comprise trees or shrubs with usually simple leaves, also occurring in tropical and subtropical Asia.

Collenchyma is found in the cortex; the secondary phloem contains sclerenchyma. In *Morus* the xylem vessels have spirally thickened walls and a simple vascular perforation. The wood rays are sometimes uni- or biseriate. In addition, latex elements are often found as well as unicellular hairs, calciumcarbonate and silica.

On the other hand, the ovary cells contain only one ovule, the styles are usually developed and the fruit is not winged.

The phyllotaxis is claimed in literature to be distichous or decussate and stipules are always extant. Auxiliary cells are wanting in the stomata and the latex elements show a different way of originating as well as a different anatomy.

On account of the similar characters the genera *Taxotrophis* and *Streblus* were compared. Both are distinguished by dioecy; the ♀ flowers are often solitary, the ♂, however, are, in contradistinction to *Eucommia*, arranged in spikes or racemes.

*Taxotrophis* has an ovary with a bifid style which is originally apical but ultimately becomes lateral. The plants are trees and shrubs with serrate leaves. Differences from *Eucommia*, however, are that there is a perianth, that the cotyledons are broad and rolled up, that the fruit is not winged, and that there are axillary thorns as well as stipules.

*Streblus* is found in Malaysia and southern China. In this genus the perianth is surrounding the ovary. The cotyledons are unequal, one of them being large and bilobed, the other small.

Dried material of both genera shows a slight resemblance with *Eucommia*.

7. Relation with the Cannabaceae and the Urticaceae.

*Eucommia* is agreeing with the Cannabaceae regarding the ovary in unisexual flowers of dioecious species, as well as regarding the anatomical characters mentioned under the Ulmaceae and the Moraceae. In Cannabis the phyllotaxis is originally spiral.
Points of difference are the perianth, the single ovule, the capsule, the palmately nerved leaves and the stipules.

In the Urticaceae the stigmata are sometimes sessile and papillate. In some cases the leaves are spirally arranged. The single basal and atropic ovule, however, leads to the conclusion that in the Urticaleae the Urticaceae are undoubtedly the least related family in comparison with Eucommia. It is difficult to mention a genus which shows some direct relation with Eucommia. Perhaps those species of Memorialis from Malaysia may be quoted here which show a winged fruit but they are, for the rest, much different.

On the other hand, it may be stated that there are only few families in which the latex elements are so much resembling those of Eucommia as is the case in the Urticaceae and the Cannabaceae. In the two last-named groups unicellular and unbranched tubes are formed just below the vegetation point. This way of originating was first described for Eucommia by Weiss (32) and is, for the rest, only known in Cannabis and Humulus (Zander l.c.) and in Urtica and further in Vinca (Schaffstein 24). Yet, in Eucommia there is a point of distinction in that additional tubes are formed by the cambium and that they are also found in the roots.

8. Relation with the Euphorbiaceae.

With this family Eucommia has only little in common. It is true that in the table several characters have been printed in heavy type but these can as a rule not be said to be essential for the whole family, since most of them are occasional phenomena. The following characters may be considered evidential: plants dioecious, perianth sometimes none, two apical anatropic ovules in the cell, albumen extant, leaves alternate and mostly simple, stomata often with auxiliary cells, cortex with collateral phloem sometimes provided with sclerenchyma bands, xylem vessels with always simple and sometimes moreover with scalariform perforations. Latex elements are found in many Euphorbiaceae. However, they are either multicellular vessels or unicellular tubes. In the last-named case they originate in a definite number in the embryo (Chauveaud 1, Schaffstein l.c.) and they are branched. In these respects the latex elements of Eucommia, therefore, show no relation with those of the Euphorbiaceae.

Weiss (l.c.) makes the remark that if Eucommia, as is the opinion of Oliver (1891), should be related to the Euphorbiaceae, it would have to be placed in the Crotonoideae, since latex elements are wanting in the Phyllanthoideae. More exactly, its place would be near the Johannesieae or, if we should lay as much stress on the structure of the latex elements as is done by Pax (19), between the Johannesieae and the Hippomaneae. According to Chauveaud’s classification of latex elements (c.f. Weiss, l.c. page 253), however, we might associate Eucommia with either Cannabis, Urtica or Vinca. It must be stated, however, that Weiss himself considers these suggestions very doubtful on account of the fact that the structure of the flower of Eucommia was not yet known.

From the way of originating and the anatomical structure of the latex elements in Eucommia it is obvious that a relationship with the
Johannesieae and the Hippomaneae in this respect can hardly be considered.

On comparing the morphological characters of the two groups mentioned with those of Eucommia we meet with the following resemblances and differences. Johannesia, Annesijoa and Hevea are distinguished by compound leaves with entire leaflets. They are monoecious, a calyx and a corolla are found in the two first-named genera; in Hevea only a calyx is extant. In all three genera the filaments are connate. The ovary is 3-celled in Annesijoa and Hevea, 2-celled in Johannesia. It appears from this enumeration of characters that the Johannesieae are very much different from Eucommia.

The Hippomaneae show some more resemblance in their general characters (c. f. Pax, 20). The following points are supporting the relationship: woody plants, rarely undershrubs, leaves mostly alternate, provided with glands at the teeth, unicellular latex tubes, stomata with two auxiliary cells lying parallel to the aperture, unicellular hairs rarely extant, vessel perforation simple, perianth always apetalous, entirely wanting in Adenopeltis (this is the only essential point of resemblance between Adenopeltis and Eucommia).

The following points are those in which Eucommia is differing from the Hippomaneae: The latter group has a different leaf shape, small caducous stipules and extrafloral nectaries. They are monoecious and possess terminal inflorescences, stamens mostly 3—2, pistil with 3—2 carpels, fruit a dehiscent capsule of which the central axis is remaining, latex tubes unicellular and branched.

Reduction of the ovary to one cell with 3—2 short bifid styles is found in the Crotoneae, to wit in the American genera Crotonopsis and Eremocarpus. In Crotonopsis the petals are wanting in the female flowers and the small capsule is not dehiscent. These are annual herbs with distichous or decussate leaves. Further unicellular hairs with a scale-like dilatation at the base are occurring here. Others tribes or genera in the Crotonoideae with eventual resemblances with Eucommia could not be traced.

The Phyllanthoideae have, like Eucommia, two apical anatropic ovules in the cell. They are, however, differing by the lacking of latex as well as by most of their morphological characters. A 1-celled ovary is found in the dioecious genera Antidesma, Cometia and Drypetes. They never show any trace of abortive cells.

It is true that Hymenocardia possesses a winged fruit which more or less reminds us of that of Ulmus and Eucommia but this fruit is a 2-celled dehiscent capsule with a permanent central axis.

9. Relation with the Hamamelidaceae.

Solereder in 1899 inserted Eucommia in the Hamamelidaceae on account of the following characters: flowers unisexual without a perianth, connectives apiculate, two connate carpels with apical anatropic ovules and fairly well developed stigmata, embryo large. Certain anatomical
characters were given in support to this opinion: scalariform vessel perforations, libriform with bordered pits and narrow uniseriate wood rays.

To these points we may add that in the Hamamelidaceae the fruit is mostly 1-seeded and that the seed is containing endosperm. In this family there is a great number of trees and shrubs occurring in central and southern China. The cortex often contains a collenchyma tissue and the stomata possess auxiliary cells.

In spite of these similarities, Eucommia would hold a rather isolated position in the Hamamelidaceae, as was already remarked by Solereder, on account of the solitary ♀ flowers and the entirely different fruit. We may add the following points of difference. Dioecy is very rare in the Hamamelidaceae and the perianth is only wanting in a very few genera. It is true that the pistil consists of 2 carpels but the condition that one of these is regularly abort is not known.

Regarding the anatomical characters the following differences may be enumerated. In the Hamamelidaceae latex elements are unknown. Solereder considers this character unimportant although, in my opinion, it is essential and constant in many families. Furthermore, Eucommia possesses scalariform vessel perforations only in the primary xylem. The secondary xylem exclusively shows simple perforations. The latter are, therefore, not exceptional, as was claimed by Solereder.

It appeared from the keys to the genera of the Hamamelidaceae given by Harms in Engler & Prantl, that the following genera might show some relation with Eucommia: Distylium, Altingia, Sinowilsonia, Parrotia, Eustigma and Fortunearia. Of these Distylium is probably the nearest of kin by the unisexual flowers, the lacking of the petals, the eventual abortion of the calyx, the oblong anthers with elongated connective and the 2-celled ovary with subulate stigmata. The embryo is almost as long as the albumen, the flat cotyledons almost twice as long as the straight radicle. The leaves are often serrate towards the apex. In addition, one species of Distylium is found in China (Hupeh), viz. Distylium chinense Diehl.

Yet, on considering the following characters, the resemblances prove to be very superficial. The plants are monoecious, the flowers of both sexes being arranged in short axillary spikes or racemes, mostly with a bisexual terminal flower. There is one ovule in each cell of the ovary and there are two subulate styles. The fruit is a tomentose bivalve capsule, the valves being bifid. There are stipules which are caducous. Latex elements are wanting and stellate hairs are found on the innovations.

Altingia has likewise apetalous unisexual flowers while the calyx is also wanting in the male flowers. Exceptionally, female flowers (with a 2-celled ovary) are found solitary in the axils of the uppermost leaves. As in Eucommia the albumen is scanty and the cotyledons are flat and oblong.

However, the inflorescences are very much different. The ♂ flowers are combined into terminal thyrses with sometimes 1—3 female flowers at the base. For the rest, the female flowers are forming globular capitula; their calyces bear on the rim small connate scales which ultimately indurate. The flower is perigynous, the ovules are numerous and are
inserted in 4 rows at the septum. As in Distylium the fruit is a bivalvate capsule with bifid valves.

From a comparison of dried material of Allingia chinensis Champ. from Kwantung and of A. excelsa Nor. from Assam and western Malaysia it appeared that the Chinese species showed the least resemblance with Eucommia. The latter has, namely, obovate serrate leaves. On the other hand, the ovate and serrate leaves of A. excelsa strongly recall those of Eucommia. Finally, A. gracilipes Hemsl. from southern China may be mentioned which, according to the description, is distinguished from the other species by the small serrate leaves. Material of this species was not available for examination.

Sinowilsonia from China, which in many respects resembles Distylium, is distinctly less related to Eucommia than Distylium. Parrotia from northern Persia has still fewer characters in common with it. The flowers are apetalous but bisexual. The anthers are apiculate, the ovary is 2-celled. The leaves are often unequal at the base and coarsely serrate towards the apex. Eustigma and Fortunearia from China need no further consideration. Of the former only the subulate and densely papillate stigmata resemble those of Eucommia.

10. Relation with the Trochodendraceae (sensu v. Tieghem).

Even a superficial glance at the table shows that Eucommia has but very few characters in common with Trochodendron, the sole genus of the family. The principal points of resemblance are the wanting of the perianth, the apical anatropic ovules, the albumen and the simple leaves without stipules.

Points of difference are the entirely different inflorescences, flower parts, fruits, phyllotaxis and leaf shape. The leaves of Trochodendron are characterized by very long petioles. In addition, Eucommia is differing in a great number of anatomical characters enumerated by Van Tieghem (l.c.). Among these the lacking of vessels in the xylem and of latex elements in Trochodendron seem to be the most striking. In my opinion, Solereder en Van Tieghem were therefore right to exclude Eucommia from the Trochodendraceae. In recent publications this relationship has no longer been mentioned.

11. Summary (cf. the Table).

Summarizing, it appears that Eucommia has the greatest number of characters in common with the Urticales. This is shown by the similarity of the inflorescences as well as by the unisexual flowers and the dioecy. In both groups the pistil consists of 2 connate carpels and the ovary is usually 1-celled by abortion, while the stigmata are generally papillate.

Further general points of relation with the Urticales are the originally spiral phyllotaxis, which becomes later on pseudo-distichous, simple vessel perforations, libriform with bordered pits, unicellular hairs and the occurrence of calciumcarbonate and silica as well as of latex elements.

Yet, it seems difficult to indicate any particular family in the
Urticales to which Eucommia should be most related. While the fruit recalls Ulmus and the latex elements Urtica and Cannabis, the spirally thickened vessel walls remind us of some Morus species. In addition, Eucommia is isolated by the facts that in the Urticales the perianth is never entirely wanting, that there is only one ovule in the cell of the ovary, that stipules are very frequent, that calciumoxalate is characteristic (it is wanting in Eucommia) and that the superficial suberization is sub-epidermal in the Urticales and epidermal in Eucommia.

After the Urticales the Euphorbiaceae-Hippomaneae seem to be the nearest of kin, on account of a number of anatomical and morphological characters. However, the Euphorbiaceae usually possess a 3-celled ovary, a 2-celled one occasionally occurs in the Hippomaneae. Next follow the Hamamelidaceae which have, however, two fertile carpels but of which Distylium and Altingia show a reduction in the perianth and the latter moreover a similar leaf shape.

12. Conclusions.

1. Eucommia ulmoides Oliv. is strongly isolated in the system.
2. The view of Van Tieghem (1900) to accept a separate family for this species seems justified.
3. It is suggested to insert this family in the order of the Urticales.
4. The Ulmaceae and among these Ulmus are considered the nearest of kin of Eucommia.
5. There is some slight relation with the Euphorbiaceae-Hippomaneae, and still less with the Hamamelidaceae in which Eucommia was inserted by Solereder in 1899.
6. There is no relation whatsoever with the Trochodendraceae (sensu van Tieghem).

Literature.

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