THE PHYLLOTAXY OF METASEQUOIA, SEQUOIA AND TAXODIUM

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LIANG, CHOW & AU (1) describe in their paper entitled: *Properties of a »Living Fossil« Wood (Metasequoia glyptostroboides* Hu et Cheng) in the first place the xylotomy of *Metasequoia;* however, simultaneously they charachterize the most important external morphological properties of the tree as follows: »Morphologically, *Metasequoia* leaves and cone scales stand opposite, having the most important family characters of *Cupressaceae* . . . It has been suggested that *Metasequoia* might be an intermediate link family *»Metasequoiaceae«* between *Cupressaceae* and *Taxodiaceae.«*

Their establishment that the disposition of the leaves and the scales of the cone of the *Metasequoia* is opposite and decussate respectively and that this that plant is an intermediate link between *Cupressaceae* and *Taxodiaceae* should be emphasised.

In his excellent review: *On Metasequoia, living and fossil* FLORIN (2) also referring to the establishments of various other authors HU & CHENG (1948), STEBBINS (1948), MORLEY (1949), THENG (1948), STERLING (1949), MIKI & HIKITA (1950), CHANEY (1951) writes concerning the leaves of the *Metasequoia* among other things on pp 5—6 „Foliage leaves monomorphous, deciduous, decussate uninerved, each made up of a lamina and a decurrent portion . . . . Leaves on short shoots generally much more closely spaced than those in long shoots, but a short shoot will sometimes grow rapidly, with widely spaced leaves. The decussate phyllotaxy is most apparent on the vertical stem and in the basal region of the main lateral branches in the distal region of the latter the leaf pairs bend on their bases towards the horizontal, and approach a two-ranked position. The foliage leaves of the short shoots are also decussately arranged; as each successive leaf pair grows larger and opens outward from the bud, its »node« twists, however, bringing the leaf bases into a plane approximately parallel to the ground. *Alternating »nodes« rotate respectively clockwise and counter-clockwise, whereby the leaf bases are all brought into the same plane with an angular twist of about 90° between any two »nodes«.*"

»According to MORLEY's and my own observations, leaves which are not quite opposite one another at the »node« occur rather frequently. MORLEY has found, however, that the groove extensions of the leaf gaps in the xylem of the axis confirm the decussate phyllotaxy. The amount of twist between »nodes« may also vary, but such differences are compensated by a bending of

each leaf on its base towards the horizontal, making all short shoots appear flat-ranked.«

»As regards the *female strobilus* he states: Conelet oblong-elipsoid, composed of up to about 20—30 decussate, ovate cone scales, each with a broard stalk-like portion, an apex broadly angled in tangential view and a large distal resin cavity.« On this basis and mainly referring to CHANEY he establishes the most important morphological differences prevailing between *Metasequoia, Sequoia* and *Taxodium*, as follows:

1. »Leafy shoots of the ultimate order oposite and disposed distichously in *Metasequoia;* spiral and disposed distichously in *Sequoia* and *Taxodium.*

2. Needle-like foliage leaves on shoots of the ultimate order decussate and disposed distichously in *Metasequoia,* spiral and usually disposed distichously in *Sequoia* and *Taxodium.*

3. Cone scales decussate in *Metasequoia, s*pirally disposed in *Sequoia* and *Taxodium.*

In »Fortschritte der Botanik« MÄGDEFRAU (5) draws essentialy the same conclusion.

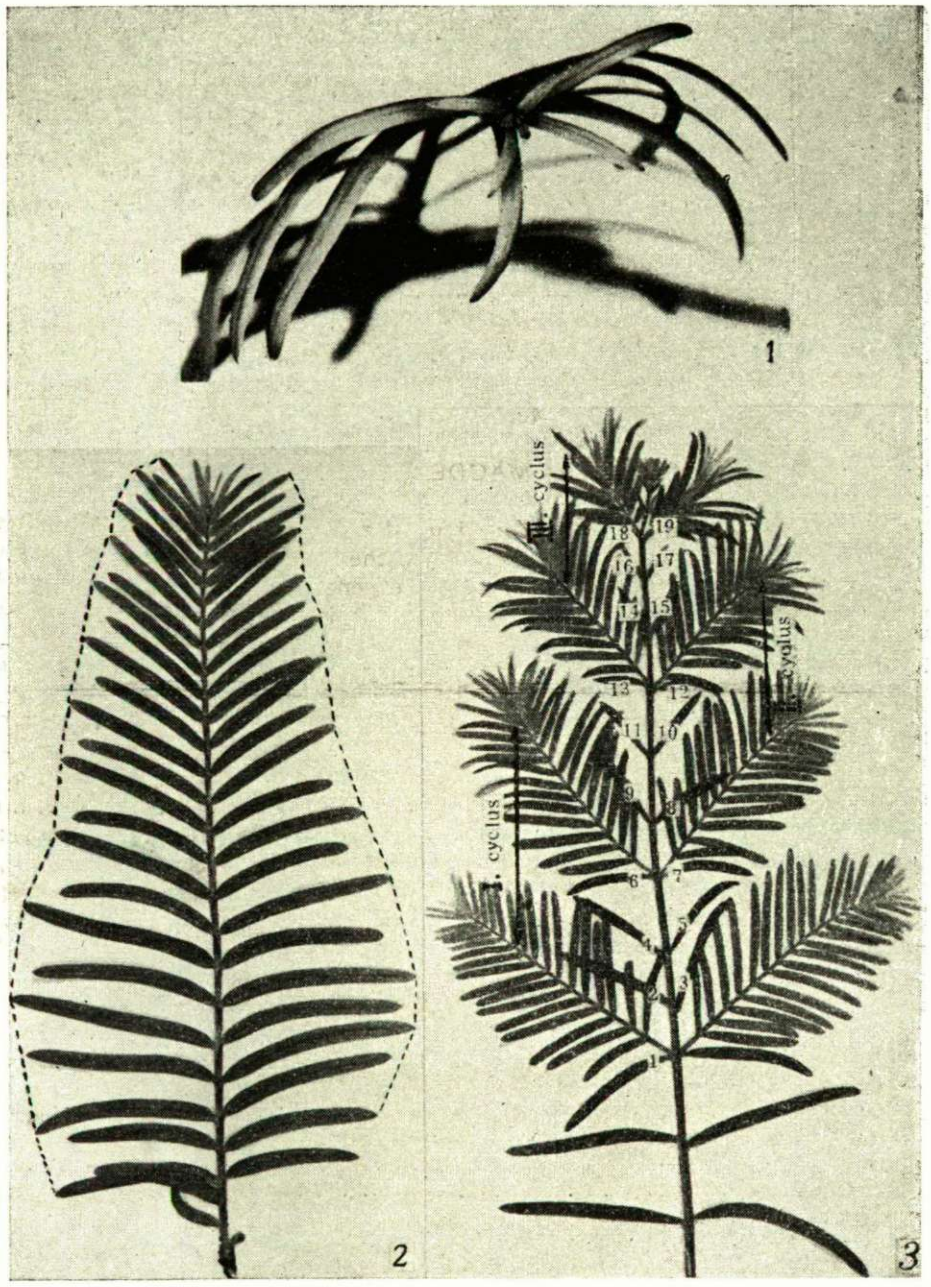
The above data have been adopted by the literature in general and are therefore accepted as genuine. The author of the present paper was, however, able to examine each species of all the three genera not only from the xylotomous point of view, (4) but had also the opportunity of investigating the living plants and to make comparative studies concerning the morphology. On the basis of these precise observations the author came to the interesting conclusion that in contradiction to the above establishments the foliage leaves of the *Metasequoia* were not originaly opposite, as well as that the disposition of the leaves of the *Sequoia sempervirens* is exactly 2/5 and that their leaves arrange only ultimately on the side branches apparently in two rows. *Taxodium mucronatum* has esentially also 2/5 leaf disposition. The leaves of the *Taxodium mucronatum* are essentially also spaced at a 2/5 distance and are apparently only, in two rows on the short shoots. The autohr believes that the same holds true for the scales of the cones. Thus he believes on the basis of his observations that *Metasequoia* and *Cupressacea* cannot be brought into genetical correlation.

Discussion

This statement will be confirmed by the following facts:

The phyllotaxy of the foliage leaves. If the 3 illustrations published in FLORIN's (2) paper are studied carefully it becomes immediately visible that in none of the species do the leaves originate exactly from the nodus, but one originates somewhat higher or lower than the other; this has also already been observed by FLORIN (2). This fact, in the case of all species, to a certain extent support the conclusion that the leaves do not stand quite opposite.

a) On the summits opposite of the growing branches the leaves of *Metasequoia* are not yet opposite as they appear to be in the middle and the lower parts of the short shoots. This can be well seen in *Fig. 1.* If, namely, the young leaves on the summits of the growing plants would already initially sohw an opposite, or a transverse, decussate disposition then, viewed from above, only



The Legend of the Illustrations Phot. Simoncsics

Figure 1. The summits of a short *Metasequoia* shoot viewed from above. The disposition of the young leaves is not decussate as more than four orthostichons are visible (2/1).

„ 2. On the short shoots one of the leaves of the leave pairs is always smaller than the other they occur alternatively. (1/1).

„ 3. The origin of the side branches. The side branches always originate after two leave pairs from the axil of the third, corresponding to cycle 2/5. (1/1).

2 or 4 orthostichon developments could be observed on the summits. However, the photo evidences quite the opposite, as on the living summits the leaves are not arranged in four, but in more rows, which can be considered as representing a spiral disposition. Another important circumstance also supporting the spiral phyllotaxy is that on the living summits one of the apparently decussate leaves is always somewhat larger than the other *(see Fig. 1.)*. This can also be considered as a proof contradicting the decussate, or transverse decussate, arrangement of the foliage leaves. Furthermore, another evidence in favour of the spiral phyllotaxy is that, of the two leaves situated at the same nodus, one is always more advanced in its development than the other, a fact which can only occur in the case of the disposition of the leaves being spiral.

This slight difference can also be observed later, inasmuch as the still undeveloped leaves on the short shoots-standing apparently opposite — are always different in size, alternately one of them always being 1—3—4 mm larger than the other. In *Fig. 2.* the summits of the larger leaves are connected on both sides by lines. On the photo it can be clearly seen that the larger leaflet on the one side is always smaller than its pair on the ohter side showing that they are not equal in their development which phenomena also provide evidence contradicting a genuine opposite leaf disposition. Still further evidence in favour of spiral phyllotaxy is furnished by the fact that on the vertical stem as well as on the developed short shoots, the nodes of the leaves rarely coincide the one always being about 0.3—1—2 mm higher than the other. On the illustrations published by FLORIN (2) this phenomenon can also be seen on some places.

b) Sequoia. The spiral phyllotaxy can be observed still more plainly on the closest relative of *Metasequoia*, the *Sequoia*, more precisely the *Sequoia sempervirens (see Fig. 5.)*. Similary to the *Metasequoia*, on the young side branches of the developed *Sequoia sempervirens* the leaves are also distichous, i. e. the phyllotaxy is apparently 1/2. However, in this case, too, this is only apparently so, as actually on the young shoots as well on the short ones the 2/5 arrangement is well visible, this is also proved and confirmed by the photo. On the photo the succession of the leaves is denoted by numbers 1—18. All the cycles are designated by the white connecting lines, (1—5, 2—6, 3—7, 4—8, 5—9 etc.) while the nodes of the leaves are connected by the white line twisted around the vertical stem. The 5 vertical white lines, i. e. the 5 orthostichons clearly show that the phyllotaxy of the *Sequoia sempervirens* is spiral, i. e. it is exactly 2/5. This can also be seen fairly well on photo No. e. of the paper published by FLORIN (2).

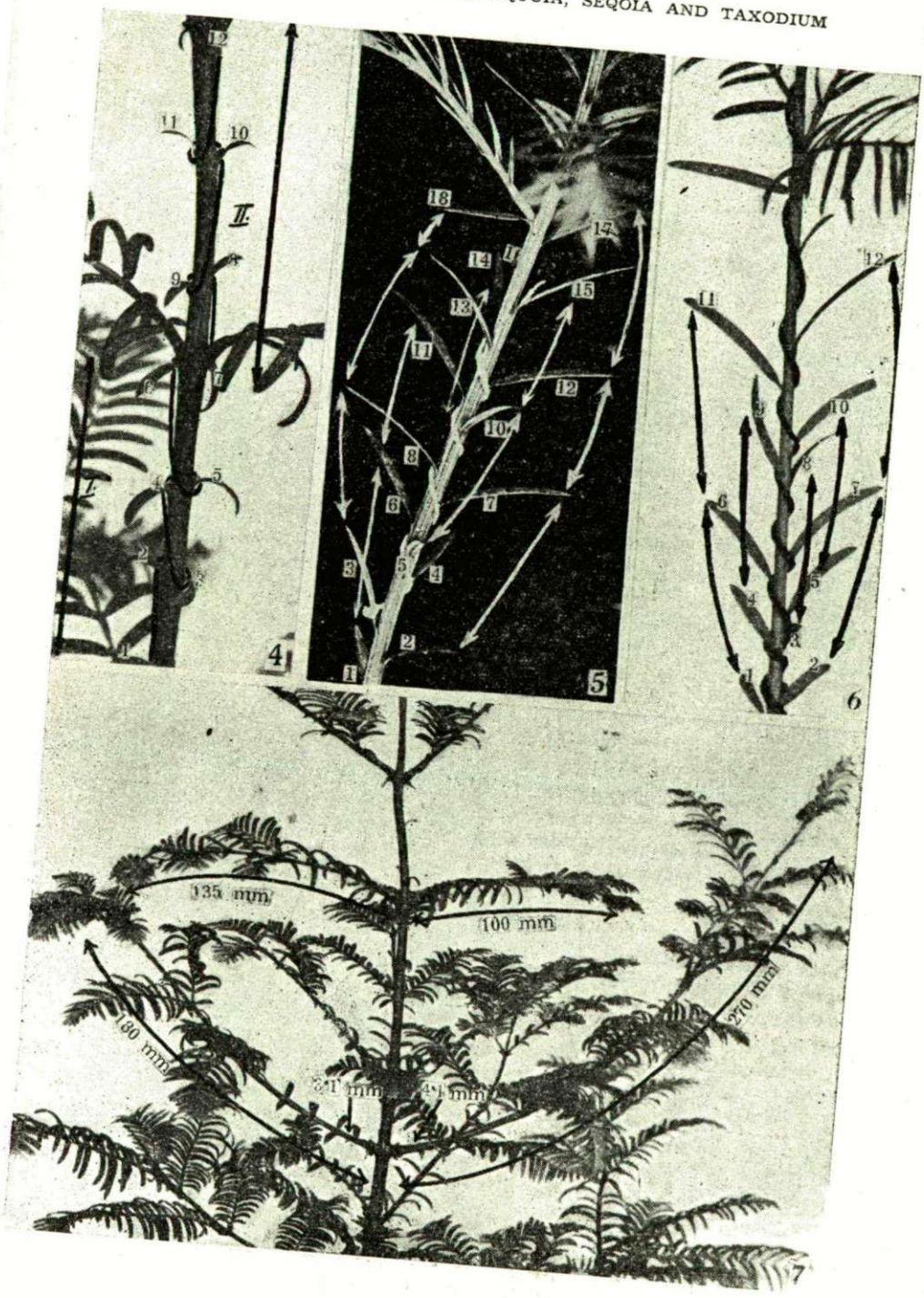
The Legend of the Illustrations

Figure 4. The phyllotaxy of *Metasequoia*. Leaves No. 1—6 illustrate the I. and those numbered 7—12 the II. cycle. In cycle I. the spiral proceeds clockwise in II., counter-clockwise. (2/1).

„ 5. The phyllotaxy of the *Sequoia*. The five vertical white lines denote the five orthostichons, the line sections above one another the different cycles. The white spiral line encircling the stem connect the *noduses* of the leaves. (1/1).

„ 6. On the young shoots of the *Taxodium mucronatum* the disposition of the leaves is exactly 2/5. The five vertical black lines denote the five orthostichons, the black line sections above one another the cycles (1/1).

„ 7. A part of a young *Metasequoia* near the summit. The length and thickness of the opposite side branches is not equal. (1/2).



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c) Taxodium. The photo No. 6. showing a shoot of *Taxodium mucronatum* also provides evidence in favour of the spiral, and against the opposite disposition of the foliage leaves. This photo shows clearly that the nodes of the leaves on the main stalk are situated at different levels, thus they are not opposite, but, similarly to those of the *Sequoia* and *Metasequoia,* spirally arranged in a 2/5 manner. Hence also here, probably owing to adaptation to the light conditions, the distichous phyllotaxy only resulted later like the phenomenon well known in the case of the *Abies, Taxus* etc.

Accordingly, it can be established that in the case of *Metasequoia* as well as in that of the *Taxodium* and *Sequoia* the phyllotaxy was originally spiral, more precisely it occurred in a 2/5 manner and that on the side branches the leaves lined up in two rows only later. This establishment is from the phylogenetic point of view of great importance as it rules out the supposition that on the basis of the disposition of the leaves the 3 otherwise very closely related genera can be brought into genetical connection on supposing that the *Metasequoia* represents the missing link between them and the verticillate, opposite *Cupressaceae.* So, in the opinion of the author, this assumpiton must undergo revision.

The evolution of the side branches. The evolution of the side branches is also closely correlated with the phyllotaxy. The following precisely checked data justify the statement that the development of the side branches of the *Metasequoia* is not either genuinely opposite or deccusate but, as regards its origin, rather spiral. Namely, according to the corresponding succession of the disposition of their foliage leaves the side branches originate from the axils of the leaves which is also well illustrated by *Fig. 3.* This photo, too discloses that the side branches always originate on the main shoot and generally after every two pairs of leaves, hence on the third nodus, always of course, from the axil of the leaf. If, however, the succession of the development of the branches is more closely investigated it can be established that the side branches always develop corresponding to the 2/5 disposition of the leaves rotating at the end of each cycle clockwise and counter-clockwise respectively (see FLORIN (2) p. 6.), this is characteristic for *Metasequoia.* On the photo the leaves are also denoted by the serial numbers 1—19 and the cycles by numbers I—IV. The first cycle involves numbers 1—6, the second 7—12 and the third 13—18 and it should be noted that the III. cycle is above the I. and the IV. above the II., i. e. the site of the origin of the side branches also seems to support the fact that the phyllotaxy of the side branches of *Metasequoia* corresponding to the disposition of the leaves is 2/5 and not 1/2 as would have to be assumed in the case of typical opposite phyllotaxy.

The dimensions of the thickness and difference in length of the branches situated at the same level also supports the view that there is no genuine decussate disposition, and these data were also precisely checked. The following *Table 1.* illustrates the result of such a measurement. Attention should be drawn to the fact that the juxt-aposed numbers denote the thickness of the branches at the same level at a distance of about 2 mm to the site of their origin. The third column shows in mm the difference between the opposite branches at the same level, whereas the fourth column represents the differences of the values expressed in per cents.

The values expressed in per cents show that the difference between the young branches is greater than that between the older ones. The former may amount to 34 per cent, whereas in the case of the latter it is merely 10 per cent, thus on the average it is 23 per cent.

Table 1.

Succession of the origins	The thickness of the opposite branches expressed in mm		Difference expressed in mm	Values in per cents
I.	3,8	4,9	1,1	29
II.	5,	4	1	25
III.	5,	6,7	1,7	34
IV.	6,5	5,4	1,1	20
V.	5,8	7,2	1,4	24
VI.	8,	6,5	1,5	23
VII.	7,2	9	1,8	25
VIII.	10,9	8,9	2	22
IX.	10,	11,9	1,9	19
X.	13,2	12	1,2	10
The total thickness of I—X branches	75·4	76·5		Average 23·1 per cent s

In *Fig. 7.* the diameter of one of the branches is 3.1 mm whilst that of the opposite one is 4.1 mm. These data prove also undoubtedly that the branches situated opposite one another do not develop identically, hence in the case of *Metasequoia* there is no genuine decussate branching, in the strict sense of the word.

The length of the opposite branches is in close correlation with their thickness, too, which can be well seen in *Fig. 7.*, for instance the length of one of the branches situated at the same level was 13.5 cm and that of the opposite one only 10 cm, in the case of another level the lengths were 18 and 27 cm respectively. Among the lower branches the one was 66, and the other 82 cm long. This rather supports also the fact that we are dealing with monopodial ramification and not with a genuinely decussate one. It should be emphasised that these morphological characteristics and differences are not fortuitous representing exceptions but occur always representing one of the characteristic of *Metasequoia.*

The disposition of the sporophylls: In the author's opinion, similarly to the regularity that can be observed regarding the phyllotoxy, ramification, thickness and size of the side branches, a very close correlation must also exist as regards the disposition of the sporophylls, hence also concerning that of the male strobili and the cone scales too.

The male strobili: We succeeded in detecting male strobili as buds only. The buds of the male strobili in youth are covered with bud scales arranged in

four rows. It could be established beyond doubt that when the male strobilus was only budding the leaves, i. e. the leaves of the bud of the scale are actually arranged in four rows one above the other, these four rows are not quite parallel to the axis, they deviate to a very slight extent from it. Namely, when the scales of the bud were picked the regularity mentioned above was confirmed. Of the scales of the bud situated at the same level one is somewhat smaller than the other. For example the one was 2.1 mm high and 2.3 mm broad, whereas the one opposite to it was 1.8 mm high and 2 mm. This also supports the view that the scales of buds at the same level are not quite equally developed hence they cannot be of exactly the same value either. We did not succeed in precisely observing the arrangement of the stamen or sporophylls on the axis; it seems, however, likely that also in this case these phenomena occur.

The structure of the female cone. Essentially the same conditions could be observed in the structure of the female cone. We succeeded in observing the size of the single cone scales. The maximum thickness was measured at the middle of the single scone scales of each cone scale pair, on ortostichon four *(see Table 2.)*.

Table 2.

Origin of the cone scales	Orthostichon			
	I.	III.	II.	IV.
7			**4,9**	4,3 mm
6	**5,1**	4,6		
5			3,9	**4,9** „
4	4,0	4,9		
3			**5,1**	4.3 „
2	**4,8**	4,2		
The total height of 3 scales	13,9	**13,7**	13,9	13,5 mm

The thnickness of the scales of the scones fluctuated between 4—5.1 mm. In the case of row I. and III. opposite to it the total height of the 3 scales was 13.9 and 13.7 respectively, and in the alternative rows II. and IV. the 3 scales were almost precisely identical with 13.9 and 13.5, respectively. This is not astonishing at all. It is merely remarkable that the thickness of the four scales above each other was exactly *alternative* showing that scales at the same level develop to a different extent and so are not of precisely the same value which can only be due to thein having developed in spiral succession. If this is so, from the point of view of their development they are arranged in several parastichons although in the cone of the *Metasequoia* on the cone axis the leaves of the scales are arranged as 4 orthstichons. Hence, in the cone of the *Matesequoia* the disposition of the leaves of the scales is similary to that of the

Sequoia and the *Taxodium* — though scens from the exterior apparently decussate — rather spiral.

The above literature unequivocally states that the cone scales of the *Metasequoia* are decussate, whereas those of the *Sequoia* and *Taxodium* are arranged in spirals; this is also the reason why certain authors bring them into genetical correlation with the *Cupressacae,* the only coniferae family for which the genuine verticillate or opposite phyllotaxy respectively, is characteristic.

At any rate it seems desirable that thorough and precise investigations should be carried out in order to reach a final decision concerning this very important problem. If the cone scales in the cone of the *Metasequoia* would really be decussate and equally developed, this single common feature would indeed support the assumption that there exists some genetical relation between *Metasequoia* and *Cupressaceae* as was suggested by LIANG, CHOW and AU (3) in the paper mentioned above. However, the author believes that in the light of the observations mentioned regarding the disposition of the leaves, as well as that of the cone scales, there is no definite morphological basis suggesting a genetical relation between *Metasequoia* and *Cupressaceae,* but on the contrary, all essential data contest the possibility of such a relation. *Metasequoia* has such characteristically *Taxodiaceaous* features that in the opinion of the author of the present paper to lift it out from this family and to classify it as a separate family does not seem to be by any means justified. On the basis of all its more important characteristics the *Metasequoia* certainly must be regarded as a member of the *Taxodiaceae* family and cannot be considered to be an intermediate link between *Taxodiacae* and *Cupressacae.*

Summary

Summarising the above establishments is seems desirable to modify the hitherto existing views concerning *Metasequoia* as follows:

1. Considering its origin the phyllotaxy of the *Metasequoia* is not genuinely opposite, but similarly to that of the *Taxodium* and *Sequoia* probably spiral 2/5. The distichous phyllotaxy is probably due to adaptation to light. Of two leaves situated at the same level the one is larger than the other affording evidence of contesting opposite phyllotaxy.

2. Corresponding to the phyllotaxy, the ramification of the shoots of *Metasequoia* is not either exactly opposite, or transversely decussate, this in only apparently the case. Of the branches situated opposite one another the one is always better developed and longer, than the other.

3. Concerning the development of the scales of the cones situated at the same level, in the cone of the *Metasequoia* they are like those of the *Taxodium* and the *Sequoia* arranged rather on parastichons. Of the opposite cone scales one is always better developed than the other, which also contradicts the opposite phyllotaxy concept.

4. Based on the above statements the *Metasequoia* completely fits into the *Taxodiaceae* family and its classification as a new family is quite unjustified and it cannot be considered to compose a genetical link with *Cupressaceae,* either.

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