ACTA BOTANICA NEERLANDICA, Vol. 4 (3), 1955

THE STORIED-STRUCTURE-FEATURES AND THE TAXONOMIC RANK OF THE LEGUMINOUS TAXA

BY

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(*received June 7th, 1955*)

INTRODUCTION

In a former paper by the author and RIJSDIJK (1955) it was shown that the leguminous taxa can be readily distinguished by wood anatomical characters. A key for identification was included. The *main* features separating the taxa are the presence or absence of gable ended parenchyma strands and of storied structure, the structure of rays and the number of cells in the parenchyma strands. No opinion was expressed about the taxonomic rank of the taxa. The present investigation was undertaken to ascertain the extent to which a knowledge of the distribution of the storied-structure-features among the taxa might allow suggestions concerning their category.

The storied-structure-features were only known superficially when in 1931 JANSSONIUS published the important results of his own investigations and in fact introduced the storied-structure-features ('Stockwerkmerkmale') and the storied-structure complex into wood anatomy because of the many correlations involved. The first concept includes storied structure itself and the units of the complex. The units of the complex were presented in sequence of importance and frequency. The units are:

(1) Wood parenchyma strands and fusiform wood parenchyma cells with gable ends on tangential section, on radial section the end cells rectangled. Pitting often markedly more abundant on the gable-ends.

(2) A low number of cells in the strands, often not more than 2.

Janssonius did not specify what precisely was meant by: a low number of cells. To the author's opinion a number of 1–4 cells or lower will represent the unit, the presence of which will be recorded in the third column of the Tables. Next to this figure in the Tables the percentage of strands with 1–2 cells will be recorded. In the text the latter subunit will be called unit 2a and the former one 2b.

(3) Middle part of the libriform fibres in horizontal layers, so that on cross section radial rows of wide middle parts are typically alternating with rows of narrow parts (Fig. 1).

(4) The fibres abruptly tapering to one-sided slender ends (fibres with shoulders, Fig. 2 and Fig. 3).

(5) The pitting of the radial walls of the fibres sub 4. more abundant in the vicinity of the slender ends and the latter without pits or barely with any.
(6) Short vessel members and parenchyma strands and fusiform parenchyma-cells, low rays and short middle part of libriform fibres.

Storied structure in a wood is often accompanied by one or more special features. By JANSSONIUS (1931) such features were also found in

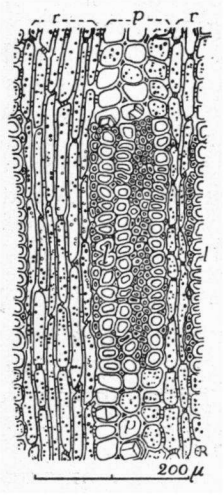

Fig. 1

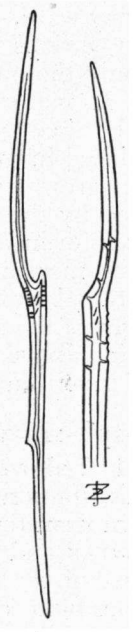

Fig. 2

Fig. 3

Fig. 1. Unit 3. of the storied-structure complex. On cross section radial rows of wide middle parts of the libriform fibres alternating with irregular rows of the slender ends of the fibres from higher and lower stories. l: libriform fibres; r: wood ray; p: wood parenchyma. From REINDERS (1951).

Fig. 2. *Dialium sp.* Libriform fibres with shoulders, the left one with a short middle part. Extreme, and rather extreme case. From REINDERS (1951).

Fig. 3. *Hymenaea courbaril* L. A less extreme case of a libriform fibre with shoulders.

the nearest allies in which the storied structure itself was not present. For this reason Janssonius attached great value to the storied-structure features from a taxonomic point of view.

MATERIAL

Material for this investigation was taken from the Surinam wood collection of this Laboratory. This includes authenticated specimens from the Collection Welvaartsfonds Suriname (WS), which were obtained through the courtesy of Prof. Dr J. F. Kools; from the

Collection sampled by the late Prof. Dr G. Stahel in Surinam; and from the Surinam Collections sampled by Ir I. A. de Hulster (de H and dHS[1]). Used also were some specimens from older collections (G) and (S) from Surinam, also obtained through the courtesy of Prof. Kools.

For their assistance in preparing the microtome sections and macerated material the author is indebted to Ir J. F. Rijsdijk, Miss R. Ubels, Mr B. W. Smit and Mr N. Stegman; to Miss Dr J. de Zeeuw for preparing the drawings used as illustrations and to all other members of the staff for help in many ways.

Sections were made at various points in the specimens. For this investigation, however, only those cut at a distance as far as possible from the core were used. In many cases specimens of small diameter were the only ones available (see JAPING, 1955). The distance from the core, in the Tables, is enlisted in number of growth rings (gr. r.) and in cm whenever possible; growth rings were counted by Ir Rijsdijk and the countings checked by the author. A 0 in the Tables means that growth rings are absent or invisible to the handlens; a – indicates that accurate counting and measurement was impossible because the core is missing. An additional capital letter in the WS specimens is informing about the height of the specimen in the tree, A indicating the lowest log, and the line above or below whether the specimen is taken at the top or at the bottom of the log.

DISTRIBUTION OF THE STORIED-STRUCTURE-FEATURES

For the purpose aimed at above the numbers 2, 3, 4 and 6 were studied only, since the distribution of nr 1a and 1b (gable ends and storied structure) is known from the work of JANSSONIUS (1914, 1918) and of REINDERS-GOUWENTAK and RIJSDIJK (1955). Of nr 6 only the length of the middle part of the fibres was studied.

In the Tables the various figures are inserted in the same sequence. For the % of 1–2 cells within the parenchyma strands and the variation of total number of cells 40–50 strands were examined in the bands or in the vasicentric parenchyma at a distance of 2 cells from the vessels. This procedure is necessary because strands close to the vessels mostly have a greater number of cells.

Whether the middle parts of the libriform fibres are placed in horizontal layers is studied on cross sections. In that case radial rows of wide fibres are typically alternating with rows of narrow fibres (Fig. 1). It often is a matter of appreciation whether the middle parts of libriform fibres are placed in such horizontal layers. A + in the Tables means presence of horizontal layers, a — that no such layers are present. When the layers are locally present the fact is noted with + & —. A ± in the Table means that the unit is not quite absent.

For the determination of the % of fibres with shoulders and the % of fibres with short middle part 100 fibres were examined. Short means that the middle part has about the length of the vessel members. Fibres showing such shoulders as pictured in Fig. 2 do not present any

[1] The author is indebted to Dr H. C. D. de Wit for identification of the herbarium sampled with the dHS specimens of woods.

difficulty. This is not so with less extreme cases one of which is shown in Fig. 3. In such a case every author will draw the line elsewhere. This means that the dates represent but rough estimates. Furthermore it is important to bear in mind that in families-without-storied structure that neither have near allies with storied structure, 25 %–30 % of the fibres may show shoulders.

TABLE I

Storied-structure-features in the Mimosaceous taxon.

	Parenchyma strands		Libriform fibres		
	2a	2b	3	4	6
Name of Plant Coll. Nr Distance from Core (gr. r.; cm)	% 1–2 cells	number of cells	middle part in hor. layers	% with shoulders	% with short middle part
Parkia pendula (Willd.) Benth. de H 66 (± 27; ± 11) . .	**37**	**1–4**	+	28	6
Parkia nitida Miq. St. 85 (21?; 10?)	24	(1)**2–4**	+	27	?
Parkia ulei (Harms) Kuhlm. St. 316 (–; –)	16	2–5	+	19	?
Pentaclethra macroloba (Willd.) Kuntze; de H 24 (–; 10) .	**100**	**1–2**	—	**51**	24
Piptadenia suaveolens Miq. dHS XV (± 50; 27) . . .	± 18	1–4 (5, 6)	—	3	0
Inga alba (Swartz) Willd. WS 75C (± 39; 21) . . .	**48**	**2–4**	—	18	0
Inga sp.; de H 38 (± 15; 13)	**37**	1–6	—	19	3
Inga sp. (coriacea (Pers.) Desv. (?)); dHS VII (0; 21,5)	25	2–4 (5)	—	17	3
Inga rubiginosa (A. Rich.) D.C. St. 162 (± 13; ± 6) . . .	20	2–4 (5)	—	24	0
Inga splendens Willd. de H 108 (–; –)	27	**2–4**	—	21	7
Inga edulis Mart. WS 45B (± 40; 17,5) . .	19	2–5	—	30	18
Inga bourgoni (Aubl.) D.C. de H 25 (–; –)	**35**	**2–4**	—	10	0
Pithecellobium (Zygia) cauliflorum (Willd.) Mart. St. 284 (> 20; 6–7?) . . .	25	2–4 (5)	—	8	0
Pithecellobium (Abarema?) racemosum Ducke St. 72 (> 20; –)	0	3–5	—	8	0
Pithecellobium (Arthrosamanea) corymbosum (Rich.) Benth. WS 46C & WS 47B (±40; 26)	**100**	**1** [1])–2	—	27	12
Pithecellobium (Arthrosamanea) gonggrijpii Kleinh. dHS III (0; 23)	**38**	2–4 (5)	—	20	8
Pithecellobium (Macrosamanea) pedicellare (D.C.) Benth. WS 59A (83; 35)	**42**	**1–4**	+	28	2

[1]) 1-celled: 72 %

JANSSONIUS (1931) p. 104 writes '. . . .könnte man fragen ob es überhaupt noch Familien gibt in welchen der Stockwerkartige Aufbau ganz fehlt'. Certainly meant with 'Stockwerkartige Aufbau' is: storied structure features. In translation: '. . . .one could ask whether there are families without any of the storied structure features'. Janssonius's answer is that there are such families and he even found, that there is a positive correlation between absence of the features and presence of fibretracheids and scalariform perforations in the vessels.

As long as no further details are available it seems best to accept a percentage of about 45 at least before recording presence of storied-structure-features in the *fibres*.

In Table I the results of the countings and measurements are recorded for the Mimosaceous taxon. Here 17 species are included from 5 genera or from 8 genera if *Zygia*, *Abarema*, *Arthrosamanea* and *Macrosamanea* would be recognized as distinct genera.

The percentage of parenchyma strands with 1–2 cells in 8 species is higher than 30 and will reach JANSSONIUS's (1931) qualification 'often'. As regards unit 2b, in *Pithecellobium*(*Arthrosamanea*?) *corymbosum* and in *Pentaclethra macroloba* the number of cells is 1–2 and in 7 species it is 2–4. In 4 species 5 cells rarely occur and most strands have 2–4 cells. In 4 species only, *Parkia ulei*, *Inga sp.*, *Inga edulis* and *Pithecellobium* (*Abarema*?) *racemosum* 5 or 6 cells in the strands are a common phenomenon. So the units 2a and 2b are present to a high degree in the Surinam species of the Mimosaceous taxon. Such is not the case with the libriform units.

Horizontal layers of middle parts of libriform fibres are present in 4 species. A high percentage of fibres-with-shoulders was found in *Pentaclethra macroloba* only. None of the species showed a large amount of fibres with short middle part.

As to the distribution of units in the species, *Pentaclethra macroloba* with 3 units has the largest amount of storied-structure-features, closely followed by *Pithecellobium pedicellare* and *Parkia pendula*.

Within the genus *Inga* the parenchyma-strand units will perhaps prove to be important as identification features. Some of the species of this genus do, some do not possess a high percentage of 1–2 cells in the strands.

It can be seen from Table II, that in the Caesalpiniaceous taxon (inclusive Swartzioideae) a high percentage of 1–2 cells in the strands is present only in 6 species of the 19 species-with-parenchyma (in *Sclerolobium albiflorum* parenchyma practically is absent). It is noteworthy that the unit is absent in *Dialium*, *Dicorynia* and *Martiusia* which genera have a distinct storied structure even in the rays. As regards unit 2b a number of 2–4 cells in the strands is present only in *Copaifera*, *Hymenaea*, *Peltogyne pubescens* and *Sclerolobium albiflorum* and in 2 *Swartzia* species.

So the storied-structure units often occurred more in the parenchyma strands of the Mimosaceous taxon than in the Caesalpiniaceous species or genera.

In none of the species was the horizontal-layer unit present every-

TABLE II

Storied-structure-features in the Caesalpiniaceous taxon.

	Parenchyma strands		Libriform fibres		
	2a	2b	3	4	6
Name of Plant Coll. Nr Distance from Core (gr. r.; cm)	% 1–2 cells	number of cells	middle part in hor. layers	% with shoulders	% with short middle part
Dimorphandra conjugata (Splitg.) Sandw. dHS I (0; 25)	0	3–9	—	13	0
Dimorphandra pullei Amsh. dHS XVIII (± 50; 29) .	1	(2) 3–6	—	29	7
Mora excelsa Benth. S 26 (± 84; 39)	10	2–5	—	9	0
Mora gonggrijpii (Kleinh.) Sandw. WS 88B (± 90; 29) . . .	25	2–4 (5)	±	6	0
Copaifera guianensis Desf. dHS V(± 96; 22)	12	**2–4**	+ & ±	**82**	**77**
Hymenaea courbaril L. WS 85D (± 104; 29,5) . .	26	**2–4**	—	**45**	31
Peltogyne pubescens Benth. dHS XI (± 60; 19½) . .	12	**2–4**	—	9	0
Peltogyne venosa (Vahl) Benth. S 25 (± 50; 23)	**35**	1–7	—	2	3
Eperua falcata Aubl. S 20 (0; 28)	**85**	2–(3, 4, 5)	—	19	15
Dialium guianense (Aubl.) Sandw.; St. 245 (> 10; –) .	3	(2)3–5(6)	—		
Dicorynia paraensis Benth. = *D. guianensis* Amsh. G 100 (0; –)	0	(3)4–7	±	**44**	23
Martiusia parviflora Amsh. St. 145 (> 20; –)	3	(2)3–8	+ & —		
Vouacapoua americana Aubl. S 2 (> 65; –)	2	(2)3–7	±	0	0
Sclerolobium melinonii Harms WS 73A (± 70; 24) . . .	[1]	[1]	—	5	0
Sclerolobium albiflorum R. Ben. WS 70B (± 40; 20,5) . .	**100**	**1–2**	—	0	0
Swartzia benthamiana Miq. St. 369 (–; 4,5)	**31**	1–4(5)	—	38	19
Swartzia remigifer Amsh. St. 169 (–; –)	2	(2)3–4(5)	—		
Swartzia tomentosa D.C. WS 84A (± 60; 26) . . .	7	2–4(5)	—	**47**	27
Swartzia prouacensis (Aubl.) Amsh.; St. 69 (–; 8?) . . .	**100**	**2**	—	**69**	**66**
Swartzia bannia Sandw. St. 173 (–; –)	**58**	**2–3(4)**	—	**85**	**60**

[1]) Parenchyma practically absent.

where in the sections. In *Copaifera guianensis* and in *Martiusia* the unit was locally present; in *Mora gonggrijpii*, *Dicorynia paraensis* and in *Vouacapoua*[1] *americana* the unit had to be recorded as ±.

So the horizontal-layer unit of the libriform also occurred more often in the Mimosaceous taxon.

A high percentage of fibres-with-shoulders was found in 6 species, 3 of which are *Swartziae*. As for the short-middle-part unit a high percentage occurs in 3 species, in *Copaifera guianensis* (perhaps also in *Hymenaea courbaril*) and in 2 *Swartziae*.

So the libriform-units other than the horizontal-layer unit *less* often occur in the Mimosaceous taxon than in the Caesalpiniaceous.

JANSSONIUS (1918, 1931) and REINDERS-GOUWENTAK and RIJSDIJK (1955) did not find gable ends nor storied structure (units 1a and 1b) in the Mimosaceous taxon. These are the units that by Janssonius are considered to be the most important ones among the storied-structure-features. These units Janssonius found in two Javanese species of the Caesalpiniaceous taxon. In the Surinam species examined by Reinders-Gouwentak and Rijsdijk storied structure and gable ends occur in the Swartzieae, in *Dialium guianense*, *Dicorynia paraensis*, *Martiusia parviflora*, and in one of the specimens of *Peltogyne pubescens*. With the exception of the *Swartzia* species-with-gable-ends only, the parenchyma strands have gable-ended cells as well as conical end cells.

The presence of the gable-end unit and the storied structure unit in the Caesalpiniaceous taxon indicates that some members of this taxon possess storied-structure-features to a higher degree than would appear from the figures in Table II. Thus some at least of the *Swartzia* species show about 4 or 6 features and in the Caesalpiniaceous species s.s. *Copaifera* and *Dicorynia* then have 3 à 4 units, *Hymenaea* 2 or 3.

Of the 14 species of the Papilionaceous taxon examined for Table III a high percentage of 1–2 cells was found in 50 % of the species. In 8 species the second parenchyma-strand unit is also present and in the 2 *Pterocarpus* species and in *Lonchocarpus* 100 % of the strands contain 1–2 cells. Fusiform parenchyma strands often occur in this taxon and the number of cells varies from 1–6. The same occurs in the Mimosaceous but practically does not occur in the Caesalpiniaceous taxon.

From these facts it appears that the storied-structure units in the parenchyma strands of the Papilionaceous taxon occur in the same percentage or in a slightly higher one than in the Mimosaceous taxon. The horizontal-layer unit was found many times and so here also occurs more often than in the Mimosaceous taxon.

A high percentage of fibres-with-shoulders is shown by 3 of the 14 species, the short-middle-part unit in 2 or perhaps 3 species. So here practically to the same extent as in the Caesalpiniaceous taxon.

As regards the gable-end feature, it appeared from our former work cited above that gable-ends were found in all of the Papilionaceous

[1] *Vouacapoua* in agreement with PULLE (1939–1940) has been included in the Caesalpiniaceous taxon.

TABLE III

Storied-structure-features in the Papilionaceous taxon.

Name of Plant Coll. Nr Distance from Core (gr. r.; cm)	Parenchyma strands		Libriform fibres		
	2a	2b	3	4	6
	% 1–2 cells	number of cells	middle part in hor. layers	% with shoulders	% with short middle part
* *Sweetia nitens* Benth. G 68 (–; 20)	24	**2–4**	—	12	3
Diplotropis purpurea (Rich.) Amsh.; S 17 (0; ± 20) .	2	2–7	+	25	1
Clathrotropis brachypetala (Tul.) Kleinh.; dHS XVI (> 30; ± 16)	14	1–5(6)	—	32	30
Ormosia coutinhoi Ducke WS 25Ā (0; 18)	**64**	**1–4**	—	24	18
Alexa wachenheimii R. Ben. dHS VIII (± 60; 25) . .	0	3–7	+	**75**	**73**
Vatairea guianensis Aubl. WS 91Ā (± 40; 24) . . .	13	2–8	—	26	16
* *Pterocarpus officinalis* Jacq. de H 8 (> 15; > 10) . .	**100**	**1–2**	+	**93**	**87**
* *Pterocarpus rohrii* Vahl St. 252 (> 8; > 2) . . .	**100**	**1–2**	—		
* *Platymiscium trinitatis* Benth.; dHS VI (0; 24)	**85**	**2–4**	±	34	13
* *Hymenolobium flavum* Kleinh. G 65 (0; 14)	1	(2)4	+	**69**	26
* *Lonchocarpus hedyosmus* Miq. WS 90Ā (± 50; 18) . .	**100**	**1–2**	—	9	28
Andira coriacea Pulle S 13 (0; 23)	27	2–4(5)	—	22	0
* *Andira surinamensis* (Bondt) Splitg.; deH 45 (–; ± 16) .	**46**	**(1)2–4**	—	13	7
* *Dipteryx odorata* (Aubl.) Willd.; S 19 (± 50; ± 18)	**42**	**2–4**	+ & —	12	9

species. The feature is typical for the taxon as was also noted by JANSSONIUS (1918) in all of the Javanese species examined by him. Storied structure by RIJSDIJK (unpublished) was found in many species, which in Table III are marked with an asterisk.

From these facts it appears that the storied-structure features are more abundant in the Papilionaceous taxon than in the Mimosaceous and Caesalpiniaceous taxa.

DISCUSSION

In reviewing the distribution of the units of the storied-structure-features as revealed in this investigation it can be stated that:

(i) The parenchyma-strand features occur in a lessening degree from the Papilionaceous to the Mimosaceous to the Caesalpiniaceous taxon.

(ii) The horizontal-layer-feature of the libriform fibres occur in the same sequence.

(iii) The other two features in the libriform fibres occur in a lessening degree from the Papilionaceous to the Caesalpiniaceous to the Mimosaceous taxon.

It is significant in this connection that JANSSONIUS (1918) found the same sequence for the taxa as recorded in (i) from his research on Javanese Leguminosae. Unfortunately no data are available about (ii) and (iii). In a later paper JANSSONIUS (1931) has given a general survey about the occurrence of what he introduced as the storied-structure-features. Janssonius in that survey considers the gable-end feature to be the most important one of the storied-structure complex.

The reason for this is clear. Gable ends appeared to occur in such families only as also show storied structure in at least some of the members. This unit did not appear in families where storied structure does not occur. This, as has been stated on p. 464 cannot be said of the other units; therefore, the present author awaiting further research, in the mean time proposed to require a certain percentage for presence of the latter ones.

Storied-structure itself was not recognized by Janssonius as a very important feature, since he found incidental exceptions to the rule that Papilionaceae are characterized by presence of storied structure and Caesalpiniaceae by absence of that feature. In this point the writer does not agree with Janssonius. Storied structure occurs more often in the Caesalpiniaceous taxon and much less in the Papilionaceous taxon than Janssonius could suppose from the accidental genera and species examined by him.

As regards the taxonomic rank of the Leguminous taxa from a wood anatomical point of view, with the evidence at hand, each one of the three common classification schemes could be adopted. Choice depends on the value that is attached to the various characters present in the taxa.

In such a highly specialized group as the Leguminosae it cannot be expected that the families will differ as much among each other in wood anatomical structure as is the case in unspecialized groups. As appears from the work of REINDERS-GOUWENTAK and RIJSDIJK (1955) the taxa have many features in common but are specifically different with regard to the most important ones of the storied-structure features.

When accepting Janssonius's view about the significance of presence or absence of gable end cells in the parenchyma strands and accepting the importance of the storied structure, the distance between the Mimosaceous taxon on one side and the other two taxa together on the other side is greater than the differences among the three taxa separately. From this point of view, there would be two distinct families, the Mimosaceae and the Papilionaceae, the latter with two subfamilies: Caesalpinioideae and Lotoideae (Papilionatae). This classification agrees with the scheme of PULLE *et al.* (1939–1940) from exomorphic data.

If, on the other hand, taxonomists in future would agree upon a

family status of the taxa, wood anatomy could also lend support to this conclusion if it would only drop the belief in the importance of the gable-end and the storied-structure feature. Then, the distance between the Mimosaceae on one side and the rest of the taxa on the other side would become less evident and quantitative only. The Mimosaceae thus would be the family with the least number of storied structure features, closely followed by the Caesalpiniaceae; and the Papilionaceae would be largely different from both through the great number of features.

REINDERS-GOUWENTAK and RIJSDIJK (1955) admit the presence of vestigial storied structure in the Mimosaceous taxon in the immature wood. Storied structure was found in the immature wood of *Plathymenia* in a slide obtained on loan from the wood collection of the Imperial Forestry Institute, Oxford. METCALFE and CHALK (1950) even mention more genera, without, however, indicating whether mature or immature wood was investigated. Neither Janssonius nor Reinders-Gouwentak and Rijsdijk recorded storied structure in mature Mimosaceous woods. JANSSONIUS (1931) stated that in a family (e.g. Moraceae) where storied structure occurs in some genera or species some of the taxa may not show storied structure and only possess one or more features of the storied structure complex. From this point of view the three taxa could be also treated as subfamilies. However, in this case also the gable end feature and the storied-structure feature itself would have to be considered minor features of the same rank as those examined for this investigation.

Which one of the three possibilities will be the most desirable one from a wood anatomical point of view can only be determined after a closer examination of the occurrence of gable ends and the minor features in not only more genera and species of the Leguminous taxa but also in other families. The correlation between the occurrence of the features and the classification scheme to be adopted by taxonomists should also have got to be studied.

SUMMARY

The distribution of the minor storied-structure features in the Leguminous taxa is recorded. The features mentioned in the first three columns of the Tables occur in a lessening degree from the Papilionaceous to the Mimosaceous to the Caesalpiniaceous taxon. The other features occur in the sequence Papilionaceous, Caesalpiniaceous, Mimosaceous taxon.

From a wood anatomical point of view the taxa may be elevated to family rank or divided into 3 subfamilies or 2 families may be distinguished viz. Mimosaceae and Papilionaceae, the latter family subdivided into 2 subfamilies.

Which classification is desirable cannot be decided at present, although the distribution of the major storied-structure features might be in favour of accepting two families.

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