RAY TERMINOLOGY IN WOOD ANATOMY

BY

CORNELIA A. REINDERS-GOUWENTAK

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§ 1. Introduction.

The present author in an earlier article (9) discussed a classification of rays into homogeneous and heterogeneous rays, both groups containing many rays of distinct structure (see this paper fig. 1). At the same time there appeared a paper prepared by Miss M. M. CHATTAWAY who proposes an alteration of the definition of homogeneous and heterogeneous rays in the Glossary of terms of 1933 (5). The revised definitions differ from those presented by JANSSONIUS (7, vol. IV) and commented by the present writer in her earlier article.

Miss CHATTAWAY's definitions are based on cell shape and cell functions the latter being gathered from cell contents, pitting and staining properties of the wall. The rays in which all the cells, which adjoin the *same* elements, are similar regarding cell shape, contents and pitting, are homogeneous rays. Heterogeneous are the rays in which one or more of these conditions are not fulfilled. However, under such conditions it is evident that the term homogeneous can only seldom be applied. All the conditions required for homogeneity will almost never be present.

To all probability Miss CHATTAWAY is right in assuming functional differences between pitted and unpitted ray cells and between ray cells with different cell contents, but it is not a reason for involving physiology in anatomical classification matters. The stem of a Cactus has a photosynthetic function, but in morphological studies Cactus stems are not classified with the leaves of non succulents. And there is even more to say against Miss CHATTAWAY's concept of homogeneity.

According to Miss CHATTAWAY a homogeneous ray should be a ray composed of procumbent cells or of erect cells only provided all of the cells are also similar in "function" when in contact with the same elements. For example: in a homogeneous ray the cells contiguous to vessels are all of them pitted or all of them not pitted at all, but where the ray cells are adjoining fibres the pitting may be another one than where the ray cells are in contact with vessels.

The question might be asked whether the pits of all the cells which are in contact with a vessel or fibre etc. are all of them of the same shape, dimension, number? Certainly not so. But why not these requirements too? Why draw the limit elsewhere? What, moreover, do such definitions of homogeneous and heterogeneous rays help in the urgent need for supplying identification features of woods? Miss CHATTAWAY in collecting these cell features highly contributed to the increase of our knowledge about rays but the features mentioned are features in detail and not likely to be of use for ray classification purposes.

No cell details but structure of rays should be used for the classification of rays. A first step was already done by RECORD and CHATTAWAY (8) and one may only wonder why Miss CHATTAWAY did not continue her investigations of *structural* specialization of rays.

From a structural point of view rays have been classified into homogeneous and heterogeneous rays by JANSSONIUS (7) but with the german terms: einfache and zusammengesetzte Markstrahlen. Thanks to our present knowledge of rays JANSSONIUS' work could be supplemented and the results recorded in a key for identification of homogeneous and heterogeneous rays (9).

A key though easy for manipulation is not the form to be used in a glossary of terms. This paper, therefore, presents definitions of homogeneous and heterogeneous rays as covered by the key but which now might be included in a glossary of terms. In connection with Miss CHATTAWAY'S recent work a review of the author's previous article will precede the definitions.

§ 2. Discussion of the terms homogeneous and heterogeneous and allied terms.

Miss CHATTAWAY in concluding her paper states "that there are good grounds for discontinuing the use of these terms and replacing them with something entirely different". The present author cannot agree with her. To discontinue the use of the terms homogeneous and heterogeneous would lead to too many sequels. The terms homogeneous type and heterogeneous type of KRIBS (6) would have to disappear too, what with the work of KRIBS well introduced in literature would rather be a disadvantage. Furthermore, KRIBS proposed the terms homocellular and heterocellular to replace the terms homogeneous and heterogeneous of the Glossary (5). Recently the terms homogeneous ray and heterogeneous ray (REINDERS-GOUWENTAK (9)) were proposed for various rays constituting the homogeneous types and heterogeneous types of KRIBS; this third type of terms then would have to disappear too. To the present authors opinion all the terms are entirely adequate ones if one can only divorce the words from their proper meaning what in many cases (wood) anatomists appear to have done with other terms.

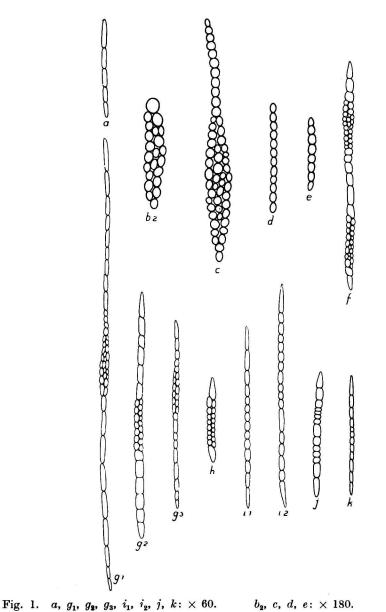
Properly speaking KRIBS proposed the term *homocellular* for rays formed of procumbent cells only, but extending the usage to rays composed of erect (square) cells seems adequate. The term *heterocellular* has to be applied to a ray composed of both types of cells, the erect (square) and the procumbent cells. Now, according to p. 5 of her recent paper Miss CHATTAWAY objects to using such terms as erect and procumbent. But how serious is this objection? Is not the point missed? The terms "erect" and "procumbent" surely are not meant to cover transitional stages too. There will be always cells which are neither erect nor procumbent; erect to procumbent would be the proper term for them. Do these difficulties arise only in wood anatomy or has not morphology to deal with the same trouble in applying such terms as circular, elliptical, oblong etc. for the indication of special shapes of leaves?

The terms homogeneous type of rays and heterogeneous type of rays introduced by KRIBS (6) indicate specific ray combinations, each combination a constant feature in genera or families. Leaving the question of terminology to others KRIBS enumerated rays constituting the homogeneous and heterogeneous types. For example, the heterogeneous type I in Dillenia. In this wood the ray tissue consists of high uniseriate rays composed of very large elongated cells and of multiseriate rays composed of a middle multiseriate portion of procumbent cells and very long marginal extensions which are composed of cells identical with those of the uniseriate rays.

REINDERS-GOUWENTAK (9) in joining JANSSONIUS' concept of ray structure established that for example KRIBS' rays of the heterogeneous type I are represented by the rays which are reproduced in fig. 1 of this paper in a and g_1 , a being identical with the uniseriate extension in g_1 . All the other rays of KRIBS' combinations and even more than are mentioned by him may be found in fig. 1, 2 (p. 1268 and 1269), 3 (p. 1270) and 4 (p. 1271). In Dillenia there are also present rays identical with h (fig. 1). The rays g_1 are, as it were, composed of three individual rays. The uniseriate extensions are identical with the uniseriate ray a, the multiseriate portion is similar in structure to a separate multiseriate ray h.

JANSSONIUS (7, Vol. IV, p. 403) writing in german designated such rays a as "einfache" rays of the first kind, the multiseriate rays as "einfache" rays of the second kind and rays g_1 as "zusammengesetzte" rays. The present writer in her previous article (9) proposed homogeneous rays of the first kind, homogeneous rays of the second kind and heterogeneous rays as english terms.

It is clear that another meaning is attached now to the terms homogeneous and heterogeneous than in the Glossary. In the latter the terms are used to indicate the presence of a specific cell shape within rays; now they are used for purposes of emphasizing different structural composition. The writer is fully aware of the objections there may be made to an alteration of definitions but retaining of terms. Yet, in her opinion, the advantages of preserving the terms for ray classification are still greater. In the sense now attached to them the terms may prove a success together with the terms homocellular and heterocellular, homogeneous type and heterogeneous type of KRIBS. Confusion is already so great that for years to come we cannot do without mentioning author's names in all matters concerning terminology of rays. It may be thought that it will help to reduce confusion or rather prevent.



f, $h: \times 90$.

- a. Homogeneous ray of the first kind; all cells upright.
- b_2 . Homogeneous ray of the second kind; all cells procumbent.
- c. Heterogeneous ray, with uniseriate tier of procumbent cells.
- d. Homogeneous ray of the first kind; all cells procumbent.¹)
- e. Homogeneous ray of the second kind; all cells procumbent.¹)
- f. Heterogeneous ray composed of 5 tiers.
- g_1 . Heterogeneous ray composed of 3 tiers; the uniseriate tiers very high.
- g_2 . Heterogeneous ray composed of 3 tiers; the uniseriate tiers lower.
- g_3 . Heterogeneous ray composed of 3 tiers; the uniseriate tiers with radial rows of procumbent cells.
- h. Homogeneous ray of the second kind. See also fig. 4, f on p. [1271].
- i_1 . Heterogeneous uniseriate ray of 3 tiers.¹)
- i_2 . Heterogeneous uniseriate ray of many tiers.
- j. Heterogeneous uniseriate ray of 5 tiers.
- k. Homogeneous uniseriate ray of the first kind 1) with radial rows of procumbent cells.

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¹) The rays d and e are quite identical and so are the rays i_1 and k, but an examination of all ray types in the same sample shows them to belong to different kinds: d occurs with c, e with b_2 ; k with g_3 , i_1 not with g_3 (for explanation of kinds, see text).

1269

§ 3. Homogeneous and heterogeneous rays.

In many woods there are (among others) rays which are composed of two, three or more vertically arranged stories, alternately composed of uniseriate tiers of erect cells or of erect and procumbent cells, and of multiseriate tiers of mainly procumbent cells. Such rays are examples of the most simple form of heterogeneous rays of 3 stories (fig. 1: g_1, g_2, g_3), of 2 (fig. 2: a, b) or of more than 3 stories (fig. 1: f). In a wood containing

Fig. 2. Sarcocephalus cordatus Miq. All × 60.
a. Heterogeneous ray composed of two tiers. The uniseriate tier of upright cells is short.
b. As a, but the uniseriate tier is longer. (Reproduced by permission from Med. Landbouwhogeschool Wageningen, 1949).

such heterogeneous rays, there occur always or nearly always uniseriate rays (locally biseriate) too made up of erect cells only (fig. 1: a) or of erect cells and procumbent cells (fig. 1: k). These rays are homogeneous rays of the first kind (cf. § 2).

Sometimes, for example in Ficus and in Acer (fig. 1: c) some or all of the multiseriate rays are made up of a multiseriate storey of procumbent cells and a uniseriate storey of procumbent cells too. To the authors opinion these rays too are *heterogeneous rays*, although the rays are homocellular. That it is the right thing to do is proved by the presence of multiseriate rays with a uniseriate margin of both erect and procumbent cells or of erect cells only in the same or in allied species (fig. 3), while in that case uniseriate rays occur which are identical with the margins of the multiseriates. These uniseriate rays are all of them *homogeneous rays of the first kind*, although in some of them erect cells occur mingled with procumbent ones and so the rays are heterocellular. But *homocellularity* and heterocellularity are not the criteria for homogeneity and heterogeneity; only the structural relations between rays are.

The length of the uniseriate extension is important. When only 1 cell is forming the uniseriate parts whether procumbent (fig. 1: b_2) or erect (fig. 1: h), the ray is considered a homogeneous ray of the second kind, even when some or all of the cells of the first (or of the first and second) row of the multiseriate part which are contiguous to the erect uniseriate part of the ray are erect too (fig. 4: f). So it is only the number of the cells in the uniseriate part which determines whether the ray is to be considered a homogeneous ray of the second kind or a heterogeneous ray, and so ray g_1 , g_2 and g_3 of fig. 1 are heterogeneous rays (composed of three stories) and ray a and b of fig. 2 are heterogeneous rays too (composed of 2 stories) and ray b_2 and h of fig. 1 are homogeneous rays of the second kind. According to JANSSONIUS the length of the uniseriate extension, however, is only important for rays which are composed of two or three parts,

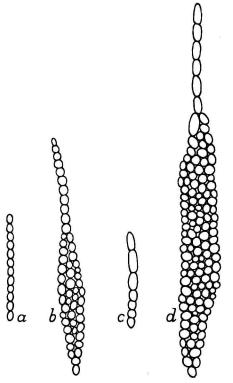


Fig. 3. Acer campestre L. All \times 180.

- a. Homogeneous ray of the first kind but composed of procumbent cells.
- b. Heterogeneous ray, the uniseriate tier composed of procumbent cells as the ray of 3a.
- c. Homogeneous ray of the first kind, composed of upright cells with radial rows of procumbent cells.
- d. Heterogeneous ray, the uniseriate tier composed of upright cells.

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in rays composed of more parts (see fig. 1: f) one cell is already forming a storey.

In specific cases a uniseriate ray composed of both erect and procumbent cells (arranged in tiers) is itself a heterogeneous ray (fig. 1: i_1 , j), viz. if the uniseriate rays are not identical with the uniseriate margins of multiseriate heterogeneous rays present.

Heterogeneous rays. It may be clear that a heterogeneous ray can be made up of both erect and procumbent cells or of procumbent cells only and is always characterised by showing a marginal extension that is uniseriate or locally biseriate. But for the same reasons a ray made up *entirely* of erect cells may be a heterogeneous ray too provided it is composed of a multiseriate part of erect cells and one or two uniseriate extensions of erect cells. The present author stated this already in a footnote of her previous paper (9) p. 224 and she agrees here completely with JANSSONIUS (7) who suggested it (Part VI p. 290).

Homogeneous rays of the first or of the second kind. A uniseriate ray

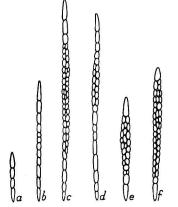


Fig. 4. Alstonia scholaris R.Br. All \times 60.

- a. Homogeneous ray of the first kind. Upright cells only.
- b. Homogeneous ray of the first kind. Upright cells and radial rows of procumbent cells.
- c. Heterogeneous ray. The uniseriate tiers composed as 4a.
- d. Heterogeneous ray. The uniseriate tiers with radial rows of procumbent cells (as 4b).
- e. Homogeneous ray of the second kind with one uniseriate row of upright cells at the margins; see text.
- f. Homogeneous ray of the second kind with one uniseriate row of upright cells at the margins; one of the uppermost radial rows of the multiseriate part with an upright cell on tg. face.

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which is composed of either erect (fig. 1: a) or procumbent (fig. 1: d, e) cells is always a homogeneous ray. If it is also present as uniseriate margin in another uniseriate ray, as in i_1 (fig. 1) or in a multiseriate ray as in g_1 , c (fig. 1) of the same wood species, the uniseriate is a homogeneous ray of the first kind (a, d). But, if in the same wood species, it is not present as a margin the uniseriate ray is a homogeneous ray of the second kind (fig. 1:e). Consequently homogeneity of uniseriate rays may be reached along two different paths. For purposes of emphasizing the difference in homogeneity JANSSONIUS distinguished the two kinds of homogeneous rays. The present writer in suggesting these english terms in her recent publication (9) wrote she would have preferred the word type instead of kind, but could not because of KRIBS having the term type already used in another meaning.

Homogeneous rays of the first kind. For reasons of compilation we may now repeat that homogeneous rays of the first kind comprise the rays which in the same wood species are accompanied by heterogeneous rays in the uniseriate extensions of which they are mirrored. As a rule the homogeneous rays of the first kind are uniseriate but sometimes locally biseriate; they are either composed entirely of erect cells (*Diospyros*, *Dillenia*, *Alstonia* (fig. 4: a)) or they are made up of erect cells mingled with procumbent cells (*Sarcocephalus*, *Alstonia* (fig. 4: b), *Acer* (fig. 3: c)) or they possess procumbent cells only (*Acer* (fig. 3: a); *Ficus*).

Homogeneous rays of the second kind. In the second kind of homogeneous rays are placed the uniseriate homogeneous rays which are not accompanied by the heterogeneous rays mentioned. The uniseriate homogeneous rays of the second kind may be constituted of either erect or procumbent cells. If made up of erect cells they are more or less similar in shape and size to the homogeneous rays of the first kind as depicted in fig. 1: a and possibly only occur in semi-shrubs and herbs (BARGHOORN (1)); these rays had not yet been fitted into the key for identification of homogeneous and heterogeneous rays (9). If constituted of procumbent cells (fig. 1: e) the rays are similar in shape to such homogeneous rays of the first kind as depicted in fig. 1: d. In the second kind of homogeneous rays are also placed the *multiseriate* rays without a uniseriate extension and those where the uniseriate extension is only 1 cell high (fig. 1: b_2 , h) or/and those where the first or second upper(lower)most row(s) of the multiseriate part contain erect cells too (fig. 4: f). In connection with the multiseriate heterogeneous rays mentioned above which are entirely composed of erect cells the rays which are identical with the body of erect cells of these heterogeneous rays are also homogeneous rays of the second kind (Pipturus).

Miss CHATTAWAY's question in the Newsletter (2) p. 2 where we are to fit the rays of *Pipturus* etc. has been answered now. In the highly specialised woods of some of the Urticaceae, the Loganiaceae etc. the homogeneous rays of the second kind are constituted of erect cells. This is probably due to a transformation of ray initials to the more fusiform type of cambial cells and as such a step towards complete elimination of rays (cf. BARGHOORN (1)).

Sheath cells and tile cells do not interfere with the classification of rays, but are merely identification features in the description of wood specimens. The rays of some woods, for example those of the *Flacourtiaceae* and *Rubiaceae*, contain single erect cells or rows of such cells between the procumbent cells of the multiseriate part of a heterogeneous ray or of a homogeneous ray of the second kind; these erect cells must not be taken into account in ray classification matters. But of course they too deserve attention as special identification features in woods. The same may be said about pitting and contents of ray cells.

In all rays mentioned one ray cambium is involved. By the superposition of two or more ray cambia vertically fused rays are the result of their activity (fig. 5: a and b). The constituent rays of the vertically fused ray must be classified separately. The writer has been able to discern vertically fused rays from heterogeneous rays in most cases studied. HUBER (4) perhaps did not see enough examples of these kinds of rays to arrive at the same conclusion.

It should be well borne in mind that ray structure has to be studied in those places, where the rays are embedded in libriform or fibertracheid

Fig. 5. $a, b \ (\times 60)$. Vertically fused rays, each formed by two ray cambia. In a the cambia somewhat more fused and forming a 2-storied heterogeneous ray and a homogeneous ray. In b both the constituent parts are homogeneous.

tissue, as their cells are often different in shape where contiguous to vessels or to parenchyma. Since the rays in the inner secondary xylem differ often in structure from the rays in the outer, wood samples should not be taken too near to the primary xylem. That because of this rays should not show reliable features for wood identification as BARGHOORN (1) expects has not been evidenced (see also CHOWDHURY (3)).

In a previous paper (REINDERS-GOUWENTAK (9)) the ray characteristics enabling a classification into homogeneous and heterogeneous rays have been recorded in key form. However, definitions suiting more the concise form of a glossary are not an impossibility. But with such far from simple structures definitions cannot be short nor are they easily read and for routine purposes the key mentioned will perhaps prove more useful than the ponderous definitions.

§ 4. Definitions.

Heterogeneous rays.

I Multiseriate rays composed of 2 (fig. 2), 3 (fig. 1: g) or more (fig. 1: f) vertically arranged tiers, alternately uniseriate (locally biseriate) and multiseriate.

The uniseriate tiers composed of:

- 1. erect cells (fig. 1: g_1 ; fig. 3: d; Urticaceae),
- 2. procumbent cells (fig. 1: c),

3. erect and procumbent cells (fig. 1: g_3).

The multiseriate tiers composed of:

- 1. procumbent cells (fig. 1: g, c),
- 2. procumbent cells with 1 or 2 upper- and/or lowermost rows of erect cells,
- 3. procumbent cells with crect cells or rows of cells scattered between,
- 4. erect cells only (Urticaceae etc.).

II Uniseriate rays composed of 2, 3 or more alternating tiers of erect and of procumbent cells and not being present also as the uniseriate marginal tier of another ray (fig. 1: i_1 , i_2 , j).

Homogeneous rays of the first kind: uniseriate or locally biseriate rays, which are identical with the uniseriate (or locally biseriate) margin of another ray.

Composed of:

- 1. erect cells (fig. 1: a; cf. fig. 1: g_1 and fig. 3: d),
- 2. procumbent cells (fig. 1: d cf. fig. 1: c),
- erect cells mingled with procumbent cells (fig. 1: k, cf. fig. 1: g₃; fig. 3: c).

Homogeneous rays of the second kind: uniseriate (locally biseriate) rays not occurring also as marginal tiers of other rays, and multiseriate rays without uniseriate extension(s) or with a uniseriate extension one cell in height.

If uniseriate (locally biseriate), composed of:

- 1. erect cells (probably only in semishrubs and herbs),
- 2. procumbent cells (Leguminosae fig. 1: e; Quercus),

If multiseriate, composed of:

- 1. procumbent cells (admitting local presence of sheath cells or of erect cells scattered between) (fig. 1: b_2),
- 2. procumbent cells with one uniseriate row of erect cells forming the upper or/and lower margin (fig. 1:h) (admitting local presence of sheath cells or of erect cells in the body),
- 3. as 2, but also in the first and/or second upper and/or lower row(s) of the multiseriate part erect cells (fig. 4: f),
- 4. erect cells (admitting local presence of procumbent cells), e.g. Urticaceae.

Summary.

KRIBS' proposal to replace the terms heterogeneous and homogeneous in the Glossary with heterocellular and homocellular is sustained with a slight alteration in application.

The terms homogeneous ray and heterogeneous ray are introduced again but now to indicate different structural composition, the heterogeneous ray though formed by one ray cambium, yet, as it were, composed of two homogeneous rays.

Vertically fused rays consist of several rays which, as viewed tangentially, have not become confluent and are each of them formed by a separate ray cambium.

KRIBS' homogeneous and heterogeneous types are formed by two or more single homogeneous or homogeneous and heterogeneous rays. Definitions of homogeneous and heterogeneous rays are composed and recorded into such a form as renders them suitable for a Glossary of woodanatomical terms.

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