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## Using the InsideWood web site: Potentials and pitfalls

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### ABSTRACT

The InsideWood web site is a freely accessible resource for research and teaching in wood anatomy and includes a multiple-entry key to aid in wood identification. Its database has over 9400 descriptions of fossil and modern woody dicots, representing over 10 000 species and 200 plant families, and is accompanied by over 50 000 images. The descriptions and the multiple key use the numbered features of the *IAWA List of Hardwood Features for Wood Identification*. The background for creating this web site, the rationale for how descriptions in the database were created, and the basics for using the multiple-entry key are given. The potentials of the ever-expanding and continuously edited database for microscopic wood identification are enormous. Yet many users experience problems when attempting the identification of an unknown sample. The main reasons for this are (1) erroneous or ambiguous interpretation of the IAWA Hardwood features; (2) incomplete coverage of the infraspecific wood anatomical variation in the literature for numerous entries in the InsideWood database. Against this background, we review all individual features of the IAWA Hardwood List and give their frequency in the database, and we suggest how to use their presence or absence in the multiple-entry key. All this is done with an awareness of the limitations of the IAWA Hardwood List and InsideWood. We give two examples of using InsideWood to try to identify an unknown wood. It cannot be overemphasized that it is necessary to consult reference materials (slides, literature descriptions) to verify the identification of an unknown.

**Keywords:** wood identification; IAWA Hardwood List; *Thespesia*; *Pistacia*.

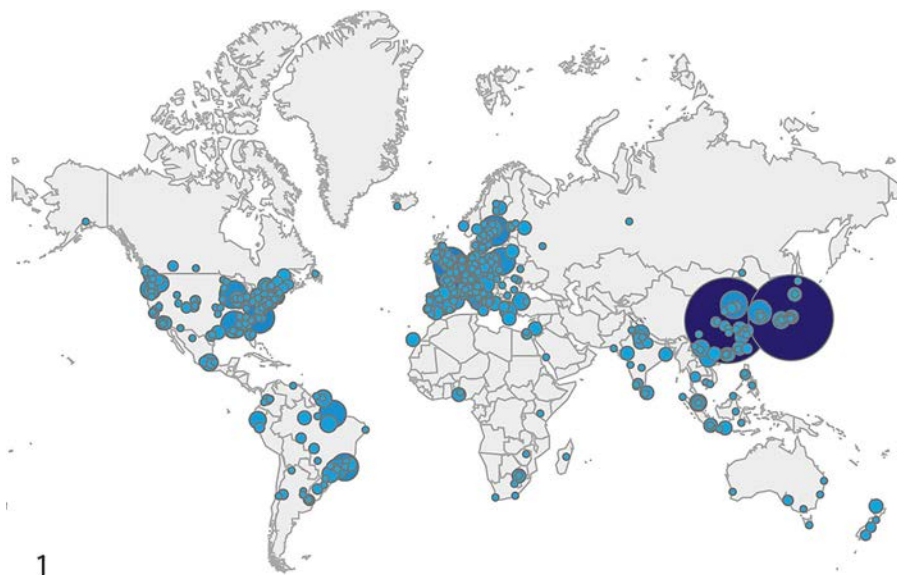


Figure 1. Map showing locations (cities) of InsideWood users in January 2020. The larger and darker the circle the more users at that location. Within a large dark circle representing a location with many users, there may be smaller circles representing localities with fewer users, for example in eastern Asia, the large dark circle for Chuo City encompasses smaller circles representing Hichioji, Tsukuba, and Yokohama.

## INTRODUCTION

InsideWood (2004-onwards) is arguably the most successful web-based tool for microscopic wood identifications and/or retrieving wood anatomical data on a large number of extant and fossil angiosperm trees, shrubs and lianas. Its use is literally worldwide (Fig. 1), and with use increasing in recent years from 8948 individual users and 32 096 sessions in 2014 to 12 326 individual users and 38 240 sessions in 2019. In 2019, there was a monthly average of 1245 active users from 67 countries. Despite its success, many users experience problems — partly due to limitations of the database, partly due to misunderstandings of feature definitions in the IAWA Hardwood List (IAWA Committee 1989) which are at the core of InsideWood. This paper aims to clarify these issues, and thus assist both beginners and seasoned users of InsideWood.

Our experiences in teaching short courses in wood anatomy, reviewing manuscripts, and interacting with individuals interested in wood identification have made us think that it would be useful to share how we describe an unknown for wood identification, such as coding the presence/absence of selected features. The majority of this paper describes issues with individual features and details how they are coded in the InsideWood database. Anyone who uses InsideWood should be aware of its limitations, be willing to be flexible, and recognize that there is no single best way to search InsideWood to identify an unknown.

Using InsideWood is but a start to an identification and it is essential to confirm your identification by consulting the literature and, if available, slides or blocks of vouchered wood samples. This paper will be most useful to those with some familiarity with the IAWA Hardwood List (IAWA Committee 1989) and the InsideWood web site (<https://insidewood.lib.ncsu.edu>), but it also serves as an introduction to using the InsideWood web site.

## BACKGROUND

### *History of the InsideWood database*

This project was started in the 1980s to help with identifying fossil dicotyledonous woods. For the reasons given below, when working with fossil woods or woody remains of unknown origin, it is important to use a multiple-entry key that has broad geographic coverage and gives flexibility in choosing which features to use and in what order they are used.

1. Fossil woods may be related to present-day taxa that today occur on a continent other than the one where the fossil was found, so it is important to consider woods of different geographic areas.
2. Many dichotomous keys use specific gravity or colour, features that aren't useful for fossil woods or subfossil woods that have been buried for many years.
3. Not all diagnostic features may be visible in a fossil wood or archaeological sample because it is not well-preserved.

Chalk's Oxford cards and the family by family wood anatomical descriptions in *Anatomy of the Dicotyledons* (Metcalf & Chalk 1950) provided such broad coverage.

Chalk recorded data on punch cards (one species or species group per card) as per Clarke (1938) that could be sorted by feature and used as a multiple entry key. In the 1980s, these Oxford card data were recorded in a format that could be searched by a mainframe computer (Pearson & Wheeler 1981). Subsequently, data were added from the Princes Risborough lab (Brazier & Franklin 1961), the CTFT atlases (Normand & Paquis 1976; Détienne & Jacquet 1983), and post-1950 literature coded at N.C. State University. This resulted in the OPCN database, which used the same features as the Oxford cards. The OPCN database was accompanied by the GUESS search program and distributed on diskettes for use on personal computers (Wheeler *et al.* 1986; LaPasha & Wheeler 1987).

With the development of the world wide web and the IAWA Hardwood List, a logical next step was to translate the OPCN database into a database using the *IAWA List of Microscopic Features for Hardwood Identification* and make the database publicly accessible and searchable. The translation from the Oxford Card features to the IAWA Hardwood List was done using a computer program. The IAWA List has more features than the Oxford cards, consequently, some IAWA features were translated as unknowns — a “?” follows the feature number. Since that initial translation, the database has continually been edited and many “?”s have been replaced by data. A pdf (translation.pdf) with details of the translation is available at <https://insidewood.lib.ncsu.edu/databasedetails>.

InsideWood has been available online since 2004 and since that time descriptions have been added and corrections continue to be made. In 2007, images were added to the web site to serve as a virtual reference collection of photomicrographs. Not all descriptions are accompanied by images and not all images are linked to descriptions (Wheeler 2011).

Paleobotanists who work on Paleogene or Cretaceous woods have objectives somewhat different from those who are trying to identify commercially important woods or trying to determine the species and geographic source of an antique or archaeological wooden object. For older fossil woods, a search of InsideWood that results in 100 or fewer suggested matches often is good enough and can indicate to which families and orders the fossil may belong.

For modern woods, it is important to go back to the literature used to prepare the InsideWood descriptions and also look at reference images in the InsideWood database. You should be suspicious of getting a single match (genus or species), although this sometimes happens for woods with a distinctive combination of features (*Acer* or *Zelkova*).

#### *Descriptions in the InsideWood Database*

The anatomical descriptions in the IW database are in the tradition of multiple entry card keys: only features present are stored and displayed. The descriptions use features from the *IAWA List of Features for Hardwood Identification* (IAWA Committee 1989). Because the objective of the InsideWood web site is primarily wood identification, some descriptions represent multiple species because those species share similar wood anatomy and information to date indicates it is not possible to distinguish them based on their microscopic anatomy, such as different species of the red oaks. On the other hand, some species have more than one record. These species are ones that are commercially important or common and widespread modern species that have been described by multiple authors, or fossil woods that occur at different localities (each occurrence of a fossil species is treated as a separate record).

Investigators interested in incidences of features need to be aware that if they search for a particular feature, the number of descriptions retrieved does not equal the number of species with that feature. Some publications did not provide information on some features, such as vessel-ray parenchyma pits or vessel element lengths; in such cases, the feature numbers are followed by a “?”.

#### *Variability*

Wood is variable, and most descriptions are based on only a few samples or even a single specimen. Consequently, an InsideWood database description surely does not represent the full variability of a species. Although this database is relatively large, certainly not all woody species are represented; an unknown wood may belong to a species not represented in the database. Also, not only is wood variable, but wood anatomists vary in their interpretations and descriptions, especially of fibre pits, growth ring distinctiveness, and porosity. InsideWood users need to be aware of these different sources of variability that affect the coding of the database.

If a feature is present in some samples of a species but absent in others, or if a feature is borderline with a tendency to show a feature, that feature will be coded as variable in the database with the feature number followed by a “v”. For example, gv indicates that the wood sample is close to having exclusively solitary vessels but does not meet the criterion of >90% solitary.

### *Basics of searching*

There are two options for searching the InsideWood database — use the menu or enter feature numbers followed by p for present, a for absent, r for required present, e for required absent. Features coded v in the database will match searches using either p’s (present) or a’s (absent), but not r’s (presence required) or e’s (absence require). Features coded “?” in the database will also match searches using either p’s (present) or a’s (absent), but not r’s (presence required) or e’s (absence required).

You can search for an exact match to a description of an unknown, so that only taxa that have all the features designated as present and all the features designated as absent are in the results of a search. Alternatively, you can allow mismatches and search for taxa that differ in one or more features from the unknown.

We appreciate that it can be frustrating to use InsideWood for identification, especially for present-day woods where you would like to be presented with only a few possibilities. If a large number of possibilities results from a search, continue to add features until a number that you feel comfortable working with is returned. Exporting the results as a tab-delimited file (TSV file) and then converting it to an Excel file you can sort allows you to look at how the possible matches differ and can help in deciding which additional features to use. Details on how to export are available in the slide set ‘About InsideWood’ on the InsideWood welcome page. If the majority of the results are for only a few families, the next best step would be to look at the literature on those families and go to the image collection to browse through the images for those families.

It is not uncommon, especially if you use a large number of features in a search, to get this message “No results found for search criteria. Please try a different search.” If this happens, one useful option is to do subsequent searches allowing for one or more mismatches between the features you coded and the description in the database, if you allow for one mismatch the results will include woods that have all but one of the features used. The results of a search using mismatches will list the mismatched features for each taxon. The subsequent section on the InsideWood features can help you decide if the mismatched features are significant. For example, if the unknown had scalariform perforation plates, you could exclude the taxa that mismatched in having exclusively simple perforation plates.

### COMMENTS ON INDIVIDUAL FEATURES IN THE *IAWA LIST OF MICROSCOPIC FEATURES FOR HARDWOOD IDENTIFICATION*

The IAWA Committee (1989) defined and illustrated 163 wood anatomical features and gave extensive explanatory comments and caveats on how to use or not to use them in a wood identification procedure. Below we discuss some problems that may arise when using the numerical codes defined in the IAWA Hardwood List and comment on the diagnostic value

of most features. For each set of features, we give in parentheses the sections in which the features are visible — transverse (TS), tangential longitudinal (TLS), radial longitudinal (RLS). We give background on how different features were recorded in *InsideWood* descriptions and make recommendations on how to code features when attempting an identification (ID), noting particular issues with fossil woods. Table 1 gives the incidence of each feature in the *InsideWood* database. After the discussion of the features, we give two examples of how we have used *InsideWood* to try to identify an unknown.

#### GROWTH RINGS (TS)

1. Growth ring boundaries distinct
2. Growth ring boundaries indistinct or absent

Seemingly, these should be easy features to code. However, these two features generated the most discussion at the workshop creating the IAWA Hardwood List. Pierre D tienne (formerly of CIRAD) with his considerable experience with Neotropical and Paleotropical hardwoods did not think these features were generally useful for species identification. Meanwhile, an extensive literature is developing on growth periodicity in tropical woods (Silva *et al.* 2019), showing that a high proportion of tropical trees have growth rings even in rainforests with only a mild dry season. All present-day, above-ground, temperate-zone woods have distinct growth ring boundaries, and no one seems to have a problem accepting that feature 1 applies to these species. However, it isn't particularly easy to make decisions about these features in tropical woods because rainfall periodicity may cause irregular density variations or discontinuous marginal parenchyma bands that some might describe as distinct while others might call them indistinct. In the literature reviewed to add descriptions to *InsideWood*, some tropical species were described as having distinct growth rings, yet the illustrations of these woods did not show distinct growth rings as seen in temperate zone woods. The descriptions of these woods in *InsideWood* usually include a 1v. If you search *InsideWood* for the presence of both features 1 and 2 (1p 2p) in present-day woods, you will recover 1,456 descriptions. When a species has a wide geographic range, the growth ring boundaries may be distinct at higher latitudes and in regions with variation in rainfall, but indistinct in rainforests at lower latitudes. In case of doubt, don't use these features in an identification (ID) procedure.

In the Cretaceous and Paleogene, it is believed that seasonality was less pronounced in what are now temperate areas. Because of this, we recommend not using Feature 2 when looking for relationships of woods of those ages because the present-day relatives could have distinct growth rings. Growth rings can be wide in fossil woods, so small thin sections might not capture what appeared to the unaided eye to be distinct growth ring boundaries; distinct vs indistinct boundaries should be determined microscopically.

#### POROSITY (TS)

3. Wood ring-porous
4. Wood semi-ring-porous

### 5. Wood diffuse-porous.

Because ring-porous and semi-ring-porous are uncommon features (Table 1), they are useful for narrowing a search; coding for their presence eliminates over 90% of the InsideWood records. However, as emphasized by the IAWA Hardwood Committee, there is an intergrading continuum from diffuse-porous, via semi-ring-porous to ring-porous, and individual species may range from semi-ring-porous to ring-porous, or from diffuse-porous to semi-ring-porous. For instance, *Quercus virginiana* (live oak) usually is semi-ring-porous, but some samples could be described as diffuse-porous. *Tectona* (teak) is an extreme example of variation in porosity, no doubt related to where it is grown. In the literature, it usually is described as semi-ring-porous, but some samples appear or tend to be diffuse-porous, and yet others appear or tend to be ring-porous. There are some woods in which the very last portion of the growth ring has narrower vessels, the Hardwood List recommends coding these woods as diffuse-porous. However, for *Fagus* spp., descriptions in InsideWood include 4v as well as 5 because the region of narrow latewood vessels is relatively distinct and some students and publications have considered *Fagus* to be semi-ring porous.

Some wood anatomists from the tropics occasionally have described woods as semi-ring-porous or even ring-porous although the illustrations in those papers do not match the Hardwood List definition. Apparently, they were so described because they had distinct growth rings. In InsideWood, the descriptions of these woods are based on what the illustrations show, not the text description.

If a Cretaceous or Paleogene fossil wood is semi-ring-porous, it may be best to do one search using 4p and another search using the absence of 'wood diffuse-porous' (5a). The rationale is that because of the differences between present and past climates, the nearest living relatives (NLR) could be either ring-porous or semi-ring-porous.

## VESSEL ARRANGEMENT (TS)

### 6. Vessels in tangential bands

### 7. Vessels in diagonal and/or radial patterns

### 8. Vessels in dendritic pattern

The default condition is that tangential, radial, diagonal, and dendritic patterns are absent. The rare incidence of these features makes them quite useful in narrowing down a search; they often are restricted to the latewood of ring-porous (or semi-ring-porous) woods. These features can co-occur and a relatively high proportion of the occurrences of these features are recorded as variable (Table 1), indicating that vessel arrangement patterns often are only weakly expressed. When coding an unknown, we recommend using the presence of these patterns only when they are distinct. If the wood does not have any of these vessel arrangement patterns, then code the unknown as 6a, 7a, 8a. These individual features are not common but searching for the absence of all three features eliminates approximately 1000 records of modern woods. Vessel arrangement is used for woods with exclusively solitary vessels as well as for woods with some solitary vessels and vessel multiples.

Table 1.  
Frequency of the IAWA Hardwood Features in the InsideWood database.

IAWA Feature	%	Present includes the V's and ?'s			
		Present	V	?	
<b>Growth rings</b>					
1 Growth ring boundaries distinct	42.6%	3140	719	29	633 have 1 and 2
2 Growth ring boundaries indistinct or absent	76.7%	5652	66	20	
<b>Vessels</b>					
<i>Porosity</i>					
3 Wood ring-porous	4.6%	342	47	-	158 have 3 and 4
4 Wood semi-ring-porous	9.7%	714	278	1	41.4 have 4 and 5
5 Wood diffuse-porous	92.8%	6837	86	-	
<i>Vessel arrangement</i>					
6 Vessels in tangential bands	3.7%	274	100	-	75 have 6 and 7
7 Vessels in diagonal and/or radial pattern	13.1%	965	423	-	
8 Vessels in dendritic pattern	2.9%	215	68	-	198 have 7 and 8
<i>Vessel groupings</i>					
9 Vessels exclusively solitary (90% or more)	17.4%	1284	281		
10 Vessels in radial multiples of 4 or more common	11.5%	850	445		
11 Vessel clusters common	8.7%	641	230	3	
<i>Solitary vessel outline</i>					
12 Solitary vessel outline angular	33.5%	2468	1124	621	
<i>Perforation plates</i>					
13 Simple perforation plates	88.4%	6513	33	-	608 have 13 and 14
14 Scalariform perforation plates	19.5%	1440	328	2	
15 Scalariform perforation plates with ≤ 10 bars	6.3%	461	266	42	368 have 15 and 16
16 Scalariform perforation plates with 10–20 bars	6.3%	467	163	44	258 have 16 and 17



Table 1.  
(Continued.)

	IAWA Feature	%	Present includes the V's and ?'s			
			Present	V	?	Notes
17	Scalariform perforation plates with 20–40 bars	5.4%	396	74	23	176 have 17 and 18
18	Scalariform perforation plates with $\geq 40$ bars	2.5%	168	34	24	
19	Reticulate, foraminate and/or other types of multiple perforation plates	0.4%	269	152	3	
	Intervessel pits: arrangement and size					If vessels are exclusively solitary then often "?" for intervessel pit type.
20	Intervessel pits scalariform	9.5%	698	109	35	
21	Intervessel pits opposite	12.8%	941	135	67	503 have 20 and 21
22	Intervessel pits alternate	90.1%	6690	64	51	446 have 21 and 22
23	Shape of alternate pits polygonal	69.2%	5098	971	3079	
24	Minute ( $\leq 4 \mu\text{m}$ )	27.0%	1991	151	135	
25	Small (4–7 $\mu\text{m}$ )	53.3%	3931	236	580	1073 have 24 and 25
26	Medium (7–10 $\mu\text{m}$ )	46.0%	3388	237	619	1711 have 25 and 26
27	Large ( $\geq 10 \mu\text{m}$ )	24.3%	1788	206	462	1361 have 26 and 27
	Vestured pits					
29	Vestured pits	27.1%	1999	19	–	
	Vessel-ray pitting					
30	Vessel-ray pits with distinct borders; similar to intervessel pits in size and shape throughout the ray cell	68.2%	5028	191	54	
31	Vessel-ray pits with much reduced borders to apparently simple: pits rounded or angular	8.3%	2463	251	60	1864 have 31 and 32
32	Vessel-ray pits with much reduced borders to apparently simple: pits horizontal (scalariform gash-like) to vertical (palisade)	31.8%	2345	231	46	
33	Vessel-ray pits of two distinct sizes or types in the same ray cell	4.2%	311	76	111	

Table 1.  
(Continued.)

	IAWA Feature	%	Present includes the V's and ?'s			
			Present	V	?	Notes
34	Vessel-ray pits unilaterally compound and coarse (over 10 µm)	5.1%	375	118	172	
35	Vessel-ray pits restricted to marginal rows	11.5%	845	32	762	
	Helical thickenings					
36	Helical thickenings in vessel elements present	13.4%	991	217	2	
37	Helical thickenings throughout body of vessel element	11.8%	877	170	5	
38	Helical thickenings only in vessel element tails	1.4%	109	62	2	
39	Helical thickenings only in narrower vessel elements	3.1%	231	45	4	
	Tangential diameter of vessel lumina					
	Mean tangential diameter of vessel lumina					
40	≤50 µm	21.8%	1606	107	31	896 have 40 and 41
41	50–100 µm	50.8%	3747	300	43	1002 have 41 and 42
42	100–200 µm	48.2%	3552	311	43	652 have 42 and 43
43	≥200 µm	13.5%	992	167	15	
45	Vessels of two distinct diameter classes wood not ring-porous	10.4%	768	372	217	
	Vessels per square millimetre					
46	≤5 vessels per square millimetre	21.4%	1575	136	8	1179 have 46 and 47
47	5–20 vessels per square millimetre	51.4%	3787	301	998	707 have 47 and 48
48	20–40 vessels per square millimetre	29.3%	2160	243	126	635 have 48 and 49
49	40–100 vessels per square millimetre	23.1%	1704	149	217	505 have 49 and 50
50	≥100 vessels per square millimetre	13.7%	1007	166	130	
	Mean vessel element length					
52	≤350 µm	55.0%	4051	63	2635	3117 have 52 and 53

Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s		
		Present	V	?
53 350–800 µm	76.3%	5623	133	2824
54 ≥800 µm	37.2%	2739	60	1722
Tyloses and deposits in vessels				
56 Tyloses common	17.1%	1257	222	13
57 Tyloses sclerotic	1.4%	100	49	–
58 Gums and other deposits in heartwood vessels	17.6%	1300	196	2
Wood vesselless				
59 Wood vesselless	0.1%	7		
Tracheids and fibres				
60 Vascular/vasicentric tracheids present	12.5%	922	181	17
Ground tissue fibres				
61 Fibres with simple to minutely bordered pits	75.2%	5541	130	9
62 Fibres with distinctly bordered pits	30.2%	2228	175	12
63 Fibre pits common in both radial and tangential walls	32.0%	2356	183	644
64 Helical thickenings in ground tissue fibres	2.8%	207	59	3
Septate fibres and parenchyma-like fibre bands				
65 Septate fibres present	25.8%	1904	225	13
66 Non-septate fibres present	85.8%	6324	161	6
67 Parenchyma-like fibre bands alternating with ordinary fibres	2.4%	177	54	5
Fibre wall thickness				
68 Fibres very thin-walled	16.0%	1177	180	153
69 Fibres thin- to thick-walled	76.4%	5629	185	167

Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s		
		Present	V	? Notes
70	Fibres very thick-walled	2595	349	43
	Axial parenchyma			
75	Axial parenchyma absent or extremely rare	1157	103	1 258 have 75 and 76 513 have 75 and 78
	Apotracheal axial parenchyma			
76	Axial parenchyma diffuse	2595	367	2 1172 have 76 and 77
77	Axial parenchyma diffuse-in-aggregates Paratracheal axial parenchyma	1705	157	3
78	Axial parenchyma scanty paratracheal	2713	225	1 840 have 78 and 79
79	Axial parenchyma vasicentric	2367	287	1 974 have 79 and 80
80	Axial parenchyma aliform	1613	386	1
81	Axial parenchyma lozenge-aliform	945	303	117 438 have 81 and 82
82	Axial parenchyma winged-aliform	835	288	112
83	Axial parenchyma confluent	1578	318	– 1245 have 80 and 83
84	Axial parenchyma unilateral paratracheal Banded parenchyma	247	109	–
85	Axial parenchyma bands more than three cells wide	872	251	6 355 have 85 and 86
86	Axial parenchyma in narrow bands or lines up to three cells wide	1684	371	4
87	Axial parenchyma reticulate	520	219	158
88	Axial parenchyma scalariform	301	99	83
89	Axial parenchyma in marginal or in seemingly marginal bands Axial parenchyma cell type/strand length	1860	671	29
90	Fusiform parenchyma cells	500	85	20 476 have 90 and 91

Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s		
		Present	V	? Notes
91 Two cells per parenchyma strand	36.8%	2709	176	422 2314 have 91 and 92
92 Four (3-4) cells per parenchyma strand	70.0%	5162	227	581 3091 have 92 and 93
93 Eight (5-8) cells per parenchyma strand	57.0%	4201	289	568 1131 have 93 and 94
94 Over eight cells per parenchyma strand	17.4%	1280	154	504
95 Unlignified parenchyma	0.5%	35	-	-
Rays				
Ray width				
96 Rays exclusively uniseriate	16.9%	1248	117	1 388 have 96 and 97
97 Ray width 1 to 3 cells	56.6%	4171	645	4 985 have 97 and 98
98 Larger rays commonly 4-to 10 seriate	41.5%	3062	608	4 230 have 98 and 99
99 Larger rays commonly >10-seriate	6.0%	442	98	1
100 Rays with multiseriate portion(s) as wide as uniseriate portions	4.6%	341	172	19
Aggregate rays				
101 Aggregate rays	1.1%	81	23	1
Ray height				
102 Ray height > 1 mm	30.3%	2230	403	153
Rays of two distinct sizes				
103 Rays of two distinct sizes	13.7%	1012	306	15
Rays: cellular composition				
104 All ray cells procumbent	28.0%	2066	269	11
105 All ray cells upright and/or square	8.0%	592	124	25
106 Body ray cells procumbent with one row of upright and/or square marginal cells	44.7%	3294	498	40 925 have 104 and 106

Table 1.  
(Continued.)

	IAWA Feature	%	Present includes the V's and ?'s			Notes
			Present	V	?	
107	Body ray cells procumbent with mostly 2-4 rows of upright and/or square marginal cells	43.7%	3221	267	110	2055 have 106 and 107
108	Body ray cells procumbent with over 4 rows of upright and/or square marginal cells	30.8%	2267	209	94	1231 have 107 and 108
109	Rays with procumbent square and upright cells mixed throughout the ray	16.6%	1221	245	279	
110	Sheath cells	13.5%	994	386	9	
111	Tile cells	1.3%	96	17	-	
112	Perforated ray cells	11.7%	863	75	507	
113	Disjunctive ray parenchyma cell walls	9.9%	732	33	534	
114	Disjunctive ray parenchyma cell walls Rays per millimetre	11.3%	832	49	81	413 have 114 and 115
115	4-12/mm	70.7%	5214	105	255	867 have 115 and 116
116	≥12/mm	33.9%	2501	130	197	
117	Wood rayless	0.3%	20	-	-	
118	Wood rayless					
	Storied structure					
	All rays storied	4.6%	342	57	2	

Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s			Notes
		Present	V	?	
119 Low rays storied high rays non-storied.	2.3%	172	45	2	
120 Axial parenchyma and/or vessel elements storied	11.0%	812	117	-	
121 Fibres storied	3.1%	230	47	47	
122 Rays and/or axial elements irregularly storied	3.4%	248	78	1	
Secretory elements and cambial variants					
Oil and mucilage cells					
124 Oil and/or mucilage cells associated with ray parenchyma	3.3%	241	53	3	
125 Oil and/or mucilage cells associated with axial parenchyma	2.3%	173	24	6	
126 Oil and/or mucilage cells present among fibres	1.2%	85	13	3	
Intercellular canals					
127 Axial canals in long tangential lines	1.2%	84	7	11	
128 Axial canals in short tangential lines	0.7%	55	9	12	
129 Axial canals diffuse	0.9%	64	22	-	
130 Radial canals	3.3%	242	49	3	
131 Intercellular canals of traumatic origin	2.4%	174	19	-	
Tubes/tubules					
132 Laticifers or tanniferous tubes	2.7%	199	47	-	
Cambial variants					
133 Included phloem concentric	0.9%	66	5	-	
134 Included phloem diffuse	1.3%	95	5	-	
135 Other cambial variants	0.6%	42	3	-	

Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s		
		Present	V	? Notes
<b>Mineral inclusions</b>				
<b>Prismatic crystals</b>				
136 Prismatic crystals present	52.2%	3847	481	7
137 Prismatic crystals in upright and/or square ray cells	25.5%	1879	287	233
138 Prismatic crystals in procumbent ray cells	17.4%	1281	323	257
139 Prismatic crystals in radial alignment in procumbent ray cells	3.3%	240	71	105
140 Prismatic crystals in chambered upright and/or square ray cells	8.2%	600	140	94
141 Prismatic crystals in non-chambered axial parenchyma cells	11.6%	856	228	155
142 Prismatic crystals in chambered axial parenchyma cells	29.1%	2143	307	162
143 Prismatic crystals in fibres	4.0%	292	61	47
<b>Druses</b>				
144 Druses present	2.4%	176	62	3
145 Druses in ray parenchyma cells	1.8%	135	43	10
146 Druses in axial parenchyma cells	1.0%	73	25	8
147 Druses in fibres	0.1%	8	1	7
148 Druses in chambered cells	0.4%	27	4	8
<b>Other crystal types</b>				
149 Raphides	1.3%	98	20	1
150 Acicular crystals	2.1%	153	24	106
151 Styloids and/or elongate crystals	2.9%	213	27	100
152 Crystals of other shapes (mostly small)	3.4%	251	36	109
153 Crystal sand	2.9%	213	39	112
<b>Other diagnostic crystal features</b>				
154 More than one crystal of about the same size per cell or chamber	3.6%	268	91	26



Table 1.  
(Continued.)

IAWA Feature	%	Present includes the V's and ?'s		
		Present	V	? Notes
155 Two distinct sizes of crystals per cell or chamber	1.3%	98	34	24
156 Crystals in enlarged cells	4.3%	314	133	5
157 Crystals in tyloses	0.5%	36	9	9
158 Cystoliths	0.1%	7	3	-
Silica				
159 Silica bodies present	7.4%	549	66	3
160 Silica bodies in ray cells	7.0%	519	64	4
161 Silica bodies in axial parenchyma cells	2.1%	157	62	2
162 Silica bodies in fibres	0.2%	12	3	
163 Vitreous silica	0.4%	26	9	-
Geographical distribution				
164 Europe and temperate Asia	13.3%	987		
165 Europe excluding Mediterranean	1.5%	109		
166 Mediterranean including Northern Africa and Middle East	3.2%	239		
167 Temperate Asia (China, Japan, USSR)	10.0%	743		
168 Central South Asia	8.8%	656		
169 India, Pakistan, Sri Lanka	8.0%	599		
170 Myanmar (Burma)	4.4%	330		
171 Southeast Asia and the Pacific	21.3%	1590		
172 Thailand, Laos, Vietnam, Cambodia (Indochina)	10.6%	789		
173 Indomalaysia: Indonesia, Philippines, Malaysia, Brunei, Papua New Guinea and Solomon Islands	15.1%	1122		
174 Pacific Islands (including New Caledonia, Samoa, Hawaii and Fiji)	3.2%	238		

Table 1.  
(Continued.)

	IAWA Feature	%	Present includes the V's and ?'s		
			Present	V	?
175	Australia and New Zealand	6.7%	498		
176	Australia	5.2%	389		
177	New Zealand	1.7%	129		
178	Tropical mainland Africa and adjacent islands	25.1%	1866		
179	Tropical Africa	16.2%	1204		
180	Madagascar and Mauritius Réunion and Comores	10.1%	756		
181	Southern Africa (south of the Tropic of Capricorn)	2.3%	175		
182	North America north of Mexico	4.8%	359		
183	Neotropics and temperate Brazil	29.6%	2208		
184	Mexico and Central America	9.0%	670		
185	Caribbean	4.3%	317		
186	Tropical South America	22.6%	1683		
187	Southern Brazil	3.5%	262		
188	Temperate South America including Argentina Chile Uruguay and S. Paraguay	3.8%	286		
	Habit				
189	Tree	85.8%	6321		915 have 189 and 190
190	Shrub	23.9%	1764		
191	Vine/liana	3.0%	221		60 have 190 and 191
192	Wood of commercial importance	27.7%	2061		

Percentages based on the August 2019 database which had 7371 descriptions. V, number of that feature of variable occurrence present in some samples absent in others or showing a tendency to having the feature; ?, number of that feature whose status is unknown.

## VESSEL GROUPINGS (TS)

9. Vessels exclusively solitary (90% or more)
10. Vessels in radial multiples of 4 or more common
11. Vessel clusters common

Vessels solitary and in short radial multiples is the default condition for dicot woods. This condition was — perhaps unwisely — not given its own feature number in the Hardwood List. A search for such woods would use 9a 10a 11a; which eliminates approximately 1700 of the about 7300 descriptions in InsideWood. The presence of Features 9–11 is useful in a search because all are of limited occurrence.

In the database, woods that have mostly solitary vessels (say 80%) usually are described as 9v, so that they would match a search for either presence or absence. One problem with features 10 and 11 is that “common” means different things to different observers. Descriptions and illustrations in the literature sometimes were ambiguous about the presence of these features so that made it difficult to decide if features 10 or 11 were present in a species, consequently, there is a high proportion of these features recorded as variable in the InsideWood database. When coding for an unknown we recommend using vessel grouping features only when distinct.

Occasionally, users of the Hardwood List ignore the adjective “exclusively” and erroneously use feature 9 present when some solitary vessels are present.

## SOLITARY VESSEL OUTLINE (TS)

12. Solitary vessel outline angular

Distinctly angular vessels are infrequent; searching the InsideWood database for 12r returns just 10% of all entries in the InsideWood database. A very high number of species has been recorded as variable, reflecting the continuous variation from angular to slightly rounded. In a search, only use presence or absence of feature 12, when the type of vessel outline is very distinct. The separation of red and white oaks is a classic example of the diagnostic value of solitary vessel outline: the latewood vessels in white oak are angular in outline and are recorded as having feature 12, while the latewood vessels of the red oaks are rounded in outline so feature 12 is not part of their description. A search for vessels rounded in outline would use 12a.

Feature 12 has not been used in the fossil wood database because fossil woods often are compressed or otherwise distorted.

## PERFORATION PLATES (RLS, TLS)

13. Simple perforation plates
14. Scalariform perforation plates
15. Scalariform perforation plates with  $\leq 10$  bars

16. Scalariform perforation plates with 10–20 bars
17. Scalariform perforation plates with 20–40 bars
18. Scalariform perforation plates with  $\geq 40$  bars
19. Reticulate, foraminate, and/or other types of multiple perforation plates

Perforation plates are most easily seen in radial sections where they are visible face-on. Generally, the wider the vessel the more horizontal (less oblique) the perforation plate is. Type of perforation plate is a key feature for wood identification and should always be used in a search. Scalariform perforation plates are the less common type (Table 1). The combination of both simple and scalariform perforation plates is even less common. However, be aware that rarely occurring scalariform perforations in woods with predominantly simple perforation plates might have been overlooked in the original literature description on which the InsideWood data is based. In woods with exclusively scalariform perforations, the range of the number of bars can be quite diagnostic, but often more than one category occurs. For such woods, it may be worthwhile to start with just 14p and use features 15–18 at a later stage. If it is obvious there are fewer than 20 bars, code for 17a and/or 18a. Similarly, if you are sure the unknown has more than 20 bars, code for 15a.

Feature 19 is rare and usually occurs in combination with simple and/or scalariform perforation plates. If seen, it is useful for narrowing down possibilities. However, because it is not common and can be overlooked and might not have been described for a species, it is not a good idea to search for its absence. Often, bars in perforation plates are torn during sectioning, so it might not be possible to get a correct count of the number of bars in a scalariform perforation plate. It can be useful to search for 14p 15a when it is obvious that the number of bars exceeds ten, but it is not possible to determine if the unknown has features 16, 17, and/or 18.

In some woods with prominent helical thickenings, like *Ilex aquifolium*, wall thickenings and bars of perforation plates might be confused.

#### INTERVESSEL PITS: ARRANGEMENT AND SIZE (TLS, RLS)

20. Intervessel pits scalariform
  21. Intervessel pits opposite
  22. Intervessel pits alternate
23. Shape of alternate pits polygonal

Because most woods have some radial multiples, their shared walls are visible in tangential section, and so that section is most likely to have intervessel pits visible. For woods with vessels tangentially arranged, the radial section is as likely to expose common walls and intervessel pits.

There are times when alternate and opposite pits intergrade, and some caution is needed to determine if the pits are aligned in relatively straight rows (opposite) or if they

are staggered/alternating/in helical rows. See Table 1 for the frequency occurrence of each feature and number of co-occurrences.

We recommend not using feature 23 in an identification search, because we are not sure how reliable the data are in InsideWood. Feature 23 was not an Oxford feature and it was initially recorded as “23?”. Perceptions of whether the pit shape is polygonal depend on the focal plane and we recommend focusing on the maximum pit chamber diameter. When pits are minute, it can be difficult to determine whether or not they are polygonal in outline.

In woods with exclusively solitary vessel elements, vessel elements are only in contact towards the end of the element, and intervessel pits might not be observed. Thus, the descriptions in InsideWood for these woods often have these features recorded as unknowns (“20?”, “21?”, “22?”, “23?”). If a wood has exclusively solitary vessels and vasicentric tracheids, the pitting between these two cell types has been recorded as for intervessel pits.

#### INTERVESSEL PIT SIZE (ALTERNATE AND OPPOSITE) (TLS, RLS)

- 24. Minute ( $\leq 4 \mu\text{m}$ )
- 25. Small (4–7  $\mu\text{m}$ )
- 26. Medium (7–10  $\mu\text{m}$ )
- 27. Large ( $\geq 10 \mu\text{m}$ )

The IAWA Hardwood List uses horizontal diameter of a pit chamber at the broadest point. Because transitional (scalariform to opposite) and scalariform intervessel pits have horizontal diameters that are too variable to be meaningful, some publications report vertical diameters (Richter 1981, Helmling *et al.* 2018). The information for intervessel pit sizes from these publications has been recorded in InsideWood; it seems that for alternate pits the vertical diameter more or less equals horizontal diameters. For descriptions recently added to InsideWood, the “Anatomical Note” will mention if the pit sizes are for vertical diameters.

As is true for all the quantitative features, a single species may have more than one feature recorded. When coding an unknown, just code the most common type or size class. It is unwise to code adjacent features differently, for example, coding 24p 25a is not a good idea because this would not catch species that were described as having intervessel pits 3–5  $\mu\text{m}$  across and have both features 24 and 25 recorded in the InsideWood database. It can be useful to search for absences, if pits are not minute or large, you can search for 24a and 27a, which will return descriptions of woods that have been reported as having small and/or medium-sized pits. It is probably best to measure the pit size from pits in the middle of vessel elements.

#### VESTURED PITS (TLS, RLS)

- 29. Vested pits

The presence/absence of vested pits is useful for distinguishing between families whose macroscopic appearance is similar. As noted in the Hardwood List, Combretaceae,

most Leguminosae, Lythraceae, Myrtaceae, and Rubiaceae have vested pits. Thus, if an unknown has non-vested pits then it is unlikely to belong to those families (NB: some Leguminosae have non-vested pits). When pits are minute to small, vestures can be difficult to detect with a light microscope, (*Gonystylus* and *Aquilaria*). In case of doubt, it is well worth taking the extra trouble to use an oil immersion objective or SEM because this feature is so diagnostic. Using an oil immersion lens may be troublesome when using temporary glycerin mounted slides of unknowns when the coverslip is not affixed. Vestures may become detached during the pulping process, so this is not a good character to identify vessel elements in pulp and paper (Helmling *et al.* 2018).

Caution is needed to not to mistake “pseudovestures” for true vesturing (Gale 1982). Pseudovestures likely are a result of extractive deposition, with accumulations around a pit aperture and on pit membranes.

This feature is not used in the Fossil Wood Database, as determining whether vestures are present/absent in fossil wood is extremely difficult. If a wood is exceptionally well-preserved and the pits are medium to large, sometimes it is possible to tell. In some instances, mineralization results in the appearance of vesturing.

#### VESSEL-RAY PITTING (RLS)

30. Vessel-ray pits with distinct borders; similar to intervessel pits in size and shape throughout the ray cell
31. Vessel-ray pits with much-reduced borders to apparently simple: pits rounded or angular
32. Vessel-ray pits with much-reduced borders to apparently simple: pits horizontal (scalariform, gash-like) to vertical (palisade)
33. Vessel-ray pits of two distinct sizes or types in the same ray cell
34. Vessel-ray pits unilaterally compound and coarse (over 10  $\mu\text{m}$ )
35. Vessel-ray pits restricted to marginal rows

Vessel-ray pitting, as viewed in radial sections, is among the most important features for identifying a hardwood. The most common feature is for the vessel-ray pitting to be distinctly bordered, and similar in shape and size to the intervessel pits (feature 30), occurring in 68% of the InsideWood descriptions. Feature 30 had a direct counterpart in the Oxford cards. Features 31–35 did not, initially, these features were translated to “?”. The Oxford cards had a feature 44 “vessel-ray parenchyma pits large” and the presence of this feature was translated to both IAWA Features 31 and 32. These two features overlap, and the occurrence of only 31 or only 32 is rare. Please note that some woods with scalariform intervessel pits have large vessel-ray parenchyma pits with borders that are not that much reduced. However, the descriptions in InsideWood have them recorded as 32. Features 33 and 34 are not comprehensively recorded.

As noted in the Hardwood List, “If a wood has predominantly solitary vessels, comparison of vessel-ray pits with intervessel pits often is not possible. If the vessel-ray parenchyma

pits in such woods are uniform in size and shape and have borders, then use feature 30; if not, any of features 31–35 may apply”, so searching for 30a would be appropriate.

Coding for feature 35 is a problem because radial sections of multiseriate rays with wide central portions and narrow uniseriate margins may not expose the ‘outside’ of the multiseriate ray that is in contact with the vessels, so it is not possible to determine whether this feature is present or not. Be sure to examine a number of rays to determine whether this feature applies or not.

If an unknown has features 31 and/or 32, we recommend using the absence of feature 30. We do not recommend using features 33, 34, or 35 in initial searches.

In radial sections of poorly preserved fossil woods sometimes it is not possible to see vessel-ray parenchyma pitting, but you might observe vessel-axial (paratracheal) parenchyma pitting. Because vessel-ray parenchyma pits and vessel-axial parenchyma pits usually are similar, you can use the appearance of the vessel-axial parenchyma pits to code for features 30–35.

#### HELICAL THICKENINGS (RLS, TLS)

- 36. Helical thickenings in vessel elements present
- 37. Helical thickenings throughout body of vessel element
- 38. Helical thickenings only in vessel element tails
- 39. Helical thickenings only in narrower vessel elements

Presence of helical thickenings is a feature for 13% of all InsideWood entries, but almost a quarter of those are recorded as variable. The occurrence of helical thickenings is a feature whose incidence correlates with the environment; helical thickenings are less common in tropical and subtropical woods than in temperate woods. Feature 37, helical thickenings present throughout the body of the vessel element, is the most common condition for helical thickenings.

Feature 38 is the most difficult to determine and generally is found only in those species with elongate vessel element tails (*Cercidiphyllum*, *Liquidambar*).

In ring-porous woods, helical thickenings, if present, primarily occur in the narrow latewood vessels (feature 39), so be sure to examine the radial section of an unknown, which should include both earlywood and latewood.

It should be noted that decay of the cell wall, such as soft rot cavities, can give the impression of helical thickenings. If coalescent pit apertures are common, they might also be confused with helical thickenings. Carlquist (1988) discussed elongated grooves that interconnect pit apertures, a feature more likely to be observed with an SEM than with a light microscope. These are not associated with wall thickenings and feature 36 would not apply to this phenomenon.

In fossil wood, these features are ones that should only be used in the positive sense. If a wood is not well-preserved, then it is not possible to be sure about the presence/absence of helical thickenings. Moreover, in Cretaceous and Paleogene woods, taxa that today have

helical thickenings might not have developed this feature in the less seasonal climates of those times.

#### TANGENTIAL DIAMETER OF VESSEL LUMINA (TS)

Mean tangential diameter of vessel lumina

40.  $\leq 50 \mu\text{m}$

41.  $50\text{--}100 \mu\text{m}$

42.  $100\text{--}200 \mu\text{m}$

43.  $\geq 200 \mu\text{m}$

Overall, vessel lumen diameter varies strongly with plant size (Olson *et al.* 2014), with cambial age (narrower vessels occur in juvenile wood near the pith), as well as with habitat. We therefore recommend using this feature with caution. It is relevant to note that many InsideWood descriptions are based on the older forest products literature (Pearson & Brown 1932), which described woods from large diameter tree trunks from old-growth forests. More recent timber samples from smaller-diameter trees of the same species usually have narrower vessels (Gasson and Baas, personal observations).

Another confounding factor is that it is likely that some vessel diameter measurements were for vessel lumen plus vessel wall, not just vessel lumen. This would be of more consequence for species with narrower vessels where the vessel wall thickness would represent a higher percentage of the lumen width. Schweingruber and Crivellaro (2016) noted that the IAWA Hardwood List size classes are too broad, particularly for describing shrubs, a group of plants whose identity can be of special importance to ecologists and archaeobotanists.

Charcoals have undergone shrinkage and usually, this results in narrower vessel lumina (Scheel-Ybert & Gonçalves 2017), so for this material use quantitative vessel features with extreme caution and rely on qualitative features.

When a wood is ring-porous (feature 3) or has two distinct diameter classes (feature 45), the IAWA Hardwood Committee recommended recording the tangential diameter of the earlywood vessels or the larger of the two size classes. The data in InsideWood follow that recommendation.

However, when trying to identify a semi-ring-porous unknown, vessel diameter is a feature to use cautiously. The data for semi-ring porous woods in InsideWood likely do not match the IAWA Hardwood Committee recommendation “measure along a radial transect through a growth ring. For semi-ring-porous woods, it is recommended that more than 25 vessels be measured; a larger standard deviation is expected for such woods.” Most publications do not specify the procedure they used to measure mean tangential diameter of semi-ring porous woods; some publications report the average for the first half of a growth ring.

Some descriptions in InsideWood are based on publications in which only the range of tangential diameters was reported, in such cases, usually, the category near the middle of the range was recorded for the InsideWood description. Unfortunately, it was a tradition



in Indian paleobotany to only report ranges for tangential diameters, making it difficult to evaluate the hydraulic traits of some significant older angiosperm fossil woods.

Yet after taking all these limitations into account, vessel diameter is still a useful diagnostic feature, especially when vessels are very narrow (feature 40:  $\leq 50 \mu\text{m}$ ) or very wide (feature 43:  $\geq 200 \mu\text{m}$ ). When uncertain about the precise range and average value of tangential diameter, it can be helpful to simply code for absence of the extreme categories (40a and/or 43a), thereby eliminating 35% of potential matches.

Because there is variability within species, and many entries in InsideWood are coded as having adjacent features (40 and 41; 41 and 42; 42 and 43) it is unwise to code adjacent categories differently. If an unknown has an average vessel diameter of  $45 \mu\text{m}$ , it would not be a good idea to search for 40p 41a because whatever species is a match for that unknown might have some samples that have an average of  $52 \mu\text{m}$ . This particular unknown might best be described by coding for the absence of wider vessels 42a 43a. Similarly, an unknown with an average of  $170 \mu\text{m}$  might best be described by coding for the absence of narrow vessels (40a 41a).

#### 45. Vessels of two distinct diameter classes, wood not ring-porous (TS)

Feature 45, vessels of two distinct diameter classes, wood not ring-porous. occurs in only 10% of all world woods, but over half of the entries with feature 45 are coded as variable in InsideWood, reflecting the arbitrary nature of the descriptor “two distinct sizes”. This was not a feature of the Oxford cards, so this information was added subsequently. This feature primarily occurs in woody vines. However, there are 85 descriptions that have this feature but are not vines (45p 191a) and another 352 descriptions of erect trees and shrubs that are recorded as having a tendency to this feature (45v).

#### VESSELS PER $\text{MM}^2$ (TS)

46.  $\leq 5$  vessels/ $\text{mm}^2$

47. 5–20 vessels/ $\text{mm}^2$

48. 20–40 vessels/ $\text{mm}^2$

49. 40–100 vessels/ $\text{mm}^2$

50.  $\geq 100$  vessels/ $\text{mm}^2$

As for vessel lumen diameter, vessel frequency varies with cambial age and ecology. There can be an inverse relationship between vessel diameter and vessel frequency. As Table 1 shows many descriptions have two overlapping ranges, reflecting their natural infraspecific variation. Feature 46 ( $\leq 5 / \text{mm}^2$ ) is typically restricted to lowland tropical forest trees (and lianas) that have wide vessels; Feature 50 ( $\geq 100 / \text{mm}^2$ ) is typical of cool temperate to boreal and arctic species and shrubs. Keep in mind that if an unknown is a small fragment, which may or may not represent a mature individual, vessel frequency is not a good feature to use.

In a search, coding for absence of extreme character states may be more useful than coding for presence of a single category. Many publications do not report an average number of vessels per square millimetre, but a range, so the *InsideWood* descriptions for these species include all the categories mentioned.

As is pointed out in the *Hardwood List*, all vessels should be counted. If in a single field of view there are 3 solitary vessels, 4 radial multiples of 2, and 2 radial multiples of 3, then that field has a count of 17 vessels.

#### MEAN VESSEL ELEMENT LENGTH (TLS)

52.  $\leq 350 \mu\text{m}$

53.  $350\text{--}800 \mu\text{m}$

54.  $\geq 800 \mu\text{m}$

The literature and *InsideWood* are deficient on reliable data for vessel element length. As Table 1 shows, over half of the descriptions in *InsideWood* lack information on vessel element length. Ideally, vessel element lengths should be measured using macerations. However, many studies report lengths measured from sections, which is the only option for fossil woods. In sections, it might not be possible to see the actual tips/tails of vessel elements, so the lengths recorded would be shorter than measured from macerations. Another difficulty is that when tyloses are present they may obscure the position of perforation plates and lead to erroneous measurements. Vessel element length is thus of limited value in wood ID searches.

#### TYLOSES AND DEPOSITS IN VESSELS (TS, RLS, TLS)

56. Tyloses common

57. Tyloses sclerotic

58. Gums and other deposits in heartwood vessels

For unknowns, we do not recommend searching for the absence of these features because the unknown might represent sapwood in which neither tyloses nor gums have formed. Here, as is true for other features and many descriptions, the modifier “common” is problematic. Different people may have different interpretations of ‘common’.

For fossil woods, if any presence of tyloses was mentioned in a publication, usually feature 56 was recorded as present.

A traditional distinction between the white oak and red oak groups is that white oaks commonly have tyloses while red oaks do not, nonetheless some red oaks do have some tyloses. The occurrence of abundant tyloses usually is correlated with large vessel-ray parenchyma pits (Bonsen & Kučera 1990; De Micco *et al.* 2016).

In ring-porous woods, tyloses occur most frequently in the earlywood vessels. Because tyloses are not always closely spaced, a small transverse section might not show tyloses,

while the radial and tangential sections do, so presence of tyloses should be verified using longitudinal sections.

Sclerotic tyloses (feature 57) is one of the rarest in the database (1.4%); it has been reported for some high-density commercial hardwoods such as Bornean Ironwood, *Eusideroxylon zwageri*, and Snakewood, *Brosimum guianense*. The presence of sclerotic tyloses will greatly reduce the number of possibilities; their absence should never be used to confirm an identification. Of the 100 entries with this feature in InsideWood, 49% are coded as variable, possibly because the full sclerification of tyloses takes a long time (see DeMicco *et al.* 2016 for a review of gums and tyloses). The feature is probably under-recorded in InsideWood, in part because it was not an Oxford card feature; it is likely to be less rare in species restricted to nutrient-poor soils (Bhiki *et al.* 2016; Baas 2017).

Gums are easiest to see in longitudinal sections because they often collect on end walls of vessel elements. NB, boiling a modern wood before sectioning might remove gums.

#### WOOD VESSELLESS

##### 59. Wood vesselless

At present, relatively few (only 7) of the uncommon vesselless angiosperm woods have descriptions in InsideWood; one of them (*Tetracentron*) is CITES-listed. Vesselless angiosperms have much wider rays than extant conifers.

#### TRACHEIDS AND FIBRES

##### 60. Vascular/vasicentric tracheids present (TLS, RLS)

Tracheids are imperforate. Vascular tracheids usually occur in clusters grouped with narrow vessels. In sections, it can be difficult to distinguish them from narrow vessel elements. Searching the modern wood database for the combination of vessel clusters (11p) and feature 60, reduces the number of potential matches to 189, so that using a few additional features should reduce the number of families and genera to which the unknown could belong.

As their name implies, vasicentric tracheids surround vessels. They have distinctly bordered pits on both tangential and radial walls. Sometimes they have a wavy outline as they wrap around vessels (*Quercus*, *Castanea*) whereas they are relatively straight in *Calophyllum* and *Eucalyptus*. Because these cells are thin-walled and surround vessels, in transverse section, they have been mistakenly interpreted as vasicentric parenchyma; this is a problem when using image analysis to determine the percentage of different cell types. This cell type often co-occurs with exclusively solitary vessels that are relatively wide (*Calophyllum*, *Dryobalanops*, *Eucalyptus*, *Gymnostoma*, *Shorea*, and Quercoideae of the Fagaceae).

#### GROUND TISSUE FIBRES (RLS, TLS, TS)

##### 61. Fibres with simple to minutely bordered pits

##### 62. Fibres with distinctly bordered pits

63. Fibre pits common in both radial and tangential walls

64. Helical thickenings in ground tissue fibres.

Features 61–63 distinguish fibre types on the basis of interfibre pitting and require high magnifications to be interpreted correctly. Simple to minutely bordered pits (pit borders < 3  $\mu\text{m}$ , feature 61) are usually restricted to the radial walls and characterize so-called libriform fibres; distinctly bordered pits (borders > 3  $\mu\text{m}$ , feature 62) characterize so-called fibre-tracheids — or “true tracheids” *sensu* Carlquist (2001) — and often are common in the tangential walls as well (feature 63). Feature 63 was not on the Oxford cards, so many InsideWood descriptions are coded “63?”. Feature 63 should be used late in a search; the information on its presence or absence in the database is far from complete. The Annonaceae and Vitaceae have multiple species having the unusual combination of features 61 and 63.

Feature 64 — helical thickenings in ground tissue fibres — is a very rare feature occurring in about 3% of all InsideWood descriptions but is coded variable for a quarter of these entries. When distinct in an unknown it is a powerful diagnostic feature.

All too often, fossil woods are not well enough preserved to determine the type of fibre pits or whether helical thickenings are present.

#### SEPTATE FIBRES AND PARENCHYMA-LIKE FIBRE BANDS

65. Septate fibres present (TLS, RLS)

66. Non-septate fibres present (TLS, RLS)

67. Parenchyma-like fibre bands alternating with ordinary fibres (TS, RLS)

In InsideWood, some descriptions have exclusively septate fibres (65p 66a; ca 16%), many have exclusively non-septate fibres (65a 66p; ca 77%), and some have both septate and non-septate fibres (65p 66p; ca 12%). Determining whether septate fibres are present requires careful microscopic observation. Care is needed not to confuse septa in fibres with transverse walls in parenchyma strands. Septa are deposited after completion of secondary wall deposition and terminate at the junction with the secondary wall. In contrast, transverse walls in axial parenchyma strands have a compound middle lamella that is continuous with the compound middle lamellae of the side walls.

For fossil and decayed woods, one problem with deciding whether or not septate fibres are present is the occurrence of fine fungal hyphae crossing through fibres. Usually, fungal hyphae do not take a straight path across fibres as would a septum.

Feature 67, parenchyma-like fibre bands, is rare (2.4% of InsideWood entries). It may be weakly expressed (several Lythraceae) or quite distinct (a few Celastraceae). About one-third of the entries with feature 67 are coded as variable for this feature. When distinct, the parenchyma-like fibre bands can easily be confused with true parenchyma bands, and this feature can only be confidently recorded from viewing a combination of transverse and longitudinal (especially radial) sections. Parenchyma-like fibres can be distinguished from fusiform parenchyma by their intrusive tips.

## FIBRE WALL THICKNESS (TS)

- 68. Fibres very thin-walled
- 69. Fibres thin- to thick-walled
- 70. Fibres very thick-walled

Feature 69 (thin- to thick-walled fibres) is by far the most common feature (76%). Feature 70 (very thick-walled fibres) characterizes 35% of the entries, and Feature 68 (very thin-walled fibres) is the least common (16%). Some entries have two fibre wall thicknesses reported for them (Table 1).

In practice, most of us do not take the time to measure lumen width and double cell wall thickness to strictly apply the definitions for fibre wall thickness given in the Hardwood List, but just use our impression as to which category applies to an unknown. It is probably best to code for the presence or absence of but a single fibre wall thickness category (68a or 70a). If you are not sure if the unknown fits feature 68 or 69, but you are sure that it does not have very thick-walled fibres, it would be best to code for absence of feature 70. Similarly, if you are not sure if an unknown is a best fit for feature 69 or 70, but you are sure the fibres are not very thin-walled, just code for absence of feature 68.

Fibre wall thickness is not a feature in the fossil wood database because cell wall appearance can be altered during preservation, especially if there has been any fungal or bacterial degradation of the cell wall. Sometimes the S2 wall layer, which is the least lignified of all cell layers, is decayed first and the cell wall collapses to appear thinner-walled than it originally was; alternatively, the cell wall may swell and so appears thicker.

## FIBRE LENGTHS

- 71.  $\leq 900 \mu\text{m}$
- 72.  $900\text{--}1600 \mu\text{m}$
- 73.  $\geq 1600 \mu\text{m}$

Fibre lengths should be measured in macerations; it is not practical to measure them in sections. Data on fibre lengths in InsideWood are so sparse that we do not recommend using these features in an identification procedure and they are not included in Table 1. Many systematic wood anatomy publications do not include data on fibre lengths. Consequently, many InsideWood entries do not have information on fibre lengths. Fibre length also shows considerable infraspecific and intra-tree variation (Zobel & van Buijtenen 1989) and despite the very broad categories of the IAWA Hardwood List, individual descriptions may have two length categories recorded.

## AXIAL PARENCHYMA

The Hardwood List's general comments about axial parenchyma warrant repeating:

*“When identifying an unknown, use the most obvious type of parenchyma pattern first and then the less evident type or types. Be sure to use a broad field of view when determining the*

*predominant parenchyma pattern(s) from the transverse section. Various combinations of the three general types (Apotracheal, Paratracheal, and Banded) described below may be present in a given wood (IAWA Committee 1989, p. 270).*

Table 1 bears out the last sentence of this quote. Axial parenchyma patterns can be extremely useful in wood identification, especially for tropical woods.

#### 75. Axial parenchyma absent or extremely rare (TS, TLS, RLS)

This is a good diagnostic feature as it occurs in only 16% of the InsideWood entries. Some InsideWood descriptions have both features 75 and 76 (axial parenchyma diffuse) recorded when the diffuse parenchyma is uncommon. Some have both features 75 and 78 (scanty paratracheal) recorded when there are only a few cells associated with vessels. It is always useful to check the longitudinal sections to see whether you might have missed the parenchyma in transverse sections. This is especially true for woods with thin-walled fibres.

### APOTRACHEAL AXIAL PARENCHYMA (TS, TLS, RLS)

#### 76. Axial parenchyma diffuse

#### 77. Axial parenchyma diffuse-in-aggregates

Most woods that have feature 77 also have feature 76. Given that samples within a species may vary in whether they have either or both 76 and 77, it is generally not advisable to code for the presence of one and the absence of the other. That being said, if you are sure that only diffuse is present and diffuse-in-aggregates is absent, it can be useful to code an unknown as 76p 77a to narrow down the possible matches. Note that feature 77 overlaps with feature 86 (Axial parenchyma in narrow bands or lines up to three cells wide) and feature 87 (Axial parenchyma reticulate).

If you only observe diffuse or diffuse-in-aggregates parenchyma in an unknown and no obvious paratracheal parenchyma, it is useful to also code for the absence of obvious paratracheal parenchyma arrangements to reduce the number of suggested matches. Many species with predominantly paratracheal parenchyma also have some diffuse and/or diffuse-in-aggregates axial parenchyma. A search for just 76p yields 2596 results, while a search for 76p 79a 80a 83a yields 1847 matches.

When fibres are very thin-walled, it may be difficult to determine from a transverse section if features 76 and 77 are present, so we recommend examining the longitudinal sections to confirm their presence/absence. In modern woods, axial parenchyma cells may sometimes be distinguished from thin-walled fibres in transverse sections if the parenchyma cells retain their contents (IAWA Committee 1989, Fig. 84, p. 271).

### PARATRACHEAL AXIAL PARENCHYMA (TS)

#### 78. Axial parenchyma scanty paratracheal

#### 79. Axial parenchyma vasicentric

- 80. Axial parenchyma aliform
- 81. Axial parenchyma lozenge-aliform
- 82. Axial parenchyma winged-aliform
- 83. Axial parenchyma confluent
- 84. Axial parenchyma unilateral paratracheal

These features intergrade and often co-occur, particularly within the Leguminosae. It is unusual for only one of these features to be present. It is especially common that aliform and confluent co-occur (Table 1). Features 81 and 82 were not on the original Oxford cards. An effort has been made to record those features using post-1950 literature and observations, however, as Table 1 shows, features 81 and 82 have more unknowns than the other paratracheal parenchyma features.

To confirm whether scanty paratracheal parenchyma is present or absent, it is important to check the longitudinal sections to see if there are axial parenchyma strands next to the vessels. Unilateral parenchyma is the least common of the parenchyma features.

Although some of these characters are distinctive and easy to recognize, they work best at narrowing down a search when used in combination with other features. For example, a search for aliform (80p) and confluent (83p) yields 1246 records, while a search for 80p, 83p, and rays storied (118p) yields only 135 matches. This is an illustration that it is important to try different combinations of features to see what results you get.

#### BANDED PARENCHYMA (TS)

- 85. Axial parenchyma bands more than three cells wide
- 86. Axial parenchyma in narrow bands or lines up to three cells wide
- 87. Axial parenchyma reticulate
- 88. Axial parenchyma scalariform
- 89. Axial parenchyma in marginal or in seemingly marginal bands

Banded axial parenchyma has been classified into five not mutually exclusive types. Bands more than three cells wide (85p; 12%) may co-occur with narrow bands or lines up to three cells wide (86p; 23%). Reticulate (87p; 7%) and scalariform (88p; 4%) are special types of banded parenchyma that intergrade and have a high percentage of variable entries. Confluent parenchyma (feature 83) may intergrade with features 85 and 86.

All too often woods have bands that are 3–4 cells wide and so do not neatly match features 85 or 86. Such woods have descriptions with both features 85 and 86 recorded, sometimes as variables 85v 86v. If an unknown has bands 3–4 cells wide, at first just try searching for 85p or 86p.

Marginal parenchyma bands (feature 89; 25%), are growth ring markers that typically, but not always coincide with distinct growth rings (feature 1). In tropical and subtropical species, it can be difficult to decide if a parenchyma band is marginal or not, especially

when the bands are widely spaced. This partially accounts for over a third of the entries with marginal bands recorded as variable in the InsideWood database. Also, there is variation in the occurrence of this feature within a species due to variations in rainfall seasonality in the tropics and subtropics. In ID-searches only use marginal parenchyma (89p) when distinct.

In the database, if marginal parenchyma is present, the cell width of those bands often has not been recorded, so it is best to not to code for both marginal parenchyma and band width, if the only parenchyma bands are marginal parenchyma (for instance in *Afzelia* or *Magnolia*).

#### AXIAL PARENCHYMA CELL TYPE/STRAND LENGTH (TLS)

- 90. Fusiform parenchyma cells
- 91. Two cells per parenchyma strand
- 92. Four (3–4) cells per parenchyma strand
- 93. Eight (5–8) cells per parenchyma strand
- 94. Over eight cells per parenchyma strand

This is another case of most species having 2 or more of these categories recorded (Table 1), so there are different strategies to use. If one category dominates, we recommend only coding for presence of that category. If an unknown has strands of 2–5 cells or 3–5, we recommend coding 90a and 94a, instead of coding 91p 92p 93p. If only few strands have been observed in the unknown, it may also be effective to code for absence of features well removed from the observed condition.

Not used in the Fossil Wood Database because very few descriptions have mentioned strand lengths.

- 95. Unlignified parenchyma

This feature is extremely rare (23 records only). Some of its reported occurrences need to be verified: when slides were examined of some species described in the literature as having unlignified axial parenchyma, it appeared that the parenchyma cell walls were in fact lignified. Do not confuse unlignified parenchyma with included phloem and its associated conjunctive parenchyma (features 133 and 134).

#### RAY WIDTH (TLS)

- 96. Rays exclusively uniseriate
- 97. Ray width 1 to 3 cells
- 98. Larger rays commonly 4- to 10-seriate
- 99. Larger rays commonly >10-seriate
- 100. Rays with multiseriate portion(s) as wide as uniseriate portions



Ray width should be determined in tangential sections and applies to the widest parts of the rays. Rays exclusively uniseriate is highly diagnostic and occurs in 17% of the InsideWood descriptions. In some genera described as having exclusively uniseriate rays with 96 recorded in their descriptions (*Castanea*), biseriate rays may rarely occur. Ray width 1 to 3 cells is the most common condition (57%); very broad rays (> 10 cells) are rare (6%) and highly diagnostic. When coding an unknown, use only one code for the maximum ray width or when in doubt code for absence of the extreme features.

Many species have variable ray widths. For example, some samples of a species may have exclusively uniseriate rays, while other samples have 1-2-seriate rays, and so in the database are described as 96 97 or 96 97v or 96v 97. It is not uncommon for some species to have samples with the wider rays only 3-seriate, while other samples have 4-seriate rays. In the InsideWood database, such species have both categories recorded, for example 97 98 or 97 98v or 97v 98. Because of this, when searching for an unknown, do not code adjacent features differently, do not code 97p 98a because you might lose a potential match. If it is difficult to decide which category applies, you could do one search using 97p and no other ray width features, and then subsequently use 98p and no other ray features, or just search for 96a 99a.

Feature 100 occurs in less than 5% of the InsideWood entries, but half of them are recorded as variable. When coding an unknown, only use this feature when distinctly present. This feature was intended to apply to woods with alternating uniseriate and multiseriate portions, not to rays with just the marginal ray cell(s) being the same width as the adjacent multiseriate portion.

#### AGGREGATE RAYS (TLS, TS)

##### 101. Aggregate rays

This feature is one of the rarest (1.1%) in InsideWood. If an unknown has aggregate rays, use of 101p quickly reduces the number of possible matches. As noted in the Hardwood List: "Aggregate rays may be relatively infrequent in the taxa in which they occur, so they may be easily overlooked or absent in a small sample; therefore, this feature should preferably be used positively only."

This feature was recorded as variable when aggregation of broad rays intergrades with very broad rays being occasionally dissected by axial elements as in evergreen oaks (*Quercus*). In other species (*Platanus*, *Vitis*), woods with large rays that are dissected into a vertical series of large rays have not been recorded as having aggregate rays.

#### RAY HEIGHT

##### 102. Ray height >1 mm (TLS)

This feature is defined as "the large rays commonly exceeding 1 mm in height." Again, what constitutes commonly is debatable. The detail given on ray height varies by author; some gave total ranges; others gave averages and standard deviations. If a species was described as having a ray height range that went over 1 mm, that species usually will have

at least 102v recorded in the InsideWood description. Some publications report ray height in cell number. For descriptions based on these publications, illustrations with scale bars were used to determine the occurrence of feature 102.

The IAWA Committee (1989) did not take advantage of the great diversity in ray height categories, which certainly is a pity for groups of commercial timbers with low rays or distinguishing between woods of interest to archaeologists or museum conservators. Presence or absence of feature 102 can be useful, but should not be coded for an unknown when the maximum ray height is close to 1 mm.

#### RAYS OF TWO DISTINCT SIZES (TLS)

##### 103. Rays of two distinct sizes

A useful diagnostic feature because it occurs in only 14% of the InsideWood descriptions. The presence or absence of this feature is based on a general impression, rather than a plot of the ray widths (and heights) to see if there is a bimodal distribution of ray sizes. Table 1 shows a relatively high proportion of 103v recorded for this feature. Consequently, only use this feature (presence or absence) in a search when you are sure of its status. Remember that if you were unsure of its presence or absence and did not use this feature in a search, you can look at the results of a search and see if any of the suggested matches were described as 103v and that could help with confirming an ID.

#### RAYS: CELLULAR COMPOSITION (RLS, TLS)

##### 104. All ray cells procumbent

##### 105. All ray cells upright and/or square

##### 106. Body ray cells procumbent with one row of upright and/or square marginal cells

##### 107. Body ray cells procumbent with mostly 2-4 rows of upright and/or square marginal cells

##### 108. Body ray cells procumbent with over 4 rows of upright and/or square marginal cells

##### 109. Rays with procumbent, square and upright cells mixed throughout the ray

Ray cellular composition varies with stem age and should preferably only be used for identifying mature wood. In juvenile wood close to the pith, ray cells tend to be more upright or less procumbent than in more mature wood and rays tend to have more marginal rows of upright and/or square cells.

In InsideWood many descriptions have two or three adjacent ray composition features. It is not unusual for a single radial section to have rays with one, one or two, and two to four marginal rows of square/upright cells.

We recommend coding unknowns only for the most common ray composition type present, or in case of doubt, just code for absences of strongly contrasting types from what you find in the unknown. If an unknown has some rays with all procumbent cells (104) and some rays with a single marginal row of square/upright cells (106), one option is to code

105a 107a 108a 109a, which would return a list of species that have either or both 104 and 106. The same logic would apply for unknowns with 2–5 marginal rows, with an option of searching for 104a 105a 109a.

Features 105 and 109 had no equivalents in the Oxford cards, so the information on these features in InsideWood may not be accurate for all descriptions. Feature 105 is the least common type (8%), with a relatively high incidence in shrubby species. As pointed out in the Hardwood List, feature 109 does not apply to woods with alternating uniseriate and multiseriate ray portions as in feature 100. To determine the presence of feature 109 requires careful observation in perfectly radial sections.

The IAWA Hardwood List illustrates these features with photographs of radial sections. Given that a radial section may not reveal the entire ray margin, it helps to check the tangential sections to better see ray margins, mindful of the fact that a relatively high marginal cell in tangential view is not necessarily an upright or square cell in RLS.

#### SHEATH CELLS (TLS)

##### 110. Sheath cells

This feature occurs in 14% of the InsideWood entries, but with a relatively high proportion of those entries (30%) recorded as variable. This is because there is a gradation from conspicuous sheath cells to poorly differentiated sheath cells that hardly differ in size and shape from the more central ray cells (as seen in tangential section). Only use this feature in an ID search if you are sure of its presence/absence.

If you are unsure whether sheath cells are present, but think they might be, first search for the features you are sure of, then check the descriptions of the suggested matches to see if they include 110v, which may help confirm the ID.

#### TILE CELLS (RLS, TLS)

##### 111. Tile cells

An extremely useful feature because tile cells are restricted to the order Malvales. Note that not all Malvaceae have tile cells. Weakly developed tile cells have been recorded as variably present in the genus *Hopea* (Dipterocarpaceae) which also belongs to the Malvales *sensu* APG (Angiosperm Phylogeny Group).

#### PERFORATED RAY CELLS (RLS, TLS)

##### 112. Perforated ray cells

Perforated ray cells are recorded in 12% of the InsideWood descriptions. Because these cells often occur in very low frequency and usually are not obvious at lower magnifications we think they have been underreported in the literature. InsideWood most surely does not record all occurrences of this feature, so the absence of this feature in the IW database is not a reliable indicator of its absence in a species.

This feature is not used in the Fossil Wood Database.

## DISJUNCTIVE RAY PARENCHYMA CELL WALLS (RLS)

## 113. Disjunctive ray parenchyma cell walls

We are sure this feature is underreported in the literature and is more common than is shown in Table 1 (only 10% of the *InsideWood* descriptions). Often, when we have gone back and checked radial sections of woods with heterocellular rays with multiple marginal rows of upright/square cells, we have observed this feature. This feature appears to be associated with a marked difference in the radial widths of the procumbent and upright cells.

This feature is not used in the Fossil Wood Database.

## RAYS PER MILLIMETRE (TLS, TS)

114.  $\leq 4$ /mm

## 115. 4-12/mm

116.  $\geq 12$ /mm

An ocular micrometer will help with orientation for counting the number of rays along a straight line perpendicular to the rays' axes. Some anatomists (PB, PG) only use tangential sections to measure rays per mm. Others (EW) use transverse sections, especially for fossil woods.

For woods with aggregate rays (feature 101) or with very broad rays and two distinct size classes (features 99 and 103) the data on rays/mm are not consistent. Some descriptions of woods with these features report the number of rays in between the aggregate rays or in between the very wide rays; while others report a value based on surveying a wide area that includes the wide rays. For narrowing down the number of possible matches for an unknown, the value of features 101p (aggregate rays) and 103p (rays of 2 distinct sizes) far outweigh the value of rays per mm, so we advise not using features 114-116 for such woods.

## WOOD RAYLESS (TS, TLS, RLS)

## 117. Wood rayless

Woods without rays are extremely rare: only 20 entries (approximately 0.3%) in *InsideWood* have this feature, mostly shrubs in chiefly herbaceous groups that are secondarily woody (Carlquist 1985, 2001; Lens *et al.* 2013).

## STORIED STRUCTURE (TLS)

## 118. All rays storied

## 119. Low rays storied, high rays non-storied

## 120. Axial parenchyma and/or vessel elements storied

## 121. Fibres storied

## 122. Rays and/or axial elements irregularly storied

The presence/absence of storied structure should be determined only from the tangential surface. Storied structure is uncommon and is highly diagnostic, being especially useful for some commercial hardwoods belonging to the Bignoniaceae, Dipterocarpaceae, Leguminosae, Malvaceae, and Zygophyllaceae. Features 118-122 are not mutually exclusive. If rays are storied, then axial parenchyma usually is storied as well; there are only a few descriptions with storied rays and without storied axial parenchyma (Table 1). As noted in the Hardwood List, these features are variable in occurrence, with *Swietenia* being an often-cited example of variation in occurrence of storied rays (White & Gasson 2008).

Feature 119 mainly occurs in the Malvaceae and Leguminosae (the faboid and caesalpinoid legumes). In some species, such as *Thespesia populnea* and *Hibiscus tiliaceus* (Malvaceae), there is variation in how common the tall rays are, and a small sample might not include the tall rays.

As expected, and almost by definition, feature 122: rays and/or axial elements irregularly storied is often recorded as variable (Table 1). This feature is easily overlooked in microscope sections and may be easier to see at low magnifications (dissecting microscope or hand lens).

#### OIL AND MUCILAGE CELLS (TLS, RLS)

- 124. Oil and/or mucilage cells associated with ray parenchyma
- 125. Oil and/or mucilage cells associated with axial parenchyma
- 126. Oil and/or mucilage cells present among fibres

This is a useful feature for identification because these idioblasts only occur in a few families, particularly within the magnoliids (Magnoliales: Annonaceae, Degeneriaceae, Eupomatiaceae, Magnoliaceae; Laurales: Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae; Cannellales: Canellaceae, Winteraceae). Within the Lauraceae, these idioblasts can occur in just one location or in more than one; Richter (1981) noted some infraspecific variation in the family. In the other families, they rarely occur in more than one location; for example, in the Annonaceae, they are usually in the interior of the ray; in the Magnoliaceae, in the ray margins. In tangential section, marginal ray cells sometimes appear enlarged relative to the body cells, so it is wise to verify oil cell presence using radial sections.

#### INTERCELLULAR CANALS

- 127. Axial canals in long tangential lines (TS)
- 128. Axial canals in short tangential lines (TS)
- 129. Axial canals diffuse (TS)
- 130. Radial canals (TLS)
- 131. Intercellular canals of traumatic origin (TS)

Features 127–130 occur in but a few families and so are useful in narrowing a search. Species described as variable for these features are not so much variable for presence or absence, but variable or intermediate for their distribution within a single piece of wood. A small section of a wood that has few or widely spaced canals may not show the feature.

There are intergradations between features 127–129. Axial canals occur primarily in the Dipterocarpaceae and are especially important for distinguishing genera or species groups within the family. They are also an obvious feature of several non-papilionoid Leguminosae genera.

While most Anacardiaceae and Burseraceae (order Sapindales) have radial canals, not all do, so the absence of this feature can help with identifying some genera within those families. Of the 242 Anacardiaceae descriptions in InsideWood, 84 do not have radial canals and 11 are described as variable because the canals are rare and could be overlooked; there are 94 Burseraceae descriptions in InsideWood, 36 do not have radial canals and three are described as variable.

The absence of Feature 131 (Traumatic canals) should not be used in a search because they are not a consistent feature and do not occur in all samples of a species. It is assumed that these canals are formed in response to an injury of some sort to the cambium. In InsideWood, there are 15 families recorded as having species with traumatic canals, notably the Meliaceae, Rutaceae, and Simaroubaceae (Sapindales), Combretaceae and Vochysiaceae (Myrtales), Rosaceae and Eleagnaceae (Rosales), Leguminosae (Fabales), and Malvaceae (Malvales).

#### TUBES/TUBULES

##### 132. Laticifers or tanniniferous tubes

These are rare and can be difficult to find. Laticifers are restricted to Apocynaceae (including the former Asclepiadaceae), Euphorbiaceae, and Moraceae; tanniniferous tubes to Connaraceae, three genera of Leguminosae (Stepanova *et al.* 2017), Myristicaceae, and the genus *Pteroceltis* (Cannabaceae; Zhong *et al.* 1992). The Hardwood List notes that these tubes often are of the same size as the surrounding ray cells in tangential so that they may be easier to recognize in radial sections because they have much longer radial dimensions than adjacent procumbent ray cells.

There are some species with large laticifers/tanniniferous tubes, which might initially be thought to be radial canals (*Alstonia congensis*, *Couma macrocarpa*, *Dyera costulata*, *Parahancornia fasciculata*). It may be helpful to check at higher magnifications for presence of epithelial cells. However, large laticifers may modify the pattern of the developing surrounding ray cells, creating the false impression of an epithelium.

#### CAMBIAL VARIANTS

##### 133. Included phloem, concentric

##### 134. Included phloem, diffuse

##### 135. Other cambial variants

These features (133–135) involve soft tissues (phloem and unligified parenchyma) that will be affected by drying. In dried samples and thin sections, phloem strands may only appear as holes. Nonetheless, their distributions and appearance still have some diagnostic value, in CITES-listed, incense producing Gaharu or Agarwood belonging to the genera *Aquilaria* and *Gyrinops* of the Thymelaeaceae for example.

The IAWA Hardwood Committee (1989) used terms for cambial variants that have become obsolete. The IAWA Bark List uses the currently acceptable terminology: ‘phloem strands produced by successive cambia’ (~concentric included phloem, 133), and ‘phloem strands produced by a single cambium’ (~diffuse included phloem, 134) (Carlquist 2001; Angyalossy *et al.* 2016). Feature 135, other cambial variants, is a mixed bag of features, mostly associated with the lianescent habit, including phloem wedges typical of many climbing Bignoniaceae (Angyalossy *et al.* 2016).

#### MINERAL INCLUSIONS (136–163)

The IAWA Hardwood List recognizes many features for type and distribution of mineral inclusions, and yet one can easily encounter variants that are not easy to match with one of the IAWA Codes. A single wood may exhibit multiple features of the long list of possibilities (136–163). We recommend using polarized light when searching for crystals. Presence, type and distribution of crystals are highly diagnostic, but abundance and absence often are not.

#### PRISMATIC CRYSTALS (RLS, TLS)

- 136. Prismatic crystals present
- 137. Prismatic crystals in upright and /or square ray cells
- 138. Prismatic crystals in procumbent ray cells
- 139. Prismatic crystals in radial alignment in procumbent ray cells
- 140. Prismatic crystals in chambered upright and/or square ray cells
- 141. Prismatic crystals in non-chambered axial parenchyma cells
- 142. Prismatic crystals in chambered axial parenchyma cells
- 143. Prismatic crystals in fibres.

Prismatic crystals are by far the most common type of crystals and occur in 52% of InsideWood entries. The various features for their distribution (137–143) are not mutually exclusive. Most hardwoods with crystals have them in procumbent (138) and/or square and upright ray cells (140) or non-chambered and chambered axial parenchyma cells (141, 142). Radial alignment in procumbent ray cells (feature 139; 3%) and crystals in fibres (142; 4%) are rare.

If hydrofluoric acid (HF) was used to soften a wood for sectioning, calcium oxalate crystals can be dissolved. However, the lignified thin integuments that surround crystals in

several plant families retain their shape ('crystal ghosts') and indicate that crystals were present.

The Oxford cards had only two features for prismatic crystals, as compared to the IAWA Hardwood List's eight features. Descriptions have been edited to try to get details on crystal location in line with the Hardwood List; however, it is probable the information for features 137-142 is incomplete, as Table 1 shows there are still descriptions with some features recorded as "?". Crystal occurrence and abundance varies within a species, so we do not recommend searching for the absence of these features.

#### DRUSES (RLS, TLS)

- 144. Druses present
- 145. Druses in ray parenchyma cells
- 146. Druses in axial parenchyma cells
- 147. Druses in fibres
- 148. Druses in chambered cells

Druses are rare (2.4% of the InsideWood descriptions) and so their presence is useful for reducing the number of possible IDs for an unknown. As the IAWA Hardwood List (p. 313) notes, many publications report the presence of druses, but do not provide information on location. Consequently, information on features 145-148 is not complete, and using the absence of the features for druse locations is not recommended.

#### OTHER CRYSTAL TYPES

- 149. Raphides
- 150. Acicular crystals
- 151. Styloids and/or elongate crystals
- 152. Crystals of other shapes (mostly small)
- 153. Crystal sand

The only one of these features used in the Oxford cards was "Raphides". Information on features 150-153 is incomplete. However, these features have great diagnostic potential, for example 150 in *Gmelina arborea* (Lamiaceae); 151 in ray cells of *Gonystylus* (Thymelaeaceae); 152 in some genera of Lauraceae and Oleaceae; 153 in *Bumelia obtusifolia* (Sapotaceae) and assorted Solanaceae and Boraginaceae.

#### OTHER DIAGNOSTIC CRYSTAL FEATURES (RLS, TLS)

- 154. More than one crystal of about the same size per cell or chamber
- 155. Two distinct sizes of crystals per cell or chamber



156. Crystals in enlarged cells

157. Crystals in tyloses

158. Cystoliths

The only one of these features used in the Oxford cards is “crystals in idioblasts”, which equates with feature 156. Information on the other features is incomplete, but worth exploring because of their very high diagnostic potential (especially features 157 and 158).

#### SILICA (RLS, TLS)

159. Silica bodies present

160. Silica bodies in ray cells

161. Silica bodies in axial parenchyma cells

162. Silica bodies in fibres

163. Vitreous silica

The Oxford cards had a feature for “silica bodies” but did not provide information on their location. Information on features 160–162 is incomplete. Another problem with the silica features is that some labs used hydrofluoric acid for softening woods and this would have dissolved the silica bodies meaning descriptions based on these samples would never have included information on silica features. Whether or not silica bodies would be visible in permineralized fossil wood is not clear.

Vitreous silica seems to be exceptionally rare and there is little information on its occurrence. It was not an Oxford card feature. Vitreous silica is difficult to see in sections and because most wood anatomical studies have used only sections, it is unlikely to be reported. We recommend not to use presence of vitreous silica in an ID procedure.

#### GEOGRAPHICAL DISTRIBUTION

164. Europe and temperate Asia (Brazier and Franklin region 74)

165. Europe, excluding Mediterranean

166. Mediterranean including Northern Africa and Middle East

167. Temperate Asia (China), Japan, USSR

168. Central South Asia (Brazier and Franklin region 75)

169. India, Pakistan, Sri Lanka

170. Myanmar (Burma)

171. Southeast Asia and the Pacific (Brazier and Franklin region 76)

172. Thailand, Laos, Vietnam, Cambodia (Indochina)

- 173. Indomalasia: Indonesia, Philippines, Malaysia, Brunei, Papua New Guinea, and Solomon Islands
- 174. Pacific Islands (including New Caledonia, Samoa, Hawaii, and Fiji)
- 175. Australia and New Zealand (Brazier and Franklin region 77)
  - 176. Australia
  - 177. New Zealand
- 178. Tropical mainland Africa and adjacent islands (Brazier and Franklin region 78)
  - 179. Tropical Africa
  - 180. Madagascar & Mauritius, Réunion & Comores
- 181. Southern Africa (south of the Tropic of Capricorn) (Brazier and Franklin region 79)
- 182. North America, north of Mexico (Brazier and Franklin region 80)
- 183. Neotropics and temperate Brazil (Brazier and Franklin region 81)
  - 184. Mexico and Central America
  - 185. Caribbean
  - 186. Tropical South America
  - 187. Southern Brazil
- 188. Temperate South America including Argentina, Chile, Uruguay, and S. Paraguay (Brazier and Franklin region 82)

The Hardwood Committee chose to use the geographic regions of Brazier and Franklin's multiple entry key (1961) and with some subdivisions. The Brazier and Franklin regions were similar to those used by Clarke (1938) and Chalk (Metcalfe & Chalk 1950). The geographic regions recorded in a description are for the taxon's native range, not where it is cultivated or has become naturalized. For example, *Robinia pseudoacacia* (Black Locust) is native to the central and eastern U.S., but has been introduced to Africa, Asia, Australia, Europe, and southern South America, at times being invasive. The only geographic area recorded for it in InsideWood is 182 (North America). Some species have wide ranges and occur in more than one region.

The percentages in Table 1 are percentages of descriptions in InsideWood, not percentages of species. Some individual descriptions in InsideWood represent multiple species that have similar wood anatomy.

In the future, it would be useful to have more precise searchable locality data in InsideWood and to link descriptions to global databases such as GBIF (<https://www.gbif.org>) and Kew's Plants of the World *online* (<http://www.plantsoftheworldonline.org>).

#### HABIT

- 189. Tree

190. Shrub

191. Vine/liana

If the unknown obviously is from a tree, using 189p is helpful. There are relatively few descriptions of lianas (Table 1), but if you are sure the unknown is a vine, it is helpful to code 191p. For small isolated samples, as recovered by archaeologists and paleobotanists, it is difficult to know the habit of the source material.

NON-ANATOMICAL FEATURES (192–221)  
WOOD OF COMMERCIAL IMPORTANCE

192. Wood of commercial importance

It seems best to repeat the Hardwood List's comments: "This category is intended for woods of both historical and current commercial importance. The term 'of commercial importance' is somewhat vague and should be used with caution when identifying an unknown. But when identifying certain wooden artefacts, such as furniture, it can be helpful to segregate commercial species from noncommercial species" (IAWA Committee 1989, p. 322). However, data on this feature likely are not complete because systematic wood anatomical papers do not necessarily include information on whether a species is commercially important. Commercial importance was not an Oxford card feature. It might have been wise to automatically code this feature as an unknown, but it was not. Information was added post-2004. Some woods that are not widely traded but used locally are coded as variable for this feature (192v).

SPECIFIC GRAVITY

193. Basic specific gravity low,  $\leq 0.40$

194. Basic specific gravity medium,  $0.40-0.75$

195. Basic specific gravity high,  $\geq 0.75$

HEARTWOOD COLOUR

196. Heartwood colour darker than sapwood colour

197. Heartwood basically brown or shades of brown

198. Heartwood basically red or shades of red

199. Heartwood basically yellow or shades of yellow

200. Heartwood basically white to grey

201. Heartwood with streaks

202. Heartwood not as above

## HEARTWOOD FLUORESCENCE

## 204. Heartwood fluorescent

## WATER &amp; ETHANOL EXTRACTS: FLUORESCENCE &amp; COLOUR

## 205. Water extract fluorescent

Only some InsideWood descriptions for commercially important timber species include information on non-anatomical features. Most systematic anatomy papers do not include such information and many of InsideWood's descriptions are based on this literature. Therefore, the non-anatomical features cannot be relied upon to help with identifying an unknown. In InsideWood, there are more descriptions with information on specific gravity and heartwood colour than on features 205–221 because the former are commonly mentioned in publications from forestry and wood science institutions (Détienne & Jacquet 1983; Gérard *et al.* 2016). Miller's (2007) paper on fluorescent woods of the world was used to record the presence of features 204 and 205.

## TWO EXAMPLES OF USING INSIDEWOOD'S WOOD MULTIPLE ENTRY KEY

Example 1 shows the importance of allowing mismatches and referring to the image collection and other literature to reach an identification. Example 2 is a rare case of finding a Paleogene fossil wood to have characteristics of a single present-day genus. This fossil had a combination of features that Table 1 shows as relatively uncommon and this made it relatively easy to narrow down its identification to a single genus.

**1. *A recalcitrant hairpin***

While we were preparing this paper, we were approached by Caroline Van Santen with a request for non-destructive identification of ethnic art from the Pacific in the collections of the British Museum. One of our institutes, the Naturalis Biodiversity Center, had acquired an advanced micro-CT scanner. We tested its usefulness in finding features for wood identification by gathering medium-resolution transverse, radial, and tangential scans of a wooden hairpin bought at a tourist market on Marquesas Islands (Fig. 2). The scans showed diffuse-porous wood (5), vessels with simple perforations (13), vessel-ray pits similar to intervessel pits (30), non-septate fibres present (66), parenchyma diffuse-in-aggregates (77) and in narrow bands/lines (86), strands of 2 cells (91), rays 1–3-seriate (97), body ray cells procumbent with one row of upright and/or square marginal cells (106), sheath cells present in some of the rays (110), all rays storied (118), axial parenchyma and/or vessel elements storied (120), prismatic crystals present in upright ray cells (136, 137), and wood from the Pacific region (174). Entering all those features in InsideWood does not produce a single match. Allowing one mismatching feature produces two matches — *Thespesia populnea*, a common pantropical coastal tree (the mismatching feature is 118: all rays storied), and *Kleinhovia hospita*, a commonly cultivated ornamental tree (mismatching in feature 110 tile cells).

The InsideWood entries for *T. populnea* include feature 119: tall rays nonstoried, low rays storied — a reason why we initially rejected *T. populnea* as a possible ID of the hairpin.

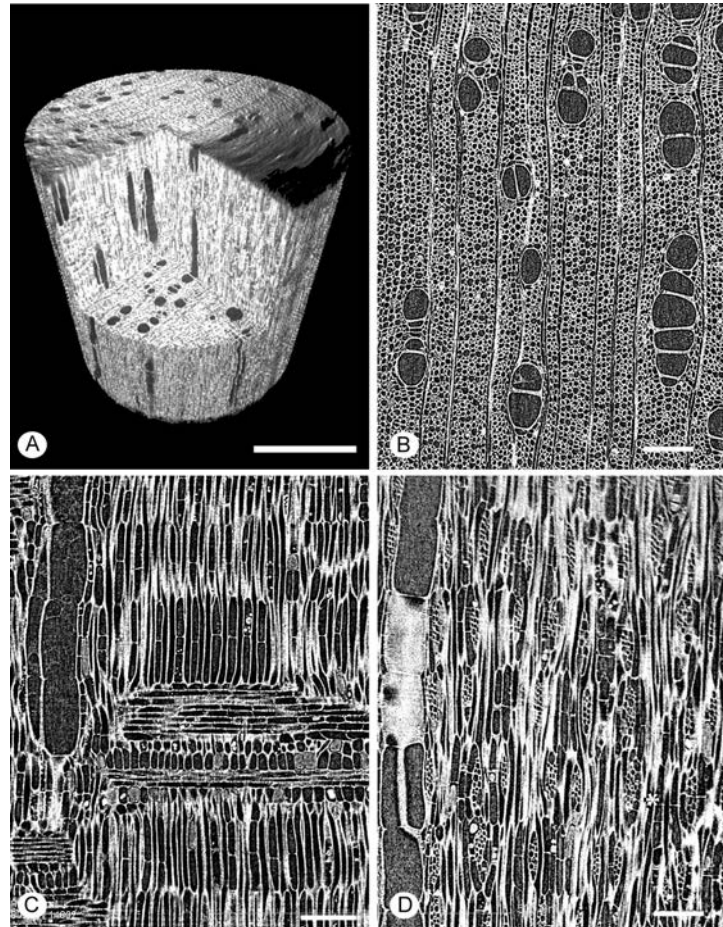


Figure 2. Micro-CT scans of a wooden hairpin from Marquesas Islands. (A) 3-D reconstruction. (B) Wood diffuse-porous (5p), vessels solitary and in radial multiples, axial parenchyma diffuse-in-aggregates (77p) and narrow lines (88p), TS. (C) Rays with procumbent body cells and one row of square/upright cells, asterisk to the right of the upright cell with prismatic crystal, RLS. (D) Rays and axial parenchyma storied (118p, 120p), rays mostly 2–3 seriate (97p). Axial parenchyma strands of two cells (91p), TLS. Asterisk (\*) to the right of the ray with sheath cells (110p). Scale bars: 1 mm in (A); 100  $\mu\text{m}$  in (B, C, D).

The InsideWood descriptions were based on information from Détienne & Jacquet (1999), Louppe *et al.* (2008), and Sosef *et al.* (1998). In InsideWood *K. hospita* is coded to lack sheath cells, and more significantly to have tile cells, which on inspection appear to belong to the distinct *Durio* type (cf. IAWA Committee 1989). Allowing two mismatches yields a number of other Malvaceae: *Camptostemon*, *Desplatsia*, *Hibiscus*, and even a few *Dalbergia* species (Leguminosae). The extra mismatches usually concerned geographical distribution, as well as sheath cells, ray width or parenchyma distribution. At this stage, we were informed by

Caroline Van Santen that on the basis of ethnobotanical and circumstantial evidence the hairpin was most likely carved from *Thespesia* wood.

Further literature searches revealed that Illic (1991) and Rudall & Cartwright (2019) had illustrated *T. populnea* samples with all rays storied, and tall rays absent or very rare. Images in InsideWood show considerable variation in frequency of tall non-storied rays; no tall rays are visible in FPAw ngf.5439 and Uw 4807; tall rays are present, but rare in Kw 21890 and CTFTw 27648; tall rays are common in BWCw 8770. Two slides in a Leiden research collection of *T. populnea* from Mauritius showed extremely contrasting ray patterns: one with almost all rays low and storied, and the other (juvenile) sample with virtually all rays tall and non-storied. These specimens were also variable for presence/absence of tile cells of the *Pterospermum* type (cf. IAWA Committee 1989). In conclusion, we accept *T. populnea* as the most likely identification, and modified InsideWood's description of it to better reflect its infraspecific variation; 118 was added to the description.

It cannot be emphasized enough that geographically widespread species, such as *T. populnea*, can be variable in some features. InsideWood entries, unfortunately, may not fully reflect that variability. Also, because the images in InsideWood are added separately from the descriptions, there can be differences between the photos and descriptions in some features. Whenever such differences are noted, please contact EW so the InsideWood coded descriptions can be modified.

## 2. A late Eocene (approximately 36 Ma) wood

Late Eocene fossil woods from Post, Oregon, are the subject of ongoing investigations by Wheeler & Manchester (Wheeler et al. 2006; Wheeler & Manchester 2007, ms. in preparation). One well preserved wood type (Fig. 3) was used as a test case by two of us (PB and PG).

PB recognized the following features: distinct growth rings (1), ring-porous (3), vessel clusters common (11), simple perforations (13), vessel-ray pits with much-reduced borders, rounded (31), helical thickenings in vessel elements (36), tyloses common (56), larger rays 4 cells wide or wider (98), body ray cells procumbent with one row of square/upright marginal cells (106), radial canals (130), prismatic crystals in upright/square ray cells (137). Searching the modern wood database gave four matches, all *Pistacia* species.

Searching the fossil wood database for these features yields one match from the Eocene Post Oregon (UF locality 279) — the actual test sample. The InsideWood coding also has vascular tracheids (60) present, and parenchyma scanty paratracheal (78) and vasicentric (79), features that are visible in Fig. 3. Allowing one mismatch to the above search, yielded two other fossil Anacardiaceae (*Pistacioxylon*) in the InsideWood database, strengthening confidence in the outcome of this search: the UF 279 sample will be assigned to the genus *Pistacia* (Wheeler & Manchester, ms. in preparation).

Independently of PB, PG chose the following features and put them into the search in one go: Distinct growth rings (1), ring-porous (3), vessels in diagonal/radial pattern (7), radial multiples (10) and clusters (11), simple perforations (13), helical thickenings (36, 37), vessel-ray pitting circular with reduced borders (31), fibres thin- to thick-walled (69), rays

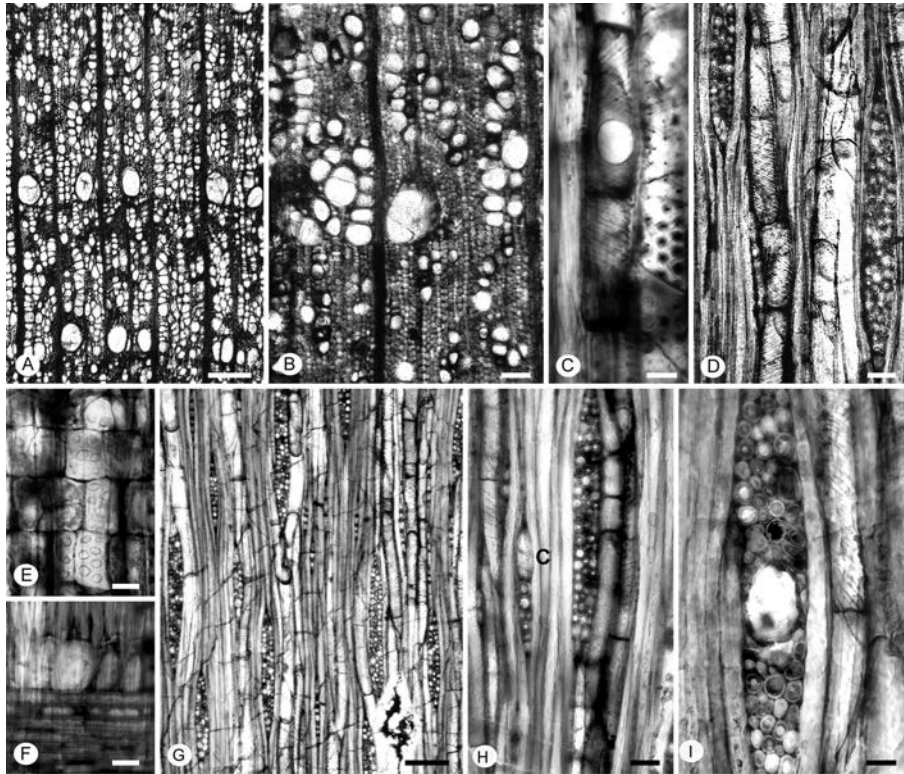


Figure 3. Late Eocene *Pistacia* wood. (A, B) Ring-porous wood (3p) with latewood in clusters (1up) and radial multiples of 4 or more (10p), fibres thin- to thick-walled, TS. (C) Simple perforation plate (13p), alternate intervessel pitting (22p), TLS. (D) Helical thickenings in vessel element (36p), multiserial rays four cells wide (98p), TLS. (E) Vessel-ray parenchyma pits with reduced borders and rounded in outline (31p), RLS. (F) A single marginal row of square/upright cells (106p), crystals in upright ray cells (137p), RLS. (G) Rays 1–4 (5) seriate, commonly 3–4 seriate, TLS. (H) Crystal (C) in upright marginal ray cell (137p), TLS. (I) Radial canal (130p). Scale bars: 200  $\mu\text{m}$  in (A, G); 100  $\mu\text{m}$  in (B, D); 50  $\mu\text{m}$  in (C, I); 20  $\mu\text{m}$  in (E,F).

1–3 (97) and 4–10 cells wide (98), one row of uprights (104a, 105a, 106p, 109a; PG was not certain that there was only one row of uprights, hence the use of absences), radial canals (130). Searching modern woods resulted in only three matches, all *Pistacia*. He then searched the modern and fossil database and got exactly the same result.

This example shows that coding slightly different character combinations still yields the same identification result.

PG did not search for crystals. *Pistacia* is now known from Europe, Asia and Malesia, the southern U.S. and Central America (Mabberley 2017). The current distribution supports the identification; many Eocene age fossils of the Pacific Northwest are related to present-day taxa with a disjunct distribution.

## CONCLUDING REMARKS

The descriptions and images in InsideWood have particular value in answering yes/no questions, such as *Does this wood belong to genus X? or family Y?* Using the keyword search or the *Browse by Taxonomy* option will retrieve descriptions and images to help answer such questions. Answering the question — *What is this wood?* — especially when the geographic origin is unknown is considerably more challenging. To effectively use InsideWood's multiple entry key requires:

1. An understanding of the definitions of the IAWA Hardwood features (IAWA Committee 1989).
2. Knowing that coding for absence of features can be as helpful as coding for presence, for example describing the common pattern of vessels solitary and in short radial multiples and not arranged in any pattern use 6a 7a 8a 9a 10a 11a or if a wood has only diffuse (76p) and diffuse-in-aggregates parenchyma (77p), code for absence of obvious paratracheal parenchyma (79a 80a 81a 82a 83a) and parenchyma in wide bands (85a).
3. Table 1 suggests that — if present — using the following features that are relatively rare and relatively straightforward to recognize can quickly reduce the number of possibilities. The features are ring-porosity (3), any of the vessel arrangement or vessel grouping features (6-11), scalariform perforation plates (14), scalariform or opposite intervessel pitting (20 or 21), minute (24) or very large intervessel (27) pits, very wide vessels (43), axial parenchyma absent or extremely rare (75), rays exclusively uniseriate (96) or commonly  $\geq 10$ -seriate (99), aggregate rays when a relatively large sample is used so as to not overlook them (101), all ray cells procumbent (104), tile cells (111), all rays storied (118), oil cells (124–126), radial canals (130). Even if none of these uncommon features are observed, attempts to identify woods with such common features as diffuse porosity (5p), simple perforations (13p), alternate pits (22p), non-septate fibres (66p) with simple to minutely bordered pits (61p), and 1–3-seriate heterocellular (97p) non-storied rays (118a) are often successful, with the addition of a few extra features like vessel diameter and frequency, axial parenchyma distribution, and crystal location.
4. Recognizing there are some features with potential for narrowing a search, but that should be used later on and with caution, because information on them in InsideWood is incomplete: some vessel-ray parenchyma pit features (33–35), sclerotic tyloses (57), perforated ray cells (112), disjunctive ray parenchyma cell walls (113), other crystal types such as acicular, elongate, of other shapes, and crystal sand (150–153), and some of the other diagnostic crystal features (154, 155, 157, 158).
5. Knowing there is no single correct way to use InsideWood's multiple-entry key. One strategy is to start with the presence or absence of a few features and then add additional features in small numbers or one by one until you get a number of possible matches you can work with to do comparative work. An alternative strategy is to enter the presence or absence of all the features you are sure about, and, if no matches are found, allow mismatches until you reach a number you can work with.



6. While it is good that InsideWood has broad coverage and includes many non-commercial woods, this means that sometimes a large number of possible matches can result from a search. This is true in part because within some relatively large families (Anacardiaceae, Annonaceae, Leguminosae, Lauraceae) some genera and species have similar anatomy.
7. If you get a small number of matches, we recommend looking at the descriptions and images of other members of those taxa in InsideWood, as well as the literature cited, to help with getting to the most likely identification. When we report on our identification work, we often say the unknown has features of this taxon, rather than say it is this taxon. This acknowledges that there are many species not described in InsideWood.
8. Be comfortable with the incontrovertible fact that wood anatomy and wood anatomists are variable. This translates into recognizing that having an unknown being one feature off from an InsideWood taxon description in such features as vessel diameter, vessel frequency, ray cellular composition may not be a good reason for excluding that taxon as a reasonable identification.
9. Please never hesitate to question the descriptions in InsideWood and write EW with those questions. Also, please send pdfs of publications that are not represented in InsideWood and non-copyrighted images so that InsideWood's content can become more comprehensive.

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