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Towards a standardised terminology for taxonomically important morphological characters in the Umbelliferae

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Taxonomically important structural characters and their states are given in an attempt to clarify and standardise the confusing and ambiguous terminology that is currently used in descriptions and identification keys of Umbelliferae taxa. The proposed terms to be used for characters and character states are listed, illustrated and discussed.

Introduction

A considerable limitation in the current descriptive work in the Umbelliferae (Apiaceae) is the incompleteness and/or incompatibility of descriptions in protologues, various monographs and regional Floras, as well as the use of inadequate terminology in identification keys. In the classical treatments of Drude (1898) and Koso-Poljansky (1914), explanations of terms were sometimes quite detailed, but the number of taxonomic characters was rather small (the full complexity was not yet known at the time), and different character states were not always precisely given and distinguished.

With the appearance of computer methods in taxonomic botany (initially numerical taxonomy, and later cladistics or numerical phylogeny), more precise formulation of character states for classification and phylogeny construction became necessary. The Umbelliferae were not unaffected. For instance, for classification of some complex genera or generic groups of Old World Umbelliferae by multivariate methods, some of us (e.g. Pimenov 1968, Pimenov *et al.* 1981, Pimenov and Kljuykov 1981, Lavrova *et al*. 1987, Tomkovich and Pimenov 1987, Ostroumova and Pimenov 1997, Pimenov *et al*. 2000) prepared lists of characters with two or more states. Similar efforts were also made by other researchers such as Roux *et al.* (1978), Small (1978), Spalik (1996), Van Wyk *et al.* (1996), Van Wyk (2001), Henwood and Hart (2001) and Menemen and Jury (2001) but all of them were not universal for the family as a whole. On the other hand, Gilmartin (1980) proposed a very long list of Umbelliferae characters arranged according to presumed plesiomorphic and apomorphic states, i.e. suitable for cladistic analysis. The well-known and popular DELTA system (and similar computer identification systems) used to produce compatible descriptions and computer keys also requires complete and standardised sets of character states. Serious attempts have been made to do this for some large families, such as the Gramineae, as well as to compile descriptions of the families of the World flora (Watson and Dallwitz 1992).

Below we attempt to enumerate and illustrate diagnostic structural characters and their states that can be used for descriptions of genera, species and other taxa within the Umbelliferae and for identification keys. This may be viewed as a first step towards a complete, standardised glossary for the family. It will hopefully encourage different workers to survey as many of these characters as is practically possible, in order to promote comparable data sets and to use the same descriptive terminology. The list is, of course, preliminary and open to addition and correction.

Discussion

The Umbelliferae (Apiaceae) display several unique features of the inflorescence, flower and fruit (schizocarp) and therefore a family-specific terminology has developed over many years in attempts to accurately and unambiguously describe various structural details.

The terminology used now in the Umbelliferae description has a long history of development, in which the names of Hoffmann (1814, 1816), Lagasca (1821), Koch (1824) and Baillon (1879) are to be noted as founders. The early terms were critically summarised by Drude (1898), the author of the most comprehensive classification of the family, which has been widely used up to now, despite its obvious shortcomings. Many authors (some perhaps unknowingly) followed the terminology used by Drude. Some additional terms were proposed by Koso-Poljansky (1914, 1916), Briquet (1926), Klan (1947), and an attempt to streamline carpological terminology was made by Tamamschian (Tamamschian and Vinogradova 1969). The selection of the terms proposed below is somewhat subjective, but we care-

fully considered historical developments and also the most common current usage, as reflected in several recent papers that are referred to below.

Vegetative structures

Various characters and character states of the vegetative morphology, including those relating to habit (life-form), seedlings, roots, stems, leaves (petioles, laminas and stomata) are listed in Table 1. Various states are illustrated here, such as the petiole type in transverse section (Figure 1), terminal leaflet shape and margins (Figure 2) and stomata types (Figure 3). Most of these are not specific to the Umbelliferae and require no further discussion.

Inflorescences and flowers

In general, the synflorescence in the Umbelliferae is an umbel (simple or compound). The family was firstly separated just on the basis of this inflorescence type (Morison

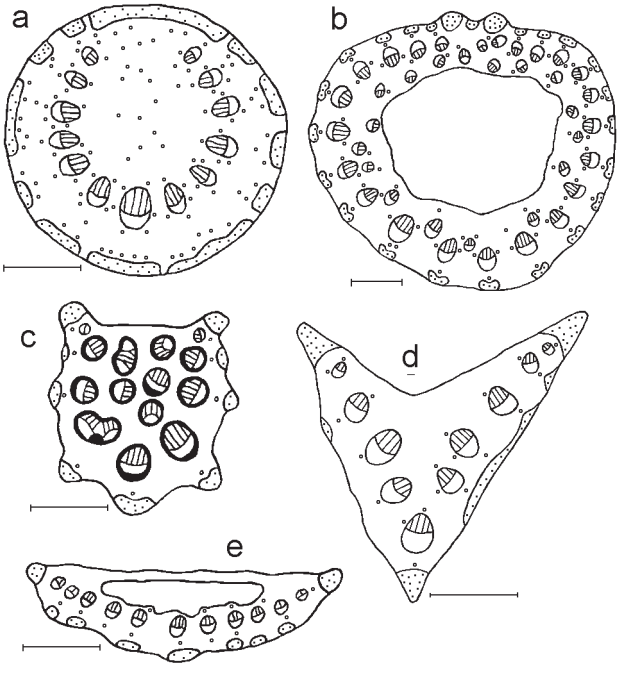

Figure 1: Transverse sections of petioles. a — *Eryngium maritimum* L.: glabrous (**31**, *1*), terete, without groove on adaxial side (**32**, *1*), smooth (**33**, *1*), solid (**34**, *1*), vascular bundles only marginal (**35**, *1*), parenchyma not lignified (**36**,*1*). b — *Smyrniopsis aucherii* Boiss.: glabrous (**31**, *1*), terete, with a small groove on adaxial side (**32**, *2*), smooth (**33**, *1*), hollow (**34**, *2*), vascular bundles marginal and central (**35**, *2*), parenchyma not lignified (**36**, *1*). c — *Echiniphora orientalis* Hedge et Lamond: glabrous (**31**, *1*), terete, with a broad groove on adaxial side (**32**, *3*), ribbed (**33**, *3*), solid (**34**, *1*), vascular bundles marginal and central (**35**, *2*), parenchyma not lignified (**36**, *1*). d — *Ostericum maximowiczii* (F.Schmidt ex Maxim.) Kitag.: glabrous (**31**, *1*), triangular, with adaxial groove (**32**, *4*), smooth (**33**, *1*), solid (**34**, *1*), vascular bundles only marginal (**35**, *1*), parenchyma not lignified (**36**, *1*). e — *Lipskya insignis* (Lipsky) Nevski: glabrous (**31**, *1*), adaxially flattened, with adaxial groove (**32**, *5*), smooth (**33**, *1*), hollow (**34**, *2*), vascular bundles only marginal (**35**, *1*), parenchyma not lignified (**36**, *1*). Scale bar = 1mm

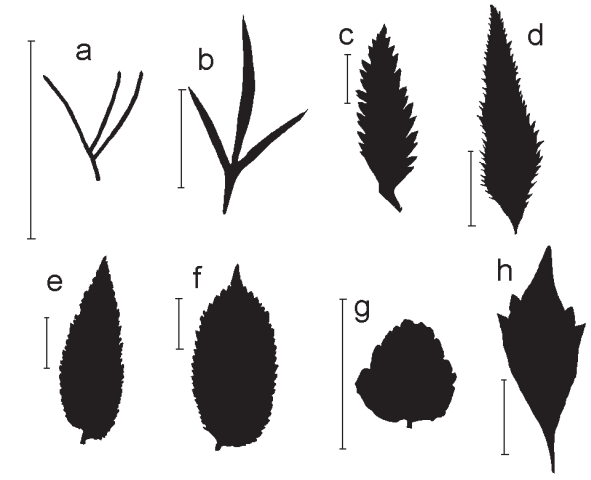

Figure 2: Terminal leaflets. a — *Rupiphila tachiroei* (Franch. et Savat.) Pimenov et Lavrova: filiform (**38**, *1*) with entire margin (**39**, *1*) and acute apex (**40**, *3*). b — *Ostericum maximowiczii* (Fr. Schmidt ex Maxim.) Kitag.: linear (**38**, *2*) with entire margin (**39**, *1*), acute apex (**40**, *3*) and decurrent base (**41**, *6*). c — *Pleurospermum uralense* Hoffm.: oblong (**38**, *3*) or narrowly ovate, serrate (**39**, *3*) with acute apex (**40**, *3*) and cuneate base (**41**, *3*). d — *Cryptotaenia japonica* Hassk.: linear-lanceolate (**38**, *4*), serrate (**39**, *3*) with acute apex (**40**, *3*) and cuneate base (**41**, *3*). e — *Angelica genuflexa* Nutt. ex Torr. et A.Gray.: lanceolate (**38**, *5*) with serrate margin (**39**, *3*), acute apex (**40**, *3*) and rounded base (**41**, *2*). f — *Angelica indica* Pimenov et Kljuykov: elliptic (**38**, *6*), serrate (**39**, *3*) with attenuate apex (**40**, *5*) and rounded base (**41**, *2*). g — *Magadania victoris* (Schischk.) Pimenov et Lavrova: ovate (**38**, *7*), crenate (**39**, *2*) with blunt (obtuse) apex (**40**, *4*) and slightly cordate base (**41**, *4*). h — *Ostericum sieboldii* (Miq.) Nakai: rhombic (**38,** *11*), dentate (**39,** *5*) with acute apex (**40**, *3*) and cuneate base (**41**, *3*). Scale bar = 2cm

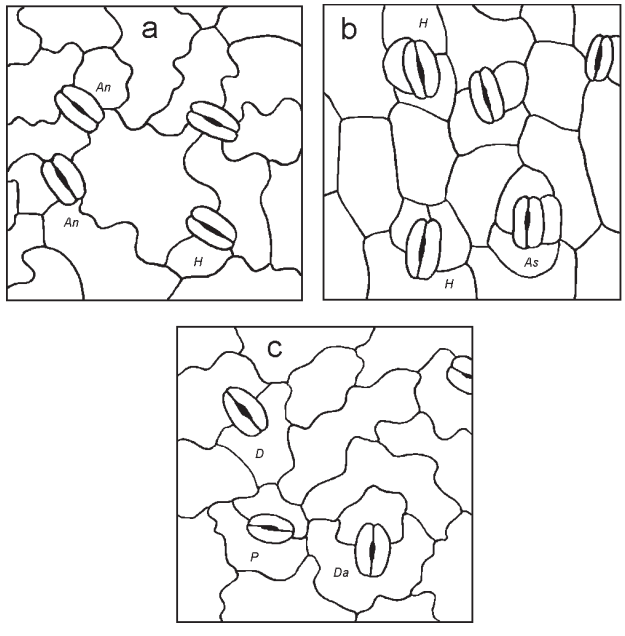

Figure 3: Stomata. a — *Hymenolaena badachschanica* Pissjauk. anomocytic (An) rarely hemiparacytic (H) (**44**, *1*). b — *Schrenkia golickeana* (Regel et Schmalh.) B.Fedtsch.: hemiparacytic (H) and anisocytic (As) (**44**, *2*). c — *Hydrocotyle javanica* Thunb.: diacytic (D), diallelocytic (Da) and paracytic (P) (**44**, *4*)

Table 1: Taxonomic characters and character states of the *Umbelliferae*

1. Life form
1. Tree. *2*. Shrub. *3*. Perennial polycarpic herb. *4*. Perennial monocarpic herb. *5*. Biennial herb. *6*. Annual herb.

2. Seedlings (cotyledon number)
1. One. *2*. Two.

3. Seedlings (cotyledon shape)
1. Linear. *2*. Lanceolate. *3*. Elliptic or ovate.

4. Seedlings (cotyledon tube)
1. Present. *2*. Absent.

5. Underground part
1. Taproot, not thickened. *2*. Taproot, thickened, turnip-shaped (tuberous). *3*. Rootstock (caudex, vertical branched rhizome). *4*. Tubers radical, hypocotylary, basal. *5*. Taproot not developed, roots adventitious, thin. *6*. Adventitious roots thickened. *7*. Rhizome horizontal, short. *8*. Rhizome horizontal, elongate. *9*. Horizontal stolons.

6. Stem (development)
1. Well developed. *2*. Not developed.

7. Stems (number)
1. Solitary. *2*. Few to several.

8. Stem (height in cm)

9. Stem (diameter at the base)

10. Stem (base)
1. Lignified. *2*. Covered with fibrous remains of petioles. *3*. Covered with scaly remains of petioles. *4*. Herbaceous, without petiole remains.

11. Stem (shape in transverse section)
1. Terete, smooth. *2*. Terete, grooved. *3*. Ribbed.

12. Stem (presence of cavity)
1. Hollow in all internodes. *2*. Hollow at the base. *3*. Solid.

13. Stem (in transverse section)
1. Without medullary vascular bundles. *2*. With medullary vascular bundles.

14. Stem (nodes)
1. Trilacunar. *2*. Multilacunar.

15. Stem (secondary thickening)
1. Present. *2*. Absent.

16. Stem (position)
1. Decumbent (prostrate). *2*. Ascending. *3*. Erect.

17. Stem (presence of leaves)
1. Without leaves. *2*. Leafy.

18. Stem (pubescence)
1. Glabrous. *2*. Hairy, covered with short hairs only under umbel. *3*. Covered with short hairs along full length. *4*. Hispid. *5*. Covered with reflexed hairs. *6*. Covered with stellate hairs.

19. Stem (branching)
1. Not branched. *2*. Alternate in the upper part. *3*. Opposite and/or verticillate in the upper part. *4*. Branching from the middle. *5*. Branching from the base.

20. Leaf (dissection)
1. Without blade. *2*. Simple, peltate. *3*. Simple, without distinct petiole. *4*. Simple, distinctly petiolate. *5*. Ternate. *6*. Biternate. *7*. 3-4-ternate. *8*. Pinnate or pinnatifid. *9*. Bipinnate. *10*. 3-4-pinnate. *11*. Palmate.

21. Stipules
1. Present. *2*. Obsolete

22. Leaves (arrangement)
1. Opposite. *2*. Alternate. *3*. Rosulate.

23. Leaf blade (shape in outline)
1. Circular. *2*. Ovate. *3*. Obovate. *4*. Deltoid. *5*. Rhombic. *6*. Triangular. *7*. Elliptic. *8*. Oblong. *9*. Lanceolate. *10*. Linear.

24. Leaf blade (length in cm, minimum)

25. Leaf blade (length in cm, maximum)

26. Leaf blade (width in cm, minimum)

27. Leaf blade (width in cm, maximum)

28. Leaf sheath
1. Not distinct. *2*. Linear-lanceolate. *3*. Inflated.

29. Leaf sheath (pubescence)
1. Glabrous. *2*. Hairy on the veins only. *3*. Hairy all over.

30. Leaf sheath (margin)
1. Herbaceous. *2*. White-membranaceous.

31. Petiole (pubescence)
1. Glabrous. *2*. Sparsely covered with short hairs. *3*. Densely covered with short hairs. *4*. Sparsely covered with long hairs. *5*. Densely covered with long hairs.

32. Petiole (transverse section)
1. Terete, without adaxial groove (Figure 1a). *2*. Terete, with narrow adaxial groove Figure 1b). *3*. Terete, with broad adaxial groove (Figure 1c). *4*. Triangular, with adaxial groove (Figure 1d). *5*. Adaxially flattened, with broad adaxial groove (Figure 1e).

33. Petiole (ribbing, excluding any adaxial groove)
1. Smooth (Figure 1a, 1b, 1d, 1e). *2*. Furrowed (sulcate). *3*. Ribbed (Figure 1c).

34. Petiole (presence of cavity)
1. Solid (Figure 1a, 1c, 1d). *2*. Hollow (Figure 1b,1e).

35. Petiole (vascular bundles)
1. Marginal only (Figure 1a, 1d, 1e). *2*. Marginal and central (Figure 1b, 1c).

36. Petiole (central tissue)
1. Not lignified. *2*. Lignified.

37. Leaf blade (primary segments/leaflets)
1. Sessile. *2*. Petiolulate.

38. Leaf blade (terminal leaflets in outline)
1. Filiform (Figure 2a). *2*. Linear (Figure 2b). *3*. Oblong (Figure 2c). *4*. Linear-lanceolate (Figure 2d). *5*. Lanceolate (Figure 2e). *6*. Elliptic (Figure 2f). *7*. Ovate (Figure 2g). *8*. Obovate. *9*. Deltoid. *10*. Circular. *11*. Rhombic (Figure 2h).

39. Leaf blade (leaflet dentation)
1. Entire (Figure 2a, 2b). *2*. Crenate (Figure 2g). *3*. Serrate (Figure 2c–f). *4*. Twice serrate. *5*. Dentate (Figure 2h). *6*. Twice dentate. *7*. Wavy *8*. Sinuate. *9*. Lobed.

40. Leaf blade (leaflet apex shape)
1. Awned. *2*. Mucronate. *3*. Acute (Figure 2a–e, 2h). *4*. Blunt (obtuse) (Figure 2g). *5*. Attenuate (Figure 2f).

41. Leaf blade (leaflet base shape)
1. Truncate. *2*. Rounded (Figure 2e, 2f). *3*. Cuneate (wedge-shaped) (Figure 2c, 2d, 2h). *4*. Cordate (Figure 2g). *5*. Attenuate. *6*. Decurrent (Figure 2b).

42. Leaf blade (pubescence)
1. Glabrous. *2*. Hairy below (along veins only). *3*. Sparsely hairy below. *3*. Sparsely hairy on both sides. *4*. Densely hairy below, glabrous or sparsely hairy above. *5*. Densely hairy on both sides.

43. Upper stem leaves
1. Dissected. *2*. Entire.

44. Stomata (predominant type)
1. Anomocytic (Figure 3a). *2*. Hemiparacytic (Figure 3b). *3*. Anomocytic + diacytic + paracytic. *4*. Diacytic + paracytic (Figure 3c).

45. Synflorescence as reproductive unit
1. Anthoid (flower-like). *2*. Head. *3*. Simple umbel. *4*. Compound umbel.

46. Flowers (arrangement by sexual condition) (Figure 4a–j, respectively)
1. All hermaphroditic. *2*. Predominantly hermaphroditic, some male. *3*. Andromonoecious. *4*. Monoecious.

Table 1 cont.

5. Gynomonoecious. *6*. Polygamonoecious. *7*. Dioecious. *8*. Androdioecious. *9*. Gynodioecious. *10*. Polygamodioecious.

47. Bracts (Figure 5a)
1. Present. *2*. Highly reduced. *3*. Absent.

48. Bracts (position)
1. Appressed to umbel rays. *2*. Reflexed.

49. Bracts (number)

50. Bracts (dissection)
1. Entire. *2*. Toothed (dentate). *3*. Pinnate. *4*. 2-3-pinnate.

51. Bracts (shape)
1. Filiform. *2*. Linear. *3*. Lanceolate. *4*. Elliptic. *5*. Circular. *6*. Ovate.

52. Bracts (apex shape)
1. Obtuse, enlarged at the apex. *2*. Obtuse. *3*. Mucronate. *4*. Acute. *5*. Attenuate.

53. Bracts (pubescence)
1. Glabrous. *2*. Scabrous. *3*. Sparsely hairy. *4*. Densely hairy.

54. Bracts (texture)
1. Herbaceous. *2*. Narrowly white-margined (banded). *3*. Broadly white-margined. *4*. White membranaceous. *5*. Spine-like.

55. Rays (Figure 5a) (number, minimum)

56. Rays (number, maximum)

57. Rays (relative size)
1. Equal (of the same length). *2*. Unequal.

58. Rays (pubescence)
1. Glabrous. *2*. Scabrous. *3*. Sparsely hairy. *4*. Densely hairy.

59. Rays (length)

60. Rays (surface)
1. Smooth. *2*. Grooved. *3*. Ribbed. *4*. Angular.

61. Bracteoles (Figure 5a)
1. Present. *2*. Absent

62. Bracteoles (connation)
1. Free. *2*. Connate at the base.

63. Bracteoles (relative size)
1. Shorter than pedicels. *2*. More or less equal to pedicels. *3*. Longer than pedicels.

64. Bracteoles (number)

65. Bracteoles (dissection)
1. Entire. *2*. Toothed. *3*. Pinnate. *4*. 2-3-pinnate.

66. Bracteoles (shape)
1. Filiform. *2*. Linear. *3*. Lanceolate. *4*. Elliptic. *5*. Circular. *6*. Ovate.

67. Bracteoles (apex)
1. Obtuse, enlarged at the apex. *2*. Obtuse. *3*. Sharpened. *4*. Acute. *5*. Attenuate.

68. Bracteoles (pubescence)
1. Glabrous. *2*. Scabrous. *3*. Sparsely hairy. *4*. Densely hairy.

69. Bracteoles (texture)
1. Herbaceous. *2*. Narrowly white-margined (banded). *3*. Broadly white-margined. *4*. White membranaceous. *5*. Spine-like.

70. Pedicels (Figure 5a) (number, minimum)

71. Pedicels (number, maximum)

72. Pedicels (pubescence)
1. Glabrous. *2*. Scabrous. *3*. Sparsely hairy. *4*. Densely hairy.

73. Pedicels (length)

74. Calyx teeth (Figure 5b) (presence/absence)
1. Prominent. *2*. Obsolete.

75. Calyx teeth (size)
1. Short. *2*. Equal to stylopod(ium) (Figure 5b). *3*. Exceeding stylopod(ium).

76. Calyx teeth (shape)
1. Filiform. *2*. Linear. *3*. Linear-lanceolate. *4*. Lanceolate. *5*. Ovate. *6*. Pinnatifid.

77. Calyx teeth (pubescence)
1. Glabrous. *2*. Pubescent.

78. Petals (inflexed lobe*; = lobulum inflexum*, Figure 5b)
1. Absent. *2*. Present.

79. Petals (base)
1. With claw. *2*. Without claw.

80. Petals (shape in outline)
1. Ovate. *2*. Round. *3*. Obovate. *4*. Obcordate. *5*. Spathulate. *6*. Lanceolate. *7*. Dissected.

81. Petals (tip)
1. Obtuse. *2*. Mucronate *3*. Attenuate and incurved. *4*. Attenuate.

82. Petals (relative size)
1. Equal. *2*. Unequal (outermost/marginal radiant).

83. Petals (pubescence)
1. Glabrous. *2*. Dorsally sparsely hairy. *3*. Dorsally densely hairy.

84. Petals (colour)
1. White. *2*. Blue. *3*. Pink. *4*. Red. *5*. Greenish-yellow. *6*. Yellow. *7*. Maroon or purple.

85. Petals (secretory ducts)
1. Absent. *2*. Solitary. *3*. Branched or several.

86. Anthers (colour)
1. White. *2*. Red. *3*. Yellow. *4*. Brown. *5*. Black.

87. Pollen grains (in outline)
1. Elliptic. *2*. Equatorially constricted. *3*. Rhomboid. *4*. Rectangular.

88. Fruits (separation at maturity, Figure 5c)
1. Mericarps separating. *2*. Mericarps not separating.

89. Fruits (shape/outline)
1. Ovate. *2*. Orbicular. *3*. Elliptic. *4*. Lanceolate. *5*. Linear-lanceolate. *6*. Linear.

90. Carpophore (Figure 5c)
1. Bifid (2-cleft) to the base. *2*. Bifid (2-cleft) to the middle. *3*. Entire. *4*. Absent (obsolete).

91. Mericarps (length, minimum)

92. Mericarps (length, maximum)

93. Mericarps(width, minimum)

94. Mericarps(width, maximum)

95. Mericarps (symmetry, Figure 6)
1. Equal (homomorphic). *2*. Unequal (heteromorphic).

96. Mericarps (in transverse section)
1. Strongly compressed dorsally (mericarp width more than three times the thickness) (Figure 7a). *2*. Slightly compressed dorsally (mericarp width less than three times the thickness) (Figure 7b–d, 7g, 7h). *3*. Not compressed (terete) (Figure 7e, 7f). *4*. Compressed laterally (Figure 6a).

97. Mericarps (ribs: primary, secondary)
1. Primary only (Figure 6b, 6c and Figure 7a–e, 7g, 7h). *2*. Primary and secondary (Figure 7f)

98. Mericarps (primary ribs)
1. All ribs equal (Figure 7e, 7g, 7h). *2*. Dorsal ribs (median and the two laterals) distinct from marginal ribs (Figure 7a–d, 7f). *3*. Lateral ribs broader than marginal and median ribs.

99. Mericarps (median rib)
1. Obsolete (Figure 7a, 7e). *2*. Keeled (Figure 7b, 7f, 7h). *3*. Winged (Figure 7c, 7d, 7g). *4*. Composed of hairs or spines. *5*. Thickened.

Table 1 cont.

100. Mericarps (marginal ribs)
1. Obsolete (Figure 7e). *2*. Keeled (Figure 7h). *3*. Winged (Figure 7a–d, 7g). *4*. Composed of hairs or spines. *5*. Thickened.

101. Mericarps (lateral ribs, if distinct from median)
1. Obsolete. *2*. Keeled. *3*. Winged (Figure 6c). *4*. Composed of hairs or spines. *5*. Thickened.

102. Mericarps (secondary ribs)
1. Obsolete. *2*. Keeled (Figure 7f). *3*. Winged. *4*. Composed of hairs or spines.

103. Mericarps (ribs)
1. Entire. *2*. Wavy. *3*. Plicate (transversely folded).

104. Mericarps (rib margin)
1. Smooth. *2*. Toothed.

105. Mericarps (pubescence)
1. Glabrous. *2*. Scabrous. *3*. Sparsely pubescent on ribs. *4*. Sparsely pubescent all over. *5*. Densely hairy. *6*. Spiny (Figure 7f). *7*. Covered with hooked (uncinate) prickles. *8*. Covered with scales (squamae). *9*. Tuberculate.

106. Stylopodia (Figure 5)
1. Present. *2*. Obsolete.

107. Stylopodia (shape)
1. Narrow conical. *2*. Conical. *3*. Low conical. *4*. Flat.

108. Styles (length)

109. Styles (shape)
1. Erect, parallel. *2*. Spreading. *3*. Recurved.

110. Exocarp/epidermis (adherence to mesocarp)
1. Adhering (Figure 8a). *2*. Separating at maturity (Figure 8b).

111. Exocarp/epidermis (cell size)
1. Small (Figure 8a). *2*. Large (Figure 8b).

112. Commissure (Figure 6) (width)
1. Narrow, exocarp almost reaches carpophore (Figure 7d–f, 7h). *2*. Intermediate (Figure 7c, 7g). *3*. Broad, exocarp stops near edges of marginal ribs (Figure 7a, 7b).

113. Mesocarp (presence of hypendocarp — inner fibrous mesocarp).
1. Present (Figure 7a, 8a). *2*. Obsolete (Figure 7b–h).

114. Mesocarp (excluding hypendocarp)
1. Not lignified (Figure 7b, 7e, 7f, 7h). *2*. Parenchyma cells lignified, with pitted walls (Figure 7a, 7c, 7d, 7g). *3*. Mesocarp with lignified cell groups.

115. Mesocarp (vascular bundle arrangement)
1. At primary rib/wing bases (Figure 7b, 7c, 7f). *2*. In middle of primary ribs/wings (Figure 7a). *3*. In distal part of primary ribs/wings (Figure 7d). *4*. Vascular elements diffuse, not forming bundles (Figure 7g).

116. Rib secretory ducts (Figure 6a, 6b)
1. Small, present in all ribs (Figure 7g). *2*. Large. *3*. Small, present in some ribs only (Figure 7b, 7c). *4*. Obsolete (Figure 7a, 7d, 7e, 7f, 7h).

117. Vittae (= 'secretory ducts', excluding those in the ribs). (Figure 6b, 6c)
1. Obsolete in mature fruit (Figure 7e, 7h). *2*. Vallecular and commissural (Figure 7a–d, 7f). *3*. Cyclic (Figure 7g). *4*. Diffuse (Figure 7g). *5*. Branching and anastomosing.

118. Vittae
1. Separate. *2*. Branching and anastomosing.

119. Vittae
1. Septate. *2*. Non-septate.

120. Vittae (vallecular vittae, Figure 6b, 6c)
1. Solitary (Figure 7a, 7d, 7f). *2*. 2–5 in each furrow (Figure 7b, 7c). *3*. Obsolete (Figure 7e, 7h).

121. Vittae (commissural vittae, Figure 6b, 6c)
1. Two (Figure 7a, 7d, 7f). *2*. 4–10 (Figure 7b, 7c). *3*. Obsolete (Figure 7e, 7h).

122. Endocarp (inner epiderm, Figure 6a, 6c)
1. Not lignified (the common state in Apioideae). *2*. Somewhat lignified. *3*. Strongly lignified (the common state in Hydrocotyloideae).

123. Endosperm (groove on commissural side)
1. Emarginate, flat, slightly convex or slightly concave (Figure 7a–d). *2*. With broad, shallow groove. *3*. With broad, deep groove (Figure 7e). *4*. With narrow, deep groove (Figure 7h). *5*. Mushroom-like (Figure 7f, 7g).

124. Crystals in pericarp
1. Obsolete. *2*. Cyclic (usually absent on commissural side). *3*. Diffuse. *4*. Commissural only.

1672), and its name is derived from the word 'umbel' (Constance 1971, Hedge 1973).

Froebe (1971) proposed, on the basis of comparative studies, that the typical umbel is actually derived from a thyrse (i.e. a monotelic inflorescence system). The flowers are most commonly all bisexual (hermaphroditic) as shown in Figure 4a. Another fairly common state is the presence of peripheral male flowers around the central, bisexual ones (Figure 4b). An interesting feature, often found in *Centella* and other members of Drude's Hydrocotyloideae, is the complicated reproductive systems, which may include andromonoecious (Figure 4c), monoecious (Figure 4d), gynomonoecious (Figure 4e) and polygamonoecious (Figure 4f) or even dioecious, androdioecious, gynodioecious or polygamodioecious types as shown in Figure 4g–j, respectively. Drude (1898) used the terms *endständige Dolde* and *Zweigdolden* to refer to the terminal and lateral umbels respectively. In Figure 5a the general structure of an umbel is shown including the position of the rays, pedicels, bracts (often referred to as involucral bracts) and bracteoles.

The pentamerous flower with its inferior ovary (Erbar and Leins 2004) is highly characteristic for the family and shows a few taxonomically useful discontinuities, including the presence, size and vestiture of the calyx teeth and petals (Figure 5b). A unique feature is the so-called stylopodium (an enlargement, often disc-like, at the base of the styles) that persists in the fruit, showing various possible states as listed in Table 1.

Fruits

The dry, bilocular fruits (schizocarps) usually split at maturity into two mericarps (Figure 5c), borne on a so-called carpophore, which may be entire or split (forked). The carpophore originates from the vascular bundle in the central part of the fruit (see below). If present, the carpophore is usually comprised of two vascular bundles (Figure 5c). Schizocarps vary considerably in size, shape and in the form

of the ribs. The shape in transverse section is of particular importance in distinguishing major groups of Apiaceae: either laterally compressed or dorsally compressed, as shown in Figures 6a, 6b and 6c respectively. The two mericarps are usually identical (homomorphic, Figures 6a and 6b) or rarely dissimilar in shape and wing configuration (heteromorphic, Figure 6c — Tilney and Van Wyk 2002, Winter and Van Wyk 1996). Terms used to describe ribs include dorsal, median, lateral, marginal and commissural. It is important to note the lack of consistency of these terms in the literature. The dorsal ribs are generally considered to be the three ribs on the dorsal side of the mericarp, as opposed to the two marginal (= commissural) ones. The term *dorsal rib* is therefore ambiguous, as it may refer to any of these three ribs (but often used for the median one only, e.g. Liu *et al*. 2003). We propose that the terms *median rib* and *lateral ribs* be used for the three dorsal ribs (Figure 6). Some authors (e.g. Theobald 1971) used *lateral rib* or *lateral wing* for the structures we here call *marginal rib* and *marginal wing*, while others have used the term *commissural rib* (e.g. Drude 1898). Commissural and marginal are synonymous and the term marginal is hereafter consistently used. Usually there are five mericarp ribs, but occasionally additional ribs may be present. Among them some ribs have vascular bundles; i.e. they do not differ from usual primary ribs (Figure 6a), so-called secondary ribs usually have no vascular bundles.

The various layers in the fruit wall (pericarp) are the exocarp (= epidermis), mesocarp (the inner part of which is sometimes fibrous, and then called an hypendocarp), and the endocarp (Figures 6, 7 and 8). The last-mentioned has one or several cell layers and is usually not lignified (the common state in Apioideae), somewhat lignified (in some basal groups of Apioideae) or strongly lignified (the common state in Hydrocotyloideae). The term hypendocarp is traditionally used for fibrous cells in the mesocarp (Figure 8) even though hyperendocarp may be seem linguistically more correct.

The oil ducts in the fruit (described as *Ölgängen* or *Secretcanale* by Drude 1898) are of particular interest. Three basic types (Figure 6) are distinguished: (1) vallecular vittae, present in each furrow between the ribs (the *Vittae valleculares* of Drude 1898); these are usually solitary, but sometimes two or more (up to five); (2) commissural vittae, present in the commissural region (the *Vittae commissurales* of Drude 1898); they may be solitary to several; (3) rib oil ducts, found in the fruit ribs, nearly always external to the rib vascular bundle; these are generally small or obsolete in the subfamily Apioideae but are often large in the Saniculoideae. Rib ducts are of different origin in comparison with the two other types, and they differ in their secretions. Rib secretory ducts are a part of the general secreto-

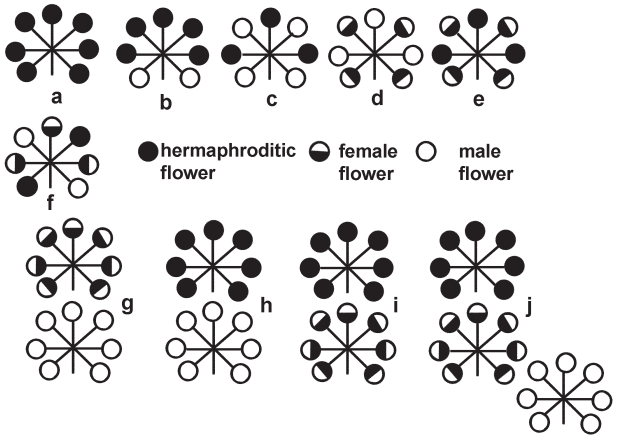

Figure 4: Arrangement of flowers by sexual condition in an inflorescence or in a single plant (a–f) or on different plants (g–j). a — all hermaphroditic (**46**, *1*). b — predominantly hermaphroditic, some male (**46**, *2*). c — andromonoecious (**46**, *3*). d — monoecious (**46**, *4*). e — gynomonoecious (**46**, *5*). f — polygamonoecious (**46**, *6*). g — dioecious (**46**, *7*). h — androdioecious (**46**, *8*). i — gynodioecious (**46**, *9*). j — polygamodioecious (**46**, *10*)

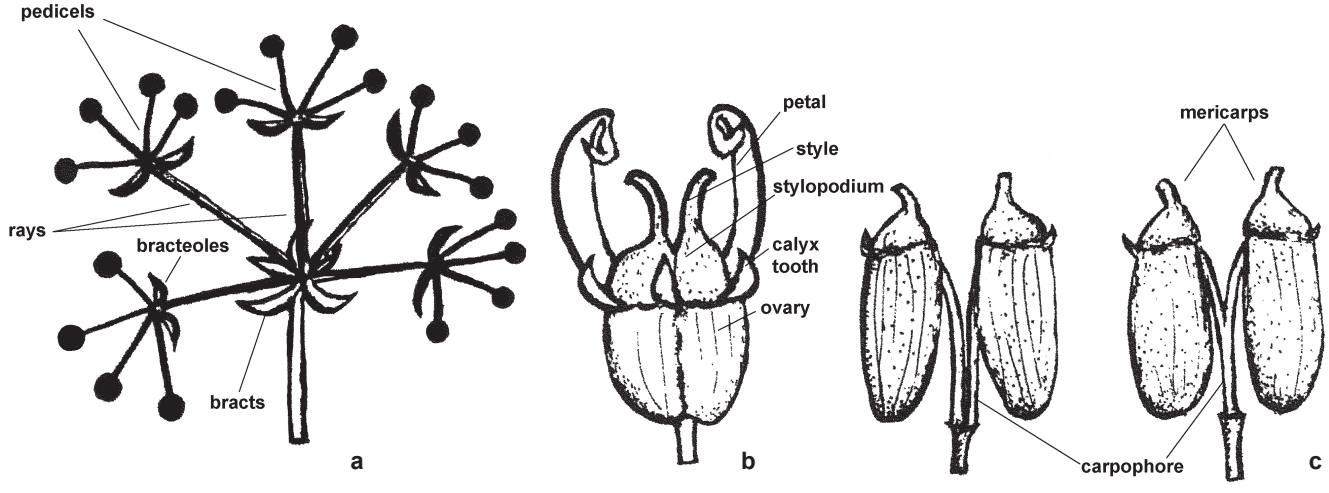

Figure 5: Inflorescencence, flower and fruits of Umbelliferae, to show general terminology. a — inflorescence (compound umbel), showing bracts (**47**), rays (**55**), bracteoles (**61**), pedicels (**70**). b — flowers, showing calyx teeth (**74**), petals (**78**) with inflexed lobe (**78**, *2*). c — fruits, showing mericarps separating (**88**, *1*), with the carpophore bifid to the base (**90**, *1*) or bifid to the middle (**90**, *2*)

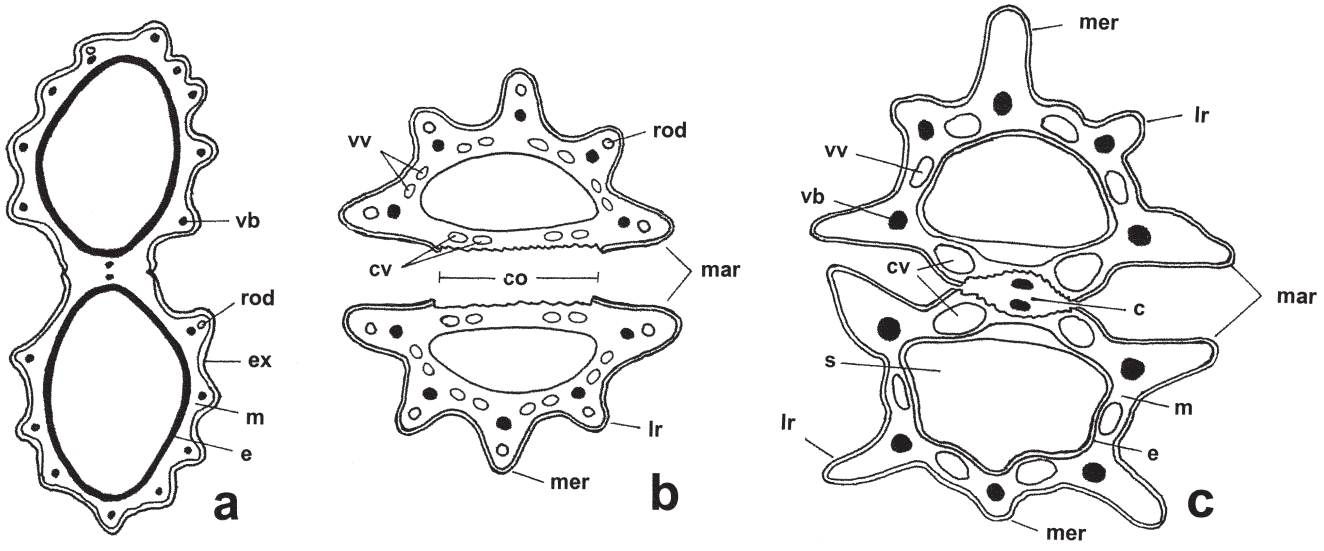

Figure 6: Transverse sections of fruits (schizocarps) of Umbelliferae, to show general terminology. a and b — equal (homomorphic) mericarps (**95**, *1*), a — compressed laterally (**96**, *4*), b and c — compressed dorsally (**96**, *1*). c — unequal (heteromorphic) mericarps (**95**, *2*). c = carpophore; co = commissure; cv = commissural vittae; ex = exocarp; m = mesocarp; e = endocarp; lr = lateral rib; mar = marginal ribs; mer = median rib; rod = rib oil duct; s = seed; vb = vascular bundle; vv = vallecular vittae

ry system of the plant, being associated with vascular bundles. The diversity of the fruit secretory system is not limited to these three types. In some taxa, other types of secretory ducts are observed (*Berula*, *Prangos*, some species of *Angelica*). In *Prangos* and its satellite genera, additional short secretory ducts are found dispersed in the mesocarp.

The endosperm often has a groove on the inner (commissural) side, showing various modifications (Figure 7). Crystals are relatively rare in the *Apioideae* (except in some basal groups, such as the woody African genera, nowadays included in the tribe Heteromorpheae) but are characteristic for the subfamily *Saniculoideae*. More work is needed on the homology of various types of crystals and their distribution in the family.

The terms used for the various characters and character states in Table 1 have become well established through common usage although a few appear to be disputable. Our proposal is given in Table 1 below and is also an invitation to discuss the terminological problems in *Umbelliferae* descriptions and diagnostics so that a consensus may eventually be reached.

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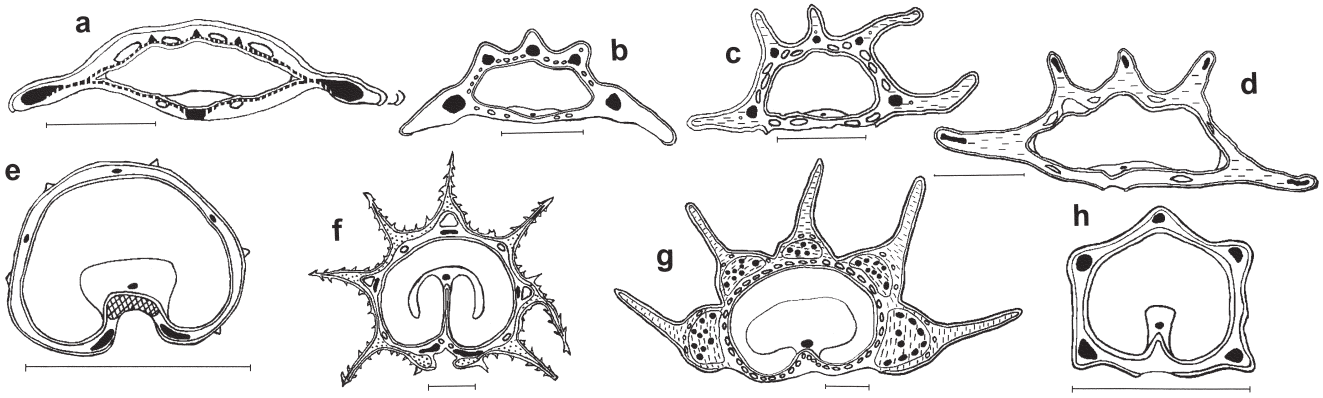

Figure 7: Transverse sections of mericarps. a — *Pastinaca pimpinellifolia* M.Bieb.: strongly compressed dorsally (**96**, *1*), ribs only primary (**97**, *1*), three dorsal ribs (= median and two lateral ribs) distinct from marginal ribs (**98**, *2*), median ribs small or obsolete (**99**, *1*), marginal ribs broadly winged (**100**, *3*), lateral ribs small or obsolete (**101**, *1*), glabrous (**105**, *1*), commissure broad (**112**, *3*), hypendocarp present (**113**, *1*), mesocarp parenchyma lignified with pitted walls in marginal ribs (**114**, *2*), vascular bundles in middle portion of marginal ribs (**115**, *2*), rib secretory ducts obsolete (**116**, *4*), vallecular and commissural vittae present (**117**, *2*), vallecular vittae solitary (**120**, *1*), commissural vittae 2 (**121**, *1*), endosperm flat or slightly convex on commissural side (**123**, *1*). b — *Lomatocarpa korovinii* Pimenov: slightly compressed dorsally (**96**, *2*), ribs only primary (**97**, *1*), three dorsal ribs distinct from marginal (**98**, *2*), median ribs keeled (**99**, *2*), marginal ribs winged (**100**, *3*), lateral ribs keeled (**101**, *2*), glabrous (**105**, *1*), commissure broad (**112**, *3*) hypendocarp obsolete (**113**, *2*), mesocarp not lignified (**114**, *1*), vascular bundles at rib bases (**115**, *1*), rib secretory ducts small, not in all ribs (**116**, *3*), vallecular and commissural vittae present (**117**, *2*), vallecular vittae 2–5 in each furrow (**120**, *2*), commissural vittae 4–10 (**121**, *2*), endosperm flat on commissural side (**123**, *1*). c — *Oreocome involucellata* Pimenov et Kljuykov: slightly compressed dorsally (**96**, *1*), ribs only primary (**97**, *1*), three dorsal ribs (median plus two lateral) distinct from marginal (**98**, *2*), median ribs narrow-winged (**99**, *3*), marginal ribs broadly winged (**100**, *3*), lateral ribs narrow-winged (**101**, *3*), glabrous (**105**, *1*), commissure intermediate (**112**, *2*), hypendocarp obsolete (**113**, *2*), mesocarp parenchyma lignified with pitted walls only in ribs (**114**, *2*), vascular bundles at primary rib bases (**115**, *1*), rib secretory ducts small, not in all ribs (**116**, *3*), vallecular and commissural vittae present (**117**, *2*), vallecular vittae 2–5 (**120**, *2*), commissural vittae 4–10 (**121**, *2*), endosperm flat on commissural side (**123**, *1*). d — *Conioselinum tataricum* Fisch. ex Hoffm.: slightly compressed dorsally (**96**, *1*), ribs only primary (**97**, *1*), three dorsal ribs distinct from marginal ribs (**98**, *2*), median ribs narrow-winged (**99**, *3*), marginal ribs broadly winged (**100**, *3*), lateral ribs narrow-winged (**101**, *3*), glabrous (**105**, *1*), commissure narrow (**112**, *1*), hypendocarp obsolete (**113**, *2*), mesocarp cells lignified with pitted walls (**114**, *2*), vascular bundles in distal part of primary ribs (**115**, *3*), rib secretory ducts obsolete (**116**, *4*), vallecular and commissural vittae present (**117**, *2*), vallecular vittae solitary (**120**, *1*), commissural vittae two (**121**, *1*), endosperm flat on commissural side (**123**, *1*). e — *Anthriscus cerefolium* (L.) Hoffm.: terete (**96**, *3*) or slightly compressed, ribs only primary (**97**, *1*), primary ribs equal (**98**, *1*), median ribs obsolete (**99**, *1*), marginal ribs obsolete (**100**, *1*), lateral ribs obsolete (**101**, *1*), scabrous (**105**, *2*), commissure narrow (**112**, *1*), hypendocarp obsolete (**113**, *2*), mesocarp not lignified (**114**, *1*), rib secretory ducts obsolete (**116**, *4*), vittae obsolete in mature fruits (**117**, *1*), vallecular vittae obsolete (**120**, *3*), commissural vittae obsolete (**121**, *3*), endosperm with a broad deep groove on commissural side (**123**, *3*). f — *Turgenia latifolia* (L.) Hoffm.: not compressed (terete) (**96**, *3*), ribs primary and secondary (**97**, *2*), three primary dorsal ribs distinct from marginal (**98**, *2*), median ribs keeled (**99**, *2*), marginal ribs obsolete (**100**, *1*), lateral ribs keeled (**101**, *2*), secondary ribs keeled (**102**, *2*), spiny (**105**, *6*), commissure narrow (**112**, *1*), hypendocarp obsolete (**113**, *2*), mesocarp not lignified (**114**, *1*), vascular bundles at primary rib bases (**115**, *1*), rib secretory ducts obsolete (**116**, *4*), vallecular and commissural vittae present (**117**, *2*), vallecular vittae solitary (**120**, *1*), commissural vittae two (**121**, *1*), endosperm with a mushroom-like groove on commissural side (**123**, *5*). g — *Prangos lipskyi* Korovin: slightly compressed dorsally (**96**, *2*), ribs only primary (**97**, *1*), primary ribs equal (**98**, *1*), median ribs winged (**99**, *3*), marginal ribs winged (**100**, *3*), lateral ribs winged (**101**, *3*), glabrous (**105**, *1*), commissure of intermediate length (**112**, *2*), hypendocarp obsolete (**113**, *2*), mesocarp parenchyma lignified with pitted walls (**114,** *2*), vascular elements diffuse (**115**, *4*), rib secretory ducts small, present in all ribs (**116**, *1*), vittae cyclic and diffuse (**117**, *3 & 4*), endosperm with a mushroom-like groove on commissural side (**123**, *5*). h — *Conium maculatum* L.: slightly compressed dorsally (**96**, *2*), ribs only primary (**97**, *1*), primary ribs equal (**98**, *1*), median ribs keeled (**99**, *2*), marginal ribs keeled (**100**, *2*), lateral ribs keeled (**101**, *2*), glabrous (**105**, *1*), commissure narrow (**112**, *1*), hypendocarp obsolete (**113**, *2*), mesocarp not lignified (**114**, *1*), rib secretory ducts obsolete (**116**, *4*), vittae obsolete in mature fruits (**117**, *1*), endosperm with a narrow deep groove on commissural side (**123**, *4*). Scale bar = 1mm

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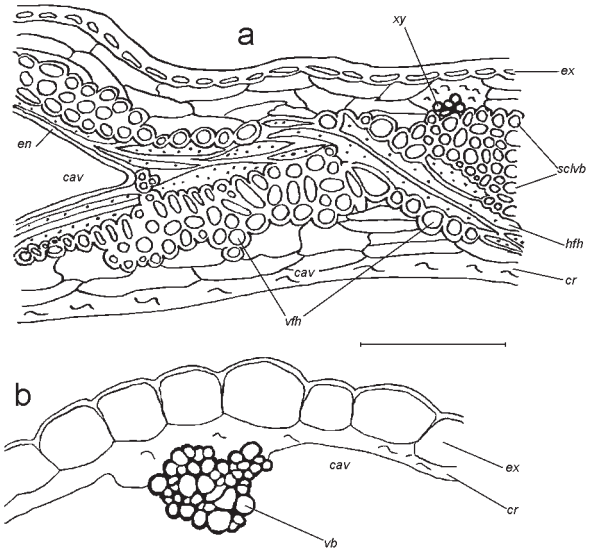

Figure 8: Transverse sections of mericarps with details of wall structure. a — *Pastinaca pimpinellifolia* M.Bieb.: exocarp adhering (**110**, *1*), exocarp cells small (**111**, *1*), hypendocarp present (**113**, *1*). b — *Ostericum scaberulum* (Franch.) Yuan ChangChi et Shan RenHwa: exocarp separating (**110**, *2*), exocarp cells large (**111**, *2*). *cav* = cavity, *cr* = crushed cells, *en* = endocarp, *ex* = exocarp, *hfh* = horizontal fibres of hypendocarp, sclvb – sclerenchyma of vascular bundle, *vb* = vascular bundle, *vfh* = vertical fibres of hypendocarp, *xy* = xylem. Scale bar = 0.1mm

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