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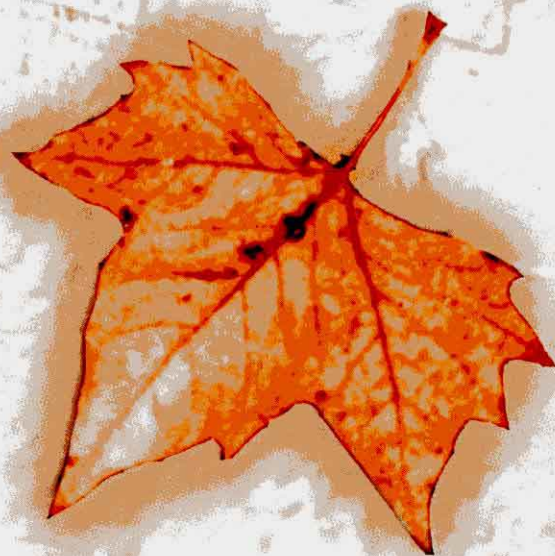
СОВРЕМЕННЫЕ ПРОБЛЕМЫ ПАЛЕОФЛОРИСТИКИ, ПАЛЕОФИТОГЕОГРАФИИ И ФИТОСТРАТИГРАФИИ

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Международной палеоботанической конференции

Москва, 17-18 мая 2005 г.

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МОСКОВСКОЕ ОБЩЕСТВО ИСПЫТАТЕЛЕЙ ПРИРОДЫ

Московское отделение
ВСЕСОЮЗНОГО ПАЛЕОНТОЛОГИЧЕСКОГО ОБЩЕСТВА

СОВРЕМЕННЫЕ ПРОБЛЕМЫ ПАЛЕОФЛОРИСТИКИ, ПАЛЕОФИТОГЕОГРАФИИ И ФИТОСТРАТИГРАФИИ

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Современные проблемы палеофлористики, палеофитогеографии и фитостратиграфии. Труды Международной палеоботанической конференции. Москва, 17–18 мая 2005 г. Вып. 1. – М.: ГЕОС, 2005. – 384 с., илл. ISBN 5-89118-354-4

В выпуск вошли статьи, подготовленные по докладам на палеоботанической конференции “Современные проблемы палеофитогеографии и фитостратиграфии”, организованной лабораторией палеофлористики Геологического института РАН (17–18 мая 2005) в связи с 50-летием создания лаборатории и основания палеоботанической школы Геологического института РАН. Публикуемые материалы посвящены общим проблемам палеоботаники, результатам изучения растительных мегафоссилий, проблемам дочетвертичной и четвертичной палинологии, палеоальгологии. Эти направления исследований являются определяющими в деятельности лаборатории в настоящее время.

Выпуск рассчитан на палеоботаников, палинологов, стратиграфов, геологов, а также широкий круг лиц, интересующихся вопросами палеоботаники, стратиграфии и палеогеографии.

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This issue includes scientific reports, presented to the International Palaeobotanical Conference “Modern problems of Palaeofloristics, Palaeophytogeography and Phytostratigraphy”. This Conference was organized by Laboratory Palaeofloristic Geological Institute RAS, connection with 50-years foundation of this Laboratory and Palaeobotanical school of the Geological Institute RAS. The most of papers are included materials on the General Palaeobotany, Macroflora, Pre-Quaternary and Quaternary Palynology, Palaeoalgology. These papers represent the main aspects of the research activities of the Laboratory at the recent time.

This issue is intended for palaeobotanists, palynologists, stratigraphers, geologists, botanists and also for wide audience who are interested in natural science.

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ОПЫТ РЕКОНСТРУКЦИИ РАННИХ ЭТАПОВ МОРФОГЕНЕЗА ПЛОДОВ АРХАИЧЕСКИХ ЦВЕТКОВЫХ

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Анализ строения плодов архаических групп магнолиофитов позволяет заключить, что морфогенетические преобразования этой уникальной структуры цветковых происходили на базе двух исходных типов. Один из них – это листовка в узком понимании: апокарпный плод, образованный вентрально вскрывающимися плодиками с гистологически дифференцированным перикарпием. Листовка (s. str.) характерна как для древнейших ископаемых цветковых растений (*Archaeanthus*, *Archaeofructus*), так и для большинства исследованных нами современных архаических рецентных покрытосемянных – Magnoliaceae, Illiciaceae, Myristicaceae, Lactoridaceae, Anaxagoea и *Xylopi* (Annonaceae). Наиболее близким к вентрально вскрывающейся многолисточке производным типом плода является сочная многолисточка, в перикарпии вторично невскрывающихся плодиков которой сохраняются рудименты механизма вскрывания (большинство Annonaceae, Schisandraceae). Второй впервые установленный нами базальный тип плода – это винтерина: апокарпный плод, образованный плодиками с очень слабо дифференцированным перикарпием, изначально лишённым каких-либо механизмов вскрывания. Такой тип плода выявлен у Degeneriaceae, Trimeniaceae и большинства представителей Winteraceae–Winteroideae, а его синкарпный и паракарпный производные подтипы – у *Zygogynum* (Winteraceae–Winteroideae) и *Takhtajania* + Canellaceae соответственно.

The problem of the origin of angiosperms is the subject of heated discussion since the times of Ch. Darwin. With the accumulation of factual data on fossil and recent plants very different hypotheses of their origin and early evolution were proposed. A number of attempts were made to ally angiosperms with different groups of fossil and some recent seed plants. As Magnoliophyta is the youngest in geological respect group of higher plants, all other taxa of these plants could be theoretically treated as ancestral ones. Currently, the hypothesis of origin of angiosperms from seed ferns is widely accepted [Stewart, Rothwell, 1993].

The oldest fossil angiosperms are dated by the beginning of Cretaceous or even the boundary of Jurassic and Cretaceous. Almost all described by present time well-preserved cretaceous fossil angiosperms could

be with certainty placed in recent families. The determination of their affinities bases on unique within the family features of reproductive organs' structure [Zhou et al., 2001; Gandolfo et al., 2004 etc.]. The angiosperms differ from other seed plants by the presence of perianth (in most cases), peculiar ultrastructure of sporoderm and forming of carpels and subsequently fruits. Nevertheless, the perianth and structure of pollen grains do not always allow to make a decision on affiliation of the fossils to Magnoliophyta. The perianth is an exceptionally evolutionary plastic structure, which readily origins and reduces in evolution; possibly it could had never originated in some groups of angiosperms with achlamydous flowers. L. Van der Pijl [1960; 1961] underlined that the main function of the perianth is the primary attraction of pollinators. The

sporoderm structure does not always allow to ascribe fossil pollen to the flowering plants on account of some “delicate” parallelisms of ultrastructural characters (e. g., sporoderm structure of *Sahnia* (Pentoxylales) [Osborn et al., 1991] and recent Nymphaeaceae (N.R. Meyer-Melikian, pers. comm.). On the other hand, the carpel and fruit structure are so much distinctive, that allow to describe any fossils as flowering plants with high probability. Namely the carpel and derived from it fruit are universal, unique and evolutionary conservative characteristics of flowering plants which are very important for phylogenetic reconstructions [Garcin, 1890; Vikhireva, 1952; Melikian, 1981; 1996]. The greatest importance of carpel and fruit is explained by their functioning as the system, which secures 1) constant conditions of ovules development from the moment of their origin and until the completion of seed development, and 2) taking care of the descendants (including dissemination). Thus, we suggest that namely the data of comparative carpology will assist to solve the problem of Magnoliophyta origin.

We have studied fruits of representatives of the families, which are treated as basalmost by morphologists and molecular scientists [Cronquist, 1981; Takhtajan, 1997; APG..., 2003]: Magnoliaceae, Illiciaceae, Schisandraceae, Degeneriaceae, Winteraceae, Canelaceae [Romanov, 2004; Romanov et al., 2004; Romanov, Bobrov, 2005], Trimeniaceae [Bobrov et al., 2002], Annonaceae [Romanov, 2004], Myristicaceae [Melikian et al., 2002], Amborellaceae [Melikian, Bobrov, 1997; Bobrov et al., 2005], Lactoridaceae [Bobrov, Romanov, 1999], Lauraceae [Melikian, Dhalilova, 2003], Monimiacae [Bobrov, Romanov, 2002; Bobrov et al., 2003], Atherospermataceae [Bobrov et al., 2003; 2004]. In some representatives of pointed families the fruits are apocarpous dry polyfollicles, formed by dehiscent (in type) fruitlets which expose the seeds. Such fruits are generally recognized by most evolutionary morphologist and systematists as the most archaic fruit types in view of the fact of their similarity with conduplicate megasporophyll of hypothetical groups of seed ferns [Bailey, Smith, 1942; Takhtajan, 1964; Stewart, Rothwell, 1993]. Palaeobotanical data are generally accorded with such view. Such fruits are the character of *Archaeanthus* [Dilcher, Crane, 1984] – one of the most well-studied fossil angiosperm. Polymerous polyfollicle of *Archaeanthus*, formed by 100–130 ventrally-dehiscent fruitlets, in which the pericarp is differentiated into exocarp, mesocarp (in which nests of radially-elongated fibers were found) and endocarp (represented by tangentially-elongated fibers), could be treated as ancestral fruit type. The fruits of the most ancient fossil angiosperm – *Archaeofructus* [Sun et al., 1998; 2002; Friis et al., 2003] to a certain extent resemble the *Archaeanthus*'s ones. The

finding of so ancient angiosperms with dehiscent follicles provide evidence for treating follicles as basal fruit type. Nevertheless, the assumptions of some investigators [Gottsberger et al., 1980] that early angiosperms could develop flesh polyspermous indehiscent fruits similar to recent Winteraceae – are of great interest. At first these fleshy fruits could be dispersed by reptiles and later – by birds and mammals.

The developmental investigations of fruit morphology and anatomy in archaic angiosperms brought us to the conclusion that in parallel with “classical” dry dehiscent follicle there is the second basal fruit type in angiosperms – the winterina [Romanov, 2004]. Winterina differs from follicle by morphology and anatomical structure of pericarp. Two basal fruit types, which are generally treated as the same one, fundamentally differ by anatomical differentiation of pericarp and consequently have different ways of dissemination. We suggest to use the term follicle for those apocarpous (poly-, oligo-, and monomerous) fruits, in which the pericarp is differentiated into exocarp (epidermal tissue), mesocarp (parenchyma with nests of sclereids) and lignificated endocarp (from many to one layer of fibers or sclereids). This type of differentiation of pericarp predetermines fruit dehiscence, and in this case the diaspora is the seed. In this new treating the follicle is the character of Magnoliaceae s. strss. (Pl. b, g) and Illiciaceae (Pl. Ic, e) [Romanov, 2004; Romanov et al., 2004], Lactoridaceae [Bobrov, Romanov, 1999], Anaxagorea and *Xylopi* (Pl. Id) Annonaceae, [Romanov, 2004]. Indicative is the similarity of morphological and anatomical features of fruits of *Paramanglietia aromatica* (Dandy) Hu, W.C. Cheng (Pl. Ia; fig. 1a) with the fruits of *Archaeanthus* [Romanov, 2004; Romanov et al., 2004]. Being the very conservative character the anatomical structure of pericarp does not sufficiently changes in monomerous follicles of Myristicaceae [Melikian et al., 2002] and in syncarpous (oligo-) polyfollicle of *Pachylarnax* [Romanov, Bobrov, 2005].

Spiral polyfollicles of *Illicium* (Pl. c, f) demonstrate some morphological similarity with the fruits of *Archaeanthus*, however anatomical structure of these polyfollicles is somewhat different. The endocarp in *Illicium* is formed by one layer of radially elongated sclereids, which imply the specialization (fig. 1b). This type of polyfollicle could be treated as basal for some other apocarpous fruit types. For instance if we assume the reduction of dehiscence of polyfollicles of *Illicium*-type under the preservation of general plan of pericarp differentiation the polydrupes of Monimiacae will be received, for example polydrupes of *Hedycarya arborea* J. R. Forster and G. Forster (fig. 1c; Pl. f) or *Peumus boldus* Molina [Bobrov, Romanov, 2002; Bobrov et al., 2003]. Further monomerization of the gynoecium brings to formation of (mono)drupes

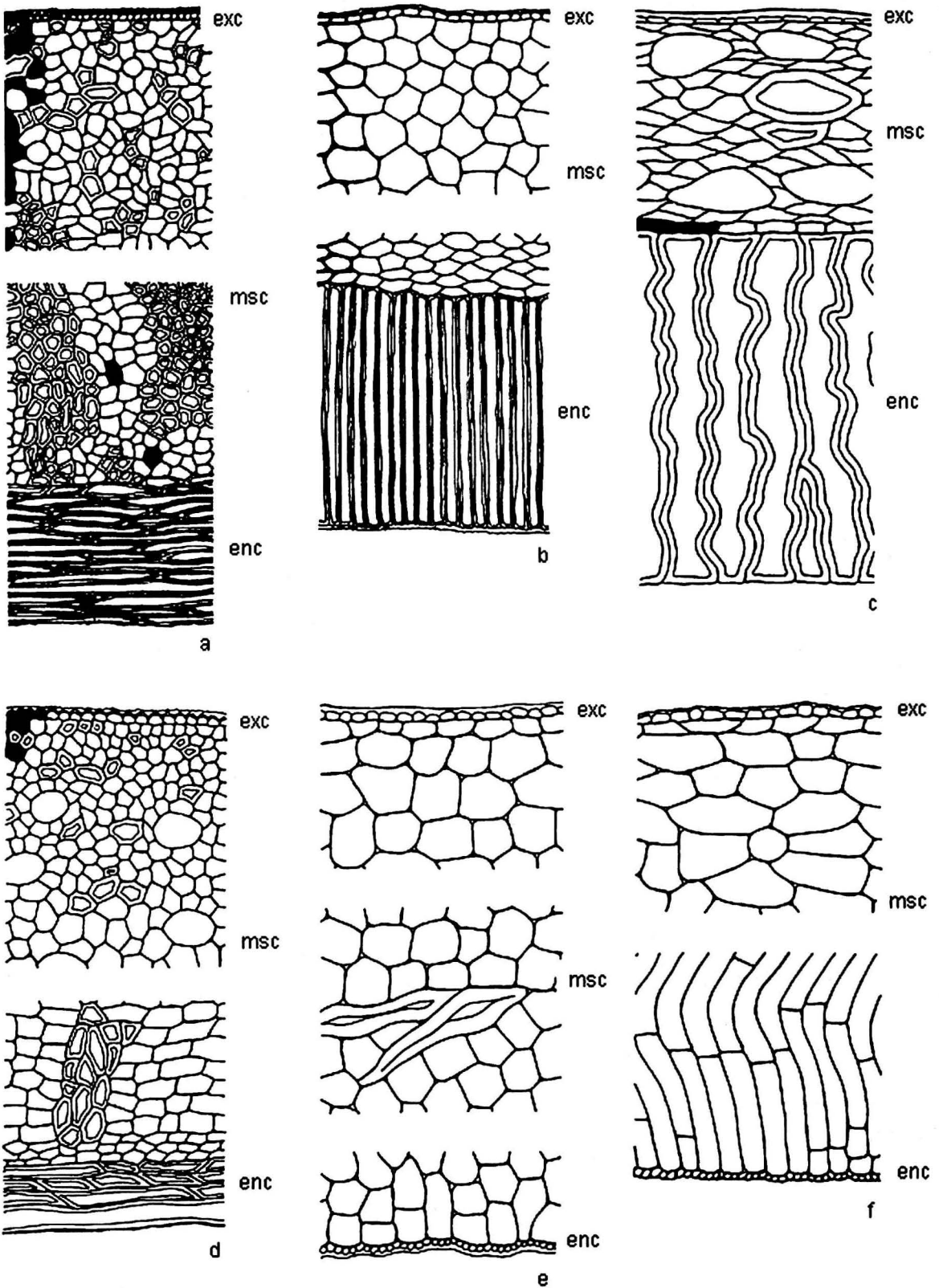


Fig. 1. a – cross section of pericarp of *Paramanglietia aromatica* (Dandy) Hu and W.C. Cheng; b – cross section of pericarp of *Illicium cambodianum* Hance; c – cross section of pericarp of *Hedycarya arborea* J.R. Forster and G. Forster; d – cross section of pericarp of *Magnolia hypoleuca* Siebold and Zucc.; e – cross section of pericarp of *Kadsura japonica* (L.) Dunal; f – cross section of pericarp of *Schisandra sphenanthera* Rehder and E.H. Wilson in Sarg

of Lauraceae, e. g., *Cinnamomum camphora* (L.) Nees and Eberm [Melikian, Dhalilova, 2003]. In spite of extreme reduction of pericarp in Atherospermataceae and fruit adaptation for anemochory the anatomical differentiation of pericarp allows determining these fruits as extremely specialized polydrupes [Bobrov et al., 2003; 2004]. On the other hand the parenchymatization of pericarp of follicles of Magnoliaceae-type brought to origin of flesh indehiscent polyfollicles of Schisandraceae (Pl. j) [Romanov, 2004], Himantandraceae [Buchheim, 1962; Endress, 1983], Austrobaileya-ceae [Endress, 1983], most Annonaceae-Annonoideae, Hydrastida-ceae [Chernokh, 1998], some species of *Dillenia* L. [Corner, 1976]. The inability of fruitlets to dehiscent in pointed taxa is the secondary character, which is supported by persistence of mechanism of dehiscence in endocarp.

The second basal fruit type is winterina – the indehiscent apocarpous polymerous, oligomerous or monomerous fruit in which primary pericarp differentiation of fruitlets does not secure their dehiscence. Winterinas are characterized by peculiar anatomical differentiation of pericarp: exocarp and endocarp are represented by epidermis and the mesocarp comprises parenchyma with sclereids (or without sclerenchymatic elements) in peripheral zone and secretory cells in the inner zone (fig. 2a–c) [Romanov, 2004]. The single-layered unligificated endocarp of winterina does not secure the fruitlet dehiscence and there are no rudiments of mechanism of dehiscence in pericarp of winterinas. Dissemination of polywinterinas is endo- or synzoochory and barochory, and unlike polyfollicles s. str. the diaspore is the whole fruitlet with few to many seed within – *Bellium*, *Bubbia* p. p., *Drimys* (Pl. k), *Pseudowintera* p. p., *Tasmannia* p. p. (Winteraceae). By some reasons winterina is not widely distributed as the fruit type in angiosperms. Traditional modi of fruit transformations brought to origin of monowinterinas – *Bubbia* p. p., *Pseudo-wintera* p. p. и *Tasmannia* p. p. (Winteraceae), *Degeneria* (Degeneriaceae) and taxa of Trimeniaceae [Bobrov et al., 2002; Romanov, 2004; Romanov et al., 2004]. Apocarpous polywinterinas were also the basis for formation of hemisyncarpous (*Exospermum* van Tiegh.) and syncarpous polywinterinas (*Zygogynum* Baill. – Pl. l; fig. 2c). In parallel the paracarpous winterinas of *Takhtajania perrieri* (Capuron) Baranova and J.-F. Leroy and Canellaceae evolved. In all cases anatomical differentiation of winterina remained intact [Romanov, 2004].

Thus, in the result of comparative carpological investigations of basalmost angiosperms two basal fruit types were revealed – the follicle s. str. and the winterina. The follicles are developed in representatives of Magnoliaceae and Illiciaceae and derived taxa of archaic angiosperms, which are primarily distributed in the Northern Hemisphere, at the territories of former

Laurasia. In Cretaceous they migrated from Asia to North America (e. g., *Archaeanthus*), and then subsequently to South America and later to Africa. On the other hand the representatives of Degeneriaceae, Winteraceae, Canellaceae, and Trimeniaceae are primarily distributed at the South Hemisphere. Supposedly namely there the main evolutionary transformations of ancestors of Winteraceae took place and were accompanied by migration processes [Doyle, 2000]. Thus, the evolution of two groups of taxa of archaic angiosperms – the family Magnoliaceae and related taxa on one side and the families Degeneriaceae and Winteraceae and allied taxa on the other – supposedly took place at the geographically separated territories of the earth.

Received carpological materials are of great importance for phylogenetic systematic and do not support the monophyletic origin of angiosperms. Supposedly the ancestors of flowering plants are some until recently unknown groups of seed ferns with adaxial ovule position on the megasporophyll and with a tendency for conduplication of the last one. Basing on the received data and materials on seed anatomy [Corner, 1976; Takhtajan, 1988] we propose a new outline of phylogenetic relationships of the families of archaic angiosperms (fig. 2d).

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¹ Здесь и далее в тексте выпуска четыре инициала сопровождают фамилию Алексея Владимировича Боброва в ее латинском написании. Так, он предпочитает публиковаться во всех без исключения англоязычных журналах и в отечественных публикациях на английском языке.

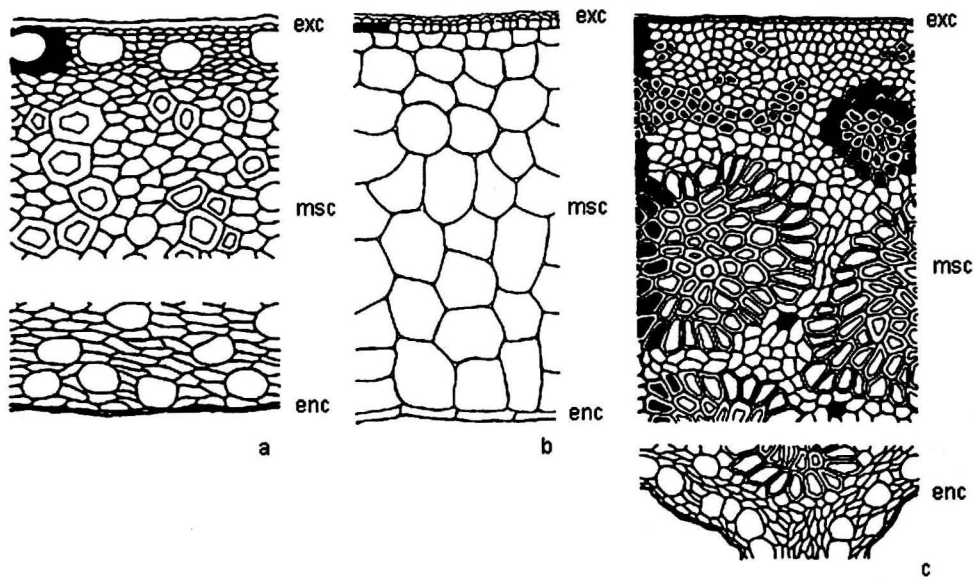


Fig. 2. a – cross section of pericarp of *Bubbia balansae* (Baill.) Van Tiegh.; b – cross section of pericarp of *Drimys winteri* J.R. Forster and G. Forster; c – cross section of pericarp of *Zygogynum bicolor* Van Tiegh.; d – scheme of hypothetical relationship of basal angiosperms

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THE RECONSTRUCTION OF EARLY STAGES OF FRUIT MORPHOGENESIS IN ARCHAIC ANGIOSPERMS

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The investigation of fruit structure of basal angiosperms allowed to conclude that morphogenetic transformation of this unique organ of flowering plants are based on two basal fruit types. The first basal fruit type is the follicle in narrow sense which is formed by dehiscent fruitlets with numerous sclerenchymatic elements in mesocarp and lignified endocarp. The follicles s. str. were revealed in most archaic fossil plants (*Archaeanthus*, *Archaeofructus*), and in a number of recent angiosperms – *Magnoliaceae*, *Illiciaceae*, *Myristicaceae*, *Lactoridaceae*, *Anaxagorea* and *Xylopia* (*Annonaceae*). Flesh polyfollicles of most *Annonaceae* and *Schisandraceae* are treated as derived from those of *Magnoliaceae*-type that is supported by presence of rudiments of mechanism of dehiscence in their pericarp. The second basal fruit type is the winterina – apocarpous fruit formed by indehiscent fruitlets with some (or without) sclerenchymatic elements in mesocarp and parenchymatic one-layered endocarp. Original differentiation of pericarp and the absence of rudiments of mechanism of dehiscence in pericarp allow to treat fruitlets of winterinas as originally indehiscent. This fruit type have been revealed in *Degeneriaceae*, most representatives of *Winteraceae*–*Winteroideae*, and *Trimeniaceae*; in *Zygogynum* (*Winteraceae*–*Winteroideae*) and *Takhtajania* + *Canellaceae* syncarpous and paracarpous winterinas were correspondingly formed.



a



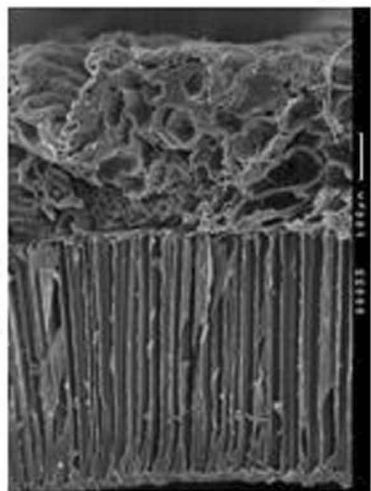
b



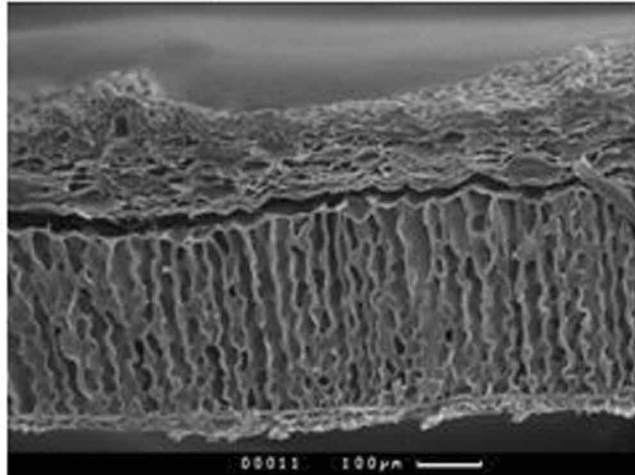
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f



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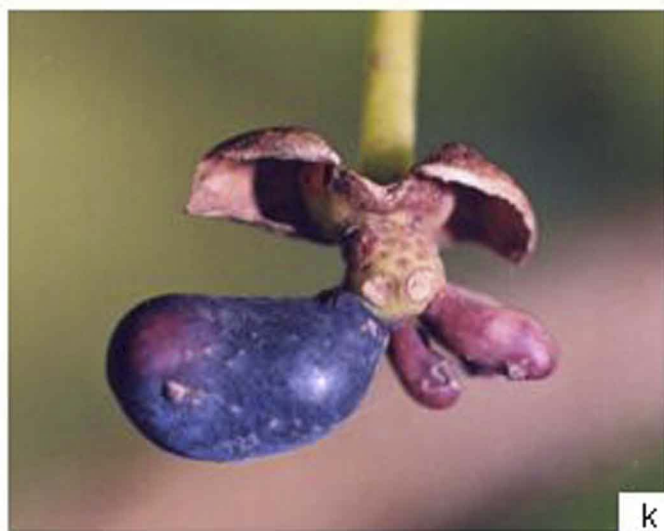
h



i



j



k



l

Table. a - *Paramanglietia aromatica*; b - *Magnolia carpunii* M.S. Romanov and A.V. Bobrov; c - *Illicium floridanum* J. Ellis.; d - *Xylopia aromatica* Mart.; e - cross section of pericarp of *Illicium cambodianum*; f - cross section of pericarp of *Hedycarya arborea*; g - *Magnolia hypoleuca*; h - *Michelia compressa* (Maxim.) Sarg.; i - *Kadsura japonica*; j - *Schisandra sphenanthera*; k - *Drimys winteri*; l - *Zygogynum bicolor*

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