FRUIT STRUCTURE OF THE GENUS *TORICELLIA* DC. (*TORICELLIACEJIE)* AND ITS TAXONOMIC POSITION IN THE ORDER APIALES

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Abstract: The genus Toricellia DC. with 2 species - T. tiliifolia DC. and T. angulata Oliv. - is represented by dioecious trees or shrubs with alternate exstipulate leaves and morphological differences between male and female flowers. Its fruit (pyrenarium) is ovoid or obliquely ovoid, crowned by a persistent calyx. Toricellia has 2-4-loculed yet 1-seeded pyrenaria, developed from the inferior ovary (pseudomonocarpous fruits). Outer walls of sterile locules have rounded openings. A very peculiar stone ("pyrene ") consists of two zones: the outer is very thick, consisting of multilayered lignifed sclereids; the inner is one-lavered, fiber-formed, inconspicuous. Thus, in species of Toricellia, the endocarp proper composes only the inner part of the pyrene, while the outer part is made of mesocarp elements, so the "pyrene " is of combined mesoendocarpic origin. The only seed is of the same shape as the locule - oblong and cur\'ed. Seed coat of a few cell layers. Some features shared by Toricellia and other related genera (Aralidium Miq., Griselinia For St., Melanophylla Baker) are discussed along with Toricellia s possible taxonomic relations.

Keywords: Toricellia, Toricelliaceae, fruit anatomy, pyrenaria, Apiales, Cornales, taxonomic position

Introduction

The genus *Toricellia* DC. with 2 species - *Toricellia tiliifolia* DC. and *T. angulata* Oliv. - is represented by dioecious trees or shrubs with alternate exstipulate leaves and morphological differences between male and female flowers. The pentamerous flowers are in lax axillary paniculate inflorescences. These plants' distribution range is confined to southeastern Asia, including Bhutan, China, northern India, Nepal and Sikkim; one of the two species is endemic to China.

Toricellia, described and validated by A.P. de Candolle in late 1830, was named after an Italian naturalist, physicist and mathematician Evangelista Torricelli. This peculiar Chinese-Himalayan genus was attributed to the family Comaceae by H. Harms in 1898 [4] and W. Wangerin in 1910 [14] - they placed it in the tribe Toricellieae. However, W. Wangerin pointed out marked morphological differences existing between the only genus of this tribe and other 15 representatives of Comaceae sensu Harms [4] *(Cornus* L., *Nyssa* L., *Helwingia* Willd., *Auciiba* Thunb., *Garrya* Douglas ex Lindl., *Mastixia* Blume, etc.). Based on these differences (multi-celled glandular trichomes, specific hanging axillary paniculate inflorescences, free stylodia, etc.), X.S. Hu was able to describe a new family Toricelliaceae in 1934. Later, the advisability of this placement was confirmed by wood and bark anatomy research by Adams [1] who noted relative primitiveness of *Toricellia s* characters treating the genus as a climax point of a long and independent evolutionary line. Out of genera of Comaceae sensu Harms (1898), *Griselinia* Forst. and *Helwingia* were most often related to *Toricellia,* and some authors would remove *Toricellia* from Comaceae circle of affinity and relate it to Apiales. A.L. Takhtajan [9, 10] was convinced

that *Toricellia* is even more distant from Comales and related orders, therefore placing the genus in the order of its own, Toricelliales, between Aralidiales and Araliales (Apiales).

The results of recent molecular research provided new insights into *Toricellia's* taxonomic position [2,6]. Based on these data, currently the family Toricelliaceae is described to include three genera - *Toricellia, Melanophylla* Baker (formerly a member of Comaceae sensu Harms and Melanophyllaceae within no longer existing order Hydrangeales) and *Aralidium* Miq. (previously representing a family and an order of its own, Aralidiaceae and Aralidiales, respectively).

Even though Harms's concept of Comaceae of 1898 [4] is now considered outdated and more molecular-based classifications have been and are being proposed, the clear-cut circumscription of the this circle of related or unrelated genera is still to be completed. Therefore, for the purposes of convenience and methodology, hereinafter we are still going to use "Comaceae sensu Harms", which is known to include 15 genera (*Cornus*, *Aucuba, Alangium* Lam., *Camptotheca* Decne, *Corokia* A. Cunn., *Curtisia* Aiton, *Davidia* Baill., *Helwingia*, *Garrya, Griselinia, Kaliphora* Hook, f., *Mastixia, Melanophylla*, *Nyssa* and *Toricellia).* We do acknowledge thought that this concept cannot be valid in the phylogenetic sense.

As we can see from the above cited references, *Toricellia* has been studied well in terms of its vegetative structure and molecular aspects, but very regretfully, fruit structure has been omitted in these studies. However, it is broadly accepted that fruit structure (especially fruit anatomy) is an important taxonomic marker because carpological traits are known to be very constant and not much variable under the influence of environmental factors. Our present work in fruit and seed structure of *Toricellia* and related genera is aimed at bridging this gap and searching for traits of high taxonomic value that would be able to contribute to the clarification of *Toricellia'*s status and position within flowering plants.

Materials and methods

For morphological and anatomical research, mature fruits of *Toricellia tiliifolia* and *T. angidata* were used. The material was obtained from botanic gardens and carpological collections of herbaria (carpological collection of Komarov Botanical Institute, St. Petersburg, Russia (LE), Herbarium of Royal Botanic Gardens Edinburgh, UK (E).

Plant material was fixed in 70% ethyl alcohol and freehand transverse (cross) sections were made. Dry fruits were previously rehydrated in Strassbourger mixture (water, glycerol and 70% ethyl alcohol in equal proportions) at 50°C or boiled and cooled down repeatedly. Further treatment of sections was performed according to traditional anatomical techniques [5, 8] and included the following:

1. Phloroglucinol + HC1 (concentrated) - test-reaction to reveal lignification;
2.12 + KI - test-reaction for proteins and starch;
3. Sudan III (IV) - test- reaction for lipids (including cutin and suberin).

After test-reactions and staining, if needed, the sections were embedded in glycerolgelatin and studied with the help of light microscope (Primo Star by Carl Zeiss). Suitable sections were photographed and drawn.

Transverse fruit sections and surface ultrasculpture of *Toricellia* fruit was studied at the Inter-department laboratory of electron microscopy of the Faculty of Biology, MSU named in honour of M.V. Lomonosov, by means of scanning electron microscopes (SEM) Hitachi S-405A and JSM-6380 LA. The plant material was prepared for SEM investigations according to the techniques used in the Inter-department lab of MSU. SEM research was documented by microphotographs.

Results

Fruit morphology

Toricellia fruits are often referred to as drupes (or 'drupaceous') but this term is imprecise as true drupes are only known to occur in the subfamily Prunoideae of the family Rosaceae where the fruit develops from a single-carpelled apocarpous gynoeceum [7]. For plants with syncarpous gynocea, just like the majority of Comaceae sensu Harms, a more suitable term "pyrcnarium" is used (for a detailed substantiation of the terminology applied to Comaceae and related families as well as explanation of the crucial developmental aspects of such fruits see works by E. Yu. Yembaturova and co-authors [15, 17]).

The fruits of *Toricellia* are small inferior pyrenaria, 5-8 mm in length and 4-5 mm in diameter in dry condition; their shape is somewhat asymmetrical (flattened on one side and bulging on the other. Two to three protruding projections (unrelated to vascular bundles) are found on the bulging side. Dry fruits are black in colour; in natural conditions, a mature fruit is dark purple [12]. The fruit's single stone possesses 2 to 4 locules (triangle in cross section) with only one of them being fertile and bearing a single seed capable of reaching full maturity [12; original data].

Pericarp histology

At the first glance, the pericarp of *Toricellia* is very simple in structure (Figure IB, 2B), but since the fruit develops from the inferior ovary, five histological zones can be distinguished in it:

1. Exocarp is represented by the epiderm (originating from the outer hypanthial epiderm) and subepidermal underlying tissue. The pigment determining the fruit colour is localized in exocarp cells.
2. Parenchymous mesocarp of tissues of hypanthial origin.
3. Parenchymous mesocarp of outer carpellary tissues with vascular bundles and their derivatives.
4. Stone, or pyrene, made of supporting tissue (sclereids).
5. Endocarp proper - the inner layer of fibers (different from the sclereids) derived from the inner carpellary epiderm. The endocarp is an integral part of the stone.

The border between the hypanthial and the carpellary zone of the fruit wall is quite pronounced: the former consists of larger cells whereas the latter is in general made of minute, often compress cells that partially obliterate in the mature fruit *(T. tiliifolia).* Vascular bundles derivatives form one or two circles. They tend to be located towards the inner part of the fleshy mesocarp of carpellary origin. The above mentioned projections appear to be formed out of all tissues present in the fleshy part of the pericarp. In total, the fleshy part of the pericarp (of exomesocarpic origin) is constituted by 6 to 10 cell layers.

The stone in most studied specimens is composed of 10 to 12 layers of well-lignified sclerenchymous elements (of rounded or irregular shape in cross section) with moderately thickened walls (Figure ID, 2D) while the endocarp proper is not very conspicuous but nevertheless present; fibers in its structure are readily distinguishable from other sclereids of the pyrene (Figure 1C, 2C); their walls are canaliculated. No secretory structures were found in mature fruits of *T. tiliifolia* The pericarp histology of both studied species is found to be very similar.

As far as the fruit surface ultrasculpture (Figure 1A, 2A) is concerned, the primary sculpture is flattened, showing rhombic or trapeziform outlines of epidermal cells. The

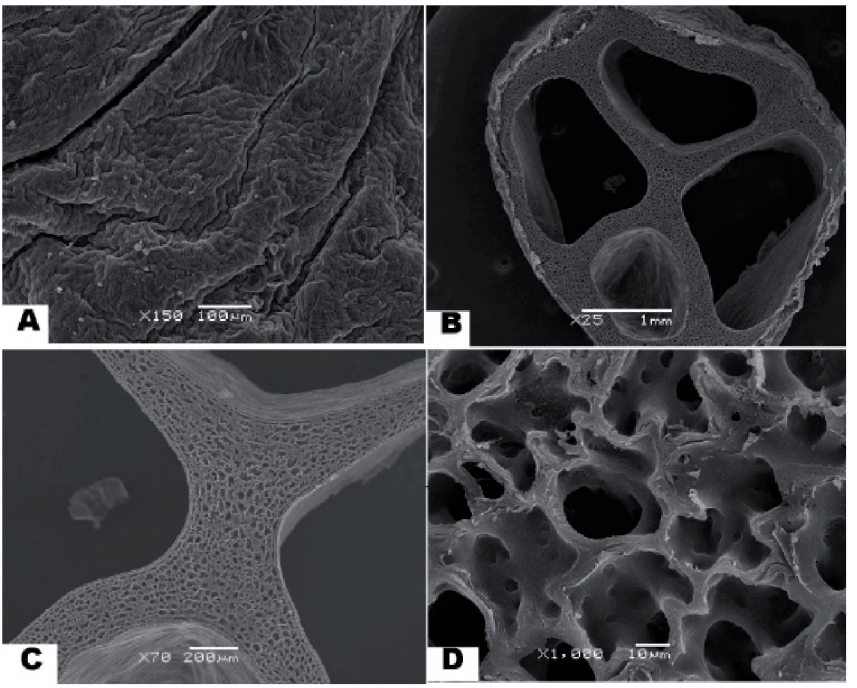

Fig. 1. Fruit structure of *T. tiliifolia* (SEM photographs): A - fruit surface, x150; B - fruit cross section, x25; C - pyrene structure: endocarp fibers and mesocarp sclereids, x70; D - sclereid-like lignified elements of mesocarpic origin

cuticle is slightly plicate. A few stomata or sparse thin simple trichomes can be observed. Very few globoid or differently shaped granules of epicuticular wax are seen on the fruit surface (Figure 1A, 2A).

Seed structure

The seed structure in *Toricellia* has been described previously [12]. The seed develops from a single ovule hanging down from the top of the fertile locule. Its short funiculus possesses an outgrowth. At maturity, the seed can easily be removed from the locule. According to our observations, in certain parts of the fertile locule wall, the stone is not fully continuous and apparently, the seed simply falls out of the stone when full maturity is reached and the outer fleshy tissues are destroyed. This peculiar trait has not been observed in any representatives of Comales or Apiales studied to date.

The seed coat is rather thin and filmy however, it is much more pronounced than in representatives of Comaceae and related families with thick bony endocarps (*Cormis*, *Alangium, Nyssa,* etc.) due to the correlation between the endocarp and seed coat thickness characteristic to fleshy drupaceous fruits [13].

Discussion

As shown by our investigation, fruit structure of *Toricellia* is very peculiar and differs greatly from that of most other Apiales or Comales genera studied previously. The most striking features are: quite thin fleshy part of the pericarp (exocarp and part of mesocarp)

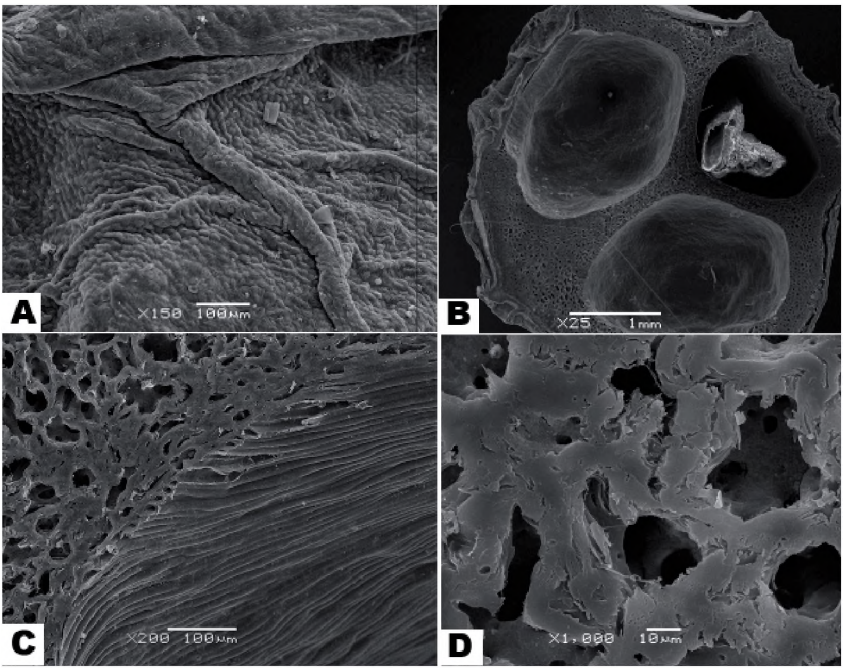

Fig. 2. Fruit structure of *T. angulata* (SEM photographs): A - fruit surface, x150; B-fruit cross section through the middle part, x25; C-pyrene structure: endocarp fibers and mesocarp sclereids, x70; D - lignified elements of mesocarpic origin

and a four-loculed pyrene of relatively thin-walled and moderately lignified (in comparison to most other Comaceae sensu Harms) sclereids. In the pyrene, only one locule is fertile and seed-bearing, but the other two or three sterile locules retain their shape and do not compress. Moreover, it was interesting to observe almost discontinuous structure of the stone wall which could allow the seed to literarily fall out of it.

Pyrene structure. The majority of Comaceae sensu Harms (except *Curtisici, Kctliphorct* and *Helwingia* [17]) are known to possess pseudomonomerous pyrenaria (with only one of two or more locules and seeds reaching full development). In many genera, *(Cormis* and its segregates, *Nyssct, Corokict, Dctvidict)* all locules besides the fertile one are markedly compressed. However, there are some taxa in this circle of affinity where sterile locules retain their shape and size. One of them *is Melanophylla,* in which the seed-bearing locule is the smallest of three, two other ones being large and somewhat inflated [11]. Just like in *Toricellia,* the seed *of Melanophylla* copies the shape of the locule. It is known to have copious endosperm and a tiny embryo, differently from *Toricellia,* where the embryo is much bigger in size. Another feature shared by the two discussed genera is the relatively small thickness of the pyrene wall.

Discontinuous pyrene. The opening (or discontinuity) in the wall of the fertile locule, noted in *Toricellia,* is seemingly a peculiar trait not found in any studied representatives, related to *Toricellia* now or before. One must note though that openings, more or less rounded in shape, have been reported by R. Eyde [3] in the walls of sterile locules. According to this botanist, the germination in *Toricellia* occurs by means of a triangle valve. Almost discontinuous pyrene (however, much bigger in thickness) was observed in

Kaliphora [16], which was closely related to *Melanophylla* within Hydrangeales [11] in the past. Similar traits (locules discontinuous from outside) have been revealed in a saniculoid genus *Petagnaea* Caruel [A.I. Konstantinova, unpublished data].

Fleshy part of the pericarp. Even though in *Toricellia's* supposed relatives by Comales (*Cornus*, *Alangium, Nyssa. Curtisia, Mastixia, Corokia,* etc.) the fleshy zone of the fruit wall is always very well-developed, there are some representatives in which the reduction of this part has been noted. More distinctively this trend of exomesocarp reduction, together with more pronounced histological zonality and distinct specialization of the zones, is observed in more specialized fruits of Apiales.

The absence of *secretory structures* in the mature pericarp points out *Toricellia*'s difference from Apiales, where they are present in abundance. However, they have not been found in mature fruits of *Helwingia. Aralidium*, *Kaliphora* and *Griselinia.*

All carpological traits taken together suggest comparing the studied genus with yet another representative of Comaceae sensu Harms - *Griselinia.* These plants have many features in common, e.g., they both tend towards pyrene reduction in thickness and the degree of cell wall lignification of sclereid-like elements (Figure ID). Both of them have rather uniform structure of the fleshy exomesocarp. where no secretory canals are found at maturity and derivatives of vascular bundles can be seen and help to identify the borderline between the carpellary and hypanthial zones of the fruit wall. However, differences are present, too - most importantly, in *Toricellia* all three or four locules are well-developed in the stone whereas in *Griselinia* only one of them is pronounced and obviously dominating. *G. scandens* Taub. is known to possess sclereids in the fleshy part of the pericarp - this feature is common for many Comales but not found in *Toricellia.* The seed of *Griselinia* is bigger in size and the embryo develops to a much more advanced stage. The seed coat structure is similar in both of the discussed genera, but it seems thicker and less compressed in *Griselinia,* suggesting a parenchotestal type of the seed in the genus.

Apart from carpological traits, there is a biochemical feature shared by *Griselinia* and *Toricellia.* Both of them have been reported to accumulate an iridoid compound

Comparative analysis of fruit structure traits in *Toricellia* and possibly related genera

Traits	*Toricellia*	*Griselinia*	*Aralidium*	*Melano-phylla**	*Kaliphora*	*Schefflera*
Number of locules	3-4	1	1	2-3	2	From 2 to many
Number of fully developed seeds per fruit	1	1	1	1	2	From 2 to many, seeds may mature only in some of the locules
Borderline between hypanthial and carpellary zone	Present; more pronounced in *T.angulata*	Poorly defined, the most pronounced in *G. jodinifolia*	Present, well seen	…	Present, well seen	
Secretory system	Absent	Absent	Absent	…	Absent	Usually well-developed

Table - ending

Traits	*Toricellia*	*Griselinia*	*Aralidium*	*Melanophylla**	*Kaliphora*	*Schefflera*
Discontinuity of the stone	Present, in the distal part of the fruit (outside)	None	None	Present, in the proximal part of the fruit (inside)	Present, in the proximal part of the fruit (inside)	In some species (rarely) in the proximal part (inside), in the distal part or both
Presence of endocarp (as carpel's inner epiderm)	Present as a single layer of fibers lining the pyrene made of sclereids	Absent, obliterated or indistinct in the mass of pyrene-composing sclereids (*G. lucida*)	Present as a layer of obliterated parenchyma cells	…	Absent, obliterated or indistinct in the mass of pyrene-composing fibers	Absent, obliterated or indistinct in the mass of pyrene-composing fibers (from several layers to one)
Seed coat	Thin, non-differentiated	Thin, non-differentiated	…	More or less differentiated into exo-, meso- and endotesta	Thin, non-differentiated	Thin, non-differentiated
Presence of griselinoside	Present	Present	Present	…	…	…

* Data on fruit structure of *Melanophylla* are taken from V.I. Trifonova's paper [11].

griselinoside [3, 9]. This substance has also been found in *Aralidium* [9], which is united with *Toricellia* within one family - Toricelliaceae according to one of the most recent treatments of Apiales based on molecular research [2, 6].

Data on fruit structure in some of the above discussed genera, currently placed in or related to Apiales are given in the Table. *Schefflera* J.R. Forst. & G. Forst. is shown here as atypical and the most numerous representative of the order Apiales.

Conclusions

The genus *Toricellia* has demonstrated a unique combination of features that does not give an immediate suggestion of its close relationship to any of the genera ever considered as *Toricellia's* possible relatives. The genera of its family, *Aralidium* and *Melanophylla.* do share some traits with *Toricellia* however, still remaining rather different.

Our carpological investigation has revealed some interesting features, one of the being the locules discontinuous from outside. A similar trait has been found in *Griselinia,* which has also been transferred from Comales to Apiales, and a saniculoid genus *Petagnaea.*

The absence of secretory structures in mature fruits of *Toricellia* links it to *Aralidium* and *Griselinia.* However, this carpological evidence is not in favour of *Toricellia's* affin-

ity with Apiales as representatives of this order are known to have a variety of secretory structures in their fruits.

An interesting peculiarity of *Toricellia* is the accumulation of griselinoside. This iridoid compound is also found in *Griselmia* and *Toricellia s* suggested family-mate *Aralidium*. This peculiar trait, as well as the other above listed characters, definitely requires further investigations.

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ОСОБЕННОСТИ СТРОЕНИЯ ПЛОДОВ ПРЕДСТАВИТЕЛЕЙ РОДА *TORICELLIA* DC. (*TORICELLIACEAE)* И ВЗГЛЯДЫ НА ПОЛОЖЕНИЕ ТАКСОНА В СИСТЕМЕ ПОРЯДКА APIALES

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Аннотация: представители рода Toricellia DC — T. tiliifolia DC. и T. angulata Oliv. - двудомные деревья и кустарники с очередными листьями без прилистников и отличающимися по морфологии мужскими и женскими цветками. Плоды этих растений (пиренарии) неравнобокие, яйцевидные или почти шаровидные, на верхушке с неопадающей чашечкой. Отличительная особенность Toricellia - развитие из нижней завязи плода с 2-4 гнездами, только одно из которых несет семя (псевдомономерный плод). Характерно наличие округлых отверстий в наружных стенках стерильных гнезд. В косточке («пирене») различаются две гистологические зоны: наружная, часто очень мощная, состоящая из склереид, и слабо выраженная внутренняя зона из одного слоя волокон. Таким образом, у видов Toricellia собственно эндокарпий составляет лишь внутреннюю часть пирены, тогда как наружная образована элементами мезокарпия, так что происхождение пирены мезоэндокарпическое. Единственное семя повторяет форму фертильного гнезда - продолговатое и в разной степени согнутое. Спермодерма малослойная. В статье обсуждаются признаки, отмеченные у рода Toricellia и сближаемых с ним родов (Aralidium Miq., Griselinia Forst., Melanophylla Baker), а также взгляды на систематическое положение изучаемого таксона.

Ключевые слова: Toricellia, Toricelliaceae, анатомия плода, пиренарии, Apiales, Cornales, систематическое положение.

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