

## CARPOLOGY AND PHERMATOLOGY OF *GOMORTEGA* (*GOMORTEGACEAE*): SYSTEMATIC AND EVOLUTIONARY IMPLICATIONS

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**ABSTRACT.** *Carpology and phermatology of Gomortega (Gomortegaceae): Systematic and evolutionary implications.* The anatomy and morphology of the fruits and seeds of *Gomortega keule* (Mol.) Baill., comprising a monotypic genus in the monogeneric family *Gomortegaceae* Reiche, have been studied in an effort to clarify its systematic position. The fruits are fleshy inferior coenocarpous drupines, giving the appearance (due to the lateral concrescence of spirally arranged 2—6 carpels) of mostly 2—3-locular or rarely pseudomonomerous syncarpous fruit. Seeds are flattened, exarillate, abundantly albuminous with a small embryo, originate from hemianatropous crassinucellate, bitegmic ovules. The seed coat is endotestal-endotegmic; the endotesta, only testal layer preserved in the mature spermoderm, is of tracheotestal type, having peculiar numerous spiral or annular projections penetrating into the cell cavities. Evidence, mainly from seed anatomy and morphology, emphasizes phylogenetic unity of *Gomortega* having aberrant inferior fruits with *Monimiaceae s.l.* or more correctly, a group of the families *Monimiaceae s. str.*, *Amborellaceae*, *Hortoniaceae*, *Siparunaceae*, and *Atherospermataceae*. *Gomortegaceae* especially have common roots with *Atherospermataceae*, sharing similar tracheotestal endotestal type of seed coats, albuminous seeds with small embryos, similar chromosome number, morphology of sieve-element plastids, palynomorphology, xylem anatomy, and distinctive staminodial appendages and valvular dehiscence of anthers. With the addition of more data on the fruit and seed anatomy and morphology of *Atherospermataceae*, the interrelationships of *Gomortega* and *Atherospermataceae* would be defined more precisely.

**Key words.** *Gomortega keule* (Mol.) Baill., keule (queule), carpology, pericarp, seed anatomy and evolution, *Gomortegaceae*, *Atherospermataceae*, *Monimiaceae*, *Lauraceae*, *Magnoliidae*, *Ranunculidae*, *Caryophyllidae*, *Hamamelididae*, *Rosidae*, *Dilleniidae*.

**RESUMEN.** *Carpología y morfología de la cubierta de la semilla de Gomortega (Gomortegaceae): implicaciones sistemáticas y evolutivas.* En un esfuerzo de clarificar la posición sistemática del género *Gomortega*, en el presente trabajo se estudia la morfología y anatomía de los frutos y semillas de *Gomortega keule* (Mol.) Baill., perteneciente al género monotípico anteriormente citado, de la monogénica familia *Gomortegaceae* Reiche. Los frutos son drupas cenocárpicas carnosas, que ofrecen la apariencia de frutos sincárpicos bi- o triloculares, o más raramente uniloculares, debido a la concrescencia lateral de los 2—6 carpelos que lo componen y que se encuentran espiraladamente dispuestos. Las semillas son aplanadas, desprovistas de arilo, con albúmen abundante y embrión pequeño, originadas a partir de primordios seminales bitégmicos, anátropos y crasinucelados. La cubierta de la semilla es endotestal-endotégmica; la endotesta (sólo la base testal se preservó en la espermodermis madura) es de tipo traqueotestal, presentando la peculiaridad de poseer numerosas proyecciones anulares o espiraladas que penetran en las cavidades celulares. Las evidencias encontradas, fundamentalmente en base a la morfología y anatomía de las semillas, apoyan la relación filogenética existente entre *Gomortega*, con frutos íferos aberrates, y *Monimiaceae s.l.* o, más correctamente, con el grupo de las familias *Monimiaceae s. str.*, *Amborellaceae*, *Hortoniaceae*, *Siparubaceae* y *Atherospermataceae*, que comparten un tipo similar de cubierta seminal

endotestal y traqueotestal, semillas albuminadas, con embrión pequeño, similar número de cromosomas, morfología de los plastidios de los elementos cribosos del floema, morfología polínica, anatomía del xilema, los apéndices de los estaminodios y la dehiscencia valvar de las anteras. Con la aportación de una mayor cantidad de datos sobre la morfología y anatomía de los frutos y semillas de *Atherospermataceae*, las interrelaciones existentes entre *Gomortega* y *Atherospermataceae* podrían ser definidas de manera más precisa.

Palabras clave. *Gomortega keule* (Mol.) Baill., keule (queule), carpología, pericarpo, anatomía seminal y evolución, *Gomortegaceae*, *Atherospermataceae*, *Monimiaceae*, *Lauraceae*, *Magnoliidae*, *Ranunculidae*, *Caryophyllidae*, *Hamamelididae*, *Rosidae*, *Dilleniidae*

## INTRODUCTION

The arborescent Chilean plants Queule (Keule) are currently well-known in systematic botany as *Gomortega keule* (Mol.) Baill., that comprises a distinct monotypic family *Gomortegaceae* Reiche. They were at first time described by Molina (1782) under the name of *Lucuma keule* Mol. Since the genus was turned out to be composed of unrelated members, the name has been rejected in a favour of published later *Gomortega nitida* Ruiz & Pav. (Ruiz López & Pavón, 1794), and then corrected according to the established rules of botanical nomenclature by Baillon (1867/1869) on *G. keule* (Mol.) Baill. (cf. Johnston, 1924; Espinosa Bustos, 1948; Gunckel, 1972). In old botanical literature of XIX century these plants were often, but invalidly named as *Adenostemum nitidum* (Ruiz & Pav.) Pers., since Persoon (1805) renamed the genus, treating the name *Gomortega* as invalid later nomen to *Ortega* L., which has been already established by Linnè (1753) to honour the name of Casimir Gómez-Ortega, professor of the Royal Botanical Garden in Madrid. Later Molina (1810) proposed once more invalid name for these plants: *Keulia chilensis* Mol.

Likewise the confused nomenclature of the species, the taxonomic position was also indefinite and complicated. Ruiz López & Pavón (1794) and Persoon (1805) placed *Gomortega* into artificial Linnaean 10th class *Decandria monogynia* together with *Cercis* L., *Bauhinia* L., *Parkinsonia* L., *Caesalpinia* L.,

*Cassia* L., *Gaertnera* L., *Zygophyllum* L., *Monotropa* L., *Pyrola* L., *Styrax* L., and even *Rhododendron* L. Endlicher (1836/1840) synonymized *Gomortega* with *Peumus* Nees (now in *Monimiaceae* Juss. s.l.), which he included in *Cryptocarya* R. Br. (*Lauraceae* Juss.). Lindley (1853) accepted this taxonomic re-arrangement. Philippi (1864/1865) refuted phylogenetic relationships of *Gomortega* with *Lauraceae*, emphasizing occurrence of mostly trimerous inferior ovary and abundant endosperm in seeds. Later Philippi (1868) supposed a monimiaceous affinity for a doubtful genus, regarding it as a connecting link between *Lauraceae* and *Monimiaceae*. Mez (1888) agreed with Philippi (1864/1865, 1865, 1868) and transferred *Gomortega* into *Monimiaceae*. But Bentham & Hooker (1883) suggested a quite another, curious affinity to *Euphorbiaceae* Juss., seeing a resemblance in trimerous construction of gynoecea. Nevertheless, Reiche (1896) regarded this resemblance as superficial and therefore erected a distinct family *Gomortegaceae*, emphasizing thereby its differences with both closely allied *Lauraceae* and *Monimiaceae*.

Hallier (1912) rejected a distinct family for *Gomortega* and included it into *Monimiaceae* [as did Mez (1888)], connecting with *Calycanthaceae* Lindl., *Lauraceae*, and *Chloranthaceae* R. Br. ex Lindl. Later Swamy (1953) also thought it possible to reveal some close phylogenetic relationships with *Chloranthaceae*. Bessey (1915) and Engler & Gilg (Engler, 1919), representatives of two

antagonistic approaches to the classification of flowering plants, agreed to place distinct family *Gomortegaceae* near mostly *Myristicaceae* R. Br.: Bessey placed it in *Ranales* between *Lactoridaceae* Engl. and *Myristicaceae*, in a similar way Engler & Gilg positioned *Gomortegaceae* between *Myristicaceae* and *Monimiaceae* in special suborder Magnoliineae. Hutchinson (1926) included *Gomortegaceae* into *Laurales* along with *Monimiaceae*, *Lauraceae*, *Hernandiaceae* Blume, and again *Myristicaceae*.

Garratt (1934), studying wood anatomy of *Gomortega*, suggested an affinity with atherospermataceous genera *Atherosperma* Labill., *Daphnandra* Benth., *Doryphora* Endl., and *Laurelia* Juss. of *Monimiaceae* s.l. (= *Atherospermataceae* R. Br.). These close phylogenetic relationships have been later confirmed by chromosome analysis (Goldblatt, 1976) and morphology of sieve-element plastids (Behnke, 1988). Nevertheless, Metcalfe & Chalk (1950), on the basis of wood anatomical characters, agreed with general lauralean affinity, but pointed out to a possible relationship of *Gomortega* to *Canellaceae* Mart. Later Stern (1955) in a thorough study of xylem structure rejected any idea of canellaceous relationships and suggested that 'most likely *Gomortegaceae* is closely allied to *Monimiaceae* through a *Hortonia*-like forebear with valvate anthers'. This point of view is accepted in most modern systems of angiosperms (Dahlgren, 1989; Cronquist, 1992; Thorne, 1992; Takhtajan, 1997). Nonetheless, Gottwald (1977) on the basis of again xylem characteristics placed *Gomortegaceae* in his 'Hamamelidal-Dillennial' (!) Group within magnolialean families.

There are no record of carpological descriptions of *Gomortega*, except for some general dissections of the fruits presented by Ruiz López & Pavón (1794) and Reiche's (1896) discovery of the spiral arrangement of carpels in syncarpous gynoecium. The same is

true for seeds (Corner, 1976; Fedotova, 1988) except for corrections of Reiche (1896) of some previous erroneous descriptions of embryo as small (Philippi, 1868); the spermoderm is till described only as 'thin and brittle'. Recently Endress & Igersheim (1997) described several additional details of the general morphology and anatomy of ovules and carpels constituting the inferior ovary of *Gomortega*. Here we attempt to elucidate the phylogenetic relationships of *Gomortegaceae* using the additional carpological and phermatological features of *Gomortega*.

## MATERIALS AND METHODS

Mature fruits containing ripe seeds of *Gomortega keule* (Mol.) Baill. were obtained from the Herbario, Departamento de

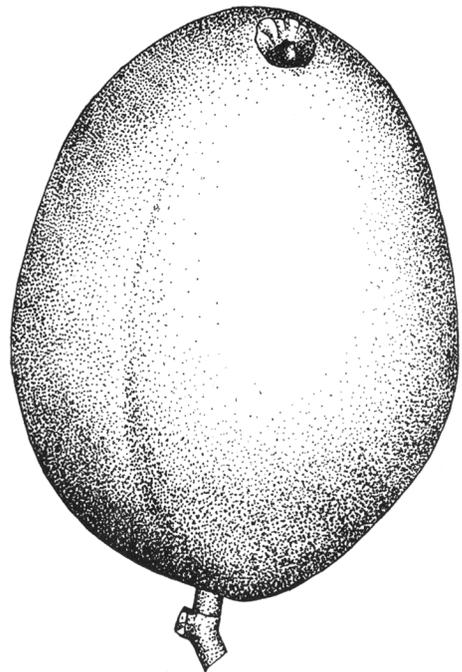
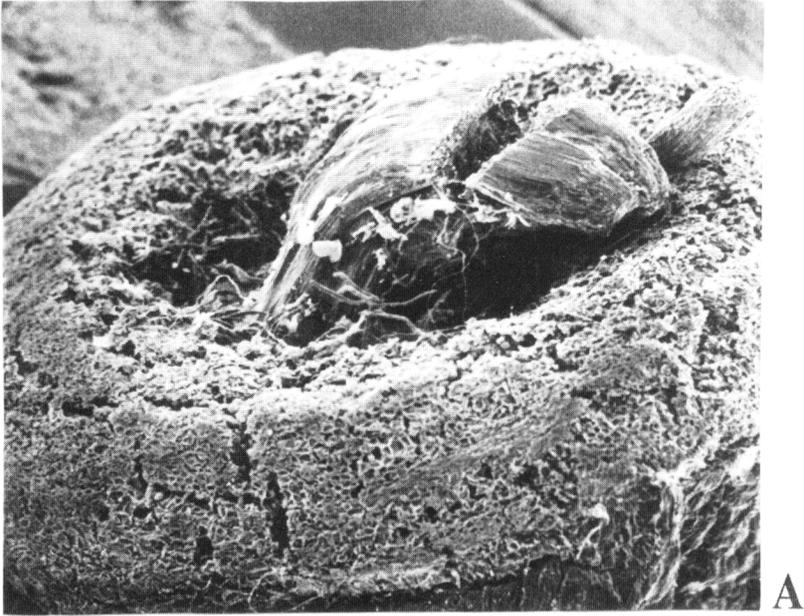


Figure 1. General view of the mature fruit of *Gomortega keule* (Mol.) Baill., x 15.



A



B

Figure 2. SEM micrographs of the fruit top of *Gomortega keule* (Mol.) Baill. A, frontal view of two styles, x 75; B, the same, but from the upper, x 75.



Figure 3. SEM micrograph of the striped surface of style, x 380.

Silvicultura, Universidad de Chile (EIF). The collections were made by Rodolfo Gajardo on 23 February 1986 in Chile, Ramadillas, Altos de Tregualemu, 36° 00" S, 72° 40" W at 520 m elevation. The voucher specimens were housed in the Carpotheca of the National Institute of Carpology (Gaertnerian Institution), Moscow [NICAR]. Drawings were made with an assistance of PA-4<sup>®</sup> camera lucida from microtome serial cross-sections 5610  $\mu$ m thick, prepared by the usual paraffin method and stained with safranin-fast green (O'Brien & McCully, 1981). Scanning Electron Microscope (SEM) observations were made with a HITACHI S-405 A at 15 kV after sputtercoating with platinum-palladium.

## RESULTS

### *Fruit*

*Mature fruits.* The mature fruit (fig. 1) is yellow, obovoid or globose, 3.567 cm long and 3.5—5 cm wide, fleshy, indehiscent, drupaceous, (1—) 2—3-locular with 2 (—3) styles (figs. 2, 3); originates from the (2—) 3 (—6)-merous coenocarpous inferior ovary (fig. 4). The fruit surface is rough due to the fruit shrivelling; fruit sculpturing is striped (figs. 5). The carpels are spirally arranged, some of them (mostly basal) abortive; the number of carpels is varying from 3—6 to more usual condition of fertile 2—3 (Reiche, 1896;

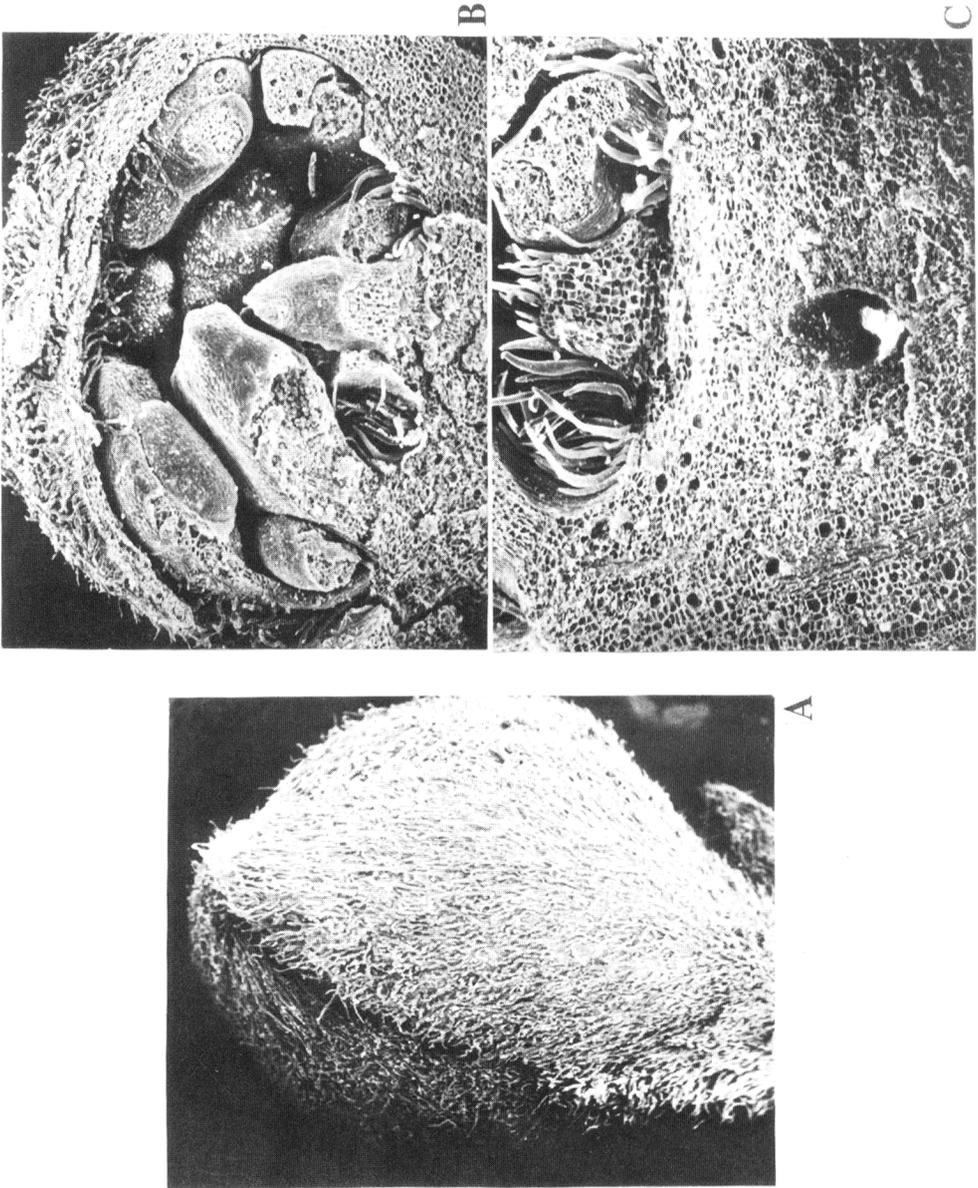
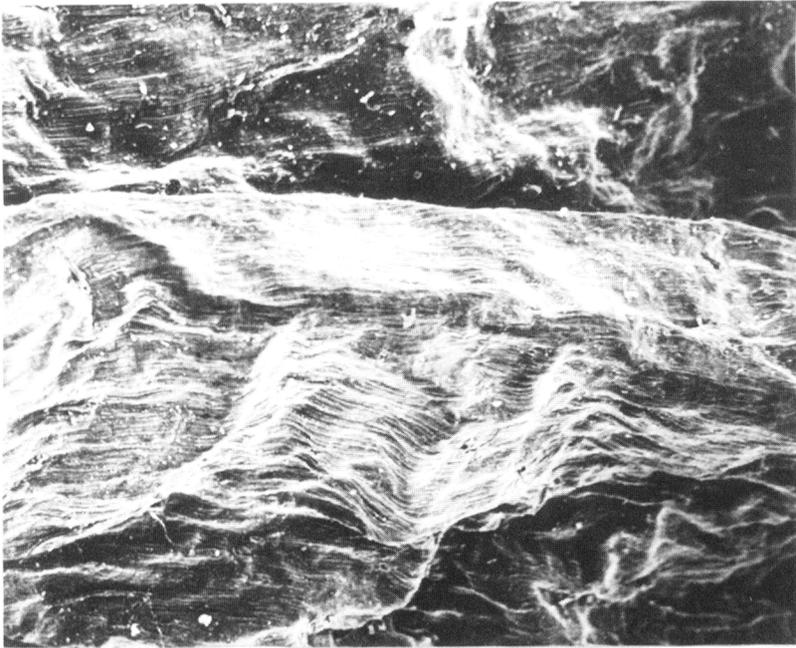
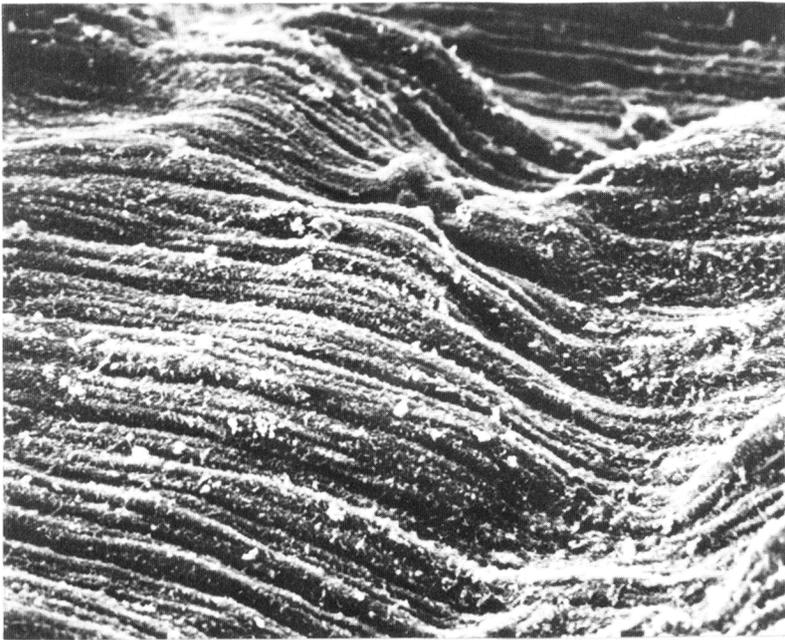


Figure 4. SEM micrographs of the developing ovary of *Gomortega keule* (Mol.) Baill. A, general view of the bud, x 30; B, upper part of the longitudinal dissection of the bud of *Gomortega keule* (Mol.) Baill., x 75; C, the same, but lower part, showing carpellary cavity, x 75.



A



B

Figure 5. SEM micrographs of the fruit surface of *Gomortega keule* (Mol.) Baill. A, general rough sculpture, x 75; B, striped sculpturing, x 380.

Brizicky, 1959), thus giving the appearance of mostly 2—3-locular or even pseudomonomerous syncarpous fruit. Due to the lateral concrescence of carpels during anthesis the locules of the fruit are narrow, slit-like with marginal placentation of one (rarely two) ovules. The vascular skeleton of the fruit (fig. 6) is represented by numerous (>30) vascular bundles in two circles, laying in the outermost fleshy part of pericarp, giving off numerous traces for spirally arranged (5—) 7—9 tepals, 7—9 (—13) stamens and (1—) 3 (—4) staminodia, and independently originated distinct vascular supply to every carpel, which is consisted of one ventral trace and one dorsal, not extending upwards into the style (*cf.* also Leinfellner, 1968).

*Pericarp.* This is differentiated into three to six layered exocarp, with up to 100 layers (c. 1.2—1.4 cm) of mesocarp composing of two distinct zones (fleshy and stony), and a 4—5-layered lignified fibrous endocarp (fig. 7—8). Such a sclerified mesendocarp-like construction of the whole pericarp is typical of drupaceous fruits (Garcin, 1891), and therefore the inferior fruit type of *Gomortega* should be redefined as a *drupine* according to a new system of fruit classification and terminology (Doweld & Sorokina, 1997), but not a *drupe* (Reiche, 1896; Spjut, 1994).

The parenchymatous exocarp is composed of thin-walled cells filled with tannin-like dark substances (fig. 7 A). The mesocarp is differentiated into two distinct zones: the outer (fig. 7 B), remaining parenchymatous (c. 3—3.5 mm), and massive sclerified inner one (c. 0.9—1.1 cm) (fig. 7 C). The outermost parenchymatous part of mesocarp, adjacent to exocarp, is also characterized by the occurrence of 1—2 zones of tannin-bearing cells, interrupted by the layers of colourless parenchyma (fig. 8 A). In the thin-walled mesocarpic parenchyma there are numerous spherical secretory oil-cells with relatively

thin, but sometimes lignified walls (fig. 8 C). In the zone of numerous vascular bundles there are one or sometimes two layers of lignified macrosclereids (fig. 7 C) with pitted walls. The inner part of mesocarp is represented by mostly radially elongated brachysclereids with heavily thickened and pitted walls (Figs 7 D, 8 B). The endocarp is represented by heavily thickened lignified and pitted fibres oriented parallelly to the axis of fruit (fig. 7 D).

### Seed

*Mature seeds.* These are relatively large, 10—14 mm long, 6—8 mm wide and 4—6 mm thick, flattened, obcordate to elliptic-lanceolate, slightly elongated, exarillate, brown (fig. 9 A). The hilum is black and large, basal. The raphe or antiraphe are not morphologically differentiated. The vascular skeleton is reduced and represents by small single vascular bundle terminating in chalaza under a large cup-shaped hypostase (fig. 9 B). There are no marks of pachychalaza reported by Igersheim & Endress (1997). The mature seeds are albuminous, with a small straight dicotyledonous embryo (fig. 9 C).

*Spermoderm.* The seed coat (fig. 10) is formed from both integuments of the hemianatropous (suborthotropous) crassinucellate ovules. It is endotestal-endotegmic. The seed sculpturing is rough, with numerous remnants of outer testal parenchyma (fig. 11).

The *testa* consists of 2—3 layers, one or two outermost of which are often obliterated in mature seeds, being composed of thin-walled parenchyma. The only mechanical layers is represented by tangentially elongate tracheidal thick-walled cells with numerous spiral or annular projections penetrating into the cell cavity [‘Spiralzellenschicht’ of Schleiden, 1839; *tracheotesta*].

The *tegmen* is composed of 3—4 layers of

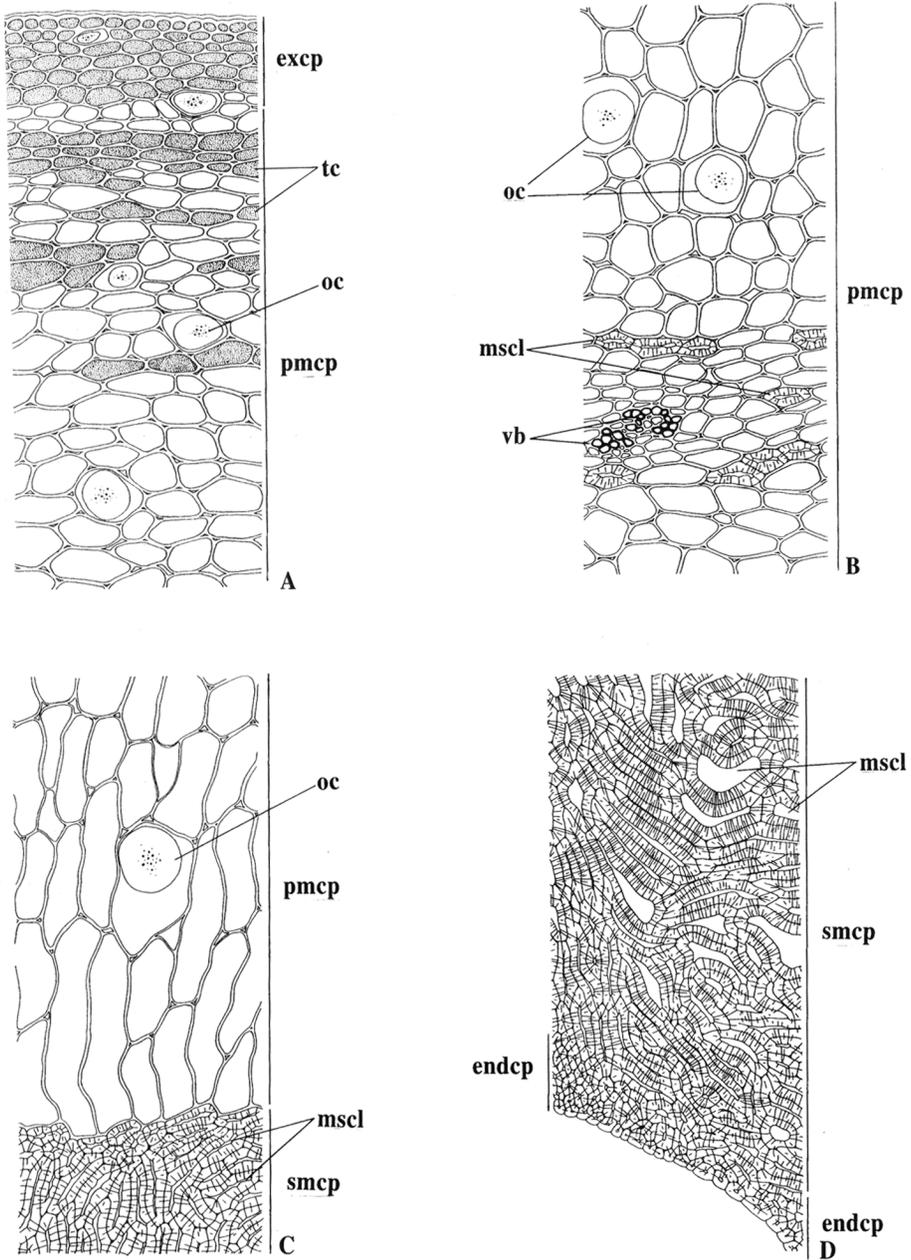


Figure 7. Cross-sections of the pericarp of *Gomortega keule* (Mol.) Baill., x 160. A, outermost part (incl. exocarp); B, mesocarpic parenchyma (outer parenchymatous part of mesocarp); C, zone of transition between parenchymatous and sclerenchymatous parts of mesocarp; D, innermost part of sclerified mesocarp and sclerendocarp. Abbreviations: excp, exocarp; pmcp, parenchymatous (outer) part of mesocarp; smcp, sclerified (inner) part of mesocarp; endcp, endocarp, oc, oil cells; tc, tanniferous cells; mscl, macrosclereids, vb, vascular bundles.

thin-walled, only the innermost tanniferous layer (endotegmen) of large, slightly tangentially elongate cells, does not crush in mature seeds. Other layers of parenchymatous tangentially elongated cells are collapsed, and only remnants are visible.

The remnants of the *nucellus* are represented by approx. one or two (rarely more) layers of large, thin-walled colourless cells, separated from the tegmen by a cuticular layer.

## DISCUSSION

### *Relationships with Canellaceae*

Metcalf & Chalk (1950) on the basis of xylem anatomy suggested that *Canellaceae* and *Gomortegaceae* are closely related. But as has been later stated by Stern (1955) and Gottwald (1977) the occurrence of homogeneous vascular rays and both apotracheal and paratracheal parenchyma in *Canellaceae* clearly distinguishes the latter taxon and places it into quite another structural group by xylem specialisation ['Myristical' of Gottwald, 1977]. Other characters of *Canellaceae*, such as monosulcate pollens (Walker, 1974 a, b; 1976), trilacunar nodal anatomy (Money, Bailey & Swamy, 1950), pentamerous floral construction, including 465 sepals and 265-carpellate superior paracarpous berry (Parameswaran, 1962), numerous seeds with ruminant endosperm, specialized exotestal seed coat construction (*Canella* P. Browne: Nemirovic-Dancenکو, 1988) point out to the lack of any close phylogenetic relationships with *Gomortegaceae* having inaperturate pollens (Walker, 1974 a, b, 1976; Hesse & Kubitzki, 1983), unilacunar nodal anatomy, mostly trimerous (although remaining indefinite) floral construction with numerous tepals and inferior ovary of drupaceous type (Buchheim, 1958; Brizicky, 1959), and quite distinct (in origin and morphogeny) endotestal-

endotegmic spermoderm. Thus the idea of canellaceous affinity for *Gomortega* should be ruled out.

### *Relationships with Chloranthaceae*

Hallier (1912) and later Money, Bailey & Swamy (1950) and Swamy (1953) advocated an idea of the existence of close phylogenetic relationships between *Gomortega* and *Chloranthaceae*. In reality, *Chloranthaceae* possess some similar principal characters with *Gomortegaceae*, such as unilacunar nodes, secretary oil cells, primitive xylem structure,  $\pm$  similar trimerous floral construction [tripartite gynoecium in *Hedyosmum* Swartz. (Yamazaki, 1992)], albuminous seeds originating from  $\pm$  orthotropous ovules, and pollen grains inaperturate (*Sarcandra* Gardn.) to monocolpate (*Ascarina* Foerst.) and even polycolpate with a tendency towards again inaperturate (*Hedyosmum*, *Chloranthus* Swartz.). However, the suggested affinity appears to indicate only some distant relationships between these taxa. The occurrence of inferior ovary in *Gomortega* with a somewhat varying (indefinite ?) number of constituting carpels (from two to six), while in the *Chloranthaceae* the monocarpellary gynoecium is prevailing (Endress, 1987), the coenocarpous drupaceous type of fruit in contrast to mostly apocarpous baccate or rarely syncarpous assaraceous inferior (*Hedyosmum*) in *Chloranthaceae*, large, differentiated embryo of *Gomortega* vs. small, with slightly differentiated cotyledons in *Chloranthaceae* emphasize a certain distinctness of *Gomortegaceae* from *Chloranthaceae*. However, these differences do not upset the integrity of this possible single, though heterobathmic evolutionary line, because these families, being allied by a number of similarities in nodal and xylem anatomy as well as palynomorphology, display a specific similar tracheotestal, endotestal seed coat type,

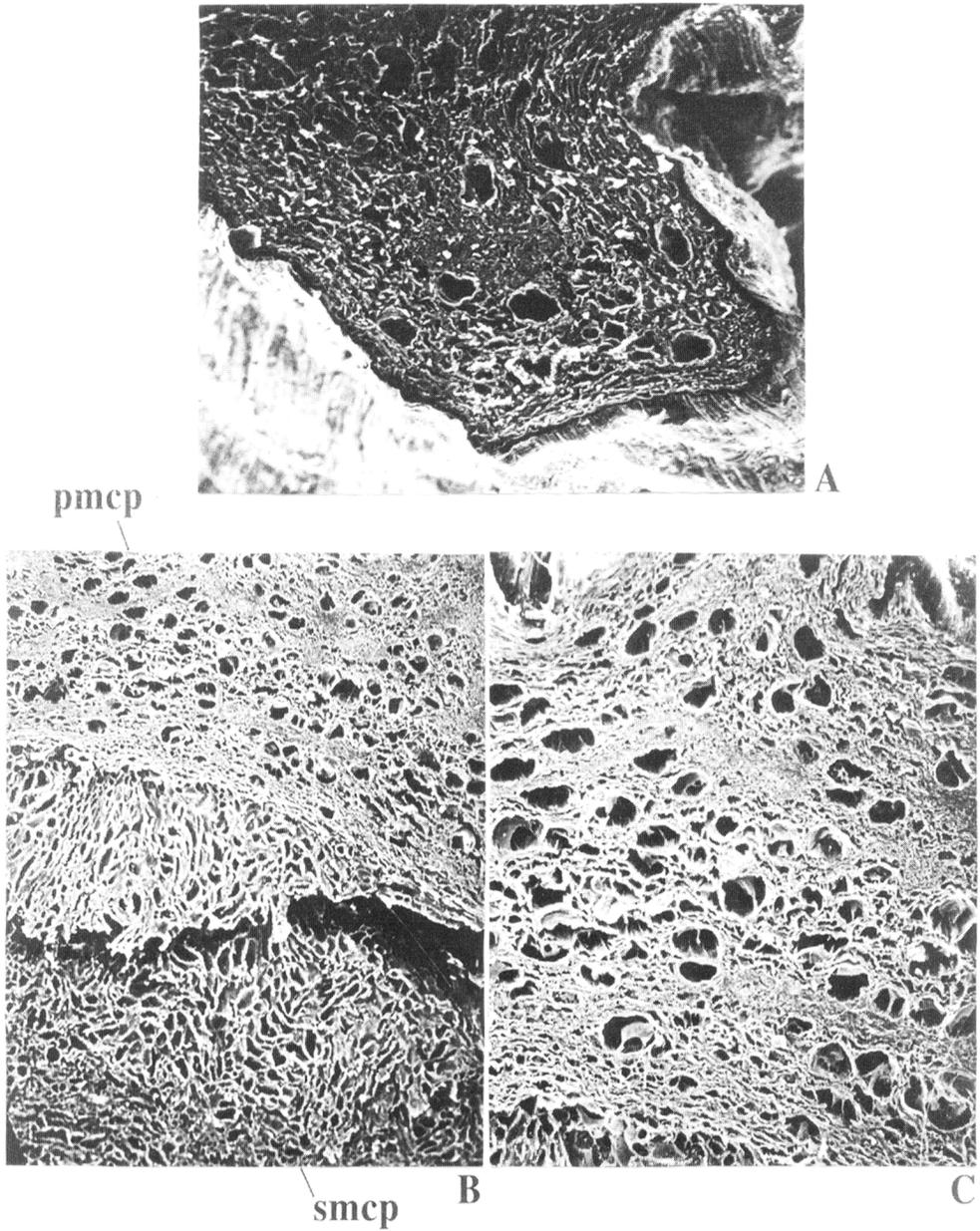


Figure 8. SEM micrographs of the pericarp tissues of *Gomortega keule* (Mol.) Baill. A, fleshy exomesocarpic parenchyma of the outermost part of pericarp, x 100; B, sclerified (smcp) and parenchymatous (pmcp) parts of mesocarp, x 150; C, mesocarpic parenchyma, x 200.

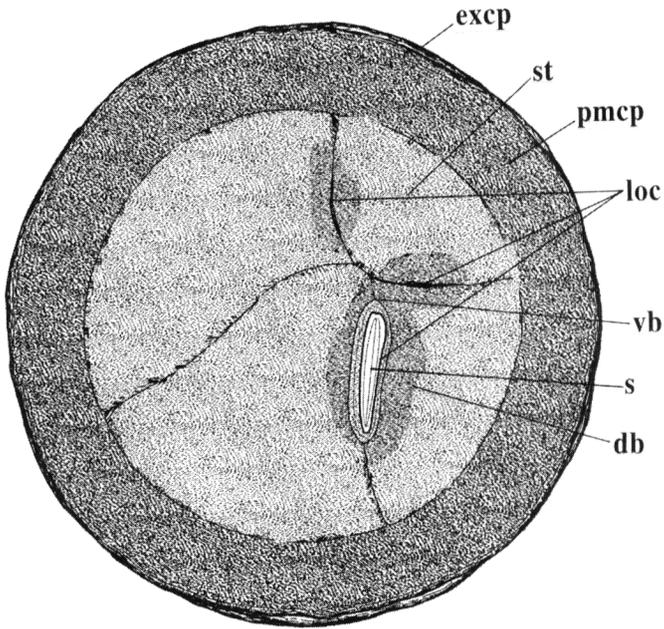


Figure 6. Cross-section of the fruit of *Gomortega keule* (Mol.) Baill., x 20. Abbreviations: excp, exocarp; s, seeds; loc, locules; vb, ventral vascular bundles; db, dorsal vascular bundles; st, sclerified tissues of pericarp; pmcp, parenchymatus part of mesocarp.

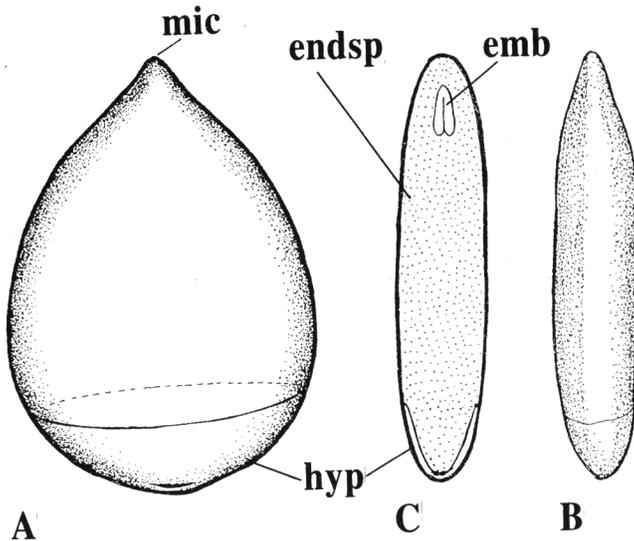


Figure 9. The seed of *Gomortega keule* (Mol.) Baill. A, general view, x 20; B, vascular skeleton and cup-shaped hypostase, x 20; C, longitudinal section of the seed, x 20. Abbreviations: hyp, hypostase; endsp, endosperm; emb, embryo; mic, micropyle.

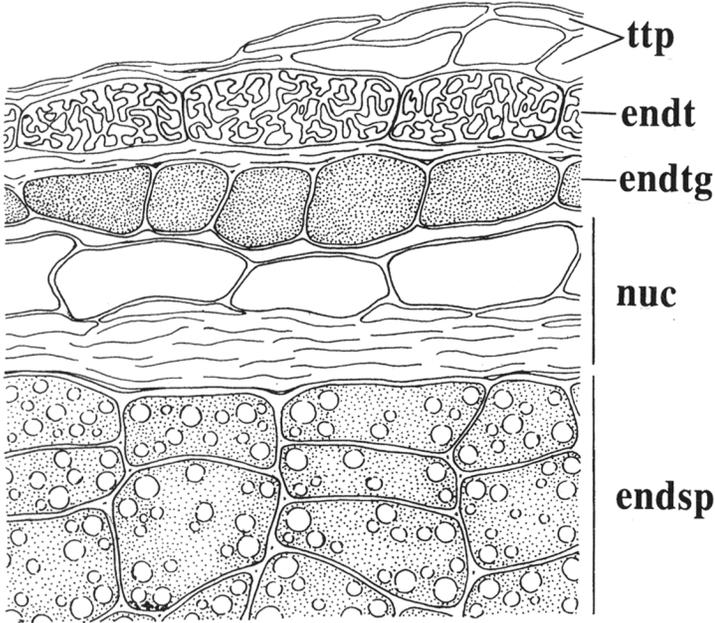


Figure 10. Cross-section of the seed coats of *Gomortega keule* (Mol.) Baill., x 800. Abbreviations: ttp, testal obliterated parenchyma; endt, endotesta; endtg, endotegmen; nuc, remnants of nucellus; endsp, endosperm.

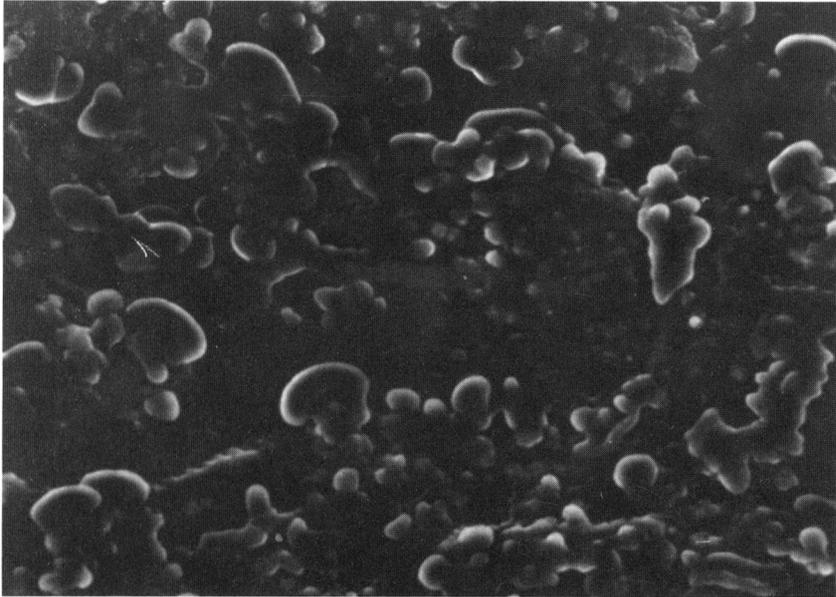


Figure 11. SEM micrograph of the seed surface of *Gomortega keule* (Mol.) Baill., showing obliterated testal parenchyma, x 380.

which is occurred in a very limited number of archaic families of angiosperms.

The family *Chloranthaceae* is diverse in seed coat types (Lodkina, 1988): the multilayered exotegmic type with a rudimentary thickened endotesta has been reported for *Ascarina* (Corner, 1976), the endotestal-exotegmic one for *Chloranthus* and *Sarcandra* (Vijayaraghavan, 1964; Lodkina, 1988), and highly advanced, unspecialized seed coat (parenchotestal-parenchotegmic) has been described in *Hedyosmum* (Edwards, 1920). The chloranthacean endotesta, being representing by sclerified, tangentially elongate cells filled with 'internal cellulose processes as a fibrillar network' (Corner, 1976 : 96) and crystals of calcium oxalate (appearing at the stage of progressive despecialization of sclerified structures), has all marks of the derivation from the tracheidal endotesta, similar to that of *Gomortega*. This principal key-character is indicative of a common ancestry for both taxa, though the appearance of unspecialized spermoderm in assare of *Hedyosmum* and gradual transference of the mechanical function from endotesta to tegmen with multiplicative sclerified exotegmen in series of *Chloranthus*—*Sarcandra*→*Ascarina* (endotestal-exotegmic→(endotestal)-exotegmic) confirm the distinctness of *Gomortegaceae* and *Chloranthaceae*. From the stand point of seed coat anatomy, these families definitely belong to the single, ancient and highly irradiated phylum of archaic *Magnoliidae*.

#### *Relationships with Lauraceae*

The recognition of the monocarpellary nature of the gynoecium in *Lauraceae* led Mez (1888) to exclude *Gomortega* from the family an reject any idea of close relationships between both taxa. Nevertheless, both families have a somewhat similar endotestal (tracheotestal) seed coat type, which is supplemented by

additional similarities in unilacunar nodes, secretory oil cells, similar xylem structure (Stern, 1954, 1955), (trimerous floral plan, mostly bilocular anthers, inferior ovary (only in lauraceous *Hypodaphnis zenkeri*), inaperturate pollen grains, single pendulous ovule. But the monomy of the lauraceous gynoecium together with the differentiated two circles of six tepals, three stamens (or 32 in *Cinnadenia*) arranged in four circles, fruit (capsule) with only differentiated 1-layered endocarp from the inner epidermis of pericarp (not a drupe !), exalbuminous seeds with a greatly developed pachychalaza (e.g., up to  $\pm \frac{2}{3}$  of the seed in *Laurus nobilis* L.) call into question the phylogenetic closeness.

The seed coat of *Lauraceae* has a similar mechanical system of endotestal tracheidal layer, but with unspecialized and practically completely obliterated tegmen (Sastri, 1962; Corner, 1976). The number of layers in lauraceous testa (5—8 (—20)) and tegmen (2—4) is somewhat distinct from that of gomortegaceous (2—3 and 3—4 respectively); the enormous development of highly vascularized pachychalaza (Le Monnier, 1872; Corner, 1976) leads to the substitution of the usual bitegumentary system in most part of seed. These differences confirm phylogenetic distinctness of the *Lauraceae* from *Gomortegaceae*, and families seems represent quite different vectors in the evolution of similar distinctive endotestal seed coats, although they remain to be clearly affiliated with a single evolutionary line in *Magnoliidae*.

#### *Relationships with Monimiaceae*

The *Monimiaceae s.l.* comprising 6 subfamilies *Hortonioidae* (= *Hortoniaceae*), *Atherospermatoideae* (= *Atherospermataceae*), *Siparunoideae* (= *Siparunaceae*), *Glossocalycoideae*, *Mollinedioideae*, and *Monimioideae* (Philipson, 1987, 1988; Takhtajan, 1997), represent a quite unnatural,

combined taxon with varying floral and fruit morphology; the delimitation of the family and splitting into several natural families (Pichon, 1948; Schodde, 1969, 1970; Smith, 1972) is ignored in recent systems of classification. The below positioned comparison of *Gomortega* with heterogeneous family emphasises the artificial circumscription of *Monimiaceae s.l.* Gomortegaceae, as practically all *Monimiaceae s.l.*, are exstipulate with a decussate leaf arrangement, unilacunar nodes, and albuminous seeds with endotestal seed coats. But the combination of inferior coenocarpous ovary with a single ovule, spirally arranged stamens and carpels, primitive wood, valvular dehiscence of the anthers, relatively large embryo somewhat distances the family from the monimiaceous diverse alliance. Among all subfamilies of *Monimiaceae s.l.*, *Gomortega* shows some similarities to *Atherospermatoideae* in having spirally arranged perianth, androecium and gynoecium, staminodial appendages (this feature is also shared with *Hortonia* Wight), carpels with a persistent styles, characteristic valvular dehiscence of anthers, *Pcsf*-type of sieve-element plastids (Behnke, 1988; much like also those of *Calycanthaceae*); but dramatically differs in having inferior ovary, although atherospermataceous genera, e.g. *Doryphora* Endl. and *Dryadodaphne* S. Moore, have a distinctive deeply concave, cupuliform receptacle, showing a prominent tendency toward epigyny, and thereby reducing a phylo-morphogenetic gap between two taxa. The endotestal (tracheotestal) type of seed coat, typical for all *Monimiaceae s.l.* (except for parenchotestal *Siparunoideae*: Heilborn, 1931), almost with a rudimentary perichalazy, is indicative of a close phylogenetic relationship of *Monimiaceae* to *Gomortega*.

Although detailed descriptions of the monimiaceous pericarp are mostly missing or controversial (Foreman, 1984), the occurrence of the drupaceous differentiation of the whole

pericarp in the drupeta of *Hortonioideae* (Corner, 1976), hypodrupeta of *Siparunoideae* (Heilborn, 1931) and *Monimioideae* (Corner, 1976) might be regarded as a connecting feature (nonetheless, one should be emphasized that monimiaceous taxa have apocarpous fruits in contrast to coenocarpous ones of *Gomortega*). The formation of the receptaculihiscent, mostly polymerous hypodrupeta in 'higher' *Monimiaceae* (*Glossocalycoideae*, *Mollinedioideae*, and some *Monimioideae*) represents itself a quite distinct vector in the evolution of fruits within *Monimiaceae*, starting from the archaic non-perigynous drupeta of *Hortonia* and some half-perigynous *Atherospermatoideae*. The latter taxa, as has been once proposed (Schodde, 1969, 1970), seems are rather most primitive 'splinters' of the massive endotestal evolutionary promonimiaceous line, and therefore, revealing close phylogenetic relationships with a distinct family *Gomortegaceae*, should be considered as distinct families having a common ancestry. The distinct familial rank of *Gomortega* showing close affinities to *Atherospermatoideae* and *Hortonioideae* precludes a possibility to consider them in the *Monimiaceae s.l.* Although Philipson (1987) thought that *Gomortega* might be united with *Monimiaceae s.l.* ('if its syncarpous inferior gynoecium is not considered sufficient to separate it decisively from the *Monimiaceae*'), this idea absolutely has not support in the structure of seed coats and fruits in general.

### Systematic position

The traditional inclusion of the *Gomortegaceae* in *Laurales* (Cronquist, 1992; Thorne, 1992; Takhtajan, 1997) is fully supported by fruit and seed coat anatomy in particular. The drupaceous, though inferior and coenocarpous, fruits, albuminous seeds with endotestal-endotegmic spermoderm of *Gomortega* reveal a certain similarity with

fruits and seeds of the *Monimiaceae s.l.*, or more correctly, a group of the families of monimiaceous alliance. Although monimiaceous families are characterized by apocarpous fruits, the trend towards gomortegaceous epigyny is evident in the formation of specialized perigynous drupeta (hypodrupeta), the indehiscent and few-carpelled forms of which with indefinite number of carpels have a principal construction like those in *Gomortega*. The available carpological and phermatological data on *Gomortegaceae*, together with data on palynomorphology (Agababian, 1973; Walker, 1974 a, b, 1976; Hesse & Kubitzki, 1983), chromosome analysis (Goldblatt, 1976), and morphology of sieve-element plastids (Behnke, 1988) question the unity of *Monimiaceae s.l.* (*sensu* Philipson, 1987, 1988), requiring to split the heterogeneous family into series of smaller natural groups in which characters are easily grasped. In this case, the relationship of *Gomortega* is definitely with the family *Atherospermataceae*, having a distinctive staminodial appendages and valvular dehiscence of anthers, somewhat similar pollen morphology (Sampson & Foreman, 1988), karyotype  $n = 22$  (Goldblatt, 1976), drupaceous differentiation of pericarp, endotestal seed coat construction, copious endosperm (Sampson, 1969 a, b), similar xylem (Garratt, 1934; Stern, 1955), and nodal anatomy (Money, Bailey & Swamy, 1950), specific *Pcsf*-type of sieve-element plastids (Behnke, 1988). With the addition of more data on carpology and phermatology of *Atherospermataceae* and other monimiaceous taxa, the close relationships and common origins of *Gomortega* and *Atherospermataceae* would be more evident.

Amongst *Magnoliidae*, the similar *Pcsf*-type of sieve-element plastids *Gomortega* shares also with *Calycanthaceae* representing a single order *Calycanthales* (Takhtajan, 1997). This circumstance emphasises the validity, in my opinion, of the argued splitting of the

*Monimiaceae s.l.* Nevertheless, *Calycanthaceae* are more remote phylogenetically from *Gomortegaceae* than *Atherospermataceae*, because they have more advanced structure of markedly perigynous (Baccarini, 1885; Tiagi, 1963) fruits (hypassareta with sclerified exo- and endocarp only: Lignier, 1892), exalbuminous seeds, though also endotestal and rudimentary perichalazal (? pachychalazal: Brofferio, 1930). The large embryo with massive convolute cotyledons also points to a high specialisation of *Calycanthaceae*. Using fruit and seed coat structure of *Calycanthaceae*, it is impossible to support the close phylogenetic proximity of *Gomortega* to this family which, perhaps, represents a relic and early diverging side-branch to monimiaceous ancestry. Therefore, the occurrence of the similar type of sieve-elements plastids in *Gomortega* and *Calycanthaceae* are not indicative of very close phylogenetic relationships.

The same remote, though not so far, phylogenetic relationships *Gomortega* shows to eulauralean families, *Lauraceae* and *Hernandiaceae* (incl. *Gyrocarpaceae*) (Takhtajan, 1997), the unicarpellate gynoecium of which precludes any possibility to affiliate *Gomortegaceae* with this group of families. The endotestal seed coat construction in both families (except for parenchotestal *Hernandioideae* & *Hernandiaceae*) may serve as a connecting link between monimiaceous and lauraceous phyla (Mohana Rao, 1986). However, within eulauraleans there are: progressive development of pachychalaza (*Lauraceae*), epigynous fruit construction on the basis of unicarpellate gynoecium (*Hypodaphnis* Stapf in *Lauraceae* and all *Hernandiaceae*), more specialized pericarp differentiation (i.e. formation of the assaraceous inferior pericarp in *Hernandioideae* & *Hernandiaceae* together with preservation of the initial capsular structure of the whole pericarp with a single-layered

sclerified endocarp typical for apocarpous *Lauraceae*), exalbuminous seeds with massive embryos having labyrinth, folded or spirally twisted large cotyledons. All these characters are markers of the great advance of *Lauraceae* and *Hernandiaceae* in comparison to archaic *Gomortegaceae*, connecting it with more primitive families of monimiaceous alliance.

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## REFERENCES

- AGABABIAN, V.Sh. -1973- *Pollens of the primitive angiosperms*. Erevan: Izdatelstvo Akademii Nauk Armjanskoj SSR. [In Russian].
- BACCARINI, P. -1885- Osservazioni anatomiche sopra alcuni ricettacoli fiorali. *Annuar. R. Istit. Bot. Roma* 1(1884): 66–88.
- BAILLON, H. -1867/1869- *Histoire des Plantes*. Vol. 1. *Renonculacées, Dilléniacées, Magnoliacées, Anonacées, Monimiacées, Rosacées*. Librairie Hachette et C<sup>ie</sup>, Paris.
- BEHNKE, H.D. -198- Sieve-element plastids, phloem protein, and evolution of flowering plants: III. Magnoliidae. *Taxon* 37: 699–732.
- BENTHAM, G. & J.D. HOOKER -1883- *Genera plantarum ad exemplaria imprimis in Herbariis Kewensibus servata definita*. Vol. 3. *Monochlamydearum, Gymnospermeorum et monocotyledonum ordines LXXIII*. Londini: L. Reeve & Co.
- BESSEY, C.E. -1915- The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109–164.
- BRIZICKY, G.K. -1959- Variability in the floral parts of *Gomortega* (Gomortegaceae). *Willdenowia* 2: 200–207.
- BROFFERIO, I. -1930- Osservazioni sullo sviluppo della Calycanthaceae. *Ann. Bot. (Roma)* 18: 387–394.
- BUCHHEIM, G. -1958- Bemerkungen zum Andrözeum der Gomortegaceae. *Willdenowia* 2: 27–31.
- CORNER, E.J.H. -1976- *The Seeds of Dicotyledons*. Vols 1, 2. Cambridge University Press, Cambridge.
- CRONQUIST, A. -1992- *An integrated system of classification of flowering plants*. 2nd ed. Columbia University Press, New York.
- DAHLGREN, G. -1989- An updated angiosperm classification. *Bot. J. Linn. Soc.* 100: 197–203.
- DOWELD, A.B. & E.A. SOROKINA -1997- A terminology of the principal types of the fruits in flowering plants. *Naucn.-Tekhn. Terminol.* 1997(1): 33–39. [In Russian].
- EDWARDS, E.S. -1920- Flower and seed of *Hedyosmum nutans*. *Bot. Gaz.* 70: 409–424.
- ENDLICHER, S. -1836/1840- *Genera plantarum secundum ordines naturales disposita*. Apud F. Beck Universitatis Bibliopolam, Vindobonae.
- ENDRESS, P.K. -1987- The Chloranthaceae: reproductive structures and systematic position. *Bot. Jahrb. Syst.* 109: 153–226.
- ENDRESS, P.K. & A. IGRSHEIM -1997- Gynoecium diversity and systematics of the Laurales. *Bot. J. Linn. Soc.* 125: 93–168.
- ENGLER, A. -1919- *Syllabus der Pflanzenfamilien*. 8 ed. Gebrüder Borntraeger, Berlin.
- ESPINOSA BUSTOS, M.R. -1948- Estudios botánicos. 2. Nomenclatura del Queule. *Bol. Mus. Nac. Hist. Nat.* (Santiago de Chile) 24: 70–79.
- FEDOTOVA, T.A. -1988- Gomortegaceae. In *Anatomia Seminum Comparativa*. Vol. 2. Edited by A.L. Takhtajan. Nauka, Leningrad. pp. 68. [In Russian].
- GARCIN, A.G. -1891- Contribution à l'Étude des péricarpes charnus. Du noyau des drupes. Histologie et histogénèse. *Ann. Soc. Bot. Lyon* 17(1890): 27–39.
- GARRATT, G.A. -1934- Systematic anatomy of the

- woods of the Monimiaceae. *Trop. Woods* 39: 18–44.
- GOLDBLATT, P. -1976- Chromosome number in Gomortega keule. *Ann. Missouri Bot. Gard.* 63: 207–208.
- GOTTWALD, H. -1977- The anatomy of the secondary xylem and the classification of ancient dicotyledons. *Pl. Syst. Evol. Suppl.* 1: 111–121.
- GUNCKEL, H. -1972- Plantas chilenas descritas como nuevas por Juan Ignacio Molina y sus concordancias con la nomenclatura botánica actual. *Noticiar. Mens. Mus. Nac. Hist. Nat. (Santiago de Chile)* 197: 3–11.
- HALLIER, H. -1912- Lorigine et le système phylétique des Angiospermes exposés à laide de leur arbre généalogique. *Arch. Néerl. Sci. Exact. Nat. Sér. 3B (Sci. Nat.)* 1: 146–234.
- HEILBORN, O. -1931- Studies on the taxonomy, geographical distribution and embryology of the genus Siparuna Aubl. *Svensk Bot. Tidskr.* 25: 202–228.
- HESSE, M. & K. KUBITZKI -1983- The sporoderm ultrastructure in Persea, Nectandra, Hernandia, Gomortega and some other lauralean genera. *Pl. Syst. Evol.* 141: 299–311.
- HUTCHINSON, J. -1926- The families of flowering plants. I. Dicotyledons. Arranged according to a new system based on their probable phylogeny. MacMillan & Co, London.
- JOHNSTON, I.M. -1924- Taxonomic records concerning american spermatophytes. 4. On the validity of Molina's scientific names. *Contr. Gray Herbarium* 70: 90–92.
- LE MONNIER, G. -1872- Recherches sur la nervation de la graine. *Ann. Sci. Nat. Sér. 6, Bot.* 16: 233–305.
- LEINFELLNER, W. -1968- Über die Karpelle verschiedener Magnoliales. VI. Gomortega keule (Gomortegaceae). *Öster. Bot. Zeitschr.* 115: 113–119.
- LIGNIER, O. -1892- La graine et le fruit des Calycanthacées. *Bull. Soc. Linn. Normandie. Sér. 4* 5(1891): 19–33.
- LINDLEY, J. -1853- The Vegetable Kingdom; or, The structure, classification and uses of plants, illustrated upon the natural system. 3rd ed. Bradbury & Evans, London.
- LINNÉ, C. -1753- Species plantarum, exhibentes plantas rite cognitatas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. T. I. Laurentii Salvii, Holmiæ.
- LODKINA, M.M. -1988- Chloranthaceae. In *Anatomia Seminum Comparativa*. Vol. 2. Edited by A.L. Takhtajan. Nauka, Leningrad. pp. 89–92. [In Russian].
- METCALFE, C.R. & L. CHALK -1950- Anatomy of the Dicotyledons. Leaves, stem, and wood in relation to taxonomy with notes on economic uses. Vols 1, 2. Clarendon Press, Oxford.
- MEZ, C. -1888- Lauraceae Americanae monographice descriptae. *Jahrb. K. Bot. Gart. Mus. Berlin* 5: 1–556.
- MOHANA RAO, P.R. -1986- Seed and fruit anatomy in Gyrocarpus americanus with a discussion of the affinities of Hernandiaceae. *Israel J. Bot.* 35: 133–152.
- MOLINA, J.I. -1782- Saggio sulla storia naturale del Chili. Stamperio di T. d'Aquino, Bologna.
- MOLINA, J.I. -1810- Saggio sulla storia naturale del Chili. 2<sup>nd</sup> ed. Tipografia de' Fratelli Masi e Comp., Bologna.
- MONEY, L.L., I.W. BAILEY & B.G.L. SWAMY -1950- The morphology and relationships of the Monimiaceae. *J. Arnold Arbor.* 31: 372–404.
- NEMIROVIC-DANCENKO, E.N. -1988- Canellaceae. In *Anatomia Seminum Comparativa*. Vol. 2. Edited by A.L. Takhtajan. Nauka, Leningrad. pp. 31–32. [In Russian].
- O'BRIEN, T.P. & M.E. MCCULLY -1981- *The Study of Plant Structure: Principles and selected Methods*. Termarcarphi and Pty. Ltd., Melbourne.
- PARAMESWARAN, N. -1962- Floral morphology and embryology in some taxa of the Canellaceae. *Proc. Indian Acad. Sci. Sect. B* 55: 167–188.
- PERSOON, C.H. -1805- Synopsis plantarum seu Enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum. Pt. I. Apud C. F. Cramerum, Parisiis Lutetiorum; Apud J. G. Cottam, Tubingae.
- PHILIPPI, R.A. -1864/1865- Plantarum novarum Chilensium centuriæ, inclusis quibusdam Mendocinis et Patagonicis. *Linnaea* 33: 1–308.
- PHILIPPI, R.A. -1865- Descripción de algunas plantas nuevas chilenas. *Anal. Univ. Chile* 26: 638–650.
- PHILIPPI, R.A. -1868- Über die Adenostemum nitidum. *Pers. Bot. Zeit.* 26: 217–221.

- PHILIPSON, W.R. -1987- A classification of the Monimiaceae. *Nordic J. Bot.* 7: 25–29.
- PHILIPSON, W.R. -1988- A classification of the Monimiaceae: an additional note. *Nordic J. Bot.* 8: 24.
- PICHON, P. -1948- Les Monimiacées: famille hétérogène. *Bull. Mus. Nat. d'Hist. Nat. Paris*, Sér. 2 20: 383–384.
- REICHE, K. -1896- Zur Kenntniss von *Gomortega nitida* R. et Pav. *Ber. Deutsch. Bot. Ges.* 14: 225–233.
- RUIZ LÓPEZ, H. & J. PAVÓN -1794- Flora peruviana, et chilensis prodromus, sive, Novorum generum plantarum peruvianarum, et chilensium descriptiones, et icones. Descripciónes y láminas de los nuevos géneros de plantas de la flora del Perú y Chile. Imp. de Sancha, Madrid.
- SAMPSON, F.B. -1969a- Studies on the Monimiaceae. II. Floral morphology of *Laurelia novae-zelandiae* A. Cunn. (subfamily Atherospermatoidae). *New Zealand J. Bot.* 7: 214–240.
- SAMPSON, F.B. -1969b- Studies on the Monimiaceae. III. Gametophyte development of *Laurelia novae-zelandiae* A. Cunn. (subfamily Atherospermatoidae). *Austral. J. Bot.* 17: 425–439.
- SAMPSON, F.B. & FOREMAN, D.B. -1988- Pollen morphology of *Atherosperma*, *Daphnandra*, and *Doryphora* (Atherospermataceae [Monimiaceae]). *Grana* 27: 17–25.
- SASTRI, R.L.N. -1962- Studies in Lauraceae. III. Embryology of *Cassytha*. *Bot. Gaz.* 123: 197–206.
- SCHLEIDEN, M.J. -1839- Botanische Notizen, 9. über die Spiralzellenschicht in der Frucht der Laurineen. *Arch. Naturgesch. Jahrg.* 5 1: 288–290.
- SCHODDE, R. -1969- *A monograph of the family Atherospermataceae* R. Br. Vols 1, 2. Thesis, University of Adelaide.
- SCHODDE, R. -1970- Two new suprageneric taxa in the Monimiaceae alliance. *Taxon* 19: 324–328.
- SMITH, A.C. -1972- An appraisal of the orders and families of primitive extant angiosperms. *J. Indian Bot. Soc.* 50A: 215–226.
- SPJUT, R.W. -1994- A systematic treatment of fruit types. *Mem. New York Bot. Gard.* 70: 1–182.
- STERN, W.L. -1954- Comparative anatomy of xylem and phylogeny of Lauraceae. *Trop. Woods* 100: 1–73.
- STERN, W.L. -1955- Xylem anatomy and relationships of Gomortegaceae. *Amer. J. Bot.* 42: 874–885.
- SWAMY, B.G.L. -1953- The morphology and relationships of Chloranthaceae. *J. Arnold Arbor.* 34: 375–411.
- TAKHTAJAN, A.L. -1997- *Diversity and classification of flowering plants*. Columbia University Press, New York.
- THORNE, R.F. -1992- Classification and geography of the flowering plants. *Bot. Rev.* (Lancaster) 58: 225–348.
- TIAGI, Y.D. -1963- Vascular anatomy of the flower of certain species of the Calycanthaceae. *Proc. Indian Acad. Sci. Sect. B, Biol. Sci.* 58: 224–234.
- VIJAYARAGHAVAN, M.R. -1964- Morphology and embryology of a vesselless dicotyledon — *Sarcandra irvingbaileyi* Swamy, and systematic position of Chloranthaceae. *Phytomorphology* 14: 429–441.
- WALKER, J.W. -1974a- Evolution of exine structure in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 891–902.
- WALKER, J.W. -1974 b- Aperture evolution in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 1112–1137.
- WALKER, J.W. -1976- Comparative pollen morphology and phylogeny of the ranalean complex. In *Origin and early evolution of Angiosperms*. Edited by C.B. Beck. Columbia University Press, New York. pp. 241–295.
- YAMAZAKI, T. -1992- Floral morphology of *Hedyosmum orientale* Merr. et Chun (Chloranthaceae) and phylogenetic significance of its perianth. *J. Jap. Bot.* 67: 257–269.

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