ON CORNERIAN AND OTHER TERMINOLOGY OF ANGIOSPERMOUS AND GYMNOSPERMOUS SEED COATS: HISTORICAL PERSPECTIVE AND TERMINOLOGICAL RECOMMENDATIONS

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Summary

A revision of Corner's (1976) classification of angiospermous (especially dicotyledonous) seeds is given in outline form according to the histology of the seed coat, namely, exo-, meso-, and endotestal seeds versus exo-, meso-, and endotegmic seeds. This revision is presented in the context of a historical perspective, and with certain explanations and caveats for the use of the classification. A digression pursues the terminology of the gymnospermous seed coat, in particular its division into sarco-, sclero-, and endotestal layers. An appendix lists published reviews of Corner's 1976 book The seeds of dicotyledons.

In 1976 there appeared a milestone work by Professor E. J. H. Corner on the morphology and anatomy of dicotyledonous seeds. This work has been generally enthusiastically received (see references in Appendix) and its findings and terminology have increasingly been used in both synthetic accounts (e.g., Boesewinkel and Bouman, 1984; Dahlgren and Thorne, 1984) and detailed studies (e.g., Boesewinkel and Been, 1979; Boesewinkel and Geenen, 1980; Grootjen, 1983; Mohana Rao, 1978; Schmid, 1978a, b; Schmid et al., 1984).

Corner's two-volume work is wide ranging. The text in the first volume contains chapters on methodology, seed morphology, seed-coat anatomy, seed evolution, and the relationships of seed anatomy and morphology to the classification of dicotyledons. Most of this volume gives summary details for 243 families. The second volume is an atlas of 634 diagrams specially prepared by Corner. The figures are beautifully drawn, with as many as 15 subunits per figure. Numerous figures show fruit and even floral structure. Unfortunately, their captions are brief and their labels very few. The scanty index is especially deficient in listing structures.

A terminologically most important part of Corner's opus is his 17-page chapter on seed-coat anatomy (pp. 8–24), which proposes some novel terms or modifies definitions of some old terms. The abundance of terminology in this chapter makes for some rough sledding. Consequently, to facilitate use of this chapter in particular, and of Corner's invaluable work in general, I not only discuss Cornerian and other seed-coat terminology in a historical context, but also give a guide (Table 1) to the "Cornercopia" of histological terminology. Both in this guide and in the following discussion various terminological recommendations are made. In addition, because the seed-coat terminology of angiosperms is related to that of gymnosperms, I also deal with the latter.

The recent review article by Boesewinkel and Bouman (1984) on seed-coat structure, it might be noted, largely adopts Corner's terminology. This review, which appeared after the present account had been substantially written, is only selectively cited in the sections below. However, Table 1 and the following remarks also largely apply to this review.

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Corner's Testal-tegmic Terminology for Angiosperms: Historical Perspective and Terminological Recommendations

Corner properly distinguished between the integuments of the ovule and the integuments of the seed. The latter, of course, involve various modifications after fertilization of the ovule. Corner referred to the outer integument of the seed as “testa,” and the inner integument of the seed as “tegmen.” Hence seeds with a characteristic testa can be called “testal,” those with a characteristic tegmen “tegmic.” Bitegmic seeds by definition have both a testa and a tegmen. By fiat unitegmic seeds have strictly a testa (see comment #2 in section on caveats). Actually, Corner (1976: 8) restricted “outer integument” and “inner integument” to ovules and used their counterparts, “testa” and “tegmen,” for seeds. In contrast, Corner used “bitegmic” and “unitegmic” for both ovules and seeds. In addition, some specialized groups, for example, Santalales, have greatly reduced ovules that lack integuments and other features (e.g., nucellus); that is, the ovules and seeds are “ategmic” (Bhojwani and Bhatnagar, 1978; Boesewinkel and Bouman, 1984; Bouman, 1984; Corner, 1976; Cronquist, 1981; Dahlgren, 1975; Eames, 1961; McLean and Ivimey-Cook, 1956; Netolitzky, 1926). In such cases, the Cornerian testal-tegmic terminology obviously does not apply.

The division of the angiospermous seed coat (for gymnosperms see later section) into an outer integumental testa and an inner integumental tegmen is actually in line with the mainly taxonomic distinction of yore, for example, by Crozier (1892), Gaertner (1788), Gray (1879, and the earlier editions), Heining (1899), Jackson (1928, and the earlier editions), Lawrence (1951), Le Maout and Decaisne (1873), de Mirbel (1815), and Stearn (1983). Very old works, for example, the pre-1900 ones just cited, frequently use other terms for the two parts of the seed coat, especially “exopleura” for testa and “endopleura” for tegmen, which are both based on the Greek “pleura,” meaning “side.”

Gaertner (1788) was the first to divide the seed coat into a “testa” and a “tegmen,” which are Latin nouns meaning, respectively, “shell” and “cover.” Gaertner actually originated the botanical usage of “testa,” but he called the tegmen the “membrana interna.” It was de Mirbel (1815) who proposed “tegmen,” although he discarded “testa” for his new term “lorica” (actually “lorique”). “Endopleura” originated with de Candolle (1827—also in 1841) as a substitute for “tegmen,” “testa” being retained by him, but “mesospermum” being suggested for an intervening layer (“exopleura” was proposed later, by whom I do not know). Raspail (1827) and Richard (1808, 1811, 1819) had similar interpretations of seed-coat structure, but with completely different nomenclatures. However, most early botanists (see preceding paragraph) favored the concept of two rather than three layers in the mature seed coat (Bouman, 1974, 1978). Bouman (1974, 1978) gives a masterful excursion through the nomenclatural jungle of semenology, the aforenoted terms being just the tip of the seminal iceberg.

In contrast, the increasingly common and chiefly anatomical and morphological tendency is to use testa for the entire seed coat of angiospermous seeds, for example: Benson (1979), Bewley and Black (1985), Bouman (1974, 1978), Cutter (1971), Eames (1961), Elizens (1985), Esau (1965, 1977), Fahn (1982), Foster and Gifford (1974), McLean and Ivimey-Cook (1956), van der Pijl (1982), Scagel et al. (1984), and Swamy and Krishnamurthy (1980). Lindley (1848, and the earlier editions back to 1832) and Raspail (1827), it should be noted, were systematists, and among the rare early ones, favoring this approach. Raspail (1827) apparently originated usage of “testa” (he actually used “test”) for the inclusive seed coat. Among modern anatomists and morphologists, on the other hand, Bhojwani and Bhatnagar (1978), Boesewinkel and Bouman (1984), Boesewinkel and Geenen (1980, in abstract only), Bold et al. (1980), Mohana Rao (1978), Schmid et al. (1984), and Tsinger (1958) favored the Cornerian distinction of testa versus tegmen, although Tsinger (1958), a highly obscure work in Russian, avoids these specific designations. Among modern systematists, Dahlgren et al. (1985) and Dahlgren and Thorne (1984) have also adopted Corner's testal-tegmic subdivision of the seed coat, although the former sometimes lapse.
Table 1. Key to types of angiospermous seed coats based on Corner (1976).¹

I. Ovule/seed with single integument—unitegmic ovules/seeds: see leads IIA and IIB2a following²

II. Ovule/seed with two integuments—bitegmic ovules/seeds
   A. Mechanical layer absent—"undifferentiated seed-coats" sensu Corner (1976: 18) and Boesewinkel and Bouman (1984: 585)³
   B. Mechanical layer(s) present⁴,⁵
      1. Outer testa or entire testa pulpy, often juicy and edible—sarcotestal seeds, which may be testal, tegmic, or both: see lead 2 following
      2. Testa not pulpy or juicy—non-sarcotestal seeds
         a) Mechanical layer(s)⁴ in outer integument of seed—testal seeds (Figs. 1–3)
            (1) Mechanical layer in outer epidermis of outer integument—exotestal seeds (Fig. 1): mechanical layer (a) a palisade (i.e., a layer of columnar cells perpendicularly elongate to the seed surface), (b) a fibrous layer, etc.⁵
            (2) Mechanical layer in mesophyll of outer integument—mesotestal seeds (Fig. 2): mechanical layer (a) an outer hypodermal palisade, (b) a diffuse layer of cuboidal sclerotic cells, (c) a diffuse fibrous layer, etc.⁵
            (3) Mechanical layer in inner epidermis of outer integument—endotestal seeds (Fig. 3): mechanical layer (a) a palisade, (b) a tracheoid layer⁶ (its tangentially elongate cells with helical or annular thickenings), (c) a multiple layer of sclerotic cells, (d) a single layer of cuboidal sclerotic cells, etc.⁵,⁷
         b) Mechanical layer(s)⁴ in inner integument of seed—tegmic seeds (Figs. 4–7)
            (1) Mechanical layer in outer epidermis of inner integument—exotegmic seeds (Fig. 4):
               mechanical layer (a) a palisade (its cells more or less prismatic with angular, isodiametric or shortly oblong facets, or its cells tubular or radially elongate but with stellate-undulate or lobate facets), (b) a fibrous layer, (c) a tracheoid layer,⁶ etc.⁵,⁸
            (2) Mechanical layer in mesophyll of inner integument—mesotegmic seeds (Figs. 5, 6):
               mechanical layer (a) a fibrous layer, (b) a tracheoid layer,⁶ etc.⁵,⁹
            (3) Mechanical layer in inner epidermis of inner integument—endotegmic seeds (Fig. 7):
               mechanical layer (a) a palisade, (b) a layer of cuboidal sclerotic cells, etc.⁵

¹ Based on Corner (1976: 10 left especially, also right 10–18 and 46–47). Boesewinkel and Bouman (1984) largely follow Corner. See text for explanation and caveats. This classification and terminology obviously do not apply to ategmic seeds, which lack a seed coat.
² Unitegmic seeds either lack a mechanical layer or have one and then by fiat are regarded as "testal seeds," with the terminology in Part IIB2a. For elaboration see comment #2 in text.
³ The "undifferentiated" designation clearly refers to the absence of a mechanical layer (which may have a slight exotestal tendency), but it is, nevertheless, unfortunate as other types of histological differentiation may occur in the seed coat. Consequently, seeds with a mechanical layer or layers (i.e., IIB in key) should not be referred to as "differentiated seed coats."
⁴ Two or more mechanical layers may occur in one seed so that, as exemplified in Figs. 5, 6, and 8, and as indicated in note 9 below and in comment #4 in the text, hybrid terminology can be applied to the seed coat.
⁵ Additional subtypes probably occur; see comment #3 in text for elaboration.
⁶ I substitute "tracheoid" for Corner's (1976) and Boesewinkel and Bouman's (1984) "tracheidal" because the former refers to tracheary elements in general whereas the latter refers to just tracheids. In discussions of the angiospermous seed coat (Corner, 1976; Netolitzky, 1926), as exemplified in note 8 below, and also in histological discussions of "tracheid bars" (these occur in seeds—see Boesewinkel and Bouman, 1984: 602), "storage tracheids," "tracheid idioblasts," "tracheid idioblasts," "tracheoids," and the like (Cutter, 1971; Esau, 1965, 1977; Fahn, 1982; Rao and Das, 1979), tracheids are universally assumed to be present. Fahn (1982: 219) refers to "tracheide-like cells (tracheoids)." However, in all these cases one might ask if always tracheids and never vessel elements are present (this terminological question obviously does not apply to gymnosperms other than Gnetophyta). Consequently, "tracheoid" seems the preferable term for use as both a noun and an adjective ("tracheoidal" as an adjective is actually redundant).
⁷ Corner (1976) presented on his p. 12, in addition to that presented on his p. 10, a more detailed classification of endotestal seeds with eight subtypes based on the shape of the endotestal cells, their manner of lignification or thickening, and their arrangement whether a single layer or multiple layer
into using an inclusive “testa” (e.g., compare, respectively, pp. 16, 170, 172, 194, 207, 222, 226, 277, 372, 379 with 111, 124, 160, 164, 170, 240, 326, 342, 379, 384).

**Terminological recommendations.**—There might be a satisfactory dual resolution of the foregoing terminological differences involving the seed coat. In general anatomical and morphological treatments, as in the works cited in the preceding paragraph, and also in general systematic works, it seems clearer, especially from a pedagogic viewpoint, to use “testa” for the inclusive seed coat. However, recent elementary botany textbooks, for example, Raven et al. (1981), tend to avoid “testa” entirely and use just “seed coat.” This approach has also been favored in some technical works, for example, Boesewinkel and Been (1979), Boesewinkel and Geenen (1980, except in abstract), Bouman and Calis (1977), Bouman and Schier (1979), Grootjen (1983), Netolitzky (1926) [the old bible of semenology to which Corner’s opus is dedicated], Quisumbing (1925), Schnarf (1937), Singh and Dathan (1980), Singh (1978), and Wunderlich (1967). Alternatively, in detailed, technical accounts of the seed coat, as in the works cited in the first paragraph of this paper, I believe it appropriate to cite Corner (1976) and to adopt his terminology [Boesewinkel and Been (1979) and Grootjen (1983) avoided “testa” and “tegmen” whereas Schmid (1978a, b) used “testa” in a broad sense for unigamic taxa, but all used other Cornerian terminology, as outlined below].

Corner’s Other Seed-coat Terminology for Angiosperms: Historical Perspective and Terminological Clarifications

According to Corner (1976: 9–10), the distinctive feature of seed-coat anatomy lies in the structure and especially the position of the main mechanical layer or layers, which are thick-walled regions, though not necessarily lignified ones. The mechanical layer(s) of the seed coat may variously occur in the testa (outer integument of a bitegmic seed, or the single integument of a unigamic seed) or in the tegmen (inner integument of a bitegmic seed) or in both, and in the integument may additionally variously involve the outer epidermis, the inner epidermis, or the intervening layers. Corner referred to the last as “mesophyll,” which may well be a novel application of a term usually reserved for leaves and floral and other leaflike appendages. Thus, on the basis of the position of the mechanical layer, one can designate seeds as “exotestal,” “mesotestal,” “endotestal,” “exotegmic,” “mesotegmic,” “endotegmic,” or combinations of these (see comment #4 in section on caveats), as shown in Figs. 1–8 and in Table 1. The nature of the mechanical layer varies appreciably; for example, it can be a layer of columnar cells perpendicularly elongate to the seed surface (i.e., a palisade) or a layer of fibers, sclerotic cells, tracheoid elements, etc. (see Table 1 and its notes 6–8).

Corner (1976: 8; see also Boesewinkel and Bouman, 1984: 578) also used “hypodermis” and “outer and inner hypodermal layers” to refer to seeds. If the mechanical layer is strictly

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8 On his p. 10 Corner (1976) indicated three subtypes of exotegmic seeds but on his pp. 13 and 16 only two subtypes. Thus on Corner’s p. 10 there is a major subtype “with stellately lobed cells” coordinate with the “palisade” subtype but on his p. 13 the former is subordinate to the latter.

In addition, Corner terminologically confused matters with the “fibrous layer” or “fibrous exotegmen,” which may have “tracheidal fibers” with helical (not “spiral”) or annular wall thickenings “as if the fibres were elongate tracheids” (p. 15). Such fibers are corrupted on pp. 16–18 into occurring in a “tracheidal exotegmen,” on p. 17 into occurring in “exotegmic tracheidal seeds,” and on p. 18 into occurring in a “fibrous-tracheidal exotegmen.”

9 According to Corner (1976: 10, 13) and Boesewinkel and Bouman (1984: 584), mesotegmic seeds are rare, always occurring in conjunction with exotegmic or endotegmic ones. Strictly speaking, these would be, respectively, exo-mesotegmic and meso-endotegmic seeds.
Figs. 1–8. Diagrams (after Corner, 1976) showing for an anatropous seed the main types of seed-coat structure involving position of the mechanical layer(s) in the testa (outer integument) and/or tegmen (inner integument). Mesotegmic seeds occur only in conjunction with exotegmic or endotegmic seeds (Figs. 5, 6). Compare with Table 1. Not shown are certain “hybrid” types, for example, exo-mesotestal, exo-endotestal, mesotestal-exotegmic, or exo-endotegmic seeds; see comment #4 in text for elaboration.
cotesta,” which he defined (p. 24) as “a convenient descriptive term for the pulpy and edible testa or outer part of it, which simulates the aril” (Boesewinkel and Bouman, 1984: 590, adopt a similar definition). The Linnean term “aril” in turn was defined (Corner, 1976: 23) as “the pulpy structure which grows from some part of the ovule or funicle after fertilization and invests part or the whole of the seed,” a usage of the term originated by Gaertner (1788). As Corner admitted, this broad and widely accepted definition of “aril” has been criticized (see also Boesewinkel and Bouman, 1984; Dahlgren and Clifford, 1982, Dahlgren et al., 1985; Eames, 1961; Endress, 1973; Kapil et al., 1980; McLean and Ivimey-Cook, 1956, van der Pijl, 1982, and Schnarf, 1937).

Seeds with a characteristic sarcotesta are called “sarcotestal seeds” and those with an aril “arillate seeds” (Boesewinkel and Bouman, 1984; Corner, 1976), the former being more preferable to “sarcotesta seeds” (van der Pijl, 1982, and earlier editions). The sarcotesta occurs in a variety of positions in the testa, but it never occurs in the tegmen (Corner, 1976: 53). It represents (1) exotesta in the mesotestal-exotegmic seeds of *Punica*, (2) mesotesta in the endotestal seeds of *Magnolia* and in the exotegmic seeds of *Baccaurea*, (3) exo-mesotesta in the endotestal seeds of *Ribes*, some species of which are arillate, and in the arillate, exo-mesotegmic seeds of *Carica*, or (4) the entire testa in the exotegmic seeds of *Aporosa* (Boesewinkel and Bouman, 1984; Corner, 1976; Netolitzky, 1926). An aril occurs in *Myristica* and many other taxa (references in preceding paragraph), though contrary to Corner (1976) not in *Actinidia* (see Schmid, 1978a). Other taxa have both sarcotesta and aril (Corner, 1976: 54). For example, in various members of Connnaraceae, Meliaceae, and Sapindaceae the aril and sarcotesta are both of chalazal origin.

Of the seven terms of the seed coat used by Corner with considerable frequency, namely, “sarcotesta,” “exo-testa,” “endo-testa,” “mesotesta,” “exo-tegmen,” “mesote-gmen,” and “endo-tegmen”—and their adjectival derivatives, the last four terms appear to be new. At least I have not seen their antecedent use in the literature. The first three terms, however, have had extensive earlier usage for gymnospermous seeds, as elaborated in the next section. I am not certain to what extent the preceding testal terminology has been applied to angiospermous seeds by pre-Cornerian botanists. (59) Netolitzky (1926) occasionally used “endo-testa” and especially “sarcotesta,” and Dahlgren et al. (1985) and van der Pijl (1982, and earlier editions), respectively, rarely and extensively used the latter term. “Mesotesta” seems a term restricted to angiospermous seeds, and perhaps used no earlier than Corner, whereas “sclerotesta,” as detailed below, seems a term restricted to gymnospermous seeds. Corner (1976: 59) used the latter term once and then only for gymnospermous seeds.

**Seed-coat Terminology for Gymnosperms: Historical Perspective and Terminological Recommendations**

“Sarcotesta,” “sclerotesta,” “endo-testa,” and, to a lesser extent, “exo-testa” have had great applicability in studies of gymnospermous seeds, especially in the paleobotanical literature cited below. For example, Taylor (1981: 558, 562) in his glossary defined “sarcotesta” as “the outer parenchymatous layer of the integument in some seeds,” “sclerotesta” as “the fibrous [usually “middle” –see pp. 344, 433] layer of the integument of some seeds,” and “endo-testa” as “the delicate, innermost layer of the integument of some seeds.” [Stewart’s (1983) recent book lacks a glossary. Although these terms are not as clearly defined by Stewart (see esp. p. 262), his application of them is similar.] Such terminology has also been applied to seeds of extant gymnosperms (Brongniart, 1874; Corner, 1976; Oliver, 1902, 1904; van der Pijl, 1982; Rodin and Kapil, 1969; Schnarf, 1937; Scott, 1923; Scott and Maslen, 1907; Seward, 1917; Singh, 1978; Sporne, 1965: 19 only; Stewart, 1983; Trivedi and Singh, 1969; Williamson, 1876a, 1877). I have not encountered “mesotesta” used for gymnospermous seeds.

Brongniart (1874) actually introduced “sarcotesta” and “endo-testa” for the seeds of fossil and extant gymnosperms and used these terms in a sense equivalent to the aforenoted
modern definitions of “sarcotesta” and “sclerotesta.” Williamson probably introduced “exotesta” (in 1876a, b, 1877) and “sclerotesta” (only in 1876b). Williamson (1876a, b, 1877) actually had four applications for the two outer layers of the seed coat of living and extant gymnosperms (the inner fleshy layer was generally not reported in paleobotanical studies of this vintage—see also remarks at end of this section), namely: (1) Brongniart’s (1874) “sarcotesta” and “endotesta” (in Williamson, 1877, but not in 1876a, b), for example, for the seeds of Ginkgo (as Salisburia adiantifolia) and the Paleozoic Pachytesta (as Trigonocarpus) and Malacotesta; (2) “exotesta” (in Williamson, 1877, equated with “sarcotesta”—see especially caption to his Figs. 95–99) and “endotesta” (Williamson, 1876a, b, 1877), for example, for his same material of Pachytesta and Malacotesta and also for the seeds of Ginkgo and Mitrospernum (as Cardiocarpus—also for some specimens of the lycopod Lepidocarpon misidentified as the cordaite—see Scott, 1923: 306); (3) “exotesta” and “sclerotesta” (in Williamson, 1876b, the latter equated to “endotesta”—see pp. 71–72, “sclerotesta” not in Williamson, 1876a, 1877), for example, for his same material of Pachytesta; and (4) “exotesta” for the entire testa (only in Williamson, 1877, “exotesta” in this sense used strictly in the figure captions), for example, for the seeds of Lagenostoma.

Of these four testal terms, namely, “exotesta,” “sarcotesta,” “endotesta,” and “sclerotesta,” the last did not really catch on until after 1900, beginning with Oliver’s (1902) paper (see citations below) and the burst of mainly British activity involving studies of Paleozoic seeds (Oliver, 1904, 1909; Scott and Maslen, 1907; for other early work see especially Schnarf, 1937; Scott, 1923; Seward, 1917). Probably significantly, “sclerotesta” appears in the 1909 edition of Scott’s textbook (the 1923 edition of which is cited here) but not in the 1900 edition, where Brongniartian seed-coat terminology is used (p. 438).

Two further terminological digressions seem desirable: First, if gymnospermous seeds are regarded as consistently unitegmic (Bold et al., 1980; Corner, 1976; Foster and Gifford, 1974; Leisman, 1964; Oliver, 1904, 1909; Scagel et al., 1984; Scott, 1923; Scott and Maslen, 1907; Seward, 1917; Stewart, 1983; Taylor, 1965, 1981), they are strictly “testal,” never “tegmic.” In the same context only “testa,” and rarely “tegmen,” has been applied to the seed coat of gymnosperms. It should be noted, however, that some gymnosperms, especially Pteridospermophyta and Gnetophyta, have been interpreted as having bitegmic or even tritegmic ovules and seeds (Datta, 1966; Lawrence, 1951; Quisumbing, 1925, especially for review; Rodin and Kapil, 1969; Schnarf, 1937; Singh, 1978; Sporne, 1965; Trivedi and Singh, 1969).

Secondly, in most gymnosperms the seed coat is divided on largely histological rather than developmental criteria into two and especially three regions, which are either fleshy or stony, and which may be rudimentary or absent (see especially Schnarf, 1937). Some gymnospermous seeds, as those of Thujopsis and Physostoma discussed below, have a strictly fleshy testa. The “fleshy layer” has also been called “flesh,” “soft layer,” “pulpy layer,” “parenchymatous layer,” “papery layer,” “fleshy layer,” etc. In contrast, the “stony layer” (see especially Quisumbing, 1925) has also been designated “stone,” “hard layer,” “bony layer,” “woody layer,” “fibrous layer,” “sclerous layer,” “sclerotic layer,” “sclerenchymatous layer,” etc. In both cases “lining,” “region,” “membrane,” “zone,” “coat,” or “shell” may replace “layer.”

The fleshy layer (both outer and inner) of gymnospermous seeds may contain small amounts of sclerenchyma either as scattered (idioblastic) or clustered sclerenchyma elements (fibers and sclereids), as in the seeds of Gnetum (Rodin and Kapil, 1969; Schnarf, 1937; Singh, 1978; Trivedi and Singh, 1969) and Pachytesta (Taylor, 1965). In view of this, and also the facts that the fleshy layer can be only one or a few cell layers thick, as in the seeds of Cupressaceae (Quisumbing, 1925; Schnarf, 1937), or that the seed coat can consist entirely of parenchymatous cells that are not appreciably succulent, as in the seeds of Thujopsis dolabrata (Schnarf, 1937) and Physostoma (see item “5” below), “fleshy layer”
clearly is used in a somewhat loose sense, essentially one meaning not at all sclerenchymatous, or not appreciably sclerenchymatous.

There are several possibilities for the occurrence of these fleshy and stony layers in the gymnospermous seed, to wit:

(1) An outer fleshy layer, a middle stony layer, and an inner fleshy layer: These layers are often referred to by only or by chiefly these designations, especially in general morphology textbooks (e.g., Bold et al., 1980, except p. 554; Datta, 1966; Foster and Gifford, 1974, except p. 410; Quisumbing, 1925; Scagel et al., 1984; Sporne, 1965, except p. 19; Trivedi and Singh, 1969, except pp. 2, 55–56). However, traditionally these layers have been called, respectively, “sarcotesta,” “sclerotesta,” and “endotesta” (Oliver, 1902: 148; Rodin and Kapil, 1969; Schnarf, 1937; Seward, 1917; Singh, 1978; Stewart, 1983; Taylor, 1965, 1981), with variations as follows: Seward (1917: 27 only), Sporne (1965: 19 only), and Trivedi and Singh (1969: 2, 56 only) replaced “endotesta” with “inner sarcotesta.” Bold et al. (1980: 554 only), Scott (1923), and Scott and Maslen (1907) and usually Seward (1917) and Taylor (1965) replaced “endotesta” with “inner flesh.” Schnarf (1937) usually replaced “endotesta” with “innere fleischige Schichte” or “Innenhütchen.” This is the typical situation in gymnospermous seeds and occurs in cycads, Ginkgo, Cephalotaxus; and many other fossil and extant taxa.

(2) An outer fleshy layer and an inner stony layer: As noted above, Brongniart (1874) and Williamson (1877) called these, respectively, “sarcotesta” and “endotesta,” and Williamson also called them, respectively, “exotesta” and “endotesta” (Williamson, 1876a, b, 1877) or “exotesta” and “sclerotesta” (Williamson, 1876b). However, the more usual designations are, respectively, “sarcotesta” and “sclerotesta” (Schnarf, 1937; Scott, 1923; Scott and Maslen, 1907; Seward, 1917; and others listed in the next paragraph).

(3) An outer stony layer and an inner fleshy layer: Oliver (1902: 148) and Seward (1917: 323–325) called these, respectively, “exotesta” and “endotesta” (but see Williamson’s usage in “2” above). However, these layers have been more typically designated, respectively, “sclerotesta” and “endotesta” or else “sclerotesta” and “inner flesh” (Oliver, 1902: 153, 1904; Schnarf, 1937; Seward, 1917: 326; Singh, 1978; Taylor, 1965).

(4) A single stony layer: As elaborated below, this situation is common for casts of fossil seeds and also is the apparent condition for mature seeds of some extant taxa. The post-1900 paleobotanical literature cited above generally refers to this layer as “sclerotesta.”

(5) A single fleshy layer: This occurs, for example, in the seeds of Thujaopsis dolabrata (Schnarf, 1937) and also in Physostoma, where the integument is parenchymatous and “essentially uniform and nonsclerified” (Leisman, 1964: 1072, for the quotation; Oliver, 1909; Schnarf, 1937: 42; Seward, 1917; Sporne, 1965; Taylor, 1981; Williamson, 1876a, 1877). However, the literature is reticent in applying “sarcotesta” to such cases (see also preceding comments on these taxa), although the original account of Physostoma by Williamson (1877) mentions a doubtful “endotesta.”

In situations “2” and “3” the inner fleshy and outer fleshy layers, respectively, are frequently artfactually absent in fossils due to poor preservation. For example, compare descriptions of the seeds of Pachytesta incrassata or P. olivaeformis (synonyms = Trigonocarpus olivaeformis and T. parkinsoni) having a two-parted (Brongniart, 1874; Williamson, 1876b, 1877—see above) versus a three-parted integument (Schnarf, 1937; Scott, 1923; Scott and Maslen, 1907; Seward, 1917; Sporne, 1965; Taylor, 1965), the latter based on more recent findings. In extant taxa, and conceivably in extinct ones, the fleshy layer may be rudimentary or developmentally absent, for instance, the rudimentary outer fleshy layer in Pinus and many other conifers versus this layer absent in the taxads (Bold et al., 1980; Foster and Gifford, 1974; Oliver, 1902; Quisumbing, 1925; Schnarf, 1937; Singh, 1978; Trivedi and Singh, 1969). In addition, in situation “2” the inner fleshy layer (endotesta) may be present in both fossil and extant taxa but may, especially in evolutionary discussions.
Terminological recommendations. — Because “sarcotesta,” “sclerotesta,” and “endotesta” (or comparable terms, as noted above) are purely descriptive designations, with no real developmental basis, I feel that they should be applied from a strictly topographic viewpoint, with no implications about phylogeny or homology. Thus, if the seed coat (testa) is three-parted, as it typically is in gymnosperms, then “outer fleshy layer,” “middle stony layer,” and “inner fleshy layer” (or their comparable vernacular expressions, as noted above) or, preferably, their respective equivalents of “sarcotesta,” “sclerotesta,” and “endotesta” can be used. If the seed coat is two-parted, either artificially or naturally so, then “sclerotesta” or “stony layer” can be used for the sclerenchymatous layer, depending whether the parenchymatous layer is external or internal to the former, then, respectively, “sarcotesta”/“outer fleshy layer” or “endotesta”/“inner fleshy layer” can be used. And if the seed coat is one-parted, either artificially or naturally so, then “sclerotesta” or “stony seed coat” (“stony testa”) can be used if the testa is sclerenchymatous whereas “sarcotesta” or “fleshy seed coat” (“fleshy testa”) can be used if the testa is not at all sclerenchymatous, or not appreciably sclerenchymatous.

Terminological ramifications. — The preceding usage for “fleshy layer” and especially “sarcotesta” is, as warned above for the former term, applied in a somewhat loose sense. In addition, the usage for “sarcotesta,” “sclerotesta,” and “endotesta” need not imply anything about homology, for example, in a sclero-endotestal seed that the sclerotesta is necessarily derived from the sarcotesta. And finally, such usage for these testal terms would bring their application (but not especially nomenclature) in line with the “exocarp” (“epicarp”), “mesocarp” (“sarcocarp”), and “endocarp” (“sclerocarp”) of fruit morphology and anatomy (see especially de Candolle, 1827, 1841, who perhaps originated “mesocarp”; Cutter, 1971; Esau, 1965, 1977; Fahn, 1982; Richard, 1808, 1811, 1819, who proposed “epicarp,” “sarcocarp,” and “endocarp”; Roth, 1977; Schmid, 1982).

A Classification of Angiospermous Seed Coats Based on Corner: Explanation and Caveats

With Corner’s (1976) seed-coat terminology and the preceding discussion in mind, the key in Table 1 can be presented for the classification of seeds according to the histology of their seed coat (see also Figs. 1–8). The use of this key requires several explanations and caveats:

1. While the classification in Table 1 follows that in Corner (1976: 10 left especially, also right 10–18 and 46–47), I have clarified items, rearranged phrases, and used terminology that is more accurate from an anatomical viewpoint (e.g., Esau, 1965, 1977; Fahn, 1982), for example, the use of “tracheoid” versus “tracheidal” (see note 6 in Table 1) or the use of “helical” for reference to structures circling the surface of a cylinder versus “spiral” for reference to structures circling around from a central point.

2. My classification of seed coats is more complete than Corner’s (1976: 10), which dealt solely with bitegmic seeds, and which is equivalent only to Part IIB2 in Table 1. I have added entries for unitegmic seeds, sarcotestal seeds, and seeds lacking a mechanical layer, and, as elaborated in comment #5 below, also include monocotyledonous seeds. Although Corner had extensive treatment of sarcotestal seeds (see above and also, for an opposing viewpoint, van der Pijl, 1982), he included little about seeds lacking a mechanical layer (see note 3 in Table 1) or about unitegmic seeds. Bouman and Schier (1979) and
Singh and Dathan (1980) remarked on Corner's neglect of, and disinterest in, the unitegmic and sympetalous families of dicotyledons. The intimation from Corner (1976: 49) is that, by fiat, unitegmic seeds have strictly a testa and that the “testal” terminology in Part IIB2a of Table 1 can thus be applied to them. However, Corner (1976: 49) commented that on developmental grounds unitegmic seeds “can be called exotestal.” There is, in fact, no reason why unitegmic seeds should be excluded from the classification in Table 1 or why all of its “testal” terminology cannot be applied to them. After concluding this, I was gratified to read that Singh and Dathan’s (1980) paper arrived at the same conclusion. In addition, these workers called attention to the mesotestal seeds of Bignoniaceae, Caprifoliaceae, and Verbenaceae, to which might be added Acanthaceae, Apocynaceae, Loganiaceae, Martyriaceae, Polemoniaceae (Cobaea), Scrophulariaceae, and Solanaceae (Bouman and Schier, 1979; Corner, 1976, especially p. 50; Netolitzky, 1926), but, contrary to Corner, not Convolvulaceae (see Bouman and Schier, 1979). Another argument favoring the inclusion of unitegmic seeds in Corner’s classification is, as noted by Singh and Dathan (1980), their occurrence in many predominantly bitegmic families (see especially Bouman, 1974, 1978; Bouman and Calis, 1977; Corner, 1976; Dahlgren, 1975; Eames, 1961; Netolitzky, 1926).

Compared to the classification in Table 1, Corner (1976: 10, 46–47) more formally recognized distinct histological seed types for both the position and the structure of the mechanical layer, the latter being of secondary importance. That is, Corner placed the “(a),” “(b),” “(c),” and “(d)” entries in Table 1 on separate lines. In contrast, I have run these together, and have also added to the six main seed-coat types in Part IIB2 of Table 1 the word “etc.” For each of these six types there certainly must be other structural possibilities than the “(a),” “(b),” etc., situations noted. There is no point in the present state of still very inadequate knowledge of seed-coat histology of conveying that there are only these few stated cases for the nature of the mechanical layer.

In fact, Corner himself was at times erroneous, inconsistent, or incomplete. For example, Knema laurina has an endotestal-exotegmic seed (Fig. 8) with an exotegmic layer of sclerotic cells and an endotestal palisade, which was incorrectly captioned as “exotestal” in Corner’s Fig. 414. The exotegmic characterization is from the caption to Corner’s Fig. 414; in contrast, his text description on p. 200 refers to the outer epidermis of the tegmen as “a narrow layer of longitudinally elongate, lignified, tracheidal cells with transversely pitted walls.” Neither the text nor the caption possibility noted for the exotegmen actually appear in Corner’s key (Corner, 1976: 10) or in the derivative version in Table 1, that is, entry IIB2b1 therein.

Moreover, it is clear from Corner’s detailed discussion (his pp. 10–47) of familial relationships and of the six main seed-coat types listed in Part IIB2 of Table 1 that additional subtypes based on structure of the mechanical layer do occur, for example, cuboidal sclerotic cells in the exotesta, tabular cells with stellate-undulate facets in the endotesta, or fibers in the endotesta or endotegmen (see especially the outlines of seed-coat types on pp. 12–47 of Corner). Notes 7 and 8 to Table 1 detail additional inconsistencies in Corner’s classification of seed-coat subtypes.

According to Corner (1976: 10), seeds of most taxa can be placed in one of the categories in Part IIB2 of Table 1 because one mechanical layer predominates in the seed. Some seeds, however, have two or more mechanical layers. Such seeds can be referred to by appropriate hybrid terminology, for example, the endotestal-exotegmic seeds (Fig. 8) of certain Geraniaceae and Myristicaceae, including Knema laurina discussed above (Boesewinkel and Been, 1979; Corner, 1976; Netolitzky, 1926). Exo-mesotegmic and meso-endotegmic seeds are shown in, respectively, Figs. 5 and 6. Additional examples are the mesotestal-exotegmic seeds of Punica and the exo-mesotegmic seeds of Carica discussed earlier under “sarcotesta.” Corner (1976: 46–47) has yet other “hybrid” examples, for example, his “exo-mesotestal,” his “exotestal-endotestal,” and his “exotegmic and endo-
tegmic.” I would shorten the latter two types to, respectively, “exo-endotestal” and “exo-endotegmic.”

(5) Although Corner’s classification of the seed coat (Table 1) was formulated with specific reference to the dicotyledons, it can also be applied to the monocotyledons, as suggested by Corner (1976: 10) himself. Monocotyledons, however, exhibit much less structural diversity of the seed coat, according to Corner, having exotestal and endotestal seeds but few, if any, tegmic ones. Dahlgren and Clifford (1982) and Dahlgren et al. (1985) used various seed characters in their comparative survey of the monocotyledons, and the latter adopted Corner’s testal-tegmic subdivision of the seed coat (but see end of second section). However, they did not use other terminology of the seed coat sensu Corner (“exotesta” in Dahlgren et al., 1985: 277, seems a slip for “sarcotesta”—see, e.g., pp. 16 and 280), even though Dahlgren has extensively used Corner’s data and terminology elsewhere, for example, in Dahlgren and Thorne (1984). Cronquist’s (1981) recent compilation is also not helpful in this respect. Surprisingly, Boesewinkel and Bouman (1984) likewise did not use monocotyledenous examples with Cornerian seed-coat terminology. However, a recent work on Marantaceae (Grootjen, 1983) is distinctive in its use of Cornerian seed-coat terminology.

(6) Finally, Corner’s classification of the seed coat and Table 1 are based on analysis of the mature seed, which, of course, is the only thing possible with herbarium material and even most pickled material. However, as elaborated below, developmental studies are really essential because ontogenetic events may lead to histological endpoints that are not necessarily indicative of the apparent situation in the mature seed.

**Summary Discussion**

Although a number of reviews of Corner’s 1976 work have appeared (see Appendix), and although his work is now frequently cited (e.g., see *Science Citation Index*), there has been little critical, in particular negative comment, on Corner’s classification of the seed coat as outlined in Table 1. Bouman and Schier (1979) and Singh and Dathan (1980), who were discussed in the preceding section under comment #2, and Boesewinkel and Bouman (1984), who are discussed below, are important exceptions in this respect. In contrast, almost all of the significant criticism of Corner’s book has applied to his fervent espousal of his exotic “durian theory” or to his views on the relationships of dicotyledonous taxa.

Nevertheless, Bouman (1974: 27, 1978: 21–22) in his masterful review of the studies of the ovule and seed noted that “the two layers [of the seed coat] have mostly been indiscriminately called testa and tegmen . . . , and they were erroneously [my emphasis] interpreted as derivatives of the outer and of the inner integument, respectively.” Bouman (1974: 28, 1978: 22, quotation from the former) continued:

> It is clear that only a global comparison and identification is possible and that a careful checking of the writings of each individual worker and of every single described species of seed is required before the true morphological status of the recognised layers (in terms of derivation from, or a complete or partial identity with, the outer or inner integument, the nucellus or perisperm, the endosperm, and/or the embryo) can be established. However, most of the early introduced terminologies were not or [else were] badly defined, and the classificatory criteria contradictory and often almost exclusively founded on differences in texture (consistency), and the more or less easy mechanical separation into two or more concentric layers, of the envelope of ripening or mature seeds.

After pleading for more developmental studies of ovular and seminal structures Bouman (1974: 163–164) concluded that:

> In detailed embryological descriptions the use of such terms as the outer epidermis, the subdermal cell layers, and the inner epidermis of the integuments or of the testa, must be avoided if these qualifications are not based on ontogenetic studies. . . . Characters derived from the structure of the
mature seed coats are of doubtful taxonomic significance at and above the family level, unless they are amplified by developmental studies, because seemingly identical structures may originate by different ontogenetic pathways.

Similarly, Bouman and Schier (1979: 468) concluded for the unitegmic and sympetalous families of dicotyledons, and by implication for the angiosperms in general, that the great diversity of cell shape and of cell wall thickenings of the seed coat “can be of great help at the specific and generic level, but fails as a marker of the evolutionary lines at the familial and ordinal levels.”

For example, the ovule of angiosperms could be fairly easily unitegmy by developmentally (1) by the fusion of two integumentary primordia, which is possible only if the two integuments have the same mode of initiation, or (2) by the simple elimination of one of the two integuments by retarding or completely suppressing its development (Bouman, 1974: 163, 1984; Bouman and Calis, 1977; Bouman and Schier, 1979). These are, in fact, the two classical explanations for the origin of unitegmy from bitegmy (previous references; Bhojwani and Bhatnagar, 1978; Corner, 1976; Dahlgren, 1975; Eames, 1961; McLean and Ivimey-Cook, 1956; Netolitzky, 1926). However, as recently proposed by Bouman and Calis (1977—see also Bouman, 1984; Bouman and Schier, 1979), a third phyletic pathway might lead to unitegmy by a complex process involving (a) fusion of the two integumentary primordia into an at least partly common structure, (b) a developmental shifting of the inner integument in relation to the outer one and toward the micropyle, that is, a shifting caused by the periclinal divisions of the subdermal cells underlying the dermal initials of the inner integument, and (c) an arrested development of the inner integument. Bouman (1984), Bouman and Calis (1977), and Bouman and Schier (1979) called this third phyletic pathway one of “integumentary shifting,” in essence a process involving a dermal inner integument and a subdermal outer integument. The implication, of course, is that the unitegmic condition is not homologous throughout the angiosperms or even at lower ordinal, familial, and perhaps tribal levels (Bouman, 1984; Bouman and Calis, 1977).

Furthermore, if during the development of a bitegmic ovule into the seed, the outer integument becomes completely crushed and resorbed and the mechanical layer develops in the inner integument, what is really a tegmic seed would be characterized as a testal one. This would again raise the possibility of false homologies.

The aforecited statements of Bouman (1974, 1978; Bouman and Schier, 1979) and these developmental considerations cast some serious doubt on Corner’s classification of seed coats as presented in Table 1. However, until his recent review paper (Boesewinkel and Bouman, 1984), Bouman (1978; Bouman and Calis, 1977; Bouman and Schier, 1979; other works—see bracketed information in citation for Bouman, 1974) did not specifically criticize Corner’s classification of seed-coat types. Recently, however, Boesewinkel and Bouman (1984: 585) briefly criticized Corner as follows:

It is often very difficult to classify seeds in one or the other category [of Corner]. Frequently, there is more than one sclerenchymatous layer in the seed-coat, and several combinations are possible. There are no absolute criteria to distinguish the various layers. A slightly thickened outer layer of the testa of a relatively undifferentiated seed-coat is described as exotesta, whereas a similar layer in a seed-coat with well-developed endotesta (or other layer) is disregarded. Moreover, the function of layers with thickened cell walls is not restricted to mechanical protection, but may also be the exclusion of water, oxygen, microorganisms; and water storage or slime protection.

Boesewinkel and Bouman (1984) surprisingly did not use criticisms based on developmental criteria such as the above, other than their implication (p. 575) that developmental “knowledge is especially important for a correct interpretation of the mature seed-coat” because “seemingly identical structures may arise along different ontogenetic pathways.” Other than these criticisms and the aforenoted ones (see comment #2) about Corner’s neglect of
unitegmic seeds, no one else (see reviews in Appendix and references in Science Citation Index) has specifically criticized Corner's classification of seed-coat types.

Corner's classification then, like many another classification, is one of utility, of appreciable usefulness. As is the general case with almost all classifications involving many taxa, the general restriction to herbarium material and even much pickled material means that mature structures will play a predominant role in the classificatory criteria. Corner's classification of seed coats may well be refined by developmental studies, but it is unlikely to be superseded for quite some time. Nevertheless, there is, as discussed above, the prospect of different ontogenetic pathways yielding similar or identical structures. Hence Corner's classification should be applied judiciously, particularly at the higher taxonomic levels. Its value at familial levels and above may be more in indicating negative relationships due to structural dissimilarity than in implying positive relationships due to structural similarity.

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Appendix: Reviews of Corner (1976)
The following is a list of reviews of Corner's (1976) book. For research reports and literature reviews commenting on Corner (1976) see the discussion in text and citations in Science Citation Index.


Literature Cited


Note added in proof: Professor Corner informed me (Jan. 1986) of the tritegmic seeds of Annonaceae. Here “the middle integument appears to be unique in angiosperms and connected, perhaps, with the perichalazal structure” of the ovule (Corner, 1976:69). Table 1 did not allow for such tritegmic ovules and seeds, which, however, can be keyed out as bitegmic ones.