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The fruit of *Commiphora*

J. J. A. VAN DER WALT

SUMMARY

The fruit anatomy of *Commiphora* is described in detail and the morphological nature of the pseudo-aril is clarified. By correlation of fruit and flower characters, phylogenetic deductions are drawn.

RÉSUMÉ

L'anatomie du fruit de *Commiphora* est décrite en détail. La nature morphologique du faux-arille est clarifiée. Des conclusions d'ordre phylogénétique sont déduites à partir des caractères floraux et carpologiques.

Commiphora is the largest of the 16 genera of the *Burseraceae* recognized by Lam (1932). It consists of circa 200 species which are mainly confined to the continent of Africa and Madagascar. The genus is particularly well represented in Somalia, Kenya and Tanzania. The 26 species described from Madagascar and the Mascarenes are all endemic. In South Africa 18 species occur (Van der Walt, 1973), and in South West Africa at least 25 species, several of which are endemic.

The plants are dioecious or polygamous shrubs or trees of variable height, but most of the trees are relatively small. A peeling or flaking bark is a characteristic feature of many species. The leaves are simple, unifoliate, trifoliate or imparipinnate.

Morphology of the fruit

The fruit of *Commiphora* (Plate Ia) is an ovoid, ellipsoid or subglobose drupe of 0.4-3 cm in diameter. The two valves of unequal size are fused along a conspicuous seam (in a few species there are four valves and thus two seams). At maturity the fruit splits into two (four) valves at the seam, and the stony putamen, usually with a bright-coloured, fleshy, aril-like investment, becomes evident. The putamen itself also consists of two fused parts of unequal size and it is usually ovoid, ellipsoid or subglobose. The one face of the putamen is usually more convex than the other. The surface of the putamen can be smooth, rugose or even lumpy rugose in some species.

Oliver (1894) was the first to name the aril-like structure a pseudo-aril. It is usually reddish in colour, but an orange or yellow pseudo-aril is not uncommon. According to Ridley (1930) these are also the most common colours of true arils. The colour of the pseudo-aril contrasts well against the usually dark colour of the putamen, and is probably very conspicuous and attractive to birds. The pseudo-aril undoubtedly plays the same rôle in the dissemination of the seeds as a genuine aril.

Richard (1819) described the pericarp of fruit and its parts in general. He defined the epicarp of the fruit as the outer epidermis, the endocarp as its inner epidermis, and the intervening parenchymatous tissue as sarcocarp. In drupaceous fruits, such as the peach, he viewed the pit (putamen) as being composed of the endocarp united with an indurated portion of the sarcocarp. Afterwards the whole stony region of the drupe has come to be called endocarp, the fleshy part as the mesocarp and the skin, consisting of the epidermis and hypodermal layers, as the exocarp (Eames & MacDaniels, 1947; Esau, 1965).

Anatomy of the mature fruit of Commiphora

The epidermis is covered with a cuticle of variable thickness. Trichomes in the form of glandular and non-glandular hairs are present in some species. The hypodermal layers usually consist of collenchymatous cells, some of which contain druses of calcium oxalate, other secretions or plastids.

There is no sharp demarcation between the exocarp and mesocarp (Plate Ib). The mesocarp is composed of large, loosely packed parenchymatous cells which often contain secretions. The spongy texture of the mesocarp is due to this parenchymatous tissue with large intercellular spaces. Large resin canals occur in the outer part of the mesocarp and in the inner part are the vascular bundles, arranged in one or two circles as seen in transverse section of the fruit (Plate IIb).

The mesocarp is separated from the cells of the pseudo-aril by a separation layer consisting of two or three layers of small elongated cells. In a transverse section of the fruit two expansions of the separation layer can be observed at two opposite poles, stretching through the mesocarp to the exocarp (Plate IIb). The cells of the separation layer disintegrate in the ripe fruit, causing the splitting of the valves.

The relatively large, thin-walled, parenchymatic cells of the pseudo-aril contain many oil droplets. There is a gradual transition between the cells of the pseudo-aril and the sclereids of the putamen. In the mature fruit the isodiametric sclereids have heavily thickened, lignified walls with numerous simple pits.

Two locules are formed in the young ovary and in each locule two ovules develop (Plate IIa). Usually only one of these ovules in one of the locules develops into a seed. The locule in which the ovule develops, enlarges much more than the other.

Two central vascular bundles, running in a longitudinal direction through the fruit, are present.

Morphological nature of the pseudo-aril

According to the literature, a consensus of opinion has not been reached on the morphological nature of the pseudo-aril. Oliver (1894) concluded that the pseudo-aril is not a distinct layer of the pericarp, but is due to a modification in texture and

substance of the bony putamen itself. Schweinfurth (1899), Engler (1931), Wild (1963) and Merxmüller (1968) designated the pseudo-aril as the mesocarp of the fruit.

An ontogenetic anatomical study of the fruit was made in order to determine the morphological nature of the pseudo-aril. Serial transverse sections of fruits in different stages of development were made.

As common in drupaceous fruits, the sclereids of the putamen are formed by derivatives of the inner epidermis (Sterling, 1953). At a certain stage these inner epidermal cells divide repeatedly forming radial files of cells (Plate IIa). As these cells enlarge, their orderly arrangement becomes obscure (Plate IIb). They gradually develop into sclereids but lignification of their walls takes only place when the fruit is almost mature.

After most of the derivatives of the inner epidermis have been formed, the cells of the pseudo-aril originate. Hypodermal cells beneath the derivatives of the inner epidermis divide and enlarge to form the cells of the pseudo-aril (Plate IIb). These cells can easily be recognized because they are much bigger and more transparent than the surrounding cells.

According to Richard's (1819) definition of the endocarp, the pseudo-aril can not be classified as part of the endocarp since it does not originate from the inner epidermis. Following the broader concept of the endocarp (Eames & MacDaniels, 1947; Esau, 1965), the pseudo-aril can well be designated as part of the endocarp. There is a gradual transition between the cells of the pseudo-aril and the sclereids of the putamen, and the cells of the pseudo-aril differ completely from the rest of the mesocarp.

From a functional point of view it is of vital importance that the pseudo-aril remains firmly attached to the putamen, otherwise it will easily be loosened by birds, with the result that seed dispersal will not take place.

Taxonomic and phylogenetic significance of the fruit

Engler published several classification systems of *Commiphora*, the last to appear in 1931. Although Engler based the ultimate division of his 43 sections mainly on leaf characters, he already realized the taxonomic importance of the pseudo-aril. The variable structure of the pseudo-aril was used as a criterion for distinguishing between two of the sections. Wild's (1959) classification, however, was mainly based on fruit and flower characters, with the pseudo-aril as the most significant fruit character.

The following fruit characters are used in the classification of the genus:

1. Number of valves in which the mature fruit splits;
2. Shape and size of the fruit;
3. Indumentum of the fruit;
4. Shape and surface of the putamen;
5. Colour and structure of the pseudo-aril; a synopsis of the variable structure of the pseudo-aril is tabulated in Figure 1.




















Subgen. <i>Opobalsamum</i>			?
Subgen. <i>Commiphora</i>			
Sect. <i>Coriaceae</i>	Subsect. <i>Ranganae</i>		
	Subsect. <i>Teretifoliolatae</i>		
Sect. <i>Spondioideae</i>	Subsect. <i>Glaucidulae</i>		
	Subsect. <i>Cupulares</i>		
	Subsect. <i>Pruinosae</i>		
Sect. <i>Commiphora</i>	Subsect. <i>Latifoliolatae</i>		
	Subsect. <i>Ugogenses</i>		
	Subsect. <i>Pedunculatae</i>		
	Subsect. <i>Quadricinctae</i>		
	Subsect. <i>Pyracanthoides</i>		
Sect. <i>Rostratae</i>	Subsect. <i>Madagascarienses</i>		
Sect. <i>Africanae</i>			

Fig. 1. — Schematic representation of the basic types of pseudo-arils and flowers occurring in the categories recognized by Wild (1959).

As shown in this table (Fig. 1), there is a definite and natural relationship between the type of fruit and the type of flower. The sections *Africanae* and *Rostratae*, as well as the subsections *Madagascarienses* and *Pyracanthoides* of the section *Commiphora*, have a pseudo-aril which covers practically the whole putamen, without distinct arms, or with four (or three) arms usually reaching almost to the apex of the putamen. A pseudo-aril without distinct arms is often relatively thin, sometimes to such an extent in some species, that it appears to be absent. In the cases where the pseudo-aril forms arms, additional isolated fragments of pseudo-aril tissue are often present. The flowers of these two sections and subsections are bisexual or unisexual and hypogynous with a free intrastaminal disc.

The remaining four subsections of the section *Commiphora*, i.e. the subsections *Quadricinctae*, *Latifoliolatae*, *Ugogenses* and *Pedunculatae*, have a pseudo-aril which

forms two long commissural arms and two (or one) shorter facial arms. The flowers are predominantly unisexual but bisexual flowers are also present. Most flowers are hypogynous with a free disc, but a few species possess a transitional type of flower in which the lower part of the disc is fused with the calyx tube and the upper part free.

The section *Spondioideae* has a cupular pseudo-aril which covers the lower part of the putamen. The flowers of this section are all unisexual and perigynous with the disc adnate to the calyx tube.

In most members of the subsection *Pruinosae* the pseudo-aril forms two commissural arms. Other members of the *Pruinosae*, as well as the subsection *Cupulares*, have a pseudo-aril with a lobed or sinuate margin. A number of species of the *Pruinosae* have flowers with only four stamens instead of the normal number of eight. The pseudo-aril of the subsection *Glaucidulae* forms two facial lobes. In some species these lobes are relatively large and thin. The putamen of the *Glaucidulae* is characteristically flattened and the flowers are characterized by a poorly developed or even undeveloped disc.

The main fruit feature of the section *Coriaceae* is the absence of a pseudo-aril in both the subsections *Rangeanae* and *Teretifoliolatae*. The flowers of the *Coriaceae* are unisexual and perigynous with the disc adnate to the calyx tube.

Wild's (1959) division of the genus into the subgenera *Commiphora* and *Opobalsamum* is largely based on the number of valves in which the fruit splits at maturity. In the subgenus *Commiphora* it splits into two valves and in the subgenus *Opobalsamum* (circa 13 species) into four valves. The pseudo-aril is apparently absent in the subgenus *Opobalsamum*. Unfortunately no flowers of this subgenus have been studied by the writer.

Conclusions

1. The hypogynous flowers of the sections *Africanae*, *Rostratae* and *Commiphora* are often bisexual and they possess a fleshy disc which is not adnate to the perianth. The perigynous flowers of the sections *Spondioideae* and *Coriaceae*, on the other hand, are always unisexual (probably by reduction since rudimentary organs exist) with the disc adnate to the calyx tube, or even completely absent. It seems likely to conclude that the flowers of the sections *Africanae*, *Rostratae* and *Commiphora* are on a whole more primitive than those of the sections *Spondioideae* and *Coriaceae*.

2. If the most primitive type of pseudo-aril should be sought among the present day species of the sections *Africanae*, *Rostratae* and *Commiphora*, it seems reasonable to choose one from the section *Africanae* which is very thin and covers most of the putamen. It is interesting that this is also the type of pseudo-aril which Engler (1931) visualized as the most primitive one. The first evolutionary tendency was probably the development of a more fleshy structure, and this was possibly followed by a reduction in size of the pseudo-aril. The reduction in size could have led to the formation of forms with arms (section *Commiphora*), then to forms where the pseudo-aril is largely restricted to the lower part of the putamen (section *Spondioideae*), and finally to the forms where no pseudo-aril develops (section *Coriaceae*). The isolated fragments of the pseudo-aril present in some members of the sections *Africanae* and *Pyracanthoides* could be considered as remnants which resulted by reduction.

3. The geographical distribution of members of the section *Africanæ*, may confirm the theory of its primitiveness. Species such as *Commiphora africana* (A. Richard) Engler and *C. schimperi* (O. Berg) Engler are extremely widely distributed. *C. africana* has been reported from more than 30 countries in Africa.

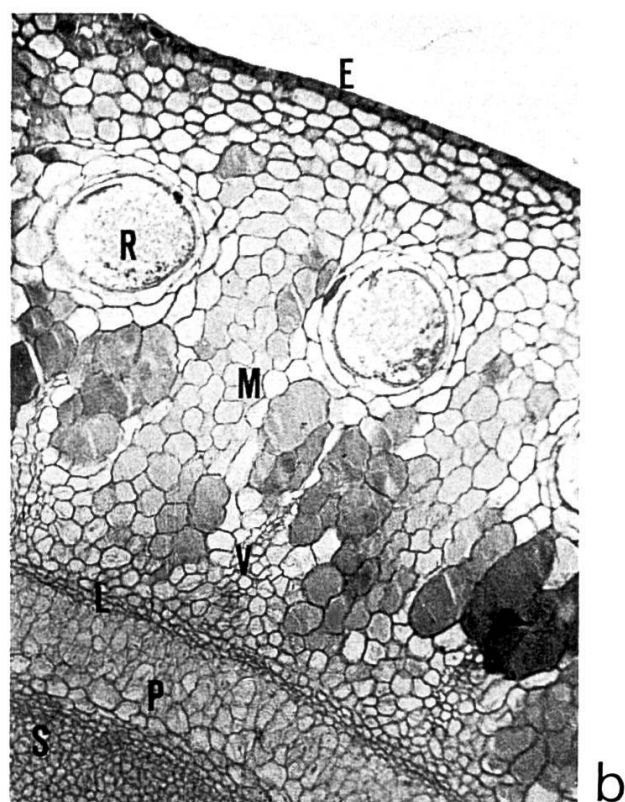
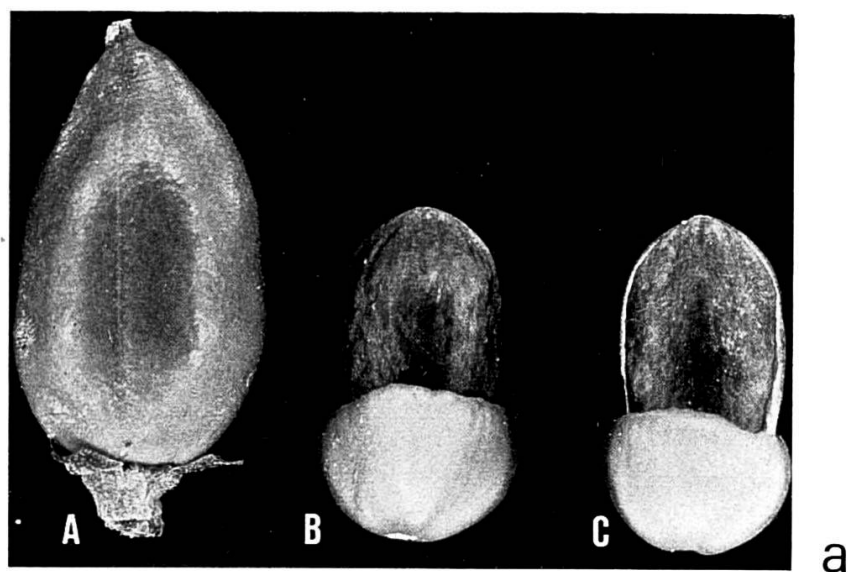
4. So far I have studied the flowers and fruits of circa 40% of the described species of *Commiphora*. Much more information is needed to draw more confident conclusions on the phylogeny of this genus. With the information at present at my disposal, however, I can not agree with the evolutionary lines proposed by Wild (1959). He concluded that the subsection *Cupulares* represents the most primitive forms as far as the present day species are concerned.

Acknowledgements

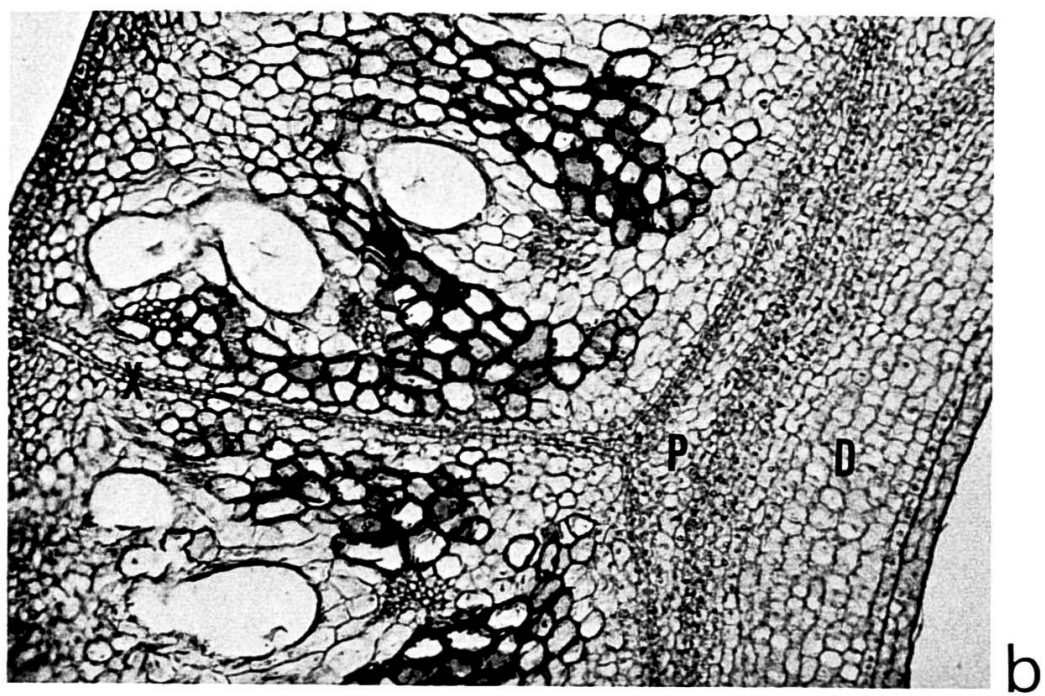
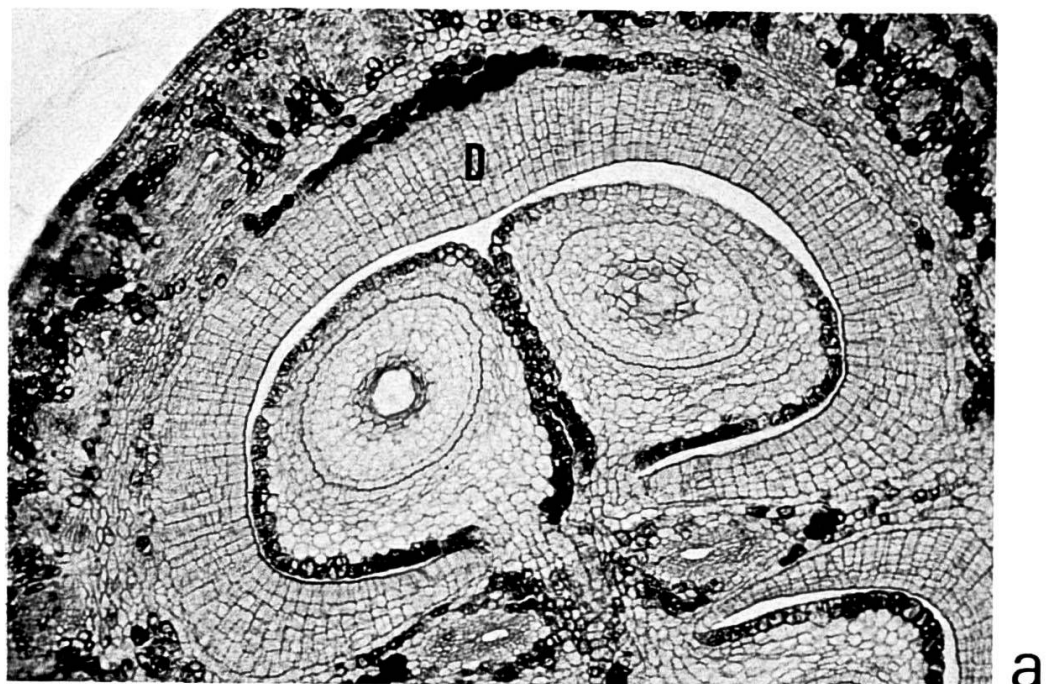
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a, fruit of *Commiphora saxicola* Engler.
A, side-view of the mature fruit; B, view of the more convex face of putamen with pseudo-aril; C, view of the less convex face of putamen with pseudo-aril.
b, transverse section of the pericarp of the almost mature fruit of *Commiphora namaensis* Schinz.
E, epidemis; L, separation layer; M, parenchymatous mesocarp; P, cells of pseudo-aril; R, resin canal; S, developing sclereids of putamen.



a, transverse section of the ovary of *Commiphora pyracanthoides* Engler.
 b, transverse section of the young fruit of *Commiphora pyracanthoides* Engler.
 D, derivatives of the inner epidermis; P, developing cells of pseudo-aril; X, expansion of separation layer.