

# Santalales-Studies V-VIII

By

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## Preliminary Observations

“ ... it should be realised that botany is no longer in need of hasty mediocre work and, furthermore, that the merit of these works lies essentially in the amount of critical, original observation they contain and in the love and care with which they have been polished.”

VAN STEENIS 1954

If useful results are to be obtained in the phylogenetic and classificatory studies, then today a thorough and evenly comprehensive recording of as many features is necessary. Premature syntheses due to studying only single character complexes might throw some highlights, but they bring no real progress in the understanding of the phylogenetic relationships. In order to draw reliable conclusions to some extent in the evaluation of the developed criteria of Phanerogams, those of anatomy, embryology and palynology can not be avoided alongside the classic morphology. Thus, accordingly such studies are long and tedious.

With the aim of gaining material for a phylogenetic and classificatory new assessment of the order Santalales, in 1957 we began to publish our Santalales studies. Previously published:

- I. Zur Stellung der Gattung *Okoubaka* Pellegrin et Normand. 1957
- II. *Daenikera*, eine neue Santalaceen-Gattung. 1957<sup>1</sup>
- III. *Amphogyne*, eine weitere Santalaceen-Gattung aus Neukaledonien. 1957<sup>1</sup>
- IV. Revisio Anthobolearum. 1959

Now may be presented four additional posts. A 1960 study trip was made possible by a subsidy of the Foundation for Scientific Research at the University of Zurich to the herbaria of Kew, London, Edinburgh and Paris and stays in Geneva and Paris in 1961 have contributed to obtaining the data provided herein.

Since the end of 1960 our research program is supported by the Swiss National Fund for Scientific Research. The Georges and Antoine Claraz-donation supported the publication of this work by a publication contribution. We thank all these institutions as well as the boards of herbaria and libraries, which enabled our studies by sending material, information and loans.

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<sup>1</sup> Together with H. HÜRLIMANN

The anatomical studies of the spicular cells the Couleae were performed by Dr. Marie-Anne GUTZWILLER. My wife, Lisa Maria Stauffer Imhoof, has created all drawings under my guidance. I am very grateful to my two employees for their constant support during the progress of these investigations.

Professor Dr. F. MARKGRAF, who introduced us to and made available for our work the Santalales Researches herbarium, library and laboratories of the Botanical Museum of the University of Zurich, and finally a release from the Botanical Museum is especially thanked.

### **African Santalaceae I: *Osyris*, *Colpoon* and *Rhoiacarpos*** (*Santalales*-Studies V)

When trying to gain from the literature an overview of the Africa Osirideae genera, I came across disagreements and contradictions; to clarify these is the purpose of the present study.

Osyrideae, found in Africa north of the Sahara, has only the genus *Osyris* L. with two species. South of the Sahara, *Colpoon* was the first genus to be described and illustrated by BERGIUS in 1767 from the Cape area with the species *C. compressum*. MURRAY 1774 directed the same plant to the new genus *Fusanus* as a single species (*F. compressus*). In 1814 R. BROWN mentioned an Osyrideae from Ethiopia as *Fusanus alternifolius*, but without description. In 1838 by Harvey the next *Fusanus* appears as another genus *Hamiltonia* MUHLENB., who said *H. capensis* is rewritten as a representative of this other American genus of the Cape. A species of the genus *Osyris* was validly published in 1851 by A. RICHARD as *O. abyssinica* HOCHST.; to HOCHSTETTER this was also expected to be a synonym of *Fusanus alternifolius* R. BR.

In 1857 ALPH. DE CANDOLLE mentions for Africa under *Osyris* Section I. *Euosiris* three species, of the genus *Colpoon* he draws as a Section II under *Osyris*, *Hamiltonia capensis* HARVEY which is the type of a new genus: *Rhoiacarpos* A. DC.

BAILLON 1862/63 again places *Colpoon* next to *Osyris*, in contrast includes *Rhoiacarpos* in *Colpoon*; he therefore expects two species in this genus. In 1880 BENTHAM (in BENTHAM et HOOKER) follow him, who also mentioned *Colpoon* with two species and (p. 226) remarked this: "*Colpoon*, Berg., by Brown connected with *Fusanus*, by Candolle with Osyride, by Baillon with *Rhoiacarpos*, and almost all of equal rights, the genera for sections *Acanthosyris*, *Santalum*, *Comandra*, *Fusanus*, *Midas*, *Colpoon*, *Rhoiacarpos* and *Osyris* very much related to each other, the sections better considered a single genus, however, it can hardly be expected for botanists to take *Santalum album* as a form of *Osyris*, versus *Osyris alba* as a species of *Santalum*, and we are forced to admit that there are several characteristics of lesser importance separated."

Important also appears a remark by this author under *Osyris* (p. 227): "*O. abyssinica*, Hochst., frequent enough in Natal southern Africa, in herbaria is often confused with *Colpoon compressum*, but can easily be distinguished from known genera by the alternate leaves and the very often 3-merous flowers."

By contrast, SIM in 1907, in turn, mentioned that *Colpoon* has two types and that he could find no separating genus or species differences between *Colpoon compressum* and *Osyris*.

HILL, the editor of Santalaceae for the Flora Capensis, discussed in 1915 the Osyrideae genera of the Cape flora and says (p. 100): "In the forthcoming volume of the Flora Capensis it has not been found possible to uphold Bergius' genus *Colpoon*; the character of the opposite leaves is far from constant, and on the same specimen leaves may be found arranged in opposite or subopposite pairs or they may be more or less alternate. In the floral characters no difference

can be noticed between plants with alternate leaves placed under *Osyris abyssinica*, Hochst., and those with more or less opposite leaves formerly placed under *Colpoon compressum*, Berg. The leaves in all specimens are flat, glaucous or gray-green and very variable in shape with mucronate apices; the inflorescences are as a rule axillary and inconspicuous, and there is no distinction between the fruits of the plants which have been assigned to the two genera." Accordingly, we find in the Flora Capensis *Colpoon compressum* synonymous with *Osyris abyssinica*, while the genus *Rhoiacarpos* is resumed.

SPRAGUE and SUMMERHAYES 1927 (S. 194) observed: "*Colpoon* is undoubtedly related to *Osyris*, to which it has been reduced by some authors, and *C. compressum* indeed resembles *O. abyssinica* so closely that it has sometimes been regarded as a mere synonym. The sessile stigma of the former, however, afford a distinguishing character which may be utilised even in the fruiting stage."

PILGER 1935 recorded *Colpoon* (with *C. compressum*) and *Rhoiacarpos* (with *R. capensis*) as monotypic genera of the Cape area, giving *Osyris* with two species of North Africa and two for Africa south of the Sahara (including *O. abyssinica*). This view finds no follower, the newer publications rather referring back to Hill, only nomenclaturally it is properly set as *Osyris compressa* (BERG.) A. DC. instead of *O. abyssinica*. PHILIPS 1951 according lists for South Africa one species each for *Rhoiacarpos* and *Osyris*.

## I.

The first question that arises in these contradictory literature data is this: does southern Africa have two or three *Osyrideae*? DE CANDOLLE, BENTHAM, and PILGER call three, HILL, PHILLIPS and other recent authors two. An investigation of the south African *Osyrideae* materials in the herbaria of Zurich, Geneva, Paris, London and Kew (BM) gave this clarification: There are three species that can be clearly distinguished morphologically and among themselves show no transitions. Table 1, supplemented by pictures, gives an overview of the most important distinctive features of the three taxa, and for the time being shall be referred to as *Colpoon compressum* BERGIUS, *Rhoiacarpos capensis* (HARV.) A. DC. and *Osyris abyssinica* HOCHST. ex A. RICH.

Table 1 Comparison of features of south African Osyrideae

	<i>Osyris abyssinica</i>	<i>Colpoon compressum</i>	<i>Rhoiacarpos capensis</i>
Phylotaxy	spiral 2/5-emplacement	decussate twin whorls, rarely the two leaves somewhat shifted	decussate twin whorls
Shoot construction	± monopodial or sympodial, but then never typical dichasial	typical dichasial	typical dichasial
Leaf	widest at or about the middle; dry flat; at the base wedge-shaped with a narrow short petiole	widest at or about the middle; dry flat; at the base wedge-shaped with a narrow short petiole	widest below the middle dry, slightly curled; at the base cordate, rounded, ± sessile
Inflorescence	axillary; stalked; one-flowered or few to moderately floriferous corymb	terminal panicle, sometimes leafy at the bottom	terminal panicle, sometimes leafy at the bottom
Bracts	abscising	abscising, rarely individually persistent (transitions to true leaves)	persistent
Sexual behavior	Flowers ♀, ♂, on separate individuals	Flowers ♀	Flowers ♀
Tepal number	3 (-4)	4-6	(4-) 5-6
Stigma lobe number (= seed primordium number)	3	4	5
Tepals on the fruit	abscising	abscising	persistent
Disk	three-lobed, flat-spherical	four-lobed, flat	five- to six-lobed, saucer-shaped
Style	long	short	long

Drawing 1. *Osyris lanceolata* HOCHSTETTER and STEUDEL (= *O. abyssinica* HOCHSTETTER ex A. RICHARD)

A-C Foliage leaves, 1: 1 (A: ROGERS 22392, B: DINTER 5508, C: ROGERS 8292)

D Inflorescence ♂, 15 : 2 (GOOSSENS 233)

E Inflorescence ♀, 15 : 2

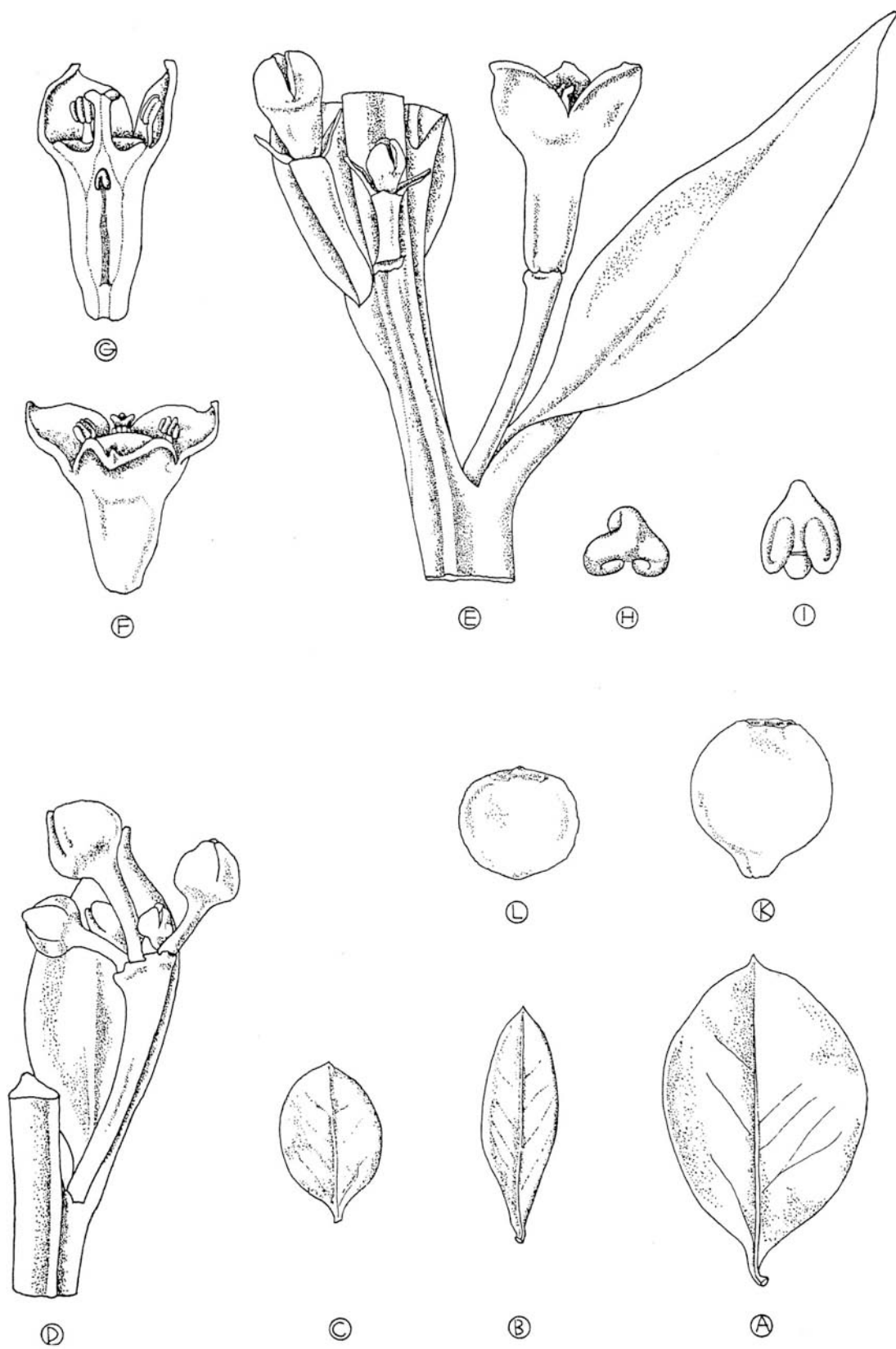
F Flower ♀, 15: 2

G Flower ♂, longitudinal section, 15 : 2

H, I Placenta, 15 : 1

K Fruit, 3 : 1

L Endocarp, 3 : 1 (E-L: DINTER 5508)



## II.

The second question that should be asked is: How are the three species to be distributed among the several genera? This question can only be solved if previously one throws a glance at the significance of the genera within the Santalaceae and specifically the Osyrideae. The genus differences are often slight. Reference should be made to the comment by BENTHAM reproduced above. An example of the subtlety of the generic differences in the Osyrideae was also discussed; it relates to *Santalum* and *Eucarya*. These genera were discussed in detail by SPRAGUE and SUMMERHAYES 1927 together with *Mida*, both SKOTTSBERG 1930 and PILGER 1935 also argue for maintaining all these genera as independent. The differences between *Eucarya* and *Santalum* is based here mainly on the level of development of the disk, the level of abscission of the tepals on the fruit, the style length and the fruit size.

If you look at Table 1, important differences between *Osyris* and the other two genera fall out at once, in the leaf position on the branch system, in the construction and position of inflorescences, and the sexual behavior of flowers. Therefore, an association of *Colpoon* and *Osyris* can not be accepted. If anything, one finds understanding of the union of *Colpoon* and *Rhoiacarpus* according to the actions of BAILLON and BENTHAM. Between these latter Osyrideae representatives are also found, however, on closer inspection, differences that have very similar number of significant conditions as the above between *Santalum* and *Eucarya*. They relate generally to the form of the disk and flower layout, style length and deciduous tendency the tepals and bracts.

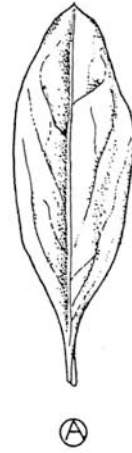
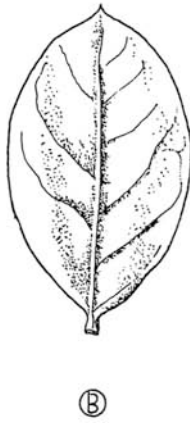
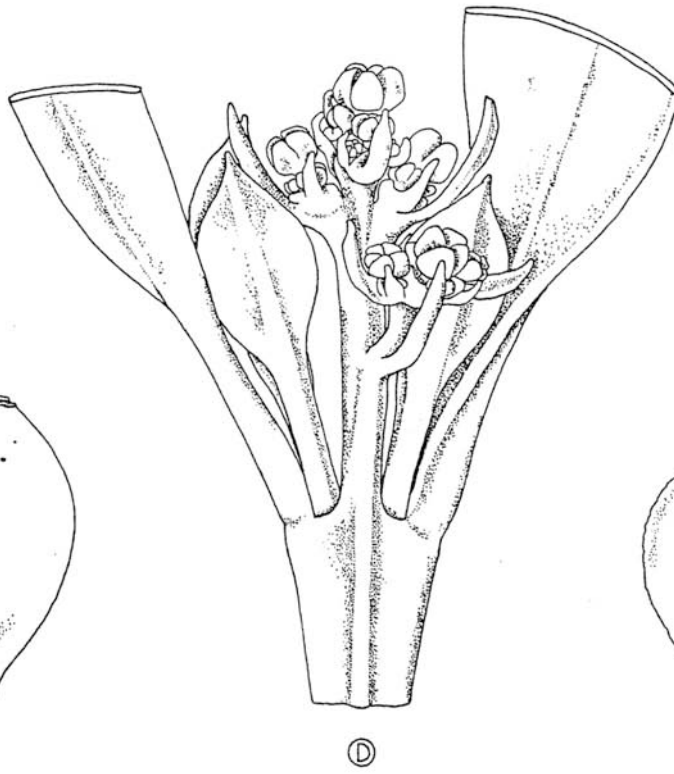
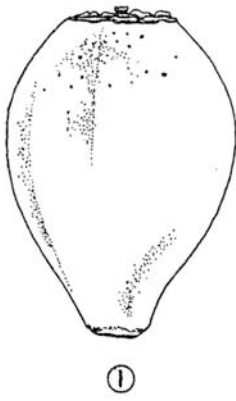
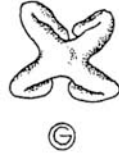
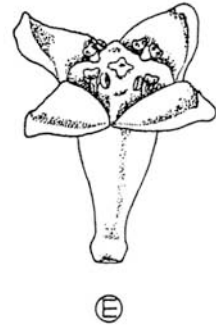
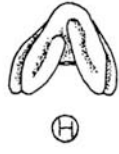
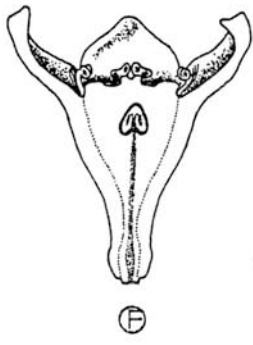
The three South African Osyrideae therefore seem entirely justified as separate genera, as long as one does not decide to make a profound generic reforms within the Osyrideae and to reduce the current twenty-six genera to about fifteen. But neither the consequent nomenclatural changes nor an objective necessity makes such a reform appear desirable, as it would be contrary to the historical development and would actually not do much for the classification, since then within the next conceived genera the former would have to be recognized again as subunits each with characteristic peculiarities.

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### Drawing 2. *Colpoon compressum* BERGIUS

A-C Foliage leaves, 1 : 1 (A: RUDATIS 1128,  
B: SCHLECHTER 286, C: ECKLON et  
ZEYHER 83.6)  
D Young inflorescence, 15 : 2 (EDWARDS  
165)

E Flower, 15 : 2  
F Flower, longitudinal section, 15 : 2  
G, H Placenta, 15 : 1 (E-H: ROGERS 27651)  
I Fruit, 3 : 1  
K Endocarp, 3 : 1 (I, K: BACHMANN 1888)



The second question we posed can therefore be answered, such that for Africa three Osyrideae genera can be expected: *Osyris*, *Colpoon* and *Rhoiacarpos*. While the latter two, as monotypic genera taxonomically and nomenclatural have no difficulties (their species are called *Colpoon compressum* BERGIUS and *Rhoiacarpos capensis* (HARVEY) ALPH. De CANDOLLE), there is a much more complicated situation in *Osyris* that I now want to shed light on.

### III.

For the genus *Osyris* so far no less than sixteen taxa for Africa have been described or indicated which are summarized in Table 2 below.

Table 2. The types of *Osyris* described or specified for Africa

		Types:
1753	<i>Osyris alba</i> LINNÉ	in Herb. LINNÉ
(1814	„Fusanus“ alternifolius R. BROWN nom. nud.	SALT in Herb. BANKS)
1832	<i>Osyris lanceolata</i> HOCHSTETTER and STEUDEL Exsicc. cum descr.	SCHIMPER
1836	<i>Osyris quadripartita</i> SALZ MANN ex DECAISNE	SALZMANN
1851	<i>Osyris abyssinica</i> HOCHSTETTER ex A. RICHARD	SCHIMPER 281
1852	<i>Osyris Wightiana</i> WALLICH ex WIGHT	WALLICH 4036
1857	<i>Osyris quadrifida</i> , SALZMANN ex A. Dc. pro syn.	SALZMANN
1857	<i>Osyris arborea</i> WALLICH ex A. Dc.	WALLICH 4035
1884	<i>Osyris pendula</i> BALFOUR	BALFOUR, COCKBURN and SCOTT 630
1892	<i>Osyris rigidissima</i> ENGLER	HILDEBRANDT 1539
1895	<i>Osyris tenuifolia</i> ENGLER	VOLKENS 1732
1910	<i>Osyris angustifolia</i> BAKER	SCOTT
1910	<i>Osyris parvifolia</i> BAKER	ROHR 84
1925	<i>Osyris urundiensis</i> DE WILDEMAN	?
1932	<i>Osyris densifolia</i> PETER	PETER 2142b
1932	<i>Osyris oblanceolata</i> PETER	PETER 43791
1932	<i>Osyris laeta</i> PETER	PETER 43561

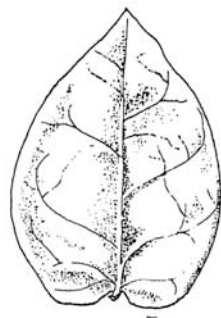
The genus can be divided into two types of inflorescence groups: the first is characterized by leaf-like bracts of the inflorescence which are spirally distributed over the entire length of the axis, so the inflorescences look like short shoots, the ♂ sex as axillary secondary flowers bearing a terminal flower, in the ♀ sex only one terminal flower. This group includes only *O. alba* L.; it comes just north of the Sahara according to Ozenda 1958 in Tefedest and Hoggar.

#### Drawing 3. *Rhoiacarpos capensis* (HARVEY) ALPH. DE CANDOLLE

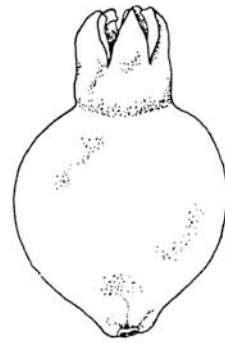
A, B Foliage leaves, 1 : 1 (A:  
SCHOENLAND 579, B: COOPER 52)  
C Young inflorescence, 15 : 2 (ECKLON et  
ZEYHER 2.4)  
D Flower, 15 : 2

E Flower, longitudinal section, 15 : 2  
F, G Placenta, 15 : 1 (D-G: ROGERS 27460)  
H Fruit, 3 : 1  
I Endocarp, 3 : 1 (H, I: BURCHELL 4111)

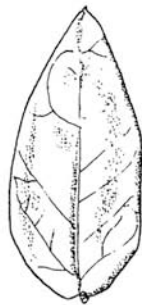




A



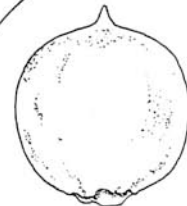
H



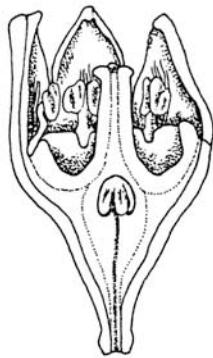
B



C



I



E



F



G



D

The second group shows reduced, deciduous bracts that are above the elongated lower internodes of the inflorescence that are all at  $\pm$  the same height and so via a multiflorous  $\text{\textcircled{M}}$  condition creates an umbel. The  $\text{\textcircled{F}}$  condition is mainly limited to the terminal flower, which can also always be found in the  $\text{\textcircled{M}}$  sex. Within this group is expected all other species reported for Africa, as well as the Asian taxa *O. nepalensis* GRIFFITH, *O. divaricata* PILGER and *O. daruma* PARSA.

These species have previously never been critically compared. A key for the whole of Africa is not available and in the individual descriptions the relationship has rarely been tested against what is already known. Separating features are mentioned: shape and texture of the leaf formation of the petiole and the blade tip, the shape and size of the fruit, degree of hairiness and growth habit. The more vouchers, however, that came into the herbaria, the more clearly one recognized the high variability in just these features, so some “species” could barely be maintained anymore.

Indicative is the list of African species in Engler 1915, which states (p. 69), inter alia: “... *O. abyssinica* Hochst, of which southwest African duplicates have the same leaf shape as *O. compressa*, while Abyssinian and others have more lanceolate leaves and the latter mentioned *O. tenuifolia* come close.” Furthermore, (p. 71) of *O. abyssinica*: “... Probably one of its ... the plant described by me as *O. rigidissima*.” For *O. tenuifolia* (p. 71): “It is the Indian *O. wightiana* Wall. (*O. arborea* Wall) very similar ...” And further (p. 71): “The *O. wightiana* approaches something like *O. lanceolata* Hochst. et Steud. by its lanceolate leaves.”

In specific publications on African flora as well, several of these species are found as synonyms (for example, in BALFOUR 1888 under *O. arborea*: *O. wightiana*, *O. abyssinica*, in PETER 1932 under *O. wightiana*: *O. tenuifolia*, in ROBYNS & LAWALREE 1948 under *O. arborea*: *O. wightiana*, *O. tenuifolia*, *O. urundiensis*, in CUFODONTIS 1953 inter alia under *O. abyssinica*: *O. rigidissima*, in BRENNAN 1954 under *O. compressa*: *O. abyssinica*, *O. arborea*, *O. wightiana*) or they disappear (as *O. angustifolia* BAKER 1910 described in Kew Bulletin, in 1911 no longer mentioned in the edited work by the same author of Santalaceae in the Flora of Tropical Africa).

Drawing 4. *Osyris*, *Colpoon*, *Rhoiacarpos*: Ramifications, Inflorescences and Floral Diagrams (compressed axis parts in black)

Ramification scheme:

- A *Osyris* (after FLECK 31Ba)
- B *Colpoon* (after BACHMANN 1431)
- C *Rhoiacarpos* (after COOPER 52)

Inflorescence scheme:

- D *Osyris*  $\text{\textcircled{M}}$  (after GOOSSENS 233)
- E *Osyris*  $\text{\textcircled{F}}$  (after SCHLIEBEN 343)

F *Colpoon* (after PHILLIPS s. n.)

G *Rhoiacarpos* (after SCHLECHTER 2657)

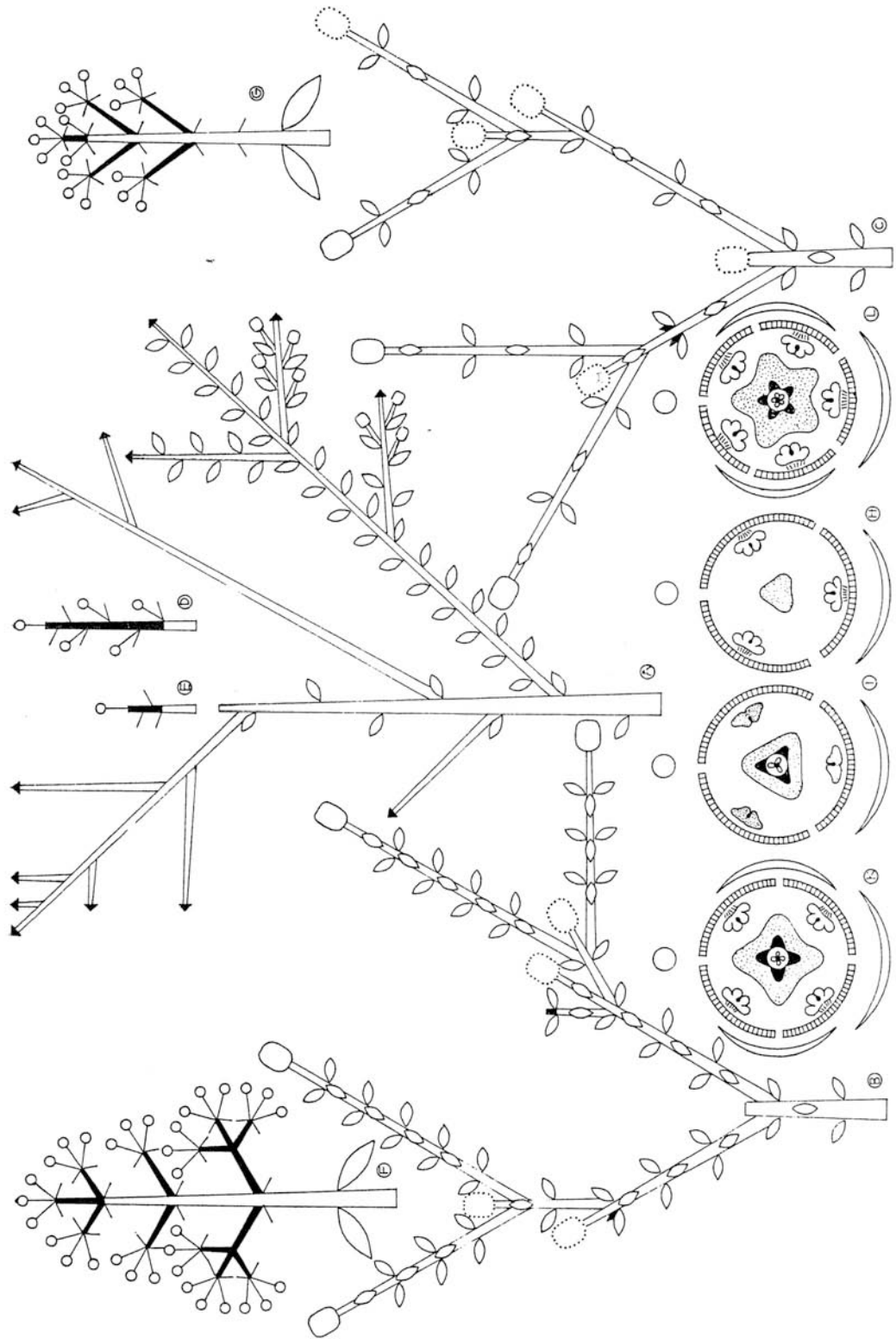
Floral diagrams:

H *Osyris*  $\text{\textcircled{M}}$

I *Osyris*  $\text{\textcircled{F}}$

K *Colpoon*

L *Rhoiacarpos*



It seemed worthwhile in this situation to consider the widest possible material of the genus. A review of *Osyris* specimens at the herbaria of Zurich, Geneva, Paris, Kew and London (BM), where also most types were included, revealed that all the supporting records of this second group of species from Africa must be reckoned as one species. Records from Morocco did not differ from those of South Africa, and in the collections there made from Ethiopia are all transitional [forms]. Characteristic is the high variability of populations throughout Africa. The Asian records belong exclusively to the same species. From various parts of individual records for some characteristics singled out in Table 3, one may show that it is not possible to distinguish several species.

Table 3. Feature comparison of various *Osyris* records

	Leaf length	Leaf width	Leaf thickness	Inflorescence length to subtending bract length	Flower number	
	(each larger leaf per record)				♂	♀
Morocco, Algeria	21-45 mm	7-16 mm	thin/thick	1/2-1/5	3-5	1(-2)
South Africa	18-55 mm	8-30 mm	thin/thick	2/3-1/3	3-10	1(-3)
Ethiopia	30-50 mm	10-27 mm	thin/thick	2/3-1/3	5-12	1(-3)
East Africa	25-53 mm	11-23 mm	thin/ moderately thick	2/3-1/4	3-8	1
China, Tonkin	30-53 mm	8-21 mm	thin/ moderately thick	2/3-1/4	3-8	1(-3)

Leaf shape, length of the petiole, texture and innervation of the leaf are all highly variable and cannot be used for the differentiation of species as well as the shape and size of the fruit and the hair on all the parts are all highly variable.

Allowedly, local forms which are emerging here and there may not be of higher rank than awarded by varieties that are likely to be mostly environmentally caused. (For example, one finds markedly thick-leaved forms in South Africa and north of the Sahara, and large-leaved forms especially in East Africa, and particularly small-leaved forms in records throughout its range.)

I therefore propose to summarize all records of the genus *Osyris* except *O. alba* under a species which must lead as the oldest validly described name *O. lanceolata* HOCHSTETTER and STEUDEL. As all other synonyms and mentioned names are cited in Table 2 other than *O. angustifolia* BAKER (= *Thesium triflorum* Thunb.), furthermore, the aforementioned Asian taxa *O. nepalensis*, *O. divaricata* and *O. daruma*.

*O. lanceolata* is common in the Iberian Peninsula, in Morocco, Algeria, Angola, West Africa, Bechuanaland [South Africa], Transvaal, Orange Free State, Natal, Rhodesia, Nyasaland, Mozambique, Tanganyika, Ruanda-Urundi, Uganda, Kenya, Equatoria [South Sudan], Abyssinia [Ethiopia], Somaliland [Somalia], Eritrea, Socotra, Arabia, Persia [Iran], India, Ceylon, Burma [Myanmar], Siam [Thailand] and southern China.

## Zusammenfassung

Die Untersuchung der afrikanischen Osyrideae hat ergeben, dass in Südafrika drei Taxa unterschieden werden können: *Colpoon compressum* BERGIUS, *Rhoiacarpos capensis* (HARVEY) ALPH, DE CANDOLLE und eine Art von *Osyris*, die bisher als *O. abyssinica* HOCHST. ex A. RICHARD bezeichnet wurde. Die Merkmale der drei Taxa werden ausführlich verglichen.

Eine kritische Durchsicht der Gattung *Osyris* hat gezeigt, dass nur zwei Arten aufrechterhalten werden können: *O. alba* LINNE, die nur nördlich der Sahara vorkommt, sowie die in Afrika und Asien weit verbreitete *O. lanceolata* HOCHSTETTER et STEUDEL.

## Summary

A study of the african Osyrideae has shown that there are three different taxa in southern Africa: *Colpoon compressum* BERGIUS, *Rhoiacarpos capensis* (HARVEY) ALPH. DE CANDOLLE and one species of *Osyris*, known hitherto as *O. abyssinica* HOCHST. ex A. RICHARD. The characters of the three taxa are discussed.

Within the genus *Osyris*, there are only two taxa that can be maintained: *O. alba* LINNÉ, occurring but in the north of the Sahara, and *O. lanceolata* HOCHSTETTER et STEUDEL, widely spread in Africa and southern Asia.

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