

Status of the Genera *Colpoon*, *Osyris* and *Rhoiacarpos* in South Africa

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Background: The taxonomic and phylogenetic status of *Colpoon*, *Osyris* and *Rhoiacarpos* (Santalaceae, Osyrideae) is reviewed.

Objectives: To resolve confusion regarding whether *Colpoon* is deserving of generic status separate from *Osyris*.

Methods: Existing morphological information was examined for the three genera as well as previously published molecular phylogenies.

Results: From both morphological and phylogenetic perspectives, *Colpoon* is distinct from *Osyris*. The status of *Rhoiacarpos* was not contentious and this genus is also easily differentiated from the other two genera in Osyrideae.

Conclusions: *Colpoon* and *Osyris* are not congeneric; therefore, floras, databases and herbarium collections should recognise these as distinct taxa.

Introduction

Over the past several decades, some confusion has surrounded the taxonomic circumscription of three genera of South African Santalaceae, tribe Osyrideae: *Osyris* L. (1753), *Colpoon* P.J.Bergius (1767) and *Rhoiacarpos* A.DC (1857). The taxonomic history and generic boundaries (from a morphological perspective) of these three taxa were discussed by Stauffer (1961). For several decades following Stauffer's work, these three genera were generally treated as distinct, as shown in 'Plants of Southern Africa: Names and Distribution' by Arnold and De Wet (1993). In 1994, Hilliard published a one-page note on *Colpoon* where she followed the treatment in Flora Capensis (Hill 1915) and reduced *Colpoon compressum* P.J.Bergius to a synonym of *Osyris abyssinica* Hochst. ex A.Rich. (= *O. lanceolata* Hochst. & Steud.). As stated by Hilliard (1994), 'There is, however, no essential differences in floral detail or in the structure of the inflorescence; those given by Stauffer (1961) are illusory'. But are the differences between the three genera given in Stauffer (1961, Table 1) real or imagined? It should be noted that Stauffer examined specimens, including the types, from Zurich, Geneva, Paris, London and Kew. His work was the most comprehensive up to that time and he concluded that the three species 'can be clearly distinguished morphologically and among themselves show no transitions'. Most web sites, recent floras and field guides that appeared after Hilliard (1994) accepted two genera for South Africa, *Osyris* and *Rhoiacarpos*, with *Colpoon* listed as a synonym of the former. Examples include Goldblatt and Manning (2000), Bean and Johns (2005), Germishuizen et al. (2006), Mucina and Rutherford (2006) and Manning (2007). This trend was reversed by Manning and Goldblatt (2012) who took into account molecular phylogenetic data that showed the three genera were distinct. Despite this publication, the concept of two Osyrideae genera for South Africa persists in herbarium collections and both popular and scientific works. Therefore, the purpose of this paper is to summarise the existing morphological and molecular information that supports recognising three distinct genera.

Molecular phylogenetic data

The first comprehensive molecular phylogenetic study of Santalaceae was by Der and Nickrent (2008) that used nuclear small-subunit ribosomal DNA and chloroplast *rbcL* and *matK*. A portion of the tree there referred to as the '*Santalum* clade' (now Santalaceae s. str.) is shown in Figure 1a. The clade composed of *Osyris*, *Nestronia*, *Rhoiacarpos* and *Colpoon* (tribe Osyrideae) is strongly supported as monophyletic. Moreover, *Osyris quadripartita* (Europe) was not sister to *Colpoon*, with *Rhoiacarpos capensis* occupying that position. It is relevant that Stauffer (1961) also saw this association based on morphology:

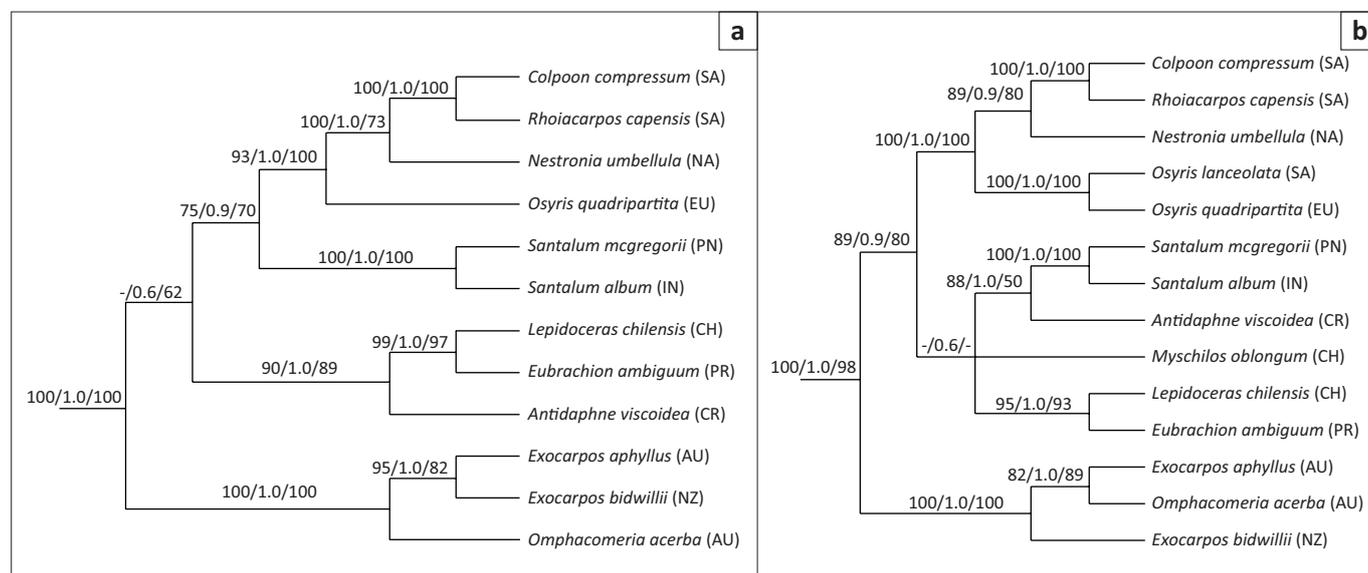
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TABLE 1: Morphological characters for some *Osyrideae*.

Morphological characters	<i>Osyris lanceolata</i>	<i>Colpoon compressum</i>	<i>Rhoiacarpus capensis</i>
Phylotaxy	alternate (spiral 2/5)	decussate, sometimes subopposite or alternate via displacement	decussate, sometimes subopposite
Leaf shape	elliptical, acute to cuneate base	elliptical, acute to cuneate base	ovate, cordate base
Leaf texture	soft	soft	coriaceous
Leaf surfaces	dull above and below	dull above and below	shiny above, dull below
Leaf margin	plane	plane	revolute
Petiole	present	present	very short
Inflorescence position	axillary	terminal	terminal
Inflorescence type	unifloral (female), monochasia (male and female), compound and compressed monochasia (male)	paniculate with compressed axes, monochasial	paniculate with compressed axes, monochasial
Inflorescence bracts	abscising	abscising or persistent below fruit	persistent below fruit
Plant sex	dioecious (androdioecious?)	flowers bisexual	flowers bisexual
Petal number	3 (4)	4 (-6)	(4) 5 (6)
Style length	to height of anthers or beyond	nearly absent (stigma sessile)	to height of anthers or beyond
Disk shape	flat, spherical	flat, lobe number equal to petal number	saucer-shaped, lobe number equal to petal number
Fruit shape	spheroid to ellipsoid	obovoid	spheroid to ellipsoid
Petals on fruit apex	not persistent	not persistent	persistent

Source: Author's own work, modified and updated from Stauffer (1961)



Source: Author's own work

Geographic abbreviations are as follows: AU, Australia; CH, Chile; EU, Europe; IN, India; NA, North America; NZ, New Zealand; PN, Papua New Guinea; PR, Puerto Rico; SA, South Africa.

FIGURE 1: A. Phylogenetics of Santalaceae *sensu stricto*. Maximum likelihood bootstrap, Bayesian posterior probabilities and maximum parsimony bootstrap values are shown at the nodes where $'\leq' < 50\%$. (a) Portion of the three-gene phylogenetic tree from Der and Nickrent (2008). (b) Portion of the seven-gene phylogenetic tree from Su et al. (2015).

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. (p. 392)

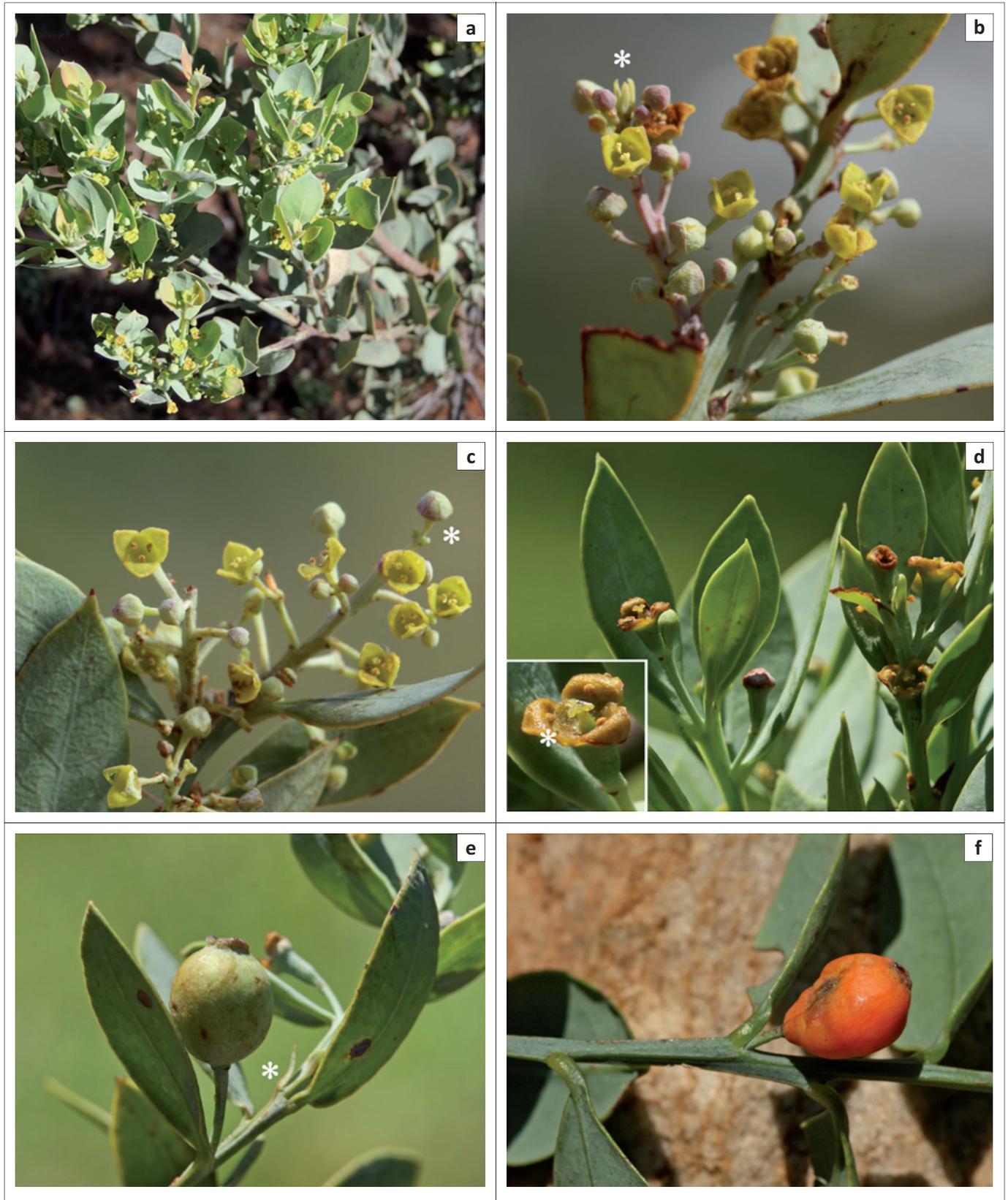
One could argue that because no South African accession of *Osyris* was included, this result should not be used to address generic delimitation in this geographic region. A seven-gene study that sampled nuclear, chloroplast and mitochondrial genes from 197 members of Santalales was published (Su et al. 2015) and a portion of the resulting tree is shown in Figure 1b. In that study, *Osyris lanceolata* from South Africa was included and it is sister to the European *Osyris quadripartita*. As before, *Osyris* is sister to a clade containing *Nestronia*, *Rhoiacarpus* and *Colpoon* with the latter two sisters.

Morphological data

A comparison of the vegetative and reproductive morphologies of *Osyris*, *Colpoon* and *Rhoiacarpus* shows that these genera share a number of features and yet differ in others (Table 1 and Figures 2–4).

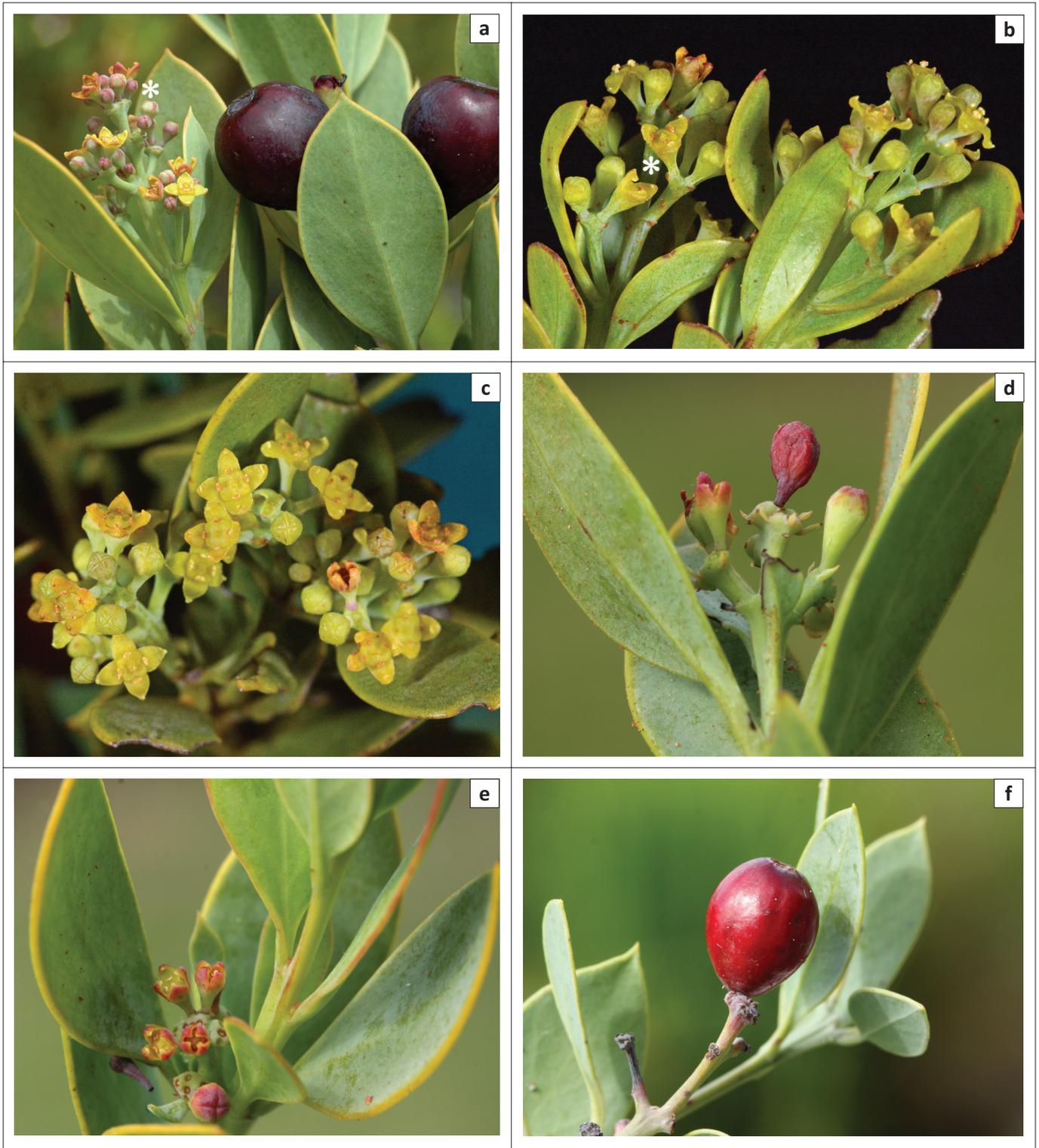
Leaves

All three genera have simple, entire leaves with mucronate apices. All show winged or ridged stems with the ridges merging with leaf petiole bases. Leaf phylotaxy was used by Hill (1915) to justify merging *Colpoon* with *Osyris* because both alternate and opposite leaves were seen in the former. Variation in phylotaxy was noted by Stauffer (1961) where *C. compressum* was scored as decussate, rarely with the two



Source: Author's own work; photos by Marinda Koekemoer

FIGURE 2: *Osyris lanceolata* vegetative and reproductive morphology. (a) Habit of plant with male flowers showing abundant axillary inflorescences. (b) Axillary male inflorescences. The left-hand shoot (*) may appear racemose but note that new leafy innovations are present at the apex. Branching of the floral peduncles indicates these units are compound monochasia (cymes). (c) Axillary male inflorescences. Although some appear dichasial (*), the lateral floral buds are of unequal age, thus indicating that these are compound monochasia with compressed axes (cf. Stauffer 1961). (d) Axillary female inflorescences. Note that the flowers occur singly or in two-flowered monochasia. The anthers in these flowers (*) do not appear functional, and hence are interpreted as staminodes. (e) Young fruit in axillary position. Note the recaulescent bracts (*) at a node opposite a leaf. (f) Mature fruit.

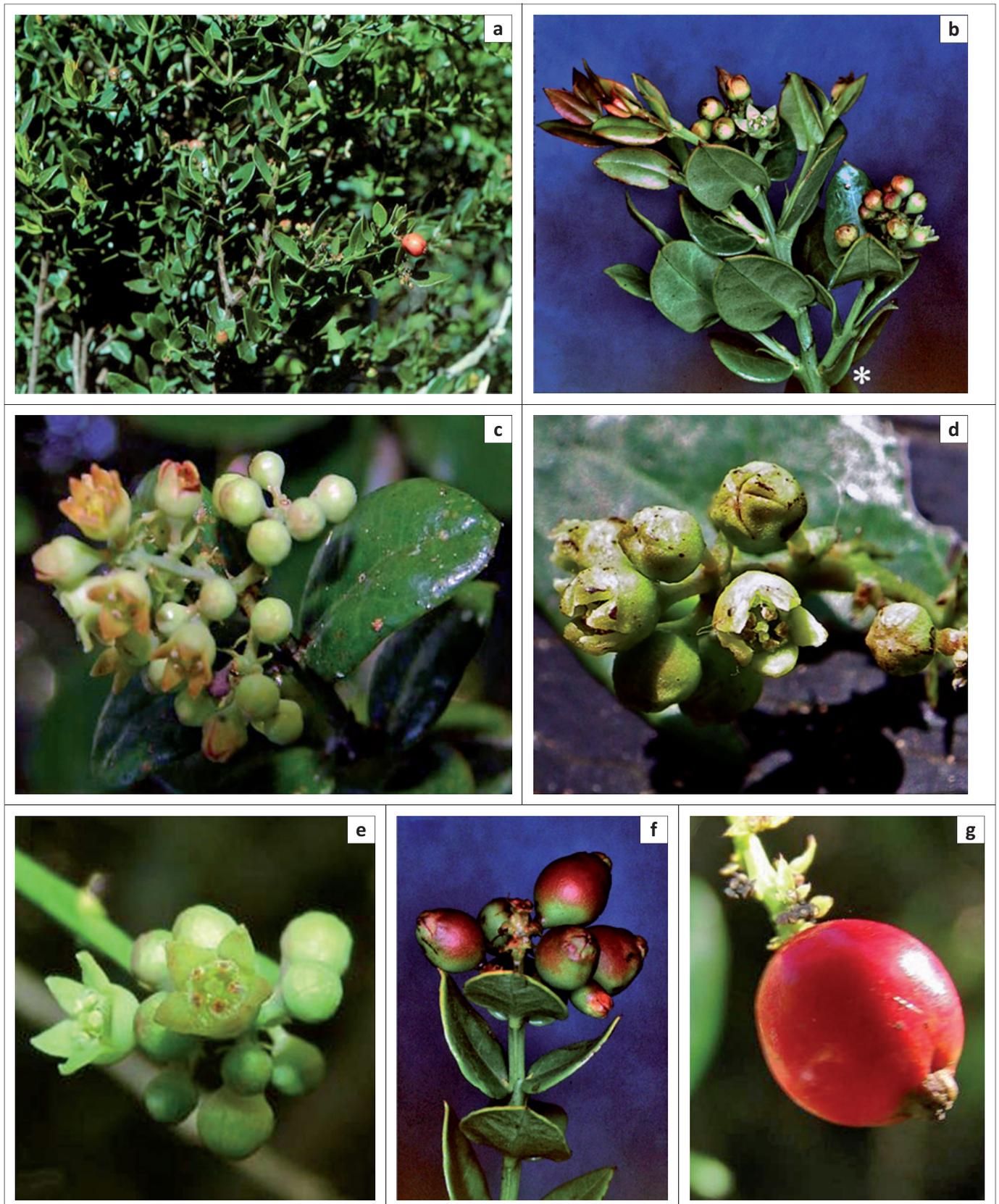


Source: Author's own work; photos (a), (b) and (c) by author and (d), (e) and (f) by Marinda Koekemoer

FIGURE 3: *Colpoon compressum* vegetative and reproductive morphology. (a) Flowering and fruiting shoots. Note the swollen termini of the panicle peduncles (*) representing compressed axes (cf. Stauffer 1961). (b) Side view of inflorescence showing compressed monochasia, minute deciduous inflorescence bracts and a 3-merous flower (*) among mostly 4-merous ones. (c) Top view of inflorescence showing all 4-merous flowers, floral disks and essentially sessile stigmas. (d) Inflorescence showing persistent bracts along edges of swollen panicle termini and flower abortion. (e) Young vegetative innovation showing metatopic displacement resulting in alternate phylotaxy. (f) Mature fruit occurring at swollen peduncular apex with scars from abortive flowers.

leaves somewhat shifted. Bean (1990) scored *C. compressum* as 'leaves usually opposite to subopposite, less often alternate' and the newly described species *Colpoon speciosum* as 'leaves as often alternate as subopposite, less often opposite'. Although *Rhoiacarpus* leaves were scored as opposite by Hill (1915),

it too can show the subopposite condition (Figure 4b). Thus, phylotaxy appears to be a rather plastic morphological feature in Osyrideae. Shifting (displacement) of leaf position through development can be a form of metatopy (Weberling 1989) possibly influenced by genetic or environmental factors.



Source: Author's own work; photos (b) and (f) by author and the remainder by Christopher Davidson

FIGURE 4: *Rhoiacarpus capensis* vegetative and reproductive morphology. (a) Habit of plant in fruit. (b) Shoot with terminal paniculate inflorescences. Note the opposite as well as subopposite (*) leaves. (c) Inflorescence. Note persistent bracts below flowers. (d, e) Closer view of the 5-merous flowers. (f) Young infructescence. Note bracts persisting on the peduncles. (g) Mature fruit showing persistent petals at apex.

Rhoiacarpos is easily distinguished from the other two genera by leaf features. Its leaves are nearly sessile, bifacial (shiny above and dull below), with cordate bases and somewhat revolute margins. The leaves of *Osyris* and *Colpoon* differ in these characters, but are quite similar to each other overall. Hilliard (1994) states for both *Osyris* and *Colpoon* 'both leaf surfaces closely and minutely white-dotted', but this feature has not been observed by this author in the field, herbarium or in photographs.

Inflorescences

The inflorescences of *Osyris* are mainly axillary whereas those of *Colpoon* and *Rhoiacarpos* are terminal. It is interesting that Hill (1915) describes the inflorescence of *Rhoiacarpos* as a panicle composed of 3-flowered axillary cymules. In Figure 4 of Stauffer (1961), both *Rhoiacarpos* and *Colpoon* are diagrammed with 3-flowered units. In other Santalales, this 3-flowered cymule unit is equivalent to a dichasium. But the situation in Osyrideae appears more complex, mainly owing to compression and reduction (loss of flowers). Hilliard (1994) indicates flowers in *Osyris lanceolata* 'may occur in 2–3-flowered dichasia'. Technically, a dichasium is 3-flowered whereas a monochasium is 2-flowered. Upon first examination, the inflorescence units may appear to be dichasial such as in *Osyris* (Figure 2c), *Colpoon* (Figure 3b), and *Rhoiacarpos* (Figure 4c), but in these cases the pair of flowers (or buds) subtending the older, terminal flower are unequal in age. Moreover, the older of the two subtending buds is often present as a lateral innovation. For these reasons, it seems best to describe these units as monochasia or compound monochasia. Simple (2-flowered) monochasia are frequently seen in the female inflorescences of *Osyris* (Figure 2d).

The terminal peduncles in the panicles of *Colpoon* are often swollen (Figure 3a and d). In his diagram, Stauffer (1961) coloured black those inflorescence axes that become compressed. Thus, the cluster of flowers seen arising from these swollen apices in *Colpoon* is interpreted as being a series of reduced monochasia (or dichasia according to Stauffer 1961). The phenomenon of syndesmy (incorporation of partial inflorescence units and their axes into the main axis) is well documented in cymoid types resulting in a coenosome (Weberling 1989). Looking at the lower inflorescence branch in Figure 3a, the six flowers and buds are of different ages: two past anthesis, one at anthesis, one older bud and two younger buds. This situation could be interpreted as two dichasia, but because the ages of the flowers are wrong, this situation might best be interpreted as three monochasia.

The components of the inflorescence axes (peduncles) are often subtended by small bracts. Stauffer (1961) indicated that these abscise in *Osyris*, abscise or are persistent in *Colpoon* and are persistent in *Rhoiacarpos*. The study by Bean (1990) confirms that the persistence of these bracts in *C. compressum* is polymorphic (compare Figure 3a and d) and further shows that in *C. speciosum* the bracts are persistent and enlarge upon fruiting.

Flowers

The flowers in *Colpoon* and *Rhoiacarpos* are bisexual, whereas in *Osyris lanceolata* flowers appear to be unisexual. Hilliard (1994) stated, 'the flowers of *Osyris lanceolata* are hermaphrodite and male, the plants being androdioecious', but no evidence was provided that supported the presence of bisexual versus female flowers. Female flowers possess stamens (Figure 2d), but if the anthers can be shown to not produce pollen, then these are staminodes and the flower is functionally female.

Flower merosity is notoriously variable in Santalaceae, often showing three or four different forms within the same inflorescence. But for differentiating the three genera considered here, this character has some value when the most common number is considered. Thus, *Osyris* generally has 3-merous flowers, occasionally having 4-merous flowers. *Colpoon* typically has 4-merous flowers, but 5- and 6-merous flowers can also be seen. Most *Rhoiacarpos* flowers are 5-merous, but 4- and 6-merous flowers are also known. The number of lobes of the glandular disk in these genera follows the number of petals.

Fruits

In all three genera, many fewer fruits develop to maturity compared with the number of flowers originally present on the inflorescence axis. In *Colpoon*, evidence of flower abortion exists (Figure 3d) such that a single fruit is present per axis with the scars of abortive flowers present at the swollen peduncle apex (Figure 3f). The fruits of *Rhoiacarpos* differ from the other two genera in having persistent petals at the apex (Figure 4f and g). A cluster of fruits is shown in Figure 4f; however, each fruit appears to be present on a separate inflorescence branch with evidence of numerous abortive flowers and their associated bracts below (Figure 4g).

In *Osyris* (Figure 2f) and *C. compressum* (Figure 3f), the petals abscise and are not persistent on the mature fruit. Bean (1990) indicates that in *C. speciosum* the petals are persistent; thus, this feature is polymorphic within the genus. Although it is not clear whether the character of fruit shape will remain valid following further observations, it appears that the fruit in *Colpoon* is more obovoid than in the other two genera that have spheroid to ellipsoid fruits.

Discussion

The decision by Hilliard (1994) to lump *Colpoon* into *Osyris* can now be addressed given the molecular phylogenetic and comparative morphology results. From the topologies of the phylogenetic trees (Figure 1a and b), one could include *Colpoon* in *Osyris*. If this was done, and monophyly was maintained, then the North American *Nestronia* and South African *Rhoiacarpos* would also have to be included in *Osyris*. This concept has never been proposed and in fact *Rhoiacarpos* has been considered a separate genus in all consulted works on South African flora. Molecular dating conducted by Vidal-Russell and Nickrent (2008) showed that *Santalum* and *Osyris*

diverged in the Paleocene, at least 60 million years ago. Although the other genera (*Nestronia*, *Rhoiacarpos* and *Colpoon*) have not been included in ultrametric trees, it is likely that they diverged from each other somewhat more recently, for example, in the Eocene, ca. 50 million years ago.

Despite the statement by Hill (1915) that 'There is also no floral difference between *Colpoon* Berg. and *Osyris* Linn'. and the similar sentiment expressed by Hilliard (1994), the evidence presented above shows that there are clear differences in vegetative, floral and fruit features among all three genera. The taxonomic conclusions reached by Stauffer (1961) are fully supported by molecular phylogenetic data; thus, *Colpoon* should be considered a genus, distinct from *Osyris*, and is composed of two species, *C. compressum* and *C. speciosum*.

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Competing interests

The author declares that he has no financial or personal relationships that may have inappropriately influenced him in writing this article.

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