

## Taxonomic position of *Rhus problematodes* (Anacardiaceae): Evidence from fruit and seed structure

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This is the first report on the structure of the pericarp and seed coat of *Rhus problematodes* Merxm. & Roessl., a curious microphyllous shrublet of very limited distribution in the southern desert region of Namibia. Mainly on the basis of macromorphology, it was hitherto considered to stand somewhat apart from other African members of *Rhus* L. (sect. *Gerontogaeae* Engl.). *R. problematodes* clearly agrees with other species of *Rhus* in its basic pericarp and seed-coat characteristics, including a single-seeded unilocular drupaceous fruit, parenchymatous mesocarp with secretory ducts, ridged outer endocarp, inner endocarp composed of three discrete layers, and an endotegmic, partially pachychalazal seed coat. The scarcity of stomata and heavy deposition of cutin in the exocarp possibly reflect adaptations to its arid habitat. Evidence from fruit and seed structure, combined with that from other sources, reconfirms the view that it is a highly specialized species of *Rhus* showing several xeromorphic, mainly macromorphological, reductions. The shared presence of glandular stellate hairs and reduced foliage leaves suggests that it might be closely allied to *R. horrida* Eckl. & Zeyh., a species from Namaqualand.

Hierdie is die eerste verslag oor die perikarp- en saadhuidstruktuur van *Rhus problematodes* Merxm. & Roessl., 'n sonderlinge mikrofiliese struikie met 'n uiters beperkte verspreiding in die suidelike woestynggebied van Namibië. Hoofsaaklik op grond van die makromorfologie, is dit tot dusver as redelik verwyderd van die ander *Rhus*-spesies in Afrika (seksie *Gerontogaeae* Engl.) beskou. Die basiese perikarp- en saadhuidkenmerke van *R. problematodes* stem duidelik met dié van ander *Rhus*-spesies ooreen; dit sluit onder andere in die enkelsadige eenhokkige steenvrugte, parenchimatiese mesokarp met sekreetkanale, geribde buitenste endokarp, binneste endokarp wat bestaan uit drie afsonderlike lae, en 'n endotegmiese, gedeeltelik-pagichalalale saadhuid. Die min stomata en swaar neerlegging van kutien in die eksokarp dui moontlik op aanpassings by die dorre habitat van die spesie. Getuigenis van vrug- en saadstruktuur, gekombineer met dié uit ander bronne, herbevestig die siening dat dit 'n hoogs gespesialiseerde spesie is wat hoofsaaklik makromorfologies in verskeie opsigte gereduseer is. Die gemeenskaplike aanwesigheid van stervormige klierhare en gereduseerde loofblare dui daarop dat dit moontlik naverwant aan *R. horrida* Eckl. & Zeyh., 'n spesie uit Namakwaland, mag wees.

**Keywords:** Anacardiaceae, fruit, hypostase, pachychalaza, seed

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### Introduction

*Rhus problematodes* Merxm. & Roessl. is a profusely branched, exceedingly squarrose shrublet from the southern Lüderitz District of Namibia, an extremely arid desert region rich in endemic plants. Most collections are from the Schwarzkalkrand, a dolomitic range just north of Witpütz. It is a most peculiar species of *Rhus* L., displaying among others such unusual characters as a decumbent habit, an indumentum with multicellular glandular stellate hairs, minute sessile leaves which are simple (usually trilobate and sometimes trifid) and clustered on short shoots, and usually solitary flowers.

The species was discovered by K. Dinter in 1934 and the still-undescribed collections of *R. problematodes* were provisionally listed under the Anacardiaceae by Merxmüller & Schreiber (1968). However, until the collection of more flowering and some fruiting specimens in 1972/73, the familial position of this material remained uncertain. On the basis of macromorphological, anatomical and palynological evidence, Merxmüller & Roessler (1973) strongly supported

a placement of the taxon in the Anacardiaceae, and described it as a new species of *Rhus* section *Gerontogaeae* Engl. Abberant features were interpreted as extreme xeromorphic adaptations.

The structure of the fruit and seed of certain members of *Rhus* was recently under consideration as part of a comparative morphological study on mainly southern African Anacardiaceae (von Teichman & Robbertse 1986; von Teichman und Logischen 1988; von Teichman 1989; von Teichman in press). Seed of *Rhus* is characterized by a relatively small size and the presence of a partial pachychalaza. In considering evolutionary trends in dicotyledonous seed, we have hypothesized that a reduction in both seed size and the extent of the chalaza may accompany adaptation to increased xeric conditions (von Teichman & van Wyk in press). Within Anacardiaceae, the large pachychalazal seed with undifferentiated seed coat of tribe Anacardiaceae probably reflects the primitive state. Tribe Spondiadeae with relatively large, distinctly partially pachychalazal seed and a seed coat showing varying

tendencies towards exo-, meso- and/or endotestal lignification is considered more advanced. The even more advanced tribe Rhoeeae, of which *Rhus* is a member, is characterized by the seed being mostly relatively small, with a less pronounced partial pachychalaza and an endotegmen, or probably only an endotegmen (von Teichman in press).

In this paper the fruit and seed structure of *R. problematodes* is described for the first time, and the new evidence is used to reassess its current taxonomic treatment. Attention is also given to the possible influence of extreme xeric conditions on the fruit and seed structure of this species, in the light of postulated evolutionary trends within the Anacardiaceae.

### Materials and Methods

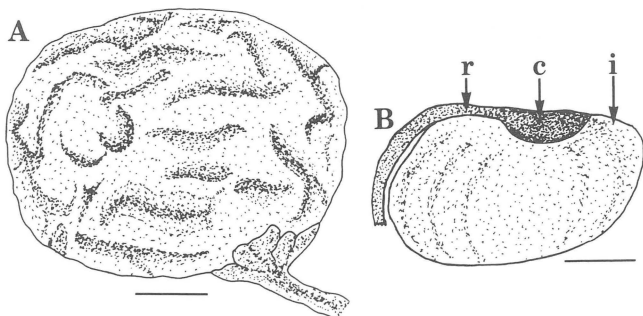
Mature fruit from the herbarium specimen *Wiss 3001*, holotype of *R. problematodes*, was kindly provided by the Botanische Staatssammlung München (M). Following rehydration in boiling water, small parts of the pericarp, seed coat and the cotyledons were fixed in 2.5% sodium phosphate-buffered glutaraldehyde, dehydrated with 2-methoxyethanol, ethanol, *n*-propanol and *n*-butanol, infiltrated and embedded in glycol methacrylate. After the periodic acid-Schiff reaction (PAS), sections were stained with toluidine blue O (Feder & O'Brien 1968). These procedures, as well as histochemical methods used for the localization of lignin, proteins and residual lipids, were described in detail by von Teichman (1987, 1988). Unstained sections and sections stained in toluidine blue were observed under crossed polarized filters to determine the presence of crystals. For detection of callose, 0.1% aniline blue was used and the sections were examined with a Nikon Optiphot light microscope (von Teichman 1990).

### Results

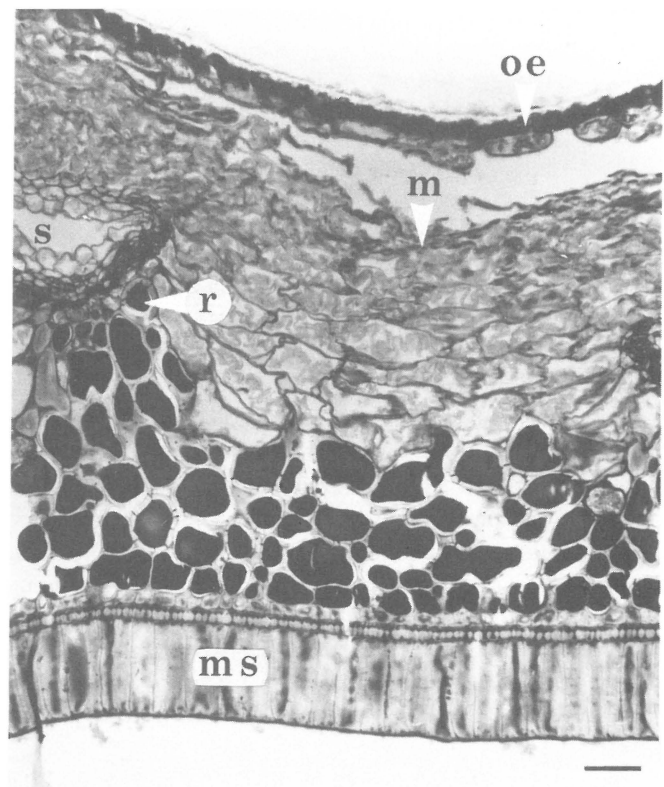
The drupes (Figure 1A) are obliquely subglobose, slightly compressed and glabrous, with remnants of the calyx and disc. A loose, papery exocarp covers the fleshy mesocarp and moderately hard endocarp. The unilocular stone contains a single seed (Figure 1B). The exocarp *s. l.* (cf. von Teichman 1989) consists of the tanniferous epidermis, a hypodermis with usually secondarily thickened, but not

lignified, cell walls, and remnants of parenchyma. The epidermal cells have thick cellulose cell walls, the outer tangential ones being serrately sculptured. Cutin is present in the well-developed cuticle which is about 8  $\mu\text{m}$  thick, and also in the outer tangential and parts of the anticlinal epidermal cell walls. There are subepidermal cuticular phlanges which are confluent in those parts where local periclinal divisions have given rise to short segments of biseriate epidermis. There are very few stomata, with the guard cells barely elevated above the outer surface of the epidermal cells.

The mesocarp consists of thin-walled parenchyma cells interspersed with secretory ducts (Figure 2). These ducts are closely associated with vascular bundles, which for the purpose of this paper are considered part of the mesocarp. The vascular tissue may also be taken as part of the endocarp, however, but this is a matter of controversy which still requires detailed consideration. The outer endocarp comprises mainly tanniferous brachysclereids with simple pits (Figure 2). In transverse section this part of the endocarp exhibits characteristic ridges, each bordering on a vascular bundle. The vascular bundles consist of a broken strand of xylem elements, surrounded on three sides by phloem. The ridged outer, together with the inner, stratified part of the endocarp, comprises the endocarp *s. l.* (cf. von Teichman 1989). The stratified inner part, or endocarp



**Figure 1** *Rhus problematodes*. Side views of the fruit (A) and seed (B), showing the remains of the calyx on the fruit, the funicle, raphe (r), as well as chalazal (c) and integumentary parts (i) of the seed coat. Scale bars = 1 mm.

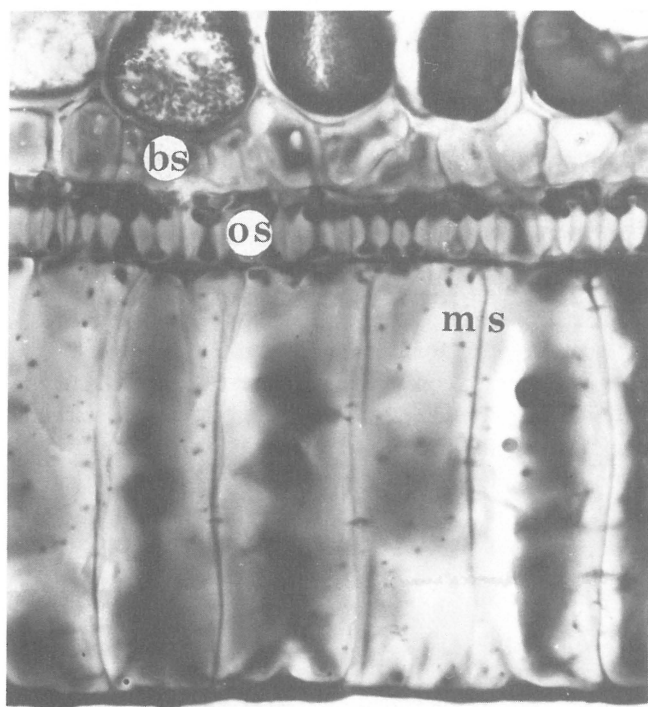


**Figure 2** *Rhus problematodes*. Transverse section of a part of the mature pericarp. Note outer epidermis (oe) with thick cuticle and hypodermal layer of the exocarp; parenchyma (m) and secretory duct (s) of the mesocarp; ridged (r) outer endocarp with tanniferous brachysclereids; three layers of the stratified inner endocarp (compare Figure 3), the macroscleireids (ms) being very prominent. Scale bar = 50  $\mu\text{m}$ .

*s. str.*, most probably develops from the inner epidermis of the ovary wall. It is structurally fairly similar to that of *Rhus lancea* L. f. (von Teichman & Robbertse 1986; von Teichman 1989), and consists of the following layers:

- an innermost layer of palisade-like macrosclereids (Figures 2 & 3), about 80  $\mu\text{m}$  in radial extent, of which the thick secondary cell walls consist mainly of cellulose and some lignin. In transverse section these macrosclereids are hexagonal in outline, with a small cell lumen;
- a middle layer of osteosclereids, about 15  $\mu\text{m}$  long, with the cell walls, except those of the capita, strongly thickened and heavily lignified (Figure 3). In longitudinal section the lumina of these sclereids are long and narrow with enlargements at both ends (bone-shaped). The enlargement (capitum) at the outer end is, however, more prominent and contains the nucleus. In a transverse section through the middle portion, these sclereids are round in outline with a small lumen;
- a uniseriate layer of brachysclereids (Figure 3) bordering the outer endocarp and averaging 10–15  $\mu\text{m}$  in radial extent. In transverse section these sclereids have star-shaped lumina and thick, wavy cell walls fitting tightly together like pieces of a jigsaw puzzle. A few parenchyma cells with prismatic crystals of calcium oxalate occur scattered within this layer.

The mature seed (Figure 1B) is laterally compressed, pale brown and characterized by a small, dark brown, saddle-shaped patch, the so-called partial pachychalaza. The thin seed coat is brittle and derived from the raphe, extended chalaza (small partial pachychalaza), and both integuments.



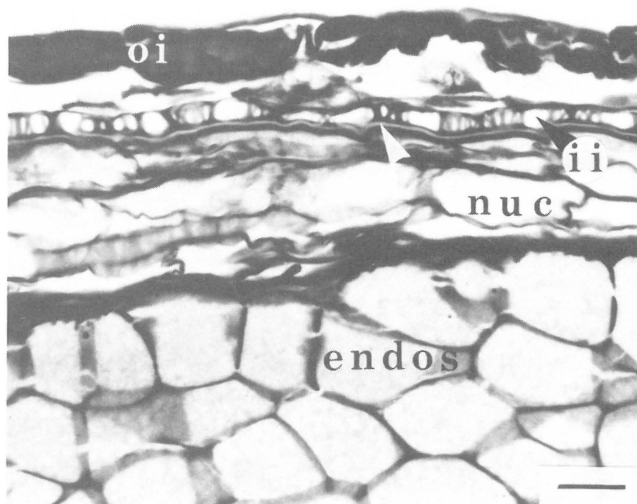
**Figure 3** *Rhus problematodes*. Transverse section of a part of the mature pericarp to illustrate parts of the inner endocarp at high magnification. Note uniseriate layers of brachysclereids (bs); osteosclereids (os) and palisade-like macrosclereids (ms). Scale bar = 20  $\mu\text{m}$ .

Brown coloration of the seed coat is due to the presence of tanniferous deposits in the outer epidermis, as well as the hypostase cells comprising the inner part of the chalazal seed coat. The relatively small chalaza-derived portion of the seed coat consists of an outer epidermis, hypodermal parenchyma with some tanniferous and crystalliferous (prismatic crystals of calcium oxalate) cells, a network of vascular bundles, and the hypostase *s. l.* (cf. von Teichman 1988). The hypostase is eight to ten cells in radial extent (thinning out towards the integumentary seed coat), and its cell walls are impregnated with both callose and lipids, probably cutin. These walls are rendered reddish-brown by the PAS-reaction and stain bluish-purple with toluidine blue O, suggesting that they possibly also contain 1,4-linked polysaccharides and phenolic compounds. Adjacent to the hypostase lies the squashed remnants of the nucellus and the *ca.* five-layered cellular endosperm.

The chalazal seed coat gradually merges into a very thin and fragile integumentary seed coat, composed mainly of the outer epidermis of the outer integument (oi), squashed remnants of the oi (absent on the antiraphal side), and the inner epidermis of the inner integument (Figure 4). This latter epidermis represents an endotegmen, the radial and tangential walls being secondarily thickened, lignified and heavily pitted. A well-developed cuticular layer (Figure 4), probably comprising the cuticles of the endotegmen and nucellar epidermis, abuts on the nucellar remnants and persistent proteinaceous endosperm. The nonchlorophyllous embryo consists of a radicle and two flattened cotyledons with fats and protein as energy reserves.

## Discussion

On the basis of fruit structure, there can be no doubt that *R. problematodes* is a member of the Anacardiaceae. This is substantiated by its drupaceous unilocular fruit which



**Figure 4** *Rhus problematodes*. Transverse section of a part of the integumentary seed coat. Note epidermis of outer integument (oi), inner epidermis of inner integument (ii) which comprises the endotegmen, adjacent cuticular layer (white arrow head), as well as the nucellar remnants (nuc) and cellular endosperm (endos). Scale bar = 20  $\mu\text{m}$ .



develops from an ovary with a single anatropous ovule, parenchymatous mesocarp with secretory ducts (resin canals) associated with the vascular tissue, and three-layered endocarp *s. str.* derived from the inner epidermis of the ovary wall. An endocarp composed of three or four discrete palisade-like layers (the so-called *Anacardium* type) is characteristic for most genera of the tribes Rhoeae, Anacardiaceae, Semecarpeae and Dobineeae (Wannan & Quinn 1990). Taxa sharing this type of endocarp are probably phylogenetically related and, within the Rhoeae, include genera such as *Astronium* Jacq., *Cotinus* Tourn., *Euroschinus* Hook. f., *Laurophyllus* Thunb., *Lithraea* Miers, *Loxostylis* Spreng. f. ex Reichb., *Ozoroa* Del., *Rhodospaera* Engl., *Rhus*, *Schinus* L., *Schinopsis* Engl. and *Toxicodendron* Mill. (Herzog 1910; Magen 1912; von Teichman & Robbertse 1986; Wannan & Quinn 1990).

The pericarp structure of *R. problematodes* is remarkably similar to that described for other species of *Rhus* (Magen 1912; Copeland & Doyel 1940; von Teichman & Robbertse 1986; von Teichman 1989; Wannan & Quinn 1990). Subsequent comparisons will be mainly with *R. lancea* L. f., the only other southern African species of *Rhus* section *Gerontogae* in which the fruit and seed structure have been described in detail.

The exocarp of *R. problematodes* differs from that of *R. lancea* mainly in the scarcity of stomata and the stronger deposition of cutin, both possible adaptations to the harsh xeric habitat. These two, as well as other species of *Rhus* mentioned by Engler (1892), have a ridged endocarp. However, as already stated by Brizicky (1963), ridged (ribbed) stones also occur in the closely related genus *Toxicodendron* (considered a subgenus of *Rhus* by him). In *Rhus problematodes* and *R. lancea* these ridges are composed of very similar brachysclereids, representing the so-called spheroidal type of monomorphic sclereid (Rao & Bhupal 1973).

Endocarp hardness is less pronounced in *R. problematodes* than in *R. lancea* with its stony endocarp. Macrosclereids of the first (inner palisade-like) endocarp layer measure about 180  $\mu\text{m}$  in *R. lancea*, whereas those of *R. problematodes* are only 80  $\mu\text{m}$  long. The latter is less than half the lowest value hitherto recorded in *Rhus* and most other members of the Rhoeae. Since the length of these sclereids may show considerable interspecific variation (Magen 1912), this character has to be used cautiously in comparative studies. A conspicuous difference between the second endocarp layers (osteosclereids) of the two southern African species of *Rhus* concerns the absence of cell wall flutes in *R. problematodes*. In *R. problematodes* the brachysclereids of the third endocarp layer resemble those of *R. glabra* L. in having wavy cell walls and a star-shaped lumen (Magen 1912). Although a pronounced crystalliferous (fourth endocarpal) layer is present in *R. lancea* and most other members of *Rhus* and the Rhoeae (Magen 1912; Wannan & Quinn 1990) included in this study, it is absent or poorly developed in *R. problematodes* and five of the fourteen species of *Rhus* studied by Magen (1912).

The exalbuminous, partially pachychalazal seed of *R. problematodes* is undeniably anacardiaceous. In the large tribe Rhoeae, as circumscribed by Engler (1892), the range of structural seed coat variation is very large (von Teichman

in press) and probably indicative of an unnatural assemblage (Wannan & Quinn 1990). However, in the species of *Rhus* studied to date, basic pericarp and seed coat structure are surprisingly similar. With regard to pericarp structure, a combination of the presence/absence/degree of development of endocarp ridges, crystalliferous layer in the stratified endocarp and structure of the osteosclereids are important in the diagnosis of the species. Interspecific differences in seed coat structure relate mainly to seed size, degree of development of the pachychalaza, presence/absence of calcium oxalate crystals, and chemical characteristics of the hypostase cell walls.

Similarities in the seed coats of *R. problematodes* and *R. lancea* (von Teichman in press) include the following:

- an endotegmen with a structure similar to that of other species of *Rhus*, as well as several other genera of the Rhoeae;
- a morphologically very similar hypostase, a tissue characteristic for the chalazal region of all anacardiaceous seed hitherto studied in detail.

Both *R. lancea* and *R. problematodes* have a seed coat with callose and lipids (cutins ?) present in cell walls of the hypostase, and a cuticular layer in the integumentary part. These may be adaptations to render the seed coat water-impermeable, thus protecting the physiologically ripe embryo against dehydration.

Differences between the seed of the two species include the following:

- calcium oxalate crystals in the hypodermal parenchyma of the chalazal seed coat are present in significant quantities in *R. problematodes* only;
- 1,4-linked polysaccharides and phenolic compounds are present in the cell walls of the hypostase in *R. problematodes* only.

Estimates of the size of the pachychalaza relative to the rest of the seed coat indicate that it is larger in *R. problematodes* (ca. 6.6%) than in *R. lancea* (ca 4.6%). Considering our hypothesis that a pachychalaza constituting the largest part of the seed coat occurs in the more primitive members of the Anacardiaceae (von Teichman & van Wyk in press), the relatively advanced state of the genus *Rhus* seems to be indicated. Unfortunately, current seed coat evidence for species of *Rhus* is too scanty to permit meaningful speculations on the possible adaptive significance of interspecific variation in the size of the pachychalaza. *Rhus longipes* Engl. represents a seemingly primitive species from eastern tropical Africa, an area considered by Engler (1881) to be the cradle of section *Gerontogae*. This species has, in addition to the regular unilocular ovaries, bilocular ovaries with up to five styles (ovary five-carpellate) as well as tri- and tetralocular ones (Fernandes 1962). A comparative study of the fruit and seed structure of this species would be most informative.

We support the view that *R. problematodes* represents a derived species adapted to extreme xeric conditions (Merxmüller & Roessler 1973). Macromorphologically, *R. problematodes* is at first glance indeed very different from all the other southern African species of *Rhus*, except *R. horrida* Eckl. & Zeyh. Although all other species of *Rhus* sect. *Gerontogae* have trifoliolate (rarely with up to five leaflets) leaves, simple leaves are known elsewhere in the



family, occurring for example in *Rhus* sect. *Trichocarpae* Engl. and sect. *Venenatae* Engl. (Engler 1892). However, the minute (3–5 mm long), sessile, trilobate to entire, and simple leaves of *R. problematodes* evidently represent a derived condition.

The possibility that *R. problematodes* might be closely allied to *R. horrida*, has apparently been overlooked by Merxmüller & Roessler (1973). The latter species also has a shrubby habit and minute leaves. Herbarium specimens of *R. horrida* studied by us revealed that the leaves are shortly petiolate and, although previously described as trifoliate (Schonland 1930), are also rarely simple and trilobate. The species also shows a preference for arid regions with a geographical range centred in Namaqualand, just south of the Namibian border. *R. problematodes* might even be considered derived from *R. horrida*, representing a further step in the reduction of leaf size, i.e. an extreme xeromorphy. Most significant is the presence in *R. horrida* of stellate glandular hairs similar to those described for *R. problematodes* (Diels 1898; confirmed by own observations). These stellate hairs were considered by Merxmüller & Roessler (1973) to be unique to *R. problematodes*. Diels (1898) also recorded similar stellate hairs in *R. magalis-montana* Sond. (= *R. burkeana* Sond.). The taxonomic significance of stellate hairs in *Rhus* requires closer scrutiny. Evidence from the present study has nevertheless confirmed that *R. problematodes* is without doubt correctly placed in the genus *Rhus*.

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