Generic position of *Protorhus namaquensis* Sprague (Anacardiaceae): evidence from seed structure

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Abstract. *Protorhus namaquensis* Sprague (Anacardiaceae, Rhoeae) is a rare, small tree of restricted distribution in an extremely arid part of southern Africa. The ovule is bitegmic, anatropous, and crassinucellar. Its hypostase extends secondarily together with the chalaza, forming a prominent part of the mature chalazal seed coat. An endotegmen, which develops from the inner epidermis of the inner integument, characterizes the integumentary seed coat and merges into the periphery of the chalazal seed coat in the partially pachychalazal seed. A comparison of the ovule and exalbuminous seed of *P. namaquensis* with those of *P. longifolia* (the lectotype of the genus *Protorhus*) and species of *Ozoroa* provides ample evidence that *P. namaquensis* is associated with members of the genus *Ozoroa*, rather than with *P. longifolia*. It is suggested that the very late impregnation with callose of the hypostase cell walls in *P. namaquensis* evolved as a response to its harsh semi-desert habitat. This callose deposition, together with the cuticular layer on the inner surface of the endotegmen, cutins in the hypostase cell walls, and deposits of tannin in the seed coat, probably constitute micromorphological survival strategies of this endemic species.

Keywords: Anacardiaceae; Callose; Endotegmen; Hypostase; Ovule; *Ozoroa*; Pachychalaza; *Protorhus*; Rhoeae; *Rhus*; Seed; Seed coat.

Introduction

In an extensive taxonomic revision of the Anacardiaceae, Engler (1892) placed the genus *Protorhus* Engl. in the tribe Rhoeae (Rhoideae). The genus is centred in Madagascar, with about 20 species. *Protorhus longifolia* (Bernh.) Engl., the lectotype of the genus (Farr et al., 1979), and *P. namaquensis* Sprague occur in southern Africa (Arnold & De Wet, 1993). These two are the only recorded species from the African continent. They have a mutually exclusive distribution and display significant morphological differences. *Protorhus longifolia* is a tree common in the subtropical forests of Natal and Kwa Zulu and it also occurs in the afromontane forests of Swaziland and Transvaal. Its fruit and seed structures were recently published (Von Teichman, 1991a,b).

Protorhus namaquensis is a multi-stemmed shrub or small tree up to about 3 m high, with simple, leathery, linear-lanceolate leaves, 28 – 45 mm long. It grows in arid mountainous terrain with very high summer temperatures and an erratic rainfall of ca. 100 – 200 mm per year, most of it falling in winter. It is dioecious and flowers in June-July. This rare and little known species is endemic to the harsh, semi-desert habitat in the lower Orange River Valley, part of White's (1983) Karoo-

Namib Regional Centre of endemism. *Rhus problematodes* Merxm. & Roessl., a curious microphyllous shrublet of the allied genus *Rhus L.* (Von Teichman and Van Wyk, 1991a), also occurs in this Centre of endemism.

When Merxmüller and Schreiber (1968) dealt with *P. namaquensis*, they justly raised doubts as to its current generic placement. The latter would have been easier if these authors had access to fruiting material. Low fruit set and the fact that this species has rarely been collected might explain their dilemma. Only in recent years has good fruiting material become available.

As shown again very recently, seed morphology, often emphasizing seed coat anatomy, is of considerable taxonomic importance (Bouman and Devente, 1992; Setoguchi et al., 1992; Tobe et al., 1992). Authors such as Boesewinkel and Bouman (1984) stress that knowledge of the ovule features and of the ontogeny of the seed coat is essential for the precise interpretation of the mature seed coat.

The purpose of this contribution, which is part of a comprehensive survey of the seed structure of the Anacardiaceae, is to describe the ovule and seed struc-

ture of *Protorhus namaquensis*. These data are used in a comparison of the ovule and seed of *P. namaquensis* with those of its alleged African counterpart, *P. longifolia*, as well as with those of species of the closely allied genus *Ozoroa* Del., notably *O. paniculosa* (Sonder) R. & A. Fernandes (Von Teichman, 1993); the aim being to evaluate the contribution of these characters for a reassessment of the generic position of *P. namaquensis*. Possible micromorphological adaptations of the seed to the semi-desert habitat are also discussed.

Materials and Methods

Flowers at anthesis and fruit at various developmental stages were collected near Goodhouse Poort in southern Namibia (voucher specimens: *Archer 1485* in PRE; *Van Wyk 8617, 8621* and *8738* in PRU). Grid reference of all the localities is 2818 CD.

Material was preserved in FAA, dissected and washed in 50% ethanol, dehydrated in ethanol, n-propanol, and n-butanol. Infiltration and embedding were done in a monomer mixture containing hydroxyethyl methacrylate (GMA), as described by Feder and O'Brien (1968). Composition of the monomer mixture, preparation and staining of the 3 µm thick GMA-sections, involving the periodic acid-Schiff's (PAS) reaction, and toluidine blue O (Tol. blue) counterstaining are described in more detail by Von Teichman (1987). Crystals of calcium oxalate and starch grains were observed under crossed polarized filters.

In addition to the PAS-reaction, starch was localized with the standard iodine potassium iodide technique. Detection of callose was done with 0.1% w/v water-soluble aniline blue in 0.1 M K_3PO_4 buffer at pH 12.4, and examined with a Nikon Optiphot light microscope equipped with epifluorescence optics. Histochemical staining for proteins was done with amido black 10B according to Bullock et al. (1980). To test for cutin, a
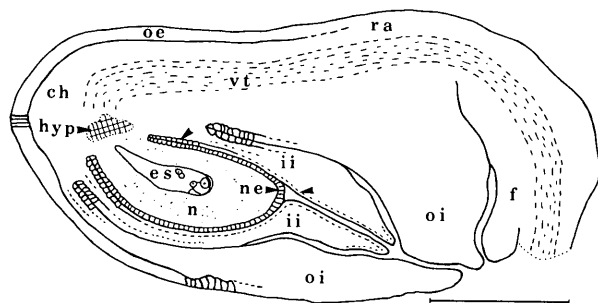

Fig. 2. Young fruit and seed of *P. namaquensis*. A) Longitudinal section. B) lateral view of young seed. Abbreviations: **e**, small embryo; **ch**, chalazal seed coat; **en**, endocarp; **ex**, exocarp; **f**, funicle; **fl**, fruit locule; **int**, integumentary seed coat; **me**, mesocarp; **s**, seed; **sd**, secretory ducts. Scale bar in A and B = 3 mm.

10-min application of a saturated solution of Sudan black B in 70% ethanol was used. After rinsing in 70% ethanol, the sections were mounted in liquefied glycerine jelly.

The terminology of the seed coat follows Corner (1976), which is widely employed (Schmid, 1986).

Fig. 3. Ripe seed of *P. namaquensis*. A) Longitudinal section of the ripe seed coat surrounding the embryo. B) Lateral view of the ripe seed showing the size and shape. For these drawings the funicle was slightly lifted. Abbreviations: **ch**, chalazal seed coat; **cot**, cotyledon; **int**, integumentary seed coat; **iz**, intermediary zone; **r**, radicle; **ra**, raphe; **sc**, seed coat. Positions of the transverse sections shown in Figures 4-6 are indicated by **a**, **b** and **c**. Scale bar = 3 mm.

Fig. 1. Ovule structure of *P. namaquensis*. Abbreviations: **ch**, chalaza; **es**, embryo sac; **f**, funicle; **hyp**, hypostase *s.l.*; **ii**, inner integument; **n**, nucellus; **ne**, nucellar epidermis; **oe**, outer epidermis; **oi**, outer integument; **ra**, raphe; **vt**, vascular tissue. Arrow heads indicate inner epidermis of the ii, i.e. the future endotegmen. Scale bar = 0.3 mm.
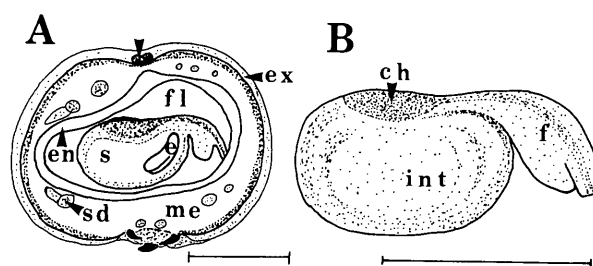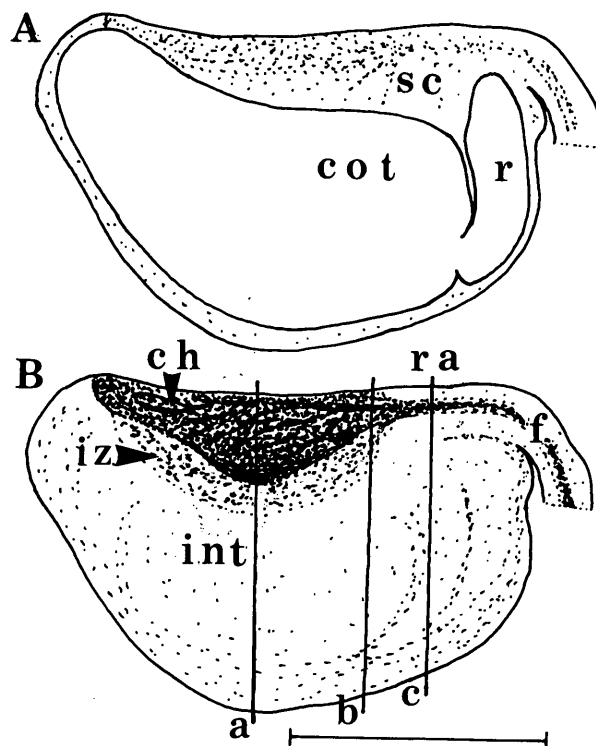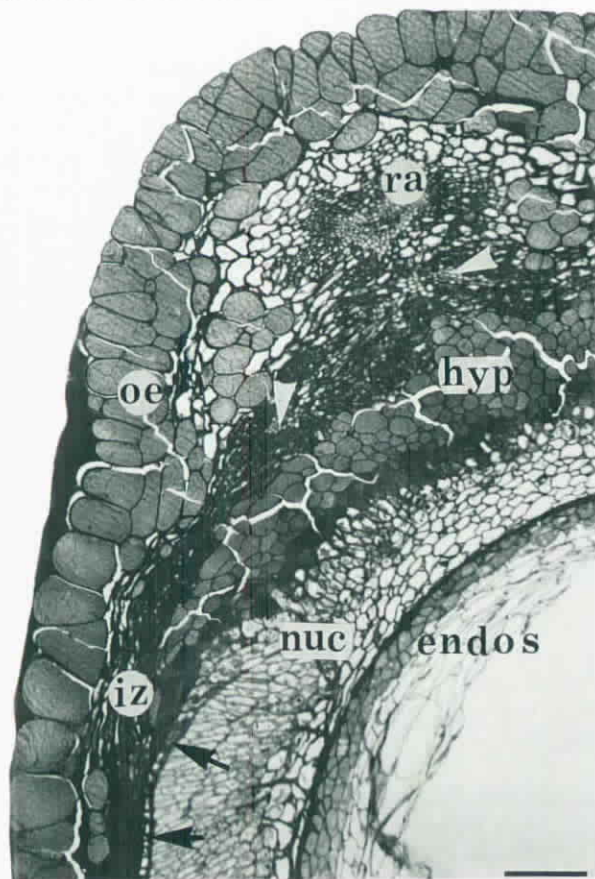
Fig. 4. Transverse section of the mature seed coat of *P. namaquensis* at position **a** in Fig. 3B. Abbreviations: **endos,** endosperm remnants; **hyp,** hypostase *s.l.*; **iz,** intermediary zone; **nuc,** nucellus; **oe,** outer epidermis; **ra,** raphe vascular bundle. White arrow heads indicate vascular tissue. Black arrows show the position of the endotegmen in the periphery of the integumentary seed coat. PAS-reaction & Tol. blue staining. Scale bar = 100 μm.

Fig. 5. Drawing of a transverse section at position **b** in Fig. 3B. Abbreviations: **endos,** endosperm remnants; **et,** endotegmen of integumentary seed coat; **hyp,** hypostase *s.l.* in chalazal seed coat; **n,** nucellar remnants; **ne,** nucellar epidermis; **oe,** outer epidermis; **ra,** raphe vascular bundle; **vt,** parenchyma with vascular tissue of chalazal seed coat. Scale bar = 400 μm.

Results

At anthesis the ovule of *Protorhus namaquensis* (Fig. 1) is bitegmic, anatropous and crassinucellar. It is further characterized by a nuclear endosperm development. A tanniniferous outer epidermis and the meristematic inner epidermis of the inner integument also characterize the ovule. The proximal part of the inner integument is 3 – 4 cell layers thick. A plate-like group of meristematic cells can be distinguished in the nucellar tissue on the chalazal side. This is the hypostase *sensu lato*. The distinction between a hypostase *sensu lato* and hypostase *sensu stricto* in the ovules of the Anacardiaceae is suggested by Von Teichman (1988). As only a hypostase *sensu lato* is present in *P. namaquensis*, it will henceforth be referred to as hypostase in this paper.

As the ovule of *P. namaquensis* is inserted on the lateral side in the ovary, the seed takes the same position in the developing fruit (Fig. 2A). As in the other Anacardiaceae, fruit development of *P. namaquensis* precedes the growth of the seed. Young seeds (Fig. 2B)
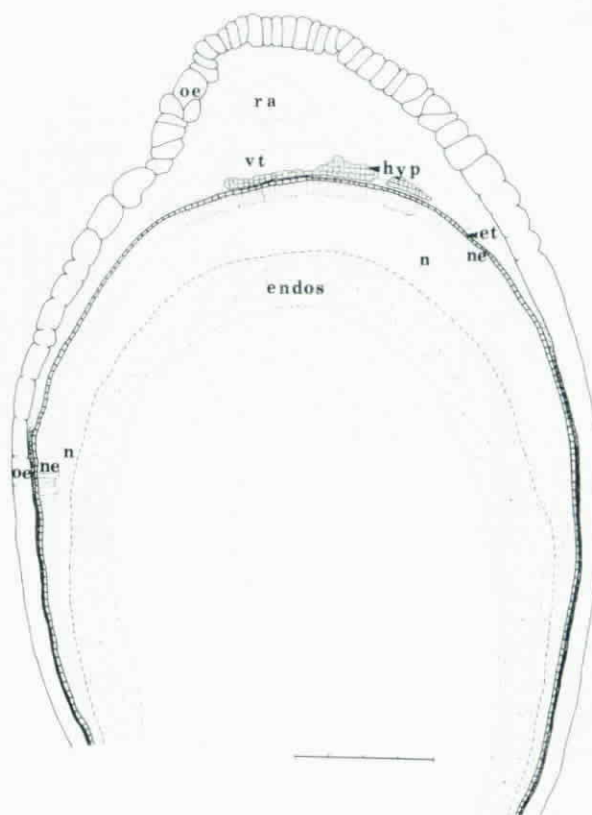
collected about nine weeks after anthesis (end of August) are laterally compressed, and they contain a small, white embryo surrounded by endosperm remnants and a thin light brown seed coat. Mature and ripe seeds were collected early in November and towards the end of December, respectively; the latter is illustrated in Figure 3. In all these seeds the funicle is tightly appressed to the seed coat. The fragile, brittle membraneous seed coat exhibits a dark brown saddle-like part. This represents the secondarily extended chalaza with tanniniferous hypostase. The seed of *P. namaquensis* is partially pachychalazal (Fig. 3B).

The seed coat anatomy in different developmental stages was studied by means of transverse sections through the lines a, b, and c indicated in Fig. 3B. Seed coat anatomy of the young seed differs from that of the ripe seed only in the degree of differentiation of the endotegmen and the degree to which cell layers have become squashed and/or the endosperm is absorbed. The mature and the ripe seed exhibit the following distinctive structural features (Figs. 4 – 6).
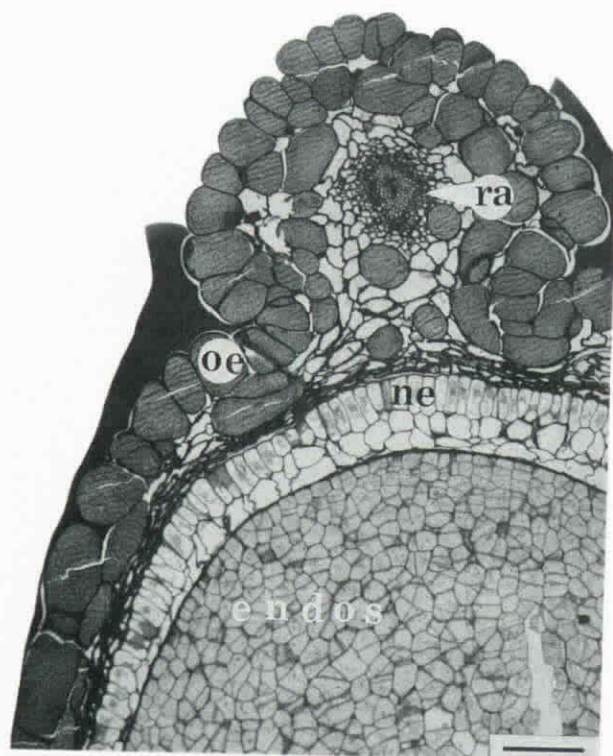
Fig. 6. Transverse section of the mature seed coat of *P. namaquensis* at position **c** (the raphe) in Fig. 3B. Abbreviations: **endos,** cellular endosperm remnants; **ne,** nucellar epidermis; **oe,** outer epidermis; **ra,** raphe vascular bundle. To the outside of the ne the cuticular layer can be distinguished in places; it is abutting on the endotegmen, which is not so well-developed here, where it borders on the raphal seed coat. PAS-reaction & Tol. blue staining. Scale bar = 100 μm.

The outer epidermal cells of the entire seed coat are densely tanniniferous. They are covered with a thin cuticle as well as partly with an outermost unidentified, possibly phenolic mucilage or resinous substance.

In the chalazal seed coat (Figs. 4 and 5), hypodermal tanniniferous parenchyma cells are followed by or lie interspersed with parenchyma and the vascular tissue. Only the tracheoids (*sensu* Schmid, 1986) are not crushed to varying degrees. Abutting on this parenchyma is the hypostase. Its cells are contiguous, thin-walled, distinctly tanniniferous and form a zone which is easily distinguishable (Fig. 4). Only in the physiologically ripe seed, the cell walls of the hypostase are secondarily impregnated with a thin layer of callose and with lipids, the latter most probably comprising cutin.

In the intermediary zone (Figs. 3B and 4), the periphery of this hypodermal tissue and the hypostase merge into the periphery of the integumentary seed coat. Besides the outer epidermis, the latter comprises the more or less compressed middle and inner layers of the outer integument, the compressed outer and middle parts of the inner integument as well as its inner epidermis, i.e.

the endotegmen. A few calcium oxalate crystals are dispersed within some of the hypodermal parenchyma cells and prevent these cells from being crushed. The endotegmen characterizes the integumentary seed coat, bordering also on the raphal part of the mature seed coat (Fig. 6). The radial and tangential cell walls of the endotegmen are secondarily thickened, lignified, and abundantly pitted.

On the anti-raphal side of the seed (see lower part in Fig. 5), the integumentary seed coat comprises the outer epidermis of the outer integument, totally crushed remnants of the middle and inner layers of the outer integument, crushed outer and middle parts of the inner integument, and the endotegmen. A well-developed cuticular layer, comprising the cuticles of the endotegmen and nucellar epidermis, abuts on the squashed nucellus. As this cuticular layer also merges into the periphery of the hypostase, the embryo of the ripe seed is completely surrounded by a protective layer of cutin.

The nucellar epidermis retains its identity (Figs. 5 and 6), except at the extreme anti-raphal side where it is crushed. Only the outermost layers of the cellular endosperm are discernible, but these also diminish at the anti-raphal side.

Sections through the raphe bundle (Fig. 6) reveal its amphicribral structure. A thick zone of cellular endosperm remnants is present here and may give some elasticity to the brittle seed coat.

Nutrient reserves in this exalbuminous seed are stored as energy-rich lipids and proteins within the cotyledons of the embryo. The hypodermal storage parenchyma is palisade-like, while secretory ducts associated with the vascular tissue occur in the mesophyll of the cotyledons.

Discussion

In species of the tribe Spondiadeae, e.g. *Lannea discolor* (Sonder) Engl., a hypostase *sensu stricto* is present in the form of a small group of cells situated between the embryo sac and the hypostase *sensu lato* (Von Teichman, 1988). In contrast to the latter, the hypostase *sensu stricto* does not take part in the formation of the seed coat.

The ovule and seed structure of *Protorhus namaquensis* will now be compared with that of *P. longifolia* and *Ozoroa paniculosa* (henceforth referred to as *Ozoroa*) (Table 1). Ovules of all three species are anatropous, bitegmic, and crassinucellar, and are characterized by a nuclear endosperm development. These character states are considered plesiomorphic for angiosperms (e.g. Bouman and Devente, 1992), and are shared by most other taxa of the Anacardiaceae studied to date, except for *Mangifera indica* L. with unitegmic ovules (Robbertse et al., 1986). There are no significant differences in the sizes of the ovules of these taxa. This also

Table 1. Comparison of ovule and seed characters in *Protorhus Longifolia*, *P. namaquensis*, and *Ozoroa paniculosa*.

Character	P. Longifolia	P. namaquensis and Ozoroa paniculosa
Ovule type	anatropous	anatropous
Number of integuments	bitegmic	bitegmic
Nucellus type	crassinucellar	crassinucellar
Endosperm development	nuclear	nuclear
Ovule insertion	apical	lateral
Pachychalazy in ovule	present	absent
Hypostase in ovule	extensive	reduced
Seed size	large	small
Degree of pachychalazy	pachychalazal	partially pachychalazal
Callose in ripe seed coat	absent	present
Embryo color	chlorophyllous	white
Principal nutrient reserves	starch	lipid and protein

applies to the general flower morphology (Von Teichman and Van Wyk, 1994). Bracteoles, however, tend to be caducous and pedicels are articulated near the apex only in *P. namaquensis* and *Ozoroa*. The latter two taxa also share a distinctly papillate floral disc and a lateral ovule insertion. In *P. longifolia* the surface of the floral disc is smooth and possesses stomata, while the ovule is inserted apically. The hypostase *sensu lato* is only extensive in the pachychalazal ovule of *P. longifolia* (compare Fig. 2 of Von Teichman, 1991b).

In all three species the funicle is appressed to the mature seed coat. The following features of the seed are shared not only by the three taxa compared, but by all of the other studied species of the Anacardiaceae:

1) Vascular bundle is amphicribral in the raphe.

2) Xylem in the chalazal vascular bundles consists of tracheoids with helical secondary wall thickenings.

3) A hypostase, consisting of contiguous, relatively small, tanniniferous and thin-walled parenchyma cells, forms an integral part of the mature chalazal seed coat

4) The mature seed is exalbuminous.

Furthermore, the mature seeds of the three taxa discussed here share similar cuticular layers, an endotegmen, and the extensive chalaza or pachychalaza. However, the degree of pachychalazy varies, and the distinctly smaller seeds of *P. namaquensis* and *Ozoroa* are partially pachychalazal, since their integuments still contribute significantly to the development of the seed coat. In contrast, the contribution of the integuments is negligible in the large pachychalazal seed of *P. longifolia*.

A secondary impregnation of the hypostase cell walls of the ripe seed often concerns lipids, most probably cutin, since they form a continuum with the inner cuticular layer. This occurs in the three taxa compared, as well

as in *Mangifera indica*, species of *Tapirira* Aubl., *Sclerocarya* Hochst. and *Spondias* L., and in *Rhus lancea* L. f. and *R. problematodes* (Von Teichman, 1990, 1991c). In *Tapirira*, the latter two species of *Rhus*, *Protorhus namaquensis*, and *Ozoroa paniculosa*, cell walls of the hypostase are additionally impregnated with callose. This callose impregnation does not occur in *P. longifolia*. It is noticeable that this callose is present predominantly in species from savannah regions (where periodical droughts occur), i.e. in *O. paniculosa* and *R. lancea*, and in species adapted to extreme arid conditions, i.e. in *P. namaquensis* and *R. problematodes*.

Recent studies of the occurrence of callose in the cell wall of microsporocytes showed that "callose apparently does not act as an impermeable barrier to the passage of high molecular weight substances such as cerous ions or cerium perhydroxide" (Rodríguez-García and Majewska-Sawka, 1992). These authors also share the opinion of Bhandari (1984), that the functional role of callose remains speculative. Vishnyakova (1991) found that callose has *inter alia* an isolating function by effectively reducing permeability, and is quite often synthesized as a response to stress. Hussey et al. (1992) concluded that callose deposition is a common wound response, thereby confirming previous studies discussed by Vishnyakova (1991).

In all the seeds of the Anacardiaceae studied to date, the secondary impregnation of the hypostase cell walls with callose occurs very late in the seed coat development, i.e. in the ripe seeds. Present data suggest that callose impregnation in these seeds probably evolved in response to stress, as part of the micromorphological strategy for survival during droughts or in extreme xeric environments.

Concerning the nutrient reserves stored in the embryo (cotyledons), starch is the main nutrient in the large, green embryo of *Protorhus longifolia*, whereas lipids

and proteins (high energy nutrients) occur in the small, white embryo of *P. namaquensis, Ozoroa* and *Rhus problematodes*. This study therefore supports the hypotheses of Von Teichman and Van Wyk (1991b) that larger-sized pachychalazal seed with starch as the main nutrient reserve occurs predominantly in species of the Anacardiaceae which are distributed in tropical and/or subtropical and generally relatively moist habitats. In contrast, a reduction in seed size, the secondary reduction of the chalaza (i.e. presence of a partial pachychalaza) and high-energy nutrient reserves characterize seeds of taxa in more temperate, arid or semi-arid habitats. Reduced seed size and a small pachychalaza are regarded as derived character states.

Conclusions

Although a few ovule and seed characters are shared by *Protorhus namaquensis, P. longifolia,* and a species of *Ozoroa,* several other characters typify *P. namaquensis* and *Ozoroa,* while the contrasting character states occur in *P. longifolia* (Table 1). A study discussing the fruit structure of these taxa indicates that features such as smaller-sized drupes, drupe morphology, presence of starch in the exocarp, modified stomata with occluded pores, and the entire endocarp structure are common only to *P. namaquensis* and *O. paniculosa,* but differ from those in *P. longifolia* (Von Teichman and Van Wyk, 1994).

This study provides ample evidence that *P. namaquensis* is related to the genus *Ozoroa* rather than to *P. longifolia,* which is the only other species of *Protorhus* in Africa. Preliminary and/or unpublished studies of fruit and seed of other species of *Ozoroa* indicate that *P. namaquensis* is most closely related to a group of *Ozoroa* species endemic to the semi-desert areas of the northwestern Cape and southern Namibia.

Abundance of tanniniferous substances in the fruit and seed coat may represent antiherbivoral, antimicrobial, or antiviral defence mechanisms. The presence of lipids and callose in the seed coat of the ripe seed suggests survival strategies to curb water loss in the harsh semi-desert habitat in which *P. namaquensis* occurs.

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從種子的結構來討論漆樹科 *Protorhus namaquensis* Sprague 屬的定位

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Protorhus namaquensis Sprague 屬漆樹科,小樹,是侷現於南非極乾旱地區的稀有種。其胚珠具雙珠被,屬倒生、厚珠心型。胚珠內承珠盤二次沿伸與接合點相接,在成熟種子接合點部位形成一明顯構造。種皮的起源來自接合點及珠被。由珠被發育而來的種皮又以內珠被內表皮衍生而來的最具特色。將 *Protorhus namaquensis, P. longifolia* 及 *Ozoroa* 三個分類群之胚珠及無胚乳種子相比較,得到足夠的証據顯示 *P. namaquensis* 與 *Ozoroa* 屬的成員較接近,而與 *P. longifolia* 較無關。此外,本文並提出二點假設,一是承珠盤在後期添加胼胝質的現象可能是對半沙漠嚴苛的環境的一種反應。此外, 這層胼胝質、內種皮內表面的厚角皮層、承珠盤細胞壁上較厚的角皮質以及種皮內單寧的沈積等可能是表現在微形態方面適應乾旱的機制。

關鍵詞:漆樹科;胼胝質;內種皮;承珠盤;胚珠;*Ozoroa*;後接合點型;*Protorhus*;*Rhoeae*;Rhus;種子;種皮。