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Two closely related species of *Caloplaca* (Teloschistaceae, Lichenes) from the Namib Desert

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ABSTRACT

The anatomical and reproductive adaptations of two closely related lichen species, *Caloplaca elegantissima* (Nyl.) Zahlbr. and *C.* **namibensis** Kärnef., sp. nov., occurring in the outer Namib fog desert, are discussed. Both species belong to the crustose forms, frequently found in the remarkably rich lichen communities, which largely depend on fog precipitation for their water supply. Both species are endemic to the Namib Desert. They are mainly distributed in South West Africa/Namibia but also extend into south-western Angola. The asexual isidiate species, *C.* **namibensis** Kärnef., is described as new.

UITTREKSEL

Die anatomiese en voortplantingsaanpassings van twee naverwante ligeenspesies, *Caloplaca elegantissima* (Nyl.) Zahlbr. en *C.* **namibensis** Kärnef., sp. nov., wat in die buitenste Namib-miswoestyn voorkom, word bespreek. Albei spesies behoort tot die korsagtige vorms wat dikwels aangetref word in die buitengewoon ryk ligeengemeenskappe wat hoofsaaklik van die misneerslag afhanklik is vir water. Albei spesies is endemies in die Namibwoestyn. Hulle kom hoofsaaklik in Suidwes-Afrika/Namibië voor maar is ook tot in suidwestelike Angola versprei. Die ongeslagtelike isidiate spesie *C.* **namibensis** Kärnef. word nuut beskryf.

INTRODUCTION

The Namib is a narrow belt of desert more than 2 000 km long, stretching northwards from the Olifants River in the Cape Province (RSA) to Mossamedes in Angola. The central Namib Desert is characterized by the world's most magnificent sand dunes. The gravel desert, occupying most of the landward parts of the central and northern Namib Desert, is usually almost devoid of higher plants. The few which occur are mainly succulents with specialized anatomical and physiological adaptations to survive in the harsh environment (Walter 1973; White 1983). Ephemeral species appear only after extremely rare rain showers.

The desert is, however, not entirely devoid of vegetation. Rock outcrops, stones and pebbles are frequently covered with colourful lichens. Even the seemingly barren soil can be covered with fruticose lichens over large areas, similar to the lichen cover which is a familiar sight in arctic or subarctic regions in the northern hemisphere. Kappen (1982) estimated the biomass in one of these areas at 250 g/m^2. The existence of this spectacular lichen vegetation is entirely due to the effect of frequent fogs. These fogs are caused by the cold Benguela current which flows northwards from the southern Atlantic Ocean along the south-western coast of Africa. Fog-induced lichen communities also occur in the coastal deserts of Peru and Baja California (Thomson & Iltis 1968; Rundel *et al.* 1972).

Lichens occurring in these coastal desert areas can evidently absorb sufficient amounts of moisture from fog to allow photosynthesis for successful reproduction and dispersal. Lange *et al.* (1970a, 1970b) studied the effect of dew on lichen communities in the Negev Desert. According to them the early morning dew provided sufficient moisture for about 3 h of photosynthesis. Apart from the effect of fog, the annual precipitation in the central Namib is not more than 30 mm, and it may not even rain every year (Kappen 1982).

More or less well known lichens occurring in the desert are *Combea mollusca* (Ach.) Nyl., *Santessonia namibensis* Hale & Vobis, *Teloschistes capensis* (L. f.) Müll. Arg., *Xanthomaculina convoluta* (Hue) Hale, *Xanthomaculina hottentotta* (Ach.) Hale and *Xanthoria marlothii* Zahlbr. All these species have various anatomical adaptations which aid in the reduction of light intensity and evaporation. Büdel & Wessels (1986) discussed the remarkable anatomical adaptions of *Xanthomaculina convoluta* (as *Parmelia hueana* Gyeln.). It is presumed that heavily pigmented layers, as encountered in *Xanthodactylon flammeum* (L. f.) Dodge, could be effective in reducing light intensity. Members of this species are less deeply pigmented in populations further south, in the Cape Province.

Teloschistes capensis (L. f.) Müll. Arg., forms extensive populations in areas north of Swakopmund, and has a deeper pigmentation than similar populations found in the Cape. Individuals which occur in the central Namib are furthermore covered by a rather dense tomentum, which is much sparser in the Cape. Presumably this dense tomentum favours the absorption of water derived from the coastal fog.

Caloplaca eudoxa (Müll. Arg.) Zahlbr. is another remarkable endemic member of the Namib lichen flora. The species is characterized by a subfruticose growth form and thick scleroplectenchymatous hyphae which cover the photobiont (Poelt & Pelleter 1984). The two *Caloplaca* species discussed in this paper, *C. elegantissima* (Nyl.) Zahlbr. and *C. namibensis* Kärnef., have

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similar anatomical adaptations. They are among the most abundant and spectacular crustose lichen species endemic to the Namib.

MATERIAL AND METHODS

The material which formed the basis of this study came mainly from my own collections made during a visit to the central Namib fog desert in January 1986. I have also studied a few collections on loan from B, BM, G, H, LISU and S. The macrophotographs were taken with an Olympus OM-2 camera, through a Zeiss dissecting microscope.

For anatomical studies, the material was sectioned on a Kryomat, Leitz freezing microtome. The sections were embedded in lactophenol cotton-blue, studied, and photographed by means of an Olympus OM-2 camera, through a Leitz, Ortholux microscope. Secondary compounds present in the material were determined by means of standardized TLC methods (Culberson 1972).

THE SPECIES

1. **Caloplaca elegantissima** *(Nyl.) Zahlbr.*, Catalogus lichenum universalis 7: 238 (1931). *Lecanora elegantissima* Nyl.: 510 (1868). Type: SWA/Namibia, 2114 (Omaruru): Lagunenberg Mountain, north-east of Mile 72 (−CC), *Kärnefelt 8605−26* (LD, neo., here designated).

Caloplaca diploplaca Zahlbr.: 268 (1932). Type: SWA/Namibia, 1927, *Kriege* sub *P. van der Byl 709* (STEU, lecto., selected here).

Caloplaca indurata Wirth & Vezda: 1 (1975). Type: Africa austro-occidentalis, Swakopmund, 15 km ad orientem urbis Swakopmund, Sept. 1974, *Volk*, in Vezda, Lich. sel. exs. 1346 (STU, holo.; iso. distributed in Vezda, Lich. sel. exs. 1346, seen in H, LD, S).

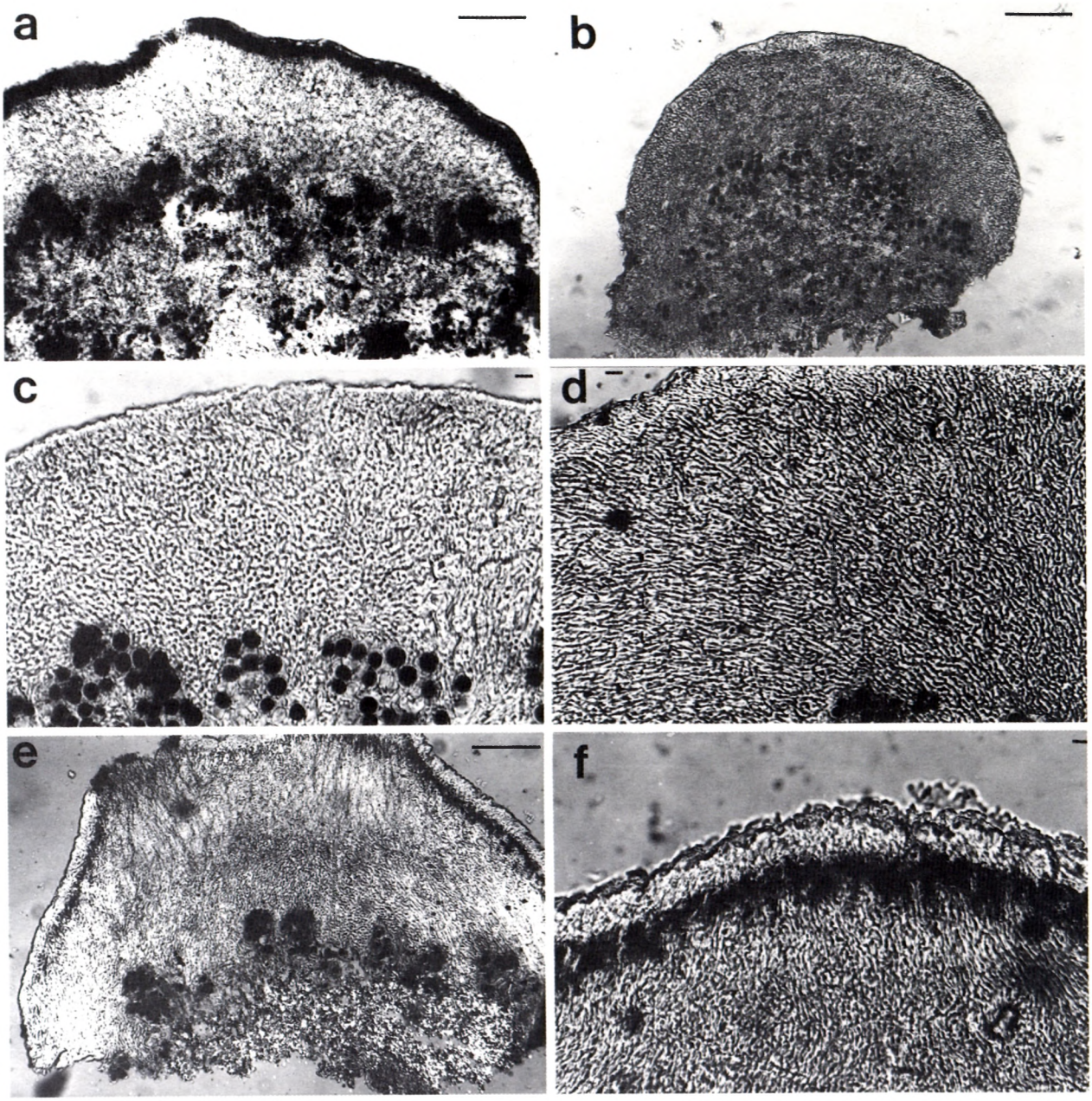

FIGURE 1.—a, *C. namibensis*, cross section, dark pigmented layer and thick cortical layer covering the darkly stained photobiont, *Kärnefelt 8602-56* (LD), bar = 100 μm; b, *C. namibensis*, cross section, *Kärnefelt 8602-56* (LD), bar = 100 μm; c, *C. namibensis*, cross section showing structure of cortical layer, *Kärnefelt 8603a-5* (LD), bar = 10 μm; d, *C. elegantissima*, cross section showing structure of cortical layer, *Desmond 25276* (LD), bar = 10 μm; e, *C. elegantissima*, cross section of specimen showing the internal pigmented layer and thick cortical layer covering the basally located photobiont, overlying a medullary layer with crystals, *Vezda*, Lich. sel. exs. 1346 (LD), bar = 100 μm; f, *C. elegantissima*, cross section showing the internal pigmented layer, Vezda, Lich. sel. exs. 1346 (LD), bar = 10 μm.

Thallus radiate, (5−)20−50(−100) mm across, the smallest occurring on pebbles, the largest on rather large rocks, composed of cartilaginous convex lobes 0,5−1,8 mm broad, 5−30 mm long, marginally distinctively effigurated, weakly dichotomously branched, secondarily becoming raised and unattached; central portions composed of short, 1−3 mm long, irregularly arranged, rather sparse lobes; short accessory lobules occasionally developed at the margins of the lobes; scarlet, orange-red to pale orange, larger individuals usually lighter pigmented at margins.

Epinecral zone 20−45 μm thick, prosoplectenchymatous, hyphae thick-walled (Figure 1d, e). *Cortex* hyaline, 150−230 μm thick, composed of strongly gelatinized hyphae, the upper 15−20 μm, orange-yellowish pigmented (Figure 1d, e, f). *Photobiont* green and spherical, 5,5−12 μm in diameter, occurring in clusters 35−75 μm large, mainly embedded in a layer of strongly gelatinized hyphae. *Medulla* 200−250 μm thick, composed of more lax hyphae, partly embedding the clustered photobiont, often containing numerous small granules, fluorescent when examined with interference contrast microscopy.

Apothecia scattered, limited mainly to central thallus portions, but may also develop marginally on the peripheral lobes, sessile, becoming slightly raised with maturity, 0,5−1,5 mm across, margin entire or occasionally irregular, several smaller apothecia occasionally fused; disc at first cupular or plane, becoming strongly convex, usually darker or of the same colour as the lobes. *Excipulum* up to 100 μm thick. *Hymenium* 75−100 μm thick, covered by a thin epihymenial layer. *Asci* 45−50 × 9−12 μm. *Ascospores* broadly ellipsoidal, 10−12 × 8−9 μm, septum ± 2 μm thick. *Paraphyses* 75−100 × 0,75 μm. *Hypothecium* up to 300 μm deep, hyaline. *Photobiont* concentrated in clusters below the hypothecium. *Conidiomata* not observed.

SWA/NAMIBIA.—2113 (Cape Cross): Skeleton Coast Park, marble ridge north of entrance gate at Ugabmund (−BA), *Kärnefelt 8609-5*; *8609-6*; *8609-22*; *8609-24*; *8609-30*; *8609-39* (LD). 2114 (Omaruru): Lagunenberg Mountain, north-east of Mile 72 (−CC), *Kärnefelt 8605-19*; *8605-20*; *8605-26* (LD); gravel flats east of Cape Cross (−CA), *Kärnefelt 8610-29*; *8610-37*; *8610-38* (LD); *Wessels 5132*; *5134a* (UNIVERSITY OF THE NORTH); 25 km north of Henties Bay Road junction, black ridge (−CA), *Nordenstam & Lundgren 2317* (S). 2214 (Swakopmund): gravel flats east of Swakopmund (−DA), *Kärnefelt 8602-33*; *8602-34*; *8602-49*; *8602-52* (LD); 15 km, in Sept.-oriente a urbe Swakopmund (−DA), 1974, *Volk* in Vezda, Lich. sel. exs. 1346 as *C. indurata* (H, LD, S); 35 km north of Swakopmund (−AD), *Nordenstam & Lundgren 2322* (S); Namib Desert (−??), *Desmond 25276* (LD).

C. elegantissima contains several anthraquinones, which were difficult to separate with the TLC method used. Extracts of *C. elegantissima* and *C. namibensis* were examined together on the same TLC plate, but the anthraquinones could not be distinguished due to the weakness of the spots (the anthraquinones are difficult to extract from the cortex). Steiner & Hauschild (1970) reported the presence of emodin (traces), parietin, teloschistin, xanthorin, erythroglaucin, fallacinal and parietinic acid in *C. elegantissima*. No material was cited, but it is presumed that the fertile species was investigated as it is the most conspicuous of the two species.

Typification

The original description of *Lecanora (Placodium) elegantissma* was presumably based on composite material involving both species discussed in this article. The short morphological diagnosis described a narrow-lobed specimen resembling *Placodium elegans* [=*Xanthoria elegans* (Link) Th. Fr.], but no isidia or similar structures were mentioned (Nylander 1868). The diagnosis, however, included a description of apothecia and ascospores and the original spore size mentioned corresponds well with my own results based on examined asci of *C. elegantissima*.

The fragment (annotated '*vestigio*') in the Nylander herbarium at Helsinki, does not belong to *C. elegantissima* but to *C. namibensis*. It therefore cannot possibly be used as the type of *C. elegantissima*. The isidia have, however, been torn off during more than 100 years of storage, leaving distinctive marks at their previous location (H-NYL 30513).

Nylander cited no material other than Welwitsch's collections from Mossamedes (erroneously spelled Monamedes). In a footnote he discussed a new species *Placodium flavorubens* Nyl. [=*Caloplaca flavorubens* (Nyl.) Zahlbr.] occurring on coastal rocks in southern Africa, which presumably is identical to *C. sublobulata* (Nyl.) Zahlbr. Since *C. elegantissima* and *C. namibensis* occur in the same habitats and occasionally also cover the same stones, Welwitsch most probably collected both species on a few of the stone samples. On Welwitsch's request, Nylander eventually studied these samples while in Paris. He must have received a mixed collection of mainly *C. namibensis*, which also included a few lobes and apothecia of *C. elegantissima*.

Other possible type material from Welwitsch's original collection is kept at BM and LISU (see Vainio 1901). The material I received on loan from these herbaria, no. 45 Welwitsch Iter Angolense, Mossamedes, near Cabo Negro, unfortunately turned out to belong to the same species described here as new, and characterized by rather narrow lobes and small isidia or fragments of isidia. Vainio (1901) also cited nos 48 and 49 as pr. p. under his *Placodium elegantissimum*, but these numbers are mainly a brown *Parmelia*, and it is not likely that Nylander used this material for his original description.

Since all known type material of *C. elegantissima* must be superseded as being in serious conflict with the protologue (Art. 8 of the I.C.B.N.), it is either possible to choose a neotype, or to have the name rejected in accordance with Art. 69 of the I.C.B.N. In fact, I did not see any material in the original collections which corresponds in any way to *C. elegantissima*, other than the type material of much younger epithets such as *C. diploplaca* Zahlbruckner (1932) and *C. indurata* Wirth & Vezda (1975).

The provisons of Art. 69 (a name must be rejected if it has been widely and persistently used for a taxon not including its type), is not really relevant in this case. I have therefore decided to select a neotype from my own collections of *C. elegantissima*.

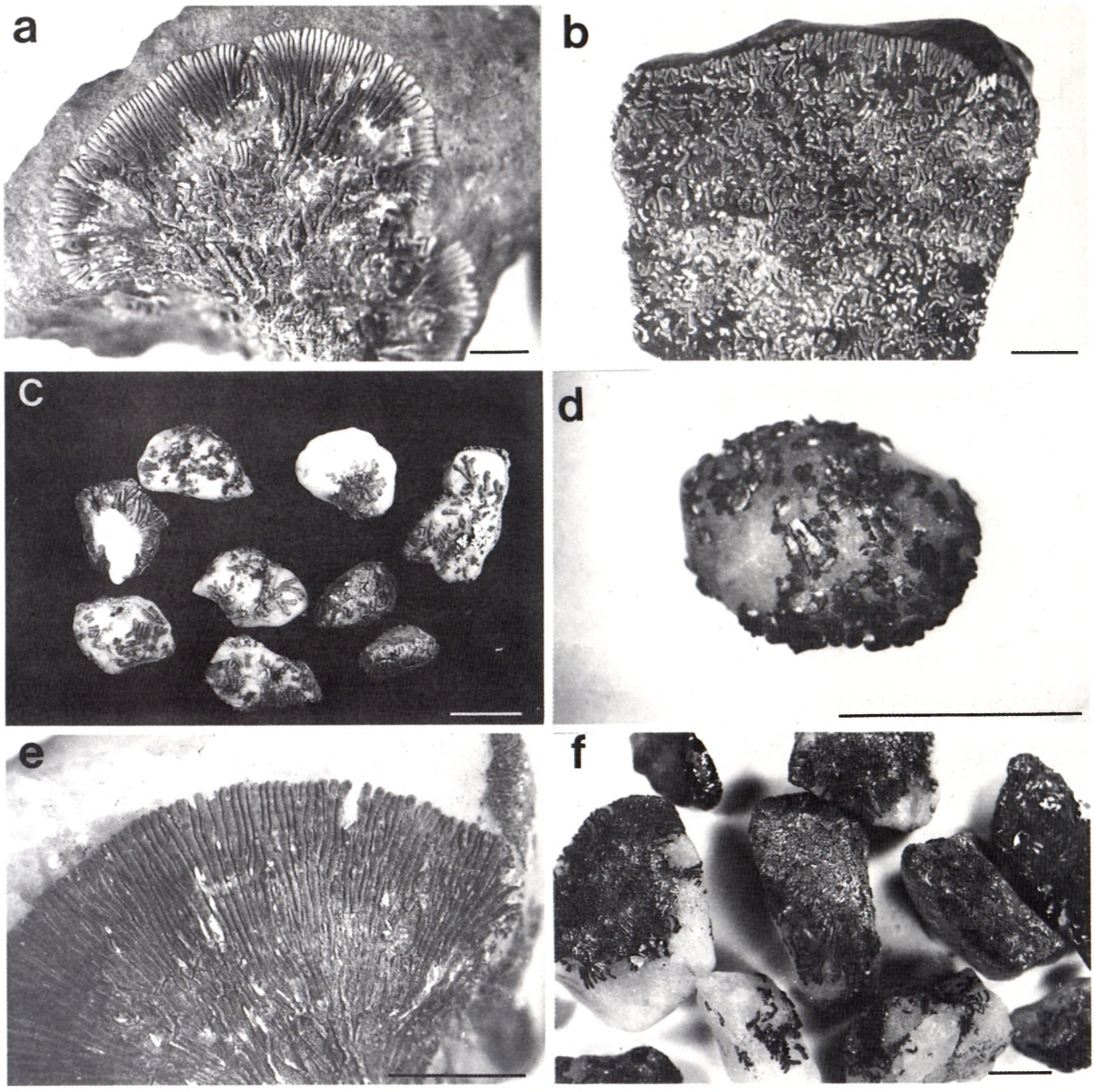

FIGURE 2.—a, *Caloplaca elegantissima*, well developed fertile specimen on dolerite, *Kärnefelt 8605-26* (LD); b, *C. elegantissima*, specimen dominated by rather short central lobes, on dolerite, *Kärnefelt 8605*-39 (LD); c, *C. elegantissima*, specimen on quartzite pebbles, *Kärnefelt 8605-19* (LD); d, *C. elegantissima* close-up of specimen on quartzite pebble; accessory lobules seen in c & d, *Kärnefelt 8605-20* (LD); e, *C. namibensis*, close-up of specimen with rather long densely arranged marginal lobes, on quartzite, *Kärnefelt 8602-36* (LD); f, *C. namibensis*, specimen on quartzite pebbles, the central portions covered with minute isidia, *Kärnefelt 8610-2* (LD). All bars = 10 mm.

2. **Caloplaca namibensis** *Kärnef.*, sp. nov.

?*Caloplaca diploplaca* Zahlbr. var. *gracilior* Zahlbr., Annales de cryptogamie exotique 5: 269 (1932). Type: SWA/Namibia [Deutsch-Südwestafrika], Haifischbucht, *Fincke* (W, not seen).

Thallus *Caloplacae elegantissimae* similis sed lobis marginalibus densioribus et angustioribus, partibus loborum centralium saepe magis areolatis et isidiis sat numerosis instructis differt.

TYPE.—SWA/NAMIBIA, 2114 (Omaruru): gravel flats east of Cape Cross (−CA), *Kärnefelt 8610-2* (LD, holo.).

Thallus radiate, (5−)10−30(−60) mm across, the smallest occurring on pebbles, occasionally up to 60 mm across on larger stones, composed of cartilaginous, rather thin, densely placed lobes, 0,2−0,5 mm wide, broadest at the lobe tips; marginal lobes usually 5−15 mm long, distinctively effigurate, weakly dichotomously branched, secondarily becoming raised and unattached; central portions composed of short, irregularly arranged or occasionally more areolated lobes, covered with simple or coralloid, rather small isidia; short accessory lobules occasionally develop at the margins of the lobes; orange to pale orange, the central portions usually pale brownish due to the accumulation of numerous small sand grains.

Epinecral zone 10−20 μm thick, prosoplectenchymatous, hyphae thick-walled (Figure 1a, c). *Cortex* 120−230 μm thick, composed of strongly gelatinized hyphae, hyaline but orange-yellowish in a thin layer above (Figure 1a, b, c). *Photobiont* green and spherical, 5,5−12 μm in diameter, occurring in clusters, 35−85 μm large,

mainly embedded in a layer of gelatinized hyphae. *Medulla* 200–300 μm thick, composed of more lax hyphae, partly embedding the clustered photobiont, often containing small granules, fluorescent when examined by means of interference contrast microscopy. *Ascomata* and *conidiomata* not observed.

Caloplaca namibensis contains several anthraquinones which were difficult to separate by means of TLC (see discussion of *C. elegantissima*). I have not seen the type material of *Caloplaca diploplaca* Zahlbr. var. *gracilior* Zahlbr. The description, however, indicates that this taxon belongs to *C. namibensis* (see Zahlbruckner 1932).

ANGOLA.—1213: Benguela, *Welwitsch s.n.*, 1859, (H-NYL 30513). 1511: Mossamedes, between Caroca and Cazimba at Cabo Negro, *Welwitsch, Iter Angolense 45* (BM, LISU).

SWA/NAMIBIA.—2114 (Omaruru): gravel flats east of Cape Cross (–CA), *Kärnefelt 8610-2*; *8610-4*; *8610-12*; *8610-15*; *8610-18–8610-20*; *8610-23*; *8610-42* (LD). 2214 (Swakopmund): gravel flats east of Swakopmund (–BA), *Kärnefelt 8602-4*; *8602-7*; *8602-12*; *8602-21*; *8602-23–8602-25*; *8602-32*; *8602-35*; *8602-36*; *8602-50*; *8602-53*; *8602-54*; *8602-56* (LD); *Wessels 5082*; *5085*; *5087* (UNIVERSITY OF THE NORTH); Omaruru flumen (–AB), *Melander 3* (H); 22 km east of Walvis Bay (–DC), *Nordenstam & Lundgren 2311* (S); between Swakopmund and Cape Cross (–??), *Mattick 6812* (B). 2315 (Rostock): Namib Naukluft Park, Gobabeb, coastal desert habitat (–CA), *Kärnefelt 8603a-3–8603a-5*; *8603a-9* (LD). 2615 (Lüderitz): Angra Pequena (–CA), 1888 *Schinz* (G).

Characteristics and differences

C. elegantissima is characterized by slightly separated, peripherally effigurated, cartilaginous, strikingly scarlet or orange-reddish lobes (Figure 2a). The central part of the thallus, especially in large well developed individuals, usually consists of short irregularly arranged lobes (Figure 2b), and the species is often fertile.

C. elegantissima differs from the closely related *C. namibensis*, by having slightly broader (0,5–1,8 mm), and more separated lobes, whereas *C. namibensis* has more closely spaced (contiguous) lobes, 0,2–0,5 mm wide, with almost no interspaces (Figure 2e, f). However, the main difference between the two species is that *C. namibensis* is isidiate, and *C. elegantissima* is not. When growing side by side, as is often the case on the gravel plains, *C. elegantissima* appears as the more robust of the two species. The specific epithet *elegantissima*, therefore describes the isidiate species better than the sexual one.

Habitat, ecology and reproduction

C. elegantissima and *C. namibensis* are two of the most common species in the Namib fog desert. As with most other species which occur in that region of the Namib Desert, they seem to be perfectly adapted to the extreme local environmental conditions.

Two other rather common crustose species, *C. volkii* Wirth & Vezda (1975) and *Lecidella crystallina* Wirth & Vezda (1975), normally occur directly on the ground. *C. elegantissima* and *C. namibensis*, on the other hand, grow on rocks of various sizes. Individuals on small pebbles, obviously a very common occurrence, can cover the substrate completely (Figure 2c, d). *C. elegantissima*, in particular, seems to occur rather frequently on small pebbles, ± 5 mm in size, whereas *C. namibensis* is more common on stones, 10 to 30 mm in size. The most luxuriant and richly fertile specimens of *C. elegantissima* were found on dolerite outcrops composed of larger stones and rocks. This observation may be correlated with the effect of drifting fog, which condenses more rapidly on cooling rock outcrops (Kappen 1982).

Sexual reproduction is presumably an important mode of dispersal for the frequently richly fertile *C. elegantissima*, whereas asexual dispersal by means of isidia must be an important mode of reproduction for *C. namibensis*, producing extensive clones. However, accessory lobules are frequently developed in both species, especially on smaller individuals growing on pebbles (Figure 2c, d). Fragmentation of the frequently raised lobes could also be interpreted as an adaptive arrangement for clonal dispersal in this regionally successfully distributed species pair.

Anatomical adaptations

The most typical environmental adaptation of these species is the anatomical structure, which is characterized by extremely thick external tissue (Figure 1). This

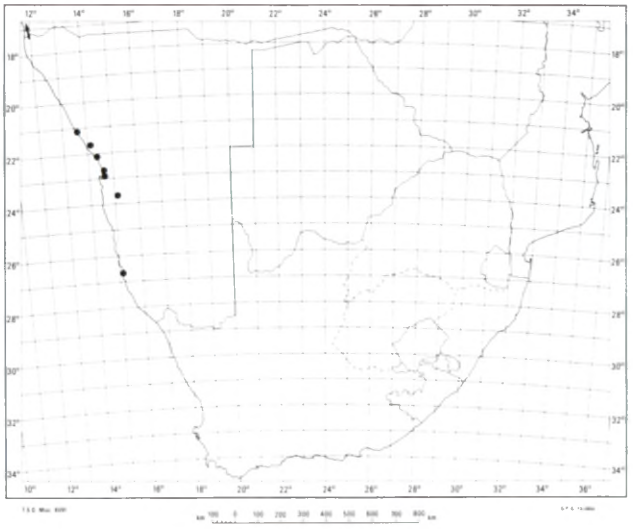

FIGURE 3.—Distribution of *Caloplaca elegantissima*. Arrow indicates localities in southern Angola.

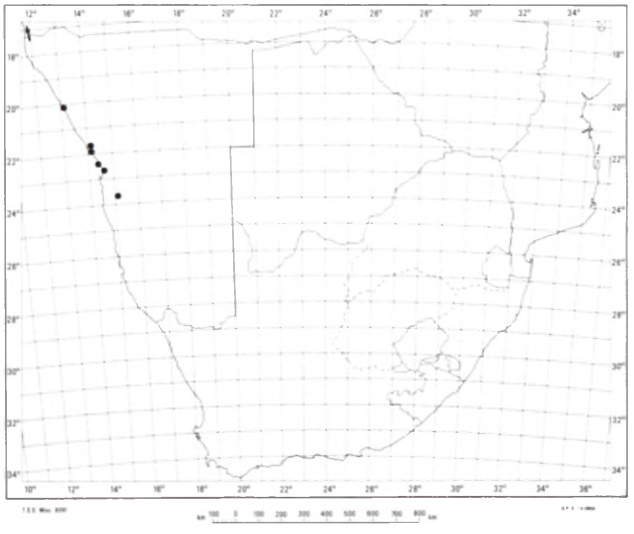

FIGURE 4.—Distribution of *Caloplaca namibensis*. Arrow indicates localities in southern Angola.

tissue, distinctively stratified into epinecral and cortical layers, is 185 to 295 μm thick in *C. elegantissima* and 130 to 250 μm thick in *C. namibensis*. The tissue forms a solid cover over the basally located photobiont (Figure 1c, d). A thick cortical layer acts mainly in reducing the intensity of light (Kappen 1973; Vogel 1955), in reducing evaporation loss and also in permitting direct absorption of water vapour from dry air (Galun 1963; Rogers 1977).

In *C. elegantissima*, the pigmented cortical zone is generally better developed than in the closely related species (Figure 1e, f). In addition, the cortex in *C. elegantissima* is composed of more strongly gelatinized hyphae, than that of *C. namibensis*.

Distribution

C. elegantissima and *C. namibensis* are endemic to the outer Namib Desert, and are known to occur from south-western Angola in the north, to the Lüderitz region in the south (Figures 3 & 4). It is suspected, however, that the area of both species may extend to the southern boundary of the Namib Desert. Closely related species from other coastal fog deserts of the world are not known.

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