

## Two new crustaceous soil lichens (Arthoniales) from the Chilean Atacama Desert, South America

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**Abstract:** FOLLMANN, G. 2008. Two new crustaceous soil lichens (Arthoniales) from the Chilean Atacama Desert, South America. – *Herzogia* 21: 25–39.

*Lecanographa azurea* (aff. *L. dimelaenoides*, Opegraphaceae) and *Roccellina ochracea* (aff. *R. accedens*, Roccellaceae) are described from the loma formations of the Atacama Desert, North Chile, South America. Among other characteristics, these lichens represent crustaceous, obligately terricolous ecotypes which are remarkably rare in those fog oases. The latter have not been found within the genus *Lecanographa* before and only once in *Roccellina*. Both taxa and the sympatric terricolous *R. terrestris* develop rhizoidal hyphae being new records at the generic level. The new species are distributed together with the many paleoendemic Roccellaceae and other Arthoniales of the Atacamian province of the Pacific-Andean floral region. Their infrageneric relations, ecological requirements, vegetational associations and biogeographical peculiarities are briefly discussed.

**Zusammenfassung:** FOLLMANN, G. 2008. Zwei neue bodenbewohnende Krustenflechten (Arthoniales) aus der chilenischen Atacamawüste, Südamerika. – *Herzogia* 21: 25–39.

Aus den Lomaformationen der nordchilenischen Atacamawüste, Südamerika, werden zwei neue Krustenflechten (Arthoniales) beschrieben, *Lecanographa azurea* (aff. *L. dimelaenoides*, Opegraphaceae) und *Roccellina ochracea* (aff. *R. accedens*, Roccellaceae). Unter anderem stellen diese krustige, obligat terrikole Ökotypen dar, welche in jenen Nebeloasen ausgesprochen selten vorkommen. Für die Gattung *Lecanographa* handelt es sich hierbei um einen Erstfund, für *Roccellina* um einen Zweitfund. Beide Arten sowie die sympatrische terrikole *R. terrestris* bilden Rhizohyphen aus, die von den genannten Gattungen ebenfalls noch nicht bekannt waren. Die neuen Sippen teilen das Areal mit zahlreichen paläoendemischen Roccellaceen und anderen Arthoniales der Atacama-Provinz der pazifisch-andinen Florenregion. Ihre infragenerischen Beziehungen, ökologischen Bedürfnisse, soziologischen Verbindungen und chorologischen Eigentümlichkeiten werden kurz erörtert.

**Key words:** *Lecanographa azurea*, Opegraphaceae, *Roccellina ochracea*, Roccellaceae, terricolous lichens, loma formations, fog oases, Pacific-Andean floral region.

### Introduction

The South American Atacama Desert, covering about 291 000 km<sup>2</sup> along the narrow coastal strip of the northern third of Chile (18°24'–29°54'S), is generally considered to be one of the most arid regions of the world. Nevertheless, due to the occurrence of roughly 50 smaller fog oases of less than 5000 km<sup>2</sup> in total, locally called “lomas”, the Atacamian flora of higher plants is so abundant and rich in endemics that the total area has been included in the international guide to “Centres of plant diversity” (DAVIS et al. 1997, DILLON & HOFFMANN 1997). According to distributional, taxonomical, ecological and vegetational studies conducted over the past 50 years, this status undoubtedly applies to the lichen population of the Atacama Desert as well (e.g. FOLLMANN 1968, 1995, 2001, 2002, FOLLMANN & REDÓN 1972, PEINE & WERNER 1995, TEHLER 1983). During

these times, a remarkable number of new, mostly endemic – and sometimes critical – lichen species has been discovered in the azonal loma formations, and more than a third of the taxa registered in the latest checklist of Chilean lichens originate from this desert region (GALLOWAY & QUILHOT 1998). Recently, two hitherto unknown soil lichens of the Arthoniales have been found in the author's collections from the Atacamian fog oases. The scarcity of comparable epigeal life forms in those loma biomes, their uncommon ecology and distribution as well as other noteworthy characteristics justify a separate description in the following report.

## Material and methods

The present account is based mainly on lichen material gathered by the author and collaborators during several study trips to the Atacama Desert between 1965 and 2003. In addition, the author's South American collections at KASSEL and KOELN (the latter now housed at B) have been used for comparison. Beyond that, selected specimens of Opegraphaceae and Roccellaceae, received on loan from the institutional herbaria BM, COLO, G, L, LD, NMW, O, PC, PRE, S, TUR, UPS, US, USM and W, were examined. Apart from PHILIPPI's (1860) delineation of his famous exploration of the Atacama Desert – still worth reading – relevant and more timely overviews on topography, geology, climatology, vegetation and other items of the operating range are detailed by BÖRGEL (1973), HARRINGTON (1961), QUINTANILLA-PÉREZ (1983), RAUH (1985), REICHE (1934–1937), RUNDEL et al. (1991), SCHMITHÜSEN (1956) and others.

All suitable specimens have been subjected to conventional spot (ST) and ultraviolet irradiation tests (UV), light (LM) and electron microscopy (EM) as well as microcrystallography (MCG), thin layer (TLC) and high performance liquid chromatography (HPLC). LM measurements were conducted to a precision of 0.5–1.0  $\mu\text{m}$  for hand or microtome sections in tap water (10–20 replicates). For co-chromatographic comparisons authentic lichen compounds were used. ST, UV, TLC and MCG examinations were repeated at least ten times, lengthy HPLC analyses five times.

Attention has also been paid to the autecology of the new species in the field, particularly the nature, consistency and pH of the substrate, altitude and orientation, exposure or protection of the site, apparent water supply, distance from the sea and influence of the marine aerosol, local distribution, abundance and gregariousness, dominance and succession. To characterize affinity, position and rank of the new taxa, all data obtained have been adjusted and integrated into previously compiled matrices and the corresponding phenograms and cladograms (EGEA & TORRENTE 1994, FOLLMANN 2001, 2002, FOLLMANN & PEINE 1999, TEHLER 1990, 1994, TEHLER & EGEA 1997).

## Results

### *Lecanographa azurea* Follmann sp. nov.

**Diagnosis:** Species nova crustacea *Lecanographae dimelaenoidis* et taxis affinibus consimilis; differt i. a. thallo cremeo-albido, effuso et fissurato nunquam areolato; strato epinecrale fino; medulla perspicue tripartita, strato inferiore instructo cum hyphis rhizoidalibus crassulis et ramosis, sufflavis usque ad suffuscis; pseudotheciis orbicularis vel polymorphis nunquam lirellatis, basi leviter constrictis, breviter stipitatis, discis applanatis, persistenter pruinosis et marginatis, modice azureis vel caesio-lividis; excipulis carbonaceis, solidis, infundibularibus, terminantibus intra stipitibus; ascis minoribus cum ascosporis procerioribus, perisporio subtiliore; substrato arenoso, subneutrali, insolato.



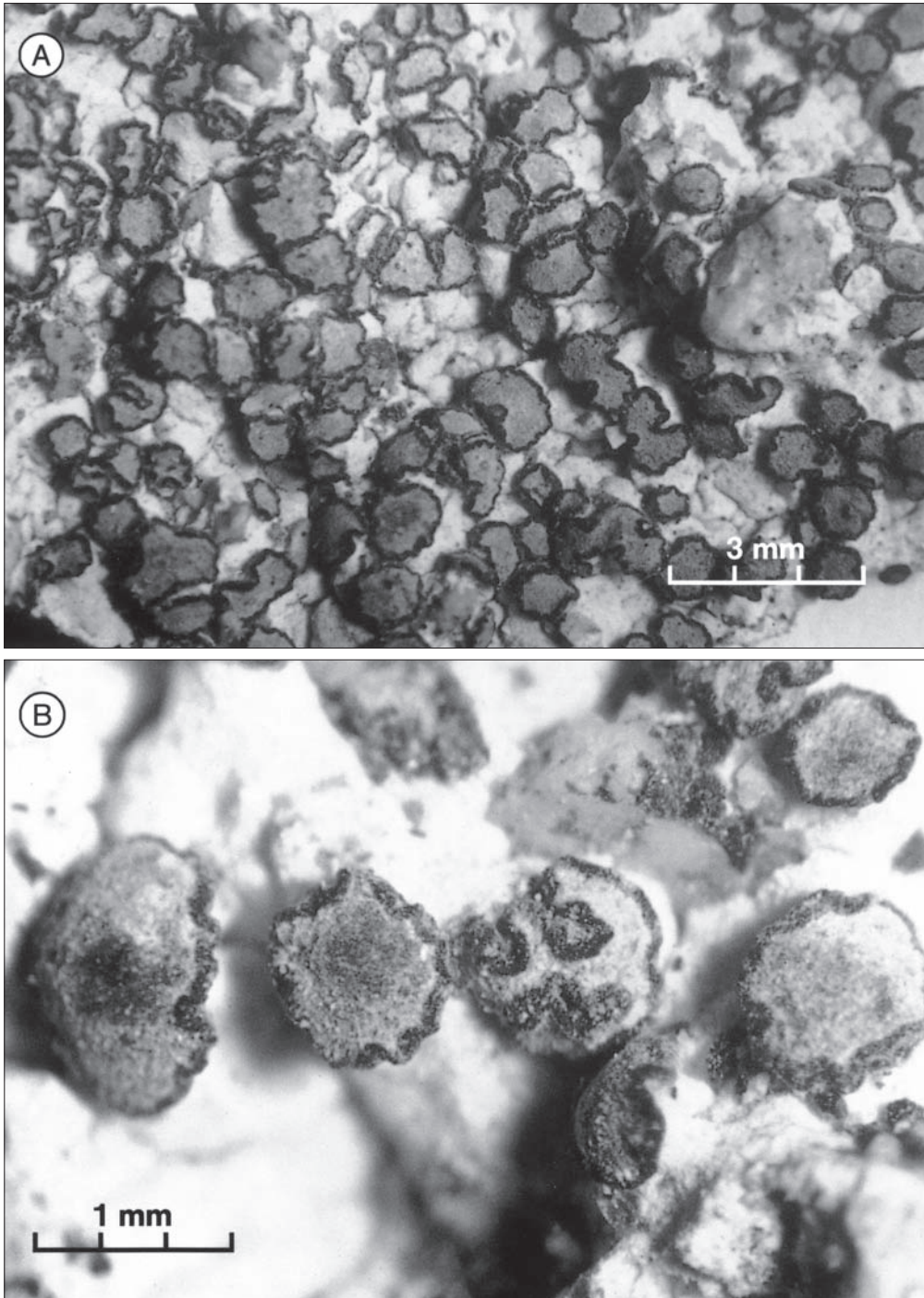
**Fig. 1:** Type locality of *Lecanographa azurea* (circle) above a SW oriented slope densely overgrown with *Tillandsia landbeckii*, southern foothills of Cerro Huantaca NE of Iquique, Province of Tarapacá, North Chile (phot. G. Follmann VIII/1993; for details see under “Holotype”).

**Holotype:** South America, Chile, Atacama Desert, Province of Tarapacá, coastal cordillera NE of Iquique, southern foothills of Cerro Huantaca, upper fog belt, open blank on the ridge above a steep slope densely overgrown with *Tillandsia landbeckii* Phil. (Fig. 1), about 850 m alt., SW exposure, scattered on slightly inclined, somewhat clayey sand interspersed with larger crystalline particles (pH 6.1), c. 15 km from the sea, associated lichens absent, but in neighbouring cushions of *T. landbeckii* various, mostly fruticulose epiphytes present; leg. G. Follmann VIII/1993 (B–35365 – holotype).

**Additional material examined:** South America, Chile, Atacama Desert, Province of Antofagasta, coastal cordillera N of Taltal, lower mountain range of the National Reserve Paposo, central fog zone, exposed niche in a fragmentary community characterized by *Euphorbia lactiflua* Phil. and *Eulychnia iquiquensis* (Schum.) Britton & Rose, c. 530 m alt., SW exposure, solitary on almost level, somewhat incrusting sandy soil (pH 6.5), c. 5 km from the sea, no terricolous companion species observed, but on the surrounding columnar cacti and spurge shrubs a luxuriant vegetation of spinicolous and corticolous lichens noted; leg. G. Follmann XII/2003 (B–35411).

**Etymology:** Specific epithet draws attention to the remarkable sky-blue to lead-blue colouration of the pseudothecial disk unique within the genus.

**Description:** Thallus crustaceous, effuse or fissured but not areolate, fragile, in top view superficially resembling the corticolous Australasian *Lecanactis platygraphoides* (Müll.Arg.) Zahlbr. (Fig. 2); without distinct prothallus or noticeable margin, soralia or isidia absent; thallus light cream-coloured, in outline roundish, 15–24 mm in diam., thickness variable, 1–2 mm in sectional view, surface undulating, rugose; cortex replaced by a comparatively delicate greyish epinecral layer without surface gel, 15–27  $\mu\text{m}$  thick; whitish medulla cretaceous, texture  $\pm$  reticular, composed of branched leptodermous hyphae, 1–2  $\mu\text{m}$  in diam., interspersed with granules and crystals, glued together by a hardly visible clear gelatinous matrix, polygonal interstices 8–12  $\mu\text{m}$  in diam., medulla appearing 3-layered in cross-section: epimedulla comparatively spongy, without considerable inclusions, 18–24  $\mu\text{m}$  thick, algal layer 150–



**Fig. 2:** Partial views of type material of *Lecanographa azurea*. **A** – Note light, slightly fissured thallus and roundish to multiform, to some extent aggregate ascomata with prominent crenated exciples. **B** – Note formation of secondary ascomata externally marked by excipular excrescences (B 35 365, phot. B. C. Werner).



190  $\mu\text{m}$  high, phycobionts trentepohliaceous, dark-green, mostly unicellular, subglobular or deformed, 7–11  $\mu\text{m}$  in diam., hyphal appressoria and haustoria present, hypomedulla compact, 290–320  $\mu\text{m}$  thick, unchanged towards the substrate, releasing single, yellowish to brownish, pachydermous, richly branched rhizoidal hyphae, 2–3  $\mu\text{m}$  in diam., detectable to almost 1 cm depth within the sandy ground, occasionally covered with adhered soil particles, especially organic detritus and various crystals, larger mineral substrate components often completely enclosed by finer secondary hyphae.

Ascomata numerous, apothecioid, representing lecideine pseudothecia, 0.5–2.0 mm in diam., mostly aggregate, basic form circular, but regardless of external pressure in many cases deviating (e.g. longish, polygonal, reniform, triangular), here and there secondarily divided (Fig. 2), slightly constricted downwards, shortly stipitate by means of conical thalline outgrowths, 0.3–0.4 mm high; disks plane, persistently pruinose, subdued sky-blue (especially when moistened) to lead-blue, somewhat glittering due to minute sharp-edged crystals; carbonaceous exciple well developed, entire, prominent and pruinose around the disks, crenated, rugged or undulated, externally covered with relatively coarse crystals, 70–100  $\mu\text{m}$  thick, in longitudinal section funnel-shaped, perpendicular axis 140–165  $\mu\text{m}$  in length, ending inside the stipes, never reaching the inferior medulla or the substrate; pseudopithecium dark-brown, 50–65  $\mu\text{m}$  high, formed by septate, branched, anastomosing and apically slightly clavate paraphysoids, 1.5–2.0  $\mu\text{m}$  in diam.; hymenium hyaline, hemiamyloid, 85–120  $\mu\text{m}$  high, paraphysoids insignificantly more delicate compared to the pseudopithecial ones, largely reticular, subhymenium brownish, about one third of the height of the hymenium; clavate asci fissitunicate, of the *Grumulosa*-type, 57–85  $\times$  12–18  $\mu\text{m}$ , exo- and endoascus comparatively thin, apex poorly developed, 8-spored, straight ascospores longitudinally arranged, oblong fusiform, of the *Lyncea*-type, 29–41  $\times$  3.5–4.5  $\mu\text{m}$ , contrary to most congeners peri-, exo- and episporic little evolved, hyaline but if over-mature somewhat brownish, 7-septate, exo- and episporic unchanged in contact with the septa, apart from the unilaterally domed terminal cells, loculi identical in form and size (concerning the spore shape cf. EGEA & TORRENTE 1994: p. 149, pl. 15 C).

Conidiomata dispersed, solitary, immersed or subimmersed, corresponding to the *Lecanactis*-type, punctiform with relatively narrow ostioles, corpus carbonaceous, subglobose, 55–65  $\mu\text{m}$  in diam., formation of conidia acrogenous, microconidia hyaline, bacilliform, straight, 5–9  $\times$  1.0–1.5  $\mu\text{m}$ , macroconidia absent.

**Chemistry:** Cream-coloured thallus surface, bluish ascomatal pruina and exposed parts of the whitish medulla UV+ faint-white; ST of epinecral layer, disks and uncovered medulla C+ reddish, KC+ scarlet-red, K+ light-yellow, P–; hymenium, especially endoasci and paraphysoids, KI+ light-blue (hemiamyloid), reduced ascus structures barely contrasted; secondary metabolites corresponding to TLC and HPLC erythrin (major specific compound), lecanoric and gyrophoric acids (traces of by-products) plus two unknowns, including the uncommon bluish pigment, insoluble in organic extractives (such as acetone, chloroform or diethylether); excipular, pseudopithecial and medullary crystals acid- and alkaline-proof (tested with HCl and H<sub>2</sub>SO<sub>4</sub> or KOH and NaOH, respectively), possibly originating from the sandy substrate; owing to the scarcity of test material, exact concentrations of the above lichen substances as yet not determined.

**Affiliation:** Apart from the sandy substrate and some adaptations relating to this (e. g. development of rhizoidal hyphae), this new species corresponds in all essential characters to the genus *Lecanographa* Egea & Torrente [Opegraphaceae s. str., typ. gen. *L. lyncea* (S.J.E.Smith) Egea & Torrente] as defined by EGEA & TORRENTE (1994) and EGEA et al. (2004). Provided that a

few taxa not definitely classified as yet are included in the account [e.g. *L. aff. farinosa* (Hepp) Egea & Torrente], the total species number amounts to nearly 30 worldwide, 13 of which occur in South America and 8 in Chile. EGEA & TORRENTE (1994) subdivided *Lecanographa* into two tentative categories, the *L. grumulosa* group and the *L. lyncea* group, leaving aside the corticolous Chilean *L. subdryophila* (Follmann & Vězda) Egea & Torrente, which shows attributes of both clusters. The lichenicolous *L. occidentalis* Egea & Torrente represents the only Chilean species of the *L. grumulosa* group, whereas all others plus *L. azurea* tend towards the *L. lyncea* group. However, obviously no direct connections exist between the previously known Chilean taxa and the new species, the last of which appearing to be more closely related to the saxicolous Californian *L. dimelaenoides* (Egea & Torrente) Egea & Torrente and *L. hypothallina* (Zahlbr.) Egea & Torrente with regard to ecological, morphological, anatomical and chemical characters.

***Roccellina ochracea* Follmann sp. nov.**

**Diagnosis:** Species nova crustacea *Roccellinae accedentis* et taxis aggregatis consimilis; differt i. a. thallo ochraceo, dense bullato-tuberculato, neque areolato neque suffruticoso, sine prothallo et margine; reactione superficiale C+ rubida et KC+ rubicunda, thallo praecipue acidum lecanoricum continenti; tegumento epicorticale acellulare; hyphis strati algarum fuscis, medulla centralis albida, medulla inferiori subnigra prope substratum, ornata cum hyphis rhizoidalibus sparsis, crassulis, scabris et suffuscis; dimensionibus pseudotheciorum exigue minoribus, discis juvenilibus albido-marginatis, non convexis, granulis pruinae crassiusculis, partim albidis partim nigris, margine et pruina evanescente; hypothecio tabuliforme non in medulla extenso, ascosporis rectis, perspicue majoribus, cum loculis dissimilibus; substrato arenoso, subacido, insolato.

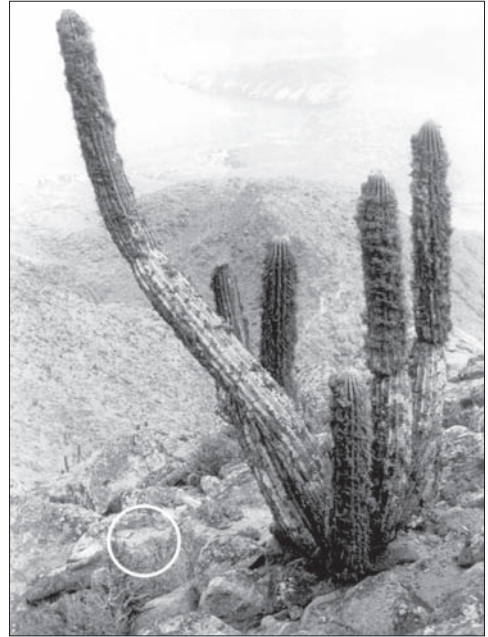
**Holotype:** South America, Chile, Atacama Desert, Province of Antofagasta, Peninsula of Mejillones, SW flank of Cerro Moreno, central fog belt, somewhat sheltered niche in a strongly contracted cactus community characterized by *Copiapoa cinerea* (Phil.) Britton & Rose and *Eulychnia iquiquensis* (Fig. 3), c. 600 m alt., SW exposure, scattered on rather level brownish-grey sandy loam intermixed with smaller fragments of crystalline rocks (pH 5.2), c. 3 km from the sea, associated terricolous lichens lacking, but nearby boulders, cacti and shrubs abounding in saxicolous, spinicolous and corticolous species; leg. G. Follmann VIII/1993 (B-35376 – holotype).

**Additional specimens studied:** South America, Chile, Atacama Desert, Province of Antofagasta, coastal cordillera N of Tocopilla, W slope of Cerro Mamilla, central fog zone, exposed clearance in a badly damaged and impoverished community of cacti distinguished by *Neoporteria recondita* (F.Ritter) Donald & G.D.Rowley and *Eulychnia iquiquensis*, c. 500 m alt., SW exposure, isolated on slightly sloping silt-filled spaces between porphyritic gravel (pH 4.8), c. 2 km from the sea, no associated lichens found, only pioneer crusts in poor condition on nearby rocks observed; leg. G. Follmann XII/2001 (B-35398). – South America, Chile, Atacama Desert, Province of Antofagasta, coastal cordillera N of Chañaral, dry valley between Cerro Cifuncho and Cerro Esmeralda, central fog belt, small bank with an eye-catching population of short-stemmed cacti dominated by *Copiapoa cinerea* var. *columna-alba* (F.Ritter) Backeberg, c. 650 m alt., W exposure, solitary on somewhat precipitous, ash-grey alluvial sand with clear marks of occasionally running water (pH 5.3), c. 10 km from the sea, associated lichens missing, but sparse roccellaceous epiphytes noted on neighbouring cacti; leg. G. Follmann XII/2003 (B-35403).

**Etymology:** Specific epithet applies to the characteristic ochraceous colouration of all external vegetative parts of this species which clearly differentiates it from other somewhat yellowish taxa of the genus.

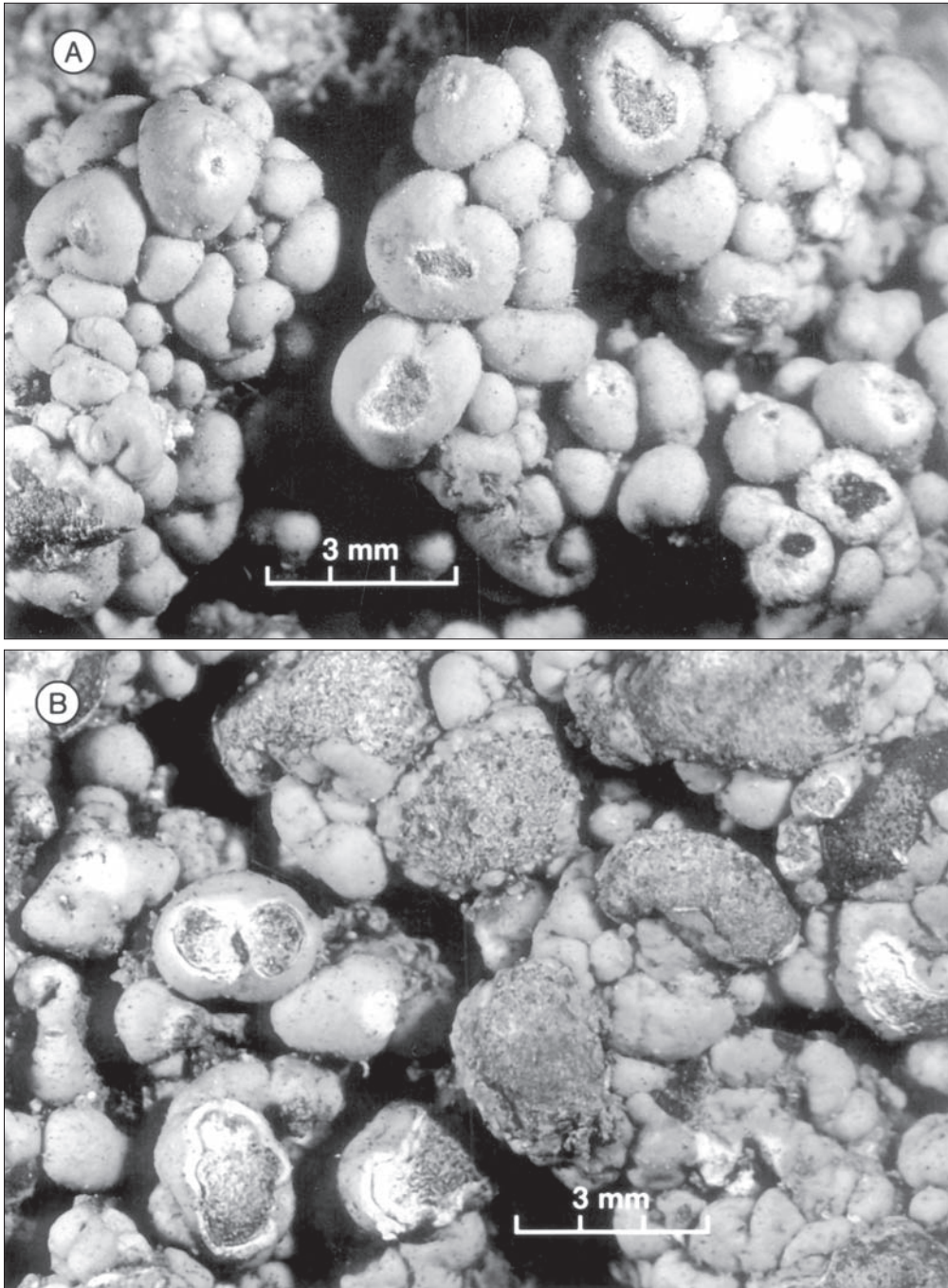
**Description:** Thallus crustaceous, initially fine-areolate but early on densely covered with bulliform tubercles (Fig. 4), occasionally vaulted but not suffruticose, friable, externally com-

**Fig. 3:** Type locality of *Roccellina ochracea* (circle), sandy niche within the dripping-zone around a solitary *Eulychnia iquiquensis* coated with *Chiodecton klementii* (whitish crusts) and *Usnea eulychniae* (dark-grey covering), southwestern flank of Cerro Moreno, Peninsula of Mejillones, Province of Antofagasta, North Chile (phot. G. Follmann IX/1997; for details see under “Holotype”).



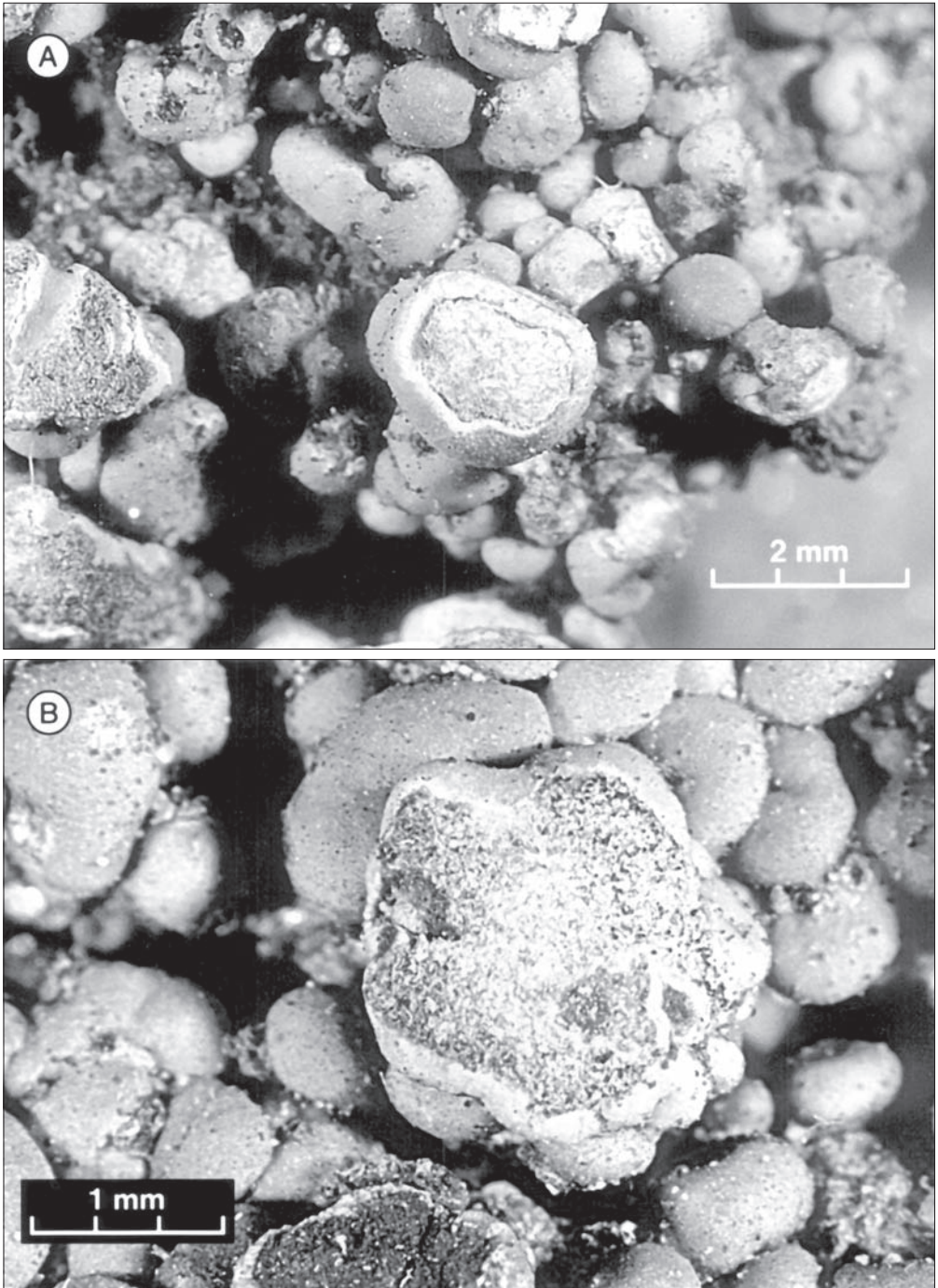
parable to juvenile stages of the sympatric *Roccellina accedens* (Nyl.) Tehler and affiliated species, surface remarkably ochraceous (particularly in the field), no distinct prothallus or effigurate margin traceable, soralia and isidia also lacking, outline irregular, 3–5 cm in diam., thickness without excrescences 1–3 mm; compact sterile and fertile tubercles hemispherical, rarely clavate, lenticular or otherwise deformed, 1–2 mm in diam., lustreless, subrugose or incompletely granulose (Fig. 5); well developed cortex 35–68  $\mu\text{m}$  thick, based on hyaline, comparatively delicate, slightly capitate but not dark-tipped, almost reticularly interwoven hyphae, only close to the epicortex these somewhat anticlinally aligned, embedded in a yellowish gelatinous matrix devoid of granules, cell-free epicortex likewise yellowish and gelatinous, 4–7  $\mu\text{m}$  thick; algal layer voluminous, apically up to 360  $\mu\text{m}$  thick, toned down by greenish-brown algal cells and darkish hyphal walls, appressoria and haustoria present, phycobionts trentepohliaceous, commonly unicellular, compressed or subglobular, 6–12  $\mu\text{m}$  in diam., rarely 2- or 3-celled, 13–26  $\mu\text{m}$  in length, whitish central medulla brittle, consisting of reticularly arranged, coarse-meshed rough hyphae, 2–3  $\mu\text{m}$  in diam., inferior medulla following the unevenness of the ground, close to the substrate greyish-brown to blackish-brown, hyphae loosely intertwined and little adhered together, equipped with single, brownish, fine-grained, scarcely branched rhizoidal hyphae with rounded or slightly flattened tips, 2–3  $\mu\text{m}$  in diam., sparsely covered with crystalloid soil particles and bunches of budding yeast cells, extending down to 0.5–1.5 cm in the sandy ground; attempts to separate thalli and substrate hardly successful without disintegration of relevant structures.

Ascomata numerous, apothecioid, representing lecanorine pseudothecia, 2–4 mm in diam., development indicated by the breakthrough of white, somewhat raised soralium-shaped excrescences at the apices of the tubercles, leaving irregularly delimited apertures which uncover immersed, greyish or blackish primordia of ascocarps (Fig. 4), mature ones commonly roundish but sometimes compressed or oblong, sessile, plane or convex, encircled by a white, elevated or undulated thalline margin of variable thickness, partly or completely disappearing during maturation (Fig. 5); disks surpassing by far the diameter of the supporting tubercles, coarse pruina consisting of a mixture of ash-grey and black, partly crystalloid granules, 6–17  $\mu\text{m}$  in diam., shedding of pruina and exposure of the deep-black epithecium largely paralleled with spore release; epithecium velvety, 34–46  $\mu\text{m}$  thick, made up of  $\pm$  erect, loosely arranged, somewhat swollen, slightly ornamented, little branched, anastomosing and septate, dark-brown to greenish-black terminal segments of paraphysoids, 2–3  $\mu\text{m}$  in diam.; hymenium hyaline,



**Fig. 4:** Partial views of type material of *Roccellina ochracea*. **A** – Marginal section with early ascoma development, note swelling of bullate tubercles, formation of white-bordered pores and openings as well as beginning exposure of discocarp primordia. **B** – Central section with advanced ascoma development, note prominent thalline margins, final disappearing of these and partial replacement by lined up secondary nodules (top centre), on the left division of younger ascoma caused by dark hypothecial excrecence (B 35 376, phot. B. C. Werner).





**Fig. 5:** Partial views of type material of *Roccellina ochracea*. **A** – Note differences in form and size between fertile and sterile tubercles. **B** – Note black and white spotted ascomatal disk and almost velvety-black one (bottom centre), besides, granular surface of tubercles, where larger, slightly raised black dots (top centre) represent conidiomata (B 35 376, phot. B. C. Werner).

hemiamyloid, 73–91  $\mu\text{m}$  thick, surrounded by a rudimentary brownish parathecium, sporadically interspersed with dark hypothecial strands and sometimes discocarps secondarily subdivided by these (Fig. 4), hymenial paraphysoids finer than those of the epithecium, 0.5–1.5  $\mu\text{m}$  in diam., brownish subhymenium inconspicuous, carbonaceous hypothecium plano-convex, at the centre 295–485  $\mu\text{m}$  thick, persistent in the whitish medullary layer; clavate asci fissitunicate, 70–80  $\times$  18–24  $\mu\text{m}$ , close to the hypothecium caudate and bent aside, apical structures little differentiated, 8-spored, straight ascospores slantwise or 3-seriately arranged, obtusely fusiform, colourless, 36–42  $\times$  5–7  $\mu\text{m}$ , epispore and septa sturdy but perispore reduced, at the epispore/septum interface barely constricted, 3-septate, loculi dissimilar, the two central ones cylindrical and of comparable size, the superior apically domed and the inferior one elongated and somewhat pointed (relating to the spore shape cf. TEHLER 1983: p. 21, fig. 13 B).

Conidiomata scattered, immersed, in places aggregate, of the *Roccella*-type, sacculiform, 165–205  $\times$  95–30  $\mu\text{m}$ , capsules and ostioles dark-brown, the first relatively thin-walled, the second uncommonly wide opened but not acervuloid (Fig. 5), conidial formation acrogenous, microconidia hyaline, filiform, crescent or sigmoid, 12–18  $\times$  0.5–1.0  $\mu\text{m}$ , macroconidia absent.

**Chemistry:** Ochraceous thallus surface and light-grey particles of the pruina UV+ faint-white, soralioid excrescences, ascomatal margins and accidental ruptures UV+ brilliant-white; ST of cortical layer, soralioid excrescences, thalline margins, light-grey portions of the pruina and medulla (except algal layer and dark medullary coating close to the surface) C+ pink-red, KC+ crimson-red, K– and P–; hymenium, particularly ascus walls, paraphysoids and epispores, KI+ light-blue (hemiamyloid), reduced apical ascus structures little accentuated; according to TLC and HPLC secondary metabolites lecanoric acid (major specific compound), erythrin and orsellinic, roccellic and schizopeltic acids (traces of by-products), plus two unknowns including the ochraceous pigment, insoluble in organic extractives (cf. *Lecanographa azurea*), due to insufficient material for analyses, precise quantities of the typical roccellaceous compounds not examined; in agreement with comparative TLC and HPLC, the absence of skyrin, characteristic sulphureous colourant of the related sympatric *Roccellina luteola* Follmann, out of question.

**Affiliation:** In conformity with TEHLER's (1983) monograph and corresponding cladistical analyses (TEHLER 1990, 1994), the new desert lichen undoubtedly ranks among the genus *Roccellina* Darb. emend. Tehler [Roccellaceae s. str., typ. gen. *R. cerebriformis* (Mont.) Tehler]. The genus includes about 25 species, 18 of which are endemic in Pacific South America with as many as 16 (!) of these showing a Central to North Chilean distribution, although a few of them radiate into neighbouring Peru. Comparable to the classification of the genus *Lecanographa* (EGEA & TORRENTE 1994), in *Roccellina* two larger, hitherto unnamed subdivisions can be distinguished, even if the number of isolated and deviating taxa appears to be larger in this case [e. g. *R. chalybea* Tehler, *R. chilena* (C.W.Dodge) Tehler, *R. mahuiana* (Follmann) Tehler, all from Chile; TEHLER 1994].

Based on all available data, *Roccellina ochracea* evidently may be incorporated into a cluster characterized by four Atacamian species: *R. accedens*, *R. nigricans* Tehler and *R. suffruticosa* Tehler, all saxicolous, as well as *R. terrestris* Tehler, until now the only soil-inhabiting representative of the genus. Supplementary anatomical examinations showed the latter species to develop rhizoidal hyphae just as *R. ochracea*. Another remarkable, yellow and suffruticose *Roccellina*, *R. luteola*, appears to be more distantly related to *R. ochracea*. On the one hand, the preceding is easily distinguished by its ochre colouration, crustaceous growth form and tuber-

culate surface as well as by the formation of epicortices and rhizoidal hyphae, the minor quantity of conidiomata, the absence of macroconidia etc. On the other hand, *R. luteola* has various similar characteristics, such as thallus stratification and wide-meshed medullary texture, early development of ascomata in and on nodular excrescences, partly identical secondary metabolites etc. This may have been one of the reasons for previously integrating *R. luteola* within the “*R. accedens* group” and for isolating it in earlier cladograms (TEHLER 1983, 1994).

## Discussion

**Ecological conditions:** The basic requirements, vegetational associations and biogeographical patterns of *Lecanographa azurea* and *Roccellina ochracea* resemble each other to such a degree that they should be treated together. However, such complex topics cannot be fully described in the present context and have to be restricted to some essential points.

As would be expected, water supply appears to be the limiting ecofactor being dependent for the most part on more or less regular moistening by dew and fog. The missing cortex and somewhat spongy epimedulla of *Lecanographa azurea* as well as the strongly enlarged surface and the wide-meshed central and inferior medulla of *Roccellina ochracea*, combined with the rhizoidal hyphae of both, possibly facilitate the absorption of condensed water and dissolved salts. Contrary to terricolous ecotypes from fairly plain habitats, saxicolous, placodioid or suffruticose lichens on inclined faces of nearby boulders and cliffs, e.g. *R. cerebriformis*, *R. luteola* or *R. nigricans*, evidently absorb more moisture under identical outer conditions. Probably this difference can be explained by the more advantageous orientation of the rock-inhabiting species. On the other hand, violent episodic rainstorms (El Niño events) may have unfavourable effects on soil lichens, rarely by washing away ground and thalli but more frequently by covering the sites with turned up loam, silt, sand etc. The consequences of such short-time damaging, if not fatal, inundations have been observed repeatedly in Atacamian fog oases (ARNTZ & FAHRBACH 1991, FOLLMANN 1995).

All stands of the two new species have been found to date at 500–850 m elevation and 2–15 km from the Pacific Ocean. Accordingly these habitats are located without exception in the central fog belt of the coastal cordilleras. Apart from the daily recurrent cloud banks, the soil lichens are in reach of the more irregularly blowing stiff breeze carrying marine aerosol. After precipitation, a delicate, barely visible hygroscopic salt film is left on the thalli which during high atmospheric humidity may contribute to their water economy (FOLLMANN 1967, HUISKES & MOERDIJK-POORTVLIET 2000, RUNDEL 1978). As a rule, the individual areas of both taxa proved to be uncommonly limited, somewhat isolated and protected niches (Figs 1, 3). The substrates traced represented throughout immature unstratified soils of minor depth with considerable amounts of quartz sand (40–70 % vol.), grit, silt, loam, clay and humus being of secondary importance (3–15 % vol.). This implies efficient water permeability as well as aeration and facilitates the development of rhizoidal hyphae, but at the same time results in reduced water accumulation and desiccation resistance.

The mean pH of the substrate below and around *Lecanographa azurea* (6.3 = subneutral) slightly differs from that of *Roccellina ochracea* (5.1 = subacid). A similar pH is characteristic of all habitats of the saxicolous Atacamian pioneer associations *Roccelletum portentosae* and *Roccellinetum cerebriformis* which have in common many species of Opegraphaceae and Roccellaceae (FOLLMANN 1964, 1997, FOLLMANN & PEINE 1999). However, substantial differences exist between the mostly fruticose morphotypes of the *Roccelletum* and the two epigeal taxa under consideration regarding their reactions to other ecofactors such as illumi-

nation or temperature. On the contrary, the Roccellinetum with its predominant crustaceous and suffruticose growth forms shows further accordances, particularly in view of exceptional photo- and thermotolerance together with outstanding xeroresistance, features which cannot be detailed here. In any case, the likewise dissimilar life-spans of members of the Roccelletum (mostly long-lived) and the Roccellinetum inclusive of *L. azurea* and *R. ochracea* (perennial but short-lived) should be taken into account in ecological considerations.

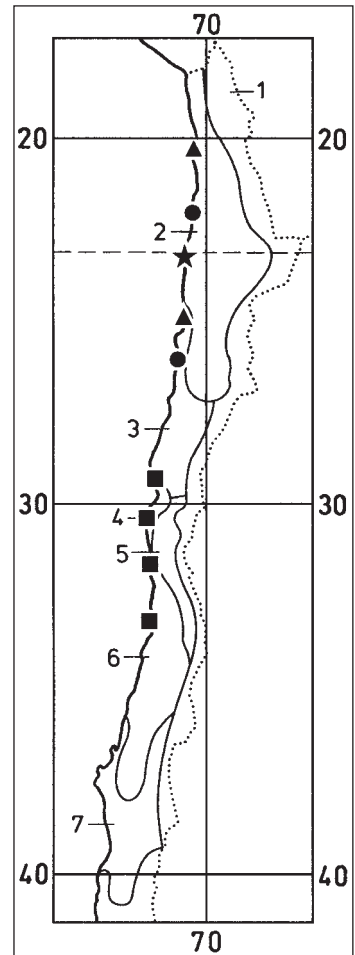
**Vegetational interrelations:** As far as is known, the new species always occur in groups of comparatively few individuals and are, most unusual, constantly surrounded with strips of barren ground (5–15 cm in diam.). At these “buffer zones” only once a trace of an orange-brown aeroterrestrial alga [*Trentepohlia* aff. *umbrina* (Kütz.) Born.] has been observed. The absence of lichens, mosses or other soil inhabitants from these open niches cannot be interpreted as allelopathic effect because secondary metabolites only reach minor concentrations and could not be detected in the immediate neighbourhood of the thalli. Notwithstanding the obviously missing sociological affinity to other lichens, inside the loose cushions of *Tillandsia landbeckii* a few metres away from the type locality of *Lecanographa azurea* (Fig. 1) some hidden individuals of mostly fruticulose epiphytes have been collected: *Heterodermia follmannii* Sipman, *Ingaderia gracillima* (Kremp.) Feige & Lumbsch, *Ramalina peruviana* Ach., *Teloschistes flavicans* (Sw.) Norman, *Tornabea scutellifera* (With.) J.R.Laundon, *Xanthoria ascendens* Kondratyuk. Such a species combination does not form part of any defined Chilean lichen community nor could it interfere with the habitat of *L. azurea*. Most probably fragments of these “foliicolous” ecotypes have been blown inland by the strong breeze.

The southern site of *Lecanographa azurea* is located in the National Reserve Paposo which has been floristically and ecologically analyzed by RUNDEL & MAHU (1976), RUNDEL et al. (1991) and others. The central section consists of open bushland with predominating *Euphorbia lactiflua* and *Eulychnia iquiquensis* loosely surrounding the habitat of the new species. Irrespective of the scattered occurrence of larger spurge shrubs and columnar cacti, a well developed corticolous respectively spinicolous Chrysotrichetum pavonii colonizes their upper branches and stems (FOLLMANN 1961). Apart from the naming species the most noticeable lichens found are *Everniopsis trulla* (Ach.) Nyl., *Heterodermia pinnata* Sipman, *Protorocella minima* (R.Sant.) Follmann, *Ramalina cactacearum* Follmann and *Roccellinastrum spongioidium* Follmann. Sporadically fallen thallus fragments of these species have been observed in different stages of decomposition on the ground partly overgrown by *L. azurea*. In view of the abundance of imported stable, biochemically active secondary products synthesized by members of the Chrysotrichetum (atranorin, calycin, lecanoric, protocetraric, psoromic, salazinic acids etc.) the possibility of allelopathic influences cannot be excluded.

The Central Atacamian fog oasis Cerro Moreno which among others supports many endemic Roccellaceae has been studied repeatedly under different aspects (FOLLMANN 1968, OLTREMARI et al. 1987, RICHTER 1995 etc.). The type of *Roccellina ochracea* originates from an impoverished succulent community with *Copiapoa cinerea* and *Eulychnia iquiquensis* where it receives some protection from loose neighbouring rocks, dried up shrubbery and solitary columnar cacti (Fig. 3). The open rock faces are partly covered with a poor Roccellinetum cerebriformis, here represented by the character species as well as *Minksia chilena* (C.W.Dodge) Redón & Follmann, *R. accedens* and *R. limitata* (Nyl.) Tehler. Contrarily, the cactus stems are often completely overgrown by a well developed lichen community which appears to be closely connected with the typically aerohygric Usneetum eulychniae (FOLLMANN 1968). At the type locality this can be recognized by the occurrence of the naming species together



**Fig. 6:** Vegetational zonation, type localities and other occurrences of three terricolous Arthoniales from the Atacama Desert (geographical order of symbols from north to south): 1 = xerophytic High Andean zone, 2 = hyperarid desert zone, 3 = subtropical dwarf shrub zone, 4 = hygrophytic shrub and succulent zone rich in spring cryptophytes, 5 = xerophytic succulent and thornbush zone, 6 = mediterranean sclerophyllous forest zone, 7 = temperate deciduous forest zone; ▲ = type locality of *Lecanographa azurea* (NE of Iquique), ● = *Roccellina ochracea* (N of Tocopilla), ★ = joint type localities of *Roccellina ochracea* and *R. terrestris* (NW of Antofagasta), ▲ = *Lecanographa azurea* (N of Taltal), ● = *Roccellina ochracea* (N of Chañaral), ■ = *Roccellina terrestris* (N of La Serena, W of Ovalle, N of Los Vilos, NE of Valparaíso).



with *Chiodecton klementii* Follmann, *Ingaderia friabilima* Follmann & M.Schulz, *Roccellaria mollis* (Kremp.) Zahlbr. and *Teloschistes flavicans* (Sw.) Norman. Since the population of *R. ochracea* grows directly in the dripping zone below *E. iquiquensis*, the condensate obtained on the ground should be tested for specific lichen substances. Compared to the type locality, the northern site provides a much more degraded plant cover with many withered cactus skeletons, while at the southern one larger columnar cacti are completely absent, being replaced by short-stemmed ones such as *Copiapoa cinerea* var. *columna-alba*.

**Biogeographical position:** Three habitats of *Roccellina terrestris* included in the outline map (Fig. 6) apply to new records for the Province of Coquimbo (20°21'–32°07'S) and one “fugitive” in the Province of Valparaíso (33°04'S, southernmost location known). Beyond that, in the same region, new occurrences have also been observed of seemingly “better understood” species such as *R. accedens*, *R. cerebriformis* and *R. luteola*. This suggests a hitherto unnoticed focal point of distribution in the southern transitional zone between the hyperarid Atacama Desert and the more temperate, subtropical dwarf shrub area.

Although there are comparatively few collections of both epigean loma lichens at present, without doubt *Lecanographa azurea* and *Roccellina ochracea* can be put on a level with the many locally endemic taxa of different affiliation appearing in the Atacamian province of the Pacific-Andean floral region. A few selected species may serve as examples of such distribution types (\* = monotypic genera): *Camanchaca corallina* Follmann & Peine (Roccellaceae), *Dolichocarpus\* chilensis* R.Sant. (Roccellaceae), *Follmanniella\* scutellata* Peine & B.Werner (Roccellaceae), *Hubbsia langei* Follmann (Roccellaceae), *Ingaderia gracillima* (Roccellaceae), *Ramalina cactacearum* Follmann (Ramalinaceae), *Roccellaria\* mollis* (Hampe) Zahlbr. (Roccellaceae), *Roccellinastrum spongioideum* Follmann (Micareaceae), *Santessonia cervicornis* (Follmann) Follmann (Physciaceae), *Usnea eulychniae* Follmann (Parmeliaceae), *Xanthoria ascendens* Kondratyuk (Teloschistaceae), *Xanthopeltis\* rupicola* R.Sant. (Teloschistaceae). Besides the appearance in the study area of a larger number of monotypic genera within the Arthoniales, the distribution patterns with many disjunctions as

well as the complete absence of corresponding taxa from the eastern slopes of the Andean barrier point to a great age, a pronounced former diversity, a high natural extinction rate and consequently a relictual endemism among the modern representatives of the order under consideration (FOLLMANN 2002, GALLOWAY 1990, 1996, WEBER 1965).

The new terricolous *Lecanographa* and *Roccellina* species have to be regarded as rare taxa, although there is still an incomplete knowledge of the Atacamian lichen flora. They must also be classified as seriously endangered, not only because of their evident scarcity, but also in view of the progressive devastation of the North Chilean fog oases caused by natural incidents and human negligence (FOLLMANN 1995). Regrettably, in the case of rare crustaceous and at first sight inconspicuous lichens, protective measures have almost always been ineffective, particularly under desert conditions.

## Acknowledgements

The author is greatly indebted to Priv.-Doz. Dr. M. Schulz, Bonn, for assistance during fieldwork and with micro-chemical analyses, to Dr. B. C. Werner, Cologne, for photographic support and to the directors and curators of institutional herbaria for loan of lichen specimens in their care and the patience they have had regarding the return of these. Special thanks are also due to Prof. Dr. M. R. D. Seaward, Bradford, for his careful linguistic revision of the manuscript, to the Association of Friends and Promoters of the University of Cologne for financial and technical aid and last, but not least, for travel grants provided by the Chancellor of the University of Cologne.

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Manuscript accepted: 1 March 2008.

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